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B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 NOVEMBER 1977

NUMBER 445

**NATURAL HISTORY OF *CERION*. VII.
GEOGRAPHIC VARIATION OF *CERION* (MOLLUSCA:
PULMONATA) FROM THE EASTERN END OF ITS RANGE
(HISPANIOLA TO THE VIRGIN ISLANDS): COHERENT
PATTERNS AND TAXONOMIC SIMPLIFICATION.**

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ABSTRACT. The eastern cerions (Hispaniola to the Virgin Islands) have, following the conventional practice for this diverse genus, been split into seven allopatric taxa. We reject this traditional scheme on the basis of a multivariate morphometric analysis (19 characters, 20 shells per sample) of 23 samples from all major areas of *Cerion*'s eastern range. We first show that eastern cerions are distinct from other members of the genus by patterns of covariation among their morphometric measures. We then demonstrate by canonical analysis that populations of each island have a distinct morphology. Were there no coherent patterns among islands, current nomenclature might be supported. However, the first canonical axis (59 per cent of all information) for an analysis by islands arrays the populations in perfect geographic order — from egg-shaped, finely and copiously ribbed shells in the east, to more cylindrical, apically pointed shells with fewer, stronger ribs in the west. The morphological direction of this cline approaches common cerion forms further west (particularly on Cuba); unique morphologies are isolated at the eastern extreme of the range. In addition, a plot of Mahalanöbis vs. geographical distance shows a remarkably tight relationship ($r = 0.96$) between geographic and morphological distance. Therefore, we synonymize all living eastern cerions into the single taxon *C. striatellum* ("Férrusac" Guérin-Meneville), reserving *C. rude* (Pfeiffer) for the rather different St. Croix fossil.

I. INTRODUCTION

Cerion has attracted the attention of eminent naturalists ever since Linnaeus designated its type species in 1758. W. H. Dall (1905), H. A. Pilsbry (1902), P. Bartsch (1920), Ludwig Plate

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(1906, 1907), W. J. Clench (1957), and Ernst Mayr (1956, 1963) invested substantial segments of their careers trying to understand the protean diversity of this unusual genus containing more than 600 described species and subspecies. So far *Cerion* has stood firm against all efforts to find coherence in the geographic distribution of its exuberant morphological variation. Elegant, oversimplified stories have collapsed (Plate, 1906), while more circumspect evolutionists speak of "crazy-quilt" distributions and random transport by hurricanes (Mayr and Rosen, 1956). The burden of available names has generally precluded a search for order and simplicity in the areas of *Cerion's* greatest diversity — Cuba, the Bahamas, and the Cayman Islands. Yet order and simplicity demonstrably exist when we trade museum trays and lists of names for the mapping of recognizable elements and their interactions in the field (Gould and Woodruff, in press, and in preparation on Little Bahama Bank, New Providence, Great Exuma, and Long Island, Bahamas).

As another strategy, we might wage some preliminary skirmishes before attacking the central areas of Cuba and the Bahamas, since *Cerion* displays markedly less variation in three peripheral areas of its distribution. The isolated populations on Aruba, Bonaire, and Curaçao have received much attention (Baker, 1924; Hummelinck, 1940; de Vries, 1974; Gould, 1969). Geographic variation in the single species, *Cerion uva* (L.), reflects both isolation (each island has a characteristic, if subtly differentiated, morphology) and local habitat; patterns have been stable for at least 50 years (Baker, 1924; Gould, 1969). This coherence allows hope for sensible interpretations elsewhere. The second peripheral area is contiguous with central regions: the Florida Keys with their single species, *Cerion incanum* (Binney). The third peripheral area is larger, more diverse, also contiguous to major centers, and equally unstudied: the essentially linear array of islands running from Hispaniola through Mona Island and Puerto Rico, to Necker and Anegada in the Virgin Islands (Fig. 1). Here 11 names are available for a basic morphology that all students of *Cerion* have recognized as unique to this Eastern area (Pilsbry, 1902). These eastern cerions provide a superb opportunity for modern study; they represent a situation intermediate between the relative simplicity of *Cerion uva* in the Leeward Islands (where we cannot practice the

art of taxonomic rectification, since no one ever successfully split the single species) to the complexity of New Providence Island with its 82 named species.

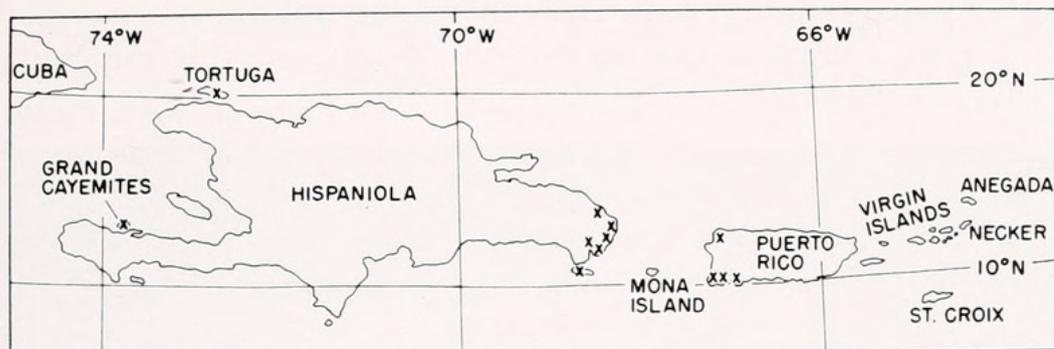


Fig. 1. The distribution of eastern cerions. Crosses indicate localities used in this study for the large islands only.

Moreover, the linear arrangement of islands leads to simple hypotheses of clinal distribution in our search for coherence, while their geographic range (980 km from Western Haiti to Anegada) permits a truly regional, not merely local, study.

II. SYSTEMATICS OF EASTERN CERIONS

Collectors of eastern cerions report that these snails share the habitat conventionally assigned to the genus (though our own observations of Bahamian forms demonstrate a much wider range); they live near the coast in limestone regions. Traditional wisdom proclaims that the animals are active on moist evenings, feeding predominantly on fungal mycelia in decaying vegetation; in drier conditions, they secrete an epiphragm and attach to plants, remaining immobile for long periods (several months in dry laboratory conditions). Beyond these basic facts of distribution, we know virtually nothing about the ecology and life history of any *Cerion*, including the eastern forms. (D. S. Woodruff has been studying two populations on Abaco Island, Bahamas during the past three and one-half years; our first adequate data will soon be available.)

Heretofore, the eastern cerions have been defined by conchological characters alone. These snails have a unique and consistent morphology (Fig. 2), rendered in most taxonomic descriptions by two characters:

1) An unusually obtuse apex, giving the entire shell a barrel or egg-shaped appearance (contrasting with the more common cylindrical form of species with pointed apices and rapid attainment in ontogeny of a definitive width; or the triangular form of species with pointed tops and continually increasing width).

2) Fine, abundant and regular ribs, evenly covering the entire surface of the shell.

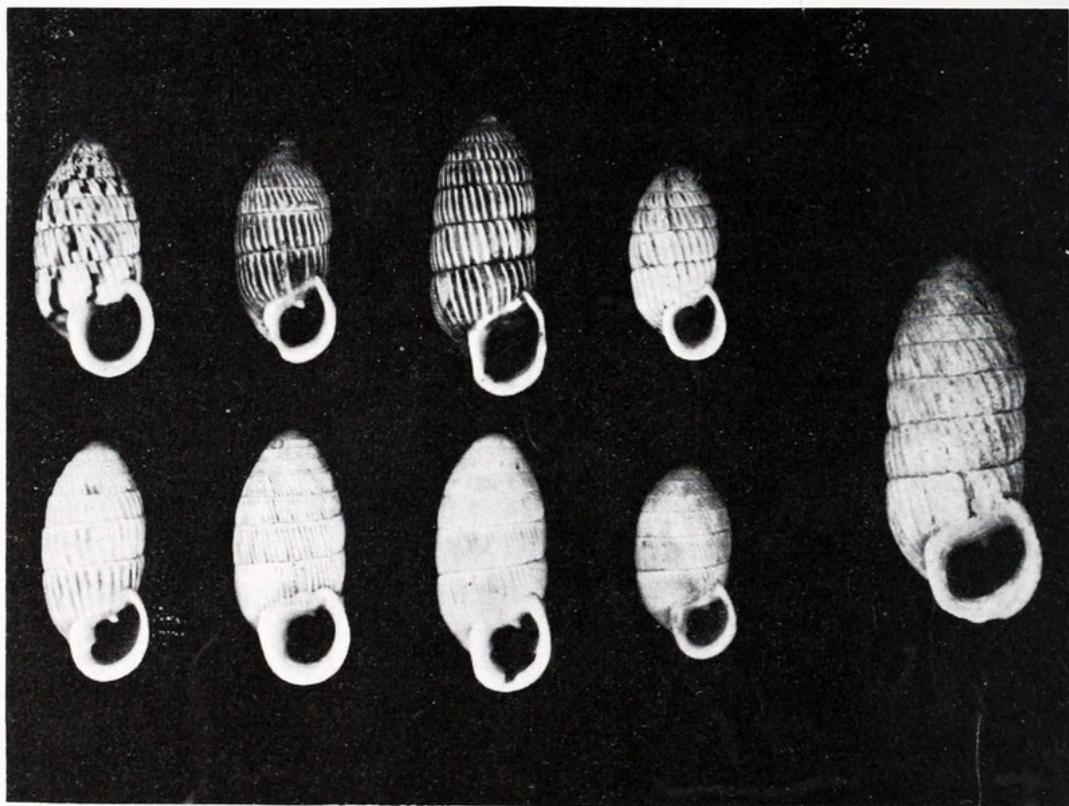


Fig. 2. Representative eastern cerions. Top row Hispaniola; second row, Mona Island (left) to Anegada (right). The large specimen at the extreme right is fossil *C. rude* from St. Croix. Note the major clinal trends from coarsely ribbed, apically pointed species in the west (Hispaniola) to copiously and finely ribbed, barrel-shaped forms in the east. Note also, the peculiarities of individual islands as described in the text — i.e., the nearly circular aperture of Puerto Rican specimens. Top row, starting from left: 1) holotype of "*C. tortuga*" (Acad. Nat. Sci. Phil. No. 146701 — locality 22 of this study); 2) holotype of "*C. yumaense ferruginum*" (M.C.Z. No. 76230); 3) paratype of "*C. yumaense*" (M.C.Z. No. 185945 — locality 18 of this study); 4) holotype of "*C. yumaense saona*" (Acad. Nat. Sci. Phil. No. 47200). Bottom row: 1) holotype of "*C. monaense*" from Mona Island (M.C.Z. No. 171019 — locality 12 of this study); Puerto Rican specimen of *C. striatellum* from locality 7; 3) from Necker Island, Virgin Islands, locality 1; 4) from Anegada, Virgin Islands, locality 2. *C. rude* is from lot No. 60564 Acad. Nat. Sci. Phil. *C. rude* specimen is 34.7 mm in height.

Pilsbry (1902), in the last comprehensive attempt to establish subgroups within *Cerion*, defined the eastern forms as one section among 11 in the subgenus *Strophioops*. He included two extraneous forms within the group:

1. *Cerion antonii* reported by Küster (1847) from the South American coast in Guyana. This species has been dutifully listed by all students of *Cerion*; comments about its anomalous geography abound. But we do not believe that it exists. The shells were described from a collector's cabinet, not from field observations. Mistaken labels in such cabinets once gave other cerions a proud range from India to China. We have no field records of living *Cerion* in South America. Moreover, Küster's shells have not been seen, so far as we can tell, by any subsequent author. All records of *C. antonii* depend upon the single poor figure published by Küster and reproduced by Pilsbry (1902) in making his assignment.

2. *C. caymanense* Pilsbry from Grand Cayman. According to Pilsbry (1902), *C. caymanense* differs from other members of the eastern group by its less obtuse apex and stouter ribs. But these are the very characters that should place it out of the group; for obtuse apices and fine ribs are the defining traits of eastern cerions. We do not understand why Pilsbry didn't include *C. caymanense* with the more similar Cuban group of *C. cyclostomum* (Küster).

The remaining taxa of Pilsbry's eastern group all reside in the geographic area of this study. Current nomenclature divides the eastern cerions according to accepted criteria within the genus: specific names have been awarded to allopatric populations of recognizable morphology. Moving from east to west among living species, cerions of the Virgin Islands (Anegada and Necker) and Puerto Rico belong to the same taxon, *Cerion striatellum* — although the phenetic distance between Puerto Rican and Virgin Island samples is greater than that between most other species in the group (see section VI). Some confusion has surrounded the appropriate name for this taxon. *Pupa striatella*, attributed to Férussac but never described by him, was defined by Guerin-Meneville in the 1829 *Regne Animal* of Cuvier (Mollusca, p. 16, plate 6, fig. 12). But Guerin-Meneville listed only "the Antilles" for a locality, and the task of deciding which cerions merited the designation fell to later authors. Küster (1847) and many others attributed Guerin-Meneville's name to the Puerto Rican specimens, but Poey

and others applied *C. striatellum* to a species from Cabo Cruz, Cuba and used Sowerby's (1875) *C. crassilabre* for Puerto Rico. Pilsbry (1902) followed Poey, but changed his mind later (1943), awarded a new name to the Cuban species (*C. cabocruzense* Pilsbry and de la Torre), and preserved the earlier *C. striatellum* for the Puerto Rican form. We follow Pilsbry's later opinion and consider *C. crassilabre* as a synonym of *C. striatellum*. This is a happy resolution since we will synonymize all living eastern cerions under this name, and since thick lips are decidedly not characteristic of many populations, whereas all are abundantly ribbed.

Moving westward from Puerto Rico, we next encounter *Cerion* on Mona Island. Clench (1951, p. 274) awarded the Mona Island population their own name (*C. monaense*) for their coarser costae and smaller size compared with Puerto Rican relatives.

Taxonomy of the Hispaniolan forms is more exuberant, but the defining criteria — size, ribbing, relative width, and shape of apex — have not been enlarged. Küster's name (1847), *Pupa striatella minor* from Haiti, is the earliest available, but all subsequent authors have ignored Küster's inadequate description, and we will not challenge this tradition. Pilsbry and Vanatta described the first full species in 1895 (p. 210): *Cerion yumaense* from the Dominican Republic — not so wide, more pointed apically, and more coarsely ribbed than the Puerto Rican populations. Maynard (1896) followed soon afterwards with *Strophia ferruginea* from Haiti, generally ranked as a subspecies of *C. yumaense* by later authors (e.g., by Pilsbry, 1902). Two additional subspecies accrued in later years: *C. yumaense sallei* (Pilsbry and Vanatta, 1896, p. 325; first attributed to *C. striatellum*, but later, and more appropriately, switched to *C. yumaense* by Pilsbry, 1902), and *C. yumaense saona* (Vanatta, 1923). Definitions involve little more than size: *sallei* is quite small, while *saona* is larger, with coarser costae than either *sallei* or the nominate subspecies. Finally, Pilsbry and Vanatta (1928) erected *Cerion tortuga* for more strongly colored, thicker lipped specimens from the nearby island of Tortuga.

In summary, living eastern cerions are generally ranked in seven taxa: *C. striatellum* ("Férussac" Guérin-Meneville) for Puerto Rico and the Virgin Islands, *C. monaense* Clench for Mona Island (between Puerto Rico and Hispaniola), and *C. yumaense* Pilsbry and Vanatta [with subspecies *C. y. yumaense*, *C. y. ferruginum* (May-

nard), *C. y. sallei* Pilsbry and Vanatta, and *C. y. saona* Vanatta] and *C. tortuga* Pilsbry and Vanatta for Hispaniola and associated islands. They are distinguished by little more than variation in the key characters used to define the entire eastern group: coarseness of ribbing, obtusity of the apex, and width of the shell.

A somewhat different fossil form has long been known from St. Croix — *Cerion rude* (Pfeiffer). [Pfeiffer's (1855) second taxon, *C. latilabre*, has been properly synonymized by all later authors as nothing more than a short specimen of *C. rude*.] *C. rude* is considerably larger than other eastern forms. It also departs from its nearest neighbors in the very characters distinguishing them from other *Cerion* — *C. rude* has a more pointed apex and fewer, coarser ribs than most living eastern *Cerion*. Yet its general appearance is still closer to the living eastern cerions than to any other group within the genus. Jacobson (1968) states that the fossil shells are buried in soils and often appear at the surface after preparation of the land for cultivation of cane. He attributes their extinction to cultivation and burning (itself, primarily, for cultivation), but we have no firmly documented record of St. Croix *Cerion* living in historic times.

III. MATERIALS, METHODS, AND INTENTIONS

Following the protocol of Gould, Woodruff, and Martin (1974), we made 19 measurements on 20 specimens (when available) for 23 samples of eastern cerions. All taxa but *C. yumaense sallei* are represented in our samples. Our measures attempt to capture the standard taxonomic characters of adult size, whorl sizes and numbers, size and shape of the aperture, shape of the spire, and patterns of ribbing. With the exception of one sample personally collected on Anegada (by C.P.), all shells come from museum collections (see Table 1). In all but two cases (Maynard's paratypes of *C. yumaense ferruginum*, and fossil *C. rude* — where we amalgamated whatever we could find from the collections of four museums to form an adequate sample), we restricted ourselves to large, recent samples collected *en masse* without obvious preference for large, unusual or attractive specimens. We gathered these data for a multivariate study of geographic variation in eastern cerions. We wished to address the following issues of distinction (at several levels) and coherence.

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Table 1. Samples used in this study.*

1.	Necker Island, 220391
2.	Anegada, 229017
3.	Anegada, collected C. Paull
4.	Anegada, 203778
5.	Near Tower Guanica Insular Forest, Puerto Rico, 212303
6.	Tamarindo Beach, Puerto Rico, 212302
7.	Guanica Insular Forest, Tower Road, Puerto Rico, 212293
8.	Cabo Rojo Colony No. 2, Puerto Rico, 212298
9.	Pt. Criollo, Guanica, Puerto Rico, 216702
10.	Cayo Maguey, La Paruera, 212292
11.	Cabo Rojo Colony No. 1, 212297
12.	Mona Island paratypes, 171020
13.	Mona Island, 190144
14.	Mona Island, Isabella Anchorage paratypes, 184052
15.	N.W. Saona Is., Hispaniola, 98829
16.	Lighthouse Cabo Engaño, Altagracia, Hispaniola, 251314
17.	North Shore Bahia de Yuma, Hispaniola, 251313
18.	Yuma River, paratypes, Hispaniola, 181967
19.	Romana Prov. 0.7 mi. east of Macao, Hispaniola, 250638
20.	N.E. Grande Cayemites Is., Hispaniola, 251161
21.	Juanilo, Altagracia, Hispaniola, 25132
22.	Tortuga Island ANSP 146701 and 146702
23.	St. Croix [composite sample: MCZ, Harvard; ANSP, AMNH (N.Y.) and Field Museum (Chicago)].

*Samples 1–21 (with the exception of sample 3 collected by C. Paull) are from the Dept. of Molluscs, Museum of Comparative Zoology (lot number indicated). Sample 22 is from the Academy of Natural Sciences, Philadelphia. Conventional identifications follow: samples 1–11, *C. striatellum*; 12–14, *C. monaense*; 15, *C. yumaense saona*; 16–19, and 21, *C. yumaense*; 20, *C. ferruginum*; 22, *C. tortuga*; 23, *C. rude*.

1. Distinction of eastern cerions from other sections of the genus: Are evident differences in morphology matched by patterns of covariation not encountered in other cerions?

2. Distinction among islands: Do the morphologies of eastern cerions record unambiguously the island of their occurrence? If so, we may identify isolation by geography as the primary correlate of morphological variation in these animals.

3. Distinction among samples: A long tradition in *Cerion* studies (amply affirmed by all our qualitative observations) holds that nearly every local population has developed its own recognizable morphology. (The older conchologists chose to recognize this pri-

mary observation by granting each form its own specific name.) Does such local differentiation exist among the eastern cerions?

4. Coherence: If cerions are distinct by island (issue 2 above), can we detect any interisland pattern (clinal or otherwise) that might suggest a common control correlated with geography (selection along climatic gradients, gene flow, or isolation by distance, for example)? The discovery of such a pattern will not permit us to distinguish among these potential explanations, for a pattern of coherence does not specify its cause, and museum specimens will not settle the issue. If we find no such pattern, current taxonomy granting autonomy to each major island must be maintained. If overall patterns exist, some consolidation may be in order, since hypotheses of direct interaction or similar responses of a single system to common factors would gain strong support from such patterns.

The subsequent definition of our measures follows Gould et al. (1974, pp. 522-524) except for 6 and 11. *Cerion* is a biometrician's delight for three reasons:

- 1) It preserves its entire ontogeny on fully exposed whorls.
- 2) It ceases growth with a definitive adult aperture. Thus we measure patterns of covariation among truly standardized adults.
- 3) We can specify comparable stages of ontogeny among specimens because the boundary between protoconch and accretionary shell provides an unambiguous, biological criterion for numbering whorls. Our characters can record both terminal sizes (for reason 2 above) and standardized traits of intermediate growth stages.

Our measures include:

1. Width of protoconch.
2. Width at the end of the fourth whorl.
3. Total number of whorls of the adult shell (with the termination of the protoconch taken as the 0th whorl).
4. Number of ribs on the fourth whorl.
5. Number of ribs on the sixth whorl.
6. Number of ribs in 40 micrometer units (2.22 mm) at the end of the first whorl.
7. Length of the adult shell, apex to lower apertural tip.
8. Maximum width of the adult shell.
9. Height of the protoconch.
10. Total height of the shell at the end of the fourth whorl.

11. Height from the end of whorl 4 to the end of whorl 6.
12. Width of the umbilicus.
13. Width of the apertural lip at its widest point (measured parallel to the plane of the aperture).
14. Thickness of the apertural lip at its thickest point (measured perpendicular to the plane of the aperture).
15. Height of the aperture.
16. Width of the aperture.
17. Protrusion of the aperture beyond the junction of aperture and terminal whorl (see fig. 5 of Gould et al., 1974) — a measure of both adult size and intensity in change of adult coiling.
18. Tilt of the aperture — a “pure” (ratio) measure of change in coiling to produce the adult aperture.
19. Weight of the shell.

IV. DISTINCTION OF EASTERN FORMS FROM OTHER CERIONS: PATTERNS OF COVARIATION

The distinction of eastern cerions on traditional criteria of static adult morphology has long been recognized (Pilsbry, 1902). We have been experimenting with the promising, but rarely-used criteria of “dynamic morphology,” or differences in the structure of covariation among variables (Gould, 1969; Gould et al., 1974). We have, so far, studied in detail only the *C. bendalli* Pilsbry and Vannatta group of Abaco cerions (Gould et al., 1974). We wish to report some interesting differences between these and the eastern cerions.

For seven samples of *C. bendalli* from Abaco we studied factor loadings on oblique axes (following varimax rotation) in separate R-mode analyses of each sample. We found that five axis solutions (recovering 70 to 75 per cent of the total information) yielded consistent and sensible interpretations with sufficient reduction of dimensions to form interesting clusters. We grouped each variable with the axis of its highest loading. In all seven samples, we obtained the same five groups, each defined by the unvarying association of two measures (see previous list of measures), and the more variable inclusion of others:

1. Adult size with whorl number (3) and shell height (7) as its focus.

2. Ribbing, with ribs on the fourth (4) and ribs on the sixth (5) whorl. This group is by far the most distinct among Abaco shells. It always occupies the second or third axis and never includes other measures (except, in two cases, the anomalous ratio measure of apertural tilt, where there can be no consistency, for measure 18 loads once positively, once negatively, and both times weakly).

3. Early whorl heights, with protoconch height (9) and height at the fourth whorl (10).

4. Later whorl sizes, with height of the middle whorls (11) and width at the fourth whorl (2).

5. Apertural lip, with lip width (13) and thickness (14).

We performed similar R-mode oblique factor analyses for 21 eastern samples with sufficient specimens, using the DUVAP program (with provision for missing data) as in Gould et al., 1974. Five axes encompass 71 to 90 per cent of all information in these samples. No new groupings appear with any consistency or frequency. Associations three through five occur with less regularity but similar composition (in 14, 10, and 11 samples respectively). We note two outstanding differences between eastern and Abaco cerions:

1. In Abaco samples, whorl number and shell height are invariably associated as the focus of a group representing adult size. We find this association in only 9 samples of eastern cerions. In 16 samples (including some of these 9), whorl number appears in *negative* association with one or more measures of shell size at standardized early whorls (measures 1, 2, 9, 10, and 11). Such a negative association appears in no sample of Abaco *C. bendalli*. We assume that this disparity reflects a difference in the control exerted via growth over final adult size. A shell may reach large size either by growing more whorls or by growing larger whorls. If final size is strictly controlled, we anticipate a negative interaction of whorl number and whorl size — as in the eastern cerions (and in our one sample of a second Abaconian species, Gould et al., 1974, p. 528). In a jigsaw puzzle with rigid borders, increase in the size of one piece must be matched by decreasing size in others. But if size is not so strictly controlled, and if all factors that increase it work in concert (or at least independently), then we expect no negative interaction — as in the seven samples of Abaconian *C. bendalli*. If the borders of the jigsaw puzzle can expand, then all pieces might increase together.

We do not know which of our characters best measures the elusive property of overall "size," but let us consider shell weight as a possible surrogate: For all nine samples of Abaconian *C. bendalli* (only seven were factor analyzed), the mean coefficient of variation for shell weight is 21.00 (range from 15.51 to 25.85). Twenty-one eastern samples yield a mean C.V. of 16.82 (range from 9.9 to 30.2, with only three samples above 20.0). This difference is significant at the 5 per cent level ($t = 2.33$ at 28 d.f.). Adult weight within samples is less variable for eastern than for Abaco cerions. Final size may be more strictly controlled in the eastern cerions.

C.V.'s for weight exhibit an interesting heterogeneity among eastern cerions. Hispaniolan samples have a mean C.V. of only 12.41 (range from 9.9 to 14.3), while all other samples average 19.02 (range from 15.0 to 30.2, no overlap with Hispaniola). The lower value for Hispaniola is correlated with stronger negative interaction between whorl number and whorl size. In factor analyses of all seven Hispaniolan samples, for example, whorl number (3) always sorts in negative association with shell height from the fourth through sixth whorls (11). We find this negative interaction in only 5 of the remaining 14 groups.

2. In Abaco *Cerion*, the ribbing measures always form a tight cluster, completely distinct from all other variables. Their association in eastern cerions is equally strong, but their group often includes other measures, almost invariably of adult size. In 18 of 21 samples, other measures group with rib numbers. Shell width (8) and umbilical width (12) join in four samples, width at the fourth whorl (2) and lip width (13) in three (but never lip thickness), apertural width (16) and apertural height (15) in two. This discovery supports our intuition that the "ribs" of eastern cerions — with their even spacing, complete coverage of the shell, and regularity of form — are not controlled in the same manner as the stronger, more irregular, and more widely spaced ribs of most other cerions. The more common pattern of other species may record environmental fluctuations and the pauses in growth that accommodate to them. Perhaps the ribbing in eastern cerions reflects a more regular, internal metabolic pattern correlated with general growth (and final size) of the animal.

We gain some support for this speculation from coefficients of variation. In Abaco *C. bendalli*, mean C.V. for ribs on the fourth whorl is 14.75 (range from 12.27 to 20.94), and for ribs on the sixth whorl, 14.83 (range from 11.93 to 17.00). Comparable figures for the same measures in eastern cerions are 8.57 (range from 3.67 to 13.59) and 8.68 (range from 3.42 to 11.27). This distinction cannot be explained by differences in absolute numbers of ribs, for the ranges are comparable in both groups (mean rib number varies from 33 to 80 in Abaco samples and from 25 to 78 in eastern samples).

V. DISTINCTIONS AMONG ISLANDS FOR EASTERN CERIONS

The traditional taxonomy of eastern cerions records primarily a distinction among islands (though we note with some surprise that no one ever split the Virgin Island from the Puerto Rican cerions). We have already reported an interesting difference in variability of shell weight between Hispaniola and other areas. Differences in variation and covariation should be pursued more vigorously (if only because they are so widely neglected); but for now we proceed along traditional lines and examine differences in form.

We performed a canonical analysis on all 23 samples (373 specimens) using D/DA, a program written by John Rhoads, Department of Anthropology, Yale University (see Gould et al., 1974). We treated each sample separately, without any prior identification of its island. Table 2 records the order of discriminating power for variables expressed in univariate ANOVA. We find a perfect correspondence between this order and the traditional criteria of taxonomic distinction: strength of ribbing (variables 4, 5), width of the shell (8, 13, and 16), and obtuseness of the apex (10). (Shells bearing obtuse apices are high at the end of the fourth whorl; whorls enlarge quickly and begin their rapid translation down the axis of coiling early in ontogeny. Triangular apices are lower at the end of the fourth whorl; the "triangle" records a slower increase in whorl size and a later incidence of the strong allometry that gives *Cerion* its characteristic shape by increasing height relative to width during post-juvenile to pre-adult growth.) The matrix of means for islands also records the rough order of discrimination. (Table 3 —

Table 2. Univariate ANOVA: discriminatory power of individual variables for all 23 samples F-ratios with 22 and 350 degrees of freedom. All are significant.

Name	Number	F-ratio
4th ribs	4	208.5
6th ribs	5	157.0
aperture width	16	102.9
width	8	102.9
4th height	10	101.8
lip width	13	67.2
aperture height	15	54.1
height	7	53.0
1st ribs	6	52.4
4-6th height	11	52.1
umbilicus	12	45.2
4th width	2	40.4
whorls	3	33.6
lip thickness	14	25.2
protrusion	17	22.7
protoconch width	1	19.5
protoconch height	9	18.8
tilt	18	3.3

not the mean of sample means, but the mean of ungrouped shells for each island.)

The first three canonical axes account for 87 per cent of the variance among sample means (45.1, 29.6 and 12.3 per cent respectively; the fourth axis falls below 5 per cent). Figure 3 displays the projection of sample centroids upon the first two axes. Samples clearly group by islands; all islands are widely separated with the exception of Hispaniola and Mona. The introduction of axis three completes the pattern; Mona and Hispaniola are now distinct (Fig. 4). We need only three components of variation to sort 23 samples unambiguously into five larger groups. The strength of determination by island is well recorded in the classification matrix: 309 of 373 specimens are correctly classified, and every misclassified specimen sorts with another sample of its island. If we redo the analysis with islands rather than samples, as groups, not a single specimen is misclassified. Each lies closest to the centroid of its own island. Geographic isolation seems to be the primary correlate of morphological variation in eastern cerions.

Table 3. Matrix of mean values for islands. Weight in grams. Linear measures in mm.

	Necker	Anegada	Puerto Rico	Mona	Hispaniola	St. Croix
Number of specimens	6	59	140	40	110	19
1. protoconch width	3.35	3.01	3.12	3.41	2.96	3.52
2. 4th whorl width	9.48	8.70	8.96	9.48	8.18	10.44
3. total whorls	7.58	6.95	7.26	6.42	6.80	8.41
4. 4th ribs	74.33	68.78	56.67	30.47	33.05	36.47
5. 6th ribs	60.50	53.78	51.09	26.02	29.70	34.68
6. 1st ribs	13.92	16.97	15.85	11.94	9.23	12.03
7. height	24.70	20.03	22.29	22.32	20.17	28.60
8. width	10.82	9.34	10.25	9.93	8.85	12.40
9. protoconch height	1.96	1.96	2.08	2.64	2.53	2.71
10. 4th height	6.63	6.48	4.10	5.32	4.51	4.61
11. 4th-6th height	7.56	7.01	5.19	7.34	5.72	4.69
12. umbilical width	4.19	4.05	4.16	4.33	3.83	6.23
13. lip width	.66	.48	1.02	1.02	.63	1.22
14. lip thickness	.99	.55	.92	1.08	.59	.87
15. aperture height	9.58	7.89	8.99	8.59	7.82	10.59
16. aperture width	7.63	6.59	8.10	7.23	6.40	9.87
17. protrusion	2.45	2.01	2.78	2.21	2.04	3.35
18. tilt	2.10	1.95	2.07	1.85	2.12	2.08
19. weight	1.20	.55	.77	.80	.56	

The matrix of factor pattern for the analysis by samples (Table 4) defines the uniqueness of each island and exhibits the morphological bases of separations in Figures 3 and 4. (The factor pattern matrix of standardized partial regression coefficients permits us to discern how the original measures vary together in distinguishing samples along the canonical axes.) We did not include shell weight (variable 19) in this analysis because we could not weigh the St. Croix fossils with their permineralized shells and filled interiors.

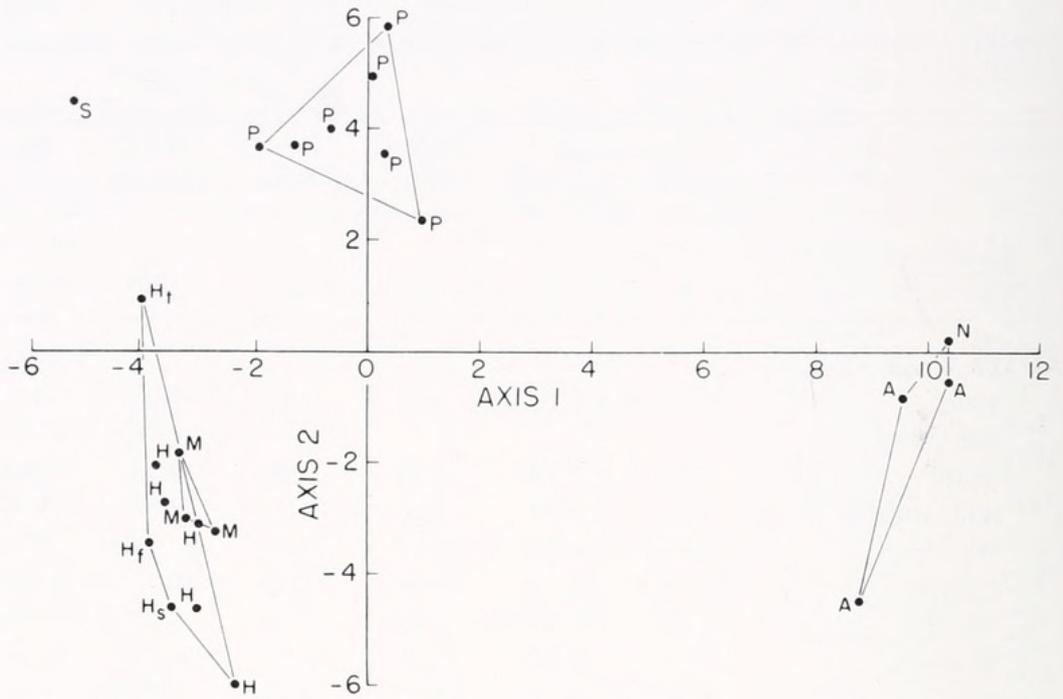


Fig. 3. Plots of centroids for all samples on first two axes of a canonical analysis (74.7 per cent of all information) to show distinction of islands and coherence within an island. Islands are circumscribed by minimum convex polygons. A—Anegada, N—Necker, P—Puerto Rico, M—Mona, S—St. Croix, and H—Hispaniola. H_f—*Cerion tortuga* (locality 23), H_f—*C. yumaense ferruginum* (locality 20), H_s—*C. yumaense saona* (locality 15).

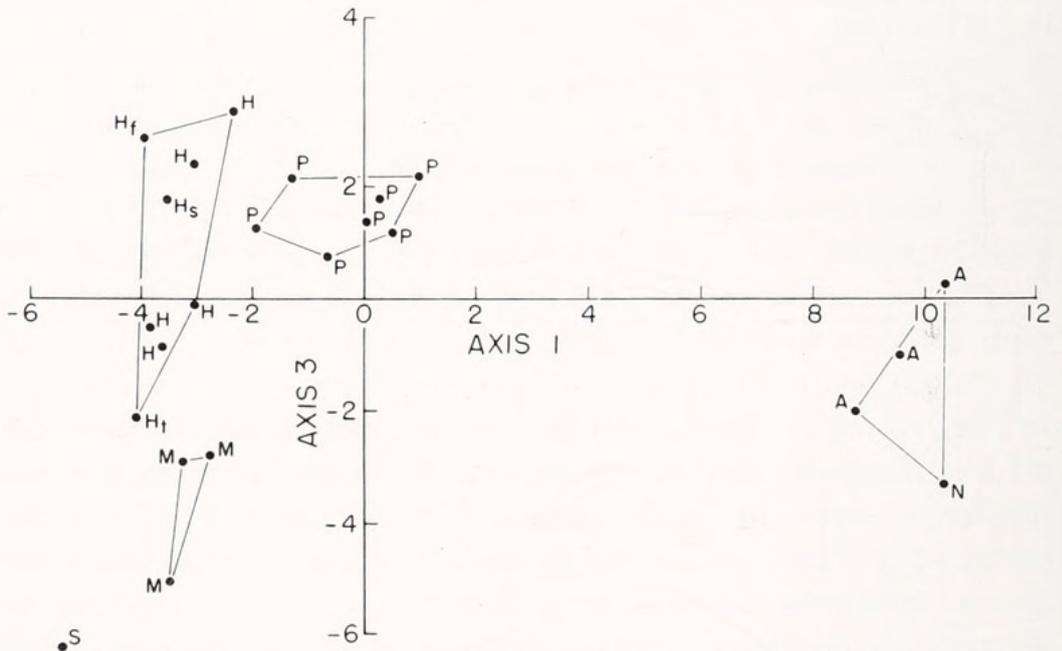


Fig. 4. Axis 1 vs. axis 3 for the same canonical analysis depicted in Figure 3. Code letters same as in Figure 3. Note that Mona and Hispaniola (overlapping in Fig. 3) are distinguished by the third axis.

Table 4. Factor pattern (structure of covariance) for original variables on first five canonical axes for all 23 samples.

No.	Name	1	2	3	4	5
1	protoconch width	-0.0430	0.1082	-0.3254	0.2116	-0.0632
2	4th width	-0.0239	0.2443	-0.4745	0.1357	-0.1085
3	whorls	-0.0047	0.2851	-0.1552	-0.4931	-0.1116
4	4th ribs	0.6196	0.4860	0.2486	-0.0291	-0.1228
5	6th ribs	0.4526	0.5397	0.2748	-0.0553	-0.2221
6	1st ribs	0.2427	0.3124	0.0459	0.2449	0.4016
7	height	-0.0968	0.3027	-0.4599	-0.1611	-0.4270
8	width	-0.0607	0.5167	-0.5713	-0.1082	-0.2853
9	protoconch height	-0.1590	-0.1151	-0.1863	-0.0339	-0.0540
10	4th height	0.3893	-0.2690	-0.4891	0.1371	0.1004
11	4-6th height	0.1832	-0.2792	-0.2773	0.4856	-0.2967
12	umbilicus	-0.0624	0.2278	-0.4813	-0.3020	0.2144
13	lip width	-0.2000	0.4035	-0.2115	0.3895	0.1607
14	lip thickness	-0.0726	0.2054	-0.1453	0.4387	-0.1463
15	aperture height	-0.0788	0.3720	-0.3568	-0.0482	-0.4348
16	aperture width	-0.1126	0.5692	-0.3769	-0.0336	-0.1512
17	protrusion	-0.0602	0.2759	-0.0882	-0.0274	-0.0037
18	tilt	-0.0180	0.0311	0.0417	-0.1369	-0.1053

The first axis separates Virgin Island samples from all others (see Figs. 3, 4). Its factor pattern records high values for measures of ribbing and whorl heights (10 and 11). Indeed, the Virgin Island samples exceed all others in their number of ribs and the obtuseness of their apices (Fig. 2). The negative loading of protoconch height (9) also reflects the obtuse apex of Virgin Island cerions (see mean values in Table 3). High protoconchs are followed by slowly expanding whorls that join the embryonic shell to produce a pointed apex with modest whorl heights; low protoconchs precede rapid expansion (high values of 10-11) and build more obtuse apices.

The second axis separates Puerto Rican samples (positive projections) from Mona Island and Hispaniola (negative projections). The factor pattern contains high positive loadings for two groups of variables: measures of ribbing (4 and 5) and shell widths, particularly aperture width (8 and 16). Whorl heights (10 and 11) load negatively. The cerions of Puerto Rico can be distinguished visually by their more circular apertures; this feature translates to high values for aperture width in our quantitative analysis. The St. Croix specimens (which also project strongly and positively on

axis two) are wide as a simple function of their large size. The ribbing measures set the major contrast between Puerto Rican samples and Mona and Hispaniolan samples. Puerto Rican cerions are abundantly ribbed (though not so abundantly as Virgin Island samples), while Mona and Hispaniolan cerions have the fewest (though strongest) ribs among eastern cerions. Puerto Rican specimens also have fairly triangular apices. This feature translates as low whorl height (10 and 11) in our measures; the negative loading of measures 10 and 11 assures the high positive projection of Puerto Rican samples on the second axis.

The third axis separates Mona and Hispaniola to complete the distinction among islands. Mona and Hispaniolan samples fell together with negative projections on the first two axes for essentially the same reason — their small number of ribs. Several measures of size — particularly of widths (2, 8, 12, and 16 — load strongly and negatively upon the third axis. Hispaniolan shells are small and especially narrow (note low mean values of 2 and 8 in Table 3); they project positively upon an axis with negative loadings for these measures. Mona samples are large and wide; since measures for size and width have negative loadings, these samples project negatively upon the axis.

Subsequent axes continue the patterns of distinction by island. The fourth axis, for example, separates Mona, having high projections, from St. Croix, having low projections. Highest loadings are for height from whorl 4 through 6 (positive) and number of whorls (negative). St. Croix specimens with their maximal number of whorls and minimal fourth to sixth whorl heights project negatively. Mona samples with their distinctively low number of whorls project positively. The fifth axis separates Virgin Island samples into their two areas of Necker and Anegada. The Necker Island sample projects strongly and negatively upon an axis with positive loadings for its low number of ribs on the first whorl (relative to Anegada), and high negative loadings for various measures of shell size.

VI. DISTINCTION AMONG SAMPLES

A persistent tradition of *Cerion* studies holds that virtually every local population bears its own distinctive morphology. This remarkable phenomenon has inspired the burden of an exuberant

specific nomenclature for these animals. Nothing we have seen in several years of study contradicts this conventional observation. We therefore predicted that samples within islands should be distinct in separate canonical analyses for each island. Our results confirm this prediction with great accuracy. The classification matrix for four Virgin Island samples correctly assigns 63 of 65 specimens to their correct sample (96.9 per cent). Only 3 of 40 specimens from Mona Island lie closest to the centroid of a sample not their own (92.5 per cent are correctly classified). Of specimens from Hispaniola, 101 of 110 are correctly allocated among eight samples (91.8 per cent). Only Puerto Rico falls below 90 per cent success — 116 of 139 specimens in seven samples (83.5 per cent).

We have, in summary, established a hierarchy of distinction among the eastern cerions. Their basic design is strikingly different — both in form and in pattern of covariance — from other cerions. Islands are distinct. Samples within islands can also be separated with little overlap.

VII. A UNIFYING THEME AND A TAXONOMIC PROPOSAL

The distinction of islands does not preclude the existence of pattern among them. We concluded that geographic separation serves as the primary correlate of morphological distinction among the eastern cerions. But does the degree of morphological separation reflect geographic distance? If so, we might expect a clinal distribution of morphology, since the islands form an essentially linear array. If we find no coherent pattern, taxonomic distinction by island should be maintained (with, God forbid, a new taxon for the Virgin Islands).

The output of our canonical analysis for islands includes a matrix of Mahalanobis distances (D^2) — a measure of separation between centroids with adjustments for variance and covariance (Table 5). Each entry is a measure of morphological distinctness (based on all variables) between shells of two islands. If we plot D^2 (see Sneath and Sokal, 1973, pp. 127, 128) against geographic separation (defined, for any island pair, as the distance between our two closest sample localities), we obtain a remarkably tight and linear relationship ($r = .96$). This calculation (Fig. 5) excludes the St. Croix fossils as representatives of another time with no expected relationship to current trends. When we plot the St. Croix

Table 5. Matrix of Mahalanobis distances (D^2) for analysis using all specimens grouped by islands.

	N	A	P	M	H	S
Necker	0					
Anegada	18.87	0				
Puerto Rico	125.33	102.90	0			
Mona	155.33	134.73	54.66	0		
Hispaniola	164.32	131.32	38.00	31.23	0	
St. Croix	214.23	187.83	65.86	65.29	57.11	0

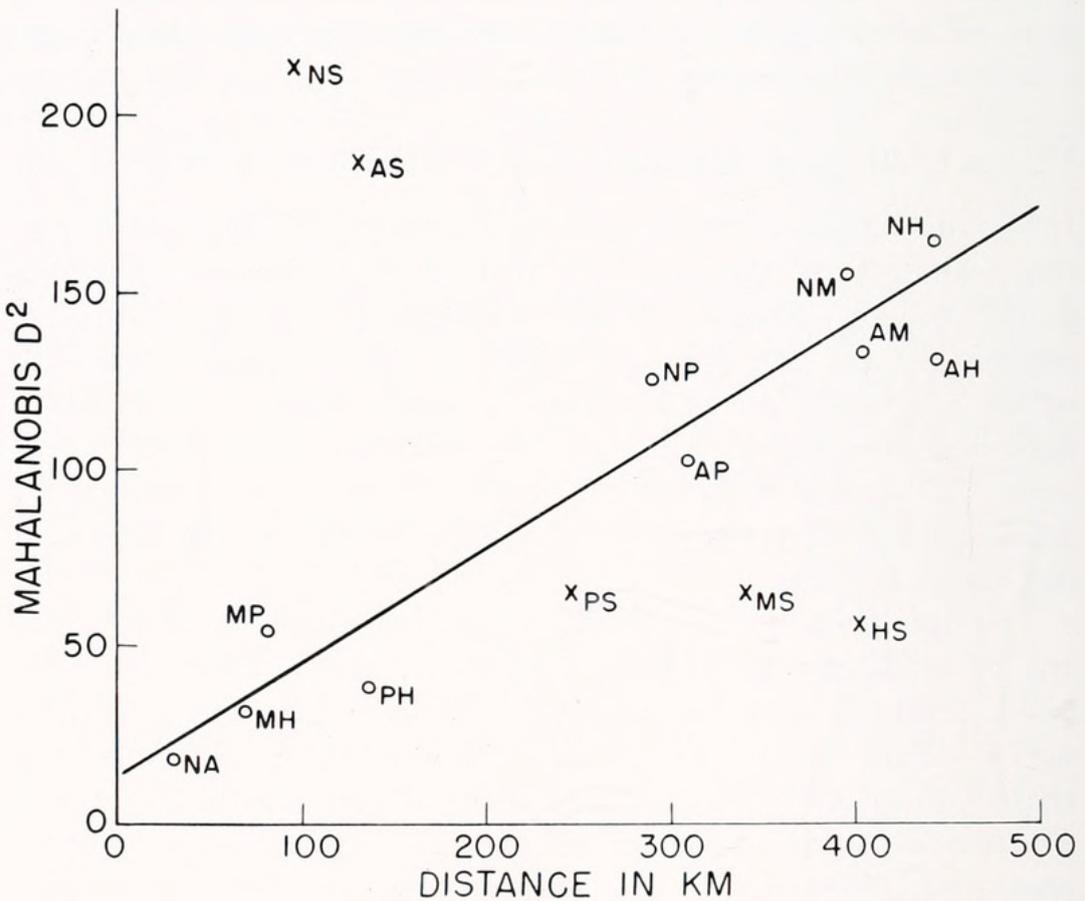


Fig. 5. Mahalanobis distance (morphological) vs. geographic separation for eastern cerions. Note the tight correlation and the departure of St. Croix fossils from the trend. A—Anegada, N—Necker, P—Puerto Rico, M—Mona, H—Hispaniola, and S—St. Croix.



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Gould, Stephen Jay. and Paull, C. 1977. "Natural history of Cerion. VII. geographic variation of Cerion (Mollusca: Pulmonata) from the eastern end of its range (Hispaniola to the Virgin Islands): coherent patterns and taxonomic simplification." *Breviora* 445, 1–24.

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