EVOLUTION AND SYSTEMATICS OF *CERION* (MOLLUSCA: PULMONATA) ON NEW PROVIDENCE ISLAND: A RADICAL REVISION

STEPHEN J. GOULD AND DAVID S. WOODRUFF

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ABSTRACT

Cerion has been described by its leading student W. J. Clench as "the most difficult genus of pulmonate mollusks to classify." No other pulmonate genus shows greater diversity of form; moreover, almost all these divergent morphologies hybridize at their areas of geographic contact. The result is a taxonomic morass that has effectively debarred fruitful biological work on these fascinating snails.

The taxonomy of New Providence Island is the most elaborate for the entire genus; more than 90 species of *Cerion* have been designated, and the distribution of existing names makes no geographic or ecological sense. We use morphometric and genetic techniques to conclude that the living *Cerion* of New Providence reduce to two semispecies, *C. glans* (the ribby morphotype) and *C. gubernatorium* (the mottled morphotype). Traces of an extinct *C. agassizi* line (a prominent taxon of fossil dunes) survive as introgressions into *C. gubernatorium* populations of southeastern New Providence. These two groups form the basis of *Cerion* faunas throughout the northern Bahamas; their separation and recognition provide a key to resolving *Cerion*'s taxonomy both here and elsewhere. Ribby and mottled morphotypes are recurrently evolved "developmental packages," not homologous taxa from place to place—thereby illustrating the importance of developmental channeling in parallel evolution.

We base our taxonomic decision upon a conciliance among many independent criteria. *Geographic distribution:* parental morphotypes occupy their expected positions, with narrow hybrid zones at predicted points of transition. *Morphology of parental populations:* differences between ribby and mottled are not simple consequences of one minor alteration in growth, but summed results of several independent covariance sets. Morphotypes differ consistently in amounts of variation and patterns of covariance. *Hybrid populations:* we find both enhanced variation and patterns of covariance based on developmental disturbance never before detected in parental populations of *Cerion*. *Genetics:* samples grouped by frequencies of electromorphs yield the same clusters of ribby and mottled populations specified by morphology. Morphotypes can be distinguished by allele frequencies, while hybrid populations contain rare alleles found in neither parental taxon. The genetic hybrid zone is wider than the morphological zone and asymmetric about it.

An appendix allocates all previously named taxa, and resolves the status of 19 designated fossil taxa, plus a new species (*Cerion clenchi*), into three successive faunas, marking waves of migration correlated with rise and fall of Pleistocene seas.

I. *CERION* ON NEW PROVIDENCE AND IN GENERAL

A. Introduction

G. B. Sowerby (1875) began his monograph on the genus *Pupa* (including *Cerion*) with a bit of doggerel expressing his awe before the bewildering diversity of these snails:

> Things that were not, at thy command,
> In perfect form before Thee stand;
> And all to their Creator raise
> A wondrous harmony of praise.

With *Cerion* alone contributing more than 600 voices (by today's count of officially designated taxa), it must have been quite a chorus.

Cerion, a West Indian land snail with centers of abundance in Cuba and the Bahama Islands, has long been famous among evolutionists for its exuberant morphological diversity (fig. 1). Except for a few hybrid samples, variation at a locality is not noteworthy in extent. But each local population tends to differ, often markedly, from all others; and virtually every potential combination of characters acts as a modal morphology for some sample. Nonetheless, fewer than five cases of sympatry between any two morphologies have been reported, and only one is adequately documented (Woodruff and Gould, 1980, p. 412). Even the most divergent morphologies interbreed freely in nature.

Sowerby might have preferred an inordinately active God, but early evolutionists emptied their barrel of available explanations in attempting to explain *Cerion*'s *erstaunlicher Formenreichtum* (Plate, 1907)—from climatic molding imposed genetically by Lamarckian means (Plate), to an unusual ca-

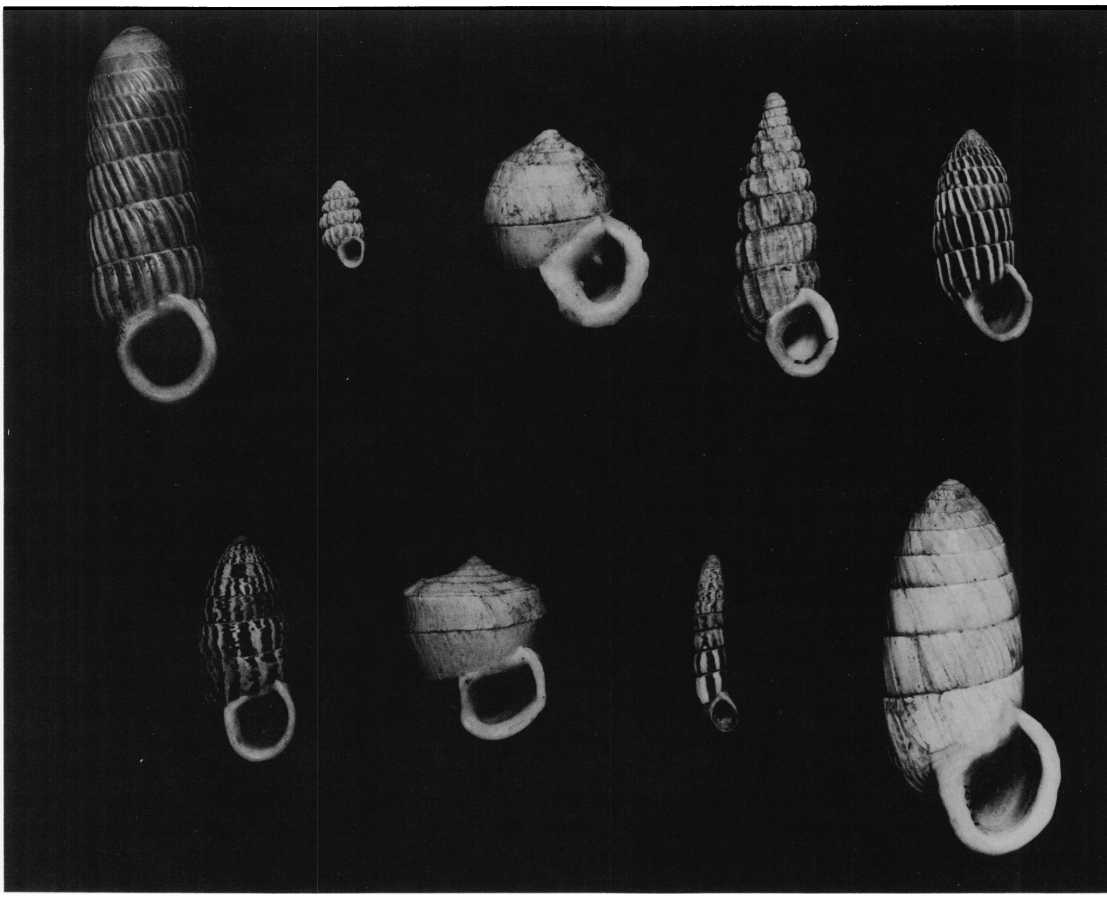


FIG. 1. The phenetic diversity of *Cerion* displayed by selecting average specimens from taxa showing extreme development of common tendencies (and by two examples of more "normal" morphology—top row, right; bottom row, left. **Top row,** from left: *C. calcareum,* Little Inagua, Bahamas; *C. turnerae,* Great Inagua, Bahamas; *C. malonei* (smooth morphotype), Long Island, Bahamas; *C.* (*Umbonis*) *johnsoni,* Cuba; *C. glans,* New Providence Island, Bahamas. **Bottom row,** from left: *C. eximium,* Cat Island, Bahamas; *C. alberti,* Cuba; *C. pauli,* Great Exuma Island, Bahamas; *C. regium,* Crooked Island Bahamas. The *C. calcareum* specimen (top row, left) is 47.8 mm in height.

pacity for differentiation following geographic isolation (Maynard), to the rapid fixation of hybrid genotypes (Bartsch).

If these early workers could not discern why *Cerion* varied in so protean a fashion, they could at least name all the manifestations of this extraordinary phenomenon. Hence, *Cerion*'s interesting biology has been buried under a thicket of taxa—and the coherence of developmental modes, the correlation of form to habitat, and the repeated pattern of geographic distribution among islands (Gould and Woodruff, 1978) have been obscured (but see Mayr and Rosen, 1956, on the Bimini cerions, the first modern evolutionary study of this genus).

C. J. Maynard, the famous amateur ornithologist and conchologist who split *Cerion* so zealously in his private publications, defended his taxonomic practice as a public service (1889, p. 2): "Conchologists may take exception to some of my new species, thinking, perhaps, that I have used too trivial characters in separating them. Believing, however, as I do, that it is the imperative duty of naturalists today, to record minute points

of differences among animals . . . I have not hesitated so to designate them, if for no other reason than for the benefit of the coming generations." But Maynard's colleagues rarely regarded his work as a favor. Pilsbry declared that "Gods and men may well stand aghast" (in Pilsbry and Vanatta, 1896, p. 324) at the "naming of individual colonies from every sisal field and potato patch in the Bahamas" (Pilsbry, 1902, p. 255). W. H. Dall labeled such splitting as "noxious and stupefying" (1896, p. 422) and added: "It is much easier to describe and name a character than it is to search out its reason for existence" (1896, p. 422). Plate also threw up his hands in frustration (1907, p. 599): "Wohin soll es führen, wenn die Zoologen sich dazu hergeben, solche Nebensächlichkeiten zu registrieren!" Nonetheless, when faced with decisions about details, all these authors compromised their bold words—none recognized fewer than half the names favored by Maynard. As Plate, who opted for a mix of species and subspecies, put it: either we use a single name for the entire genus (unacceptable for a range of form exceeding that expressed within most pulmonate families), or we recognize each local population (lesser of two evils). Moreover, at least Maynard based his decisions on populations studied in the field. Each of his species is a geographic entity defined by a sample, not a suite of aberrant individuals culled from a single habitat.

In our previous systematic works on *Cerion,* we have studiously avoided islands of densest taxonomy, choosing instead to chip away at areas of minor recorded diversity. We began in the Dutch Leeward Islands, *Cerion*'s geographic outlier, where no one has ever split *Cerion uva,* the type species of *Cerion,* and named by Linnaeus himself (Gould, 1969a, 1984a). We then moved to the eastern extremity of *Cerion*'s range (Hispaniola to the Virgin Islands) and reduced the seven living taxa to a single pattern of clinal distribution (Gould and Paull, 1977). As an opening foray in the Bahamas, we studied the seven recorded species (and many more subspecies) of Little Bahama Bank (Grand Bahama and the Abacos) and recognized but two semispecies (Gould et al., 1974; Gould and Woodruff, 1978). In each case, we found coherent patterns of morphometric (and, for the Bahamas, genetic) variation where previous authors, unacquainted with distributions in the field and relying upon an established diversity of names, had recognized a disordered "crazy quilt." In our Bahamian work, we have followed the protocol of field collection and study at all available sites followed by morphometric and genetic analysis of the same animals.

We have been pleased not primarily with the taxonomic simplification we have achieved, but with the biological patterns that such a revision reveals. Yet our method has yet to pass its most difficult test—a successful application to areas beset with large numbers of names and little reported order in distribution among them. Thus, we discuss here *Cerion*'s island of greatest recorded diversity—tiny New Providence (30 × 12 km at maximum dimensions) with its 90 species (82 listed in Clench, 1957, plus 8 dredged up by ourselves). We find among the 71 living "species" only two valid semispecies and their areas of hybridization—the same pattern that we detected on Little Bahama Bank. (The 19 fossil "species" include two additional and legitimate taxa in our opinion—the sympatric large *C. agassizi* and dwarf *C. universum.* We have also found a new species in the oldest dunes of the island—see appendix for its description.)

B. Previous Work

The confusion engendered by *Cerion* on New Providence can best be expressed by contrasting the two utterly disparate syntheses produced during this century. C. J. Maynard (1889–1896, 1919–1926) recognized more than 80 full species, convinced as he was that the smallest barriers conferred complete isolation and that separated populations invariably speciated in short order: "A comparatively narrow strip of sand, or naked soil or rock, would be sufficient to isolate a colony, and a colony so isolated, speedily acquires specific characters" (1889, p. 2). Maynard represented the great amateur tradition of close attention to nature's differences. He viewed himself naively as a mere recorder of objective entities, clearly visible to all with eyes to see and the patience to persevere. The species of *Cerion,* he wrote (1913, p. 183)

"are very real. They are not at all matters of opinion, but most decidedly matters of fact." "The matter appears perfectly clear to me" (1889, p. 132). Since Maynard was also in the business of selling shells, more species meant more items to flog. *Caveat emptor.* In any case, although Maynard worked with a clear concept of populations, his species do not conform to modern usage. He did not recognize them as reproductively isolated units, but as discontinuous morphological divisions (hence not subspecies in his view) of a geographic range. And he failed to see the general pattern of *Cerion*'s distribution on New Providence through his thicket of names.

In complete contrast, Ludwig Plate (1906, 1907), an important but dark figure[1] in the history of German evolutionary thought, tried to encompass all the New Providence cerions as expressions of a single graded cline, running west to east along the north shore. On spotty evidence of only 10 samples, he postulated an evenly graded continuum ranging from thick lipped, uniformly colored, coarsely ribbed shells on the northwest coast to thin, mottled, finely ribbed shells on the northeast. He tried to relate this morphological cline directly to climatic gradation, but presented no meteorological evidence. (In fact, he turned completely about, attributing the thick shells and coarse ribs of Western specimens to wet conditions in 1906 and to dry climates in 1907—a clear example of the pitfalls of adaptationist argument in the purely speculative mode.)

Plate, in line with most naturalists of his time, held an eclectic attitude toward evolutionary mechanisms. He found some good in all processes for continuity—Geoffroy's direct induction by environment, Lamarck's use and disuse, Darwin's natural selection—but rejected Mendelism in de Vries' version of saltatory change. For *Cerion,* however, he denied any influence to natural selection, since he could find neither predators nor differences in local substrate (although both demonstrably exist). Instead, he attributed the cline to direct climatic induction, impressed upon the germplasm and inherited in Lamarckian fashion after numerous generations had been exposed to similar influence.

In addition, Plate remained devoted to the recapitulatory thinking that evolutionists of his day often applied to problems at any scale. Ironically, after arguing that *Cerion*'s supposed cline mapped local climates, Plate turned to the conventional but inappropriate scale of long-term phyletic events and asked which characters, by the biogenetic law, could be regarded as primitive. He chose a sample near the middle of his cline as ancestral, and reinterpreted the continuum as two linear evolutionary sequences—time expressed geographically—moving out in either direction from their center of origin. The sequence of samples along the north shore of New Providence became, in his words, two "geographisch-phyletische Formenketten" (1907, p. 457).

To the burning question of his day—whether evolution is primarily powered by internal or external factors—Plate invoked *Cerion* to come down squarely in the middle. Since climate affects some taxa profoundly and others not at all, the capacity of germplasm to respond (an internal factor) must be considered—and *Cerion* must carry an unusually labile set of genetic determinants. But this capacity cannot be activated without a set of varying environments (external factors) to act either as direct agents of change in germplasm (in the Lamarckian mode that Plate favored for *Cerion*) or to set varying selective pressures in the Darwinian mode (supported by Plate as a general principle in biology, but denied in *Cerion*'s case). Plate invoked an analogy to express his middle position (1907, p. 461): "Just as the best music teacher cannot make a true artist from a student without talent and industry, so also are external factors powerless before a stable, un-

[1] Plate (1862–1937) was Haeckel's handpicked successor at Jena. But he soon forced Haeckel out of his own building and crowned the indignity by formally accusing him of stealing books (Haeckel's own, previously donated to the University, as it turned out). Plate was, by all accounts, indeed by his own writing, an aggressive superpatriot, a vicious and explicit antisemite, and a champion of fascism (see Goldschmidt, 1956, pp. 38–40, the great Jewish geneticist whom Plate tried unsuccessfully to persecute). Plate helped to establish and edit the *Archiv für Rassen und Gesellschaftsbiologie,* a leading arm of the German eugenics movement—and the organ for his publications on *Cerion.* Its last issues detail with great satisfaction the "success" of Nazi sterilization and marriage prohibition laws.

responsive germplasm. External causes call the reaction forth; internal causes determine its quality."

But Plate's work, published in an obscure German journal that later became a mouthpiece for Nazi racial policy (and finally died with it), has been ignored by almost all later students of *Cerion* (but see Mayr and Rosen, 1956). We regard Plate's "kontinuierliche Formenkette" (1906, p. 129—"continuous chain of forms") as a misrepresentation of *Cerion*'s biology equal in extent, though opposite in direction, to Maynard's nearly 90 species. Nonetheless, Plate did at least argue for coherent pattern versus a mere panoply of names. In this sense, we regret that his work achieved no notice and that Maynard's nomenclatural thicket prevailed to intimidate all subsequent workers and to leave *Cerion*'s greatest recorded diversity in a state of confusion. Clench (1957), in his indispensable catalogue of *Cerion*'s recorded names, ventures a guess that true diversity on New Providence may be five or six species (1957, p. 126). But Clench offers this opinion only as a passing comment, and he never states which taxa he would retain and why. Thus, Maynard's names remain in the literature as a block, heretofore fully effective, against biological understanding of *Cerion* on New Providence.

C. A General Hypothesis for the Taxonomy and Geographical Distribution of *Cerion*

Although Clench (1957) lists 247 names for *Cerion* from Little and Great Bahama Bank alone, we believe that more than 200 of these taxa represent only two basic "morphotypes" (and their interactions) distributed geographically within islands in a thoroughly consistent way throughout the region. The remaining taxa, representing fewer than 10 valid species, fall into five categories: (1) Fossils from Pleistocene dunes representing forms now extinct in the Bahamas. We have also collected a few undescribed fossil species (see Gould, 1984b). (2) The survival of a fossil taxon. *C. eleutherae,* not surprisingly from the island of Eleuthera, is clearly a relict of the *C. agassizi* stock, so common in the 120,000-year dunes of New Providence and Eleuthera. We have also discovered surviving *C. agassizi* on Cat Island. (3) Large white shells from Andros, called *C. sladeni.* These may also represent a survivor of the *C. agassizi* stock. (4) Incursions of the peculiar subgenus *C.* (*Umbonis*) on four islands: Andros [found by Plate and named *C. glans irregulare* (1907, p. 594), subsequently forgotten, but rediscovered in 1981 during our field work on Andros], Green Cay, Great Guana Cay (of the Exuma chain), and Cat Island (see Clench and Aguayo, 1952). (5) From two to four additional taxa [plus another *C.* (*Umbonis*) incursion] on Long Island, the southeasternmost island of Great Bahama Bank. The islands, cays, and small banks of the southeastern Bahamas contain cerions genuinely different from the two northern morphotypes. Long Island, as the island of Great Bahama Bank closest to these southeastern cerions, has received several incursions.

The two morphotypes are distinguished both by their form (fig. 2) and by their geographic distribution. Shells of the "ribby" morphotype (top row of fig. 2) tend to be uniformly colored (pure white to brown, though the ribs of brown shells may be white), ornamented with a small number of coarse ribs, thick, and shaped with a triangular apex yielding fairly abruptly to the quadrate, parallel-sided form of later ontogeny. Shells of the mottled morphotype (lower row of fig. 2), by contrast, are colored with irregular patches of white and brown, covered with numerous fine ribs (or no ribs at all in some cases), tend to be thinner, and are generally barrel-shaped, with an obtuse apex passing more smoothly to outwardly tapering whorls of mid-growth, followed by inward tapering and restriction near the aperture.

These differences, though consistent and repeated from island to island, would never have provoked our attention—for indeed we see this contrast as *the* key to unraveling the systematics of *Cerion* in the northern Bahamas—were it not for the remarkably precise correlation of form with geographic position and environment. To appreciate the correlation, we must consult a map of Pleistocene shorelines at times of low sea level (fig. 3), rather than modern physiography. The ribby morphotype lives exclusively along present seacoasts that abut the bank edges—bank-edge coasts in our terminology. With very few

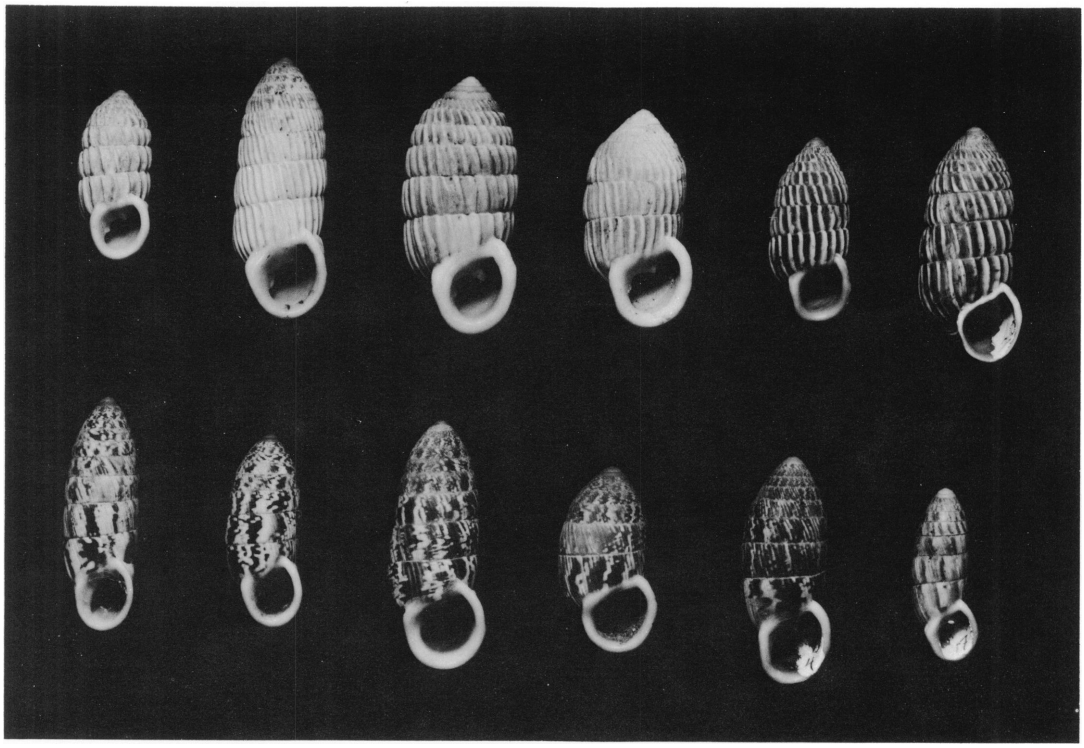


FIG. 2. Representative specimens displaying the range of variation within the two morphotypes of the Northern Bahamas. Top: ribby morphotype. Bottom: mottled morphotype. Conventional taxonomy as follows: **Top row,** left to right: *C. chrysaloides,* Grand Bahama; *C. lucayanorum,* Mores Island (holotype); *C. maynardi,* southern end of Abaco, locality 250; *C. abacoense,* southeastern shore, Abaco, locality 254; *C. glans coryi* from western end of New Providence Island; *C. salinaria,* Salt Cay north of New Providence (holotype). **Bottom row,** from left to right: *C. bendalli,* Grand Bahama, locality 200; *C. bendalli,* Abaco locality 228; *C. bendalli,* western tip of Great Abaco, locality 217; shell that could be assigned to any one of 10–15 species, Culbert's Point, New Providence Island, locality 267; shell that could be assigned to any one of 10–15 species, central New Providence, locality 275; holotype of *C. degeneri* from New Providence. The holotype of *C. lucayanorum* (top row, second from left) is 34.2 mm in height.

exceptions (including one case on New Providence), ribby populations never live more than a few hundred meters from the shore. The mottled morphotype, on the other hand, inhabits both interior areas of the major islands and present seacoasts lying within the shallow banks—bank-interior coasts in our terminology. (Older literature usually reports an exclusively coastal distribution for the entire genus, but this claim is false. *Cerion* is always more conspicuous near the coast, where it resides in impressive abundance just landward of the *Tectarius* zone, generally hanging apex down on trees, bushes, and grass blades. But snails of the mottled morphotype live at low abundance, often cryptically under rocks, throughout the interiors of major islands, sometimes exploding locally into great abundance on recently disturbed sites.)

This correlation alone would lead to a suspicion that the morphotypes are not taxa, as we believe, but mere ecophenotypic variants, developed repeatedly in response to differing environmental conditions. But we reject this hypothesis because the two morphotypes behave in the field as biological entities with defined borders and areas of interactions.

First of all, if the ribby morphotype were merely a coastal phenotype of a single genetic entity, then why—in areas inhabited by it

alone—do we never find mottled shells in adjacent interior areas that seem ideally suited for them (southern Great Abaco, most of the northern Exumas, for example)? Mottled shells are present in interior areas only on islands with coasts inhabited by both morphotypes (New Providence, northern Great Abaco, for example). In other words, the ribby morphotype seems to be an entity restricted to bank-edge habitats.

Secondly, and far more importantly, the status of ribby and mottled as two genetic entities achieves its strongest support from patterns of interaction between the two morphotypes. Ribby and mottled populations hybridize wherever they meet, but this interaction is never simply even and smooth. Invariably, some genetic or morphometric anomaly indicates that the interaction has brought together two (at least mildly) discordant entities. In some cases (New Providence at Blake Road), morphological variation is greatly enhanced, as in "classic" hybrid zones. In other cases (Abaco, see Gould and Woodruff, 1978, and in several zones on Long Island, Woodruff and Gould, in prep.), we find no increased variability, but the zones are very restricted (tens of meters to fractions of a kilometer) while parental morphologies extend unchanged on both sides for tens of kilometers. In all cases, we have found genetic anomalies in hybrid zones (Gould and Woodruff, 1978), while within-morphotype transitions, identified beforehand by geography and morphology, do not display such anomalies. Frequencies of alleles may differ drastically from either parental population and new alleles, present in no parental sample, are often found. Moreover, hybrid zones are invariably located where preferred habitats of ribby and mottled forms intersect (positions are so precise that we can usually "map" the invisible contact of bank-edge and bank-interior coasts from the position of hybrid zones). Hybrid zones may form in two situations: (1) coastally where bank-edge and bank-interior coasts meet, as on Abaco (Gould and Woodruff, 1978); (2) at the interior border of the ribby distribution where it may come into contact with interior populations of the mottled morphotype, as on New Providence at Blake Road (see section III).

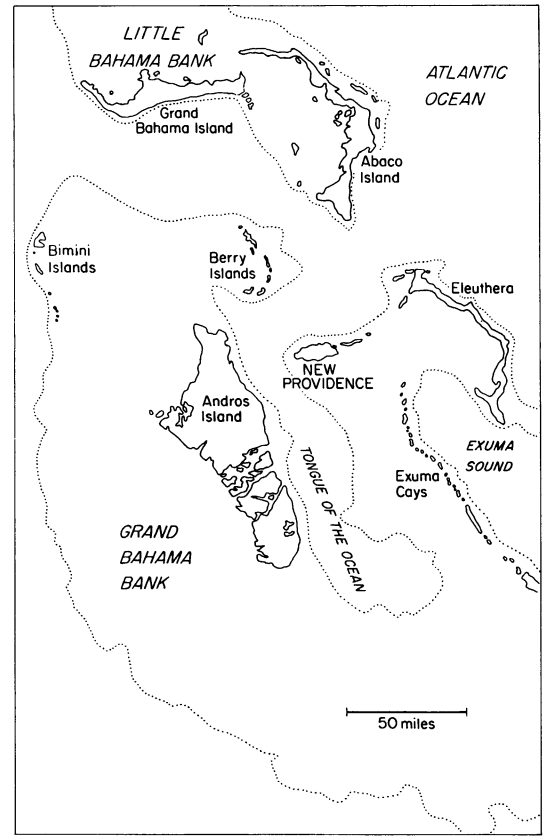


FIG. 3. The major islands of Little Bahama Bank and the northwestern part of Great Bahama Bank. Dotted lines show the bank edges. Note the current position of islands with respect to the bank edges.

We refer to ribby and mottled forms as "morphotypes" because we cannot yet decide between two hypotheses for their repeated distribution on so many islands. Previous workers (e.g., Pilsbry, 1902) have supported (by putting ribby and mottled "species" into separate sections of the genus) the conventional view that ribby and mottled populations form two phyletic branches of *Cerion* and that the morphological resemblances within each branch are homologous. Distribution on many separated islands must then be attributed either to previous connections at times of lower sea level or to accidental transport, presumably by hurricanes (Clench, 1957; Mayr and Rosen, 1956).

We suspect, however, that, at least in some cases, the ribby and mottled phenotypes have

evolved separately in response to similar habitats; each represents an ontogenetic pathway readily "called forth" from the allometric pattern of development common to all *Cerion* (see Gould and Woodruff, 1978, p. 376 for a defense of this unconventional hypothesis). We must emphasize again that ribby and mottled forms are not mere ecophenotypes of a common genotype. Ribby and mottled populations on the same island—whether introduced separately according to the first and conventional hypothesis, or developed repeatedly in situ by the second, unconventional proposal—are distinct (if only mildly discordant) genetic entities. For more than 20 years, Bartsch (1920) transplanted cerions of many morphotypes to environments inhabited by radically different forms. Invariably, the transplanted populations bred true for as many generations as Bartsch followed—unless they hybridized with the native forms.

We have recently obtained our first strong evidence for separate evolution of ribby and mottled phenotypes on separated areas of the Bahamas. In studies of genital anatomy, Chung (in press) has found that *both* morphotypes (ribby and mottled) share a similar set of features on Little Bahama Bank (Grand Bahama and Abaco), while both morphotypes share a distinctly different set of characters on islands of Great Bahama Bank (Andros, New Providence, Long Island). If genital anatomy represents homology (as pulmonate taxonomists usually assume), then our unconventional hypothesis wins strong support.

Regardless of how they arise on each island, we must still explain the precise correlation of morphotype with geography. We cannot yet decide between two hypotheses, one conventional and one unusual.

We might present a standard *ecological* argument and interpret the pattern as a short-term result of immediate habitat: ribby and mottled phenotypes are adaptations to characteristically different environments of bank-edge and bank-interior coasts. Indeed, the bank-edge coasts do tend to be ringed with cliffs (or at least low hills) and to receive a good deal of buffeting from the surf, while bank-interior coasts tend to be low and calmer, often covered with mangroves (see Gould and Woodruff, 1978, pp. 377–378, on possible adaptive meaning of the ribby-mottled distinction). On the other hand, a *historical* hypothesis would view the current distinction more simply as a relic of Pleistocene patterns at a time of emergent banks. Ribby and mottled forms made a basic division of habitat—ribby populations inhabited coasts and mottled populations the interior. As sea level rose, each form maintained its position. The peculiar distribution of modern mottled forms—interiors and bank-interior coasts—then records the interior areas of emergent banks.

In favor of the historical hypothesis, we note that coasts with unexpected properties (low, calm bank-edge or cliffy bank-interior) are still inhabited by the morphotype appropriate to their geographic position with respect to Pleistocene banks (ribby on bank-edge, mottled on bank-interior). If this historical hypothesis be generally valid, then we must drastically revise the conventional view about *Cerion*'s distribution—that it is impersistent, random, haphazard, and largely conditioned by frequent hurricane transport among islands. Instead, we would have to interpret the distribution of *Cerion* as coherent, stable over thousands of years at least, and resistant to substantial changes of local habitat (Holocene rise of sea level).

In any case, the strong correlation of geography with morphology allows us to predict the distribution of *Cerion* on New Providence, and hence, to reduce their taxonomic diversity—now greatest among all *Cerion* faunas—to the same distinction of ribby and mottled morphotypes that characterizes *Cerion* throughout the northern Bahamas. We believe that we can confirm these predictions, and we will synonymize all 71 species of living New Providence *Cerion* into the two semispecies, *Cerion glans* (Küster) (the ribby morphotype) and *Cerion gubernatorium* (Crosse) (the mottled morphotype).

D. Predictions for New Providence

New Providence Island (fig. 3) lies along the northern edge of Great Bahama Bank. It is bordered by deep water to the west (The Tongue of the Ocean between New Providence and Andros) and northwest (the northern edge of Great Bahama Bank) and by the

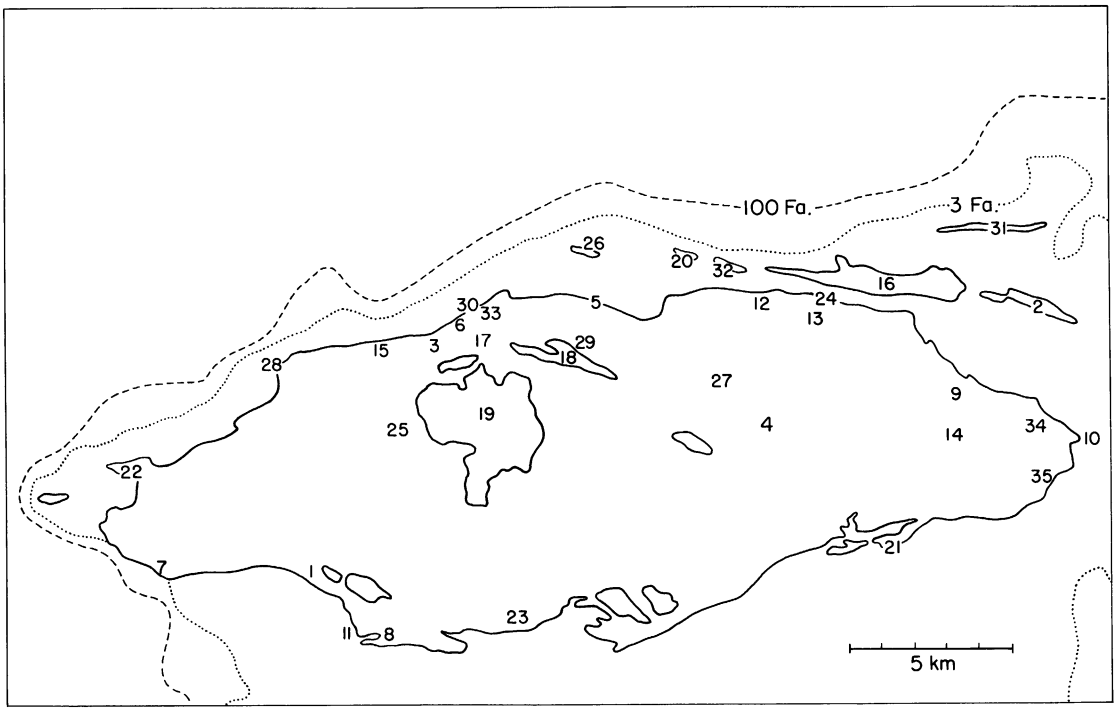


FIG. 4. New Providence island showing the bank edges by the 3-fathom (5.5-m) and 100-fathom (183-m) contours for water depth. All localities mentioned in text are shown by numbers, while the adjoining table 1 presents locations and their numbers in alphabetical order.

shallow waters of Great Bahama Bank to the south and east (fig. 3). Beginning about halfway along the northern coast (at Cable Beach) and proceeding eastward, the northern coast veers further and further away from the bank edge and comes to occupy a bank-interior position (table 1 and fig. 4). The bank edge, in this region, is marked by a series of cays, beginning with North Cay off Cable Beach and running all the way to Eleuthera—in sequence from west to east: North Cay, Long Cay, Silver Cay, Hog Cay (now, in a transformation worthy of Circe herself, called Paradise Island), and Salt Cay. The city of Nassau marks the general region of transition between a northern coast still close enough to the bank edge to harbor the ribby morphotype and a bank-interior status east of the city (table 1 and fig. 4 for all localities on New Providence).

Given this relationship of modern coastline to ancient bank, we expect the following distribution of *Cerion* if diversity on New

TABLE 1
Geographical Locations Mentioned in Text[a]

1. Adelaide	19. Lake Killarney
2. Athol Island	20. Long Cay
3. Blake Road	21. Long Point
4. Blue Hills	22. Lyford Cay
5. Cable Beach	23. Millar's Sound
6. The Caves	24. Nassau
7. Clifton Pier	25. Nassau International Airport
8. Coral Harbour	26. North Cay
9. Creek Settlement	27. Oakes Field Airport
10. East End Point	28. Old Fort Point
11. Fleeming Point	Paradise Island, See 16, Hog Island
12. Fort Charlotte	29. Prospect Ridge
13. Fort Fincastle	30. Rock Point
14. Fox Hill Road	31. Salt Cay
15. Gambier	32. Silver Cay
16. Hog (Paradise) Island	33. West Bay St.
17. John F. Kennedy Drive	34. Winton
18. Lake Cunningham	35. Yamacraw Beach

[a] Includes all places discussed except localities for the invalid taxa of Appendix 1. This table presents locations in alphabetical order. The numbers assigned are then given in figure 4.

Providence reflects the ribby-mottled distinction common to its general region:

1. The west and northwestern coasts are bank-edge and should be inhabited by the ribby morphotype. Coastal transitions to the mottled morphotypes should occur on the southwest around Clifton Pier (where the bank edge diverges away from the island) and on the northeast, in the city of Nassau itself.
2. The northeast coast (east of Nassau) and the entire southern coast east of Clifton Pier should be inhabited by the mottled morphotype.
3. The cays off the northern shore of New Providence, aligned at the bank edge, should be inhabited by the ribby morphotype.
4. Mottled populations should be the sole occupants of the island interior.
5. We should look for hybrid samples and zones of transition in three places:
   i. along the southwest coast in the region between Clifton Pier and Adelaide;
   ii. along the northern coast in the city of Nassau;
   iii. at the interior border of ribby populations where they may come in contact with mottled interior populations.
6. We should *not* find, as Plate maintained, a smooth and even transition between ribby and mottled, encompassing the entire coast in a gradual cline. Hybrid zones, if the transitions be smooth, should be restricted geographically and should not extend their morphometric effects widely into adjacent areas of parental forms. Hybrid populations, particularly if recently established, should display morphometric and genetic signs of interaction between two somewhat discordant entities.

The *Cerion* of New Providence meet these expectations in a precise and consistent way. Only one prediction cannot be confirmed with living populations, but this limitation is an artifact of human intervention. The bustle and concrete of modern Nassau have exterminated *Cerion* within city limits. The area of potential interaction between morphotypes on the north shore is now devoid of snails. But Nassau was a quieter town not long ago, and Maynard's collections from the turn of the century affirm our expectation (see section III.C). Here we encounter the supreme irony of *Cerion*'s bloated taxonomy on New Providence. Maynard was, to be sure, an extreme splitter, but he did not divide so prodigiously the snails of every island he visited. Had he been stationed along the northwest coast, where ribby shells are much of a muchness for miles, he would have constructed few species. But he set up camp in Nassau itself and concentrated his collecting right in the midst of interaction between the two morphotypes—an area of rapid transitions and odd morphologies.

We devote the rest of this monograph to a morphometric and genetic affirmation of these six expectations and to a characterization of the two legitimate taxa. We then allocate, in an appendix, the current 71 species into our two semispecies, ribby *C. glans* and mottled *C. gubernatorium.*

II. THE GENERAL MORPHOMETRIC DISTRIBUTION OF NEW PROVIDENCE *CERION*

A. Selection of Samples

Nearly all of Maynard's more than 80 species are well represented by his own specimens in the collection of the Department of Mollusks in the Museum of Comparative Zoology, Harvard University. We find two outstanding patterns in Maynard's material: (1) The general geographic distribution of ribby and mottled shells matches the predictions of the last section (and we find no taxa that do not seem to fit under the ribby-mottled umbrella). Ribby shells inhabit the northern cays and coastal areas of the main island from the southwest (at least from Clifton Pier) to the northeast, at least to Fort Charlotte in the City of Nassau (see fig. 4 for locations and table 1 for an alphabetical list). Mottled shells live east and south of Nassau, extending west-

ward on the south coast at least to Adelaide. Nassau itself contains a jumble of intermediates. (2) Diversity within the mottled morphotype greatly exceeds that within the ribby morphotype. This statement may seem to be contradicted by our allocation of more of Maynard's taxa to the ribby morphotype (see appendix), but this only reflects Maynard's taxonomic practices. Maynard always gave different names to populations on separate islands, and all the small cays, as bank-edge islands, are inhabited exclusively by ribby shells. Of 34 Maynard "species" clearly allied to the ribby morphotype, 23 inhabit the off-lying cays and only 11 were collected on the main island. All 22 "species" allied with the mottled morphotype come from the mainland of New Providence. The exuberance of names for the off-lying cays does not reflect morphology, but Maynard's decision to apply different names to all disconnected bits of real estate.

In fact, were we so inclined (as we are not), we might divide mottled forms into four geographically separated subgroups, which would then rank as subspecies under our new taxonomic proposals (fig. 5). (The geographic distribution is real enough, but we do not choose to dignify such a dynamic pattern with a set of formal names. One group is already extinct, though its shells may still be collected; another is becoming less and less common as the city of Nassau spreads eastward.)

The first group lives east of the city of Nassau along the north coast and inland at least to Winton. It is now quite rare as Nassau expands and removes suitable habitat. Shells are dark, fairly small but tall, and more strongly ribbed than any other mottled New Providence *Cerion.*

The second group once inhabited the eastern coast from East End Point south at least to Yamacraw Beach. It is, in many ways, much the most interesting of all mottled New Providence *Cerion.* In the extreme sample, *C. gubernatorium,* shells have few whorls, are short, wide, and triangular in shape, and are often white or only faintly mottled (fig. 5). They may represent a cross between mottled *Cerion* and a surviving stock of the fossil *C. agassizi* (see section IV for an affirmation of this claim). (Surviving stocks of *C. agassizi* inhabit a large area of the neighboring Cat and Eleuthera islands, where they hybridize freely and extensively with local mottled and ribby populations.) Alternatively (or complementarily), the wide and triangular shape may represent the deposition of an adult lip on shells that never fully entered the "barrel phase" of middle ontogeny because they grew such large early whorls and reached a constrained adult size before fully entering this middle phase (see p. 420). We will discuss this important issue in our section on formal taxonomy (p. 470), where we will argue that *C. gubernatorium* is an appropriate name for all mottled cerions.

The third group, one of the two abundant stocks, lives along the south coast and interior areas from the southeastern corner of the island roughly to the eastern area of Millar's Sound. These shells are the largest mottled cerions, ribless or with numerous fine ribs, strongly lipped and diffusely mottled in color. Some samples contain white and thick-lipped shells, characters otherwise found on New Providence primarily in the fossil *C. agassizi.* Since we discovered, in samples from this area, alleles otherwise unknown in *C. gubernatorium* but present in the surviving *C. agassizi* stock on Eleuthera (see section IV), and since *C. agassizi* characters are found in the morphology of samples from the geographically adjacent second group (see previous paragraph), we will conclude that *C. agassizi,* the commonest fossil of the New Providence dunes, survived until quite recently on New Providence and still makes its influence felt by introgression within *C. gubernatorium* populations of the second and third groups.

The fourth group, probably the most abundant of all, is largely a western interior stock. It lives all around the shores of Lake Killarney, extending north at least into the Blake Road hybrid zone and south probably to the coast around Coral Harbour. It is generally ribless or very finely ribbed (as in *C. degeneri*) and, most notably, mottled with sharp borders between blotches of color and the white shell ground—in marked contrast to the diffuse mottling of all other New Providence mottled cerions.

For our general morphometric survey, we chose 15 of Maynard's taxa as representative both of geographic areas and all major mor-

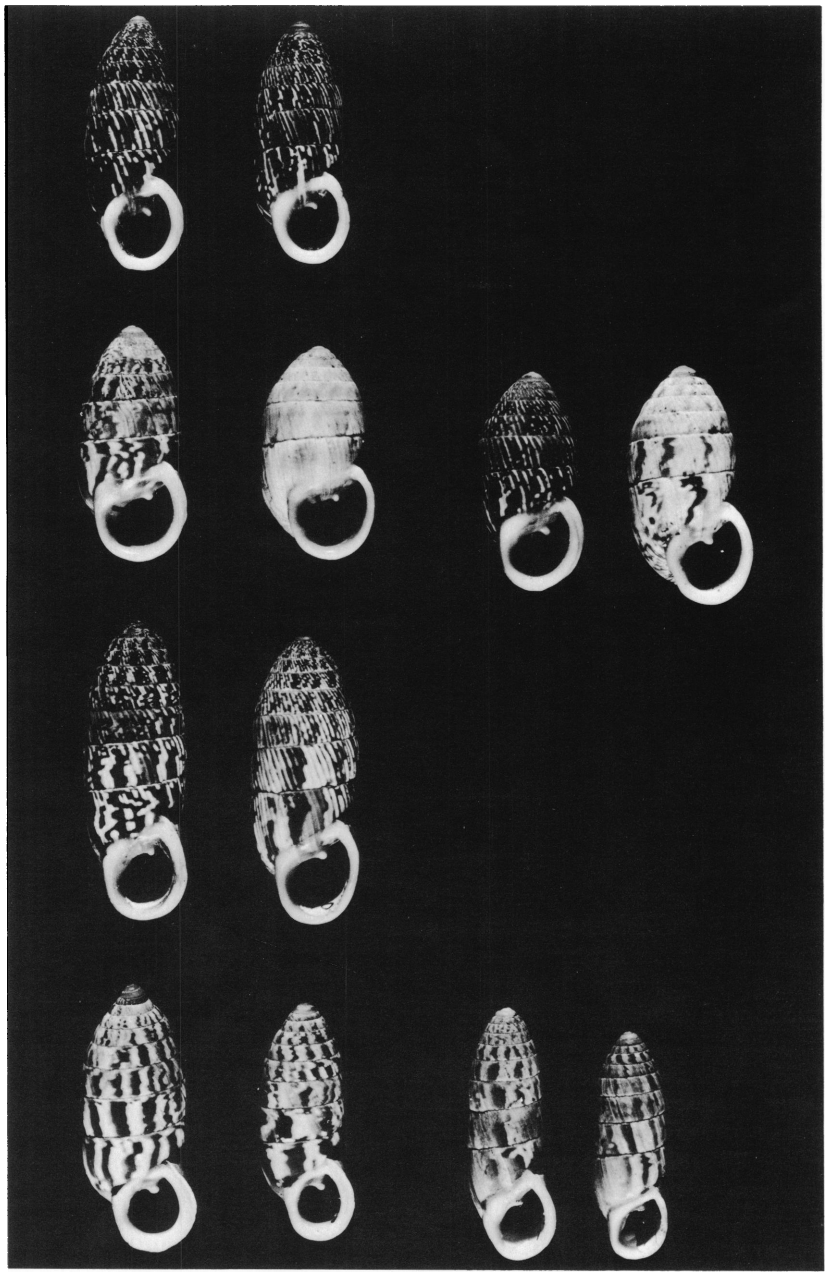


FIG. 5. Representative specimens of mottled New Providence cerions from their four major areas. **Top row,** narrow, dark colored, and relatively most ribby populations from the east coast, east of Nassau. Our locality 264. **Second row,** populations from the east end of the island—relatively wide, light colored forms traditionally called *C. gubernatorium.* Left pair: *C. gubernatorium* itself (MCZ Department of Mollusks 117723) from Southeast Point. Right pair, *C. tenui* (MCZ 107538) from Culbert's Point. **Third row,** the large, finely ribbed populations of southern interior New Providence, *C. gracila* (MCZ 76285) from Soldier's Field Road. **Bottom row,** the western interior mottled populations with their distinctive coloration in discrete stripes, rather than diffuse mottling. Left pair, our 700 from the eastern shore of Lake Killarney; right pair, paratypes of *C. degeneri* from Fleeming Point. The left specimen in the top row is 24.9 mm in height.

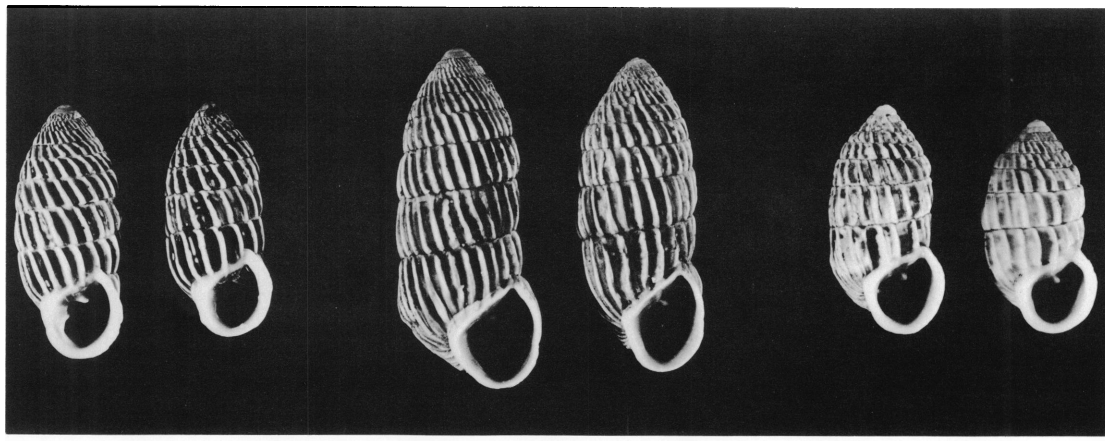


FIG. 6. Representative specimens of ribby *Cerion* showing the three major variations. **Left pair,** our number 284 from the western end of New Providence; shells are uniformly dark in ground color, but with white ribs. **Middle pair,** the larger, weakly lipped shells of the off-lying northern cays; paratypes of *C. salinaria* from Salt Cay (MCZ 76090). Right pair, the greyish ground and mottled coloration of populations from the northwest to northcentral bank-edge coast; MCZ 116573 from Cable Beach. The leftmost shell is 25.0 mm in height.

phological variants among New Providence cerions. For ribby *Cerion* (fig. 6), we chose four of Maynard's samples from the off-lying cays: *C. salinaria* from Salt Cay, *C. mutata* from Long Cay and two samples of *C. cinerea* from Hog (now Paradise) Island. (Maynard described these taxa as members of *Cerion*'s junior synonym *Strophia,* hence his feminine endings. *Cerion* is neuter, but we have not regendered the names, since we will sink them all anyway.) We also measured four samples from the bank-edge coasts of New Providence Island itself: two identified as *C. glans,* from the northeastern edge of the ribby range, and two as *C. glans coryi,* the traditional name for samples from the southwest coast (the "classic" *C. glans* with strong white ribs on a solid, dark brown background; many of the northeastern *C. glans* are greyish and discontinuously colored).

We also selected six samples of mottled shells to represent the four major forms (fig. 5): *C. purpurea* from the thin rather ribby samples of the northeast coast, east of Nassau; *C. tenui* from the peculiar short and squat samples of the eastern coast[2]; *C. agrestina* and *C. gracila* from the large-shelled southern populations; and *C. degeneri* and *C. phoenicia* (not the type location) from the discretely blotched western samples. *C. fincastlei,* an intermediate representing populations now extinct from the City of Nassau itself, formed our fifteenth sample.

We supplemented Maynard's samples with 30 from our own collections, made in April 1974. We designate these with our field sample numbers ranging between 262 and 301 (fig. 7). We attempted to collect samples at equal intervals around the coast, in order to test Plate's assertion that all *Cerion* formed an even morphological cline, at least along the entire north coast; Plate's hypothesis is the primary challenge to our proposition that two discrete taxa exist. We collected samples at more frequent intervals in the Blake Road hybrid zone (numbers 296–300).

B. MEASUREMENT OF SAMPLES

Cerion is a biometrician's dream, for four primary reasons (and a host of secondary,

[2] We rejected the name-bearer *C. gubernatorium* because we had no samples from Maynard's collection, but only some specimens gathered earlier in the 19th century, and clearly biased in their selection of large and attractive shells. Whatever one may say of Maynard, he at least collected in a "modern" and usable way—that is, he gathered all available shells from definite and restricted geographic areas.

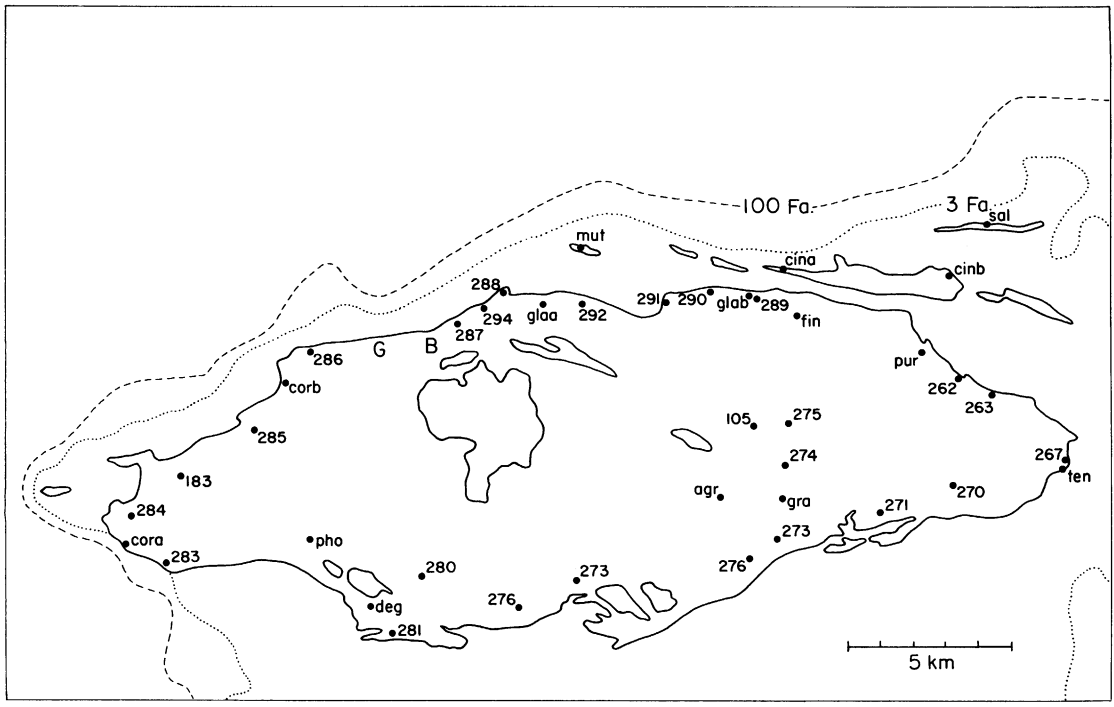


FIG. 7. Localities of all samples used in morphometric analysis on a map of New Providence showing location of the bank edges. Three-digit numbers are our field localities; lower-case letters identify Maynard's species from MCZ Department of Mollusks collections; upper-case G and B represent hybrid areas (Gambier and Blake Road) where density of sampling precludes identification of individual collection at this scale—see figure 15 for these samples.

practical points, including ease of collection and preparation, and extreme abundance of material): (1) As in all snails (and few other creatures), *Cerion* carries an entire record of ontogeny in its shell. Moreover, since whorls do not overlap extensively during growth, the major features of ontogeny are visible without further processing by X-rays or sectioning. (2) The transition from protoconch to postembryonic shell is clearly recorded as a definite point, thus providing both a biological criterion for numbering whorls and a measurable embryonic shell itself. (3) Unlike many snails with continuous growth throughout ontogeny, *Cerion* changes its angle of coiling during the last whorl, and then secretes a thickened, definitive adult lip. Thus, we can sort ontogenetic from static variation, thereby separating two components that are usually inextricably intertwined—but have such different biological meanings—in most biometrical studies of mollusks. (4) *Cerion* grows with such interesting and complex patterns of allometry that studies of covariation in ontogeny offer unusual evolutionary promise (see Gould, 1984b).

We measured 19 variables (table 2) on each of 20 specimens from each of 45 samples (we used larger samples of up to 50 shells in the hybrid populations with enhanced variability). The protocol and description of measurements follow our previous publications, and we will not repeat the details here (see Gould et al., 1974; Gould and Paull, 1977; Gould and Woodruff, 1978). We will follow the order and description of Gould and Woodruff, 1978, p. 382, throughout this paper with the following small differences: (1) We did not measure height from whorl 4 to the end of whorl 6 (measure 11 of Gould and Woodruff, 1978) for the New Providence specimens because too many samples ceased growth between the sixth and seventh whorl, thereby forming no suture at the end of the

sixth whorl (a necessary checkpoint for the measurement). Thus, the first 10 measures of this paper and Gould and Woodruff, 1978, are identical, while all subsequent measures in this work bear an identifying number one digit less than the corresponding measure in Gould and Woodruff, 1978. (2) We used a different microscope with different objectives and micrometer disk for this study. Hence, measurements in micrometer units appear at different scales. Measures 1, 9, 12, and 13 were taken at higher power with 1 mm = 30.0 micrometer units (the rib count of measure 6 was also made at this high power). Measures 2, 10, 11, 14, 15, 16, and 19 were taken at lower power with 1 mm = 10.5 micrometer units. (We have chosen to present data in micrometer units because the small but significant differences among samples are so much easier to visualize at these scales.) Measures 3, 4, 5, and 6 are counts; measures 7 and 8 were taken with calipers, directly in millimeters; 17 is a ratio; and shell weight (19) was determined with a Mettler balance accurate to thousandths of a gram.

We have chosen these 19 measures because: (1) they include the standard biometrical variables of traditional molluscan studies; (2) they have shown both minimal redundancy and interesting patterns of covariation in previous studies; (3) they encompass (insofar as we can devise means of quantification) the evident sources of phenotypic difference among cerions; (4) they permit the study of patterns of covariation in ontogeny—a subject very little exploited but capable of supplying new and important criteria of "dynamic morphology" for the study of phenotypic differences (Woodruff and Gould, 1980, pp. 394–396; Gould and Paull, 1977, pp. 10–13).

TABLE 2
Names of Variables

1. Protoconch width	10. 4th whorl height
2. 4th whorl width	11. Umbilical width
3. Total whorls	12. Width of apertural lip
4. Ribs on 4th whorl	13. Thickness of apertural lip
5. Ribs on 6th whorl	14. Height of the aperture
6. Number of ribs in 50 micrometer units on first whorl	15. Width of the aperture
	16. Protrusion of the aperture
7. Height of shell	17. Tilt of the aperture
8. Width of spire	18. Weight of the shell
9. Protoconch height	19. Distance from inner lip of aperture to previous whorl suture

C. The Basic Pattern

We computed (table 3) a vector of means for each of the 45 samples (20 specimens per sample) and used these 45 vectors as inputs for a Q-mode factor analysis of all New Providence data (see Gould and Woodruff, 1978, p. 382 for a justification of factor analysis in this situation and for a description of the programs used). The summary of figure 8 therefore represents nearly 1000 specimens and 20,000 measurements. We worked in the unconventional Q-mode (in I-space, with variables plotted against specimens—see Sneath and Sokal, 1973, p. 116) with two data transformations: (1) We approach an equalization of weights for variables by performing a percent-range transformation (table 4). The smallest mean value for a variable across all 45 samples receives a score of 0.0, the largest, 100.0; all other means are scaled between. Each variable now ranges from zero to 100, and each contributes a potentially equal weight to its vector. We know of no "ideal" procedure for equal weighting, since each introduces potentially undesirable consequences along with its benefits. In this case, we are equalizing ranges of variation. Thus, the small and random spread of variation among samples for a very stable trait will receive equal weight with the biologically significant and broadly ranging variation of another feature. This data set minimizes such problems because each entry is the mean of 20 shells, not the potentially capricious value of an individual specimen. (2) We normalize each vector (locality) by scaling it to unit length before the extraction of eigenvalues. We do this to remove the explicit effect of size (since samples range widely in mean shell size, from dwarf *C. degeneri* to the large ribby shells of northern cays). This procedure does not eliminate differences in size, but rather expresses them as proportional weights of variables in vectors of constant length for each

TABLE 3
Vectors of Means for All Samples

Sample	1 Proto-conch Width	2 4th Whorl Width	3 Total Whorls	4 4th Ribs	5 6th Ribs	6 1st Ribs	7 Height	8 Width	9 Proto-conch Height
Ribby									
cinereum a	100.03	101.15	7.76	25.15	23.90	4.70	29.40	12.23	42.25
coryi b	92.05	96.95	7.33	22.30	23.05	4.33	25.37	11.10	38.83
salinaria	95.80	101.55	7.85	28.55	27.35	5.08	29.57	12.54	37.50
292	90.00	93.55	8.14	20.95	21.60	6.53	27.87	11.79	42.93
285	93.75	89.00	8.43	22.15	22.45	4.75	28.90	11.30	40.63
287	88.55	90.45	7.57	23.05	23.05	5.13	25.43	10.67	43.05
289	90.88	96.80	7.16	23.20	21.80	5.05	23.93	10.64	39.65
291	88.03	95.40	7.63	23.70	22.85	5.03	25.65	11.28	40.03
glans b	85.67	93.45	7.33	24.10	23.55	5.35	23.77	10.72	38.58
288	91.85	94.20	7.35	24.25	23.85	5.15	24.90	10.85	38.75
294	91.78	94.70	7.23	23.20	22.75	5.40	24.14	10.56	41.03
286	90.67	89.85	7.69	24.85	23.15	5.18	25.42	10.40	37.15
283	88.15	89.35	7.86	21.95	21.50	4.88	25.30	10.28	39.28
284	89.05	90.90	7.76	22.60	21.90	4.73	24.84	10.39	40.60
mutata	93.86	96.00	7.94	31.52	29.19	6.43	27.01	11.44	37.12
coryi a	87.13	87.95	7.69	20.95	20.75	4.75	23.64	9.81	40.00
290	84.27	92.60	7.15	26.80	24.80	6.23	23.08	10.37	33.85
cinereum b	88.30	92.00	7.50	26.50	25.65	6.60	23.90	10.49	40.20
Mottled									
262	86.83	87.85	7.23	27.60	25.90	6.38	22.53	9.67	37.90
281	92.93	93.90	7.19	42.50	36.15	8.98	26.13	10.94	39.25
purpurea	97.65	94.85	6.95	48.85	45.20	8.38	23.80	10.31	37.97
gracila	95.30	93.95	7.99	61.75	53.35	8.48	27.16	10.36	36.55
263	86.58	84.92	7.39	33.75	29.55	7.28	22.12	9.78	35.58
degeneri	84.97	71.47	7.58	83.47	78.35	13.15	23.03	7.66	37.88
276	89.20	84.40	6.99	78.85	64.35	12.55	21.67	8.94	33.82
273	87.90	85.90	7.48	82.25	73.35	11.78	22.71	9.05	34.70
phoenicia	87.45	78.80	7.27	50.30	43.50	9.70	20.56	8.14	36.25
279	88.88	78.13	7.07	45.83	39.20	7.95	20.58	8.28	36.95
271	91.90	90.05	7.70	74.15	60.70	12.25	25.07	10.02	33.10
275	91.58	87.95	7.91	66.75	55.20	9.85	25.64	10.21	34.35
274	91.03	87.35	7.66	58.75	48.90	9.70	24.53	9.85	34.50
agrestina	93.67	90.15	7.78	64.45	57.05	8.65	24.55	9.77	37.03
tenui	92.53	93.85	6.46	65.90	55.40	8.93	21.18	9.81	32.85
267	92.58	88.65	6.98	52.50	46.80	10.48	22.45	9.86	36.53
280	90.84	84.44	7.76	47.38	40.88	7.97	23.52	9.08	36.75
270	91.83	89.00	7.25	52.35	45.05	8.40	22.88	9.87	35.88
278	94.95	91.80	8.16	65.90	54.60	9.68	27.21	10.88	36.35
Hybrid area									
296	84.55	86.10	6.90	42.63	39.87	7.48	20.36	9.17	36.63
297	81.20	85.20	6.93	41.50	39.38	7.40	20.34	9.39	36.92
298	87.90	92.50	7.18	32.22	29.11	5.88	23.22	10.27	40.54
299	84.78	86.95	7.07	22.45	20.80	5.40	21.82	9.54	39.40
300	90.82	86.26	8.12	41.74	43.47	7.26	26.00	10.25	41.68
301	81.15	87.00	7.11	21.55	20.00	5.58	21.61	9.95	37.08
fincastlei	85.30	84.50	7.58	38.35	31.15	7.53	22.39	9.34	36.68
glans a	82.85	91.20	7.13	23.70	22.50	4.75	21.97	10.49	36.65

TABLE 3 (*Continued*)

10 4th Whorl Height	11 Umbilical Width	12 Lip Width	13 Lip Thick-ness	14 Aperture Height	15 Aperture Width	16 Pro-trusion	17 Tilt	18 Weight	19 Aperture Suture
76.03	57.05	23.40	45.55	112.00	93.40	30.83	2.06	1.57	72.48
73.83	48.20	30.45	36.70	103.15	92.05	29.75	1.98	1.12	58.40
71.83	57.50	9.95	21.60	108.75	89.20	28.50	2.02	1.64	74.88
67.33	45.45	29.35	47.10	103.85	96.28	28.83	1.90	1.28	65.88
69.85	48.00	43.15	46.10	110.75	94.27	32.93	2.12	1.24	62.10
72.65	43.25	33.10	47.80	101.35	88.03	26.78	2.15	1.09	61.78
71.18	41.05	24.85	32.10	98.05	83.50	25.43	1.83	0.77	60.40
68.65	45.00	25.30	37.25	101.15	92.20	28.23	2.15	1.04	59.35
67.28	50.00	23.10	39.95	96.35	87.10	26.00	1.78	0.97	56.80
71.75	45.30	34.00	43.55	99.45	87.30	28.05	1.98	1.06	59.73
71.25	43.45	30.60	39.40	96.45	85.53	24.90	1.80	0.91	58.18
71.15	44.70	35.05	42.95	99.35	84.15	25.70	2.04	1.02	55.93
66.65	43.10	27.60	32.55	98.90	85.72	28.62	1.99	0.90	55.92
68.35	44.35	28.60	37.15	100.60	86.60	27.78	2.19	0.85	53.58
66.48	47.57	16.35	31.81	101.29	84.02	23.24	1.89	1.39	68.31
65.60	43.30	26.10	31.95	94.65	81.13	27.18	2.10	0.88	53.93
67.10	44.65	28.90	31.90	93.25	81.85	24.58	1.92	0.70	56.58
67.85	44.65	13.28	30.95	91.00	76.85	22.15	2.00	0.96	60.28
69.70	37.50	27.65	31.90	89.30	78.73	22.10	2.00	0.66	55.73
73.98	35.50	25.50	39.60	105.85	92.90	25.43	1.91	0.86	70.10
74.17	38.55	24.50	48.95	99.10	86.48	25.70	1.92	0.80	60.53
70.10	45.25	23.05	48.60	104.60	88.50	29.45	1.77	0.83	59.25
64.95	37.45	20.35	22.90	90.70	78.03	26.08	2.60	0.56	55.40
66.35	29.24	19.24	31.94	87.24	67.41	22.79	1.84	0.50	55.68
67.88	33.10	23.40	28.80	90.25	74.60	22.98	2.01	0.37	55.88
64.48	32.60	23.10	29.05	91.90	75.15	24.35	2.11	0.40	56.13
64.52	31.20	20.50	27.25	82.00	66.63	24.98	1.90	0.38	48.98
67.88	34.07	20.97	24.73	82.13	69.42	20.55	1.91	0.29	47.97
64.65	42.00	24.65	39.75	101.80	83.23	29.25	2.12	0.65	57.15
65.30	37.85	25.63	33.63	100.84	86.97	26.55	2.21	0.62	61.33
65.03	36.70	23.25	36.55	97.30	83.98	26.40	2.11	0.57	59.10
65.73	37.65	23.70	33.45	98.50	82.75	27.88	2.10	0.48	58.95
75.48	40.85	21.30	43.70	97.05	83.50	27.73	2.41	0.56	56.30
68.80	34.45	23.70	40.65	95.50	83.80	24.28	2.18	0.70	58.25
63.06	32.38	25.44	32.44	90.38	76.94	23.22	1.88	0.53	58.66
66.30	38.30	23.45	34.15	93.50	81.70	23.43	1.95	0.55	57.88
66.23	40.40	30.30	37.65	106.05	91.38	26.75	1.94	0.77	62.68
65.07	40.07	26.80	24.10	85.80	73.87	24.62	1.89	0.47	46.45
65.50	42.43	24.50	24.53	85.20	73.25	21.73	1.97	0.49	48.22
69.75	43.75	26.74	35.71	94.97	83.71	25.32	1.91	0.78	56.67
71.40	35.45	29.50	38.25	87.15	76.90	22.43	1.97	0.81	54.45
68.37	44.95	32.48	42.63	97.47	83.76	26.36	2.04	0.78	55.63
63.30	41.40	25.20	24.20	89.45	75.73	21.70	1.78	0.57	53.05
63.80	37.95	18.15	21.35	86.55	71.63	22.39	1.88	0.61	51.20
63.30	52.05	24.50	23.45	92.65	81.63	23.85	1.84	0.67	51.20

TABLE 4
Vectors of Means with Percent-Range Transformations

Sample	1 Proto-conch Width	2 4th Whorl Width	3 Total Whorls	4 4th Ribs	5 6th Ribs	6 1st Ribs	7 Height	8 Width	9 Proto-conch Height
Ribby									
cinereum a	100.00	98.67	65.98	6.72	6.68	4.20	98.16	93.65	92.16
coryi b	57.73	84.71	44.16	2.16	5.23	0.0	54.50	70.49	58.63
salinaria	77.60	100.00	70.56	12.16	12.60	8.50	100.00	100.00	45.59
292	46.88	73.40	85.28	0.0	2.74	24.94	81.58	84.63	98.82
285	66.74	58.28	100.00	1.92	4.20	4.76	92.74	74.59	76.28
287	39.20	63.10	56.35	3.36	5.23	9.07	55.15	61.68	100.00
289	51.54	84.21	35.53	3.60	3.09	8.16	38.90	61.07	66.67
291	36.44	79.55	59.39	4.40	4.88	7.94	57.53	74.18	70.39
glans b	23.94	73.07	44.16	5.04	6.08	11.57	37.16	62.71	56.18
288	56.67	75.57	45.18	5.28	6.60	9.30	49.40	65.37	57.84
294	56.30	77.23	39.09	3.60	4.71	12.13	41.17	59.43	80.20
286	50.42	61.10	62.44	6.24	5.40	9.64	55.04	56.15	42.16
283	37.08	59.44	71.07	1.60	2.57	6.24	53.74	53.69	63.04
284	41.84	64.59	65.99	2.64	3.26	4.54	48.75	55.94	75.98
mutata	67.32	81.55	75.13	16.91	15.75	23.81	72.26	77.46	41.86
coryi a	31.67	54.79	62.44	0.0	1.29	4.76	35.75	44.06	70.10
290	16.53	70.25	35.03	9.36	8.23	21.54	29.69	55.53	9.80
cinereum b	37.87	68.25	52.79	8.88	9.68	25.74	38.57	57.99	72.06
Mottled									
262	30.09	54.46	39.09	10.64	10.11	23.24	23.73	41.19	49.51
281	62.39	74.57	37.06	34.47	27.68	52.72	62.73	67.21	62.75
purpurea	87.39	77.73	24.87	44.63	43.19	45.92	37.49	54.30	50.20
gracila	74.95	74.73	77.67	65.26	57.16	47.05	73.89	55.33	36.27
263	28.76	44.71	47.21	20.47	16.37	33.45	19.29	43.44	26.77
degeneri	20.23	0.0	56.85	100.00	100.00	100.00	29.14	0.0	49.31
276	42.64	42.99	26.90	92.61	76.01	93.20	14.41	26.23	9.51
273	35.75	47.97	51.78	98.05	91.43	84.47	25.68	28.48	18.14
phoenicia	33.37	24.37	41.12	46.95	40.27	60.85	2.38	9.84	33.33
279	40.94	22.14	30.96	39.80	32.91	41.04	2.60	12.71	40.20
271	56.94	61.77	62.94	85.09	69.75	89.80	51.25	48.36	2.45
275	55.24	54.79	73.60	73.26	60.33	62.59	57.42	52.25	14.71
274	52.33	52.79	60.91	60.46	49.53	60.85	45.40	44.88	16.18
agrestina	66.31	62.10	67.01	69.58	63.50	48.98	45.61	43.24	40.98
tenui	60.28	74.40	0.0	71.90	60.67	52.15	9.10	44.06	0.0
267	60.54	57.11	26.40	50.46	45.93	69.73	22.86	45.08	36.08
280	51.32	43.12	66.00	42.27	35.78	41.27	34.45	29.10	38.24
270	56.57	58.28	40.10	50.22	42.93	57.48	27.52	45.29	29.71
278	73.09	67.59	86.29	71.90	59.30	60.66	74.43	65.98	34.31
Hybrid area									
296	18.01	48.64	22.34	34.68	34.05	35.71	0.22	30.94	37.06
297	0.27	45.65	23.86	32.87	33.21	34.81	0.0	35.45	39.90
298	35.75	69.91	36.55	18.03	15.61	17.57	31.20	53.48	75.39
299	19.23	51.46	30.96	2.40	1.37	12.13	16.04	38.52	64.22
300	51.22	49.17	84.26	33.25	40.22	33.22	61.32	53.07	86.57
301	0.0	51.63	33.00	0.96	0.0	14.17	13.76	46.93	41.47
fincastlei	21.98	43.32	56.85	27.83	19.11	36.28	22.21	34.43	37.55
glans a	9.00	65.59	34.01	4.40	4.28	4.76	17.66	57.99	37.26

TABLE 4 (*Continued*)

10 4th Whorl Height	11 Umbilical Width	12 Lip Width	13 Lip Thick-ness	14 Aperture Height	15 Aperture Width	16 Pro-trusion	17 Tilt	18 Weight	19 Aperture Suture
100.0	98.41	40.51	87.68	100.00	90.29	83.04	34.94	94.82	91.56
83.04	67.09	61.75	55.62	70.50	85.73	74.31	25.30	61.48	42.03
67.62	100.00	0.0	0.91	89.17	76.12	64.22	30.12	100.00	100.00
32.92	57.36	58.43	93.30	72.83	100.00	66.88	15.66	73.33	68.34
52.35	66.38	100.00	89.67	95.83	93.22	100.00	42.17	70.37	55.05
73.94	49.58	69.73	95.83	64.50	72.18	50.32	45.78	59.26	53.92
62.61	41.79	44.88	38.95	53.50	56.90	39.42	7.23	35.56	49.07
43.10	55.77	46.24	57.61	63.83	86.24	62.04	45.78	55.56	45.38
32.54	73.46	39.61	67.39	47.83	69.04	44.02	1.21	50.37	36.41
67.00	56.83	72.44	80.44	58.17	69.71	60.58	25.30	57.04	46.71
63.15	50.28	62.20	65.40	48.17	63.74	35.14	3.61	45.93	41.26
62.38	54.71	75.60	78.26	57.83	59.09	41.60	32.53	54.07	33.35
27.68	49.05	53.16	40.58	56.33	64.38	65.19	26.51	45.19	33.31
40.79	53.47	56.18	57.25	62.00	67.35	58.40	50.60	41.48	25.08
26.37	64.86	19.28	37.90	64.30	58.65	21.73	14.46	81.48	76.89
19.59	49.75	48.65	38.41	42.17	48.90	53.55	39.76	43.70	26.31
31.15	54.53	57.08	38.23	37.50	51.33	32.55	18.07	30.37	35.63
36.93	54.53	10.03	34.78	30.00	34.47	12.92	27.71	49.63	48.65
51.20	29.23	53.31	38.23	24.33	40.81	12.52	27.71	27.41	32.64
84.19	22.15	46.84	66.12	79.50	88.60	39.42	16.87	42.22	83.19
85.66	32.94	43.83	100.00	57.00	66.95	41.60	18.07	37.78	49.53
54.28	56.65	39.46	98.73	75.33	73.76	71.89	0.0	40.00	45.02
14.57	29.05	31.33	5.62	29.00	38.45	44.67	100.00	20.00	31.48
25.37	0.0	27.98	38.37	17.47	2.63	18.09	8.43	15.56	32.47
37.16	13.66	40.51	26.93	27.50	26.88	19.63	28.92	5.93	33.17
10.95	11.89	39.61	27.90	33.00	28.74	30.70	40.96	8.15	34.05
11.26	6.94	31.78	21.38	0.0	0.0	35.78	15.66	6.67	8.90
37.16	17.09	33.19	12.25	0.43	9.41	0.0	16.87	0.0	5.35
12.26	45.15	44.28	66.67	66.00	55.99	70.28	42.17	26.67	37.64
17.27	28.70	47.23	44.49	62.80	68.60	48.47	53.01	24.44	52.34
15.19	26.40	40.06	55.07	51.00	58.52	47.25	40.96	20.74	44.50
20.59	29.76	41.42	43.84	55.00	54.37	59.21	39.76	14.07	43.97
95.76	41.08	34.19	80.98	50.17	56.90	58.00	77.11	20.00	34.65
44.26	18.44	41.42	69.93	45.00	57.91	30.13	43.37	30.37	41.51
0.0	11.11	46.66	40.18	27.93	34.77	21.57	13.25	17.78	42.95
24.98	32.06	40.66	46.38	38.33	50.83	23.26	21.69	19.26	40.20
24.44	39.49	61.30	59.06	80.17	83.47	50.08	20.48	35.56	57.09
15.50	38.32	50.75	9.96	12.67	24.42	32.88	14.46	13.33	0.0
18.81	46.67	43.83	11.52	10.67	22.33	9.53	24.10	14.82	6.23
51.58	51.35	50.57	52.03	43.23	57.61	38.53	16.87	36.30	35.95
64.30	21.97	58.89	61.25	17.17	34.64	15.19	24.10	38.52	28.14
40.94	55.59	67.86	77.10	51.57	57.77	46.93	32.53	36.30	32.29
1.85	43.03	45.93	10.33	24.83	30.69	9.29	1.21	20.74	23.22
5.71	30.82	24.70	0.0	15.17	16.86	14.86	13.25	23.70	16.71
1.85	80.72	43.83	7.61	35.50	50.59	26.66	8.43	28.15	16.71

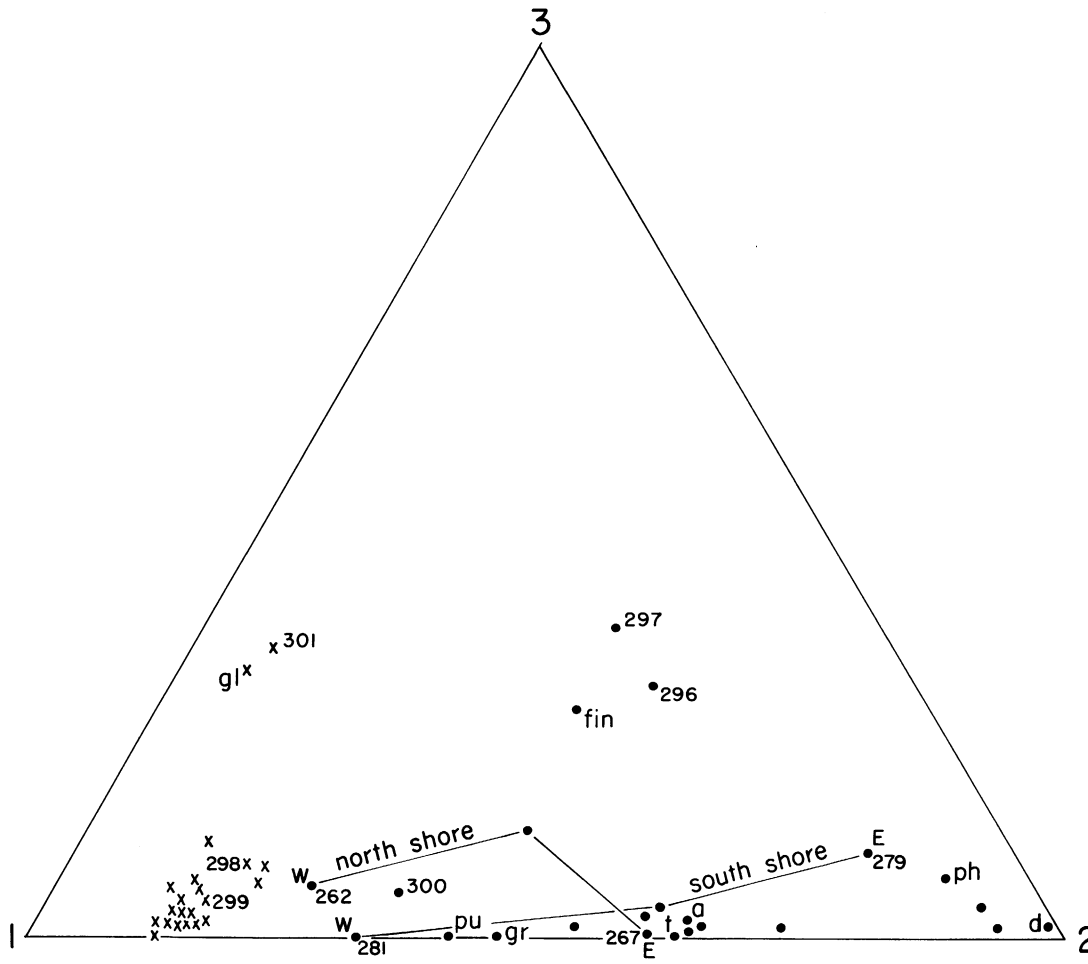


FIG. 8. Normalized factor loadings of samples for a three-axis Q-mode analysis of mean vectors for all samples. Ribby samples indicated by an X, mottled by a dot. Note that nearly all information is resolved by the first two axes acting as foci for ribby and mottled morphotypes. The intermediate field is occupied entirely by samples identified before the analysis as intermediate either in form or geography. The five samples high on axis 3 share a developmental disturbance found only in hybrid samples (see text). Southern and northern shore coastal transitions are shown by lines running W (west or ribby-influenced) to E (east and mottled). Sample 299 is just left of the number, sample 298 just right. Maynard's samples indicated by lower-case letters: gl = *C. glans*; pu = *C. purpurea*; gr = *C. gracila*; fin = *C. fincastlei*; t = *C. tenui*; a = *C. agrestina*; ph = *C. phoenicia*; d = *C. degeneri.*

sample. Some variables (numbers of ribs, size of protoconch) are very weakly, if at all, correlated with adult shell size; these will make larger contributions to vectors for small shells, since the variables correlated directly with adult size will be smaller, and will contribute proportionally less to the vector of constant length. Thus, effects of size are recorded as "shapes"—that is, as the relative sizes of individual variables among samples scaled to equal overall size. We therefore detect the important effects of size in subtle differences of proportion, not in raw effects in magnitude that can so easily swamp all other distinctions.

Since this procedure does depart from the conventional form of factor analysis—R-mode on non-normalized data—we con-

trasted a similar analysis of Little Bahama Bank cerions (Gould and Woodruff, 1978, pp. 391–392) with a conventional analysis of the same data. We found no major differences; R and Q forms of analysis are, after all, virtual mirror images.

Our factor analytic program (CABFAC, see Klovan and Imbrie, 1971) began with a 10-axis solution. The eigenvalues of the principal components solution show the usual pattern (table 5): most information falls onto the first axis (82.5% of the variance in loadings of the 45 samples—remember that in the Q-mode, loadings are samples, not variables). Of remaining axes, only the second encompasses appreciable variance (8.2%); the third (at 2.4%) initiates an even decline, with no decrement greater than 0.6 percent, to a tenth axis at 0.2 percent.

The rotated varimax solution (table 5) indicates that two axes dominate the system and encompass 85 percent of all variance: the first at 52.5 and the second at 32.5. The third, at 6.2 percent (for a cumulated total of 91.2%), merits some consideration as a general source of variance, but no subsequent axis encompasses more than 2.3 percent of the total variance and all (with one exception) owe their value almost entirely to the high loading of a single sample (see section II.D for a discussion of these minor axes and their meaning).

With three general axes to retain, we can normalize the loadings for each sample in the three-axis solution and present the three-dimensional result in the form of a ternary diagram, so beloved by geologists for the presentation of rock compositions. This diagram (fig. 8 for the samples, fig. 9 for some representative specimens) displays the primary result of the entire study: this large suite of samples, spanning an impressive range of phenotypic variation presently allocated among some 70 taxa, reduces to a matrix not very far from rank two—and the focal morphologies of the two axes in pure form are our old friends, the ribby (axis 1) and the mottled (axis 2) morphotypes. The third axis encompasses more than 15 percent of the information in only five samples. We shall see in section III that this third axis represents an interesting pattern of ontogenetic disruption characteristic of certain hybrid samples.

TABLE 5
Eigenvalues

Axis	Amount	Cumulative
A. Principal Components Solution:		
1	82.5	82.5
2	8.2	90.7
3	2.4	93.1
4	1.9	95.0
5	1.3	96.3
B. Varimax Solution:		
1	52.5	52.5
2	32.5	85.0
3	6.2	91.2
4	1.5	92.7
5	1.6	94.3
6	2.3	96.5
7	1.5	98.0
8	0.5	98.5
9	0.5	99.0
10	0.4	99.4

The third axis therefore represents patterns of interaction between the two morphotypes (see section III.C).

The most striking pattern for samples arrayed along the line of distinction between the first two axes (horizontal bottom line of fig. 8) is the marked difference in range of variation between ribby and mottled populations. All ribby samples (with the exception of two partial hybrids high on axis 3) cluster in a very tight knot in the lower left corner of the diagram. This pattern discounts Plate's proposal that all New Providence *Cerion* represent an even cline of phenotypic variation running from ribby shells in the west to mottled shells in the east. We purposely collected ribby samples at even spacing all along the coast to test Plate's assertion. All these samples cluster in no apparent order in a small section of the diagram. We note no tendency for an approach towards axis 2 in samples geographically close to the bank-interior areas inhabited by mottled shells. [The three samples that are marginally closer to axis 2, though still within the ribby cluster, show no geographic pattern. One is from Hog (Paradise) Island, another (290) from the north coast west of Nassau (but not as close to mottled samples as other ribby populations further from axis 2), and the third (298) from coastal

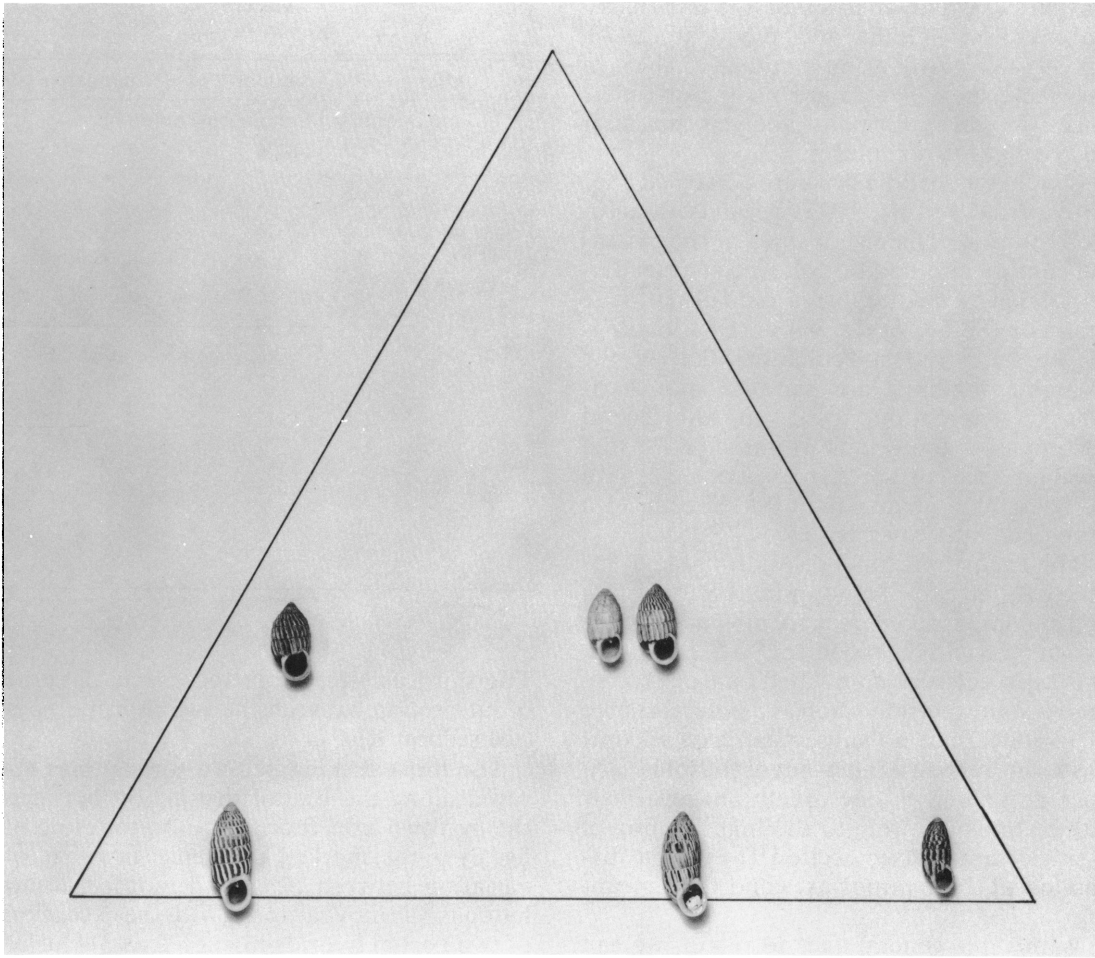


FIG. 9. Representative specimens placed in their proper position in the factor-analytic domain of figure 8. **Bottom row,** left to right, typical ribby shell with dark ground color from western New Providence; large, fine-ribbed mottled shell of *C. agrestina*; small delicate, discretely mottled shell of *C. phoenicia.* **Top row,** shells with high projections on the third axis of hybrid effect. From left to right: interior ribby shell from 301, two specimens from hybrid sample 296, showing range of ribbing in this variable sample. Note that all three hybrid shells seem to terminate growth abruptly by secreting the adult aperture upon a shell still in the middle, parallel-sided stage of growth.

populations of ribby shells just north of the Blake Road hybrid zone.] The ribby morphotype seems to encompass a phenotypically coherent and stable entity, not a fictitious modal point for one end of an even and continuous cline.

Mottled samples, as we noted qualitatively above (p. 402), form a much wider phenotypic spread, extending from four samples near the corner of the second axis, across the bottom edge of the diagram nearly to the ribby cluster itself. The factor scores for this three-axis solution (table 6) provide an explanation for differences in position and range between ribby and mottled samples. [In conventional R-mode analysis, we study covariation among variables by considering factor loadings, or the correlations of original variables with new axes. In this inverted Q-mode analysis, we study factor scores—the projection of plotted points (variables in Q-mode) upon factor axes. A cluster of high

projections in Q-mode is analogous to a cluster of high correlations in R-mode and conveys the same information about covariance.]

Most of the variables (12 of 19) project positively and quite uniformly upon the first axis with scores above 0.2, but none higher than 0.33. These 12 variables are measures of shell size, thickness, and general robustness. They include both final adult size and size at standardized whorl numbers, two sets of variables that do not always covary positively in *Cerion*. The seven highest scores are for variables that serve as the primary markers of size and general robustness: aperture height and width, general shell height and width (the four most general measures of final size), shell weight (a combination of size and thickness), thickness of the adult lip, and width at the fourth whorl (a standardized measure of size at an intermediate stage of growth). Tables 3 and 4 show that this covarying set reflects the major general differences between mottled and ribby shells: ribby shells are usually thicker, heavier, and larger at intermediate and final sizes—in general, more robust in appearance. Hence they load strongly on axis 1.

All scores below 0.2 are for variables that either participate weakly in the distinction of mottled from ribby, or have higher values for mottled shells. Total number of adult whorls (measure 3) distinguishes the two morphotypes only weakly. Ribby shells generally have more whorls, but the effect is small and inconsistent because mottled shells tend to have smaller whorls and may therefore reach their smaller final size with the same number of whorls. Protoconch width (measure 1) is a weak discriminator because differences in size between the two morphotypes tend to accumulate in ontogeny and are not marked at the outset. Lip width (measure 12) makes little contribution (while lip thickness is important) because the increased weight of the adult lip results almost entirely from its thickening, and not from its simple extension (which can be delicate and paper thin). The dimensionless measure of tilt (17, a ratio) does not distinguish the two morphotypes. Finally, the three measures of ribbing (4–6) display the only negative scores on the first axis. These are the only variables for which mottled shells show consistently higher values. (Lest this seem paradoxical, given the names of our morphotypes, we point out that ribby shells have a few strong and prominent ribs, whereas mottled forms have many fine and inconspicuous ribs.)

TABLE 6
Factor Scores for Three-Axis Varimax Solution

Name	Axis 1	Axis 2	Axis 3
1. Protoconch width	0.171	0.253	0.259
2. 4th whorl width	0.277	0.093	−0.280
3. Total whorls	0.143	0.190	−0.248
4. Ribs on 4th whorl	−0.196	0.537	−0.016
5. Ribs on 6th whorl	−0.170	0.470	−0.024
6. Number of ribs on first whorl	−0.178	0.509	−0.133
7. Height of shell	0.266	0.059	0.205
8. Width of spire	0.280	0.019	−0.201
9. Protoconch height	0.226	0.007	−0.409
10. 4th whorl height	0.247	0.086	0.213
11. Umbilical width	0.235	−0.053	−0.393
12. Width of apertural lip	0.140	0.128	−0.357
13. Thickness of apertural lip	0.284	0.162	0.344
14. Height of the aperture	0.291	0.079	0.193
15. Width of the aperture	0.331	0.055	0.072
16. Protrusion of the aperture	0.202	0.114	0.075
17. Tilt of the aperture	0.055	0.163	−0.043
18. Weight of the shell	0.271	−0.048	−0.017
19. Distance from inner lip of aperture to previous whorl suture	0.218	0.112	0.168

The second axis contains only three prominent scores—the three measures of ribbing, the only variables for which mottled shells consistently exceed ribby. Hence, mottled samples project strongly on the second axis.

With these criteria of distinction in mind, we can make sense of the variation in mottled shells across the field of variation between axes 1 and 2. The four mottled samples closest to axis 2 (*C. degeneri, C. phoenicia,* and

our 273 and 276) have the smallest shells (along with 279, the sample with the next highest projection on axis 2), and (with the exception of *C. phoenicia*) the largest number of ribs among mottled cerions (compare the sample mean vectors of tables 3 and 4 with the morphotype means of table 9). The mottled samples nearest the ribby cluster either represent unusually large shells for the morphotype (*C. gracila* and 278, both from the southern area of large-shelled populations see p. 401), or are involved in interactions with the ribby morphotype.

Of the interacting populations, *C. purpurea* is a Maynard collection from Creek Settlement, just east of Nassau (and close to our 262, which plots even closer to the ribby cluster). This area lies within the northern coastal area of interaction between the two morphotypes. Sample 300 is from the southern edge of the Blake Road hybrid zone, between the hybrids and mottled forms to the south. All other mottled samples lying close to the ribby cluster represent our collections from the coastal zones of interaction. One suite, 262-263-267 from west (ribby influenced) to east (pure mottled), is labeled north shore on figure 8; it spans the area from just east of Nassau (where we first find snails after the Nassau extinction) to East End Point (267, and well within the morphospace of mottled forms on fig. 8). The other suite, 281-280-279 and labeled south shore, represents the southern coastal transition, from Coral Harbour to Millar's Sound (see fig. 4).[3]

The morphological spread of these coastal suites is large, ranging in each case almost from the ribby cluster itself (samples 262 and 281) to well within the mottled region (samples 267 and 279). Lest this smooth transition be seen as support for Plate's assertion of even coastal clines, we point out that each area of transition represents only a small segment of the coast—about 4.0 km on the south shore and 3.5 on the north coast. Plate, on the other hand, held that the smooth cline stretched all along the north coast from extreme west to east. More than 20 km of this coast (west end to Nassau) is inhabited by snails lying entirely *within* the tight ribby cluster on axis 1.

[3] The samples labeled *C. degeneri* and *C. phoenicia* are both located west of this transition, but plot in the mottled cluster of figure 8. Both are dwarfed interior samples from mangrove areas and do not form part of the coastal transition.

D. Small (But Biologically Significant) Effects on Minor Axes

It is conventional, in factor analytic studies, to establish some quantitative criterion for the elimination of axes (dimensions) from further consideration—a test of total information (exclude an axis that encompasses less than a certain percent of the total variance), or a test of individual resolving power (eliminate an axis that fails to encompass at least a certain percent of the variance in any sample). These analogs of significance tests in standard parametric statistics often do not translate well—and may lead to a loss of biologically important information—when applied to exploratory factor analyses of the type discussed herein. We may, with good reason, be willing to take a risk of being wrong 5 percent of the time in declaring the means of two samples statistically indistinguishable. But this convention does not imply that less than 5 percent of the information in any biological system must, ipso facto, be devoid of meaning.

"Significance" has a technical definition in statistics that often does not correlate well with its vernacular meaning; a small percentage of information may have biological significance. In studies of geographic variation, for example, we may find that, for example, five samples of 100 are distinguished by a unique pattern of covariation involving only 4 of 50 variables. Now 8 percent of the variables affecting 5 percent of the samples doesn't add up to much information. In a factor analysis, this pattern may appear on a minor axis encompassing less than 1 percent of the total information. Is it therefore unimportant? It might be, if the samples have no common geographic or environmental source, and if the pattern of covariation seems accidental; the small peak of information may then represent a vagary of sampling (though patterns that seem capricious in our ignorance sometimes become the most interesting of all, once we understand their reasons). But

suppose that the samples all come from one area, or represent all the collections from a particular habitat. Or suppose that the covariance can be interpreted as a correlated response to conditions affecting only these samples. Then the information is biologically significant whatever its quantitative contribution to the entire system. If we measure 500 morphometric traits on 500 humans, including 3 albinos, the association of white skin and pink eyes will encompass a minuscule amount of variance (two traits on three people)—yet the separation of these three individuals on a small axis of a varimax solution (with high loadings for two traits only) will identify a biologically significant subgroup within the total sample. We urge morphometricians to study patterns on minor axes and not to discard them a priori.

Morphometrically, *Cerion* is so labile and so subject to local effects—the reason, after all, for its current exuberant taxonomy—that we have always detected a hierarchy of geographic coherences. Broad regions are uniquely characterized by basic patterns of form, thus disproving the older idea that haphazard transport and "crazy quilt" distributions represent the primary fact of *Cerion*'s biogeography. The basic pattern of ribby vs. mottled in the northern Bahamas (Gould and Woodruff, 1978), the cline in *C. striatellum* across its entire range from Hispaniola to the Virgin Islands (Gould and Paull, 1977), the division of *Cerion uva* into four morphometric groups representing separate islands and the two nearly separated parts of Curaçao (Gould, 1969a, 1984a), and the smooth trend surface of mottled shells on Grand Bahama (Gould and Woodruff, 1978) represent just a few examples of these broad coherences across entire islands or groups of islands.

But we also invariably find that certain geographic subregions within the range of any basic pattern can be distinguished by minor, but consistent, variations in the form of their resident snails. These subregions are either semi-isolated from the main range by geography (small islands or peninsulas) or habitat (favorable regions surrounded by unfavorable terrain for snails)—or they represent areas of unusual habitat for *Cerion* (mangrove areas that seem to induce dwarfing in mottled shells, for example). Pongo Carpet snails are semi-isolated by both habitat and geography from the more "ordinary" mottled shells that surround them on Great Abaco Island (Gould et al., 1974); *Cerion uva* from volcanic rocks (island interiors) are larger and less ribby than snails from limestone regions (island borders) in the Dutch Leeward Islands (Gould, 1969a, 1984a).

These minor, but geographically consistent, variations often sort on minor axes in factorial solutions. We found, for example, that a pattern of covariation involving protoconch height and numbers of whorls clearly distinguished the mottled samples of Treasure Cay (a peninsula) from all other mottled shells on Abaco—2 variables of 20 for 5 samples of 52, for a mere 0.95 percent of the total variance on a minor axis (see Gould and Woodruff, 1978, fig. 9, p. 390).

The full 10-axis varimax solution for New Providence cerions includes several minor axes with biologically interesting patterns. We can make no biological sense of axes 8–10. Each includes less than 0.5 percent of the total variance (see table 5), encompasses less than 5 percent of the variance for any sample and, especially, rests upon no pattern of covariance that we can recognize. Axes 4–7, however, provide (with one exception) excellent illustrations of our claim that biologically significant information can be expressed by minor axes. Each encompasses between 1.5 and 2.3 percent of the total variance. Patterns of covariation, as expressed in the matrix of factor scores for these axes (table 7), indicate that (with the same exception) these axes are based upon interactions of several variables representing definite paths of development in *Cerion*. Although two of the three interesting axes include substantial information from only one population, this sample is representative of a geographic region or a repeated response to habitat.

The fourth axis (table 7) includes three strongly positive scores for standardized measures of earliest growth stages, protoconch height and width, and height at the end of the fourth whorl. Measures of the adult aperture (height, width, and protrusion, measures 14–16) score negatively, and most other measures of adult size also score negatively, but much more weakly.

This pattern of covariation largely reflects

the loading of a single sample, number 279 (at 0.446, or 19.9% of its total information—the variance of a sample encompassed by an axis is the square of its loading). Only two other samples reach 5 percent (262 at 5.2 and 299 at 8.2). Sample 279 comes from the edge of a mangrove tract bordering Millar's Sound. As tables 3 and 4 show, shells of sample 279 average among the smallest of mottled cerions—a common characteristic of mangrove areas (Gould and Woodruff, 1978; Woodruff and Gould, 1980).

Cerion exhibits several styles of dwarfing, and the elucidation of their causes would greatly aid our understanding of *Cerion*'s outstanding plasticity (see Gould, 1984b)—for we encounter each style over and over again. We suspect that sample 279 represents the characteristic style imposed as the immediate phenotypic effect of suboptimal environments. We have often noted that mottled cerions in areas just recently subjected to unfavorable environments (long dry spells or encroaching mangroves, for example) display the two effects noted in sample 279: a large increase in variation of adult size and a general decrease in mean size. The increased variation of 279 is evident in comparing tables 8 and 9. Note that 279 exhibits an above average coefficient of variation for all measures of adult size (and a maximum among all mottled *Cerion* for the most visible measure of total shell height). However, the measures of standardized early size (protoconch height and width and height and width at the end of the fourth whorl) exhibit average amounts of variation for mottled cerions.

Combining this information on variation with patterns of covariance extracted from the scores on axis 4, we conclude that sample 279 experienced the following style of incipient dwarfing: early standardized sizes are near average for mottled cerions (37th to 41st percentile across all 45 samples in percent range transformation for the three measures scoring highly on the 4th axis—see table 4). However, measures of adult size range from the 0th only to the 17th percentile. Since our factor analysis works with data transformed to percents of ranges, this pattern explains the scores of axis 4 and the high loading of 279 upon it. Shells of 279 are relatively large (within their own mean vector) for early standardized measures and relatively small for measures of adult size. Hence, an axis with high positive scores for the standardized measures and negative scores for adult size receives a high loading from 279.

Shells of 279 begin growth at sizes near average for mottled cerions. Their unusually small final size is a consequence of stunting during later ontogeny. A marked increase in variation of final size accompanies this stunting. Could this dwarfing represent an immediate phenotypic effect following a normal early development? Will the next generation lay smaller eggs and exhibit a different style of dwarfing coordinated throughout ontogeny?

We see this style of dwarfing often in mottled cerions (mangrove areas near the north coast of Grand Bahama Island, for example). We encounter it in local populations circumscribed within immediately unfavorable environments. This style includes decrease in average size and increase in variability of size. It stands in marked contrast with a more general and profound type of dwarfing often encountered in mottled cerions. This second type, which affects populations in broader areas of more stable habitat and need not be correlated with increases in variability, produces shells that are small throughout their ontogeny, from protoconch to adult aperture. These populations have been given specific names (*C. deani* and *C. laeve* on Eleuthera, and *C. pauli* on Great Exuma) but they are clearly dwarfed mottled cerions. *C. degeneri* from New Providence—the smallest mottled *Cerion* in this study—grows in close conformity to this style; note its small size for both early standardized *and* later adult measures (tables 3 and 4).

This more global and stable style of dwarfing does not simply produce a geometrically similar, scaled-down version of mottled *Cerion*. Often, whorl number is not reduced (note that *C. degeneri* occupies the 57th percentile for whorl number, but lies well below this value for all other measures of size). These dwarf cerions reach a small final width and then add the normal number of whorls. This mode of growth leads to a unique and peculiar shape for *Cerion*: a "smokestack," long and skinny, built of numerous whorls of small and constant width (see Gould, 1984b). The

TABLE 7
Factor Scores for 10-Axis Varimax Solution

Name	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10
1. Protoconch width	0.168	0.250	0.318	0.315	−0.001	−0.010	0.232	0.257	0.604	0.048
2. 4th whorl width	0.224	0.069	−0.401	0.031	−0.194	0.006	0.141	0.018	0.324	−0.285
3. Total whorls	0.169	0.228	−0.038	0.092	0.602	0.190	0.091	−0.083	−0.018	0.301
4. Ribs on 4th whorl	−0.200	0.537	−0.070	−0.057	−0.100	−0.092	0.083	0.039	−0.077	0.075
5. Ribs on 6th whorl	−0.164	0.472	−0.072	−0.087	−0.100	−0.116	0.047	0.082	−0.220	0.073
6. Number of ribs on first whorl	−0.179	0.511	−0.129	0.023	0.013	−0.009	0.015	−0.074	−0.060	−0.258
7. Height of shell	0.274	0.083	0.237	−0.166	0.237	−0.021	0.244	−0.143	−0.123	0.246
8. Width of spire	0.236	0.005	−0.281	−0.076	−0.059	0.069	0.165	−0.143	0.075	−0.160
9. Protoconch height	0.302	0.029	−0.154	0.411	0.343	−0.028	−0.173	0.408	−0.305	−0.412
10. 4th whorl height	0.255	0.043	0.194	0.553	−0.508	−0.159	0.097	−0.103	−0.208	0.236
11. Umbilical width	0.193	−0.070	−0.518	−0.083	−0.172	−0.077	0.263	0.152	−0.200	0.296
12. Width of apertural lip	0.164	0.137	−0.347	0.208	0.090	−0.020	−0.509	−0.371	0.241	0.356
13. Thickness of apertural lip	0.351	0.177	0.287	−0.195	−0.134	−0.222	−0.513	−0.081	−0.181	−0.149
14. Height of the aperture	0.272	0.078	0.090	−0.318	−0.068	0.020	0.085	−0.048	0.031	0.065
15. Width of the aperture	0.308	0.047	−0.049	−0.276	−0.115	0.058	−0.107	−0.101	0.189	−0.148
16. Protrusion of the aperture	0.202	0.104	0.044	−0.293	−0.109	0.217	−0.170	0.632	0.062	0.229
17. Tilt of the aperture	−0.008	0.090	0.056	0.127	−0.232	0.895	−0.078	−0.110	−0.173	−0.034
18. Weight of the shell	0.269	−0.049	−0.001	−0.014	0.032	−0.012	0.239	−0.040	−0.336	0.033
19. Distance from inner lip of aperture to previous whorl suture	0.196	0.112	0.161	−0.066	0.065	0.041	0.284	−0.318	−0.015	−0.346

TABLE 8
Coefficients of Variation for All Samples

Sample	1 Proto-conch Width	2 4th Whorl Width	3 Total Whorls	4 4th Ribs	5 6th Ribs	6 1st Ribs	7 Height	8 Width	9 Proto-conch Height
Ribby									
cinereum a	4.58	5.15	5.30	8.96	8.68	18.07	6.54	4.82	9.19
coryi b	4.81	4.80	4.16	7.29	7.10	15.13	5.39	3.49	10.31
salinaria	4.86	5.87	6.28	12.00	10.22	16.69	6.16	6.00	11.00
292	4.81	4.30	4.91	11.74	11.08	30.40	5.56	4.78	10.81
285	3.87	4.78	5.78	9.52	9.08	14.29	5.60	3.18	
287	4.53	3.70	5.66	15.83	22.05	17.87	7.20	5.19	10.95
289	3.11	4.66	5.43	8.23	8.23	19.25	6.99	5.15	8.50
291	5.32	5.70	5.61	9.19	5.73	15.64	6.32	4.50	12.79
glans b	6.46	5.86	6.17	11.34	9.19	16.91	7.14	4.41	9.69
288	4.90	5.08	5.64	7.43	6.28	14.47	6.04	5.03	12.72
294	3.26	3.94	5.49	8.11	6.82	24.52	4.46	4.05	10.04
286	4.68	6.29	4.96	7.53	8.67	14.80	6.54	5.92	8.78
283	5.59	5.72	4.11	7.46	7.16	17.88	6.92	6.01	9.86
284	3.95	5.47	5.45	8.54	10.04	13.51	7.51	6.04	10.85
mutata	5.47	4.08	5.90	11.94	10.08	18.78	6.35	4.04	9.37
coryi a	5.86	6.08	5.43	8.26	6.61	25.21	6.23	4.68	9.62
290	4.86	5.01	4.49	7.80	9.12	15.30	7.74	4.70	9.88
cinereum b	4.44	4.35	6.28	10.92	8.13	19.13	7.45	4.92	10.78
Mottled									
262	6.07	5.63	6.89	9.58	9.61	22.31	5.52	4.67	11.14
281	5.27	5.43	6.32	7.84	8.43	18.39	4.68	5.35	12.15
purpurea	4.63	5.26	7.99	9.16	10.73	14.48	8.30	5.77	11.76
gracila	5.96	4.84	4.69	8.87	10.85	10.21	4.94	3.65	12.47
263	5.51	5.95	5.86	8.21	8.10	15.20	7.38	6.05	8.56
degeneri	4.53	6.00	6.14	9.15	11.07	9.10	10.01	7.24	10.53
276	5.68	4.84	6.39	12.03	14.72	17.62	8.11	4.97	12.59
273	6.20	5.55	6.71	13.19	11.90	19.41	8.31	6.84	8.65
phoenicia	6.77	5.82	4.54	25.56	29.63	12.34	6.04	5.26	14.55
279	6.10	6.51	6.07	17.84	15.59	17.58	10.28	7.38	9.72
271	5.67	5.43	4.13	16.77	18.50	13.92	6.29	6.08	14.39
275	5.20	5.01	5.50	19.61	20.56	18.79	6.97	4.50	10.31
274	3.72	4.29	5.73	13.22	9.54	17.57	8.21	5.64	8.90
agrestina	5.16	5.45	5.15	12.61	11.92	13.54	7.11	4.05	12.71
tenui	8.36	4.86	8.04	13.26	17.42	14.11	6.90	5.67	19.36
267	5.21	6.33	6.10	13.32	11.88	20.40	8.04	6.94	8.36
280	4.83	5.13	6.30		15.37	18.82	10.24	5.81	10.52
270	5.15	6.19	6.71	15.72	16.34	13.87	6.62	5.57	9.81
278	6.00	6.29	6.40	19.47	21.71	23.13	7.17	4.09	11.89
Hybrid area									
296	5.59	7.08	6.49	68.37	73.89	36.74	10.20	8.08	11.97
297	5.36	5.93	8.13	59.57	65.24	39.97	12.37	6.47	11.89
298	5.19	6.95	6.52	66.58	62.10	24.10	7.94	6.18	11.79
299	5.61	3.53	6.48	8.73	8.05	16.61	9.75	4.96	11.84
300	6.11	6.05	6.60	37.75	46.17	29.33	7.60	6.07	9.74
301	5.89	4.29	5.76	8.84	9.03	18.92	6.82	5.53	8.77
fincastlei	5.49	4.44	7.41	13.36	11.33	12.09	8.70	4.96	10.19
glans a	5.70	6.96	6.31	10.07	7.28	15.46	7.57	4.97	9.41

TABLE 8 (*Continued*)

10 4th Whorl Height	11 Umbilical Width	12 Lip Width	13 Lip Thick-ness	14 Aperture Height	15 Aperture Width	16 Pro-trusion	17 Tilt	18 Weight	19 Aperture Suture
6.88	11.06	31.66	27.54	7.35	9.45	19.32	17.11	14.70	9.23
6.63	10.53	17.91	23.95	3.93	5.69	10.98	16.36	12.94	7.33
5.38	15.57	51.71	50.10	6.52	7.44	19.90	16.63	15.62	8.45
6.37	10.50	20.27	21.98	7.58	6.63	17.02	15.90	16.51	6.02
5.54	15.72	16.67	31.79	5.81	5.90	16.74	15.83	12.76	8.64
8.24	12.97	12.93	23.82	6.03	8.56	17.58	23.69	17.36	11.55
6.17	12.03	23.40	31.46	5.92	5.64	15.74	10.03	20.31	9.87
7.59	6.65	22.58	22.15	4.52	5.71	16.81	20.77	9.72	8.90
8.01	10.60	24.24	21.66	6.43	5.65	11.86	15.62	23.57	9.10
5.95	12.63	17.18	24.95	5.68	8.09	18.71	19.40	13.24	10.09
5.68	8.85	15.99	26.82	3.58	5.72	17.57	14.07	16.18	6.83
6.97	12.26	18.66	32.28	5.51	7.32	18.20	16.62	17.09	11.86
7.54	11.64	20.64	23.77	7.02	9.55	20.12	16.59	23.94	9.51
6.13	12.03	15.19	28.77	6.56	7.32	14.11	25.48	21.72	9.45
7.77	11.98	44.16	31.45	4.03	5.50	14.98	13.30	16.29	10.79
3.06	15.83	16.90	23.37	6.62	9.78	13.39	15.56	16.65	11.57
8.41	11.10	18.10	36.68	8.09	8.39	20.79	15.62	21.08	10.58
7.39	12.70	32.04	49.60	5.80	5.60	14.56	11.45	20.62	6.83
9.66	8.37	16.61	23.68	5.01	4.94	20.19	20.77	12.95	7.48
12.34	10.16	20.61	24.34	4.65	5.65	12.24	13.78	18.91	7.69
11.85	15.44	19.21	23.88	7.76	6.66	14.15	17.36	23.22	10.75
8.45	8.89	15.06	17.66	5.31	5.68	12.48	10.56	14.20	7.18
6.43	12.33	22.11	43.92	8.14	7.64	18.27	32.85	21.29	8.14
8.13	14.03	25.30	33.69	8.04	9.77	20.87	17.35	24.85	9.69
7.41	13.26	16.72	26.02	5.82	5.79	17.42	13.69	27.92	8.10
8.42	13.98	17.25	30.02	8.99	9.36	15.70	15.45	26.17	10.45
8.68	18.06	19.16	28.32	6.00	7.04		11.61	17.59	10.45
6.61	10.62	21.31	32.64	9.00	8.61	17.93	15.45	36.39	11.17
7.22	15.37	13.31	23.27	5.64	7.54	15.48	15.13	26.95	11.56
7.43	16.33	25.09	26.84	6.10	6.38	15.60	21.27	21.40	6.17
5.38	12.32	18.77	23.86	5.38	6.94	13.17	14.80	19.72	7.61
7.67	11.60	17.43	25.23	5.53	5.69	18.73	16.40	23.86	10.65
14.45	13.42	21.39	26.15	5.84	7.44	18.93	21.48	21.22	10.00
6.85	12.26	18.68	27.96	6.42	6.94	14.88	20.46	19.83	8.58
7.17	7.72	18.21	23.59	10.45	8.04	16.15	15.74	34.63	14.10
7.20	13.10	23.42	24.65	5.84	7.10	20.17	16.80	27.60	9.41
7.21	9.41	17.20	28.14	5.09	6.23	14.70	13.10	19.77	8.47
7.54	12.00	17.73	32.33	8.71	8.87	18.13	14.91	28.12	10.45
6.42	11.15	20.81	32.32	10.04	9.38	23.59	19.65	25.70	10.14
7.30	11.11	17.28	29.99	5.43	7.81	15.85	16.43	18.85	10.56
8.34	13.68	13.63	31.67	7.71	8.47	18.15	16.33	21.40	8.36
7.90	9.88	16.40	23.94	6.37	5.18	18.66	23.57	18.87	9.26
7.36	9.12	19.97	39.63	7.20	9.40	18.87	13.40	20.71	6.82
7.31	14.37	27.13	27.78	9.71	6.58	17.46	14.98	25.57	6.92
8.66	11.21	15.70	24.06	4.78	5.06	10.11	12.44	15.33	6.68

profound difference in shape between these smokestack dwarfs and normal mottled cerions has led to the establishment of several invalid "species" for dwarfed populations. We are convinced that the differences in shape between normal mottled and smokestack dwarfs (see fig. 5) arise as a simple effect of small differences in ontogenetic style (a normal number of whorls for a shell dwarfed in all measures of size in the smokestacks), and that no taxonomic separation on this account is warranted. The smokestack style represents a general ontogenetic pattern in *Cerion*. It has evolved independently seven or eight times within four morphotypes (Gould, 1984b).

The fifth axis expresses another ontogenetic style characterizing an unusual sample within our set. Maynard's *C. tenui* displays the only high loading upon this axis (−0.507, for 25.7% of its information; no other sample reaches 5%). Only two variables score highly upon this axis (table 7): whorl number at 0.602, and height at the fourth whorl at −0.508. (Since *C. tenui* loads negatively, it grows few total whorls and unusually large height early in ontogeny.) *C. tenui,* as we mentioned before (p. 403), represents our only sample from the most divergent of the four major geographic variants within mottled *Cerion*. Shells are about average in adult size, but are short, fat, and composed of few whorls (fig. 5). Note in table 4 that *C. tenui* has fewer average whorls than any other sample, but stands near the 50th percentile for all measures of adult size except height (where it occupies only the 9th percentile).

We note here the operation of the most pervasive developmental constraint that we have identified in *Cerion* (see Gould and Paull, 1977; Woodruff and Gould, 1980; Gould, 1984a, 1984b). The form of *C. tenui* represents one extreme in the operation of this constraint. *C. tenui* begins with a flat, but wider than average protoconch. It then builds the largest early whorls among mottled New Providence cerions—96th percentile for height at the fourth whorl, 74th for width.[4] Shells subject to a general constraint upon final size encounter a forced negative correlation, for the same adult size may be reached in two different ways: by building a few large whorls, or many smaller whorls. *C. tenui* follows the first strategy, with its usual and profound consequence for adult morphology. It builds the largest early whorls among mottled cerions, but reaches an average adult size. It must therefore cease growth with few total whorls (fewest among all samples, in fact). This reduction in whorl number entails a major phenotypic consequence. *Cerion* adds height but not width in its later whorls (a result of its general form, and the reason for its generic name—from a Greek word for wax, and in reference to its beehive shape). Thus, a reduction in number of whorls produces a squat shell, "deprived" (so to speak) of its later increment of height at the expense of width. The squat shape at average size of *C. tenui* arises as a consequence of this ontogenetic style and its developmental constraint: large early whorls entailing few total whorls at a given adult size. This knowledge of ontogenetic style will help us to reach a decision in the difficult taxonomic question of whether *C. gubernatorium* (the prototype for mottled cerions of the *C. tenui* type and geographic area) represents a hybrid of mottled cerions with surviving *C. agassizi* stock, and whether it is an appropriate taxonomic name for the mottled cerions of New Providence (see pp. 470–474).

Axis 6 forms the exception to our claim that minor axes reflect significant ontogenetic styles representing broad areas or particular habitats. It exhibits a strong loading for only one sample—number 263 at 0.622, or 39 percent of its information, while no other sample exceeds 6 percent. In this case, however, the reason for 263's distinction is not a pattern of covariation representing an ontogenetic style, but the peculiarity of a single measure—number 17, the "tilt" or relative orientation of the aperture to the earlier shell. (We feel confident in labeling the high value of mea-

[4] As an unexplained but general pattern not only in *Cerion* but also in all other snails we have studied (see Gould, 1969b on *Poecilozonites*), protoconch width—not height—is strongly correlated with *height* (not width) of later whorls. In *C. tenui,* the protoconch is wide but very low, and height is far more exaggerated than width at the end of the fourth whorl. We do not understand the reasons for this phenomenon and would appreciate any suggestions.

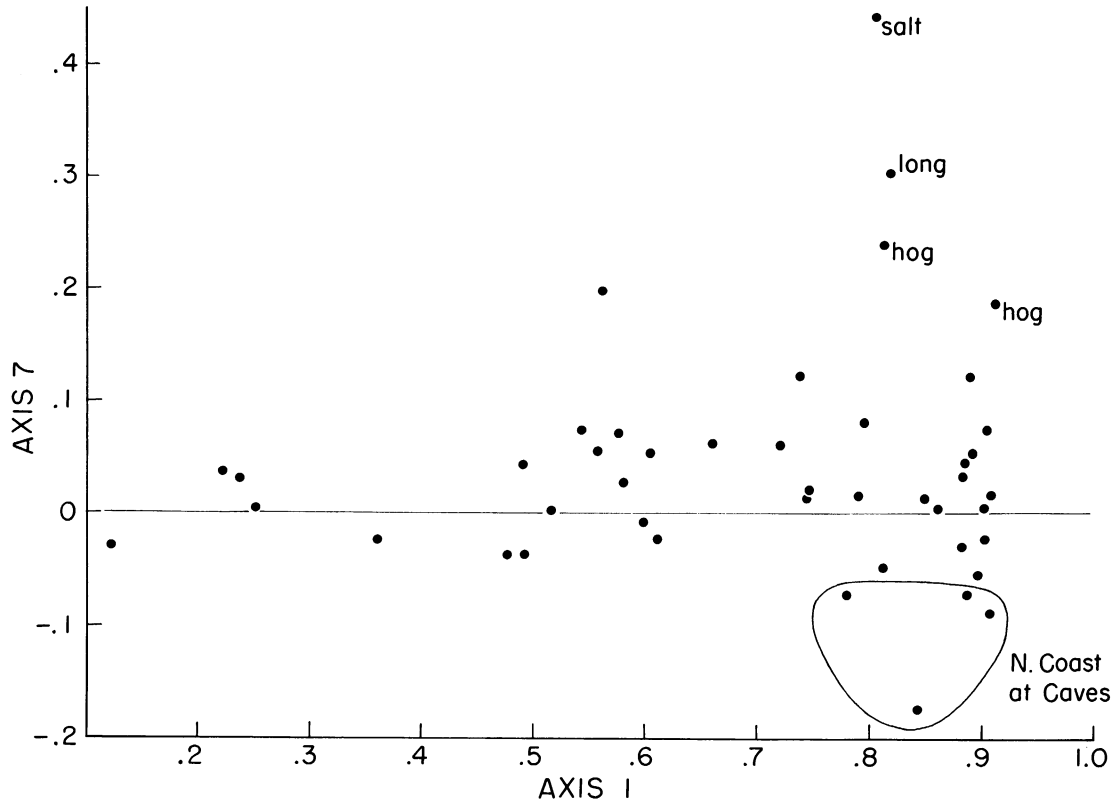


FIG. 10. Loadings of samples on Q-mode axes 1 and 7. Note how the "insignificant" axis 7 makes meaningful separations in identifying (by high projections, mostly indicating weak apertural lips) samples from the off-lying cays and (by low projections) a set of geographically adjacent ribby samples from the north coast.

sure 17 as a peculiarity because, in this case, we do not find the characteristic correlations of variable 17 with other measures of developmental intensity of the adult aperture—see Gould, 1977, pp. 263–266.) This variable scores, at 0.895, the highest for any measure on any axis; no other measure reaches 0.25 on this axis. We do not know why 263 has such a tilted aperture, but the effect seems to be a peculiarity of one sample and one variable. The effect is enhanced by one of the many unfavorable properties of ratios (measure 17 is the only ratio among our variables). In a very tilted aperture, the denominator can become quite small, even approaching zero (see Gould et al., 1974, p. 523 for a figure and definition). The measure of tilt, which normally does not stray very far from 2.0, can go "off scale" in such shells. Sample 263 contains several shells with a very high ratio for this reason; the coefficient of variation for tilt in 263 is 32.9 (see table 8), well above the next highest sample value of 25.5. The outlying status of 263 for this measure can best be seen in table 4. Measure 17 ranks at 100.0 for sample 263, while only three other samples lie above the 50th percentile, because the mean for 263 stands so far above the grand mean of all samples.

Axis 7, though it encompasses but 1.5 percent of the total variance, expresses a consistent regional effect. Its pattern of covariance (table 7) indicates a negative interaction between weakly developed adult lips (measures 12 and 13, both at −0.51 and the only strong scores on axis 7), and a set of measures related to adult size (especially shell weight at 0.24 and height at 0.24). Samples with high

positive loadings will therefore contain large shells with weakly developed lips. This combination is the virtual definition of an important suite of ribby samples—the populations on bank-edge cays off the north shore of New Providence (fig. 6). Figure 10 shows that all cay samples cluster in a unique region when we plot loadings on axis 1 against loadings on this minor axis 7. The cay samples are characterized by high joint loadings, on the first axis for their generally large size and on the seventh for their combination of large size and weak lips.

The four lowest loadings on axis 7 encompass samples 286, 287, 299, and 300, a set of ribby populations representing all our material for an area on the north coast extending from Old Fort Point to the Caves, just north of the Blake Road hybrid zone. The effect is subtle and we had not noted it in the field, but ribby shells from this area tend to have thicker and wider lips at their average adult size for ribby samples—hence their low loadings on an axis with negative scores for measures of the lip. This coherent geographic clustering (see fig. 10) accentuates the value of minor axes in picking up small but real effects easily missed in raw data and visual inspection (it is unlikely that four geographically contiguous samples would display the four lowest loadings on an axis by disconnected chance alone).

We wonder whether the cay pattern (no pun intended, though the word is pronounced "key" and not "kay") represents another general phenomenon in *Cerion* that we can document in repetitive occurrence, but do not understand in terms of the mechanics of ontogeny. Not only do the northern cays of New Providence harbor large ribby snails with weak lips, but we find the same pattern throughout the long chain of Exuma Cays to the southeast. What in the ecology of small rocky cays might favor large shells with weak lips?—for the effect is probably not a result of simple homology, but of separate evolutionary derivation. The sister populations of the New Providence cay snails must be the neighboring mainland ribby populations that do not display this effect. Since thick lips protect snails from predation by crabs, both in general (Vermeij, 1976) and for *Cerion* in particular (personal observ.), and since the land crab *Gecarcinus lateralis* is a major predator of *Cerion,* we would, as a first approach, ask whether these small rocky cays are inhospitable for land crabs. In any case, the minor seventh axis, in delineating the cay samples and detecting an unrecognized morphological pattern in snails from a coherent geographic region on the north coast, reflects once again one of the outstanding facts of *Cerion*'s biogeography: the morphological coherence, based on minor patterns of covariance, of snails from geographic subregions. *Cerion* displays strong pattern in morphology at both small and large scales. Its biogeography records no haphazard hodgepodge of accidental colonizers.

III. DEFINITION OF THE TWO MORPHOTYPES AND THEIR MODES OF INTERACTION

A. Form and Ontogeny: Differences in Means

In table 9, lines 1–4, we present the means of sample means for our 14 ribby localities on New Providence itself, for the four cay samples of ribby shells, for the 18 ribby samples considered together, and for our 19 mottled samples. We exclude the Blake Road hybrid samples from this tabulation. Line 5 then presents the percentage difference in means of sample means between ribby (N = 18) and mottled (N = 19) shells for each variable. These percentage differences were calculated as mottled minus ribby divided by the means of mottled plus ribby for each variable: a negative number therefore indicates that ribby

exceeds mottled for this variable. The variation of these percentage differences defines the basic morphological characteristics of mottled and ribby shells. The distinction of the two morphotypes is not superficial and based on an external character like ribbing alone, but affects several independently covarying sets in ontogeny.

All measures of size favor ribby samples, reflecting the basic observation that ribby shells tend to be larger. Note, however, the minimal distinction of 2.9 percent for whorl number. The larger size of ribby shells is primarily a result of larger, not more, whorls.

If size and strength of ribbing provided the only clear difference between mottled and ribby shells, we would not venture so definite a case for the distinction of morphotypes, even with our biogeographic correlations. We have, however, noted subtle but definite differences in shape that pervade all allometric phases of growth and are not correlated in ontogeny with measures of ribbing. The differences are small and not evident in all samples, but extended observation gives one a "feel" for the regularity.

In general, mottled shells exhibit a more regular outline. They are shaped like a barrel with smooth transitions between allometric phases. The initial few whorls, with their convex triangular outline (in a plane including the axis of coiling) blend smoothly into the intermediate phase of increase in height with little or no increase in width. As the "barrel" expands in width during the transition between these first two phases, it contracts with equal regularity and lack of abrupt change in the passage to the third phase, preceding the deposition of the adult aperture. Thus, the entire outline expands and contracts regularly with little sign of morphological discontinuity.

In ribby shells, on the other hand, we note subtle but definite discontinuities between all phases. The protoconch itself sticks up above the first few teleoconch whorls, which then tend to grow with a straight-sided (rather than convex) triangular outline. The transition from this triangular phase to the cylindrical stage of middle ontogeny is generally well marked, even abrupt and discontinuous, as the juvenile triangle passes into an intermediate phase that builds a parallel-sided rather than a barrel-shaped shell. In addition, this marked transition occurs at a greater relative shell width than the smoother transition does in mottled samples. Since width increases little, if at all, beyond this transition (the middle phase of ontogeny produces increase in height alone), this greater width of ribby shells is maintained throughout growth. The parallel-sided phase does not constrict gradually and pass continuously into the adult aperture (as in mottled forms); instead, the aperture grows at its divergent angle upon a shell that remains, basically, parallel-sided. All these differences—with their coordinating theme of smoother continuity in outline (for mottled shells) vs. discontinuity between allometric phases (for ribby shells)—show no apparent correlation in growth with the number and strength of ribbing. Thus, mottled and ribby shells are separated by several independent suites of characters.

These subjective impressions are all affirmed in the calculated percentage differences in means of sample means for the two morphotypes (table 9). Protoconch width differs by less than a percent, but ribby shells have a nearly 10 percent advantage in protoconch height, thus affirming that the protoconch of ribby shells "sticks up" above the first whorls of the teleoconch.

Looking at the three paired measures of width and height at similar ontogenetic stages—height and width of the protoconch, height and width of the total shell, and height and width of the aperture—we note that ribby samples are always larger than mottled, but that the difference in width always exceeds the difference in height: 7.08 vs. 3.06 percent at the fourth whorl, 12.68 vs. 8.52 percent for the entire shell, and 7.87 vs. 5.73 for the aperture alone. Thus, ribby shells are both larger *and* relatively wider than mottled.

The apparently divergent pattern for the protoconch (where difference in height exceeds width) may seem contradictory to our statement that ribby shells exceed mottled in relative width at all comparable stages of postembryonic growth. In fact, this observation reaffirms an ontogenetic correlation that we have noted again and again in *Cerion* and other pulmonates (see Gould, 1969b, on *Poecilozonites*), but that we do not understand. We have consistently found a strong

TABLE 9
Average Values and Coefficients of Variation Within and Among Samples for Ribby and Mottled *Cerion* of New Providence

Line		1 Proto-conch Width	2 4th Whorl Width	3 Total Whorls	4 4th Ribs	5 6th Ribs	6 1st Ribs	7 Height	8 Width
	Mean values								
1	Ribby N = 14	89.4	92.5	7.59	23.2	22.7	5.18	25.2	10.7
2	Ribby cays N = 4	94.5	97.7	7.76	27.9	26.5	5.70	27.5	11.7
3	All ribby N = 18	90.5	93.6	7.63	24.2	23.5	5.29	25.7	10.9
4	Mottled N = 19	91.0	87.2	7.41	58.1	50.2	9.29	23.6	9.6
5	% difference	+0.55	−7.08	−2.93	+82.38	+72.46	+54.87	−8.52	−12.68
	CV of means								
6	Ribby N = 14	2.99	3.19	4.94	6.76	4.72	11.27	6.34	4.73
7	Ribby cays N = 4	5.15	4.66	2.45	9.92	8.55	16.72	9.65	7.81
8	All ribby N = 18	4.18	4.17	4.53	11.25	9.06	12.97	7.95	6.52
9	Mottled N = 19	3.65	6.95	5.78	26.95	26.98	24.59	8.70	9.19
10	Grand average	3.92	5.56	5.16	19.10	18.02	18.78	8.33	8.06
11	% difference	−13.52	+50.00	+24.22	+82.20	+99.45	+61.87	+9.00	+33.13
	Mean of CVs								
12	Ribby N = 14	4.71	5.10	5.23	9.16	9.08	18.23	6.40	4.78
13	Ribby cays N = 4	4.84	4.86	5.94	10.95	9.28	18.02	6.62	4.94
14	All ribby N = 18	4.74	5.05	5.39	9.56	9.13	18.18	6.45	4.83
15	Mottled N = 19	5.58	5.52	6.09	13.63	14.41	16.36	7.43	5.55
16	Grand average	5.16	5.29	5.74	11.60	11.77	17.27	6.94	5.19
17	% difference	+16.28	+8.88	+12.20	+35.09	+62.15	−10.54	+14.12	+13.87
18	Sample 296	5.59	7.08	6.49	68.37	73.89	36.74	10.20	8.08
19	Sample 297	5.38	5.93	8.13	59.57	65.24	39.97	12.37	6.47

positive correlation between protoconch height and *width* at later whorls, but no (or weak) correlation between protoconch and later heights (as already noted in *C. tenui* on p. 420). The association in ribby shells of greater differences in protoconch height than width (vs. mottled shells) with greater differences in width than height during later stages of growth affirms this pattern once again.

The difference between mottled and ribby in relative smoothness of the second transition from intermediate ontogeny to the adult aperture appears, in our measures, primarily in the much larger umbilical width of ribby shells. Ribby shells constrict little, if at all, as the adult aperture forms upon the intermediate shell. The umbilicus, which remains at constant width throughout the parallel-sided stage of intermediate ontogeny, retains its high value in the adult shell. In mottled shells, however, the umbilicus constricts as the shell gradually diminishes in width before depositing the terminal lip of its aperture.

The greatest percentage differences between mottled and ribby appear in measures of ribbing and weight—the many more (but fine and inconspicuous) ribs of mottled shells, and the considerably heavier ribby shells (as a combined effect of larger general size and markedly thicker shells both in weight of the strong ribs themselves and in general thickness). But these differences are visually evident. More interesting are the subtler distinctions in shape that appear as small but consistent percentage differences in table 9. For these differences affirm that the distinction of mottled and ribby records a set of fundamental ontogenetic patterns, not just a single measure of outward (and easily changeable) adult form.

TABLE 9 (*Continued*)

9 Proto-conch Height	10 4th Whorl Height	11 Um-bilical Width	12 Lip Width	13 Lip Thick-ness	14 Aperture Height	15 Aperture Width	16 Pro-trusion	17 Tilt	18 Weight	19 Aper-ture Suture
39.6	69.5	45.0	30.0	39.0	99.8	87.6	27.5	2.00	0.99	58.5
39.3	70.6	51.7	15.8	32.5	103.2	85.9	26.2	1.99	1.39	69.0
39.5	69.7	46.5	26.9	37.6	100.5	87.2	27.2	1.99	1.08	60.8
36.0	67.6	36.6	23.7	35.0	94.9	80.6	25.3	2.04	0.59	57.7
−9.27	−3.06	−23.83	−12.65	−7.16	−5.73	−7.87	−7.24	+2.48	−58.68	−5.23
5.82	3.64	5.26	17.18	14.77	4.40	5.24	8.80	6.83	16.87	5.79
6.15	6.10	12.69	36.36	30.38	9.05	8.31	15.86	3.65	21.97	9.29
5.72	4.15	9.65	29.59	18.90	5.65	5.80	9.82	6.17	24.08	9.90
4.87	5.34	10.94	11.20	20.80	7.66	9.39	9.58	9.88	27.82	8.46
5.30	4.75	10.30	20.40	19.85	6.66	7.60	9.70	8.03	25.95	9.33
−16.03	+25.05	+12.52	−90.14	+9.57	+30.18	+47.24	−2.47	+46.20	+14.41	−12.22
10.34	6.59	11.67	18.62	26.67	5.95	7.14	16.39	17.25	17.36	9.38
10.08	6.85	12.83	39.89	39.67	5.92	7.00	17.19	14.62	16.82	8.82
10.28	6.65	11.92	23.35	29.56	5.94	7.11	16.57	16.67	17.24	9.26
11.49	8.39	12.46	19.31	27.05	6.58	7.02	16.50	17.06	23.07	9.35
10.89	7.52	12.19	21.33	28.31	6.26	7.07	16.54	16.87	20.16	9.31
+11.11	+23.14	+4.43	−18.94	−8.87	+10.22	−1.27	−0.42	+2.31	+28.92	+0.97
11.97	7.54	12.00	17.73	32.33	8.71	8.87	18.13	14.91	28.12	10.45
11.89	6.42	11.15	20.18	32.32	10.04	9.38	23.59	19.65	25.70	10.14

B. Form and Ontogeny: Differences in Variability

Cerion species have always been defined by criteria of static morphology: size, shape, color, and ornamentation of the shell at various stages of growth. Although we encounter passing statements in the literature about differences in variability, or about association of characters in ontogeny, these criteria of "dynamic morphology" have rarely been used in taxonomic work. We believe that this reliance upon static form has, in large measure, been responsible for *Cerion*'s bloated systematics. Taxa were not viewed as products of coherent developmental programs or systems of growth, but were defined only by external differences—any differences—in the forms of shells. Small distinctions that might arise by minor perturbations of a single developmental system were elevated to the status of species—though such coordinated differences surely lie within the bounds of permissible within-taxon variation.

We have therefore focused our primary work in morphometry not on the characterization of adult form, but on the study of variation. In this area of dynamic morphology, it seemed to us that two subjects offered the most promise for a better understanding of *Cerion*'s systematics: First, we have examined differences in amounts of variability between groups defined by phylogeny, ecology, and geography (that is, between morphotypes, habitats, and regions). We have already argued in this paper that mottled samples can be distinguished not only by complex differences in form from ribby shells (see last section), but also by their greater

variability among samples. Second, we have studied patterns of covariation in ontogeny. The most promising antidote against *Cerion*'s bloated taxonomy lies in our documentation that differences previously interpreted as important because they involve several characters and produce shells of strikingly different appearance are products of a simple ontogenetic change with an extensive set of automatic consequences.

Galler and Gould (1979), for example, demonstrated that the two end forms of a Cuban hybrid zone, despite impressive differences in external form, could be transformed one to the other by little more than a change in width early in postembryonic growth. And Gould (1984b) showed that complex differences in size and shape between dwarfs and normals reduce to simple consequences of one style of dwarfing–reducing the size of whorls, but not their number. By contrast, we have just argued that mottled and ribby shells on New Providence, though they differ less in outward form than the two Cuban taxa or the dwarfs and normals of Gould (1984b), are products of more complex ontogenetic disparities involving several covarying sets of characters. Since both morphotypes grow the same average number of whorls, differences between mottled and ribby cannot arise as simple results of more or less coiling. So far as we know, the differences in general size and relative width are not related as joint results of ontogenetic pathways; nor do the subtler distinctions in outline—smooth ontogenetic transitions for mottled vs. greater discontinuities for ribby—arise as consequences of variation in size or general shape.

We have continually emphasized that mottled shells present more variation among their local populations than do ribby shells (see fig. 8). If this distinction is not a simple phenotypic consequence of differences in habitat, then the two morphotypes are distinguished by patterns of variability as well as form, and our case for taxonomic distinction gains strength. In this section, we quantify these differences in variation and explore the important evolutionary question (see Sokal, 1976) of whether greater variation between samples shows any relationship with higher variability of the same characters within samples.

i. Coefficients of variation for sample means within morphotypes (CVs of means)

We calculated coefficients of variation (100 times the standard deviation divided by the mean) for each character among all samples within each morphotype considered separately. In other words, we took the mean vectors as representative of each sample and calculated CVs for mean values of each character across all samples within a morphotype. Average CVs for among-sample variation of mottled and ribby shells are recorded in lines 8 and 9 of table 9. We then (see line 11) calculated the percentage difference between CVs for mottled and ribby as the difference (mottled minus ribby) divided by the average of mottled and ribby. Positive values in line 11 therefore indicate higher values for mottled samples.

As expected, mottled samples are more variable than ribby for all but five characters. Of these five, the percentage difference of −2.47 for apertural protrusion (number 16) is smallest among all measures and not significant. We were surprised that the aperture-to-suture measure (number 19), though small in percentage difference (fourth among all measures), favored ribby samples, since all other apertural measures are more variable for mottled samples. We were also surprised by the large difference in higher variability of lip width (measure 12) for ribby samples, especially since lip thickness (measure 13) follows the usual pattern of greater variation for mottled samples. The last two exceptions are more easily interpreted: *both* measures of the protoconch show more variation among ribby samples, and at about the same percentage difference. Thus, we find the interesting (and unexplained) pattern that the protoconch exhibits more variation among ribby samples, while the postembryonic shell varies more (in almost all its many characters) among mottled samples.

For the 14 measures following the expected pattern of greater variation among mottled samples, differences between mottled and ribby are especially marked for the three measures of rib number. In all three paired measures of heights and widths (at the end of the fourth whorl, of the entire shell, and of the aperture), difference in variation of

width exceeds that of height, and the variation of width is, in itself, substantial. This pattern arises (see lines 8 and 9) because mottled samples are more variable in width than height in all three paired measures, while ribby samples exhibit about the same amount of variation for both width and height. We do not know why this is so.

ii. Coefficients of variation within samples (means of CVs)

We computed (see table 8) coefficients of variation for each measure in each sample. We then calculated the average within-sample CV for each variable within each morphotype (see table 9, lines 12–16). As for the among-sample CVs discussed in the last section, the outstanding result of lines 14 and 15 is the generally higher variation within mottled samples. In only 5 of 19 measures does CV for ribby exceed CV for mottled (see line 17 of table 9), and two of these values (for apertural width and protrusion) are effectively zero. Ribby samples are substantially more variable only for ribs on the first whorl and for the two measures of the apertural lip. Thus, mottled shells are more variable than ribby shells both within and among samples. Ribby exceed mottled for only five characters in each case, though the characters involved are interestingly different. The protoconch of ribby shells is more variable than mottled among samples, while the apertural lip of ribby shells is more variable than mottled within samples.

These within-sample CVs are very different in potential evolutionary meaning from the among-sample CVs discussed in the last section. The among-sample CVs record the extent of differences in average form from place to place; the within-sample CVs, on the other hand, record the average amount of variation for snails at a particular place—that is, within an interbreeding population. We have no clear basis for any prediction about the form of relationship between these two kinds of CVs (or, rather, positive, negative, or no correlation might be predicted on different lines of argument), though the issue of what this relationship might be in any particular case embodies a question of considerable evolutionary interest (Sokal, 1976). The rest of this section therefore treats, in order, several topics concerning within-sample CVs and their relationships with variation among samples.

1. *Differences in general levels of variation and their relationship to repeatability of measurement.* For each of the 19 measures, average within-sample CVs do not differ greatly between mottled and ribby morphotypes, and we may take the grand average between morphotypes (line 16 of table 9) as a fair expression of a general level of variability. (Only two measures exceed 30% in difference between average CV for ribby and mottled, and these may be considered as a partial exception. Number of ribs on the fourth and sixth whorls vary substantially more within mottled samples.)

Average CV among the 19 measures is 11.86. Six measures exhibit substantially higher CVs. Four of these six measure the visually most variable aspect of ontogeny, the form and angle of the adult aperture: width and thickness of the apertural lip, and protrusion and tilt of the aperture itself. Four measures—protoconch height, umbilical width, and ribs on the fourth and sixth whorls—cluster about the mean value.

The remaining nine measures all fall substantially below the mean—and these include all but one of the linear measurements of shell and whorl size. (Only protoconch height displays a higher average CV, due, we suspect, to its difficulty of measurement—see below.) Thus, linear dimensions and whorl numbers are substantially less variable within samples than weight and ribbing, thus affirming a long-standing subjective impression among *Cerion* workers. The tight clustering of basic linear measures of size between CV 5 and 7 is impressive.

Any proficient biologist could spin out a list of possible explanations for these differences in variability: potential relationships to amounts of genetic variation, to degrees of canalization, to differential susceptibility to purely phenotypic modification by direct environmental influence, for example. Before alighting upon a favorite and devoting much energy to its test, we should explore a less interesting, but more basic, methodological possibility that biometricians usually ignore at their peril: might differences be due to the human factor of relative ease and repeatability in measurement? Scales do not lie, and

TABLE 10
CV for Repeated Measurements of the Same Shell

Measure	CV	Rank
1. Protoconch width	1.01	6
2. 4th whorl width	1.05	7
3. Total whorls	0.45	4
4. Ribs on 4th whorl	1.56	10
5. Ribs on 6th whorl	2.12	12
6. Number of ribs in 50 micrometer units on first whorl	7.92	17
7. Height of shell	0.30	3
8. Width of spire	0.23	2
9. Protoconch height	3.17	13
10. 4th whorl height	2.03	11
11. Umbilical width	4.05	15
12. Width of apertural lip	5.86	16
13. Thickness of apertural lip	9.61	19
14. Height of the aperture	1.23	8
15. Width of the aperture	0.98	5
16. Protrusion of the aperture	9.46	18
17. Tilt of the aperture	3.43	14
18. Weight of the shell	0.07	1
19. Distance from inner lip of aperture to previous whorl suture	1.29	9

some measures, like shell weight, should be repeatable with high accuracy. Others, like apertural protrusion, require careful orientation of the shell or, like protoconch height and apertural width and thickness, are performed at high power on small objects. Difficulty of measurement may lead to substantial increases in CV.

To explore this possibility, a kind of null hypothesis with respect to biological explanations, Kathleen Ligare, a student of Woodruff's, performed a pilot study on repeatability of measurement. She selected three snails from Rum Cay and measured each shell nine times for each character. She did not perform a set of repeat measurements on any snail until she had fully measured 10 other snails (part of a different project). She did not refer back to any previous set of data while remeasuring the control snail. (We recognize, of course, that this experiment is far from optimal, using, as it does, people and snails not involved in the New Providence project. Our conclusions should be read as suggestive indications, rather than statistical assertions.)

We calculated the CV for repeated measurements of the same snail (N = 9 for each of three snails) and then averaged the CVs for the three snails to produce the figures in table 10. The average CV among 19 characters for repeated measurements of the same snail is 2.94; for conventional measurements of different snails, it is 11.86 for the same characters.

The correlation between CV for repeated measurements on the same shell and CV among different shells in a sample is an impressive 0.68, a value significant at the 1 percent level. Were the experimental design better, we might wish to argue that close to half ($r^2 = 0.46$) of the variation in CV among measures could be accounted for by differences in their ease and repeatability of measurement—a sobering conclusion, given the propensity of many scientists (including, formerly, ourselves) to take differences in measured variability at face value and to seek some biological explanation without considering prior alternatives.

Ease of repeatability does not, by any means, explain all the differences among CVs, as the fine structure of points on figure 11 indicates. Appeals to subjective judgment of "experts" are always frustrating to readers, for such claims cannot be evaluated rigorously, and the issue reduces, basically, to one of trust. Still, the subject cannot be avoided, as years of looking at *Cerion* shells must count for something. These subjective impressions can be partially tested in figure 11.

We have long felt that some measures are genuinely and intrinsically more variable than others, and that their measured CVs do not primarily reflect poor definition and limited repeatability. Our four primary candidates in this category are all confirmed in figure 11, for these measures lie well below the reduced major axis, indicating that within-sample variation is greater than would be predicted by repeatability as calculated from Ligare's procedure (or that repeatability is much better than predicted at the measured within-sample CV). Weight is the most highly repeatable measure (on a balance accurate to thousandths of a gram), yet it is the third most variable measure for within-sample CV. Lip thickness does not lie among the most objective measures, but we believe that its high CV reflects, for the most part, true biological variation—for adult lips in a single sample may range from nearly paper-thin to massively thickened. Lip thickness exhibits the

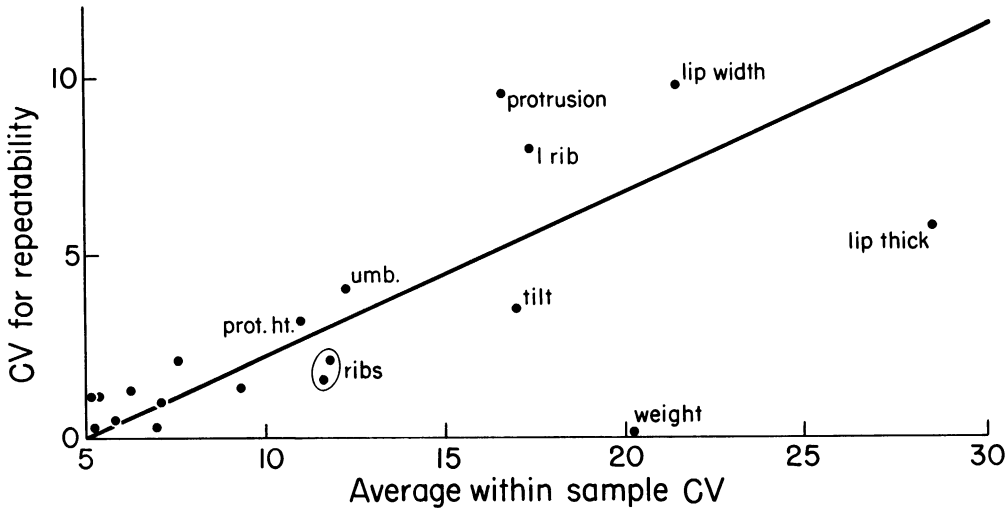


FIG. 11. The positive relationship of CV for repeated measurement of the same shell vs. average CV for the same measures among different specimens within samples.

highest within-sample CV among our measures; although it ranks fourth highest in CV for repeatability, the point for lip thickness still lies well below the line. The two rib counts on intermediate whorls also seem genuinely variable to us (particularly in mottled samples) but fairly well replicable—and their position below the line of figure 11 confirms this impression.

We have long felt that five of our measurements are considerably more difficult to make, or less well defined, than the others: height of the protoconch (taken at high power on a small object with points of definition that do not lie in a plane perpendicular to the objective of the microscope, and cannot therefore be brought into focus simultaneously); width of the umbilicus (since one border must be defined by a region of changing curvature, not a clear point); apertural protrusion (since one point of definition must be found by extrapolation and movement of the shell); ribs on the first whorl (since they are often so indistinctly defined, or even coalescent); and width of the apertural lip (a small measure, made at high power and often obscured by a bulging last whorl, so that one point of definition becomes covered in the usual orientation). We are therefore pleased to note that these five measures produce, without exception, the five points of highest joint CV lying above the line on figure 11. Much of their high within-sample CV undoubtedly reflects their difficulty of measurement, rather than their intrinsic biological variability.

Of the six measures with highest within-sample CV, four represent our entire suite of characters for allometric changes of the final phase of ontogeny: nature of the apertural lip (width and thickness) and change in orientation of the aperture (protrusion and tilt). Two of these four lie above the line (lip width and protrusion); we have previously suspected their inadequacy, but have continued to use them because they capture an important aspect of variation that we have not been able to express in a less ambiguous way. Two lie below the line (lip thickness and tilt), and are probably more satisfactory in expressing the extent of biological variation. We do not, however, believe that difficulty in repetition accounts entirely for the high within-sample CV of apertural measures. All four apertural measures covary positively in multivariate studies (see Gould, 1977), suggesting that they express differing aspects of a common process. Difficulty in measurement would not produce positive correlations, but would more likely degrade them. (Our measurers did not know the correlation structure of their variables.)

2. *The relationship of within- to among-sample CVs (mean of CVs vs. CV of means).*

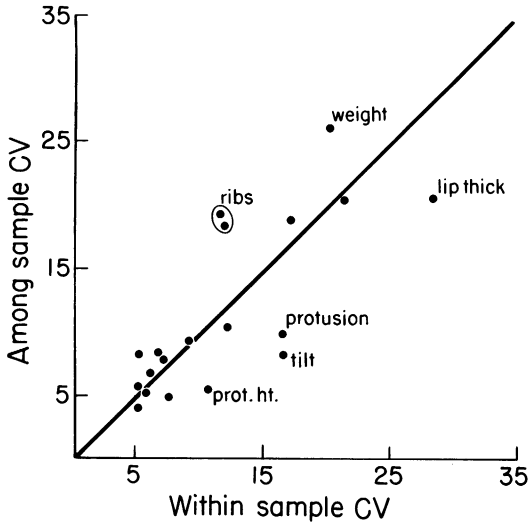


FIG. 12. The positive relationship of within- and among-sample coefficients of variation.

Since so much of evolutionary theory is fundamentally about the assumed convertibility of variation at one level into evolutionary change at the next level (viz. Fisher's "fundamental theorem"), the empirical relationship of within-sample variation (evolutionary "potential," one might argue) to among-sample variation (evolutionary "expression" perhaps) has interested many biologists.

Our extensive data on *Cerion* permit us to test this relationship with more information than has usually been available in such studies. The plot of among- vs. within-sample CV (fig. 12) shows a highly significant correlation coefficient of 0.76. We do not believe that the artifact of repeatability (see last section) can be setting this correlation for nonbiological reasons. Difficulty in repetition surely enhances some of the within-sample CVs, but it should not correspondingly raise among-sample CVs for the same measures—if we assume that measurement error in repetition is randomly distributed about a true value. Unless some samples systematically lead a measurer to under- or overestimate certain variables, among-sample CVs should not be raised by higher CVs for repetition.

The fine structure of figure 12 indicates, instead, that differences in repeatability are reflected in departure of points from the trend, not in the trend itself. The high repeatability of weight and ribs on the fourth and sixth whorls may account for their position above the line of figure 12 (unexpectedly higher among-sample than within-sample CV)—although the positive deviation for ribs only records the high (and real) among-sample variation of these measures in mottled samples (ribby samples alone lie virtually on the line). The poor repeatability of protoconch height and apertural protrusion may account for their position below the line ("abnormally" enhanced within-sample CV with no corresponding effect upon among-sample CV). Differences in repeatability cannot, however, explain all major deviations from the line of figure 12. Thickness of the apertural lip and tilt of the aperture lie *below* the line, although figure 11 demonstrates a higher repeatability than we would expect from within-sample CVs. We must therefore conclude that these measures genuinely differ less in mean value among samples than we might expect from their available within-sample variability.

Although these data provide an impressive confirmation of a positive relationship between variation within and among samples, we cannot, unfortunately, claim support for the important biological hypothesis that variation among samples (or evolutionary expression) depends upon the amount of available variation within samples, as we might propose if we had measured genetic variation directly. Our measures of phenotypic expression permit several alternative explanations for the positive relationship. In particular, the effect could be purely phenotypic if some characters are simply more subject—through poorer canalization, previous selection for variability in phenotypic expression, for example—to variation induced directly by differences in local habitat or climate. Suppose, for example that weight varies greatly within samples primarily because it records relative amounts of food or availability of lime for construction of the shell—while other characters do not vary significantly in snails that eat more or less, or find differing amounts of lime. The same propensity for variation might enhance the CV among samples as well, since some locations are relatively rich or poor in food and available lime.

Thus, we are caught in a kind of Catch-22.

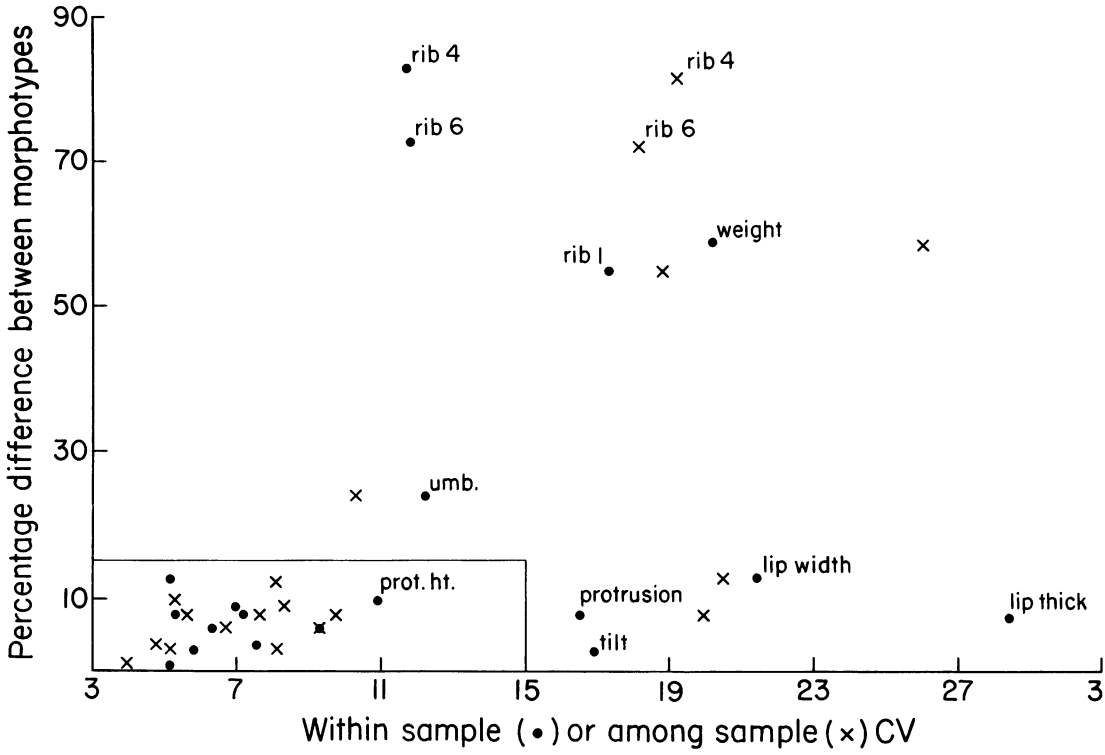


FIG. 13. Relationship of average differences between morphotype for each character and their within-sample (dots) and among-sample (Xs) coefficients of variation.

We have compiled one of the best data sets available for measuring the relationship of within- and among-sample variation. Yet the character of the measures does not permit us to reach a firm conclusion about the biological meaning of the strong relationship that we have demonstrated.

3. *Can differences in form between morphotypes be related to amounts of variation within and between samples?* We have compiled (table 9, line 5) the average percentage difference between means of ribby and mottled samples for all characters. With this information, we can look for a "conversion" of within-sample variance to a higher level of distinction than the general among-sample variance discussed in the last section: that is, we can ask whether the characters that best distinguish the ribby from the mottled morphotype are also the characters that vary most within samples (and therefore provide, if there is any correlation of genetic and morphometric variation, the most "raw material" for selection). [In this section, we use the absolute value of the percentage differences (line 5 of table 9), ignoring whether mottled or ribby score higher—for it is only the *extent* of the difference, not its direction, that concerns us here.]

The relationship between average within-sample CV (line 16 of table 9) and percentage difference between morphotypes (line 5) is weak (see fig. 13), with a correlation coefficient of 0.24.

However, when we plot the same percentage difference against the among-sample CV (line 10 of table 9), we find a reasonably strong relationship, with a significant correlation coefficient of 0.72 (see fig. 13). Moreover, this rise in correlation is not due, as we originally anticipated, only to the shift of two outlying points for ribs on the fourth and sixth whorl into the domain of positive correlation. [The within-sample CV of ribbing measures is average; the combination of this average measure with a maximal value for percentage dif-

ference between morphotypes produces two points that push the entire relationship for within-sample CV (see dots on fig. 13) toward zero correlation. But the among-sample CV of the two ribbing measures is also high, and the corresponding two points for this relationship (crosses on fig. 13), with their high joint positive values, enhance the correlation.]

The rise in correlation from within- to among-sample CV (fig. 13) is a consequence of two other changes as well. First, the four characters showing high within-sample CV (greater than 15) and low-to-modest percentage difference (less than 15%)—tilt and protrusion of the aperture, and width and thickness of the apertural lip—all move to the left for among-sample CV, since their among-sample CV is considerably lower than their within-sample CV. This shift also enhances the correlation. Thus, of the nine measures with high values on at least one of the axes in figure 13 (more than CV 15, or 15% difference), three—umbilical width, ribs on the first whorl, and shell weight—exhibit joint high positive projections on both figures, thus enhancing the correlation. Of the six points that shift substantially, all increase the correlation for among-sample CV. The two ribbing measures, with high percentage difference but average within-sample CV, move to the right and assume high joint positive positions for among-sample CV. The four measures with high within-sample CV but modest percentage differences all shift to the left, thus moving closer to regions of joint low values.

Secondly, we note a general rearrangement of points within the cluster of 10 measures with joint low values in both figures (both axes less than 15, and contained within the box of fig. 13). For example, the three lowest values for percentage differences—protoconch width, number of whorls, and height at the fourth whorl—are associated with the three lowest values for among-sample CV, but with only one of the lowest three values (protoconch width) for within-sample CV. If we compute correlation coefficients for these 10 measures alone, we obtain a strong 0.58 for among-sample CV vs. percentage difference and only 0.16 for within-sample CV vs. percentage difference.

In short, we doubt very much that this coordinated set of reasons for the rise in correlation between within- and among-sample CV—the rightward shift of ribbing measures, the leftward shift of apertural measures, and rearrangement within the cluster of low values—can represent a capricious effect.

One might concoct elaborate biological stories and conjecture, for example, that morphotype differences are converted from interdemic rather than within-sample variance, and that some "higher level" selective process may be at work. But such speculations would be fanciful, and we prefer to work first with explanations based on the methodological artifact we demonstrated above: that some measures are more repeatable than others, and that much of the variation among measures for within-sample CV reflects this artifact. We suspect that the low correlation of percentage difference and within-sample CV may record the artifact as well.

We argued above that among-sample CV should be free from this artifact, and that most major deviations from the among-sample vs. within-sample plot (fig. 12) record either unusually high repeatability (lowering within-sample CV and pushing points to the left) or poor repetition (raising within-sample CV and pushing points to the right). The deviant points of figure 13—the ones that reduce the correlation for within-sample CV to near zero—represent, for the most part, the same measures most affected by high or low repeatability in within-sample CV. Thus, the highly repeatable measures of ribs on the fourth and sixth whorls and shell weight deviate to the left for within-sample CV in figure 13 and move rightward to enhance the correlation for among-sample CV; while the poorly repeatable lip width and apertural protrusion deviate to the right for within-sample CV, but move toward the left for among-sample CV.

Curiously then, since among- and within-sample variance are so strongly correlated (fig. 12), and since among-sample variance may be free from the artifact of differential repeatability, among-sample CV probably serves as a better estimate of a truly biological within-sample CV than does the direct measure of within-sample CV itself. Thus, it is likely that both among-sample CV and a

properly corrected within-sample CV would correlate significantly with percentage differences between morphotypes.

In any case, the correlation of percentage difference with among-sample variance is strong and significant, and we must ask why the higher-level difference between morphotypes correlates with at least some aspect of variance within morphotypes. One might take a nonadaptationist view allied with the "neutralist" school of evolutionary thought and argue that higher-level divergence uses characters that are most available, not primarily what selection requires. Why else would the difference between morphotypes be constructed primarily from characters that are most variable *within* morphotypes? (Correlation with among-sample variance is less impressive than relationship to within-sample variance for this speculation, since average differences among samples may reflect adaptive requirements of microhabitats, while variation within samples may record something intrinsic about developmental possibilities.) But a selectionist will correctly respond that high among-sample variability itself may record the adaptive response of characters most crucial to survival—and that correlation of within- and between-morphotype variability might be predicted on these grounds. We cannot resolve these different interpretations with the data available. Still, we believe that a documentation of the correlation itself presents much worth pondering.

4. *Can differences in variation between morphotypes be related to differences in variation within morphotypes?* In the last section, we discussed the relationship of differences in form between morphotypes with their levels of variation. We might also consider differences in variation between morphotypes in this context, and ask whether the generally greater among-sample variation in the mottled morphotype can be related to the generally greater within-sample variance. The rough correspondence we know already: mottled shells are more variable than ribby both within and among samples. But how precise is this relationship: Are the measures that most distinguish the variation of mottled and ribby shells among samples also the measures that are most different between mottled and ribby within samples? If this relationship were strong, we might argue that the fine structure of differences in variation between morphotypes—not only their difference in form—arises from patterns of variation within samples.

We therefore correlated the percentage differences between morphotypes for within- and among-sample CVs (lines 11 and 17 of table 9). The correlation coefficient is a strong 0.59 and the points in figure 14 display what we have stated before: that mottled shells are generally more variable than ribby both within and among samples. Only 5 of 19 variables lie below zero (ribby more variable than mottled) on each axis. Mottled are more variable than ribby for 14 measures in each case, and 11 measures have a joint positive projection.

Nonetheless, figure 14 also shows why it is so important to plot points and observe fine structure, and not to rely exclusively upon such summary measures as the correlation coefficient. We note that the strong correlation of 0.59 (significant at the 1% level) is produced by three outlying points only: the high joint positive plots of ribs on the fourth and sixth whorls and the high joint negative plot of apertural lip width. The other measures, all lying closer to average variabilities, show no correlation at all.

5. *Conclusion.* We have shown, in most cases, strong correlations between levels of variation and between variation at lower levels and differences in form at higher levels. These data offer strong support for the idea that differences in variation and form at higher levels (between morphotypes or samples within morphotypes in this study) are constrained by or convertible from available variation at lower levels (within samples in this study). But, unfortunately, we do not have the necessary information for making crucial distinctions between competing biological explanations for these correlations: first, the nonselectionist interpretation that emphasizes constraints and holds that higher-level differences need not reflect active selection, but only a "playing out" of available variation, perhaps through a stochastic differentiation of form among demes within the limits of material presented by differing amounts of variation among characters; second, a variety of selectionist claims that view jointly en-

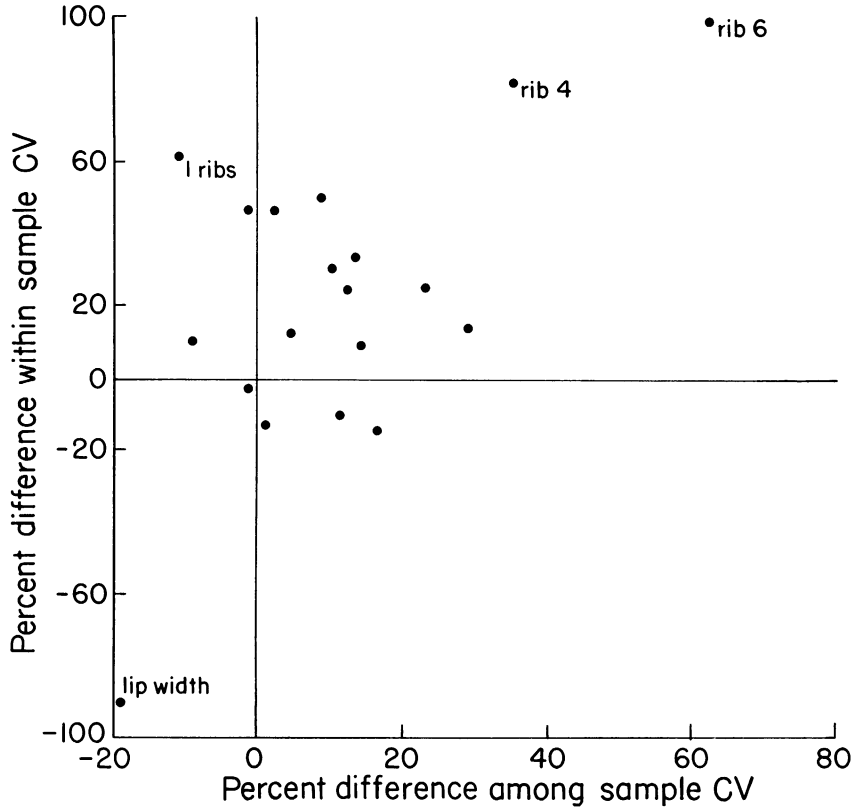


FIG. 14. Relationship of average differences between morphotypes for within-sample and among-sample coefficients of variation.

hanced or diminished variability at several levels as parallel responses to selective pressures of environmental factors acting in similar fashion within and among demes.

C. ZONES OF INTERACTION

We have demonstrated that the two morphotypes represent different entities in important biological ways. Their differences are not the superficial manifestations of such external and highly labile characters as ribbing alone. The morphotypes are distinguished by differences in form built by several independent sets of covarying characters. The morphotypes are also distinguished by differences in both amounts and patterns of variability—so that we seem to encounter two different developmental systems, not simple distinctions (however numerous) in static form. To these two classes of evidence—form and variation—we now add the third, and more direct, category of interaction in nature.

As discussed in section I, the biogeography of ribby and mottled *Cerion* and the particular configuration of New Providence Island lead us to expect that interactions between morphotypes will occur in two different situations; first, along the north and south coasts where bank-edge meets bank-interior coast; secondly, at any place along a transect perpendicular to the coast where ribby coastal samples meet interior mottled samples. The coastal zones should be fairly old and stable (at least since sea level rose above the bank edges); the coast-interior contacts should be more occasional and transient, since the habitats of ribby coastal and mottled interior forms do not generally abut, and contact therefore depends upon some local peculiari-

ty of environment—a cleared field, or absence of the usual (and snail-free) hill between appropriate coastal and interior habitats.

i. Stable coastal transitions

We have already discussed and figured (fig. 8) the even morphological transitions found along both north and south shores where bank-edge meet bank-interior coasts east of Nassau on the north and from Coral Harbour to Millar's Sound on the south. In both cases, the morphological transitions are broad and continuous over 3 to 4 km of coastline, while the much longer stretches inhabited by pure populations of ribby shells all plot with no apparent pattern in the narrow morphospace delimited by the ribby cluster of figure 8.

In our previous study of Little Bahama Bank (Gould and Woodruff, 1978), we found that old and stable hybrid zones of this coastal type do not necessarily display enhanced variation in their local samples. We also find no clear evidence of increased variation in the New Providence coastal transitions. Table 11 compares coefficients of variation for each variable in the coastal transitions 262-263-267 (north shore) and 281-280-279 (south shore) with the average CV for that variable across all samples (ribby and mottled pooled, line 16 of table 9). The intermediate sample in the northern transition does contain more variables with higher than average CV, but this pattern is not repeated in the southern transition, where the most mottled sample (279) includes more variables with higher than average CV. In both transitions, the sample nearest the ribby area (262 and 281) contains most variables with lower than average CVs, thus fitting the general observation that ribby shells are less variable than mottled within samples.

TABLE 11
Coefficients of Variation for Samples in Coastal Transitions Compared with Average CV for All Samples

Sample	No. Variables, CV > Average	No. Variables, CV < Average
North transition		
262	8	11
263	13	6
267	11	8
South transition		
281	7	12
280	10	9
279	14	5

ii. Recent and transient coast–interior transitions

Other opportunities for hybridization arise when coastal populations of the bank-edge ribby morphotype abut interior samples of the mottled morphotype. Such situations are rare on New Providence because most of the bank-edge coastline also includes a hill (a cemented fossil dune) devoid of snails on its summit and located just landward of the coast, separating populations of the two morphotypes (Garrett and Gould, 1984, on geology of New Providence). However, where the hill is absent, and when the intervening habitat between bank-edge coast and interior is suitable, hybrid populations may be found. We have located two hybrid populations in localized areas of New Providence—at Blake Road, north of the airport, and in a disused quarry near the village of Gambier (fig. 15). In both cases, the intervening area between coastal ribby and interior mottled habitats is sparsely vegetated and ideally suited to the explosive growth of *Cerion* populations that often occurs in disturbed areas.

1. *Enhanced variation at the Blake Road site.* East of Gambier and west of the caves at Rock Point, the coastal hill breaks for 100 meters or so where Blake Road (at the northwestern shore of Lake Killarney and just northeast of the airport) joins the coastal and interior roads (fig. 15). Here, just in the small area of low topography along the eastern margin of Blake Road, a field has recently been cleared and is growing back with the sparse vegetation so commonly exploited by *Cerion* for an explosive growth of populations. The bank-edge ribby snails meet interior mottled samples at this "explosion site," and the resulting population is a hybrid between the two morphotypes (see p. 459 for more details about the site).

The hybrid population inhabits an area about 200 m^2 on the low field east of Blake Road. Samples 296 and 297 were collected in the midst of this hybrid explosion (see fig.

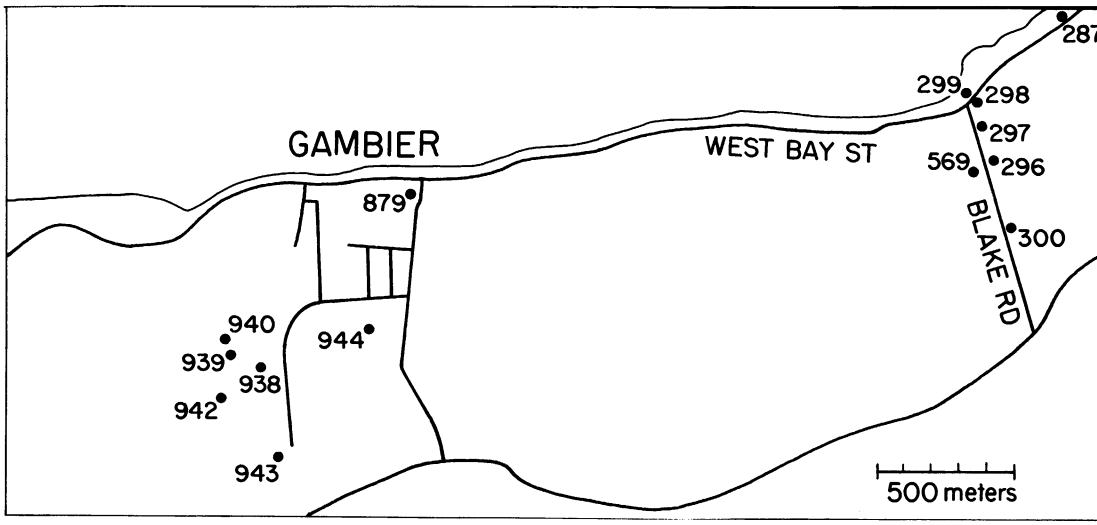


FIG. 15. Location of morphometric samples in the hybrid zones at Gambier and Blake Road.

15); 298 and 299 inhabited areas just north and south of the coastal road, respectively, still in the area of ribby *Cerion* (but in potential contact with the hybrids; sample 300 was collected on the east side of Blake Road, south of the main hybrid site (296 and 297). Here, at 300, the snails return to their normal size and do not seem as variable as samples (296 and 297) in the midst of the zone.

The center of the hybrid zone (samples 296 and 297) clearly represents a "classic" region of greatly enhanced variability. Snails are smaller than average, but their range in size greatly exceeds all but two or three mottled samples living in unfavorable habitats and subject to dwarfing. We encounter for the first time interesting styles of intermediacy in ribbing and coloration (found nowhere within the "pure" morphotypes). Most hybrid snails are either mottled or ribby, but several exhibit an intermediate pattern found in other *Cerion* hybrid zones between ribby and nonribby taxa. Intermediate specimens do not grow the same number of weaker ribs, but rather deposit more widely spaced (and therefore fewer) ribs of standard or slightly reduced strength. Color intermediates are striking since the mottled morphotype of this area develops sharply delimited flames of color (see p. 401), while the ribby morphotype is pure brown or very diffusely mottled in color. Figure 16 shows the range of intermediacy in size, color, and ribbing from samples 296 and 297.

In all hybrid samples, more than half of the variables exhibit a greater than average CV (compare line 16 of table 9 with the sample values of table 8), but the pattern is striking only for the two samples from the center of the zone (296 and 297), which both include 16 of 19 variables with higher than average CV (the other three samples have higher CVs for either 11 or 12 of 19). Most revealing are CVs for the three ribbing measures, the only values that go "off scale" in the central hybrid samples (see Mayr and Rosen, 1956, for confirmation of the generality of this phenomenon in hybrid *Cerion*). The two central samples, 296 and 297, exhibit CVs more than twice the average for ribs on the first whorl, and six times the average for ribs on the fourth and sixth whorls. By contrast, 299 from the north side of the road (and furthest from hybrid influence), exhibits average values for all three ribbing measures, while 298, from the south side of the road just 10 m from 299, displays as much increase as the hybrids for fourth and sixth whorl ribbing, and only slightly less for ribs on the first whorl. The morphological transition to hybrid effect is quite sharp, marked by the road itself. Sample 300, from south of the hybrid zone, also

exhibits strongly enhanced variation in ribbing, but at only about half the level of the central hybrids, 296 and 297.

As a general pattern, the increase of variation in 296 and 297 is greatest for ribbing, strong and consistent (but at much lower levels) for measures of overall size (whorls, height, width, aperture height and width, aperture to suture and apertural protrusion), general but not marked for standardized whorl sizes (protoconch width and height, height and width at the fourth whorl, though height at the fourth whorl is below average in 297), and not at all evident for the final allometric phase of apertural growth (tilt of the aperture, umbilical width and lip width and thickness). Thus, the four major covariance sets of *Cerion*—ribs, final sizes, standardized whorl sizes, and apertural measures—show different and consistent patterns of variability in the hybrid zone.

2. *Identification of hybrids by patterns of covariation at the Blake Road site, and for other appropriate samples.* Consider the position of Blake Road samples with respect to the zone of intermediacy between the two taxa as shown in figure 8. Sample 299, north of the coastal road and furthest removed from hybrid influence, lies firmly within the ribby cluster, though just at its right-hand edge. Sample 298, south of the road and more subject to hybrid influence, lies just detached from the ribby cluster toward the zone of intermediacy. Sample 300 falls firmly within the intermediate zone, but at a position corresponding to the ribby end of both northern and southern coastal transitions. Samples 296 and 297, the central Blake Road hybrids with enhanced variability, lie further within the intermediate zone at positions corresponding to the mottled end of both coastal transitions.

But 296 and 297 display another, far more interesting, peculiarity. In addition to their intermediate position between axes 1 and 2 (the markers of ribby and mottled samples, respectively), they also lie among the suite of only five samples with high projections on the third axis. The third axis is a "minor" contributor in total quantity of information explained, accounting for but 6.2 percent, while axis 1 encompasses 52.5 and axis 2, 32.5 percent (see pp. 414–422 on the potential biological importance of such small axes).

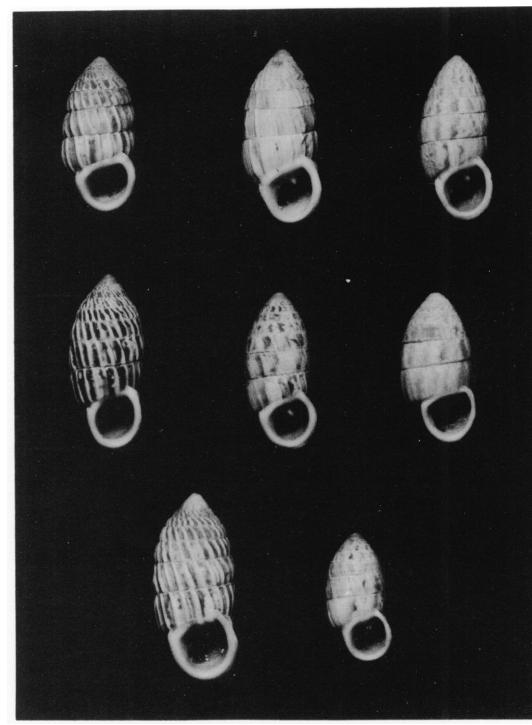


FIG. 16. Representative specimens from hybrid sample 296 (Blake Rd.) to show extent of enhanced variation. **Top row,** variation in ribbing, from pure ribby (left) to entirely smooth (right), with the curious intermediate morphology (found in no parental population) of strong but widely spaced ribs. **Middle row,** variation in color. **Bottom row,** extremes of variation in size.

But this third axis has clear and major biological significance; it is defined by a sensible and distinct pattern of covariance among its factor scores, and it includes a sensible ordering of high loadings for the five samples projecting strongly upon it.

Table 6 portrays the factor scores for figure 8. The third axis includes a grouping that we have not previously encountered in a decade's work on *Cerion.* This pattern is not, therefore, a standard covariance set for ordinary patterns of growth in *Cerion.* Protoconch widths and later heights (at the fourth whorl, total shell height and aperture height) project positively along with thickness of the apertural lip. (As a standard *Cerion* pattern, protoconch widths correlate with later heights while protoconch heights correlate more strongly with later widths—see p. 420.) Pro-

toconch heights and later shell widths (at the fourth whorl and total width), as well as umbilical width and lip width, plot with strong negative values (as does whorl number, an anomaly as we shall see). Since samples all load negatively on this axis (they are redrawn with positive projections in fig. 8), shells with high projections are relatively wide, with a wide umbilicus, and a relatively wide but thin lip.

What biological circumstance would bring about this previously unrecorded combination of characters in a coordinated way? Can we relate this circumstance to the generally smaller size of hybrids at 296 and 297? The unifying theme for both phenomena seems to be ontogeny itself. Young shells of *Cerion* are small and relatively wide, with a wide umbilicus—since *Cerion* adds height but no width in later ontogeny. (An aperture deposited on an immature shell may also exhibit its own immature character of reduced thickness at regular width—*Cerion*'s aperture first reaches full width at paper thinness, and only thickens later.) Thus, all peculiarities of the third axis can be explained by the coordinated theme of ontogenetic truncation, with deposition of a juvenilized aperture upon a shell at middle growth.

Visual inspection of specimens with high projections on the third axis confirms this interpretation (see fig. 9), for instead of decreasing gradually in width before secreting their aperture (the normal pattern for full ontogeny), these snails seem to deposit their aperture prematurely upon a shell of maximum width—that is, at mid-growth. Hybrids often exhibit various disturbances of development, a theme affirmed by the coordinated covariance of truncated ontogeny and juvenilized apertures on a factor analytic axis occupied by hybrid samples only (see following paragraphs).

The high negative score for whorl number seems anomalous, for the hybrid shells, at their smaller size and truncated ontogeny, have fewer rather than more whorls. But each variable is assessed (in the percent range transformation used here—see p. 405) as a percentage of its total vector. Therefore, if a reduction in whorl number is proportionally less than the decrease in whorl heights, a reduced number of whorls may display a negative projection. The values of table 4 (the matrix used for factor analysis) affirms this interpretation. Whorl numbers are reduced in 296 and 297, but not nearly so much as heights. In fact, their extent of reduction is closer to the decrease for widths—and whorl number therefore follows widths in negative scores on the third axis. Moreover, as table 7 indicates, the high score for whorl number is a peculiarity of the three-axis solution. At 10 axes, whorl number has a near zero projection, while the basic pattern of the third axis is already intact. Whorl number does not join the third axis at high score until the four-axis solution, after dispersal of its concentrated score on the fifth axis (see p. 420). Thus, whorl number is not a strong and invariant member of the covariance set that determines pattern on the third axis as a result of truncated ontogeny in developmentally disturbed hybrids.

The high projection of all other samples on the third axis corroborates this interpretation with independent evidence of biogeography. *Cerion fincastlei* is a Maynard collection from the 1920s. Fort Fincastle, the type locality, stands in the center of Nassau, where the coastal hybrid zone between mottled and ribby snails should be located. But *Cerion* has been extirpated in the city of Nassau, and we were frustrated by our inability to test our hypothesis of bank edges and interiors with modern material. Thus, we are particularly pleased that an old sample, collected before the intense urbanization of Nassau extinguished *Cerion* within the city, meets our expectations so well. For the *C. fincastlei* sample not only plots in the hybrid area between axes 1 and 2; it also projects strongly on axis 3 as a consequence of the same developmental disturbance found in the Blake Road hybrids.

The high position of sample 301 on the third axis is also gratifying and corroborative. With respect to the ribby–mottled transition expressed by axes 1 and 2, 301 lies entirely within the field of ribby shells. But it also projects strongly on the third axis, the criterion for developmental disturbance in samples subject to hybrid effect. Sample 301 occupies a unique geographical position for ribby snails. It represents the single exception to the rule that ribby populations are exclu-

sively coastal in their distribution, for 301 comes from an inland site along the southwestern edge of Lake Cunningham (fig. 7). We noticed no morphological peculiarity when we collected 301; we simply marked it as an anomalously placed ribby sample. But its high projection on the third axis records its anomalous geography in a region inhabited by mottled populations—and presumably, therefore, subject to some influence from them. The fifth sample with high projection on the third axis lies next to 301 in a region of ribby shells. It is a Maynard sample of *Cerion glans,* inadequately located with respect to coastal or interior position—the label simply says "5 miles W. of Nassau." From its high projection on the third axis, we would predict that this sample also inhabited the island's interior, where it interacted with surrounding mottled populations. But we know no way to test this conjecture.

3. *The Gambier hybrid zone.* Proceeding west from Blake Road, the next break in the coastal hill, and therefore the next area where coastal ribby might meet interior mottled to form a hybrid zone, occurs at the village of Gambier (fig. 15). There, in a disused quarry southwest of the village, we found a hybrid population different from Blake Road in style of intermediacy. (We discovered this population in 1981, long after completion of our morphometric work and the departure of our measurer. Unfortunately, therefore, we cannot include this hybrid zone in our morphometric analysis.) Shells in this zone are of normal size and do not seem unusually variable. Their mixed nature is most evident in patterns of ribbing, but we find few intermediately ribbed specimens. Shells are either ribby or smooth and the proportion of smooth shells increases monotonically toward the southern region of mottled populations.

The Blake Road hybrid zone is, essentially, a single exploding population of small geographic extent. By contrast, the Gambier zone spreads out for several hundred meters and never reaches the population density of Blake Road. By calculating the relative frequencies of smooth and ribby shells, we can trace invariant clinal trends running north to south through the zone—that is, from the area of pure ribby snails in the north to pure mottled snails in the south. At locality 940 (see fig. 15), at the northern end of a track leading northward from the quarry, all shells are ribby (N = 35, see table 12). Just 50 m south at 939, smooth snails constitute 22 percent of the sample (N = 41), and 23 percent (N = 39) at 938, on the north wall of the quarry itself. We collected two samples from the south wall of the quarry, 941 and 942. They yield different values, but both include a higher percentage of mottled shells than samples to the north—29 percent at 941 (N = 24) and 38 percent at 942 (N = 60). Finally, at our southernmost locality, 943, at the south end of a track running south from the quarry, the percentage of mottled shells rises to 80 (N = 40).

TABLE 12
Percent of Mottled Shells Correlated with Geography (Moving Southward) at the Gambier Hybrid Zone

Sample	% Mottled	N
940	0.0	35
939	22.0	41
938	23.1	39
941	29.2	24
942	38.3	60
943	80.0	40

Gambier differs from Blake Road in the either–or character of most shells. This distinction must lead to the objection that, perhaps, Gambier is not a hybrid zone, but an area of true sympatry between the two morphotypes. (The varying character of interactions between the two morphotypes in different situations—particularly the contrast between stable coastal and transient coastal–interior transitions already discussed—helps to explain how two interactions located so near one another can be so distinct. The Gambier quarry is overgrown and clearly much older than the recently cleared field at Blake Road.) For three reasons, however, we suspect that the Gambier interaction also represents an area of hybridization. First, intermediacy in ribbing is also rare in the Blake Road zone, where most specimens are also clearly assignable to one category or the other. Second, very few Gambier shells (3 of 239) show some intermediacy. One specimen at 938 cannot be placed in either category;

another at 939 veers toward mottled but has intermediate properties; while a third, at 942, is mottled but has fairly well-developed ribs on its last whorl. Third, and most important, all hybrid zones that we have studied in *Cerion* include rare alleles not found in either parental population (see section IV). [The Blake Road and Gambier hybrid populations are apparently discontinuous despite their geographic proximity. Sample 944, from an intermediate area within the village of Gambier itself, contains thousands of shells (all dead in this burned-over area) and all mottled as we would expect for a location at this distance from the coast. In its north–south position, sample 944 corresponds with the maximum extent of hybridization at both the Blake Road and Gambier site.]

4. *Conclusion.* We have tried to show, by morphometric analysis, that the two morphotypes of *Cerion* on New Providence are not mere ecophenotypes or geographic variants of a single taxon, but are clearly separate taxa at some level of distinction. Our criteria have been varied: differences in form built by several independent covariance sets, differences in patterns of variation as well as form, differences in covariance, and styles of interaction when the two morphotypes meet geographically. To this morphometric analysis we add, in the next section, evidence from a genetic analysis of electromorphs. We will demonstrate the existence of distinctive alleles associated with mottled and ribby morphologies, and we will show that hybrid zones, as in other cases in *Cerion* (Gould and Woodruff, 1978; Woodruff and Gould, 1980), maintain unique alleles found in neither parental taxon. We will then present a taxonomic appendix for the New Providence cerions. Since we have demonstrated that ribby and mottled morphotypes merit recognition as taxonomic entities (as semispecies, we shall conclude later), we shall henceforth use the formal names—*C. glans* for the ribby populations and *C. gubernatorium* for the mottled samples (see Appendix 1 for systematic details).

IV. GENETIC VARIATION IN NEW PROVIDENCE *CERION*

A. Introduction

Electrophoretically detectable allozymes can be used to characterize patterns of within- and between-population variation. Such data on the genetic structure of populations are invaluable in elucidating the effects of natural selection, gene flow, genetic drift, hybridization, and mating systems on the evolution of local adaptation, geographic variation, and speciation. These data are particularly useful in organisms like *Cerion* where the metapopulation is divided into small breeding units or colonies that are partially isolated from one another by distances greater than the average dispersal range of individuals.

Our earlier work has shown that *Cerion* is well suited to analyses of this type. Woodruff (1975a, 1975b) reported that *C. bendalli* from Great Abaco Island is polymorphic (*P*) at 23 percent of the 22 loci surveyed and that individual snails are heterozygous (*H*) at about 7 percent of their structural gene loci. Observed segregation frequencies for genotypes of five polymorphic loci in three populations agree with Castle-Hardy-Weinberg expectations, indicating that these anatomical hermaphrodites are outbreeding. Electrophoresis of 1575 snails representing 47 populations from the islands of the Little Bahama Bank confirmed and extended these findings (Gould and Woodruff, 1978). *Cerion abacoense* and *C. bendalli* are both moderately variable with $P = 20$–30 percent and $\bar{H} = 0.05$–0.08. Despite this underlying variability, these taxa showed little geographic variation in allozyme frequencies. In contrast, a hybrid zone between the two species on Great Abaco Island is an area of genetic anomaly. This zone of allopatric hybridization (sensu Woodruff, 1973) has been described in more detail by Woodruff (1981, and in prep.); the morphological hybrid zone between ribby and mottled morphotypes is about 0.5 km wide; but

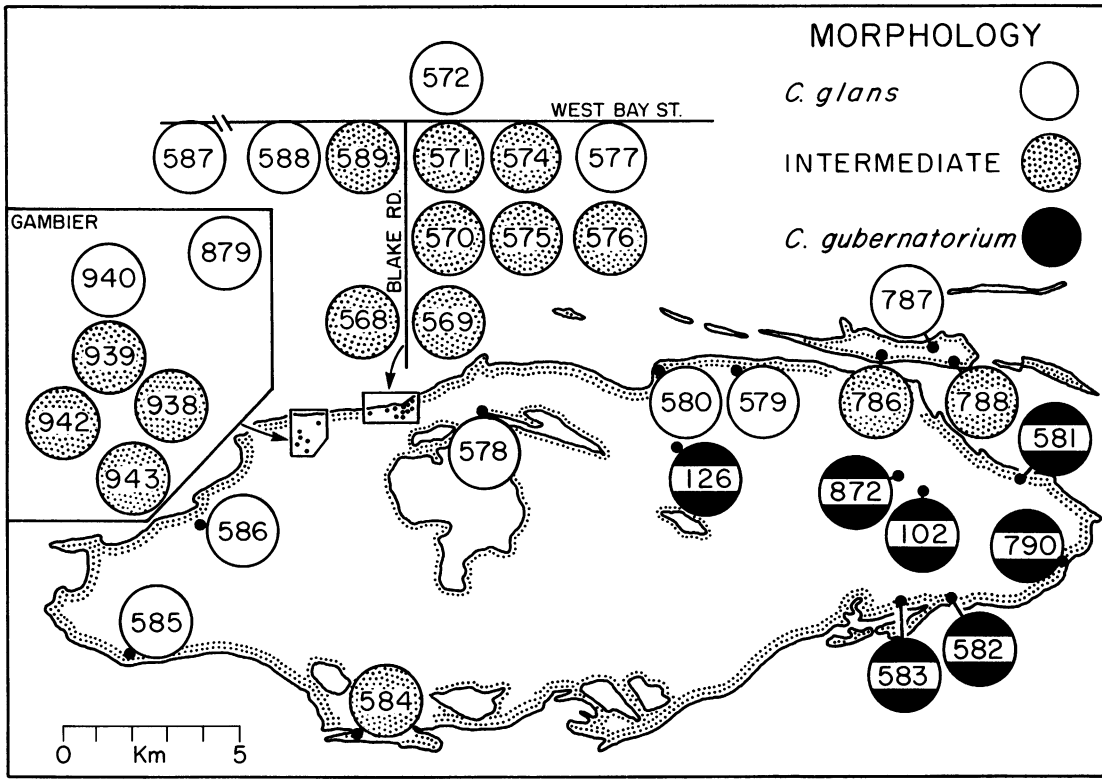


FIG. 17. Locality numbers and morphological identity of samples used in the study of genetic variation. The north coast hybrid samples from Gambier and Blake Road are offset from the main map for clarity. These 34 samples are further characterized in figures 18–28.

the genetic transition is 3–4 km wide and asymmetrically distributed around the morphological zone. Although the parental taxa are barely distinguishable genetically [Nei's (1972) genetic distance, $D = 0.01$–0.05], the hybrids were characterized by higher frequencies of unique or typically rare alleles at three loci. This observation, coupled with higher levels of mean genic heterozygosity in hybrid samples ($\bar{H} = 8.3$–11.5), defines the hybrid zone as an area of genetic anomaly connecting populations of the two morphotypes. The genetic pattern, coupled with morphometric patterns of covariation and biogeographic distribution of the two taxa, led to our decision to regard them as semispecies, and, therefore, as full species taxonomically.

With this background, we approached New Providence with some pessimism about the possibility of obtaining clear results on such a small island. New Providence today has an average north–south width of less than 7 km. Our work on Abaco had shown that, where an area of interaction is biogeographically constrained, a genetic hybrid zone may be 4 km wide. In unconstrained situations, as on Grand Bahama Island, genetic interaction between the same two semispecies may be 2–3 times as wide and may preclude the recognition of genetically pure populations in either taxon (especially on an island the size of New Providence). Thus, on New Providence where snails are distributed all around the island's periphery and across the interior in several areas, we anticipated difficulty in distinguishing the typically bank-edge populations of the ribby morphotype from the typically bank-interior populations of the mottled morphotype.

B. Samples and Methods

In our investigations of the genetics and phenetics of *Cerion,* we have typically stud-

TABLE 13
Enzyme Systems Analyzed in New Providence *Cerion*

Name (E.C. Number)	Abbreviation	Loci
Acid phosphatase (3.1.3.2)	ACP	1
Alcohol dehydrogenase (1.1.1.1)	ADH	1
Alkaline phosphatase (3.1.3.1)	ALP	1
Aspartate aminotransferase (2.6.1.1)	AAT (GOT)	2
Ceruloplasmin	CRP	1
Esterase α-naphthyl acetate (3.1.1.1)	ES	7
Glucose-6-phosphate dehydrogenase (1.1.1.49)	G6PD	1
Glucose phosphate isomerase (5.3.1.9)	GPI (PGI)	1
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GAPD	1
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	GPD (αGPDH)	1
Isocitrate dehydrogenase (1.1.1.42)	ICD (IDH)	2
Lactate dehydrogenase (1.1.1.27)	LDH	2
Leucine aminopeptidase (3.4.11 or 13)	LAP	2
Malate dehydrogenase (1.1.1.37)	MDH	2
Octinol dehydrogenase (1.1.1.73)	ODH	1
Phosphoglucomutase (2.7.5.1)	PGM	2
6-Phosphogluconate dehydrogenase (1.1.1.44)	6PGD	1
Superoxide dismutase (1.15.1.1)	SOD	2
Xanthine dehydrogenase (1.2.3.2)	XDH	1

ied shells and proteins of the same individuals. Unfortunately, most original tissue samples collected in 1973 were accidentally denatured and we therefore collected replacements in 1977. This second set of samples adequately represents the diversity in shell morphology on New Providence; in about half the cases, animals were collected from the same colonies used to study morphometric variation described above. These snails, and others collected in 1978–1982, provided 16 samples from the north coast, suitable for examination for east–west clines; 13 samples of the ribby morphotype (*C. glans*); 11 samples of the mottled morphotype (*C. gubernatorium*); 20 samples from Gambier and Blake Road where morphological evidence indicated hybridization of the two taxa; 3 samples representing interior populations of eastern New Providence; and 3 samples from Paradise (formerly Hog) Island off the northeast coast. The distribution of these localities is shown in figure 17.

In all, we surveyed electrophoretic patterns of various proteins in more than 1300 individual adult snails. We will describe the results for 1086 animals from 35 representative sites. These individuals were scored at each of the eight polymorphic loci examined.

All samples were taken by searching a small area and collecting every adult snail found. In most cases, we collected 30–50 adults; average reported sample size is 30. Most samples were collected from areas less than 10 m^2. This area is far less than the neighborhood size of *Cerion* colonies on Great Abaco, which typically range over several hundred m^2 (Woodruff and Gould, 1980). For hybrid samples from Gambier and on Blake Road, the animals were collected from areas of 2–4 m^2.

Preparation of foot-muscle tissue, biochemical specifics, and other technical aspects of our apparatus for horizontal starch gel electrophoresis are described elsewhere (Woodruff, 1975b). In this study, we report variation in 18 enzymes and one other protein. These electromorphic patterns were resolved using staining techniques presented by Shaw and Prasad (1970), Selander et al. (1971), and Harris and Hopkinson (1978). The proteins studied include metabolic function groups I, II, and III of Gillespie and Kojima (1968). The proteins, their abbreviations, and recommended E.C. numbers are shown in table 13. In the discussion that follows, capitals are used for abbreviated protein names, lower case letters for the names of 32 presumptive loci.

We used the BIOSYS-1 computer program

TABLE 14
Variation in Esterase-1 and Esterase-2 Allele Frequency

Sample	*Es-1*$^{0.83}$	*Es-1*$^{0.93}$	*Es-1*$^{1.00}$	*Es-2*$^{0.89}$	*Es-2*$^{1.00}$	*Es-2*$^{1.09}$	*Es-2*$^{1.09}$	*Es-2*$^{1.14}$	*Es-2*$^{1.16}$
102 17	–	0.15	0.85	–	0.44	0.50	0.06	–	–
126 16	–	–	1.00	–	0.87	0.12	–	–	–
568 30	–	–	1.00	–	0.76	0.10	0.03	0.11	
569 30	–	–	1.00	–	0.78	0.13	–	0.08	–
570 32	–	–	1.00	–	0.83	0.06	–	–	0.11
571 32	–	–	1.00	0.05	0.81	0.02	–	0.05	0.08
572 32	–	–	1.00	0.02	0.49	0.11	–	0.36	0.03
574 32		–	1.00		0.02	0.78	0.08	–	0.09
575 32	–	–	1.00	0.02	0.86	0.05	–	0.05	0.03
576 29	–	–	1.00	–	0.88	0.09	–	0.02	0.02
577 31	–	–	1.00	0.02	0.72	0.22	–	–	0.05
578 35	–	–	1.00	0.11	0.86	0.03	–	–	
579 32	–	–	1.00	–	1.00	–	–	–	–
580 35	–	–	1.00	–	0.94	0.06	–	–	–
581 31	–	0.24	0.76	–	0.69	0.24	0.07	–	–
582 38	0.07	0.25	0.68	–	0.26	0.57	0.17	–	–
583 22	0.02	0.32	0.66	–	0.43	0.39	0.18	–	–
584 32	–	0.17	0.83	–	0.64	0.28	0.06	–	–
585 35	–	–	1.00	–	0.96	–	–	0.04	–
586 31	–	–	1.00	0.02	0.97	–	–	0.03	–
587 32	–	–	1.00	0	0.95	–	–	0.05	–
588 30	–	–	0.00	0.93	–	–	–	0.07	
589 30	–	–	1.00	–	0.93	–	–	0.03	0.03
702 16	0.03	0.16	0.81	0.41	0.38	0.22	–	–	
786 36	–	–	1.00	–	0.83	0.10	–	–	0.07
787 31	–	–	1.00	–	0.58	0.21	–	0.21	–
788 32	–	–	1.00	–	0.45	0.27	–	0.19	0.09
790 32	–	0.22	0.78	–	0.22	0.77	0.02	–	–
872 27	–	0.07	0.93	–	0.57	0.36	0.11	–	–
879 32	–	–	1.00	–	0.94	–	–	–	0.06
937 35	–	–	1.00	–	0.83	0.10	–	–	0.07
938 35	–	–	1.00	0.01	0.97	–	–	–	0.01
939 32	–	–	1.00	–	0.92	0.03	–	–	0.05
940 25	–	–	1.00	–	0.88	0.06	–	–	0.06
942 35	–	–	1.00	–	0.97	0.01	–	–	0.01
943 22	–	–	1.00	–	0.80	0.11	–	0.05	0.04

to analyze electrophoretically detectable allelic variation (Swofford and Selander, 1981). For each sample we calculated allele frequencies and measures of genetic variability including mean number of alleles per locus, percentage of polymorphic loci (P), and the average heterozygosity per locus (H) and per sample ($\bar{H}$) by direct count and the unbiased estimate based on Castle-Hardy-Weinberg expectations (Levene, 1949; Nei, 1978). To test for deviations of genotype frequencies from Castle-Hardy-Weinberg expectations, we performed the conventional chi-square goodness-of-fit test. Where the expected frequencies in some classes were low, we pooled genotypes into three classes and repeated the chi-square test; in addition, we calculated exact significance probabilities (analogous to Fisher's exact test for 2 × 2 contingency tables). F-statistics (Wright, 1978) were used to analyze genetic differentiation within and between samples. F_{IS} is the weighted fixation index for each individual relative to its sample; it provides another estimate of deviation from panmixia. F_{IT} is the weighted fixation index for individuals relative to the total set of samples; it provides an estimate of deviation from panmixia on the island as a whole.

TABLE 15
Variation in 6-Phosphogluconate Dehydrogenase, Malate Dehydrogenase-1, and Aspartate Aminotransferase-1 Allele Frequency[a]

Sample	*6Pgd*$^{0.93}$	*6Pgd*$^{1.00}$	*6Pgd*$^{1.11}$	*Mdh-1*$^{0.72}$	*Mdh-1*$^{1.00}$	*Mdh-1*$^{1.21}$	*Aat*$^{0.7}$	*Aat*$^{1.0}$	*Aat*$^{1.3}$
102	0.24	0.29	0.47	–	0.91	0.09	–	1.00	–
126	0.09	0.72	0.19	0.19	0.78	0.03	–	1.00	–
568	–	0.86	0.14	0.07	0.93	–	–	1.00	–
569	–	0.93	0.07	–	1.00	–	0.02	0.98	–
570	0.02	0.80	0.18	0.08	0.92	–	–	1.00	–
571	0.03	0.63	0.34	0.11	0.89	–	–	1.00	–
572	0.03	0.86	0.11	0.09	0.89	0.02	–	1.00	–
574	–	0.69	0.31	0.20	0.80	–	–	1.00	–
575	0.02	0.69	0.29	0.08	0.92	–	–	1.00	–
576	–	0.64	0.36	0.16	0.84	–	–	1.00	–
577	–	0.47	0.53	0.23	0.75	0.02	–	1.00	–
578	–	0.37	0.63	0.34	0.61	0.05	0.03	0.97	–
579	0.08	0.58	0.34	0.05	0.95	–	–	1.00	–
580	0.03	0.80	0.17	0.04	0.90	0.06	–	1.00	–
581	0.13	0.50	0.37	0.13	0.77	0.10	–	1.00	–
582	0.38	0.45	0.17	–	0.84	0.16	–	0.85	0.15
583	0.27	0.45	0.28	–	0.79	0.21	–	0.86	0.14
584	0.18	0.48	0.34	–	0.89	0.11	–	1.00	–
585	0.09	0.63	0.28	0.44	0.56	–	–	1.00	–
586	0.19	0.66	0.15	0.15	0.85	–	–	1.00	–
587	0.09	0.52	0.39	0.14	0.86	–	–	1.00	–
588	0.02	0.85	0.13	0.08	0.92	–	–	1.00	–
589	0.15	0.82	0.03	0.03	0.95	0.02	–	1.00	–
702	0.25	0.44	0.31	–	0.97	0.03	–	0.91	0.09
786	–	0.44	0.56	0.06	0.94	–	–	1.00	–
787	0.03	0.36	0.61	–	1.00	–	–	1.00	–
788	0.05	0.39	0.56	–	0.98	0.02	–	1.00	–
790	0.25	0.23	0.52	–	0.87	0.13	–	1.00	–
872	0.06	0.29	0.65	–	0.93	0.07	–	1.00	–
879	0.03	0.66	0.31	0.03	0.97	–	–	1.00	–
937	–	0.87	0.13	0.06	0.94	–	–	1.00	–
938	–	0.46	0.54	0.47	0.53	–	–	1.00	–
939	–	0.44	0.56	0.28	0.70	0.02	–	1.00	–
940	–	0.56	0.44	0.42	0.52	0.06	–	1.00	–
942	–	0.50	0.50	0.29	0.68	0.03	–	1.00	–
943	–	0.46	0.56	0.18	0.73	0.09	–	1.00	–

[a] Sample sizes are the same as in Table 14.

F_{ST} is the standardized variance of allele frequency and measures the amount of differentiation among all samples. A hierarchical F-statistic analysis was also performed for various groups of samples using the formulation of Wright (1978). We examined heterogeneity among samples using the Pearson contingency chi-square statistic. Nei's (1978) unbiased measures of genetic identity (*I*) and genetic distance (*D*) were calculated for all pairwise comparisons of samples and for various groups of samples. Finally, we performed a hierarchical cluster analysis on the measures of genetic similarity using the unweighted pair-group method with arithmetic averaging (UPGMA).

C. Results

i. Allozyme variability

The 19 proteins examined electrophoretically provide evidence for variation at about 32 genes; 23 of these gave consistent and genetically interpretable results. Of these 23

TABLE 16
Variation in Ceruloplasmin, Phosphoglucomutase-2, and Glucose Phosphate Isomerase Allele Frequency[a]

Sample	*Crp*$^{1.0}$	*Crp*$^{1.2}$	*Pgm-2*$^{0.7}$	*Pgm-2*$^{0.8}$	*Pgm-2*$^{1.0}$	*Pgm-2*$^{1.2}$	*Gpi*$^{0.6}$	*Gpi*$^{0.8}$	*Gpi*$^{1.0}$	*Gpi*$^{1.4}$
102	0.10	0.90	–	–	0.91	0.09	–	–	0.97	0.03
126	0.10	0.90	–	–	0.97	0.03	–	–	0.96	0.04
568	0.17	0.83	0.03	–	0.97	–	–	–	0.95	0.05
569	0.26	0.74	0.08	–	0.92	–	–	–	0.95	0.05
570	0.17	0.83	0.14	–	0.86	–	–	–	0.97	0.03
571	0.18	0.82	–	–	1.00	–	0.03	–	0.89	0.08
572	0.47	0.53	0.02	–	0.98	–	–	0	0.70	0.30
574	0.16	0.84	0.05	–	0.95	–	0.11	–	0.87	0.02
575	0.18	0.82	0.04	–	0.96	–	–	–	0.95	0.05
576	0.23	0.77	0.02	–	0.98	–	0.02	–	0.93	0.05
577	0.35	0.65	–	1.00	–	–	–	0.92	0.08	–
578	0.63	0.37	–	–	1.00	–	–	–	1.00	–
579	0.19	0.81	–	–	1.00	–	–	–	0.94	0.06
580	0.50	0.50	–	–	1.00	–	–	–	0.91	0.09
581	0.02	0.98	–	–	0.73	0.27	–	–	0.69	0.31
582	0.13	0.87	–	0.03	0.61	0.36	–	0.03	0.86	0.11
583	0.07	0.93	–	–	0.81	0.19	–	–	0.82	0.18
584	0.23	0.77	–	–	0.94	0.06	–	–	0.89	0.11
585	–	1.00	–	–	1.00	–	–	–	0.97	0.03
586	0.15	0.85	–	–	1.00	–	–	–	0.97	0.03
587	0.16	0.84	–	–	1.00	–	–	–	0.92	0.08
588	0.42	0.58	–	–	1.00	–	0.07	–	0.86	0.07
589	0.08	0.92	–	–	1.00	–	0.07	–	0.90	0.03
702	0.19	0.81	–	–	0.53	0.47	–	0.06	0.88	0.06
786	–	1.00	–	–	1.00	–	–	–	0.98	0.02
787	1.00	–	–	1.00	–	–	–	0.97	0.03	–
788	0.03	0.97	–	–	0.97	0.03	–	–	1.00	–
790	–	1.00	–	–	0.91	0.09	–	–	0.86	0.14
872	0.08	0.92	–	–	0.87	0.13	–	–	0.89	0.11
879	0.40	0.60	–	–	1.00	–	0.03	–	0.81	0.16
937	0.14	0.86	0.10	–	0.90	–	–	–	0.98	0.02
938	0.30	0.70	0.02	–	0.98	–	0.34	–	0.66	–
939	0.25	0.75	0.03	–	0.97	–	0.44	–	0.54	0.02
940	0.30	0.70	–	–	1.00	–	0.36	–	0.64	–
942	0.13	0.87	0.09	–	0.91	–	0.33	–	0.65	0.02
943	0.10	0.90	–	–	1.00	–	0.18	–	0.68	0.14

[a] Sample sizes are the same as in Table 14.

presumptive loci, 15 were monomorphic and invariant in all New Providence *Cerion* examined: *Acp, Adh, Alp, Aat-2, Es-6, Es-7, G6pd, Gapd, Gpd, Icd-2, Mdh-2, Odh, Sod-1, Sod-2* and *Xdh*. Eight loci were variable; one locus had two alleles (*Crp*), four loci had three alleles (*Aat-1, Es-1, Mdh-1, 6Pgd*), two loci had four alleles, (*Gpi, Pgm-2*), and one locus had six alleles (*Es-2*). The remaining nine loci are not reported since they gave inconsistent or uninterpretable banding patterns (*Es-3, Es-4, Es-5, Icd-1, Lap-1, Lap-2, Ldh-1, Ldh-2, Pgm-1*).

The frequencies of various alleles at the eight polymorphic loci in 36 samples representing 34 localities are shown in tables 14–16.

ii. Levels of genetic variability

The proportion of polymorphic loci (*P*) among the 23 presumptive loci in each sam-

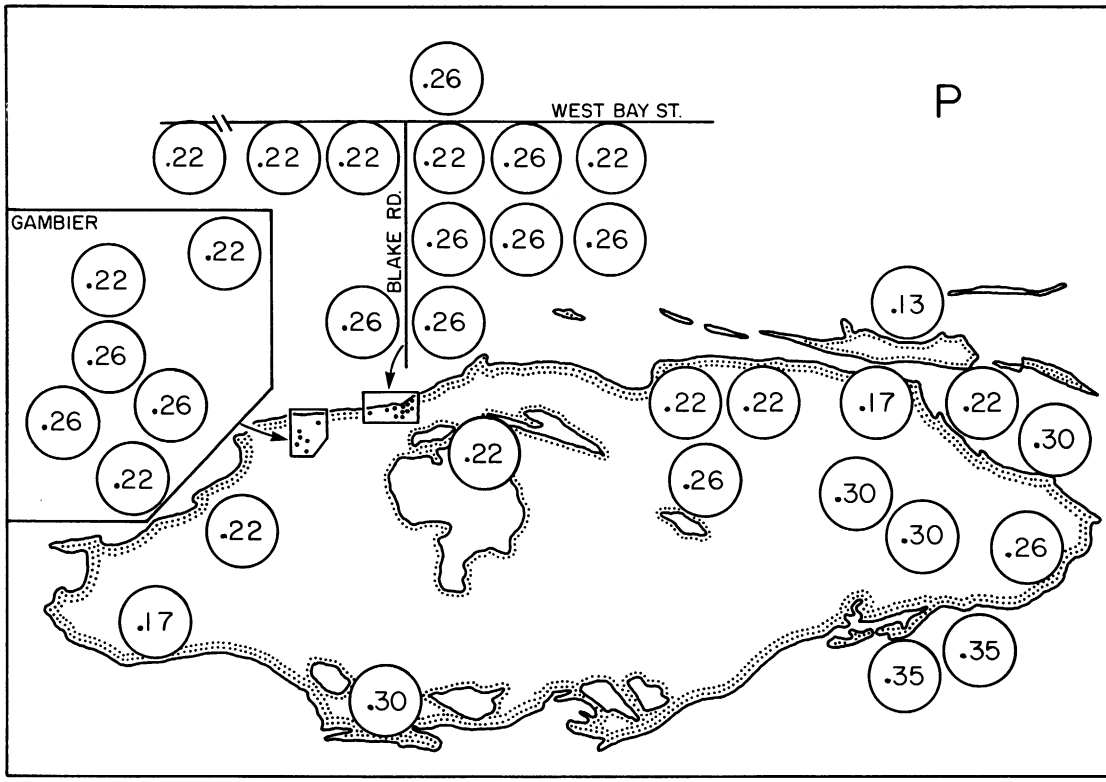


FIG. 18. Geographic variation in the proportion of polymorphic loci (P).

ple varied nearly threefold from 0.130 to 0.348 between samples from different areas (fig. 18). The most variable populations, with eight variable loci, are 582 and 583 (southeastern *C. gubernatorium*). Adjacent samples from eastern New Providence and the south coast at Coral Harbour (584) have seven variable loci. These more variable populations are characterized by multiple alleles at *Aat-1* and *Es-1,* loci that are typically monomorphic elsewhere on New Providence. The least variable populations, with 3–4 variable loci, are peripheral *C. glans* (585 in the southwest corner; and 786–787 on Paradise Island). The remaining 12 populations of *C. glans* along the north coast typically have five variable loci ($P = 0.22$). The hybrid samples at Gambier and at Blake Road exhibit one more variable locus (usually *Pgm-1*) than adjacent *C. glans* and *C. gubernatorium.* These values of $P = 0.17$–0.26 for *C. glans,* and $P = 0.26$–0.35 for *C. gubernatorium,* are very similar to those ($P = 0.15$–0.30) seen in *C. abacoense* and *C. bendalli* (Woodruff, 1975b; Gould and Woodruff, 1978).

Mean individual heterozygosity ($\bar{H}$) also varied threefold among samples and displays a pattern similar to that for P (fig. 19). Highest values, $\bar{H} = 0.148$–0.152, characterize *C. gubernatorium* from southeastern New Providence (582–583). We found slightly lower levels of heterozygosity ($\bar{H} = 0.092$–0.128) in adjacent populations from eastern New Providence and the south coast at Coral Harbour. Lowest values, $\bar{H} = 0.042$–0.066 were detected in *C. glans* populations from the north coast and Paradise Island. The morphological hybrids from Gambier are slightly more variable ($\bar{H} = 0.089$–0.104) than adjacent populations of *C. glans*; the Blake Road samples are not significantly more heterozygous. Previous estimates of heterozygosity in *Cerion* [$\bar{H} = 0.054$–0.128 on Abaco and Grand Bahama (Gould and Woodruff, 1978)] are very similar to values ($\bar{H} = 0.042$–0.152) measured on New Providence, the higher

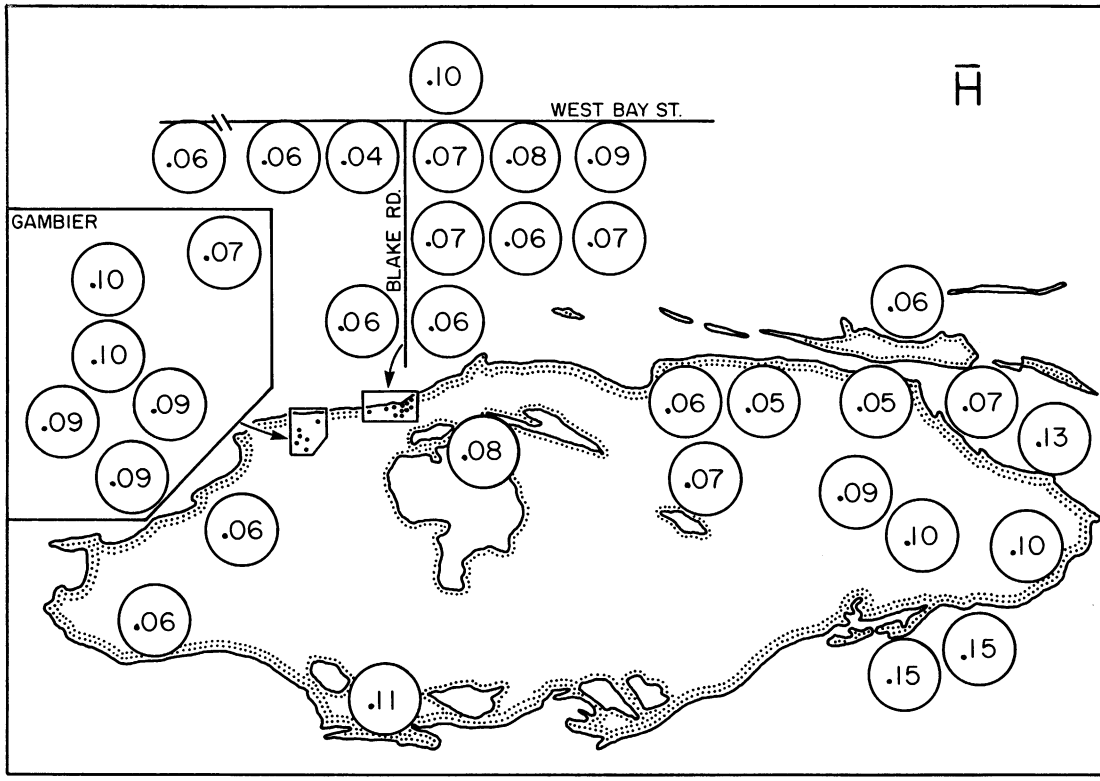


FIG. 19. Geographic variation in the mean individual heterozygosity ($\bar{H}$).

values arising from the fact that eight rather than five polymorphic loci were examined.

In conclusion, the *Cerion* of New Providence are moderately variable. Mean number of alleles per locus lies in the range 1.2–1.6 (±0.1–0.2 SE). This value, and the estimates of P and $\bar{H}$ discussed above, are minimum estimates based on single-gel electrophoretic determinations. Nevertheless, they probably reflect 80 percent of the true variability at the loci examined rather than 30 percent as suspected a few years ago (Selander and Whittam, 1983).

iii. Temporal variation in estimates of allele frequencies

During this study, we were able to analyze snails from several areas on two occasions, and thus obtain a measure of replicability in estimates of allele frequencies. This information is relevant to the following discussion of geographic variation. It also provides an indication of whether the snails used to characterize genetic variation are comparable to the animals collected 4–9 years earlier for morphological study.

Sequential samples were examined for changes in frequency of allozymes in each of four areas. Data on allele frequencies for up to seven polymorphic loci are presented for comparison (table 17). In our first pair of samples, *C. gubernatorium* from southeast New Providence, frequencies at six of seven loci are not significantly different in 1977 and 1978. At *Mdh-1,* a G-test of goodness of fit (Sokal and Rohlf, 1981) indicated a significant difference ($G = 4.218$, $p < 0.05$). In the second comparison, a hybrid site at Blake Road, frequencies at seven loci did not change significantly between 1977 and 1982. In a third comparison, for southwestern *C. glans* (the sites are 350 m apart, but far from the hybrid zone), we found no change in frequencies at three loci over four years. The final comparison, *C. glans* from Fort Char-

TABLE 17
Allozyme Frequencies in Sequential Samples

Sample:		582	702	570	937	283	585	289	579
Year:		1977	1978	1977	1982	1973	1977	1973	1977
N:		38	16	32	35	15	35	16	32
Locus	Allele								
Aat	1.0	0.85	0.91	1.00	1.00	1.00	1.00	–	–
	1.3	0.15	0.09	–	–	–	–	–	–
Es-1	0.83	0.07	0.03	1.00	1.00	–	–	–	–
	0.93	0.25	0.16	–	–	–	–	–	–
	1.00	0.68	0.81	–	–	1.00	1.00	1.00	1.00
Es-2	1.00	0.26	0.41	0.83	0.83	1.00	1.00	1.00	1.00
	1.09	0.57	0.38	0.06	0.10	–	–	–	–
	1.14	0.17	0.22	–	–	–	–	–	–
	1.24	–	–	–	–	–	–	–	–
Gpi	0.8	0.03	0.06	–	–	–	–	–	–
	1.0	0.86	0.88	0.97	0.98	–	–	–	–
	1.4	0.11	0.06	0.03	0.02	–	–	–	–
Mdh-1	0.72	–	–	0.08	0.60	–	–	0.09	0.05
	1.00	0.84	0.97	0.92	0.94	–	–	0.91	0.95
	1.21	0.16	0.03	–	–	–	–	–	–
Pgm-2	0.7	–	–	0.14	0.10	–	–	–	–
	0.8	0.03	–	–	–	–	–	–	–
	1.0	0.61	0.53	0.86	0.90			1.00	1.00
	1.2	0.36	0.47	–	–	–	–	–	–
6Pgd	0.93	0.38	0.25	0.02	–	–	–	0.09	0.08
	1.00	0.45	0.44	0.80	0.87	–	–	0.50	0.58
	1.11	0.17	0.31	0.18	0.13	–	–	0.41	0.34

lotte (collecting sites are 100 m apart), also reveals no significant changes during four years.

In summary, 21 out of 22 tests revealed no significant changes in allele frequencies during this study. Thus, our relatively small samples ($\bar{N} = 30$) provide reasonably replicable estimates of allele frequencies in these populations. Furthermore, we feel that our later genetic samples well represent the populations described morphometrically.

D. Variation within Samples and Population Structure

We used three methods to test for significant deviation in genotypic frequencies from values expected under panmixia. First, we performed a chi-square test [with Levene's (1949) correction for small sample size] on data for each variable locus in each sample (206 cases). For 20 cases, probability that observed frequencies were in Castle-Hardy-Weinberg equilibrium was less than 0.05. Eighteen of these cases gave $p > 0.05$ when rare alleles were pooled with alleles of intermediate frequency, and when the Fisher exact probabilities were calculated. In only two cases were significant departures from expectations of random mating detected: *Es-2* at 582 (*C. gubernatorium,* southeast New Providence) and 786 (*C. glans,* Paradise Island). In these cases, exact probabilities were 0.019 and 0.035, respectively. We attach no special biological significance to these two cases, since 206 total tests were performed. Furthermore, at each of these localities, all other variable loci (seven and two, respectively) exhibited segregation frequencies close to those expected under panmixia. We conclude that *Cerion* are outcrossing on New Providence.

TABLE 18

Summary of F_{IS}, a Measure of the Deviation from Random Mating Within Samples for Three Loci

Sample	*6Pgd*	*Es-2*	*Mdh-1*	Sample	*6Pgd*	*Es-2*	*Mdh-1*
102	.168	.041	−.097	585	.114	−.100	
126	−.280	−.143	−.238	586	.296[a]	−.051	.350[b]
568	−.170	−.043	4.66[c]	587	.072	−.049	−.164
569	−.071	−.106	–	588	−.156	.071	−.091
570	−.043	.162	−.085	589	−.077	.211	−.049
571	.235	−.045	−.123	702	.036	.323	−.032
572	−.132	−.204	.210	786	.213	.428[c]	.059
574	.273	.080	−.062	787	−.103	−.122	–
575	.003	.145	.349[b]	788	.054	.081	−.016
576	−.120	−.103	−.184	790	.291[a]	−.111	.429[b]
577	−.255	.062	−.308[a]	872	−.212	.072	−.080
578	−.224	−.136	−.022	879	.004	−.067	−.032
579	−.154	–	−.049	937	−.148	−.053	−.061
580	.047	−.061	.227	938	.079	−.022	−.089
581	−.029	.081	−.033	939	.238	−.063	−.246
582	.242	.230	.010	940	.351[a]	.267	−.164
583	−.058	.280	.022	942	.143	−.022	−.150
584	.140	.198	.198	943	−.100	−.038	−.269

[a] $p \leq 0.10$; [b] $p \leq 0.05$; [c] $p \leq 0.01$.

We find no evidence for assortative mating in any of the populations studied.

A second approach to the analysis of population structure involved the calculation of Wright's fixation index (F_{IS}), the inbreeding coefficient of an individual relative to its sample. Results for three loci polymorphic in almost all samples are shown in table 18. The null hypothesis, that a particular F_{IS} equals zero, was tested by Baker's (1981) method of comparing $N(F_{IS})^2$ to a chi-square distribution (df = 1). The mean F_{IS} (all loci, all samples) was 0.019, indicating that *Cerion* on New Providence as a whole form a single outbreeding metapopulation. At five sites, however, single loci showed significant ($p \leq 0.05$) heterozygote deficiencies. Marginally significant ($p \leq 0.10$) departures from Castle-Hardy-Weinberg expectations occurred at other loci for two of these sites, and at two other localities; three of these four cases also involve heterozygote deficiencies. Localities with significant positive F_{IS} values are scattered across the island: three north coast *C. glans,* three hybrids, and one *C. gubernatorium* from the southeast. In none of these localities, however, did we find any consistent and significant departure from expectations of equilibrium at all loci. We therefore conclude that the F_{IS} analysis provides no evidence for significant inbreeding in the populations studied. Occasional heterozygote deficiencies at particular loci are probably a result of our sampling technique, since samples were collected in very small areas. Since *Cerion*'s vagility is so limited, some samples may contain numerous sibs.

As a third approach, we calculated the coefficient for heterozygote deficiency (D) or excess for each locus in each sample. Figure 20 shows the mean coefficient ($\bar{D}$) at each site. Over all samples we found slightly more negative values than expected, but individual $\bar{D}$ values are not significantly different from zero. The geographic distribution of localities with slight heterozygote deficiencies forms no evident pattern, and we conclude again that genetic variation within populations points to amphimixis.

E. Interpopulation Variation in Allele Frequencies

We calculated Wright's F-statistics to estimate the degree of geographic variation on New Providence. The mean and range (for eight variable loci) are:

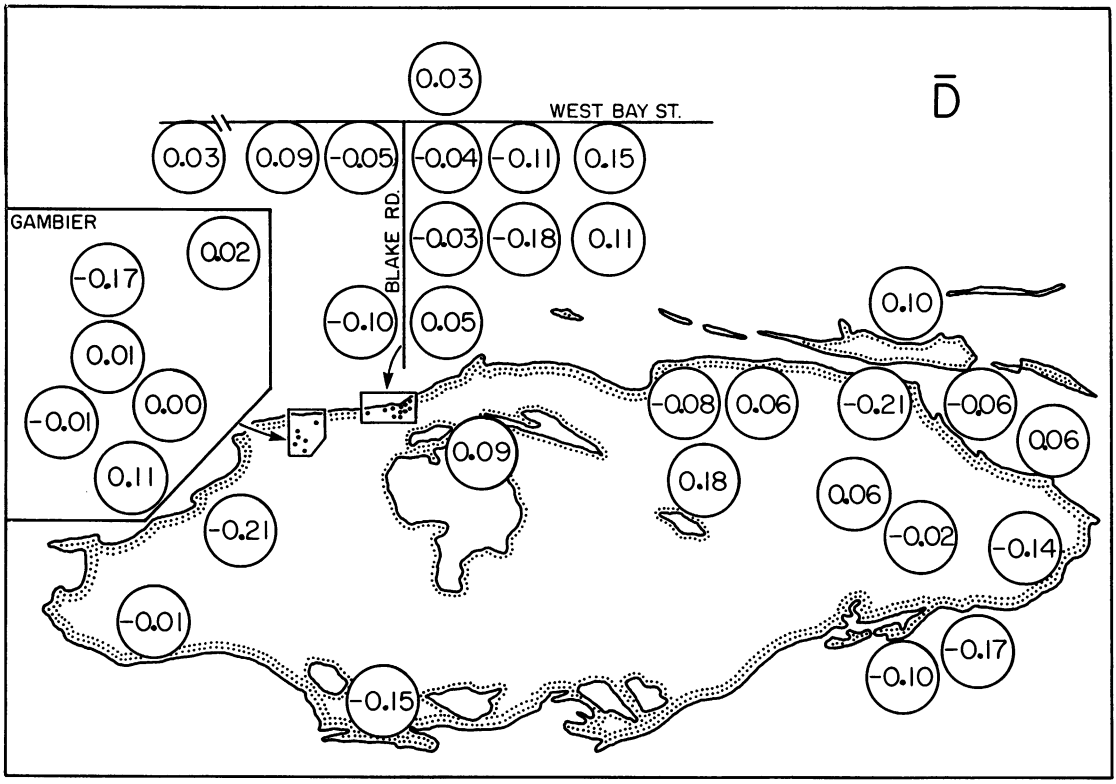


FIG. 20. Geographic variation in the coefficient for heterozygote deficiency (negative *D*) or excess (positive *D*).

F_{IS} = 0.019 (−0.067–0.067),
F_{IT} = 0.180 (0.075–0.264),
F_{ST} = 0.143 (0.109–0.219).

As noted previously, F_{IS} is the inbreeding coefficient of an individual relative to its sample. The value 0.019 is not significantly different from zero, and we therefore found no evidence for deviation from panmixia. F_{IT} provides a correlation between gametes combined within an individual snail relative to the entire population. F_{IT} = 0.18 is significantly different from zero, and is positive (as it must be when interdemic variation exists). The fixation index F_{ST} provides a measure of differentiation among demes; F_{ST} = 0.143 is significantly ($p < 0.001$) different from zero. This value indicates that considerable geographic variation exists in allele frequencies among samples on this small island.

To determine the partitioning of this variation, we calculated Wright's hierarchical F-statistics on data for each variable locus and for all loci combined. We divided the various samples into: *C. glans* [coastal and possible hybrids—Coral Harbour (584) and the coast near Gambier (879)]; *C. gubernatorium* [southeast coast and possible hybrids—interior site (126) and Paradise Island]; and "hybrids" (Blake Road and Gambier). The degree of differentiation within samples (demes, D) within areas (A) is very small: F_{DA} = 0.073 (range 0.034–0.085). This consistency across all eight loci suggests that sampling error or genetic drift, rather than local adaptation, is the primary cause of variation at this level. Estimates of variance in allele frequencies among taxa (species and hybrids, S) are twice as high: F_{DS} = 0.135 (0.087–0.168). The range is narrower (0.125–0.168) if we exclude *Aat-1,* which is only variable at four sites. Similar results were obtained when we estimated variance at the third level, between demes and the total popula-

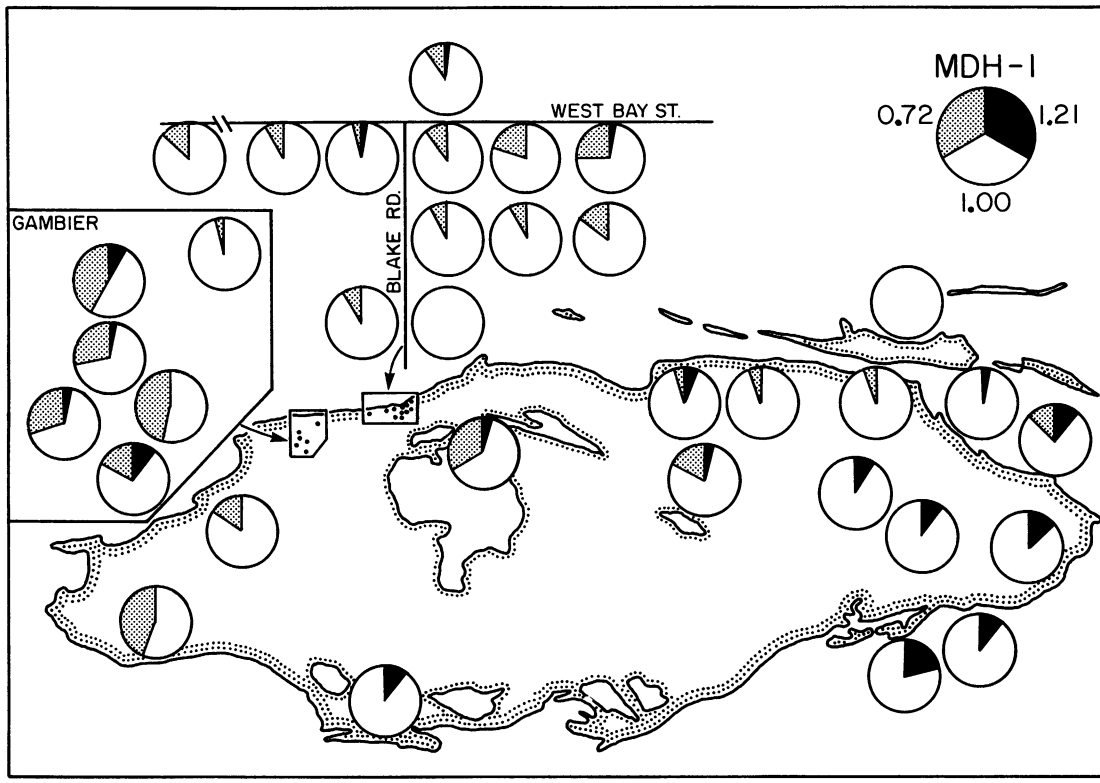
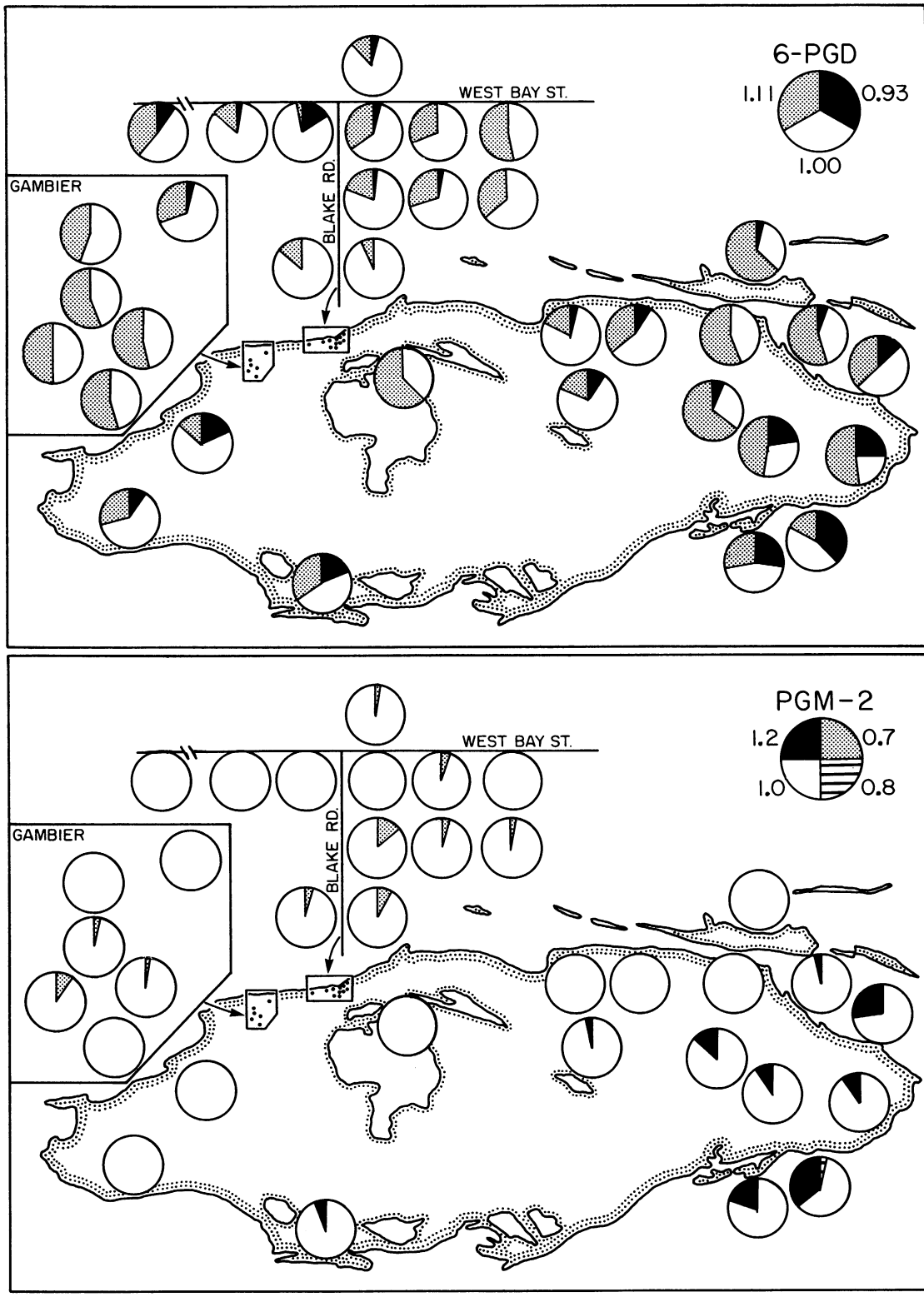


FIG. 21. Geographic variation in malate dehydrogenase-1.

tion (T): $F_{DT} = 0.149$ (0.090–0.205, 0.122–0.205 with *Aat-1* excluded). These results, and their consistency over all loci, suggest that 85 percent of the total genetic diversity can be found in snails within any given population. Conversely, about 15 percent of the total variance in allele frequencies arises from differentiation among populations. These results indicate that, although we find considerable geographic variation on New Providence, it may be difficult to discriminate the two species with these loci. We then examined patterns of variation at each locus separately.

Malate dehydrogenase-1. Three alleles were found at this locus. We show their distribution and relative frequency in figure 21. The most common allele *Mdh-1*$^{1.00}$ was found in every sample; its frequency was never less than 0.5 (typically >0.85). Its apparent fixation at two sites is probably a result of sampling error since the frequency of other alleles in adjacent populations is ≤0.08. The second most common allele, *Mdh-1*$^{0.72}$, was found in all *C. glans* samples, all hybrid samples from Blake Road and Gambier, and in two northern *C. gubernatorium* samples from eastern New Providence (126 and 581). In contrast, the third allele, *Mdh-1*$^{1.21}$, was found in all *C. gubernatorium* samples, in some intermediate samples, and in *C. glans* adjacent to *C. gubernatorium.* The faster allele is typically rare (1 or 2 heterozygotes per sample) in *C. glans* and hybrids, but rises to a frequency of 0.21 in southeastern *C. gubernatorium.* We conclude that *Mdh-1*$^{1.00}$ is a shared allele and that *Mdh-1*$^{0.72}$ and *Mdh-1*$^{1.21}$ are characteristic of *C. glans* and *C. gubernatorium,* respectively. Introgression has apparently blurred this pattern.

6-Phosphogluconate dehydrogenase. Geographic patterns for the three alleles segregating at this locus are shown in figure 22. The commonest two alleles, *6Pgd*$^{1.00}$ and *6Pgd*$^{1.11}$, were found in all samples and are quite variable in their frequencies. The slow-


6-PGD
1.11
0.93
1.00
WEST BAY ST.
BLAKE RD.
GAMBIER
PGM-2
1.2
0.7
1.0
0.8
WEST BAY ST.
BLAKE RD.
GAMBIER

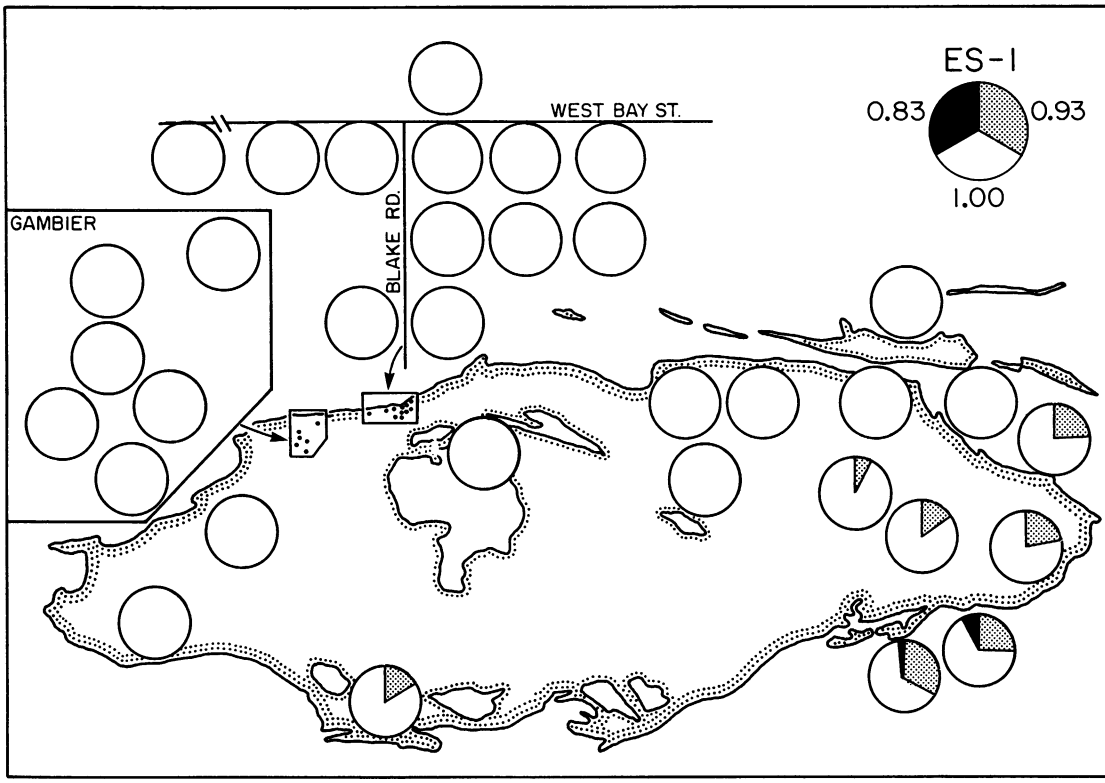


FIG. 24. Geographic variation in esterase-1.

est allele, $6Pgd^{0.93}$, is typically found at a frequency of <0.10 but rises to 0.38 in southeastern *C. gubernatorium*. It was not detected in samples of intermediate morphology from Gambier and southern Blake Road, but occurs elsewhere along the north coast in *C. glans* at low frequency. We conclude that the two taxa are poorly differentiated at this locus, but that $6Pgd^{1.00}$ occurs at slightly higher frequencies in *C. glans*, and $6Pgd^{0.93}$ at slightly higher frequencies in *C. gubernatorium*.

Phosphoglucomutase-2. Four alleles were found (fig. 23). $Pgm\text{-}2^{1.0}$ occurs at high frequency in all samples: 1.00 in all *C. glans*, >0.90 in intermediate samples, and about 0.60 in southeastern *C. gubernatorium*. $Pgm\text{-}2^{0.7}$ is a rare allele (0.02–0.14), restricted to samples of intermediate morphology from Blake Road and Gambier. $Pgm\text{-}2^{1.2}$ occurs at low to medium frequency in *C. gubernatorium*; it reaches a frequency of about 0.40 in the southeast. Finally, a fourth allele, $Pgm\text{-}2^{0.8}$, was found in two heterozygotes from sample 582 of southeastern *C. gubernatorium*. At this locus, we therefore find $Pgm\text{-}2^{1.00}$ associated with *C. glans*, $Pgm\text{-}2^{0.8}$ and $Pgm\text{-}2^{1.2}$ associated with *C. gubernatorium*, and $Pgm\text{-}2^{0.7}$ associated with some of the hybrids.

Esterase-1. Geographic variation at this nonspecific esterase locus, resolved with α-naphthyl acetate, is shown in figure 24.

←

FIG. 22. Geographic variation in 6-phosphogluconate dehydrogenase.

FIG. 23. Geographic variation in phosphoglucomutase-2.

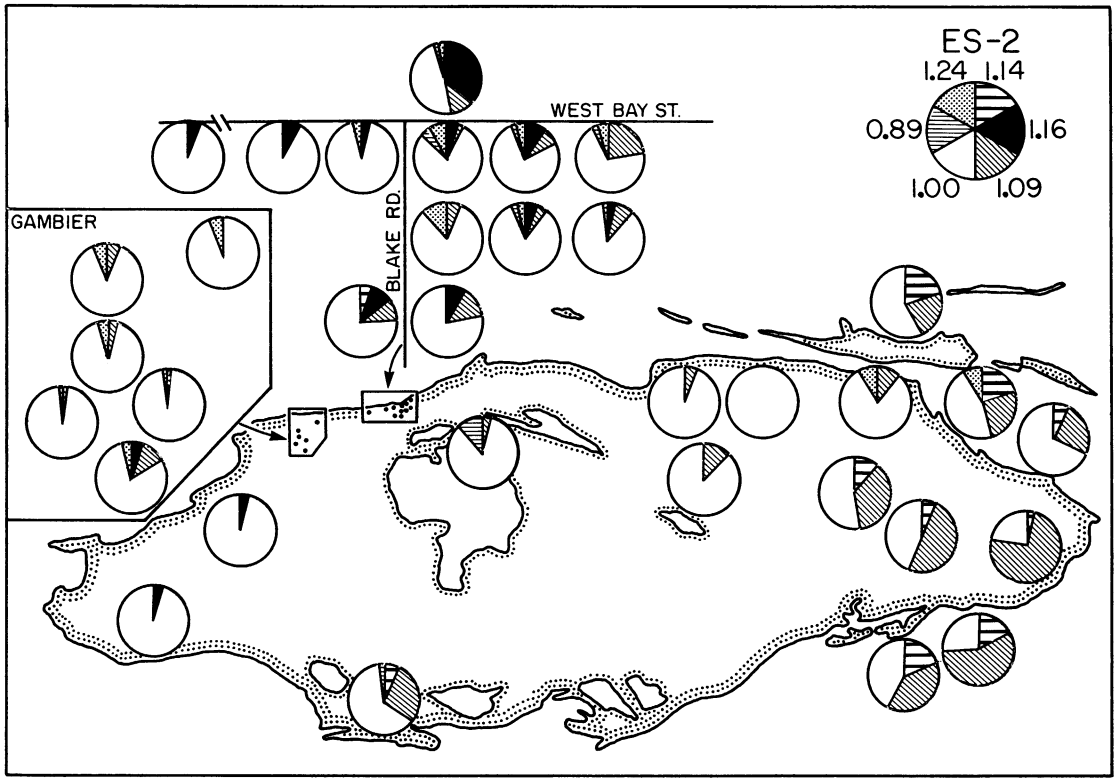


FIG. 25. Geographic variation in esterase-2.

Es-1$^{1.00}$ is common (>0.65) in all samples, and is fixed in *C. glans*. *Es-1*$^{0.93}$ was found only in *C. gubernatorium* and rises to a frequency of 0.32 in the southeast. Finally, an even slower electromorph, *Es-1*$^{0.83}$, was found in three samples from two sites (582–583) in southeast *C. gubernatorium*.

Esterase-2. A second nonspecific esterase, resolved with α-naphthyl acetate, was highly polymorphic, with five alleles segregating in some populations (fig. 25). *Es-2*$^{1.00}$ was found in all samples; in *C. glans*, it typically displays a frequency of >0.85; in *C. gubernatorium* its frequency falls to 0.22 in the southeast. *Es-2*$^{1.09}$ was also found on most of the island but shows the opposite trend, being more common in *C. gubernatorium* (up to 0.77) and absent in westernmost *C. glans*. *Es-2*$^{1.14}$ is common in southeastern *C. gubernatorium* (0.20), and extends north to the intermediates of Paradise Island, and west to the intermediates at Coral Harbour. *Es-2*$^{1.16}$ is rare in *C. glans* and intermediate samples of northwest New Providence. Its much higher frequency (0.36) in sample 572 (*C. glans* from the coast at Blake Road) was unexpected. Two other typically rare alleles were associated with samples of intermediate morphology. *Es-2*$^{0.89}$, the slowest electromorph found, was detected in half the samples from Blake Road, and as a single heterozygote at Gambier and at Coral Harbour. *Es-2*$^{1.24}$, the fastest electromorph, was found in intermediate snails from Gambier, Blake Road, and Paradise Island.

This complex pattern may be summarized as follows: *Es-2*$^{1.00}$ is shared; *Es-2*$^{1.09}$ and *Es-2*$^{1.14}$ are *C. gubernatorium* alleles that occur in intermediates to varying degrees; *Es-2*$^{1.16}$ is a *C. glans* allele that is also found in intermediates; *Es-2*$^{0.89}$ and *Es-2*$^{1.24}$ are restricted to intermediate samples.

Glucose phosphate isomerase. Two of the four alleles segregating at this locus were found across the island (fig. 26). *Gpi*$^{1.0}$ is generally common (>0.85), *Gpi*$^{1.4}$ is usually rare

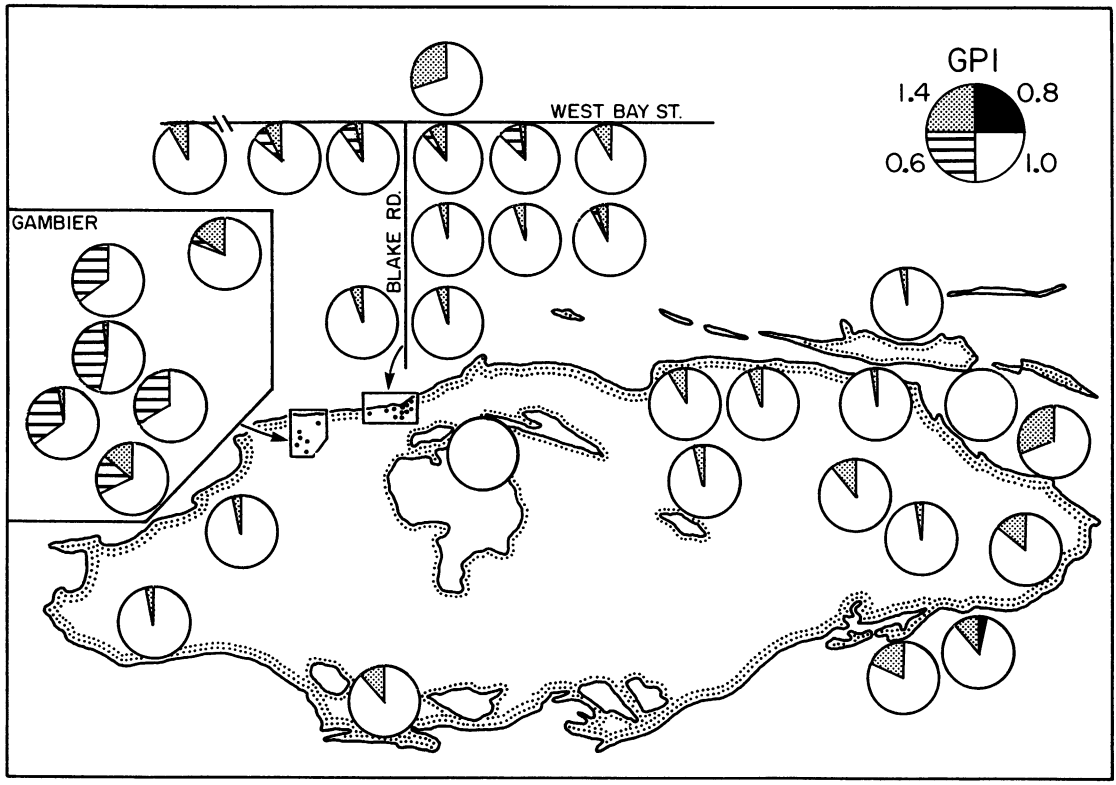


FIG. 26. Geographic variation in glucose phosphate isomerase.

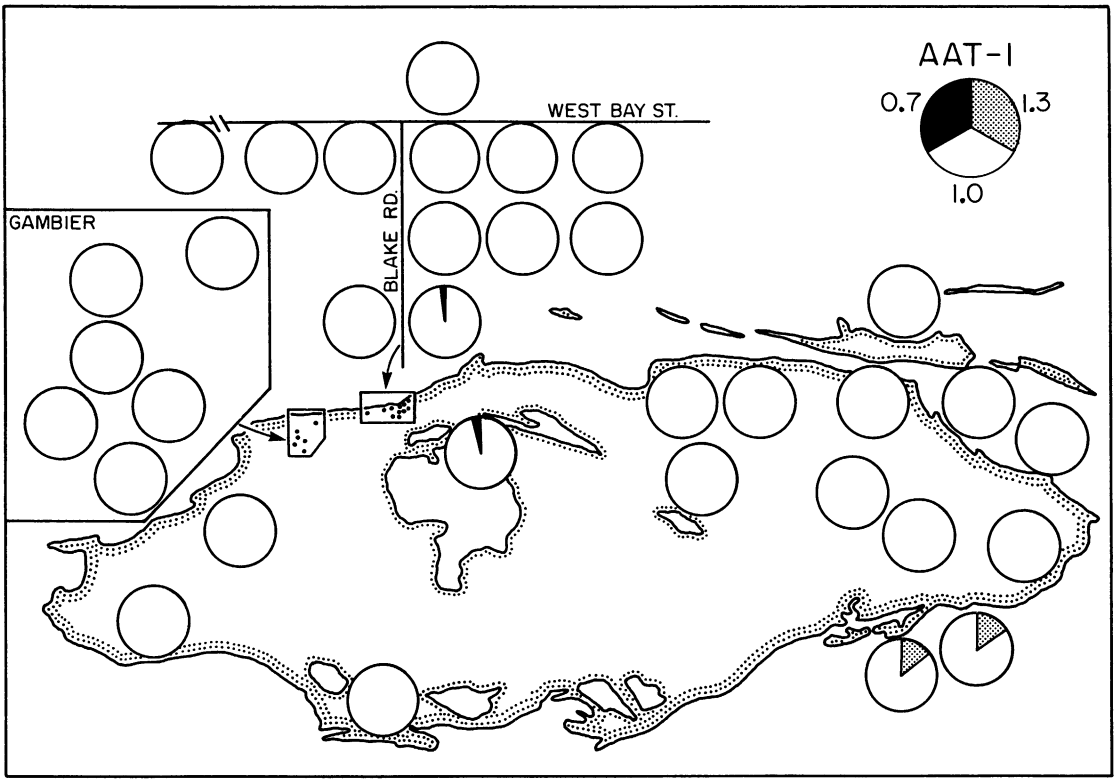
(<0.08) but locally rises to a frequency of about 0.30. We are unable to discern any clear pattern of variation in these alleles. The third and slowest electromorph, $Gpi^{0.6}$, was found in northwestern *C. glans* and in intermediates. It was rare among intermediates at Blake Road but very common at Gambier. Finally, $Gpi^{0.8}$ is a rare allele that we detected in two samples from a *C. gubernatorium* site (582) in southeast New Providence.

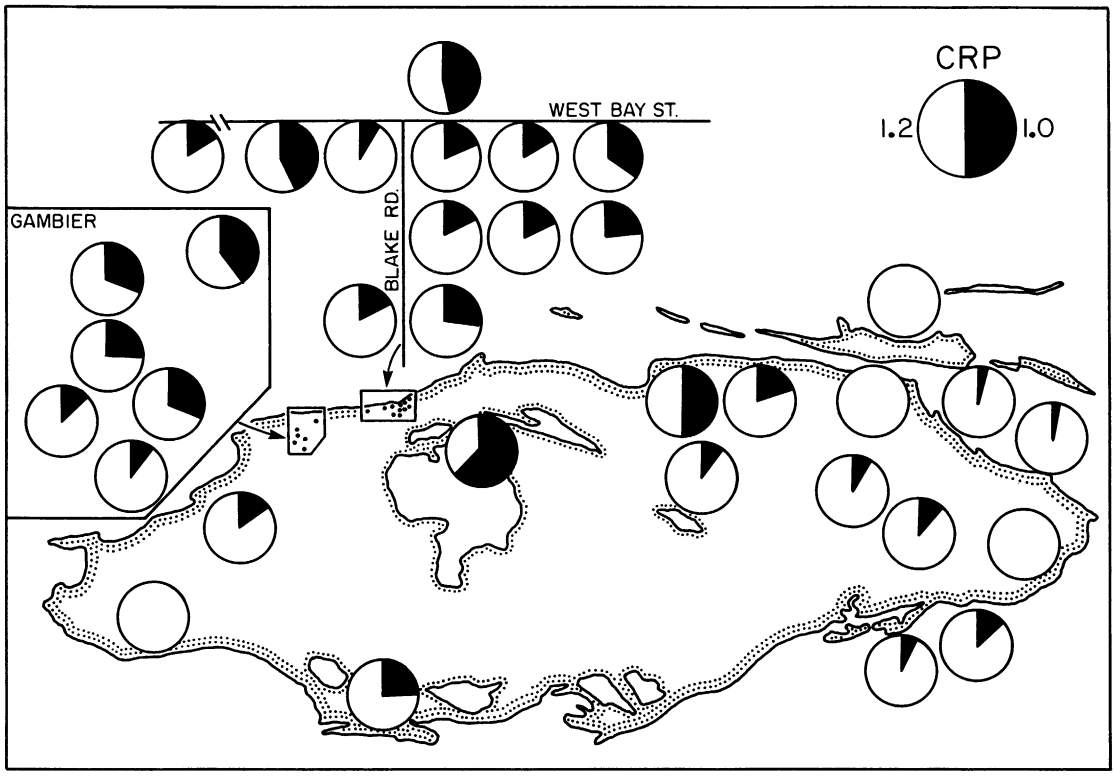
Aspartate aminotransferase-1. $Aat\text{-}1^{1.0}$ was fixed at most sites (fig. 27). A slower allele, $Aat\text{-}1^{0.7}$, was found in two heterozygotes, one from a Blake Road sample (569) of intermediates, the other from nearby Lake Cunningham (578), where snails are unexpectedly of *C. glans* morphotype but show hybrid influence in the morphometric analysis (see p. 438). A third, faster allele, $Aat\text{-}1^{1.3}$, was present at moderate frequencies (0.09–0.15) in three samples from two sites in southeastern *C. gubernatorium.*

Ceruloplasmin. We have not previously reported variation in *Cerion* for this nonenzymatic protein important in copper transport. Two codominant alleles segregate in all populations, except for four peripherally located sites (fig. 28). We cannot discern any biological meaning to the geographic pattern at this locus.

F. GENETIC DIFFERENTIATION OF *CERION* ON NEW PROVIDENCE

Four generalizations emerge from this study. First, *C. glans* is characterized by higher frequencies of $Pgm\text{-}2^{1.0}$ and $Es\text{-}2^{1.00}$, and by the presence of $Mdh\text{-}1^{0.72}$ and $Es\text{-}2^{1.16}$ not found in *C. gubernatorium.* Second, we found five alleles only in samples of intermediate morphology: $Pgm\text{-}2^{0.7}$, $Es\text{-}2^{0.89}$, $Es\text{-}2^{1.24}$, $Gpi^{0.6}$, and $Aat\text{-}1^{0.7}$. Third, *C. gubernatorium* is characterized by higher frequencies of $Mdh\text{-}1^{1.21}$ and $6Pgd^{0.93}$, and by the presence of eight alleles not found in *C. glans.*


AAT-1
0.7
1.3
1.0
WEST BAY ST.
BLAKE RD.
GAMBIER


CRP
1.2
1.0
WEST BAY ST.
BLAKE RD.
GAMBIER

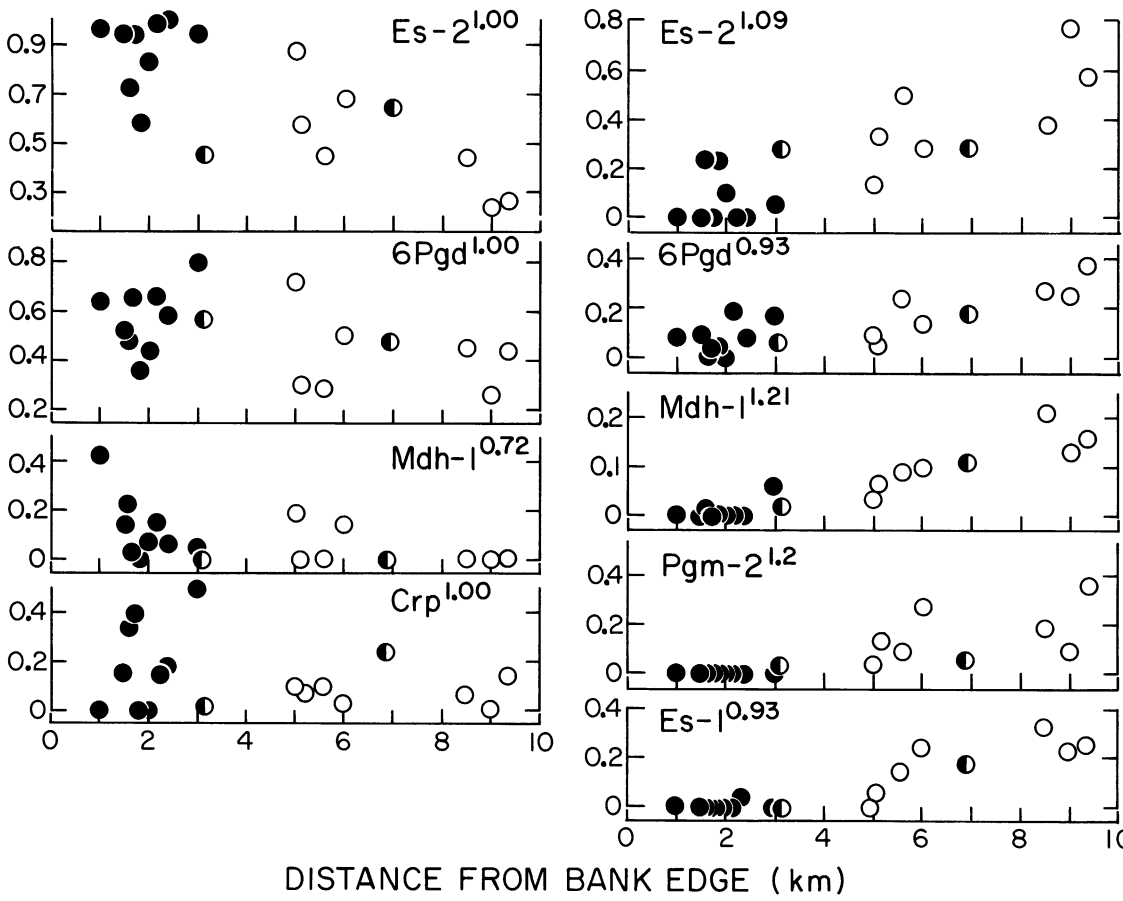


FIG. 29. Geographic trends in allele frequencies. Frequencies of nine alleles in 18 samples are plotted against the distance of each sample site from the edge of the Great Bahama Bank. Samples with *Cerion* of the *glans* morphotype are shown as dots, samples of the *gubernatorium* morphotype are shown as open circles; two samples of morphological intermediates are shown as half-closed circles. Samples included are, from left to right: 585, 587, 577, 879, 787, 786, 586, 579, 580, 788, 126, 872, 102, 581, 584, 583, 790, 582.

Four of these *C. gubernatorium* alleles are widespread (*Es-1*$^{0.93}$, *Pgm-2*$^{1.2}$, *Es-2*$^{1.09}$, and *Es-2*$^{1.14}$). The others are restricted to a small area of southeastern New Providence. These four restricted alleles (*Pgm-2*$^{0.8}$, *Es-1*$^{0.83}$, *Gpi*$^{0.8}$, and *Aat-1*$^{1.3}$) occur only at site 582, or 582 and 583 on the southeast coast.

These generalizations may overstate the genetic differences between *C. glans* and *C. gubernatorium*, since most diagnostic alleles occur at low frequency and since considerable introgression has apparently occurred. To explore this differentiation further, we studied the relationship among allele frequencies, shell morphotypes, and geography. Plots of allele frequencies against distance from the west end of New Providence provided no evidence for clinal variation of the type pro-

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FIG. 27. Geographic variation in aspartate aminotransferase-1.

FIG. 28. Geographic variation in ceruloplasmin.

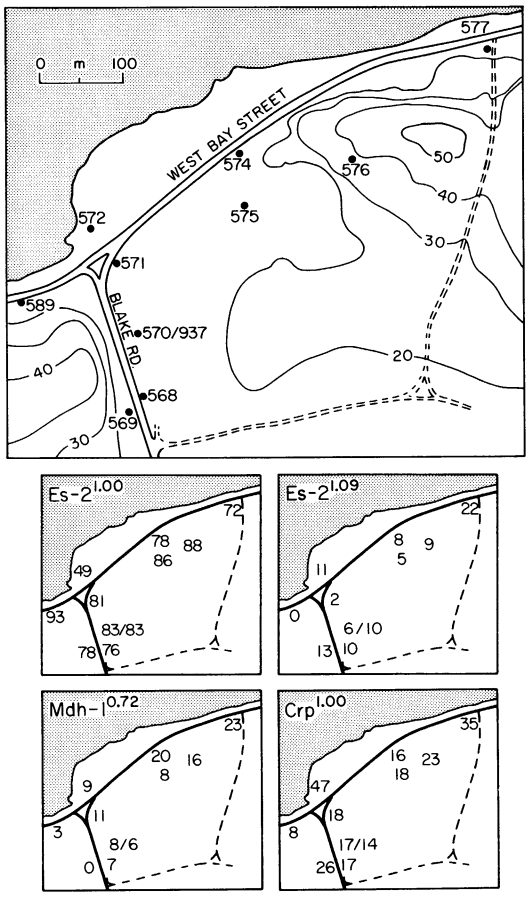

FIG. 30. Geographic variation in the area of hybridization between *Cerion glans* and *C. gubernatorium* on the north coast near Blake Road. The upper map shows the distribution of the 11 samples studied genetically relative to the ocean (shaded), roads and the coastal hill (contour intervals in meters). The lower panels show allele frequencies multiplied by 100 in each of these samples.

posed by Plate (see p. 394). Plots of frequencies against distance of each site from the present-day coast produced irregular and uninterpretable patterns. Only the relationship between allele frequencies and distance of collection sites from the edge of the island bank produced meaningful results. (Recall that during hypothermals sea level falls and water retreats over the shallow island bank to its edge.) We have previously demonstrated the importance of this paleogeographic coastline in understanding the present-day distribution of ribby and mottled morphotypes on islands of both Little and Great Bahama Banks (Woodruff and Gould, 1980). Our results for nine alleles are shown in figure 29. Only half of our samples are plotted on these graphs; we have excluded all samples of intermediate morphology from Blake Road and Gambier. (These 18 sites lie 1.8–2.2 km from the bank edge.) We regard our analysis as very preliminary, since we lack samples from areas 3–5 km from the bank edge. Much *Cerion* habitat in this region has been destroyed (by the city of Nassau, by the International Airport, and by softwood forestry), and more formal statistical analysis of the data may be misleading until we can fill this gap. Nevertheless, figure 29 shows clearly that *C. glans* and *C. gubernatorium* have quite different patterns of variation at $Es\text{-}1^{0.93}$, $Mdh\text{-}1^{1.21}$, and $Pgm\text{-}2^{1.2}$. We find more regular clinal variation at $6Pgd^{1.00}$, $6Pgd^{0.93}$, $Es\text{-}2^{1.00}$, and $Es\text{-}2^{1.09}$. We tentatively interpret these patterns as reflecting differential introgression of various alleles. The graphs indicate that the zone of genetic interaction is probably 2–4 km wide, 4–8 times wider than the morphological hybrid zones at Blake Road and Gambier. In addition, the genetic zone is asymmetrically distributed around the morphological zone (that is, it extends further inland), but this asymmetry arises necessarily (given greater width of the genetic zone) from the fact that our hybrid sites are very close to the northern bank-edge coast.

G. Genetics of Morphometrically Intermediate Samples

We studied the area of interaction between *C. glans* and *C. gubernatorium* to elucidate the extent and evolutionary significance of introgression. We looked for evidence of the Wahlund effect, for differential introgression, and, especially, at distribution and abundance of the five alleles associated geographically with the hybrid zone. We can describe the current interactions in two areas in reasonable detail and present some evidence for similar interactions occurring elsewhere on the island.

In northern New Providence the low coastal hill (10–30 m high) was originally thickly vegetated with dense scrub and woodland.

Cerion are uncommon in such dense vegetation, and this old dune separated the ranges of the two taxa. A natural gap in the dune near Cave Point provided a suitable passage for Blake Road, which connects the coast road (West Bay Street) with the inland road (John F. Kennedy Drive) to the international airport (fig. 30). The two taxa probably came into contract with one another in this natural gap long before construction of the road, but recent clearing of land has greatly increased the suitability of the intermediate area for *Cerion*. In particular, the clearing of an area approximately 200 × 200 m at the junction of Blake Road and West Bay Street has provided an ideal habitat for high-density *Cerion* populations (see photo on p. 487). We have not yet established the history of this site but suspect that the initial clearing took place in the 1950s. Today, the grass and shrubs support snail populations at densities of >10/m^2 in some areas, and probably average >1/m^2 across the whole area. South of this disturbed site, *Cerion* densities drop to <0.01/m^2 in the pine-palmetto woodland, though higher densities are encountered along the sides of Blake Road itself.

We examined electrophoretic variation in more than 350 snails from 11 samples representing eight sites within the field and two adjacent coastal sites. All samples from within the field are of hybrid phenotype. The locations of the sample sites are shown in figure 30. Recall that morphometric samples 299 (=572) and 287 (see fig. 15) are typical ribby *C. glans,* that sample 300 is predominantly mottled like *C. gubernatorium,* and that highly variable hybrids were found at 296 (=568) and 297. Morphologically, the zone of hybridization seems to be about 200 m wide and certainly not more than 400 m wide in this area.

Genetically the Blake Road hybrids are slightly more polymorphic than adjacent populations of purely ribby or mottled morphotype ($p = 0.26$ vs. 0.22), but we find no concomitant increase in average heterozygosity. Chi-square tests and calculation of the fixation index (F_{IS}) on genotype frequencies revealed no evidence for significant departure from equilibrium expectations in the area (table 18). Similarly, the coefficients of heterozygote deficiency (D) provided no evidence for assortative mating or the Wahlund effect (fig. 20).

We then examined the distribution of certain alleles that we have tentatively identified as markers of either *C. glans* or *C. gubernatorium.* Figure 30 (B–D) reveals that the frequencies of *Es-2*$^{1.00}$ and *Mdh-1*$^{0.72}$ (characteristic of *C. glans*) decline slightly with distance from the coast. We note an opposite pattern for *Es-2*$^{1.09}$ which characterizes *C. gubernatorium.* However, these clines are not well defined; moreover, in two of three cases, sample 572 gave anomalous results. This coastal ribby population is, genetically, more *gubernatorium*-like than expected. On balance, however, the data indicate that the two taxa are in full genetic contact in this area today. The marker genes have introgressed right across the morphological hybrid zone in both directions.

Our most interesting observation involves the discovery of several allelic electromorphs in the hybrid samples that are not found in either parental taxon away from the area of introgression. Figure 31 (A–E) shows the distribution of these unique and typically rare alleles. *Gpi*$^{0.6}$ is restricted to a band about 200 m long at the northern edge of the morphological hybrid zone; it was not detected 50 m further south. Its average frequency in the four adjacent samples was 0.058. *Es-2*$^{0.89}$ also has a narrow distribution along about 400 m of the northern edge of the hybrid zone. Its average frequency at five adjacent sites was 0.022. In contrast, *Es-2*$^{1.24}$ was found in almost every sample; its frequency decreases from a maximum of about 0.11 in the center of the field to much less in peripheral samples. Its average frequency over the area was 0.056. *Pgm-2*$^{0.7}$ shows a similar pattern of decrease in frequency with distance from the center of the field. Average frequency within its detected range was 0.053. Finally, *Aat-1*$^{0.7}$ was detected in a single heterozygote from the southwest edge of the field. When the frequencies of all five rare alleles are considered together, we obtain a firm image of a genetic anomaly centered on the Blake Road clearing (fig. 31F).

Three kilometers west of Blake Road we found a second area of apparent hybridization southwest of the coastal village of Gambier. We have examined more than 200 snails

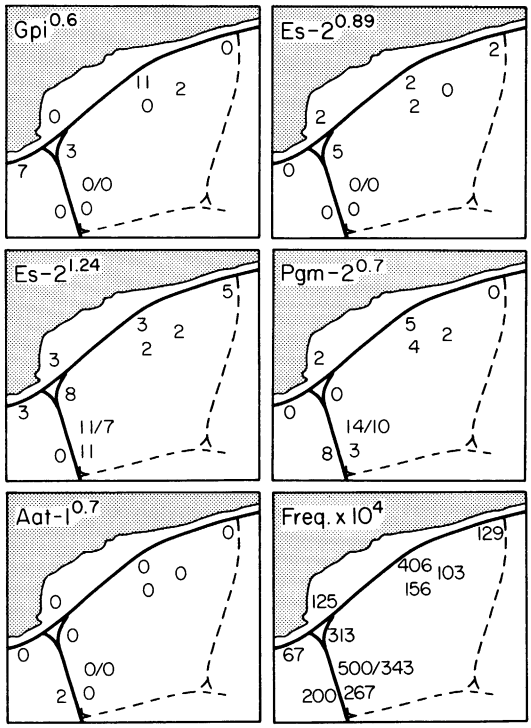

FIG. 31. Unexpected alleles at the Blake Road contact. Allele frequencies (×100) and cumulative frequencies in 11 samples are plotted on the same base map as figure 30.

from six sites along a 1-km north–south transect (fig. 32A). Sample 879 on the 25-ft coastal dune is typical ribby *C. glans*. Samples 0.4–0.9 km inland contain an increasing percentage of nonribbed, mottled *C. gubernatorium*-like snails (fig. 32B). As mentioned previously (p. 439), very few snails of intermediate morphotype were found and we first thought that the two taxa might not be hybridizing in this area today. The genetics of the situation suggests otherwise.

As at Blake Road, we found that the Gambier intermediate samples were slightly more polymorphic (P = 0.26 vs. 0.22) but not significantly more heterozygous than nearby populations of pure ribby or mottled morphotypes. As for Blake Road, we found no evidence for assortative mating, a Wahlund effect, or any other departure from panmixia. We did, however, detect several clines in allele frequency across the hybrid zone and four rare alleles associated with it.

The patterns of interest are shown in figure 32 (C–G). *C. glans* alleles $Es\text{-}2^{1.00}$ and $Mdh\text{-}1^{0.72}$ tend to decrease in frequency from north to south across the zone. Conversely, we find an increase in the frequency of *C. gubernatorium* $Es\text{-}2^{1.09}$ and $Mdh\text{-}1^{1.21}$. We also found a clinal change in frequency of $Crp^{1.00}$ from 0.4 to 0.1 across the transect. This surprised us since no such pattern was detected at Blake Road (fig. 30E) or on the island as a whole (fig. 28). The distribution and frequencies of the four rare alleles are shown in figure 33 (A–D). Three cases involve alleles detected at low frequency in or near hybrid zones and not found in populations of pure ribby or mottled morphotype. Within the Gambier zone, $Es\text{-}2^{0.89}$, $Es\text{-}2^{1.24}$, and $Pgm\text{-}2^{0.7}$ have average frequencies of 0.0026, 0.0392, and 0.0262, respectively. The fourth allele, $Gpi^{0.6}$, is exceptional in that it has risen to high frequencies at the northern edge of the morphological hybrid zone. Figure 33E shows the extent of the genetic anomaly when all four rare alleles are considered together. As at Blake Road, we find clear evidence of introgression in both directions and spreading in both directions over a distance of 0.5 km for alleles that presumably arose in the hybrid zone. Since we lack samples from further south, we cannot now estimate the width of the Gambier interaction. Nevertheless, consideration of shell (fig. 32B) and allozyme data (fig. 33E) indicates that the genetic zone is at least three times as wide as the morphological zone, and possibly even wider.

Earlier in this paper, we suggested that the Gambier contact might be older than the Blake Road interaction. The area is wooded and, except for the disused sand quarry between sites 938-939-942, affords little evidence of recent land clearing. Unfortunately, we do not have enough data to test the hypothesis that differences between the two sites are due to the varying age of interactions. We might argue, for example, that differences in mean heterozygosity between samples in the two areas (Gambier $\bar{H} = 0.094$, Blake Road $\bar{H} = 0.068$) are due to the age of each interaction. Perhaps the lower value for Blake Road results from a Wahlund effect so small that it escaped our statistical investigation. This effect would be further diminished at Gambier—hence the higher $\bar{H}$ there. In ad-

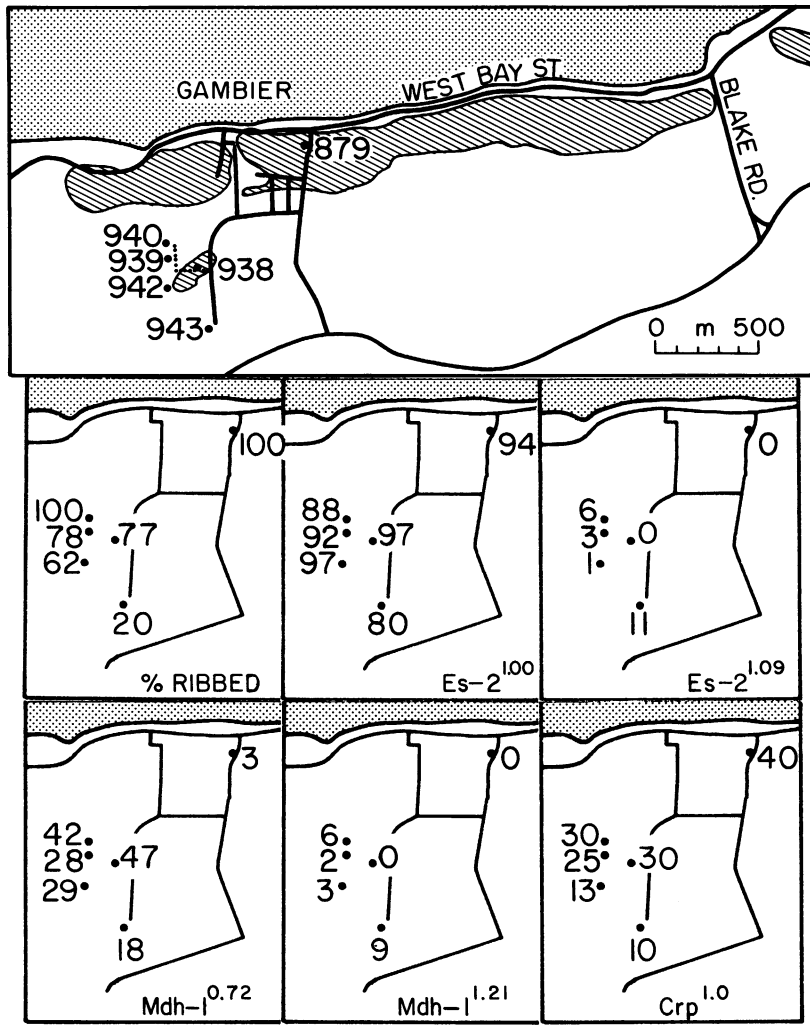

FIG. 32. Geographic variation in the area of hybridization between *Cerion glans* and *C. gubernatorium* on the north coast near Gambier village. The upper map shows the distribution and locality numbers of the six samples studied genetically. Localities are shown relative to roads and coastal hills (25 ft contour). The six lower maps show the frequency (×100) of ribby shells and of five selected alleles in each sample.

dition, we might note that we have found rare alleles spread over 900 m at Gambier but only over about 300 m at Blake. If gene flow is proportional to time, we could then argue that the Gambier interaction is older. Unfortunately, our sampling of the two sites precludes this comparison at present; we need more samples from south of the disturbed area at Blake Road (where *Cerion* densities are very low). Finally, we might compare the frequency of an unexpected allele like $Gpi^{0.6}$ in both areas and argue that it took longer to reach a mean frequency of 0.288 (range 0.03–0.44) at Gambier than 0.054 (0.02–0.11) at Blake Road. Furthermore, this allele spreads over a range of 1 km at Gambier but only about 200 m at Blake Road. But counter examples can be found: for example, $Pgm\text{-}2^{0.7}$ has twice the geographic range at Blake Road as at Gambier, as does $Es\text{-}2^{0.89}$. Until these interactions are better documented and until we have more experience with analogous in-

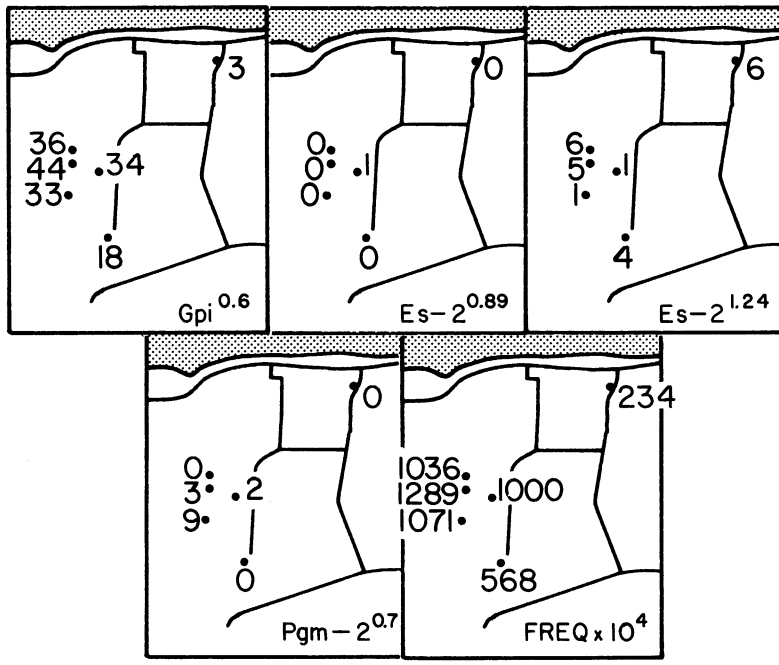

FIG. 33. Unexpected alleles at the Gambier village contact. Allele frequencies (×100) and cumulative frequencies in six samples are plotted on the same base map as figure 32.

teractions between the ribby and mottled morphotypes on other islands of the Great Bahama Bank, further speculation about the history of these two interactions is premature.

Hybridization between *C. glans* and *C. gubernatorium* is not limited to these two disturbed sites associated with gaps in the coastal dune. We find genetic evidence for introgressive hybridization at several other parts of the island. In the northeast, on Paradise Island, allozyme data show that introgression has also been occurring. Morphologically, the north coast sample from this cay (787) is a typically ribby *C. glans,* while samples from the south coast (786, 788) are intermediate in morphology and also in geographic position between ribby samples at the island's north coast and intermediate-to-mottled samples on the adjacent mainland. Inspection of figures 22–28 shows how *glans* and *gubernatorium* alleles are mixed in these three samples. Three alleles associated with *C. gubernatorium* reach Paradise Island: $6Pgd^{0.93}$, $Pgm\text{-}2^{1.2}$, and $Mdh\text{-}1^{1.21}$. We were not able to find heterozygotes between $Mdh\text{-}1^{1.21}$ and $Mdh\text{-}1^{0.72}$ (a *glans* allele) on this offshore cay, but picked them up on the adjacent main island at 580 (*C. glans*) and 126 and 581 (*C. gubernatorium*). $Es\text{-}2^{1.24}$, which we associate with hybrids at Blake Road and Gambier, was present (as might be expected) in the two southern samples. $Es\text{-}2^{1.14}$, associated with *C. gubernatorium,* was found in the two eastern samples one of which (787) exhibits the opposite morphotype. We obtain further evidence for introgression on Paradise Island from heterozygotes between $Es\text{-}2^{1.14}$ and $Es\text{-}2^{1.24}$ at site 788. The channel (Nassau Harbour) separating Paradise Island from New Providence is very shallow and the offshore populations are not significantly isolated. It is not surprising, therefore, that we can pick up genetic traces of introgression 2–3 km further inland at sites 126 and 581. Both samples are typical *C. gubernatorium* in appearance but carry *C. glans* $Mdh\text{-}1^{0.72}$ at low frequencies.

We can, on these criteria, trace this hybrid interaction west along the north coast (see fig. 17). The anomalous sample from Lake Cunningham (site 301 = 578) where *C. glans* was

found 1 km from the coast (in a region of *C. gubernatorium*) contains two of the rare alleles associated with the hybrid zones: *Es-2*$^{0.89}$ and *Aat-1*$^{0.7}$. This genetic evidence agrees with the morphometric result; recall that 301 occupied an unusual position on the third axis of our factor analysis—a region associated with Blake Road hybrids (fig. 8).

The hybrid zone between *C. glans* and *C. gubernatorium* therefore extends along the north coast of the island. Although urban development and farming have destroyed appropriate habitat in most areas, we can certainly detect its former presence from Paradise Island west for 20 km to beyond Gambier. If our central hypothesis about the relationship between location of the hybrid zone and position of the bank edge is correct (see p. 397), we would expect the zone to turn south and meet the south coast near Adelaide. This apparently occurs. Our morphometric sample from Coral Harbour (281; 2 km east of Adelaide—see fig. 7) is ribby to intermediate, while the sample from Millars Sound (279) 4 km further east is of typical mottled morphotype (fig. 7). Unfortunately, we analyzed only one sample from this area (584 = 281, Coral Harbour—figs. 7 and 17). These ribby to intermediate snails have five alleles that associate with mottled *C. gubernatorium*: *Mdh-2*$^{1.21}$, *Es-1*$^{0.93}$, *Es-2*$^{1.09}$, *Es-2*$^{1.14}$, and *Pgm-2*$^{1.2}$. Furthermore, we found *Es-2*$^{0.89}$, one of our rare alleles associated with the hybrid zone, in a single heterozygote.

H. Phantom Alleles in Southeast New Providence

We would properly conclude from the preceding discussion that New Providence is tenanted by two imperfectly isolated forms of *Cerion*. This conclusion, however, does not tell the whole story, since we also found that one of the taxa contains alleles derived from a third species no longer present on New Providence. We must first define and exclude the effects of this historical event from our comparison before reaching any taxonomic decision.

We reported in section E the unusual genetics of three samples from two adjacent sites on the southeast coast near Long Point. Sites 583 and 582 (=702 collected a year later in the same spot) are separated by 1.5 km, and display more variability than any other sample on New Providence: P = 35 percent, $\bar{H}$ = 15 percent; figures 18–19 show the lower values found elsewhere. This increased variability may be traced to the presence of four alleles found nowhere else on New Providence. Two are present only at site 582 and occur at low frequencies in heterozygotes: *Gpi*$^{0.8}$ = 0.03–0.06, *Pgm-2*$^{0.8}$ = 0.03. The other two alleles were detected at both site 582 and site 583 1.5 km to the west: *Aat-1*$^{1.3}$ = 0.09–0.15, *Es-1*$^{0.83}$ = 0.01–0.07. We found heterozygotes and homozygous individuals of these genotypes. These four alleles were not found in adjacent samples collected 3–4 km to the north and east.

In our initial view, these localized alleles characterized "pure" *C. gubernatorium* populations that had not yet introgressed with *C. glans*. This hypothesis presented several problems, however, including the need for an explanation of why *C. gubernatorium* should be nearly twice as variable as *C. glans*. Only recently, after we had nearly completed our New Providence study, a solution emerged from a different quarter. In our ongoing survey of variation in *Cerion* from other islands, we had, in 1982, turned our attention to *C. eleutherae*, which inhabits parts of Eleuthera island 100 km east of New Providence. *C. eleutherae* hybridizes in different areas with both ribby and mottled forms almost surely identical with *C. glans* and *C. gubernatorium* from New Providence. Our electrophoretic survey of these three taxa is still in progress, but one result has clearly emerged: the four electromorphs found only near Long Point on New Providence also occur in samples of *C. eleutherae* from northern Windermere Island on the east coast of Eleuthera. *C. eleutherae* is morphologically identical to, and presumably synonymous with, *C. agassizi*, which occurs abundantly as a fossil on New Providence (see pp. 478–483). Thus, we interpret the Long Point genetic anomaly as an *agassizi* effect and support this conclusion with morphometric and geographic data as well (see p. 420 and Appendix 1, Part A). The four localized alleles are phantoms of a species that once inhabited southern New Providence, but has apparently become extinct

through hybridization with *C. gubernatorium.*

I. Genetic Comparison of *Cerion glans* and *C. gubernatorium*

We estimate overall genetic differentiation of New Providence *Cerion* with Nei's (1978) unbiased coefficients of genetic identity (*I*) and genetic distance (*D*). The similarity matrix (*I*) for all pairwise comparisons of the 37 samples showed that very little differentiation has occurred among populations for the 21 loci studied. *I* values ranged from 0.942 to 1.000, with a typical value of >0.99. Our interpretation of these data has been complicated by the presence of phantom *agassizi* alleles in *C. gubernatorium* and by rare alleles associated with hybrids. We minimized the phantom effect by using site 790 at the east end of the island to characterize *C. gubernatorium.* The genetic identity between this sample and four populations of *C. glans* is:

580	Fort Charlotte	0.955
585	Southwest coast	0.958
586	North Paradise Island	0.946
588	Northwest coast	0.945

These values give us an estimate of the *glans–gubernatorium* genetic identity, *I,* of about 0.95. Alternatively, this difference may be expressed as a *D* value of about 0.05.

Patterns of genetic similarity among populations are quite coherent. We present a dendrogram of *I* values among all 37 samples in figure 34. (Note that this dendrogram includes the "tainted" samples from Long Point; interspecific similarities are consequently greater than the values estimated above.) We immediately note two well-marked clusters: *gubernatorium* and some hybrids, and *glans* and most of the hybrids. As sensible subgroups within the *gubernatorium* cluster, we find the Long Point samples (582, 583, 702) with their *agassizi* alleles, two samples of relatively pure *gubernatorium* (102, 790) from the east end of the island, and two groups of introgressed samples. One includes the Paradise (=Hog) Island populations (786–788); the other groups 581 (northeast coast) with 584 (Coral Harbour). The second major cluster also includes a number of biologically meaningful subgroups, especially the Gambier and Blake Road hybrids. Surprisingly, we find an interior *gubernatorium* sample (126) grouped with the *C. glans.* Not surprisingly, the anomalous Blake Road coastal sample (572) clusters distantly from its adjacent populations. Although the UPGMA method has some shortcomings, it does portray a pattern that we had discerned with our locus-by-locus analysis. The cophenetic correlation for the dendrogram is 0.66; the percent standard deviation, 0.96.

The quantification of a genetic distance between *C. glans* and *C. gubernatorium* at about 0.05 does not lead automatically to a taxonomic conclusion. Certainly, as an interspecific distance, this value is very low compared with measures for many genera of mammals, fish, and amphibians, where interspecific $\bar{D} \geq 0.3$ (Avise and Aquadro, 1982). It is also much lower than the interspecific distances observed in the *Drosophila willistoni* group, where *D* ranges from 0.23 to 0.66 (Ayala, 1975). From these comparisons alone, we might be tempted to synonymize *C. glans* and *C. gubernatorium,* and treat them as subspecies of a single variable species. But the simple accumulation of allelic differences may generally be irrelevant to the process of speciation. We may cite numerous cases of groups maintaining "good" species that are very poorly differentiated one from another at the structural gene level. Birds of the genera *Geospiza, Aythya,* and *Dendroica* all display $\bar{D}$ values of about 0.05 (Avise and Aquadro, 1982); for *Drosophila persimilis* and *D. pseudoobscura,* $\bar{D} = 0.05$ (Prakash, 1969); semispecies of *Drosophila paulistorum* and some

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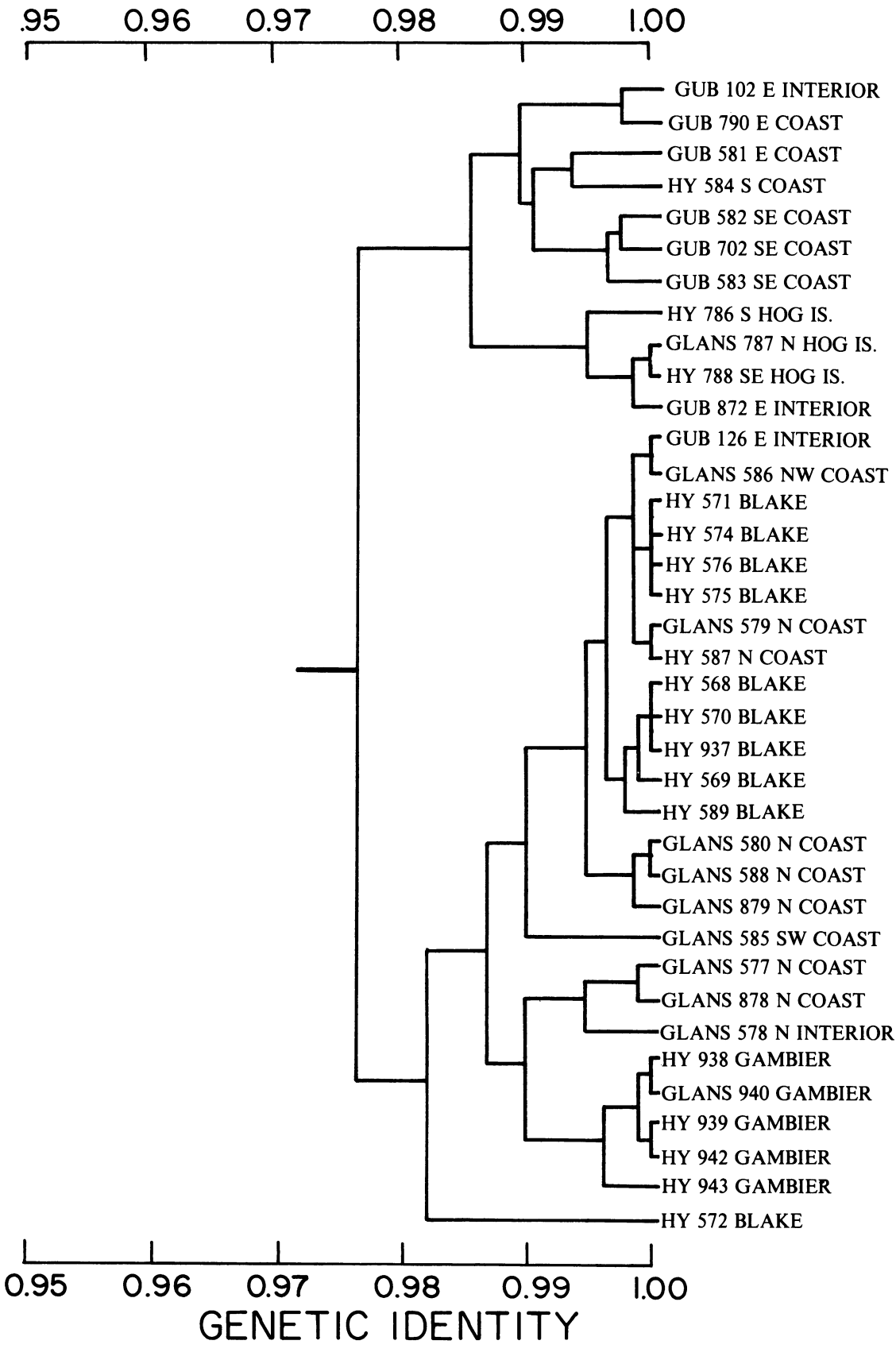
FIG. 34. A dendrogram based on UPGMA clustering of 37 samples of *Cerion* from New Providence using the unbiased genetic identity (I) of Nei (1978). Samples are identified according to their morphology (GUBernatorium, HYbrid, GLANS), locality number, and geographic location. This analysis, based on 21 loci, overestimates the genetic identity of *C. gubernatorium* and *C. glans* for reasons discussed in the text.


.95
0.96
0.97
0.98
0.99
1.00
GUB 102 E INTERIOR
GUB 790 E COAST
GUB 581 E COAST
HY 584 S COAST
GUB 582 SE COAST
GUB 702 SE COAST
GUB 583 SE COAST
HY 786 S HOG IS.
GLANS 787 N HOG IS.
HY 788 SE HOG IS.
GUB 872 E INTERIOR
GUB 126 E INTERIOR
GLANS 586 NW COAST
HY 571 BLAKE
HY 574 BLAKE
HY 576 BLAKE
HY 575 BLAKE
GLANS 579 N COAST
HY 587 N COAST
HY 568 BLAKE
HY 570 BLAKE
HY 937 BLAKE
HY 569 BLAKE
HY 589 BLAKE
GLANS 580 N COAST
GLANS 588 N COAST
GLANS 879 N COAST
GLANS 585 SW COAST
GLANS 577 N COAST
GLANS 878 N COAST
GLANS 578 N INTERIOR
HY 938 GAMBIER
GLANS 940 GAMBIER
HY 939 GAMBIER
HY 942 GAMBIER
HY 943 GAMBIER
HY 572 BLAKE
0.95
0.96
0.97
0.98
0.99
1.00
GENETIC IDENTITY

of the newest Hawaiian species have $\bar{D} = 0.03$ (Richmond, 1972; Carson, 1982). Within land gastropods, the five endemic *Partula* of Moorea and Tahiti, islands less than 1.5 million years old, show $\bar{D} = 0.09$ (Johnson et al., 1977). Clearly, taxonomic decisions do not follow directly from the estimation of *D*.

V. CONCLUSIONS

This study may seem, at first glance, merely local, parochial, and quite limited. New Providence, even by Bahamian standards, is a small island. Its *Cerion* fauna is neither particularly diverse nor peculiar—but only unusually beset with taxonomic problems, largely the work of one overenthusiastic splitter, C. J. Maynard. This monograph corrects Maynard's taxonomy and recovers a consistent biological pattern of two taxa (with sensible geographic, genetic, and morphological ordering), previously obscured by Maynard's thicket of unrelated names. Yet this monograph is the most general we have yet written on *Cerion* (hence its length) for two basic reasons.

First, it embodies a basic methodology that we have tried to apply to all our work, and that we regard as indispensable for the resolution of complex problems in natural history. William Whewell, the great 19th century British philosopher of science, noted that empirical problems generated by a complex and unobservable past history would not find their resolution in any crucial experiment or key observation. Scientists would have to seek a "conciliance of inductions"—a pattern affirmed by so many independent criteria that no other explanation could fit, even though any single criterion offered no sure resolution. Darwin understood and used the method extensively. Huxley, beguiled by the simpler models of "hard" physical sciences, did not; he pursued the chimaera of singular certainty—the "nasty, ugly, little fact" of his famous aphorism—and generally failed (DiGregorio, 1984).

We have sought conciliance by basing our studies on morphometry and genetics of the same samples personally collected from areas of known ecology and habitat. By using distributional, morphological, and genetic data on both parental and hybrid forms—and by recognizing a similar pattern strictly linked to the same geographies and habitats on all major islands of the northern Bahamas—we conclude that Maynard's 70+ names for living taxa apply to but two well-defined semispecies (the ribby and mottled morphotypes), here accorded the taxonomic status of species (*C. glans* for the ribby morphotype, and *C. gubernatorium* for the mottled morphotype). This decision is supported by recent theoretical considerations of the effects of geographically concordant multilocus clines on gene flow and differentiation of populations (Barton, 1983; Barton and Hewitt, 1983).

Any single observation or criterion would not distinguish our conclusion from the primary competitor—that ribby and mottled populations are alternative ecophenotypes of a single taxon. All criteria taken together provide adequate support (if not overkill) for the existence of two discordant *Cerion* entities on New Providence. We have used four major criteria, each with several subcategories:

1. Distribution. The restriction of ribby populations to bank-edge coasts, and mottled populations to bank-interior coasts and island interiors, is so precise that we can map the position of the subaerially invisible banks from the distribution of *Cerion.* This pattern of uninterrupted and stereotyped parental morphologies along miles of distinctive coastline, broken by narrow and variable hybrid zones located just at the geographic transition from bank-edge to bank-interior coasts, occurs both on New Providence and on all large islands of the northern Bahamas. We find similar hybrid transitions along the other predicted kind of transect—bank-edge coast inland to island interior.

2. Morphology of parental populations. We base our conclusions not on measured differences in static form of characters considered singly, but on patterns of interrelation

specified by "covariance sets" that regulate the complex, but invariant, allometries of *Cerion*'s growth. Parental morphologies are stable over the broad areas of their appropriate coasts; we find no cline gradually merging ribby into mottled samples (as previous authors had maintained). Differences in parental morphologies are not simple or superficial results of a few adaptive characters, perhaps ecophenotypically induced. The two parental morphotypes are distinguished by consistent (if sometimes subtle) differences involving *several* independent covariance sets; the morphotypes are different entities, not merely simple transformations, one into the other. The two morphotypes also differ consistently in both amounts of variation (mottled exceeding ribby both within and among samples), and in patterns of covariance themselves.

3. Morphology of hybrid populations. Hybrid samples are found only where our general theory of morphotypes (developed for other islands and, therefore, not argued in a circle for New Providence alone) predicts their origin (Gould and Woodruff, 1978). Hybrid morphologies are not simply intermediate between parentals, but show differences consistent with their status as mixtures of two discordant entities. At Blake Road, variation in size, color, and ribbing far exceeds that exhibited by any parental population. Moreover, hybrids exhibit a unique morphology (associated with a covariance set never before detected in *Cerion*), interpreted as a developmental disruption that deposits the adult aperture discordantly upon a shell still in middle growth.

4. Genetics. A general clustering of samples, based on data of electromorph frequencies alone, identifies the same two major clusters of ribby and mottled populations that morphology specified. Hybrid samples contain rare alleles found in neither parental taxon—an intriguing phenomenon noted in many other natural hybrids, and further evidence that two discrete taxa interact in the narrow hybrid zones. The genetic hybrid zone is both wider than the morphological hybrid zone, and asymmetric about it.

These criteria and subcriteria, considered together, produce a conciliance consistent only with the conclusion that but two interacting taxa constitute the contemporary *Cerion* fauna of New Providence and encompass all its 70+ available names.

Second, this monograph becomes a key, or model, for our revision of the entire genus, because it stands so neatly halfway in a process moving from comprehensible simplicity to a complexity that becomes tractable only in the light of previous resolutions.

In tackling *Cerion,* "the most difficult genus of pulmonate mollusks to classify," as its leading student maintained (W. J. Clench in litt. to Ernst Mayr, see Mayr and Rosen, 1956), we could not simply plunge *in medias res* by assaulting, from no prior experience, such a complex situation as New Providence presents. We therefore began with geographically peripheral areas harboring single taxa not suffering the burden of a bloated nomenclature. We mapped the geographic variation of *Cerion uva* from Aruba, Bonaire, and Curaçao (Gould, 1969a, 1984a), and found that each island and area housed distinctive populations defined by coordinated changes of the basic covariance sets defined by studies of *Cerion*'s growth.

We then moved to a peripheral area with established taxonomic complexity, but potential biological unity. We found a predominant cline in morphological variation of *Cerion* populations along the linear chain of islands at the eastern end of its range (Hispaniola to the Virgins), and we reduced all established names to the single taxon, *C. striatellum* (Gould and Paull, 1977).

As a first foray into truly multitaxon islands and banks, we chose the peripheral Little Bahama Bank, with fewer than 20 established taxa. There we detected, for the first time, the predominant pattern of ribby and mottled morphotypes, associated with bank-edge and bank-interior coasts, that we find repeated on all islands of the northern Bahamas, and that we now regard as a key to unraveling the general taxonomic morass of *Cerion* (Gould and Woodruff, 1978).

With this potential key in hand, we could finally mount a direct assault upon the *Cerion* dilemma in its maximal expression—multitaxon islands beset with exuberantly oversplit taxonomies. Hence, New Providence and this study. Despite the daunting complexity of received literature, we have now reduced

all 70+ taxa to the same pattern of mottled and ribby, with evidence (by introgression into mottled populations) for an extinct third taxon, once the dominant element of Pleistocene New Providence.

With this model, we can finally work toward a solution of more complex multitaxon islands in a graded and systematic way. First, two large islands near New Providence—Eleuthera and Cat—show the same pattern of mottled and ribby, but add surviving populations of the prominent fossil taxon (*C. agassizi*) that "persists" on New Providence only in introgressed form. Eleuthera contains the three taxa alone; Cat adds a fourth, a local incursion of the distinctive subgenus *C.* (*Umbonis*), now diluting by hybridization with ribby and *C. agassizi* populations at its northern and southern borders along the east coast.

The basic model of ribby and mottled also permits a resolution of the most complicated of all *Cerion* faunas—Long Island. We can understand the remarkable diversity of this island by recognizing the underlying and invariant pattern of mottled populations along the bank-interior west coast and ribby along the bank-edge eastern coast. The diversity of Long Island can be grasped when we recognize it as a set of incursions imposed upon the underlying pattern of mottled and ribby. These propagules include another taxon of *C.* (*Umbonis*), called *C. stevensoni* on Long Island, and several populations of the large, smooth, thick-shelled white cerions of the southeastern Bahamas (called *C. malonei, C. fernandina, C. nudum,* and the dwarf *C. mccleani*). Since Long Island lies closest of all Great Bahama Bank islands to the southeastern banks, these incursions occur where we would most expect them. Long Island is the major mixing ground of distinctive northern and southeastern *Cerion* faunas.

Our general approach can also resolve the existing taxonomic complexities of different *Cerion* faunas in the southeastern Bahamas. Here, the dominant element is a smooth, white, thick-shelled morphotype that invades the northern Bahamas prominently on Long Island, more distantly and less successfully, as the *C. agassizi* stocks of Eleuthera and Cat. Several islands, Mayaguana in particular, contain no other taxon. Other islands include several taxa, with the white morphotype always prominent. As *C. regina* (and a host of synonyms), this morphotype dominates *Cerion* faunas of the Turks and Caicos, while a *C.* (*Umbonis*) inhabits one island, and a long, slender, mottled taxon (*C. lewisi*) lives on a few islands of the northern Caicos. On Great Inagua, *C. columna* represents the white morphotype along exposed northern coasts, while two other taxa maintain a prominent presence—dark, ribby rosy-tipped *C. rubicundum* (and a host of synonyms), and a dwarf *C.* (*Umbonis*), now bearing two names, but ripe for synonymy as *C. rehderi.*

Thus, New Providence stands midway in a taxonomic revision of all Bahamian *Cerion.* The insights provided by *Cerion* on this little island can establish a general methodology serving as key to the revision.

This simple and sensible reordering provides satisfaction enough, but any proper systematic revision should also display its value by suggesting some evolutionary insights into the processes of change. Indeed, or so it seems to us, *Cerion* is providing hints for an unconventional hypothesis about form that might possess some general value. We are used to regarding natural similarities as either homologies passively inherited by shared descent, or analogies adaptively developed by different lineages subject to similar selective pressures. Yet a third or "intermediate" form of similarity, similar to what the classical literature called "parallelism" (as opposed to convergence), combines the historical constraint of homology with the immediate trigger of analogy. It also underscores the importance of development and its latent possibilities, the ancient, but often disregarded theme of evolution, now in the first stages of a welcome renaissance.

We find the same basic forms of *Cerion*—intricate character complexes, not just single features or bits of morphology—again and again, often in disjunct and geographically distant places. We have called these complexes "morphotypes" for want of a better term. The standard interpretation would view separated geographies of the morphotypes as an expression of homology, and develop biogeographic hypotheses of dispersal or extinc-

tion of geographically intermediate populations. Indeed, we have often drifted into this conventional language of description.

Nonetheless, if experience and history count for anything, we cannot dismiss as irrelevant the observation that both men who developed most intimate familiarity with *Cerion*—Paul Bartsch and C. J. Maynard—began with the conventional hypothesis of homology, and ended with a different interpretation. We have followed the same path in our work. In short, we believe that the complex suites of characters used to define morphotypes, despite their precision and intricacy, can arise again and again as independent responses (probably to basic adaptive requirements of different ecologies and habitats). Maynard and Bartsch developed different explanations for these separate evolutions of morphotypes, but they shared a common conclusion. For Maynard (1913, pp. 179–182), the late 19th century lawmaker, they expressed a principle of "individual" and "specific reincarnation" always latent in "dormant gemmules" inspired by Darwin's abandoned hypothesis of pangenesis. For Bartsch, they arose when hybridization broke down developmental canalization and "called to the surface submerged . . . *Cerion* strains . . . probably present in all members of the complex" (Bartsch, 1920). We may laugh at the outmoded theoretical apparatus used by Bartsch and Maynard to express their convictions, but note the underlying (and sound) conviction—that complex potential forms lie dormant and unexpressed in the developmental programs of all *Cerion*.

We have provided the first direct evidence for this unconventional concept in demonstrating, based on differences in genital anatomy (see work of Chung discussed in Gould and Woodruff, 1978), that ribby and mottled morphotypes of Little Bahama Bank are more similar to each other (in features of anatomy conventionally used as marks of homology by molluscan systematists) than to the corresponding mottled and ribby populations of Great Bahama Bank. (Correspondingly, mottled and ribby of Great Bahama Bank share a different genital anatomy.)

These separately developed similarities are not convergences—simple adaptations developed from a pliant and randomly varying ancestor as best solutions to a selective pressure. As a major conclusion of this monograph, we have shown that mottled and ribby are not simple transforms convertible one to the other as results of one trigger and its allometric consequences. The differences involve several independent covariance sets in the ontogeny of *Cerion*. The morphotypes, in short, represent preferred channels of developmental possibility—complex potentials latent in the developmental programs of (perhaps) all *Cerion*. In this sense, Maynard and Bartsch were correct in their central insight about latency. The morphotypes express a submerged and unexpressed homology brought forth by environmental triggers in similar ways—not only because they are optimal adaptations (if they are at all), but because history has impressed them into the architecture of *Cerion*'s development. In this sense, the morphotypes are a meeting ground of our ancient concepts of homology and analogy—homology to constrain and channel along paths of useful opportunity, analogy to evoke.

In studying the morphotypes of *Cerion*, we peer through a glass darkly at the interface of development and ecology that Van Valen (1973) recognized as the key to evolution, but with the wry observation that recent theory had paid little attention to either. This neglect, he noted, has been remedied for ecology, but development still languishes. The decade since Van Valen's pronouncement has witnessed a revival of interest in development and its themes of constraint, channeling, and directed opportunity. We who share a concern for development are not antiadaptationists (as often claimed). We wish only to record that organisms "push back" when selection impresses itself upon them, and that pathways of change often record the channels of inherited potential (and the interesting resultant combinations that produce real novelty in such phenomena as heterochrony), not only the creative power of selection itself.

Acknowledgments

A project of this range and complexity is more than usually dependent upon the aid

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VI. APPENDIX 1: FORMAL TAXONOMY OF NEW PROVIDENCE *CERION*

A. The Names of the Two Morphotypes

The name of the ribby morphotype is not in dispute. *Cerion glans,* the earliest name ever given to a New Providence *Cerion* (Küster, 1844—see full description of all taxonomic designations in Clench, 1957), clearly applies to ribby shells and has always been so used.

The mottled morphotype, however, presents several problems. The next name, *Pupa varius* (often neuterized within *Cerion* to *Cerion varium*) Bonnet, 1846, has since been applied by Maynard and others to samples, from Nassau and just east of Nassau, that lie in the coastal intermediate zone between ribby and mottled populations. Nonetheless, most of the Maynard samples using this name are more mottled than ribby and *C. varium* might therefore be an appropriate name for the mottled morphotype. However, Bonnet's figures show that he applied the name to a ribby shell clearly within *C. glans.* He also listed the type locality as Tasmania, and we cannot be sure that his specimen came from New Providence at all. In any case, since Bonnet applied the name to a ribby shell, Maynard's later use becomes irrelevant and *C. varium* is inappropriate as a name for the mottled taxon on New Providence.

The next available name is *Pupa gubernatoria* (again usually neuterized to *Cerion gubernatorium* for agreement with *Cerion*'s gender) Crosse, 1869. Although this name also presents a particular problem, we have determined that it is the appropriate name for the New Providence mottled cerions.

C. gubernatorium represents the extreme form within one of the four major geographic variants of mottled *Cerion* on New Providence (see fig. 5 and discussion on pp. 401–403). It can no longer be found alive on New Providence, but it did inhabit the extreme southeastern shore when Maynard made his collections. Its differences from more typical mottled shells include a generally whiter color, a larger aperture, and a more squat and triangular profile (see fig. 5). All these features are characteristics of another taxon, *Cerion agassizi.*

Cerion agassizi is a prominent fossil from the middle of three stratigraphic units on New Providence (see discussion of geology later in this section and Garrett and Gould, 1984). More importantly, *C. agassizi* continues to survive in three areas of Eleuthera (where it is known as *C. eleutherae*), hybridizing extensively in each of these three regions with both mottled and ribby populations (Gould and Woodruff, in prep.). It also survives on Cat Island under the name *C. huntingtoni* (also a hybrid with ribby populations)—though we found pure populations of *C. agassizi* type for the first time during our 1984

field season. *C. sladeni* on Andros may also be of *C. agassizi* type. The question then obviously arises: is *C. gubernatorium* really *C. agassizi* and not a mottled population, or is it a hybrid closer to *C. agassizi* than to mottled shells? In either case, *C. gubernatorium* might then not be the appropriate general name for mottled cerions on New Providence.

The large aperture and triangular profile should not, in themselves, be taken as conclusive evidence for the survival of *C. agassizi* on New Providence, for these features can arise within the spectrum of variation in mottled shells. One interesting specimen, from hybrid (but predominantly mottled) sample 569 (figs. 15 and 35), accentuates these features more than any *C. gubernatorium* shell we have seen. It is an injured specimen that grew an aperture "too early" in ontogeny, depositing it upon the midsection of the second barrel-shaped phase of growth (see p. 404). Unlike the hybrids projecting high on axis 3 (fig. 8, see p. 438), which also deposit their apertures early but are generally stunted in growth as well, this shell began growth at normal size, with all measures of early whorl sizes at or above the average. Therefore, it was still expanding in both width and height when its injury occurred and it subsequently (and precociously) laid down its aperture. This anomaly produced a squat shell, with few large whorls and a triangularly shaped outline—the very features that distinguish *C. gubernatorium* from other New Providence cerions.

Of course, as with phenocopies vs. genetically coded morphologies of identical effect (see Goldschmidt, 1940), the phenotypic production of features in one case (especially as a teratology) does not give us insight into the genetic basis of the same phenomenon in other circumstances—that is, in *C. gubernatorium*. (Though such a teratology does demonstrate that this complex of features is well within the range of potential production for standard mottled cerions—the key point in judging the appropriateness of the name *C. gubernatorium* as standard bearer for mottled cerions.)

More convincing is a demonstration that shells of *C. gubernatorium* form can appear within the normal spectrum of variation for a sample, and not as a teratologous effect. Sample 879 of *C. glans* (fig. 15) spans an unusually broad range of form and includes a shell (fig. 36) with large whorls, triangular outline, and squat appearance, well within the range of *C. gubernatorium* (and outside that of conventional *C. glans*. We also include in fig. 36 a shell from the other end of this sample's spectrum of variation). This other shell is thin and parallel-sided, far taller and with more whorls than conventional *C. glans* (see Gould, 1984b).

These two shells are opposite extremes of a determining pattern of covariance always

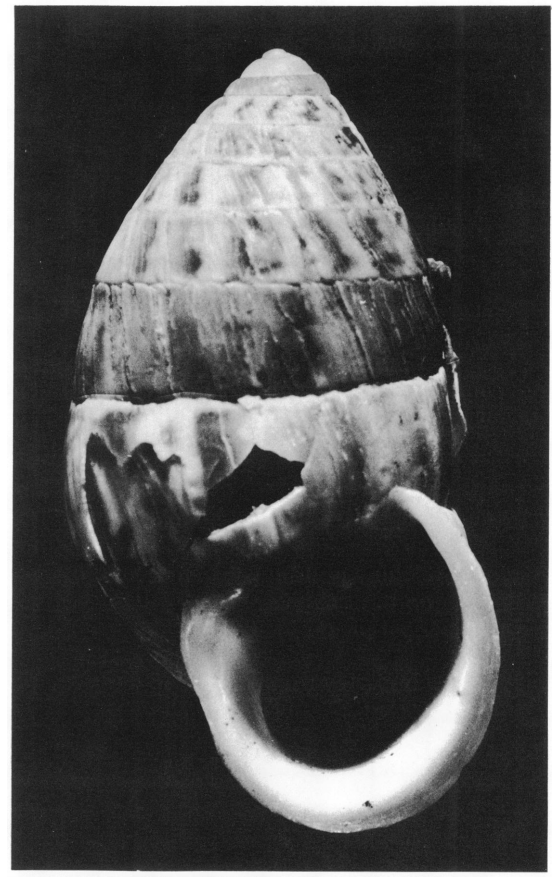

FIG. 35. An unusual specimen with large early whorls and an aperture deposited prematurely (perhaps as a response to injury) on a specimen still in the expanding phase of its spire. This pattern of growth (here a teratology) is similar to that observed normally in *C. gubernatorium*. A mottled shell from sample 569, 19.5 mm in height.

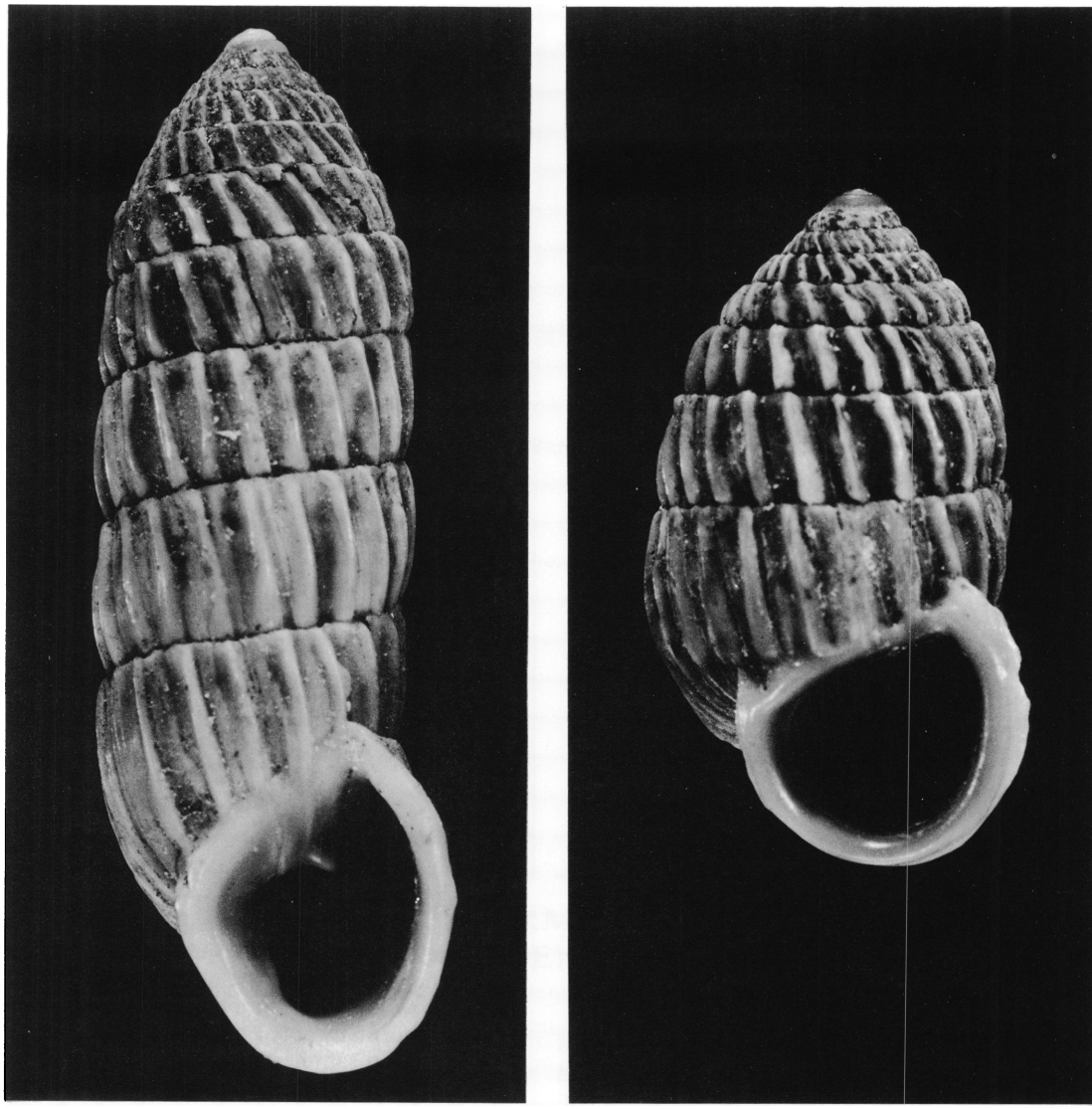

FIG. 36. Extremely tall (many whorled) and squat specimens from unusually variable ribby sample 879 (see fig. 15). The squat shell also mimics the standard growth pattern of *C. gubernatorium*. See figure 35. The tall shell is 33.0 mm in height.

detected in *Cerion* and responsible for much of its general variation in form (see discussion p. 420). When final size is constrained within a limited range, shells that begin with large whorls must end growth with few whorls and a relatively wide, squat shape because they grow their aperture upon a shell of few whorls, not far into the "barrel" phase of middle ontogeny that adds height but no width. [Alternatively, shells that begin with small whorls grow many whorls to reach the constrained size; they progress further into the barrel phase (a function of whorl number), and become relatively tall at their final size.]

This negative interaction between the whorl size and the whorl number–shell height covariance sets produces the *gubernatorium*-like shell of figure 36 as one end of its range. If this end of the range became fixed in a population through selection (or drift) for large early whorls, then this extreme form would become an average and would yield a sample

much like *C. gubernatorium*. The presence of *C. gubernatorium*-shaped shells both within mottled populations as a teratology and within ribby populations as a normal (though extreme) variant proves that this shape lies within the accomplishable range of taxa now on New Providence. Its existence as an average value in an extreme population does not indicate a new taxon and need not even imply hybridization with another taxon that exaggerates this form even more. Thus, *C. gubernatorium* could well be a mottled *Cerion* population at one end of its spectrum of normal variation.

However, two arguments strongly favor some *C. agassizi* influence. First, *C. gubernatorium* combines a shape veering toward *C. agassizi* with a tendency toward white shells also found in this species. Ribby or mottled shells of *C. gubernatorium* form usually retain the stronger, conventional color of their taxa. (But other mottled samples, with no approach to *C. agassizi* in shape, include several white shells—for example, Maynard's "*C. gracila*," see p. 477.) Secondly, as discussed in section IV, we have found alleles in living mottled samples geographically closest to the holotype population of *C. gubernatorium* (now extinct on New Providence) that occur in no other mottled population on this island, but are found in surviving *C. agassizi* stocks on Eleuthera. Thus, we have probably detected a "fossil" genetic influence of *C. agassizi* within mottled samples closest to *C. gubernatorium*.

Although the form of *C. gubernatorium* lies comfortably within the potential range of mottled cerions (though at its edge), good arguments for production of this uncommon shape through hybridization with a *C. agassizi* stock can be advanced. In any case, we regard *C. gubernatorium* as an appropriate name for mottled cerions. If it is merely a peculiar mottled sample then, of course, its use poses no problem. If it is a hybrid with a *C. agassizi* stock that survived until recently, then we may still use the name because *C. gubernatorium* clearly lies closer to conventional mottled cerions than to pure *C. agassizi*. *C. agassizi* is a very large, thick-shelled, triangularly shaped, pure white species (figs. 37, 38). *C. gubernatorium* is much smaller (within the mottled range), as thin-shelled as most mottled cerions, about intermediate in shape between both taxa, and mottled (albeit weakly) in most of its specimens. If the type sample of *C. gubernatorium* be a hybrid, the mix favors mottled influence, and its potential bastard character (given its status as first named) should not debar it as the proper standard bearer for mottled cerions.

We have studied Clench's (1957) list of all taxa to see if any potential Bahamian names for mottled cerions from other islands predate Crosse's *C. gubernatorium* and might therefore supplant it. Two candidates emerged, both from Crooked Island—*C. marmoratum* (Pfeiffer, 1847) and *C. martensi* (Weinland, 1862). Both look like mottled cerions. *C. martensi* (types seen) is finely ribbed and a bit fat for most New Providence mottled samples, but otherwise within the proper range. *C. marmoratum* (no types seen) seems clearly within the proper range and could well be taken for a set of New Providence samples. Since *C. martensi* and *C. marmoratum* are probably ripe for synonymy, the earlier name would be available as antedating *C. gubernatorium*. (*C. marmoratum* presents a problem, however, because Pfeiffer's description lists no locality and presents no figure; we do not know how it became associated with the Crooked Island samples. In any case, *C. martensi* would still be available, and it antedates *C. gubernatorium*.)

We will, however, use *C. gubernatorium* for New Providence mottled cerions because we have shown (see p. 469) that mottled shells of virtually indistinguishable form can arise independently again and again as one developmental possibility of *Cerion*'s general ontogeny. (The evidence involves anatomical similarities between ribby *and* mottled shells of Little Bahama Bank and the difference of both from ribby and mottled shells of Great Bahama Bank—see Chung, in press, and discussion on p. 398.) Therefore, when islands are widely separated by deep oceanic barriers (as are Great and Little Bahama Bank, and New Providence on Great Bahama Bank and Crooked Island well to the southeast), we should assume for now that shells of the same morphotype are independently derived, not homologous, and therefore not taxonomically appropriate for synonymy. If we later

find that the anatomy of New Providence mottled cerions cannot be distinguished from that of *C. marmoratum* on Crooked Island, we may have to revise the name, but probabilities for now seem against this resolution, and *C. gubernatorium* is the appropriate name for mottled New Providence cerions.

B. An Allocation of Maynard's Taxa (and a Few Others) for Living New Providence *Cerion*

We have located 71 names for living taxa on New Providence (the other 19 names, for fossil species, will be discussed in part C). All can be allocated without difficulty to the two taxa, *Cerion glans* (the ribby morphotype) and *Cerion gubernatorium* (the mottled morphotype). Several "species" are intermediate between the two morphotypes, but all come from the city of Nassau itself, the coastal area of known interaction between the taxa, though now devoid of living snails. Three species, ribby samples in the intermediate area (discussed on p. 476), are anomalous in their geographic distribution. All other "species" inhabit areas appropriate to their morphotype today and to the general principles of distribution for the morphotypes (see pp. 395–398). Our allocations are based on personal study of Maynard's (and other) samples in the superb collections of the Department of Mollusks, Museum of Comparative Zoology.

i. *Properly located "species" attributable to* Cerion glans

The following species should be synonymized within the ribby morphotype, *C. glans.* For each, we give locality and authorship (more details can be found in Clench, 1957). We present them in alphabetical order. For authorship, M. stands for Maynard, M. and C. for Maynard and Clapp. Unless indicated, we have personally studied both holotype and paratype material. Most species names have feminine endings because Maynard placed them in the genus *Strophia*:

1. *glans* Küster, 1844, p. 74. No locality given; no types seen.
2. *acceptoria* M., 1913, p. 185. Low Bay Cay, east of Rose Island.
3. *affinis* M., 1913, p. 184. Rose Island.
4. *agava* M., 1894, p. 152. Sisal fields west of Nassau. Clench (1957, p. 136) comments "is *C. coryi,*" but we do not know why he makes this attribution. *C. coryi* is the traditional name for *C. glans* from the extreme western end of the island, with a characteristic color pattern of white ribs on a solid dark background. *C. agava* exhibits the characteristic greyish-mottled color of its area.
5. *agava-neglecta* M., 1913, p. 192. Sisal fields west of Nassau.
6. *albata* M. and C., 1921, p. 145. Southern end of Rose Island. This is a *nomen nudum.* Maynard and Clapp list *albata* in their text but call the species *vagabunda* in their figures, prepared later. In the meantime, Maynard remembered that he had previously used *albata* (also in 1921) for a different form on Andros Island, and he renamed this population *vagabunda.*
7. *albea* M., 1894, p. 128. South side of Spruce Cay. Clench comments (1957, p. 136) "is *C. varium* Bonnet," but we disagree. *C. varium,* as discussed on p. 477 is usually used for intermediate populations from Nassau while *C. albea* seems to us clearly within the ribby range. Only paratype material seen.
8. *argentia* M., 1913, p. 191. Three Silver Cays. A large ribby form, a morphology found only on the off-lying cays.
9. *caerulea* M. and C., 1915, p. 181. Field north of Fort Charlotte.
10. *carlotta* M., 1894, p. 154. North side of hill, Fort Charlotte. Clench (1957, p. 140) comments "is *C. coryi.*" Again, and for the same reason discussed under *agava,* we disagree.
11. *cinerea* M., 1894, p. 119. Middle Bay, Hog Island (now Paradise Island). Clench (1957, p. 140) comments "is *C. varium,*" but we disagree for the same reason cited under *albea.*
12. *cinerea-varia* M., 1913, p. 185. East end of Hog Island (now Paradise Island). Maynard's name indicates (and we agree) that this sample is more confusing and intermediate in character than the more robust and more strongly ribbed *cinerea.* Only paratypes seen.
13. *coryi* M., 1894, p. 129. Extreme west end. The traditional name for distinctively colored western populations with their white ribs on a dark brown and solid background (see fig. 6, left).

14. *devereuxi* M. and C., 1915, p. 181. Devereux estate, west end of island. Although some specimens are more mottled than in pure *C. coryi,* all specimens have the white ribs so characteristic of *C. glans* at the west end of New Providence.

15. *hart-bennettii* M. and C., 1921, p. 146. Potter's Cay. This small cay lies between Hog (Paradise) Island and the mainland. Hog Island contains *C. glans* while the adjacent mainland harbors hybrid zone intermediates. Shells on Potter's Cay are quite small, almost dwarfed, an unusual status for cay forms of *C. glans.* But, though some shells show a mottled coloration, the apically pointed and later quadrate form is pure *C. glans.*

16. *hesternia* M. and C., 1915, p. 180. West end of Booby Rock. This small cay is located 16 miles northeast of New Providence in the chain of cays that joins New Providence with Eleuthera. We do not understand why Maynard thought he could distinguish this form from *C. sula.* Paratypes only seen.

17. *larga* M., 1913, p. 184. Rose Island, opposite Green Cay. A very large, straight-sided, long ribby form, characteristic of the off-lying northern cays.

18. *livida* M., 1924, p. 4. West Bay Street, opposite North Silver Cay.

19. *mobile* M. and C., 1921, p. 146. West end of Rose Island. A long thick-lipped form, rather weakly ribbed compared with most cay populations.

20. *morula* M. and C., 1915, p. 179. Spruce Cay, 4 miles east of Nassau.

21. *multa* M., 1913, p. 197. North portion of Fleming Cay about 20 miles northeast of New Providence. Smallish and whitish ribby shell of clear *C. glans* affinity. Clench (1957, p. 154) comments "is *C. exiguum.*" *C. exiguum* was described from the southern portion of Fleming Cay, but does not appear in our New Providence list because Clench (1957), whom we follow for our geographic designations, lists it with the Eleuthera species. We do not understand why he listed *multa* from the north portion of the cay with New Providence and another species from the southern portion with Eleuthera, though the cay itself lies midway between the islands. Both species, in any case, are within *C. glans.*

22. *mutata* M., 1894, p. 125. Northwest part of Long Cay (Athol Island). Clench (1957, p. 154) remarks "is *C. varium,*" but we disagree for the reasons cited under *albea. C. mutata* is lightly ribbed for a cay *Cerion,* but shows no other relation that we can discern with the intermediate shells called *C. varium.*

23. *neglecta* M., 1894, p. 150. One mile west of Fort Charlotte. Clench (1957, p. 154) remarks "is *C. coryi,*" but we disagree for the reason cited under *agava. C. neglecta* is a typical *C. glans* at the northeast part of its range—strongly ribbed and greyish-mottled in color.

24. *oberholseri* M., 1913, p. 193. Southwest Bay.

25. *obliterata,* M., 1913, p. 197. East Booby Rock, 16 miles northeast of New Providence. A *nomen nudum.* Maynard bestowed so many names on *Cerion* that he often used the same one twice, forgetting that he had previously designated another taxon similarly. In 1896, Maynard used *C. obliterata* for a Cuban population, and then applied it again in 1913 to this different Bahamian form. When he realized his error, he rechristened this population as *C. sula* in 1915.

26. *palidula* M. and C., 1921, p. 145. East end of Hog (now Paradise) Island.

27. *robusta* M., 1894, p. 121. North side of Hog (now Paradise) Island. A larger, pure ribby cay form. Clench (1957, p. 161) comments "is *C. varium,*" but we disagree for reasons cited under *albea.* Maynard described this population as a subspecies of *C. cinerea.*

28. *rosacea* M. and C., 1921, p. 139. West Silver Cay.

29. *salinaria* M., 1913, p. 184. Salt Cay. Strongest and largest of all cay *Cerion* populations.

30. *santesoni* M., 1921, p. 139. North shore west of Nassau.

31. *saxitina* M. and C., 1921, p. 145. Hog (now Paradise) Island east of Three Bays. A smallish shell, but fat, quadrate, and clearly within *C. glans.*

32. *sula* M. and C., 1915, p. 180. East Booby Rock. The new name for the *nomen nudum C. obliterata.*

33. *tracta* M., 1894, p. 123. East Point, Hog (now Paradise) Island. Again, Clench (1957, p. 165) would ally this sample with *C. varium,* but we disagree for reasons cited under *albea.* Like *C. cinerea-varia, tracta* seems

to be a name applied to Hog Island populations that are more colored and less robust than standard *C. cinerea.* The cerions of Hog Island are very variable in size, large on the north shore to quite small on the south shore (personal observation).

34. *ultima* M., 1913, p. 190. Southwest Cay.

35. *vagabunda* M. and C., 1925, p. 10. South end of Rose Island. Maynard's new name for the *nomen nudum C. albata.*

ii. *Anomalously located "species" attributable to* Cerion glans

The previous 35 names all apply to populations living within the modern range of *C. glans,* the ribby morphotype. Maynard described about 20 taxa from the city of Nassau itself, an area now devoid of living *Cerion.* Most of these names—see next category—apply to shells that are appropriately intermediate between the morphotypes since Nassau is the expected area of coastal interaction. Yet Maynard also named three species from this area that seem to fall within the range of *Cerion glans.* Of his 80 plus taxa, these are the only samples with anomalous geographic placement according to modern expectations. We do not know how ribby samples entered an area that should be the domain of intermediates. Maynard generally placed all the snails from any one spot into a single taxon—he did not separate *glans*-like from *gubernatorium*-like shells at a single place and erect sympatric taxa. Thus, we expect that these three names do apply to genuinely ribby populations that once lived in an intermediate area. Perhaps they represent incursions from off-lying cays to the north, which lie in the domain of *C. glans.*

36. *reincarnata* M. and C., 1921, p. 148. Ocean Hole east of Mackey Street, Nassau. Large, strongly ribbed shells, though a few are relatively narrow as in intermediate samples.

37. *sparsa* M., 1924, p. 3. St. James' Corner, East Nassau. Paratypes only seen. Only 20 living snails found, all large and ribby.

38. *territa* M. and C., 1921, p. 147. Methodist churchyard, two blocks west of Mackey Street, south of Shirley Street. Shells look much like *reincarnata* and lived just a few blocks away!

iii. *Intermediate "species" appropriately found in or just east of the city of Nassau*

Maynard named 13 taxa that we cannot "call" with respect to placement with *C. glans* or *C. gubernatorium.* All are appropriately placed geographically in or just east of Nassau, within a zone now devoid of snails, but predicted as the area of coastal transition between the two morphotypes.

39. *curtissii* M., 1894, p. 107. Cemetery between Waterloo and Nassau. Clench (1957, p. 142) comments "is *C. varium,*" and this time we agree, insofar as *C. varium,* though originally described for a ribby shell, has traditionally been used for populations in the Nassau intermediate zone. Shells are, typically, relatively narrow with an elongate and pointy apex and numerous fine ribs.

40. *extensa* M., 1924, p. 2. Baptist Chapel, East Nassau. Paratypes only seen.

41. *fincastlei* M. and C., 1921, p. 148. Fort Fincastle, West Nassau. This is the sample that plotted high on the third axis of hybrid influence (see p. 438).

42. *latonia* M. and C., 1921, p. 147. St. Paul's Quarry, West Shirley Street, Nassau (right downtown).

43. *mayoi* M. and C., 1921, p. 148. Field East of Mackey Street, downtown Nassau.

44. *migratoria* M. and C., 1921, p. 147. Methodist Sunday School grounds, Shirley Street, Nassau. Shells are quite ribby, some only finely so. Most shells have smoothly barreled shape of the mottled morphotype.

45. *nivea* M., 1894, p. 112. Cemetery between Waterloo and Nassau. Named as a subspecies of *C. curtissii* and described from the same locality. Applies to colorless shells.

46. *novita* M. and C., 1921, p. 148. West of Fort Montague, east of Nassau. Quite strongly but sparsely ribbed. Strongly mottled in color, with tendency to long and narrow shells, usually found in this intermediate zone.

47. *oscula* M. and C., 1921, p. 146. Old Thompson Place, Bay Street, downtown Nassau. Some specimens grow an aperture upon the truncated parallel-sided phase of mid-on-

togeny, an apparent marker of hybrid growth, see p. 438.

48. *rediviva* M., 1913, p. 187. West of St. Paul's Quarry.

49. *rubiginosa* M. and C., 1921, p. 147. Field east of Methodist Church, Shirley Street, Nassau.

50. *thorndikei* M., 1894, p. 116. Cemetery between Waterloo and Nassau. Small, relatively thin to barrel-shaped shells. Clench (1957, p. 165) comments "is *C. varium.*"

51. *varius* Bonnet, 1846, p. 71. Bonnet lists his type locality as Tasmania and depicts a shell apparently belonging to *C. glans.* We do not know how his name became traditionally associated with samples from the Nassau intermediate zone. Bonnet placed this species within the genus *Pupa,* hence his feminine ending. Applied to neuter *Cerion,* it is usually written *C. varium.*

iv. *Properly located "species" attributable to* Cerion gubernatorium

52. *gubernatoria* Crosse, 1869, p. 186. No types seen. Crosse lists his locality simply as New Providence, but his name has always been associated with the squat, thick-lipped, finely ribbed, whitish to lightly mottled samples that used to live at the southeast extremity of the island. Crosse placed this species within the genus *Pupa,* hence his feminine ending. Applied to neuter *Cerion,* it is usually rendered as *C. gubernatorium.*

53. *agrestina* M., 1894, p. 179. Six miles south of Nassau. A typical representative of the large, strongly mottled, ribless to very finely ribbed shells that inhabit the south coast south of the city of Nassau.

54. *castra* M. and C., 1921, p. 147. Field west of Williams Street. Holotype only seen. This single specimen seems closest to the skinny, ribby *C. gubernatorium* found east of Nassau. But we do not know the nature of its sample. Geography indicates that the total sample might record an intermediate population between the morphotypes.

55. *clara* M., 1924, p. 4. Church, East Bay Street to Fox Hill. Small shells, fairly ribby to smooth.

56. *degeneri* Clench, 1948, p. 50. Fleeming Point. A "smoke-stack" dwarf (see p. 416 and Gould, 1984b) of the western form of *C. gubernatorium,* with sharply marked mottling. Clench's locality note on the collecting label states "isolated 'island' in mangrove swamp," a standard environment for dwarfing in *Cerion.*

57. *delicata* M., 1913, p. 190. South Cay off Sound Point. Whitish, smooth shells.

58. *eratica* M. and C., 1921, p. 147. Fox Hill Village. Holotype only seen, but the fine-ribbed, relatively narrow form is entirely typical of coastal *C. gubernatorium* east of Nassau.

59. *fulminea* M. and C., 1915, p. 182. East of Fort Winton.

60. *gracila* M., 1924, p. 3. Soldiers Road, an interior locality 1½ miles from the south shore. Large, white to strongly mottled shells with an unusually obtuse apex, narrowing during the barrel phase of later ontogeny. Interestingly (though we don't know what it means, if anything), these are the same characters (large size and obtuse apex) found at the most interior locality of Little Bahama Bank's analog of the mottled morphotype, *C. bendalli* (locality 249, see Gould and Woodruff, 1978).

61. *macularia* M., 1913, p. 189. South shore, west side of first sound to 2 miles west to a salina.

62. *montana* M., 1924, p. 3. Sunnyside estate, East Bay Street. We did not see specimens of this taxon at all, but Maynard's description, in comparison with *C. fulminea* from the same region, indicates an even more strongly mottled shell, thinner and with fewer markings.

63. *phoenicia* M. and C., 1921, p. 149. Waterloo, East of Nassau.

64. *purpurea* M., 1913, p. 188. Creek Settlement and 1 mile east of East Point Light.

65. *repetita* M. and C., 1921, p. 149. Fields off Kemp's Road, East Nassau.

66. *rufimaculata* M., 1913, p. 189. South shore, west side of salina to Sound Point. Paratypes only seen. Large, finely ribbed southern form of *C. gubernatorium.* Large aperture and thick lip.

67. *rufula* M., 1924, p. 3. West side of Kemp's Road, St. James' Corner. Paratypes only seen. A variable population, finely ribbed to smooth.

68. *tenui* M. and C., 1915, p. 182. East

end. Very close to the traditional location of *C. gubernatorium* and clearly of the same general form (see our morphometric analysis, including this taxon).

69. *varia-nivia* M., 1913, p. 186. Eastern cemetery, Shirley Street to St. Paul's Quarry. In 1913, Maynard gave three compound names (numbers 69–71) to populations from east of Nassau that lie toward the mottled end of the intermediate coastal zone of transition between the two taxa.

70. *varia-purpurea* M., 1913, p. 188. Bay Street, east to Creek Settlement.

71. *varia-thorndikei* M., 1913, p. 186. Cemtery east of Nassau.

C. The Fossil *Cerion* of New Providence

The low, hilly topography of most Bahamian islands owes its characteristic form to a series of lithified calcium carbonate dunes (eolianite) of Pleistocene age. On most islands, a lack of exposure in cuts through the dunes precludes any geological resolution of their relatives ages, and no Bahamian island has been adequately mapped for terrestrial geology, despite voluminous attention paid by geologists to Bahamian marine environments (references in Garrett and Gould, 1984). However, the excellent road system of New Providence, which usually cuts paths through the dunes rather than running crude tracks over them as on most other Bahamian islands, provides sufficient exposure for good collections of fossils and a resolution of terrestrial geology. *Cerion* is quite common in fossil soil zones within these dunes, and can sometimes be found in the eolianite itself. We do not obtain an unbiased sample because the dunes form preferentially near rocky coasts and would, therefore, in terms of modern taxa, differentially preserve *C. glans* in preference to *C. gubernatorium,* the interior and calm-coastal form. In any case, we have made large and excellent collections of fossil *Cerion* from New Providence dunes, and the resulting information has been invaluable in permitting us to achieve the first resolution for terrestrial geology of any Bahamian island (Garrett and Gould, 1984).

Garrett and Gould have been able to divide the eolianite dunes of New Providence into three superposed units based on several criteria including distinctive *Cerion* faunas in each.

The first unit, including dunes from an episode of high sea level prior to the major 120,000 B.P. stand, crops out in a few independent hills and at the base of several dune sequences of the second unit (giving us direct superpositional information). These dunes invariably contain a previously undescribed species of *Cerion.* We will formally name it *Cerion clenchi* later in this section. Since younger dunes build out toward the coast from preexisting topography, dunes of this first unit tend to occur in the island's interior. The largest independent dune of the first unit forms the prominent hill south of Oakes Field Airport, south of the city of Nassau.

The second unit, dated to the extensive 120,000-year high stand by thorium decay in fossil corals collected from marine units correlative with the dunes (Neumann and Moore, 1975), forms the island's backbone, and includes the prominent coastal hill that runs, virtually unbroken, from East End Point to Lyford Cay ("The Hill" to residents of Nassau). *Cerion agassizi* found in eolianite caps upon some of the extensive southern marine units also dates most southern topography of New Providence Island to this unit. Two species of *Cerion* occur in dunes of this unit: the large, white, triangularly shaped *Cerion agassizi* Dall and the small dwarf *Cerion universum* Maynard, both previously named. Some localities contain just one or the other species, but several include both in the same strata, a rare case of apparent sympatry for *Cerion* species (though one locality, 183 at the western end of the island, may represent an episode of hybridization between them). Both *C. agassizi* and *C. universum* may be found in ribby or smooth state, but any local sample represents either one form or the other.

The third unit includes a few small and superficial coastal dunes of Holocene age, plastered upon the older topography. These invariably contain the modern taxon, *Cerion glans.* Maynard's collections indicate that several offlying cays contain Holocene strata, as we would expect from the principle that dunes build outward through time.

Figure 37 presents a geological range chart

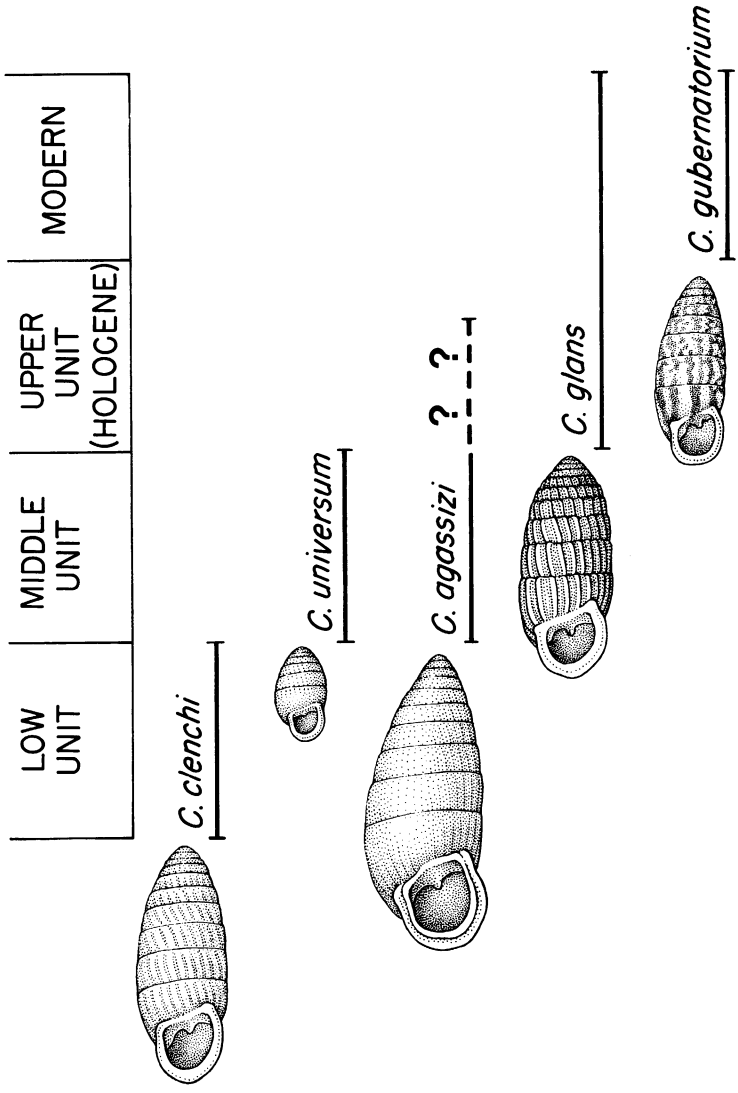

FIG. 37. Geological ranges and forms of all known *Cerion* taxa from New Providence.

for all valid taxa of New Providence *Cerion*, *C. clenchi* from the oldest unit, *C. agassizi* and *C. universum* from the middle unit, with a possible survival of *C. agassizi* into modern times, at least as a hybrid influence, *C. glans* from the upper unit to now, and *C. gubernatorium*, known only from modern evidence. (As mentioned above, we would not expect to find this interior and interior-coastal form in eolianite dunes, though fossil shells of mottled morphotype have occasionally been found on other islands, Great Exuma, for example.) Thus, we recognize five valid species for the Pleistocene and Recent history of New Providence, three fossil and two modern—and all with sensible and coherent stratigraphic distribution. We do not believe that any of these taxa can be linked in ancester–descendant relationships. Long periods of lowered sea level separate the phases of dune building, and we suspect that each new taxon represents a wave of migration to New

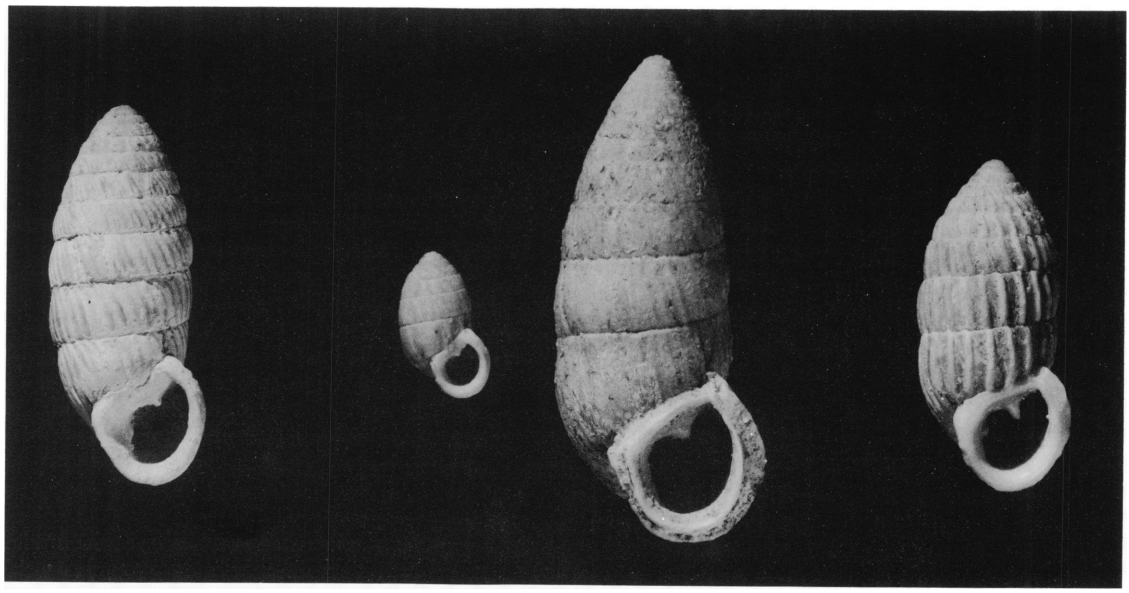

FIG. 38. Fossil *Cerion* of New Providence. **Left,** holotype of *C. clenchi* from the oldest unit (see text for details). **Middle pair,** left, dwarf, *C. universum* from locality 93 (dune ridge east of Nassau) and large *C. agassizi* from the main soil zone of the Queen's Staircase in Nassau. These species inhabit the prominent dunes of the middle stratigraphic unit. **Right,** *C. glans* from the most recent Holocene dunes at locality 850. The *C. agassizi* specimen is 38.2 mm in height.

Providence. The curious history and geographic distribution of the distinctive subgenus *Umbonis* (Clench and Aguayo, 1952; Woodruff and Gould, 1980) indicate that, even over short stretches of time, *Cerion* taxa can move extensively along sensible tracks from island to island.

We will first discuss the allocation of 19 available names for fossil taxa to four recognized species, *C. agassizi, C. universum, C. glans,* and *C. gubernatorium* (probably not true fossils). We will then describe the new and oldest taxon, *C. clenchi.* All fossil taxa are illustrated in figure 38.

A few of the allocations must be provisional. Maynard named several fossil taxa on the basis of single specimens (a strategy that, thankfully, he did not follow for living forms). Ribby shells of *C. agassizi* are not always easy to distinguish from large and strongly ribbed *Cerion glans.* Adequate samples invariably resolve the issue since, statistically, the triangular profile and thick lip of *C. agassizi* are distinctive. But an individual *C. glans* (see fig. 36) may display these characteristics as well. We will discuss these problems as they arise in the list.

v. *Fossil taxa attributable to* Cerion agassizi

72. *agassizi* Dall, 1894, p. 120. Quarry, top of Nassau ridge. Paratypes only seen. The valid name for this species was originally applied to ribless, large, thick-shelled and unambiguous specimens, presumably from the rich fossil soil zones of the Queen's Staircase in the city of Nassau.

73. *ajax* M., 1924, p. 5. In wall, village road, Shirley Street. Maynard supplied this name as a substitute for his *nomen nudum C. gigantea.* Holotype only seen, but the placement is unambiguous. This specimen represents an extreme in size, smoothness, and shell thickness.

74. *antiqua* M., 1913, p. 183. Athol Island. Holotype only seen. A difficult placement since the specimen is ribbed and smaller than standard *C. agassizi.*

75. *avita* M., 1913, p. 190. Silver Cay west

of Nassau Bar. A strongly ribbed sample. Most specimens taper outward from a triangular apex. The thick and extended aperture also indicates *C. agassizi.* The holotype itself could easily be placed in *C. glans,* however, and remains an ambiguous specimen.

76. *flacida* M. and C., 1921, p. 152. Rocks above the Queen's Staircase. The main zone of the Queen's Staircase itself contains the large, ribless, "classical" *C. agassizi.* Rocks of the same unit but stratigraphically higher contain a smaller and ribby version of *C. agassizi*—named *C. flacida* by Maynard.

77. *gigantea* M. and C., 1921. In wall, village road, Shirley Street, Nassau. This is a *nomen nudum.* Maynard originally designated these very large and thick-shelled classic *C. agassizi* as *C. gigantea* and later remembered that he had, in 1894, given the same name to different animals on Highburn Cay, Exuma. Thus, he renamed this sample *C. ajax.* (Hard to keep all your names straight when you christen so many!)

78. *leva* M. and C., 1921, p. 142. Rocks above the Queen's Staircase. Same locality and level, and same ribby form as *C. flacida.*

79. *muralia* M. and C., 1921, p. 151. In walls at East Nassau. The holotype specimen is somewhat ambiguous. It is smallish and strongly ribbed, but has the triangular outline and thickened lip of *C. agassizi.* Most of the paratypes clearly belong to *C. agassizi,* though adhering sediments indicate that they derive from a different fossil soil zone.

80. *rosea* M. and C., 1921, p. 151. Northeast end of Rose Island. Not seen, but Maynard describes a single specimen, smaller than typical *C. agassizi,* but without ribs and of *C. agassizi* shape, and therefore of fairly unambiguous placement. Since we were bothered by the ambiguous status of some species placed in this group, we were encouraged by Maynard's statement, made in his description of this taxon (and read by us after we had made our allocations), that an "*antiqua*" group includes *antiqua, muralia, agassizi, ajax* (*gigantea*), *leva,* and *flacida*—all species that we had independently synonymized within *C. agassizi.* Maynard, despite his taxonomic excesses, was a keen observer, and we welcome this independent overlap of judgment.

vi. *Fossil taxa attributable to* Cerion universum

81. *universa* M., 1913, p. 196. Green Cay, Rose Island. Paratypes are listed as "one mile north of the center of Rose Island." Maynard also records this species from Pimlico Cay, 30 miles to the east near Eleuthera. But these Pimlico shells are small *C. glans* rather than the distinctive dwarf so often found in the middle stratigraphic unit (with *C. agassizi*) of New Providence dunes. Clench also noted the superficial similarity and commented (1957, p. 166) "is *C. uniforme.*" But *C. uniforme* is a small, living *C. glans* from Little Pimlico, not the distinctive fossil *C. universum.* Maynard placed this taxon in the genus *Strophia,* hence his feminine ending. Since *Cerion* is neuter, we change it to *Cerion universum.*

82. *concina* M., 1924, p. 4. Crab holes at St. James' Corner, east of Nassau. A single small individual, presumably belonging to *C. universum.*

83. *pygmea* M., 1924, p. 4. Crab holes at St. James' Corner. Another single specimen from the same locality as *concina,* and belonging to the ribby phase of *C. universum.*

vii. *Fossil taxa attributable to* Cerion glans

84. *angustalabra* M. and C., 1921, p. 143. Fossil cliffs, west side of Rose Island opposite Green Cay. The surrounding carbonate looks very fresh and modern. As the etymology of the name suggests, the aperture is narrow and weakly developed, clearly not as in thick-lipped *C. agassizi.* Only the single holotype seen, but placement within *C. glans* seem unambiguous.

85. *crassalabra* M. and C., 1921, p. 143. Cliffs, east side of Rose Island. Another *glans*-type sample from Rose Island with a thickened lip (as in *C. agassizi,* but as in some *C. glans* as well), but with other characters clearly allied to *C. glans,* especially the relatively thin shell. The holotype, in particular, is pure *C. glans.*

86. *primigenia* M., 1913, p. 184. Beneath a sand cliff, east end of Salt Cay. Long shell typical of modern cay *C. glans* cerions. We doubt that this form is truly a fossil, though

shells may represent animals long dead in modern terms.

87. *prisca* M. and C., 1915, p. 182. East end of Salt Cay. No different, so far as we can tell, in either form (or locality) from *C. primigenia.* Shells are probably not fossils, but modern *C. glans* of cay type. Holotype, in particular, cannot be more than a semifossil.

88. *thompsoni* M. and C., 1915, p. 179. South shore, Hog (now Paradise) Island. This form, which we have also collected on Hog Island, is very difficult to call. It is a quite small, ribby shell (all characteristics of *C. glans*), but thick lipped and often relatively quite wide as in *C. agassizi.* Garrett and Gould were also unable to resolve the stratigraphic position of the Hog Island dunes—that is, we could not tell whether they represented phase 2 deposits (which would contain *C. agassizi*) or younger strata (which would harbor *C. glans*). Provisional attribution to *C. glans* seems the best course at present.

89. *vetusta* M., 1913, p. 191. Silver Cays of Nassau Bar and Pimlico Cays, Eleuthera. A large, thick-shelled ribby form of general *C. glans* characters, but again verging toward *C. agassizi* and hard to call. Some lots (not the holotype and paratype) from the wide geographic range of this pseudotaxon may represent *C. agassizi.* Clench (1957, p. 167) comments "is *C. inconsuetum*"—one of the many *C glans* synonyms from the cays between Nassau and Eleuthera.

viii. *A described fossil taxon (but probably not a true fossil) attributable to* Cerion gubernatorium

90. *minima* M., 1924, p. 4. St. James' Corner, East Nassau. Two shells found in crab holes, and almost surely not true fossils (though perhaps fairly long dead). The paratype is a clear *C. gubernatorium* of conventional thin shape and mottled color. The holotype, though small, has some *C. agassizi* characters in the triangular shape and thick lip. But several taxa within *C. gubernatorium* share these features as well.

ix. *Description of a new species of* Cerion *from the oldest geological strata of New Providence*

One dare not name a new species of *Cerion* without some apologies, especially after sinking 86 others in the previous section. But this taxon is so unambiguously distinct both in form and stratigraphic position that no other course seems possible.

This new species is found exclusively—it never occurs anywhere else and no other *Cerion* taxon occurs with it—in dunes of the oldest stratigraphic unit of New Providence (Garrett and Gould, 1984). It differs in general shape and ribbing, and usually in size, from all other New Providence *Cerion* and from members of the genus elsewhere in the Bahamas.

Cerion clenchi, new species
Figure 38

MORPHOLOGY: The general shape of *Cerion clenchi* easily distinguishes this taxon from all other New Providence cerions, for it has the smoothest and most continuous outline of any *Cerion* we have seen. From a fairly triangular apex (signifying a relatively high protoconch), it expands evenly and regularly in width, reaching a maximum two to three whorls from the aperture, unlike *C. glans,* which expands earlier near the top of the spire. From this maximum, width tapers gradually and evenly until deposition of the aperture. Thus, *Cerion clenchi* presents an almost perfect "barrel" shape in outline, with maximum width at about the spire's midpoint. By contrast, *C. agassizi,* with its triangular outline, tends to be widest near the aperture, while *C. glans* and *C. gubernatorium* are widest nearer the spire and not nearly so regular in expansion and contraction to and from the point of maximum width.

Ribbing also distinguishes *C. clenchi* from other New Providence *Cerion*s, for it displays remarkably even ribs of medium strength and constant intensity throughout growth. Most samples deposit about 40–45 ribs per whorl in the middle part of the spire, compared with 20–25 for *C. glans* and 50–60 for *C. gubernatorium.* Most *C. agassizi* samples are smooth or, if ribbed, deposit fewer, coarser ribs, as in *C. glans.* But number of ribs is not the most distinctive character of ornamentation in *C. clenchi.* Rather, the close and even spacing and constant strength of ribbing impart an unusual regularity and consistency of appearance to the shell. By contrast, ribs of *C. glans* and *C. agassizi* are always spaced

more irregularly, and exhibit more variability in strength. These two features combined—the remarkably smooth and barrel-shaped outline and the regularity of ribbing—give to *C. clenchi* a most unusual appearance of continuous and elegant form for a *Cerion.*

In size, most *C. clenchi* samples are intermediate between large *C. agassizi* and the smaller *C. glans* and *C. gubernatorium* of modern New Providence. They are higher (though not necessarily wider) than *C. glans* and *C. gubernatorium* and grow more whorls. The holotype (from locality 105 on the prominent ridge south of Oakes Field Airport) has 9⅛ postprotoconch whorls, and is 30.3 mm high and 11.8 mm wide (fig. 38)—an average specimen for this sample of average size (compare these values with means for *C. glans* and *C. gubernatorium* in table 9). A few samples, however, contain shells of smaller average size, and within the range of mean *C. glans* and *C. gubernatorium.*

The aperture of *C. clenchi* is strong, relatively thick lipped and recurved, but not otherwise distinctive. The umbilicus tends to be relatively narrow, as we would expect for a shell that reduces in width before depositing its aperture.

TEMPORAL DISTRIBUTION: Exclusively in fossil soils and eolianites of the oldest of three stratigraphic units of New Providence (Garrett and Gould, 1984). No other *Cerion* species occurs in these deposits, and *C. clenchi* has been found nowhere else on the island. We are pleased to report that *C. clenchi* also occurs in the stratigraphically oldest dunes of both Eleuthera and Cat Island, thus confirming this criterion and extending the species' range. On New Providence, *C. clenchi* has been collected at Blue Hills (type locality—the dune ridge south of Oakes Airfield), at the base of, and stratigraphically below, hills containing *C. agassizi* in their higher units at Prospect Ridge, Fort Charlotte, and the dune ridge running from the caves east of Gambier, through Gambier to Old Fort Point.

ETYMOLOGY: We are pleased to name this species to honor the memory of Bill Clench, the grand old man of *Cerion* studies. His careful, descriptive work on Bahamian *Cerion,* and his incomparable curation of the *Cerion* collection in the Department of Mollusks at the Museum of Comparative Zoology for 40 years, have formed the sine qua non of all our work. He did most of his field work during the 1930s under arduous conditions, spending days on the mailboats plying among islands, while we happily fly from place to place. It seems fitting that the oldest *Cerion* of New Providence, the basal form of the island, be named to honor the memory of this leader in *Cerion* studies.

A certain irony has not escaped our notice: we have labored so long in this work to convince readers that the modern *Cerion* fauna of New Providence contains but two slightly different, though clearly distinguished, taxa. The fossil record, with its three units, each with a distinctive *Cerion* fauna, is much richer, even though no evolutionary connections can be drawn among these faunas. The modern distinction of *C. glans* from *C. gubernatorium* almost becomes an epiphenomenon upon this richness, but a fascinating epiphenomenon in its own right—and the key, we think, to a taxonomic resolution of all modern *Cerion* in the Bahama Islands.

HOLOTYPE: Collection of fossil invertebrates M.C.Z. No. 29186.

VII. APPENDIX 2: LIST OF LOCALITIES AND REPRESENTATIVE SITE PHOTOS

Specimens described in this paper and additional samples collected in the course of this study may be found in the Museum of Comparative Zoology, Harvard University. The authors' collection sites are described below. Grid references are to the present standard Bahamas 1:25,000 map series (BLS Series 316 Edition 1: New Providence Sheet 1 and 2, 1975). The full coordinates for each locality are preceded by TC, 2 and 27; e.g., locality 102-TC 2673 27718. Localities described by three-digit coordinates are ±100 m; those described by four-digit coordinates are ±10 m. Localities 262–301 were sampled in April 1973; 568–589 in May 1977; 700–703 in May 1978; 786–790 in May 1978; 870–884 in May 1980; 102, 126 in January 1981; 937–944 in January 1982. More precise data are available from the authors.

LIST OF LOCALITIES

Loc.	Grid Ref.	General Area
102	673 718	old dune SE of Nassau, near St. Augustine Monastery
105	628 714	cut in Blue Hills on Ballou Hill Rd.
126	605 734	NW of Oakes Field Airfield, west of Nassau
183	444 696	cut through Hill on Western Rd., Lyford Cay Estates
262	689 728	junction Eastern Rd. and Fox Hill Rd., northeast coast
263	700 724	Eastern Rd., 1.3 km east of Fox Hill Rd., northeast coast
267	721 703	Culberts Point, east coast
268	680 687	south end Fox Hill Rd., southeast coast
269	714 698	north end of Yamacraw Beach, east coast
270	697 695	Yamacraw Hill Rd. near school, 1 km from southeast coast
271	668 685	landward mangrove edge near Long Point, southeast coast
273	635 679	East St. 0.4 km N of south coast
274	636 700	East St. near Airdale subdivision, 2.5 km N of south coast
275	637 715	East St. near Garden Hill Estates, 4 km N of south coast
276	628 674	South Beach Rd.
278	557 668	junction of Cow Pen and Millars Rds., 1.5 km N of south coast
279	551 658	mangrove edge Millars Sound, 0.5 km N of south coast
280	521 672	junction Coral Harbour and Adelaide Rds., 2 km N of south coast
281	511 649	Coral Harbour, south coast
283	442 673	coast of "Southwest Point," east of Clifton
284	430 685	highway near Clifton Bluff, 0.5 km from southwest coast
285	468 713	Western Rd. near Mt. Pleasant, 0.5 km from northwest coast
286	482 739	Northwest Point
287	5280 7465	West Bay St. at The Caves, 400 m E of Blake Rd., north coast
288	539 752	West Bay St. east of Rock Point, north coast
289	621 755	Fort Charlotte, north coast
290	614 757	West Bay St. at Bar Point, north coast
291	597 753	West Bay St. south of Browns Point, north coast
292	580 749	West Bay St. at Hobby Horse Race Course, north coast
294	536 751	West Bay St. at Rock Point, north coast
296	5252 7435	Blake Rd., 180 m S of West Bay St., north coast
297	5248 7441	Blake Rd., 20 m S of West Bay St., north coast
298	5248 7443	West Bay St., 10 m E of Blake Rd., north coast
299	5245 7448	West Bay St., at Cave Point, north coast
300	5255 7400	Blake Rd., 200 m S of 296, north coast
301	548 742	west end of Lake Cunningham, 1.2 km from north coast
568	5252 7435	Blake Rd., same as 296
569	5252 7425	west side of Blake Rd., opposite 568
570	5250 7435	Blake Rd., 100 m N of 568
571	5248 7443	West Bay St. at Blake Rd., same as 298
572	5245 7448	West Bay St. at Cave Point, same as 299
574	5270 7460	West Bay Rd., 200 m E of Blake Rd., north coast
575	5270 7450	50 m S of 574, north coast
576	5275 7455	50 m E of 574, above The Caves, north coast
577	5295 7475	West Bay St., 150 m E of The Caves, north coast
578	548 742	Lake Cunningham, same as 301
579	622 754	Fort Charlotte, 100 m from 289
580	597 753	Browns Point, same as 291
581	700 724	northeast coast, same as 263
582	680 687	southeast coast, same as 268
583	664 686	landward mangrove edge near Long Point, southeast coast
584	511 649	south coast, same as 281
585	446 673	South Ocean Beach Hotel golf course, southwest coast
586	468 713	northwest coast, same as 285
587	516 744	north coast on West Bay St., 1 km W of Blake Rd.

588	5205	7435	north coast on West Bay St., 300 m W of Blake Rd.
589	5235	7440	north coast on West Bay St., 100 m W of Blake Rd.
702	680	687	southeast coast, same as 268 and 582
786	664	758	Paradise Island, north of Flagler Inn
787	672	760	Paradise Island, Cabbage Beach
788	679	755	Paradise Island, southeast shore
790	714	698	Yamacraw Beach, same as 269
872	667	723	old dune SE of Nassau, Windsor subdivision, 2 km from NE coast
878	504	741	25′ coastal dune, Gambier, north coast
879	503	738	20 m W of 878, Gambier, north coast
884	4980	7350	track to sandpit, south of Gambier, 0.5 km S of north coast
937	5250	7435	Blake Rd., same as 570
938	4980	7350	Gambier sandpit, same as 884
939	4975	7355	Gambier sandpit, 50 m N on track
940	4975	7360	Gambier sandpit, 100 m N on track
941	4975	7347	Gambier sandpit, south side
942	4973	7347	Gambier sandpit, south side
943	499	732	end of track S of Gambier, 1 km S of northwest coast
944	502	736	near Gambier, 0.6 km S of northwest coast

REPRESENTATIVE SITE PHOTOS

FIG. A-1. **Top left.** *Cerion glans* estivating on trees at Cable Beach on the north coast of New Providence. Snails were found hanging up to 4 m above the ground. The two small masses of coiled feces mark other estivation sites. Locality 292; April 1973. **Top right.** *Cerion glans–C. gubernatorium* hybrids at the Blake Road contact. These *glans*-like snails were estivating on *Casuarina* trees on the north (coastal) side of the clearing. Locality 298; April 1973. **Bottom.** *Cerion gubernatorium* from southeast New Providence. Two of 12 pairs collected on the ground *in copula* at 1800 hr in an area that experienced a heavy rainstorm four hours earlier. Locality 268 (582); May 9, 1977.

FIG. A-2. **Top.** Aerial view of the clearing at Blake Road where hybrids between *Cerion glans* and *C. gubernatorium* were studied. This view looks southwest, and Blake Road is on the right (west), and West Bay Street is below (north) the clearing at the coast. See figures 15 and 30 for collecting site locations. April 1974. **Bottom.** *Cerion glans–C. gubernatorium* hybrids at the Blake Road contact. This large population from the center of the clearing contains adults with small shells and a high proportion of juveniles. Locality 296 (568); May 1977.

FIGURE A-1.

FIGURE A-2.

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