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a Multivariate Analysis of Microgastropod Diversity**

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Land Snail Communities and Pleistocene Climates in Bermuda: a Multivariate Analysis of Microgastropod Diversity

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INTRODUCTION

To students of community evolution, Scylla and Charybdis are the opposite perils of theoretical transcendence and empirical inundation. The first produces works of elegance, rigor, consistency and no relation to the world as we find it; the second buries theory in an impenetrable swamp of undigested data. These perils arise from a single source: the immense complexity of this most stubbornly multivariate of all evolutionary problems. We try to abstract and simplify, often overindulging both pursuits, or we attack head on, measure everything and understand nothing.

The obvious golden mean is an ecological situation of unusual simplicity, a natural experiment on causal parameters that can be comprehended because they are limited. It is neither by accident, nor by cynical engineering, born of a propensity for palm trees, that small islands occupy such a central role in our evolutionary literature, and that controlled experiments on tiny islets (Wilson and Simberloff, 1969) have been among the most successful.

BERMUDA AND ITS FAUNA

In a series of papers on its outstanding, endemic land snail *Poecilozonites* (Gould, 1966; 1968; 1969), I argued that Bermuda provides the simplicity required for natural experiments in paleoecology. There are three reasons for this: its isolation, the limitation of its record in space and time, and the relative simplicity of its geologic column. Bermuda, separated from the nearest land by more than 600 miles of ocean, is among the world's most isolated islands. Its native fauna is depauperate and disharmonious, an obvious result of rare transport from the West Indies and North America (Verrill, 1902). Among ground-dwelling vertebrates, only the scincoid lizard *Eumeces longirostris* gained entry and the record of animal macrofossils is virtually confined to land snails, bird bones and infrequent remains of land crabs. Bermuda's 5 main islands and many islets total just over 19 square miles, although ten times this area might have been awash during the lowest sea levels of interglacial times (Sayles, 1931). The oldest rocks now exposed date either from the early or middle Pleistocene. The volcanic foundation has recently been dated as Oligocene-Miocene (F. T. Mackenzie, personal communication).

No other Pleistocene rock suite in the western Atlantic has received such close scrutiny. Classic papers include those of Agassiz (1894), Verrill (1905), and Sayles (1931); recent articles on general geology have been written by

TABLE 1. STRATIGRAPHIC COLUMN OF BERMUDA.

Formation	Description	Interpretation
Recent Southampton	poorly developed brownish soil or crust complex of eolianites and discontinuous unindurated zones	interglacial
St. George's	red paleosol of island-wide extent	glacial
Spencer's Point Pembroke	intertidal marine, beach and dune facies extensive eolianites and discontinuous unindurated zones	
Harrington	fairly continuous unindurated layer with shallow water marine and beach facies	interglacial
Devonshire	intertidal marine and poorly developed dune facies	
Shore Hills	well developed red paleosol of island-wide extent	glacial
Belmont	complex shallow water marine, beach, and dune facies	interglacial
Walsingham	a reddened surface rarely seen in the Walsingham district highly altered eolianites	?glacial interglacial

Bretz (1960) and Land, Mackenzie and Gould (1967). The column is an alternating sequence of glacial red soils and interglacial facies mosaics of shallow marine, intertidal and eolian carbonates. Sea level is the controlling factor or independent variable (Land, Mackenzie and Gould, 1967, p. 1005). The carbonate dunes are coastal in position; they are cemented rapidly and do not migrate very far inland. In both glacial and interglacial times, dunes accumulated at the island's periphery and red soils formed in the interior as weathering products of older carbonates, augmented considerably by airborne continental detritus and phosphate leached from guano. But the dunes of glacial times are now submerged; all of modern Bermuda represents the interior of glacial greater Bermuda and only its red soils remain. In addition, Bermuda may have been so restricted during the highest interglacial sea stands, that it became, so to speak, "all periphery" and amassed dunes over its entire area. The Spencer's Point Sea, for example (Table 1), stood more than 60 feet above the present level. Thus the alternating sequence of red soils and carbonates in any one outcrop reflects the oscillating sea levels that record the advance and retreat of continental glaciers.

There exists a scattered, sporadic and inconsistent literature on the influence of environmental factors upon the form and diversity of land snails. Taylor (1965) would grant a dominant role to temperature, Geyer (1922) to moisture. Rensch (1932; 1937) and I (Gould, 1968; 1969) have been impressed by the importance of calcium availability. In terms of these factors,

the glacial red soils represent times of decreased temperature and increased moisture (Gould, 1969). In addition, while the CaCO_3 content of interglacial sediments is obviously near 100%, that of red soils has been recorded at less than 2% for some localities (Ruhe, Cady and Gomez, 1961). Since land snails build shells of lime extracted from their substrate, this distinction may be crucial for many species.

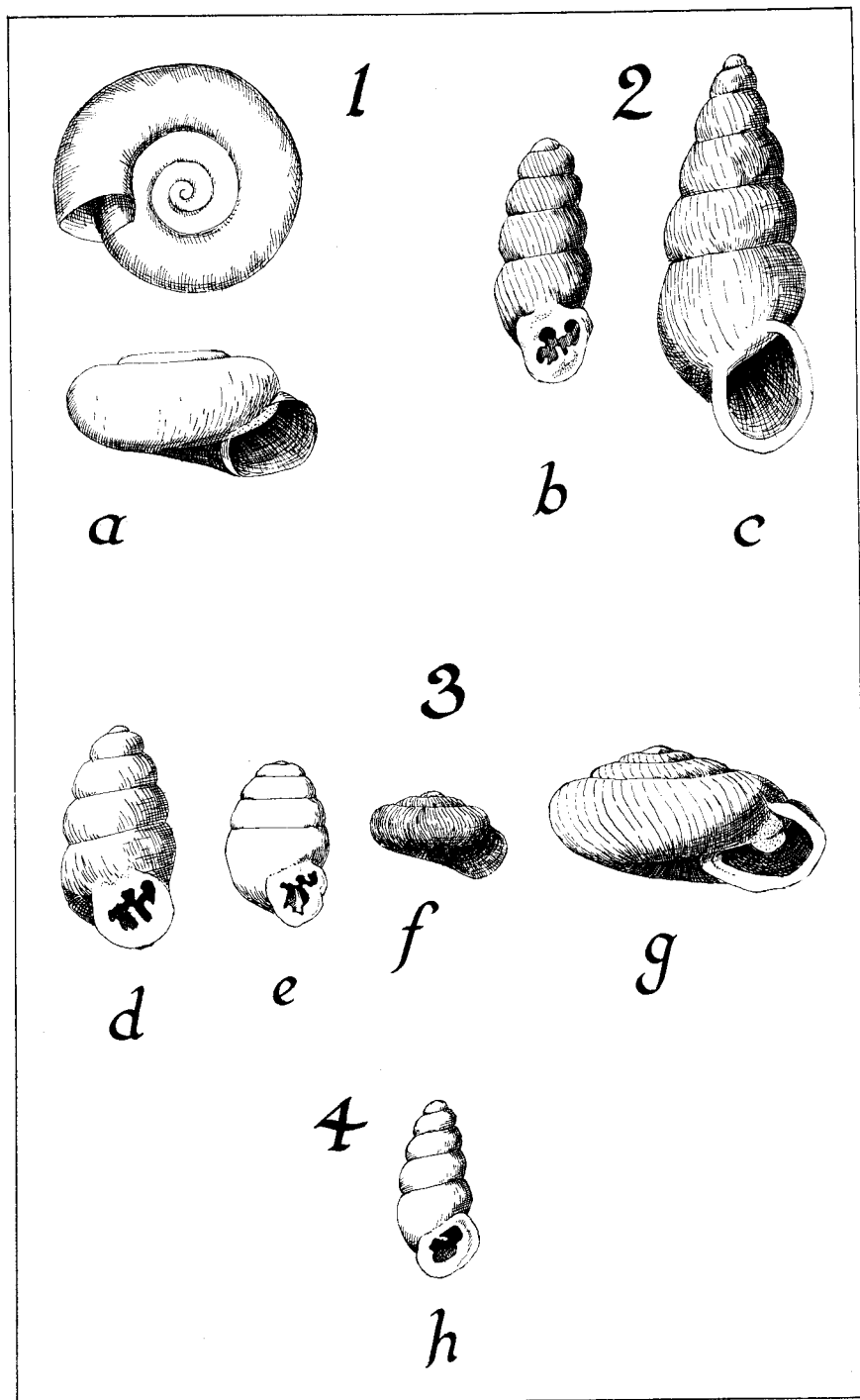
It is the alternation of these environments that produces a natural experiment. Differences in the relative abundance of snail species in Shore Hills soil and Harrington-Pembroke carbonates may, by hypothesis, be attributed to environmental differences. A repeat of the same pattern in the overlying sequence of St. George's soil and Southampton carbonates would provide an experimental replication, albeit not ideally controlled, to support the environmental hypothesis and eliminate a variety of proposals linked to major genetic changes or immigration of new species.

The fossil record of terrestrial Bermuda is little more than a history of its land snails; other remains are sufficiently rare to be labelled curiosities. Thus, a community study of Bermudian land snails represents no artificial sundering of a larger problem. Only two genera are larger than the average sediment grain size: *Succinea* with one or two species and the wonderfully diverse, endemic *Poecilozonites*, a *Geospiza* among land snails. Although I have done all my previous work on this genus, it is unsuitable for this study for two reasons. Only four species survive; these do not include the most common Pleistocene forms. To frame environmental hypotheses for differences in diversity, we need information independent of that provided by enclosing sediments on Bermuda; in other words, we need species that also live elsewhere and, preferably, live now. Secondly, this is a quantitative study of relative abundances. While it would be easy to compile presence-absence data for *Poecilozonites*, its size and abundance would require the quarrying and sieving of many cubic feet at each locality. This would render a *Poecilozonites* sample incommensurate with that of the microgastropods, for which a much smaller volume of sediment was collected.

However, lurking among the wind-blown foraminiferal tests, is a surprisingly varied and abundant fauna of microgastropods—12 species (two new) distributed among 9 or 10 genera. These have never been studied systematically. Gulick (1904) described some species and Sayles (1931) made a cursory and unsuccessful effort to identify stratigraphic ranges. Four important species

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FIG. 1. The eight major species of Bermudian microgastropods arranged according to assemblages (see text): a). *Thysanophora hypolepta*; b). *Gastrocopta pellucida hordeacella*; c). *Pupoides albilabris*; d). *Gastrocopta rupicola*; e). *Vertigo numellata*; f). *Punctum bristoli*; g). *Strobilops hubbardi*; h). *Carychium bermudense*. The *Carychium* shell is actually 1.9 mm in height. All others to same scale.



inhabit continental North America and have well defined ranges and environmental preferences; others belong to genera with characteristic habitats. I doubt that any factor beyond size is required to explain why the pulmonate fauna of Bermuda, an assemblage of chance migrants, includes such a preponderance of small forms. The fossil microgastropods of Bermuda are depicted in Fig. 1 and listed below with author and range (from Burch, 1962 for continental forms).

Subclass Pulmonata Cuvier

Order Basommatophora Keferstein

Family Carychiidae Jeffreys

- 1). *Carychium bermudense* Gulick 1904. Endemic.

Order Stylommatophora Schmidt

Family Pupillidae Turton

- 2). *Pupoides albilabris* (Adams). Maine to Florida, west to North Dakota, Colorado and Arizona.
- 3). *Gastrocopta pellucida hordeacella* (Pilsbry). New Jersey to Florida, west to California.
- 4). *Gastrocopta rupicola* (Say). South Carolina to Florida, west to Texas. This species, with its thickened peristome and tapering spire is easily distinguished from the thin shelled, elongate *G. pellucida hordeacella*. I may, however, have mixed a third species with *G. rupicola*. Some samples contain a *Gastrocopta*, similar in shape to *G. rupicola*, but with a rounder aperture and thinner peristome. This may be the *Pupa bermudensis* of Prime and *P. servilis* Gould of Pilsbry (1889). I cannot, in the absence of sympatric occurrence, distinguish true species from ecologic variants.
- 5). *Vertigo numellata* Gulick 1904. Endemic. Again, two species may be mixed under this name. One form is larger and barrel shaped, the other smaller and parallel sided; although the larger contains an additional whorl, the two are not ontogenetic variants since they differ at standardized sizes and whorl numbers. The two occur together and seem distinct in some localities, but other samples display a suite of intergrading specimens. Apertural teeth, often diagnostic for pupillids, do not differ in number or position.
- 6). *Vertigo marki* Gulick 1904. Endemic. Differs clearly from *V. numellata* in larger size, less convoluted aperture and, especially, in lacking an angular lamella.
- 7). *Pupisoma* sp. New.

Family Strobilopsidae Jooss

- 8). *Strobilops hubbardi* Brown. Georgia, Florida, Mississippi and Texas.

Family Endodontidae Pilsbry

9). *Punctum bristoli* (Gulick) 1904. Endemic.

10). Species A. New; either an endodontid or a zonitid.

Family Zonitidae Pilsbry

11). *Euconulus turbinatus* Gulick 1904. Endemic. Gulick's generic allocation may be incorrect. Peile (1926) places it in *Kaliella*.

Family Sagdidae Pilsbry

12). *Thysanophora hypolepta* Shuttlesworth. Endemic. I have not found any specimens of *Zonitoides minusculus* Binney, and I suspect that Gulick (1904) confused some members of this variable species with it. *Z. minusculus* does inhabit Bermuda today as one of the many introduced micro-gastropods.

METHODS AND PROBLEMS

Mr. Robin Houston and I collected a cubic foot of sediment from each of 74 localities in the summer of 1968; the locality numbers cited hereon refer to the map and list in Gould (1969) and the same series is used in the Appendix. After sieving and washing, each sample yielded a variable amount of material, least for red soils of high clay content and most for clean dune sands. I made no attempt to standardize the amount of material and study absolute abundance (the initial collection of 1 cubic foot is, itself, merely a matter of convenience). In fact, I can think of no criterion that would permit a meaningful comparison of absolute abundances. Equal volumes of collected material offer no similarity in duration since a foot of red soil, predominantly a weathering product, takes far longer to accumulate than a foot of dune sand. Equal volumes of sieved material, while convenient, standardize nothing of biological interest. Consequently, this study is based upon relative abundances. This limitation entails, of course, an unfortunate loss of information.

Another objection may be raised to the potentially unrepresentative nature of any sample for its locality. Species may congregate in very local areas and shells are undoubtedly subject to a variety of mechanisms for selective postmortem transport—wind, in particular. The close similarity of three samples from a mile-long Harrington exposure at Locality 41 is encouraging. However, the design of this experiment in no way requires that individual samples be average representatives of their outcrops. I am not interested in characterizing particular outcrops (which are, themselves, incomplete and imperfect representatives of general conditions at a given time), but in comparing sets of samples for different formations. A set of 20 samples, for example, might characterize its formation as well as any other even though no individual sample adequately represented its outcrop. I chose different

localities and spaced them as widely as possible in order to achieve a maximal independence in replication, not to define the peculiarities of specific localities.

Extensive postmortem transport, on the other hand, could produce serious artifacts if, for example, dunes were enriched with light shells differentially carried in from other environments. But transported particles are glazed and easily recognized, while the indigenous shells are surprisingly fresh and indistinguishable in most cases from living forms.

Miss Peggy Short picked the snails from the sieved samples and I identified and tabulated the faunas; 48 localities yielded sufficient material to be included and the complete matrix, displaying the percent contribution of each species to its locality, is presented in part A of the Appendix.

It is evident that certain species predominate in all localities while others are rarely present and never in great abundance. This raises a host of questions that I do not and cannot answer here: Why does some combination of *Thysanophora*, *Carychium*, *Gastrocopta*, and *Vertigo* dominate every locality? Why is *Vertigo* almost always less abundant than *Gastrocopta* when the two genera associate? Why are *Strobilops* and *Punctum* present almost as often as these other four, but almost never as more than 10% of the total fauna? Why do four other species occur so rarely and sporadically? Although I accept these basic patterns as given, and study variation within them, they themselves reflect the most challenging problems in ecology: competitive interactions, evolutionary strategies, ecologic balances, and so forth. They also present a potential problem for my method. My sample sizes range from 45 to 513, though with very few samples near the lower figure; rare species will be underrepresented in small samples if simple presence at very low frequency supplies much information to the system. Since species are weighted according to their percent contribution in most analyses, this problem is largely circumvented. In fact, when equal weights are supplied in the same analyses, only a very few minor differences appear.

The matrix given in part A of the Appendix is the raw data for almost all that follows. I use a variety of multivariate techniques to extract simplified patterns from this confusing array of numbers: communities are inferred from associations among species and the effects of environment are assessed by clustering localities. I think we are now past the time when each multivariate foray warranted a disquisition on its virtue and a careful explication of specific methods. General information will be found in Sokal and Sneath (1963), Seal (1964) and Reyment (1960; 1963). For computer programs used here, consult Bonham-Carter (1967) for CLUST3 (clustering by Jaccard and Simple Matching Coefficients); Dixon (1965) for BMDO4M (discriminant function analysis) and Imbrie and Van Andel (1964), Manson and Imbrie (1964) and Gould (1967; 1969) for COVAP and CABFAC (factor analysis).

I would only say that I see in these methods the promise that we can found a science of paleoecology. If science, in order to be called such, must explain according to general principles, then most of what has passed under the name of paleoecology—the correlation of organic form with sediment type and the descriptive reconstruction of paleoenvironments—is not ecology. Ecology is preeminently the causal study of organic systems in all their complexity and interaction. Until we can detect repeatable patterns amidst this complexity and relate them to general statements, we have little more than a descriptive account of some awesome phenomena.

THE RECOGNITION OF SPECIES ASSEMBLAGES

Some patterns of association are evident from the data matrix itself (Appendix: A); most outstanding is the uneven distribution of abundance (line 53). Some combination of the five species—*Thysanophora hypolepta*, *Carychium bermudense*, *Vertigo numellata*, *Gastrocopta rupicola*, and *G. pellucida hordeacella*—dominates every one of the 48 samples, being never less than 78% and more than 95% in 34 of the samples. These five species are divisible into two clear groups: 41 samples contain *Thysanophora*, *Carychium*, *Vertigo*, and *Gastrocopta rupicola* (only Locality 45, type of the Harrington Formation, departs in lacking *Carychium* and *Vertigo*); the other 7 samples are dominated by *Gastrocopta pellucida hordeacella* and, with one important exception, lack *Carychium* (25% *Carychium* at Locality 13; a single *Carychium* was also found at Locality 57, Southampton Formation). Four of these seven contain *Pupoides albilabris* in amounts ranging from 2 to 14%; elsewhere, *Pupoides* occurs only as a single specimen (.004%) at Locality 63b, Pembroke Formation. This division of localities into those dominated by *Thysanophora-Carychium-Vertigo-Gastrocopta rupicola* on the one hand and *Gastrocopta pellucida hordeacella-Pupoides albilabris* on the other should be recognized by any multivariate technique that provides a satisfactory separation of assemblages.

(I realize that this listing of exceptions begins to look ludicrous. Only two are likely to be genuine (*Carychium* at 13 and neither *Carychium* nor *Vertigo* at 45). I am not bothered by the single *Pupoides* at 63b and the one *Carychium* at 57; they are probably postmortem transports. It is, I suppose, the major frustration of analysts in this complex domain that some exception can always be ranked against a generality. I remember my friend Walter Bock once remarking that every time he propounded a sweeping synthesis, some fellow in the back of the room would raise his hand and say: "Yes, *but* there's a mouse from Michigan . . .").

Two other species, *Strobilops hubbardi* and *Punctum bristoli*, are important though not major contributors to the fauna; each is present in well over half the samples at abundances ranging up to 13% for *Punctum* at Locality 41c, Harrington Formation. The last four species—Species A, *Pupisoma* sp.,

Vertigo marki, and *Euconulus turbinatus*—are rare and exhibit no evident correlation, as does the equally rare *Pupoides albilabris*, to any major species; none is present in more than one-third of the samples and the maximum abundance is 4% for species A at Locality 48, Shore Hills Formation. Since their mean abundances over all samples range from 0.2% to 0.4% (line 53), I suspect that their presence or absence in most samples is more an artifact of sample size than an expression of any meaningful biological datum.

An extract from tables for the binomial distribution in Aiken and others, (1955) shows the probability of occurrence in samples of 50 and 400 individuals (close to my minimum and maximum) for a species ranging in actual abundance from 0.1% to 3.0%.

N	.001	.01	.02	.03	=	p
50	.05	.40	.64	.78		
100	.10	.63	.87	.95		
400	.42	.98	1.00	1.00		

In this specific example, p is the true frequency of a microgastropod species at a locality and N is the actual sample size. This tabulation assumes that any snail of any species present at a locality has an equal chance of being selected in any trial. Numbers in the body of the tabulation are probabilities that one or more individuals of a species present at probability p will appear in a sample of size N.

I could recognize little beyond this in raw data and required a factor analytic assist to fathom the more arcane associations. Both the composition of Q-mode eigenvectors and the clustering of species in R-mode analysis suggest that four biologically-important assemblages be recognized among the 12 microgastropod species.

Six axes account for 99.84% of the information in a Q-mode analysis of data normalized to depict each locality as a vector of unit length, but subjected to no other transformation. The sixth axis can be eliminated on mathematical grounds; it explains 0.23% of the total information and no more than 2.3% for any individual sample in varimax rotation. The fifth axis, dominated in composition by *Vertigo numellata* and *Punctum bristoli* (Table 2), cannot be dismissed on such grounds. It encompasses 3.72% of the total information and explains more than 30% in each of four samples (up to 78% for Locality 4, Harrington Formation). But three of these samples are from the same outcrop—a mile long exposure of the Harrington Formation extending along Bermuda's south shore, while the fourth represents the same formation, comes from the same area and may even be a continuation of the same outcrop. (See lines 13–15 and 25 in Appendix A, and note the relative abundances of *Vertigo numellata* and *Punctum bristoli* in these samples). A biologically significant association among species must transcend the peculiarities of individual localities. I have no evidence for a relationship of *Vertigo* and

TABLE 2. EIGENVECTORS FOR FIVE AXIS VARIMAX SOLUTION.

Species	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
<i>Thysanophora hypolepta</i>	-0.030	0.064	0.101	0.991	0.006
<i>Carychium bermudense</i>	0.997	-0.059	0.008	0.034	-0.026
<i>Vertigo numellata</i>	0.031	0.124	0.009	-0.005	0.977
<i>Gastrocopta rupicola</i>	0.057	0.986	0.027	-0.063	-0.131
<i>Gastrocopta pellucida hordeacella</i>	-0.007	-0.035	0.991	-0.099	-0.007
<i>Pupoides albilabris</i>	0.001	-0.008	0.080	-0.005	-0.011
<i>Strobilops hubbardi</i>	-0.003	0.036	0.025	-0.001	0.035
<i>Punctum bristoli</i>	0.021	0.037	0.000	-0.053	0.150
Species A	0.001	-0.010	0.005	-0.003	0.049
<i>Pupisoma</i> sp.	0.010	0.009	0.010	-0.017	0.018
<i>Vertigo marki</i>	0.002	-0.006	0.003	-0.002	0.026
<i>Euconulus turbinatus</i>	0.001	0.002	-0.003	-0.007	0.022

Punctum at other localities and no reason to believe that their association along the south shore during Harrington times has any environmental interest. Although the fifth axis may be "significant" in a statistical sense, this might reflect a redundancy caused by counting one tendency four times, and that tendency need not underline anything of biological interest.

The situation at four axes (95.89% of the information), however, is different. Part B of the Appendix shows the projections of each sample upon each of the four axes; the fourth axis includes high projections for samples of different times and geographic locations (though it explains only 4.82% of the total information). It reinforces, as we shall see in the next section, a consistent environmental interpretation based on other axes and is accepted as biologically significant.

The composition of the four axes is depicted in Table 3; the highest contribution for each of the eight important species is underlined. These axes form the basis for associations recognized in Fig. 1. The first is made up almost entirely of *Carychium bermudense*; the second includes *Vertigo*

TABLE 3. EIGENVECTORS FOR FOUR AXIS VARIMAX SOLUTION.

Species	Axis 1	Axis 2	Axis 3	Axis 4
<i>Thysanophora hypolepta</i>	-0.015	0.036	0.126	<u>0.974</u>
<i>Carychium bermudense</i>	<u>0.993</u>	-0.070	0.007	0.035
<i>Vertigo numellata</i>	0.115	<u>0.481</u>	0.108	-0.169
<i>Gastrocopta rupicola</i>	0.013	<u>0.866</u>	-0.039	-0.062
<i>Gastrocopta pellucida hordeacella</i>	-0.018	-0.025	<u>0.981</u>	-0.102
<i>Pupoides albilabris</i>	-0.001	-0.011	<u>0.079</u>	-0.003
<i>Strobilops hubbardi</i>	-0.001	<u>0.047</u>	0.027	-0.003
<i>Punctum bristoli</i>	0.033	<u>0.092</u>	0.013	-0.075
Species A	0.006	0.010	0.010	-0.013
<i>Pupisoma</i> sp.	0.011	0.015	0.011	-0.019
<i>Vertigo marki</i>	0.004	0.005	0.006	-0.007
<i>Euconulus turbinatus</i>	0.003	0.011	-0.001	-0.011

TABLE 4. EIGENVECTORS FOR FOUR AXIS VARIMAX SOLUTION; PERCENT-RANGE TRANSFORMATION APPLIED TO DATA.

Species	Axis 1	Axis 2	Axis 3	Axis 4
<i>Thysanophora hypolepta</i>	0.797	0.038	0.156	-0.308
<i>Carychium bermudense</i>	0.486	0.166	-0.055	0.804
<i>Vertigo numellata</i>	0.069	-0.459	0.051	0.136
<i>Gastrocopta rupicola</i>	0.226	-0.653	-0.107	-0.137
<i>Gastrocopta pellucida hordeacella</i>	-0.063	0.085	0.839	0.025
<i>Pupoides albilabris</i>	-0.030	0.063	0.321	0.037
<i>Strobilops hubbardi</i>	0.069	-0.362	0.310	-0.081
<i>Punctum bristoli</i>	-0.130	-0.344	-0.049	0.264
Species A	-0.095	-0.088	0.132	0.155
<i>Pupisoma</i> sp.	-0.175	-0.195	0.147	0.324
<i>Vertigo marki</i>	-0.060	-0.086	0.055	0.098
<i>Euconulus turbinatus</i>	-0.057	-0.147	-0.033	0.039

numellata, *Gastrocopta rupicola*, *Strobilops hubbardi*, and *Punctum bristoli* and is largely an amalgam of the second and fifth axes of the five axis solution (Table 2); the third, as predicted from an obvious relationship in raw data is dominated by *Gastrocopta pellucida hordeacella* and *Pupoides albilabris*; the fourth consists almost wholly of *Thysanophora hypolepta* (with all others but *Carychium*, including the four minor species, making a negative contribution). The reality of these associations is illustrated not so much by this aggregation into axes, but by the coherent environmental interpretation that can be drawn from them. This shall be demonstrated in the next section.

It cannot be taken *a priori* that abundant species offer more biological information than rare ones; they will, of course, contain more mathematical information when normalization is the only transformation applied to raw data. Therefore, a possible objection to the above procedure is that sample vectors are constructed almost entirely of the five abundant species; the contribution of any species to the total information of its vector is a function of the square of its percentage contribution to the fauna, thus reducing even further the weight of rare species. Some criterion for a more equal weighting of species should be used to see if major changes in axis compositions would result. Table 4 presents the eigenvectors for a four axis varimax solution; the percent-range transformation of Manson and Imbrie (1964) was applied before normalization. In this approach to equal weighting, the minimum value of each species is scored at 0, the maximum as 100 and all intermediate values as a percent of that range. Little is changed beyond the magnitude of rare species' contribution, which is still not high because these are absent from so many samples and therefore scored as zero many times. The *Thysanophora* and *Carychium* axes have reversed their positions, but all else is unaltered; the associations of Fig. 1 apply exactly.

In another approach to the identification of species assemblages, we may cluster species directly rather than view their contributions to axes that

TABLE 5. REORDERED OBLIQUE PROJECTION MATRIX FOR ALL SPECIES.

Species	Axis 1	Axis 2	Axis 3
<i>Vertigo numellata</i>	1.000	0.000	0.000
<i>Punctum bristoli</i>	0.994	-0.040	-0.274
Species A	0.933	0.215	-0.577
<i>Vertigo marki</i>	0.921	0.172	-0.491
<i>Pupisoma</i> sp.	0.875	0.410	-0.379
<i>Euconulus turbinatus</i>	0.610	-0.052	0.149
<i>Thysanophora hypolepta</i>	-0.724	-0.311	0.137
<i>Gastrocopta pellucida hordeacella</i>	0.000	1.000	0.000
<i>Pupoides albilabris</i>	-0.092	0.863	-0.138
<i>Carychium bermudense</i>	-0.339	-0.844	-0.689
<i>Gastrocopta rupicola</i>	0.000	0.000	1.000
<i>Strobilops hubbardi</i>	0.392	0.550	0.712

cluster samples. At three axes (55.7% of the total information), we cease to get axes that group only minor species. Table 5 presents the reordered oblique projection matrix for a three axis R-mode solution. Here, the criterion of orthogonality is abandoned, extreme vectors of the total set are used as axes and each vector is grouped with the axis upon which it projects most strongly. The first axis shows *Thysanophora* in negative association with two species of assemblage 3 and the four minor species (this negative relation is also evident in the composition of our Q-mode *Thysanophora* axis—number 4 of Table 3). Axis 2, predictably, groups *Gastrocopta pellucida hordeacella* and *Pupoides albilabris* in negative association with *Carychium bermudense*. In raw data, with one exception, *Carychium* does not occur (but is never otherwise absent, again with one exception) in the major presence of these two species. The third axis includes two members of Association 3. The allocation of Association 3 to two axes follows the division implied by axis 5 in Q-mode analysis. My reasons for judging this as biologically insignificant are given on page 495. Otherwise, R-mode analysis displays the four associations and suggests some interactions among them.

ENVIRONMENTAL INTERPRETATION OF ASSEMBLAGES

Bermudian stratigraphy reflects two environmental cycles: the Shore Hills glacial red soil to Harrington-Pembroke interglacial carbonates and the St. George's glacial red soil to Southampton interglacial carbonates. Red soils formed in relatively cool and moist times and are usually poor in lime; the interglacial deposits are all rich in lime, but vary greatly in the conditions of moisture they suggest. These range from the heavy vegetation of interdune lows (deep brown unindurated zones) to large foreset beds in the anterior of massive and barren dunes; most interglacial samples are from unindurated zones.

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Lines 49–52 of Appendix B give the projection upon varimax axes of hypothetical samples representing averages, for each formation, of the 41 samples dominated by *Carychium-Thysanophora-Vertigo-Gastrocopta rupicola*. The hypothesis of environmental control for species assemblages is affirmed by the even oscillation of projections upon the three relevant axes; (disregard the third axis which encompasses variability provided by the 7 excluded *Gastrocopta pellucida hordeacella-Pupoides albilabris* samples). Both the *Vertigo-Gastrocopta rupicola-Strobilops-Punctum* and the *Carychium* assemblages preferred interglacial conditions; average Harrington-Pembroke and Southampton samples have stronger projections upon their axes than either red soil sample. The *Thysanophora* assemblage (axis 4), on the other hand, is better represented in the two glacial red soils than in the interglacial carbonates.

The environmental interpretation of the four assemblages must be based both on this intrinsic evidence and on the known ecology of component species. I shall consider the groups as a series of progressive departures from glacial conditions on Bermuda.

1). The *Thysanophora* assemblage (No. 1)*: *Thysanophora hypolepta* is an endemic species. Many species of this genus live in acalcic environments. Pilsbry (1940, p. 987) reports *T. horni* from volcanic soils and Baker (1924) notes that the *Thysanophora* of Aruba, Bonaire, and Curaçao (*T. crinita* and *T. plagioptycha*) are usually found on granite and diabase soils, not on the abundant limestones that form the preferred habitat of most land snails on these islands (personal observation). Moreover, *T. hypolepta* is by far the thinnest shelled of our 12 microgastropod species; thin shells are common in land snails from acalcic habitats either as a direct phenotypic response (Rensch, 1937) or a genetic adaptation (Gould, 1969). Since *Thysanophora* shows no preference for relatively cool or wet habitats and since *T. hypolepta* is present at reduced frequencies in carbonate samples, its abundance in red soils may express its tolerance of low calcium environments that limit the numbers of more normal calciphilic species. It is then "diluted," though its absolute abundance may not decrease, in interglacial habitats.

2). The *Gastrocopta pellucida hordeacella-Pupoides albilabris* assemblage (No. 2): Both species inhabit North America, extending as far north as Ontario (Pilsbry, 1948, for *P. albilabris*) and New Jersey (Burch, 1962, for *G. pellucida hordeacella*). They thrive, therefore, at temperatures lower than that ever experienced in Bermuda during the Pleistocene. Although cold tolerant, both species extend south to Florida and into the West Indies.

*I realize that I am introducing some confusion by giving the assemblages different numbers from the axes they represent in Appendix B. Thus axis 4 of that table expresses the information of assemblage 1, axis 3 of assemblage 2, axis 2 of assemblage 3, and axis 1 of assemblage 4. I felt a need to arrange assemblages in this order since they are best understood as a series of progressive departures from conditions favored by the *Thysanophora* assemblage in the basal Shore Hills Formation.

Both prefer reasonably moist habitats, but can tolerate drier conditions (Pilsbry, 1948; Miller, 1966). *Pupoides albilabris* is a known calciphile (Pilsbry, 1948, p. 923; Leonard, 1950, p. 29); I have no information on this point for *G. pellucida hordeacella*, but Pilsbry (1916, p. 7) claims that the entire genus is calciphilic. If the *Thysanophora* assemblage is drawn to occupy the origin of a triaxial system, radiating out to greater warmth, dryness and calcium availability (Fig. 2), then this assemblage (No. 2) tolerates the relatively cool conditions of assemblage 1, but differs in requiring a limey substrate. Some samples of the generally warmer interglacials should support a fauna that thrived in relatively cool conditions. Geyer (1922) doubted that general climate had much to do with the distribution of land snails because local and temporary situations exerted such strong control. Dunes form quickly and many habitats were transient. Bermuda's interglacial winter was colder than its glacial summer and relatively cool periods, lasting several years, were probably not uncommon. Moreover, some dunes of the present island may have formed during glacial epochs, especially along Bermuda's south shore where elevation decreases so rapidly seawards that even the maximal eustatic lowering of glacial periods would not have moved the shore far from its modern position.

3). The *Gastrocopta rupicola*-*Vertigo numellata*-*Strobilops-Punctum* assemblage (No. 3): Two of these species inhabit North America but neither transgresses the Mason-Dixon line. *G. rupicola* does not occur above South Carolina (Burch, 1962) and *Strobilops hubbardi* has not been found north of Georgia. On this evidence alone, assemblage 3 seems to require warmer habitats than does assemblage 2. It was also limited by a need for limestone substrates—Pilsbry's opinion on *Gastrocopta* has already been cited—and moist conditions. *Strobilops hubbardi*, according to Pilsbry (1948, p. 851) lives on "decaying logs and dead leaves in moderately humid forest." Taylor (1960, p. 6) states, of the genus, that it is "narrowly restricted to areas with humus and dead wood . . . probably governed by available moisture, soil, and frequency of drought." *Vertigo numellata* is endemic, but the genus is hygrophilic and *V. ovata*, which Gulick (1904) placed as *V. numellata*'s nearest relative, is limited by moisture (Leonard, 1950, p. 26), living "only in moist environs afforded by shaded slopes near streams and shores of ponds" (Franzen and Leonard, 1947, p. 355). This group shares, with assemblage 2, a need for limestone substrates and moisture but requires, in addition, a warmer temperature.

4). The *Carychium* assemblage (No. 4): *Carychium bermudense* is endemic. The Carychiidae, a primitive family of basommatophoran land snails, is usually restricted to moist areas. Pilsbry (1948, p. 1059), however, reports that *Carychium exile* is tolerant of dry conditions. Intrinsic evidence suggests that *C. bermudense*, although not hygrophobic (no land snails were found in samples from the interior of massive dunes), is less limited by

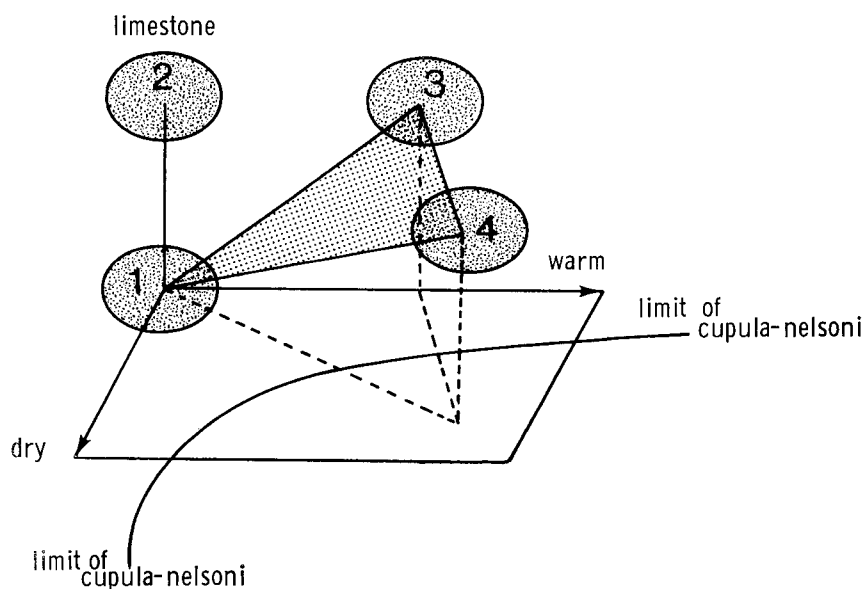


FIG. 2. Summary of environmental interpretation for assemblages, depicted as triaxial system radiating to greater lime content, warmth and dryness from the glacial environments dominated by the *Thysanophora* assemblage (No. 1). The plane joining assemblages 1, 3 and 4 indicates the minor degree of intergradation among these assemblages, compared with the uniqueness of assemblage 2 (see Fig. 7). The inferred environmental tolerances of the larger *Poecilozontes cupula* and *P. nelsoni* are shown; they did not inhabit the environments preferred by assemblage 4.

dryness than the other assemblages. It is more common in eolianites than in red soils and is particularly abundant in light colored unindurated zones thought to represent poorly vegetated habitats. Its situation may be similar to that of the larger *Succinea* which is known to thrive in relative dryness on Bermuda. The Succineidae, as a family, are always described as wet-loving, but certain species are xerophilic (Leonard, 1950, p. 24 on *S. grosvenori*; Hibbard and Taylor, 1960, p. 140 on *S. concordalis*), and Gulick (1904, p. 412) has said of Bermuda's species: "I do not think it could be proved that these snails lived under any densely shading vegetation. The humidity at Bermuda makes such a shade less necessary for snails than it is in many places. I have often seen *Succinea bermudensis* clinging to grass and to trunks of trees in such situations that I imagine an American summer day would have desiccated them." *C. bermudense* is also the thickest shelled of Bermudian microgastropods and is probably calciphilic.

Thus, in conclusion (Fig. 2), I view the assemblages as representing a series of successive departures from the relatively cool, wet, and acalcic conditions dominated by *Thysanophora*. Assemblage 2 adds limestone, assemblage 3, limestone and warmth, and assemblage 4, limestone, warmth,

TABLE 6. COMPARISON OF SAMPLES AT TOP AND BOTTOM OF CONTINUOUS SEQUENCES. CASE 1: RED SOIL-PINK EOLIANITE AT DEVONSHIRE FORT, NORTH OF LOCALITY 2; CASE 2: WHITISH UNINDURATED ZONE-BROWN UNINDURATED ZONE, AT LOCALITY 21.

Case		N	<i>Thysanophora</i> <i>hypolepta</i>	<i>Carychium</i> <i>bermudense</i>	<i>Vertigo</i> <i>nummelata</i>	<i>Gastrocopta</i> <i>rupicola</i>	<i>Succinea</i> protoconchs	<i>Punctum</i> <i>bristolii</i>	Species A
1	pink eolianite	270	34	153	16	53	4	8	2
	red soil	55	13	38	0	0	4	0	0
2	brown zone	266	33	81	46	90	10	6	0
	white zone	210	20	98	8	73	1	8	2

and dryness. I realize that it is naive and incomplete to relate such complexity to three factors alone, leaving aside an explicit treatment of such important variables as vegetation, but I do not maintain that these alone influence distribution. Rather, I am trying to see if these three encompass sufficient information to establish a useful summary of a complex situation.

This interpretation is strengthened by the two comparisons of Table 6. These contrast upper and lower units in two sequences of continuous deposition through a major environmental change. (These are not selected data; such sequences are rare and two other samples did not yield a sufficient fauna). The lower unit for case 1 is a deep red soil; this is progressively diluted upwards by an influx of eolian carbonate and the upper unit is a pinkish unindurated eolianite. All species of eolianite assemblages increase in relative abundance; *Vertigo*, *Gastrocopta*, *Punctum*, and Species A make their appearance and the ratio of *Carychium* to *Thysanophora* increases, though not significantly ($\chi^2 = 1.35$; $p < .25$). The lower unit of case 2 is a whitish unindurated zone, paralleling the foresets of an underlying dune and representing a pause in its accumulation; this grades continuously to the deep brown upper unit, a characteristic deposit of moist and heavily vegetated habitats. In our scheme, assemblage 4 should give way to assemblage 3. Indeed, *Vertigo* increases dramatically and the *Gastrocopta rupicola* to *Carychium* ratio rises ($\chi^2 = 3.39$; $.05 < p < .10$).

AN EXAMPLE OF THE UTILITY OF THIS INTERPRETATION:

I present the following example to demonstrate that this environmental interpretation of assemblages is a useful scheme for explanation. By correlating the microgastropod assemblages to the domain of Bermuda's larger land snails, we obtain a consistent story that resolves some anomalies of distribution in this larger domain and relates still more, previously disconnected information to a common explanation.



FIG. 3. The three species of *P. (Poecilozonites)*. The two species on the left (large *P. nelsoni* and small *P. cupula*) often occur together but are not found with the species on the right, *P. bermudensis*. Natural size.

The subgenus *P. (Poecilozonites)* contains four species (Fig. 3): *P. bermudensis*, *P. cupula*, *P. nelsoni*, and *P. superior* (Gould, 1969) (the last two are very closely related and are designated collectively, hereafter, as the *P. nelsoni* complex). All species are polytypic and *P. bermudensis*, in particular, contains several thin-shelled paedomorphic offshoots, derived from the central stock of *P. bermudensis zonatus* as adaptations to the acalcic environments of red soils (Gould, 1968; 1969). These species may be divided into two groups based on spatio-temporal distribution: *P. cupula* and the *P. nelsoni* complex often appear in the same sample, but *P. bermudensis* is not found with another species of its subgenus. Moreover, *P. cupula* has never been found in sediments deposited after the Spencer's Point Sea, and was presumably extinguished by some condition related to its rise. The *P. nelsoni* complex, though abundant in Harrington-Pembroke eolianites, occurs in only one area in St. George's sediments overlying Spencer's Point; it is unknown in the Southampton and presumably disappeared during St. George's time. Although two of its paedomorphic offshoots became extinct, the central stock of *P. bermudensis* passed through the Spencer's Point interval with no apparent reduction in diversity or range. What is the environmental significance of this twofold division among the four species of *P. (Poecilozonites)*?; why is only one group strongly affected by Bermuda's highest interglacial sea stand? We cannot solve the issue by studying modern forms, and gross lithology will not suffice since all species have been found both in red soils and eolianites.

A potential solution is apparent, however, when we correlate distribution of *Poecilozonites* with that for the microgastropods.

The last column of Appendix B lists the species of *P. (Poecilozonites)* that occur with microgastropods at each locality; c for *P. cupula*, n for the *P. nelsoni* complex, b for normal, nonpaedomorphic *P. bermudensis* and p for the paedomorphic offshoots of *P. bermudensis*. Table 7 shows the distribution of these *Poecilozonites* taxa among samples grouped according to maximal projections upon the four axes. All taxa that are affected by the Spencer's Point Sea (the *P. bermudensis* paedomorphs, *P. cupula*, and the

TABLE 7. SPECIES OF *P. (Poecilozonites)* AND LITHOLOGIES ASSOCIATED WITH SAMPLES GROUPED BY MAXIMAL PROJECTIONS UPON THE 4 VARIMAX AXES OF APPENDIX B.

	Species of <i>P. (Poecilozonites)</i>				Lithology	
	<i>P. bermudensis</i> non paedomorphs	<i>P. bermudensis</i> paedomorphs	<i>P. cupula</i>	<i>P. nelsoni</i> complex	red soil	collanite
Axis 1	18	4	3	1	8	17
Axis 2	2	4	6	2	2	11
Axis 3	1	0	2	2	1	4
Axis 4	2	1	1	1	3	2

(The total number of samples adds to 50 rather than 48 because two samples have both *P. cupula* and *P. nelsoni* and these were counted twice.)

P. nelsoni complex) show a tendency to occur in samples containing microgastropods of the 2nd and 3rd assemblages. The microgastropods of these assemblages are calciphilic and hygrophilic; indeed, 15 of 18 samples grouping with axes 2 and 3 in the last two columns of Table 6 are from interglacial eolian carbonates. *P. bermudensis*, on the other hand, is most often found in samples that contain microgastropods of the 1st and 4th assemblages. This taxon could inhabit all Bermudian pulmonate environments. It actually exceeds any other in both extreme faunas; the relatively cool, wet, and acalcic *Thysanophora* environment; and the warm, dry, lime rich habitats of *Carychium*.

The correlation between *Poecilozonites* and the microgastropod assemblages is depicted in Fig. 4. Here, the four axes of Table 3 and Appendix B have been reduced to three; most of *Thysanophora*'s information is eliminated. With only three axes, results can be plotted on a triangular diagram. Samples containing *P. bermudensis* paedomorphs, *P. cupula* or the *P. nelsoni* complex show a clear tendency to group with the second or third axis. Nonpaedomorphic *P. bermudensis* occurs at all three corners, but it alone is present in samples with strong projections upon the first axis.

None of these data actually contains information for *Poecilozonites* taxa; I have merely correlated the presence and absence of *Poecilozonites* with data reductions based solely on microgastropods. As explained on page 488, I did not calculate percentage abundances for *Poecilozonites* since these would not have been commensurate with similar data for microgastropods. We could, however, include both *Poecilozonites* and microgastropods in a single analysis if we used only presence-absence scoring for each locality. I therefore constructed such a matrix for 25 species at all localities: 10 microgastropods (*Thysanophora* and *Gastrocopta rupicola* are present at all localities and have no discriminating power in this analysis), *Succinea*, *P.*

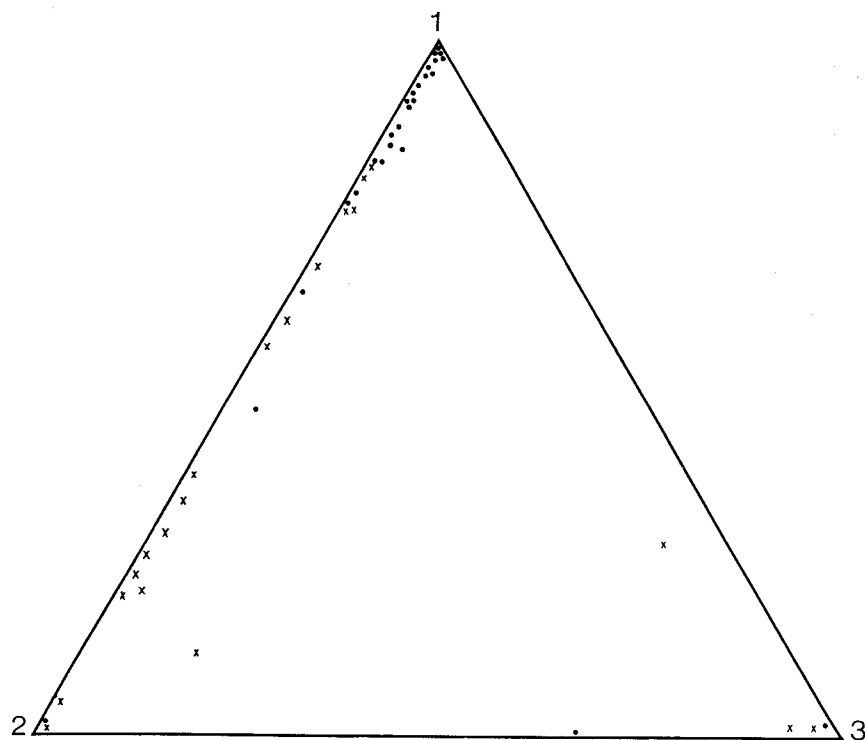


FIG. 4. All samples plotted as triangular diagram against three varimax axes. Samples marked x contain *P. cupula*, *P. nelsoni*, or *P. bermudensis* paedomorphs. Samples marked • contain only the normal, nonpaedomorphic *P. bermudensis*.

bermudensis non-paedomorphs, *P. bermudensis* paedomorphs, 5 subspecies of *P. cupula*, 2 species of the *P. nelsoni* complex and 5 species of the subgenera *P. (Gastreasmus)* and *P. (Discozonites)*.

Jaccard coefficients were computed between all pairs and the samples were clustered using Bonham-Carter's (1967) program. The Jaccard coefficient ignores negative matches, that is the absence of a species in two localities does not increase their similarity. I do not, for example, consider it interesting that all Southampton localities lack both *P. nelsoni* and *P. cupula*. These species had become extinct before the return of Southampton environments in which they would have thrived. Nevertheless, I also performed a cluster analysis with the Simple Matching Coefficient that does include negative matches in computing the similarity of two samples. There is no difference whatsoever in the composition of clusters for the two analyses; the similarity values of samples are of course, generally higher, for the Simple Matching Coefficient.

The results of this Jaccard analysis (Fig. 5) confirm previous conclusions. I have divided the clusters into seven, only slightly arbitrary, larger groups

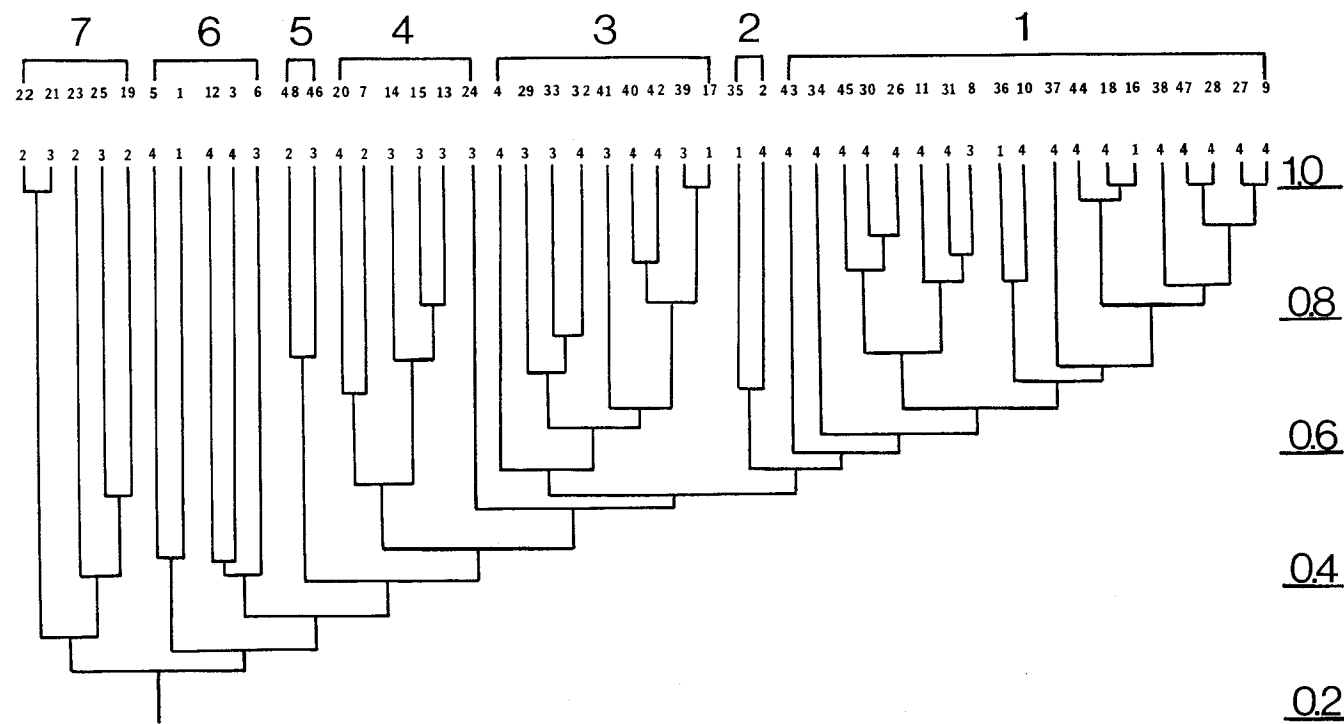


FIG. 5. Clustering of all samples based on Jaccard coefficient for presence-absence data on *Poecilozonites* and microgastropods. Large numbers 1-7 refer to groupings explained in text; smaller numbers just below identify samples (line numbers of Appendix) numbers 1-4 below identify the microgastropod assemblage of each sample. Similarity values on the ordinate. From program of Bonham-Carter (1967).

in even gradation along the array. These seven have the following composition:

1). All samples that contain both *P. bermudensis* and microgastropods of its favored 1st and 4th assemblages. The only exception is a Harrington sample (Whalebone Bay, line 8 of Appendix B) that groups with the third assemblage, but contains *P. bermudensis*.

2). The only two samples with *P. nelsoni* and microgastropods of the first and fourth assemblages (usually associated with *P. bermudensis*).

3). All samples with *P. bermudensis* paedomorphs. (I realize that the geometry of the chart is such that the positions of groups 1 and 2 could be reversed with respect to 3).

4). Samples with *P. cupula cupula*.

5). The only two samples with *P. bermudensis* that, in addition, contain *Gastrocopta pellucida hordeacella*, the chief element of assemblage 2. These are the only samples with *P. bermudensis* that do not occur in the first cluster.

6). Another group that contains only samples with *P. cupula* or the *P. nelsoni* complex.

7). All these samples either group in assemblage 2 or contain a good percentage of its species. They contain, in addition, either *P. cupula* or the *P. nelsoni* complex, but never *P. bermudensis*.

The entire array can be seen as a continuum leading from one extreme environment that favored *P. bermudensis* and the *Carychium* assemblage (No. 4) to another in which microgastropods of the second and third assemblages occur with taxa of *Poecilozonites* that were affected by the Spencer's Point Sea. Mixed samples (*P. nelsoni* with assemblages 1 or 4 and *P. bermudensis* with 2 or 3) occupy intermediate positions. The varying influence of the Spencer's Point Sea is also reflected in the distribution of samples along the array. *P. nelsoni* survived the sea stand, but its range was greatly reduced and it disappeared soon afterward. Two of its samples (including the one from post-Spencer's Point times) lie next to the main *P. bermudensis* cluster. The *P. bermudensis* paedomorphs are all in a cluster standing close to their progenitors in cluster 1. But all samples with *P. cupula* lie at the other end of the array; none appear until the fourth cluster. Four subspecies of *P. cupula* were extinguished by the rise of the Spencer's Point Sea.

We can be quite sure that it was the high sea and not the subsequent glacial environment that provoked the elimination of *P. cupula* and the *P. nelsoni* complex. Both taxa are abundant in the Shore Hills soil. In fact, Bermuda's most famous localities are the cave deposits of Shore Hills age, containing the massive *P. nelsoni* coquinas that inspired many early naturalists to effusive Victorian prose (Nelson, 1837). (Most of these have been obliterated by such signs of Bermuda's progress as garbage dumps and golf

courses and are, consequently, not included here). If we place the Spencer's Point Sea in the villain's role, it is the correlation of *P. bermudensis* with assemblage 4 that teaches us why *P. cupula* and the *P. nelsoni* complex fared so badly. When the Spencer's Point Sea rose to plus 60 m, it so greatly limited the area of Bermuda, that all parts of the island lay exposed to dune activity. This was the only time in Bermuda's recorded history during which the entire island might have been covered with dunes. For a short time, the dry-tolerant fauna of microgastropod assemblage 4 probably dominated all areas and its correlate, *P. bermudensis*, survived with no difficulty. But the existing paedomorphs of *P. bermudensis* (a new one evolved later during St. George's time), the *P. nelsoni* complex and *P. cupula* are correlated with the hygrophilic assemblages 2 and 3. The Spencer's Point Sea eliminated their habitat and hastened their demise. The presumed tolerance limits of these taxa are sketched on Fig. 2. Thus, the interpretive scheme presented on page 500 has demonstrated its utility by explaining a problem in a larger world that had yielded no solution in its own domain.

CORRESPONDENCE OF CLIMATIC AND FAUNAL FLUCTUATIONS

Taylor (1965) has discussed the recurrence of pulmonate assemblages in Pleistocene alluvial deposits of the Great Plains and has argued that these imply repeating environments. This phenomenon is so precise that "the recurrence of similar assemblages of mollusks at various times necessitates the use of independent sources of evidence to establish the stratigraphic horizon of such assemblages" (Taylor, 1965, p. 606).

We encounter the same situation in Bermuda. No microgastropod became extinct during the time recorded in Bermuda's geologic record; the calamitous effects of man's entry have extinguished some since. Neither have we any evidence that any species first gained entry during this period.

The localities of Appendix B are arrayed in temporal order so that the fluctuations upon each axis, epitomized in the averages of lines 49-53, can be readily seen. The pattern is clearest when all projections are considered, not just the underlined maxima. Thus, although only three red soil samples have their highest projection upon the fourth axis (*Thysanophora* assemblage 1), projections of other red soil samples are consistently higher than those of eolianite samples. Fig. 6 and 7 present two planar slices through the four dimensional geometry of Appendix: B. Fig. 6 plots points against the two axes representing *Carychium* and *Thysanophora*. Localities with assemblages 1 and 4 are arrayed in a band of high projections on these axes; those containing assemblages 2 and 3 are distinguished by low joint projections upon the axes. Fig. 7 is included to show the sharp distinction between assemblage 2 and all others.

We find recurrence not only for amalgamations of species abstracted as factor axes, but also for species considered individually. Table 8 presents

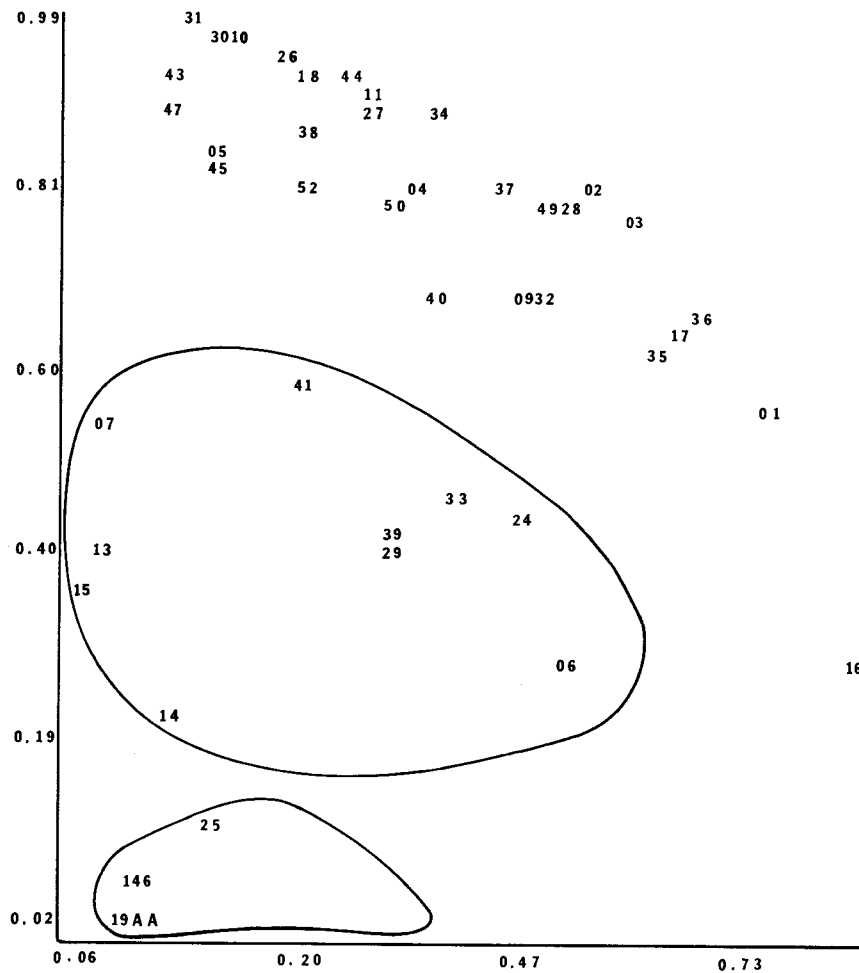


FIG. 6. All samples plotted against varimax axes 1 (ordinate) and 4 (abscissa). Samples of assemblages 1 and 4 have high joint projection on both axes. Samples of assemblage 3 in upper circle and 2 in lower circle. AA stands for samples 23 and 48. Samples identified by line numbers of Appendix.

the mean relative abundances for species in each time period. Mr. Len Vacher, in an unpublished work, has revised the stratigraphy of St. George's Island. He believes that the placement of some localities by Land, Mackenzie and Gould (1967) are incorrect and I tend to agree with him, though the issue is not completely resolved. He would place three of my St. George's localities (lines 32–34 of Appendix B) in Shore Hills times and four of my Southampton samples (lines 39–42) in Harrington-Pembroke times. Because the recurrence of assemblages is so precise, none of my conclusions are af-

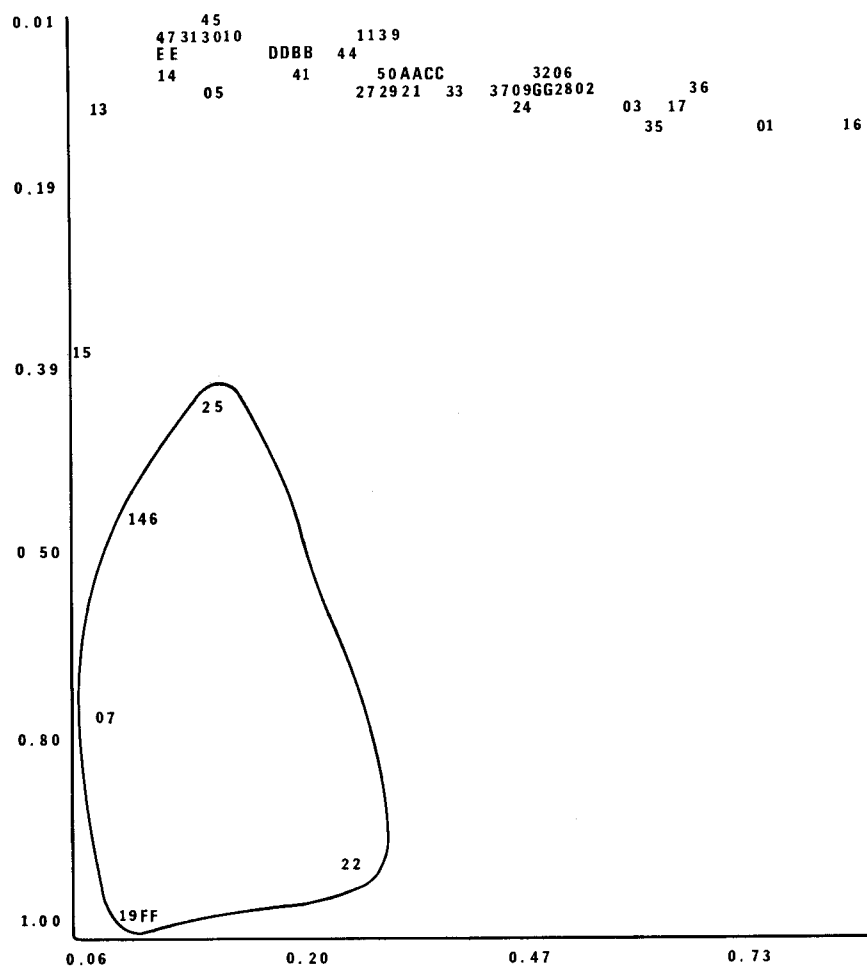


FIG. 7. All samples plotted against varimax axes 3 (ordinate) and 4 (abscissa) to show distinction between samples of assemblage 2 (circled—high projections on axis 3) and all others. Samples identified by line numbers of Appendix. AA stands for 4 and 12, BB for 18, 38, and 52, CC for 34 and 40, DD for 26 and 42, EE for 8 and 43, FF for 23 and 48, and GG for 20, 49, and 51.

ected by these changes. This table presents the same data for both stratigraphic schemes.

Time alone, therefore, plays little role in the distribution of Bermudian microgastropods. All species lived at all times and dominated their preferred environments whenever they occurred. The most fitting separation is not by temporal units, but rather by lithologies and their implied environments, and the fundamental distinction is between all interglacial, eolianite carbonates on the one hand and all glacial red soils on the other. I therefore performed

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TABLE 8. AVERAGE RELATIVE ABUNDANCES FOR CALCIPHILES AND NONCALCIPHILES IN RED SOILS AND EOLIANITES. CORRELATIONS ARE FROM LAND, MACKENZIE AND GOULD (1967) (ABUNDANCES, DERIVED USING THE UNPUBLISHED CORRELATIONS OF L. VACHER, ARE GIVEN IN PARENTHESIS).

	Shore Hills red soil	Harrington- Pembroke eolianite	St. George's red soil	South- ampton eolianite
<i>Gastrocopta rupicola</i>	.174(.208)	.312(.319)	.203(.157)	.288(.218)
<i>Strobilops hubbardi</i>	.007(.007)	.014(.013)	.005(.004)	.011(.013)
<i>Punctum bristoli</i>	.008(.005)	.030(.027)	.003(.005)	.033(.050)
<i>Thysanophora hypolepta</i>	.270(.257)	.176(.169)	.270(.297)	.105(.068)

a discriminant function analysis on these two groups (after eliminating the samples that are rendered so distinct by their abundance of *Gastrocopta pellucida hordeacella* and *Pupoides albilabris*, the components of assemblage 2). Two of 15 red soil samples were misclassified, and both of these have their highest projections on the *Carychium* axis (lines 34 and 38 of Appendix: B). Four of twenty-eight eolianite samples are misallocated; these four (lines 9, 17, 18, and 28) project strongly upon the red soil *Thysanophora* axis. The average samples for each of the four time periods appear in the middle of their groups. Mahalanobis' D^2 for the two groups is 4.208 (f at 12 and 30 d.f. is 2.506; $.025 > p > .01$). When only the four major species—*Carychium bermudense*, *Thysanophora hypolepta*, *Gastrocopta rupicola*, and *Vertigo numellata*—are used to distinguish the groups, four red soil and 6 eolianite samples are misclassified, but the means are separate at the same level of significance (Mahalanobis' D^2 is 1.474; f at 4 and 38 d.f. is 3.336; $.025 > p > .01$).

CORRESPONDENCE OF CLIMATIC FLUCTUATIONS AND FORM

The goal of this work is to explicate a natural experiment on climatic and faunal fluctuations in a system of unusual simplicity. In the last section, I demonstrated that the relative abundances of species and assemblages varied directly with climate during Bermuda's recorded Pleistocene history. Is climatic influence recorded in any other faunal parameter? Can we replicate the experiment with a new set of biological variables? In this section, I attempt to show that variation in the form of individual species is also related to climate in a very direct way.

Table 9 presents data for *Thysanophora hypolepta* and *Carychium bermudense*. These were chosen for analysis because they dominate the two extreme assemblages of the glacial-interglacial continuum of climatic preference. For *Carychium*, heights and widths were measured for 20 adult specimens in each of 19 localities (4 Shore Hills, 5 Harrington-Pembroke, 4 St. George's, and 4 Southampton). The figures of Table 9 are grand means of all sample means for each time period. In the Shore Hills red soil, *Carychium*

TABLE 9. MORPHOLOGICAL FLUCTUATIONS IN MEAN SAMPLE VALUES FOR *Thysanophora* AND *Carychium* (IN MICROMETER UNITS, 29 = 1 MM).

	Shore Hills red soil	Harrington- Pembroke eolianite	St. George's red soil	Southampton eolianite
<i>Carychium</i>				
1. Height	51.37	49.80	51.20	50.10
2. Height/Width	1.93	2.06	2.01	2.07
<i>Thysanophora</i>				
1. Umbilical width (at width = 55)	22.06	20.79	21.14	20.70

is larger and relatively wider than in subsequent Harrington-Pembroke eolian carbonates. The same sequence repeats in the overlying couple: *Carychium* is large and wide in the St. George's red soil, smaller and narrower in Southampton eolian carbonates.

For *Thysanophora*, I measured width and umbilical width for 20 specimens in the same 19 localities (among my 48 samples, these were the only ones with a sufficient number of both species for this analysis). *Thysanophora* has no recognizable adult stage and the 20 specimens were selected to encompass as wide and as even a range of size as possible. I then computed the least squares regression of umbilical width on total width using programs written in CAL for the SDS 940 by R. Chesher and myself. From the parameters of these regressions, I calculated the expected umbilical width at a total width of 55 micrometer units (1.9 mm)—a value about three quarters of maximum size and within the range of all samples. This standardized width is presented in Table 9. Again we encounter morphological fluctuation as snails from red soils are more widely umbilicate than those from eolianites. I do not know the adaptive significance of these changes; the wider umbilicus of red soil *Thysanophora* may reflect the thinner shell of acalcic habitats.

AN EXAMPLE OF PRECISE ADAPTATION IN SPECIFIC MICROHABITATS

General data of the last section do not bear upon the important issue of precision of morphological adaptation to given microenvironments. To what extent is climate such a precise determinant of form that it produces not only general trends expressed in grand means, but also predictable responses to conditions in single localities? With stronger control, for example, inter-sample variation within a time unit should be tied, in direct fashion, to a continuum of subtle climatic differences (and not simply to random variation). Also, different taxa in the same locality should be modified in the same way.

Control might be precise either because the response of snails to climate is direct, predictable and phenotypic or because environments set up such strong selective pressures that even small climatic variations produce recognizable, ordered genetic differences in morphology. Of course, the estab-

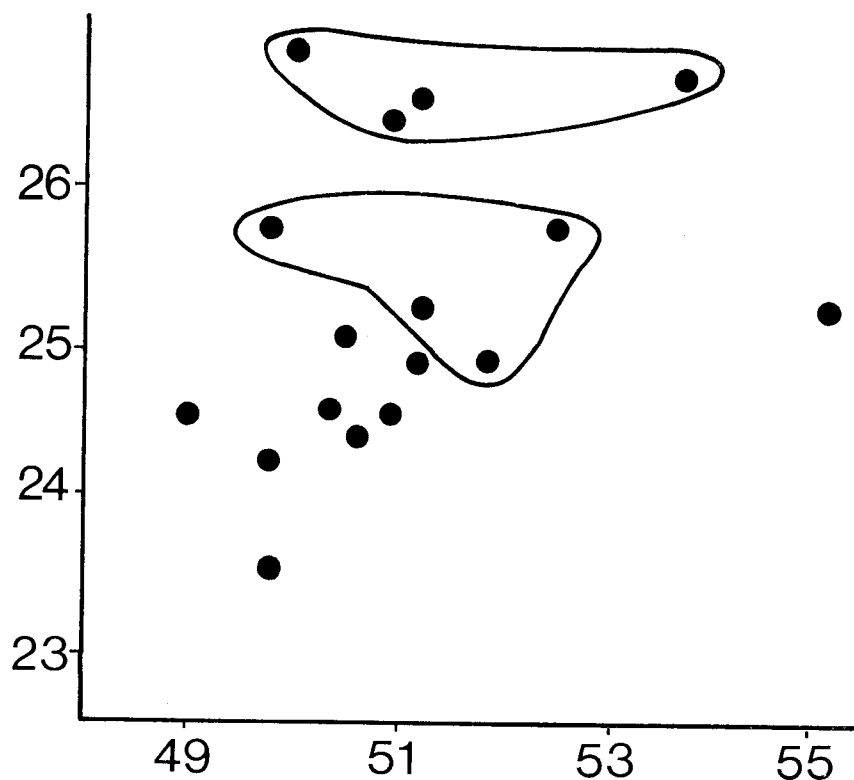


FIG. 8. Height (abscissa) versus width (ordinate) for sample means of *Carychium* adults. All Shore Hills samples in upper circle; all St. George's in lower. In micrometer units at 29 units = 1 mm.

lishment of a close correlation between environment and morphology does not, in itself, argue either for phenotypic or genetic change; it is one of paleontology's common frustrations that we can often establish the correlation and make no assessment of its genetic basis.

Individual localities do show peculiarities that extend to several taxa. Fig. 8 is a plot of mean adult width versus mean adult length for the *Carychium* populations of Table 9. (The circled groups are, from the top, all Shore Hills and all St. George's samples.) The point on the far right is for a Pembroke sample from St. David's Island (not included in Table 9 because the sample did not contain enough *Thysanophora*). These *Carychium* are unique in their extreme relative height, but this sample also contains an endemic subspecies of *P. cupula* and a very unusual, heavily callused *P. nelsoni*. The peculiarities of the three species do not correspond in any apparent way, but their very existence may testify to the influence of isolation as a prerequisite to evolutionary divergence; St. David's is an island on Bermuda's eastern periphery that was probably isolated during all interglacial high stands.

TABLE 10. RELATIVE UMBILICAL WIDTHS FOR FIVE SPECIES OF HELICOID LAND SNAILS AT TOM MOORE'S CAVE VERSUS ALL OTHER SHORE HILLS SAMPLES (IN MM).

	Tom Moore's	Average of others	Range of others	N for others
1. Large <i>Poecilozonites</i> (at height + width = 30 mm)				
a) <i>P. bermudensis</i>	3.01	2.32	2.26-2.40	4
2. Small <i>Poecilozonites</i> (at width = 9.3 mm)			one sample only	1
a) <i>P. circumfirmatus</i>	1.97	1.55	3.14-3.45	4
b) <i>P. reinianus vanattai</i>	3.85	3.34	2.34-2.70	4
c) <i>P. blandi heilprini</i>	2.80	2.53		
3. Microgastropods (at width = 1.9 mm)				
a) <i>Thysanophora hypolepta</i>	0.81	0.74	0.72-0.76	3

The modification of helicoid species in Shore Hills red soil of the Tom Moore's Cave locality is a more outstanding and intriguing case. Five helicoid species in three size ranges are found here: the large *P. bermudensis*, three middle-ranged species of *Poecilozonites*' smaller subgenera, and the microgastropod *Thysanophora hypolepta*. I calculated, by regression, the expected umbilical width at standardized sizes (30 mm for *P. bermudensis*, 9.3 mm for the small *Poecilozonites*, and 1.9 mm for *Thysanophora*) in the manner illustrated for *Thysanophora* on page 511. All five species occur in other Shore Hills samples and expected umbilical width at the standardized sizes were computed for them as well. The results are shown in Table 10. In *each* of the five species, that is, for each of five separate evolutionary events in three size ranges, umbilical width in the Tom Moore's sample exceeds that of every other Shore Hills sample! The environmental control upon pulmonate form can be impressive indeed. If, as I argued previously, *Thysanophora* is more broadly umbilicate in red soils than in eolianites because it deposits a thin shell in the absence of limestone, then, by extension, the same correlation may hold within red soil samples. The snails from Tom Moore's Cave may have had less access to lime than any others in my collection.

REPLICATIONS IN A NATURAL EXPERIMENT ON FORM AND DIVERSITY

Our natural experiment contains two types of replication. First, the climatic sequence occurred twice during Bermuda's recorded history. This established a framework within which a hypothesis of climatic control could be tested by seeing if faunal fluctuation, like that of climate, had occurred twice and in the same way. Secondly, we studied faunal events of two different, and presumably independent, types: relative abundance of species

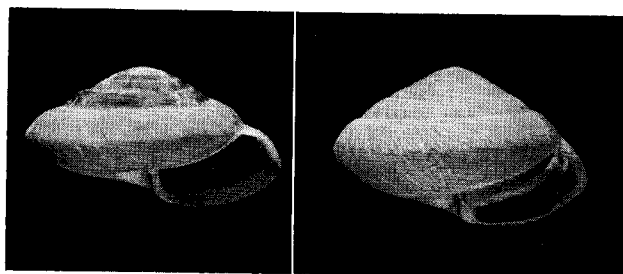


FIG. 9. Correlation of shell thickness and substrate in *P. nelsoni*. Left: *P. nelsoni nelsoni* from Shore Hills red soil. Right: Thick shelled *P. nelsoni callosus* from Pembroke eolianite. Note the remarkably thick callus of the lip. Natural size.

as an aspect of diversity; and shell morphology as an aspect of form. Replications in both categories did occur.

For diversity: the abundances of four microgastropod assemblages fluctuated in sympathy with climatic oscillations; the major species of these assemblages showed similar two-fold oscillations. In discriminant function analysis, all red soil samples were distinct from all eolianites, showing that the upper cycle of St. George's to Southampton had indeed repeated the pattern of the previous Shore Hills to Harrington-Pembroke sequence. Finally, on independent evidence, a climatic interpretation was provided for each assemblage that affirmed the climatic patterns inferred from Bermudian lithologies.

For form: Major shell dimensions of two species change in the same way in both glacial-interglacial cycles. *Carychium* is larger in both red soils than in both eolianites; *Thysanophora* has a wider umbilicus in both red soils.

To these observations on microgastropods, I add a series based on the morphology of land snails in another domain of size. For *P. (Poecilozonites)*, a catalogue of double morphologic oscillations runs to 7 events (Gould, 1969). The three most important occur in three categories of response to environment.

- 1). As (probably) direct phenotypic modification. Two separate stocks of *P. bermudensis* have thinner shells in red soils than in eolianites.
- 2). As incipient speciation in peripherally isolated populations. Thin shelled paedomorphs branched four times from the central stock of *P. bermudensis*. The two thinnest-shelled paedomorphs originated in red soils, presumably as adaptations to their low calcium content.
- 3). As persistent, stable subspecies migrating back and forth with the march of environments. Of two *P. nelsoni* subspecies, one was a thick shelled eolianite form, the other a thin shelled red soil taxon (Fig. 9).

Of all environmental factors that fluctuate with the glacial-interglacial cycles, the one that seems most important to snails is the lime content of the

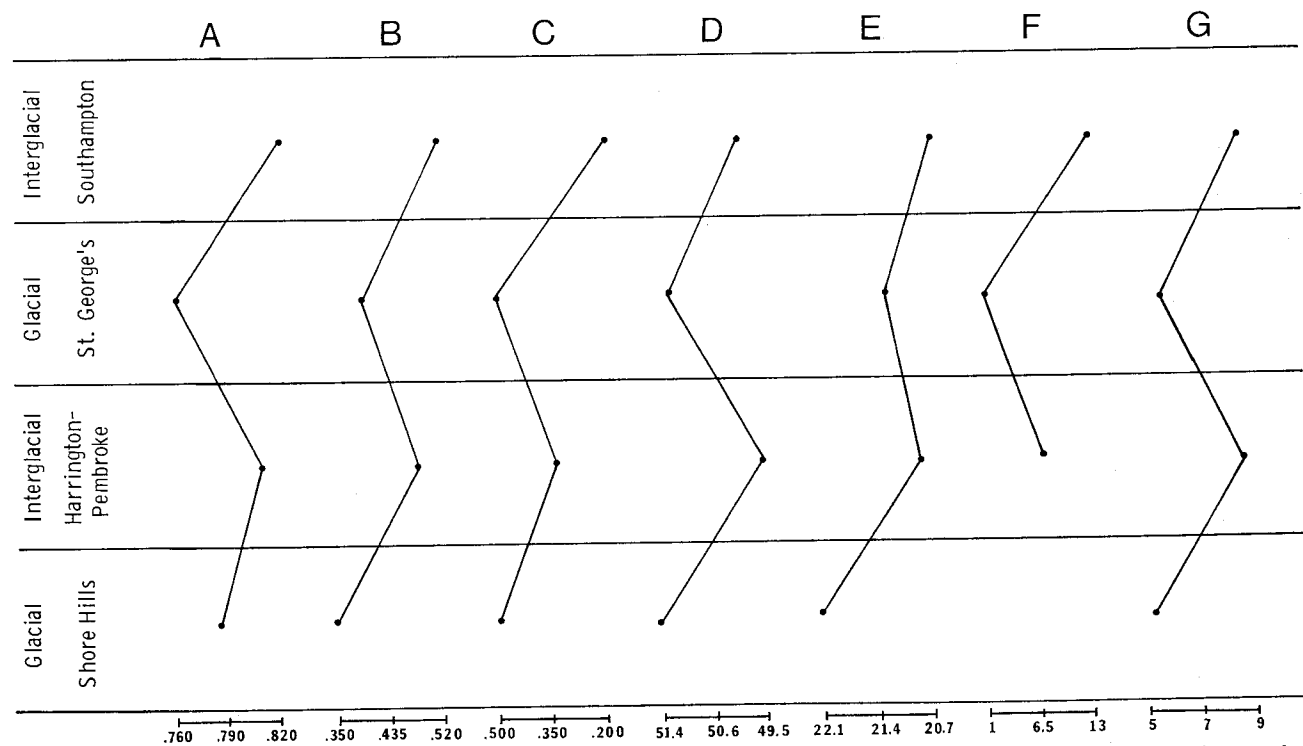


FIG. 10. Correlation of shell form, species diversity and climate in Bermuda. Seven independent events: A). Mean projections for samples of each time period upon the first varimax axis (*Carychium* assemblage of warm, dry, limestone-rich habitats); B). Same for the third axis (assemblage 2); C). Same for the fourth axis (*Thysanophora* assemblage of glacial environments); D). Height of adult *Carychium* 29 units = 1 mm.; E). Umbilical width of *Thysanophora* at width = 55 units, 29 units = 1 mm.; F). Callus thickness for *Poecilozonites bermudensis* from Western Bermuda, in mm. (From Gould, 1969); G). Callus thickness for *Poecilozonites bermudensis* from Eastern Bermuda, in mm. (From Gould, 1969).

substrate. All the *Poecilozonites* events involve thin shells in red soils and thick shells in eolian carbonates; an explanation in terms of calcium abundance is most compelling here. For the four microgastropod assemblages, the three that dominate eolian carbonates all contain calciphilic species while the fourth, most abundant in both red soils, belongs to a genus that has an established tolerance of acalcic conditions. Only for fluctuation in microgastropod form do we lack an explanation based on calcium availability, although the wider umbilicus of *Thysanophora* in red soils may record the thinner shell of these habitats.

Finally, I present as Fig. 10, a chart showing seven of these fluctuating events in diverse categories—an epitome of the success of this natural experiment.

SUMMARY

1). Bermuda is an ideal place to test hypotheses of climatic influence upon organic form and diversity. Its relatively simple environmental cycle—glacial red soils to interglacial eolian carbonates—is recorded twice in Bermuda's Pleistocene sediments. The second cycle acts as an experimental replication for correlations between climate and organisms noted in the first cycle.

2). Land snails comprise more than 95% of Bermuda's terrestrial fossils. This study deals with the twelve species of microgastropods. Forty-eight bulk samples yielded a sufficient fauna for the recognition of snail assemblages based on percentage abundances of these 12 species in all localities. I used several multivariate techniques to recognize assemblages and cluster localities on faunal criteria.

3). I recognized four assemblages in Q-mode eigenvectors for all samples, and in R-mode clusters of species. An environmental interpretation can be provided for each by noting both the lithologies (and inferred climates) of samples clustering with factor axes, and the habitat preferences of those extant species that also inhabit North America.

4). These four assemblages are:

No. 1: *Thysanophora* assemblage: preferred the cool, moist and acalcic conditions of glacial red soils.

No. 2: *Gastrocopta pellucida hordeacella-Pupoides albilabris* assemblage: preferred cool and moist conditions but also required the limey substrates of interglacial carbonates.

No. 3: *Gastrocopta rupicola-Vertigo-Strobilops-Punctum* assemblage: preferred moist conditions and required both limey substrates and warmth of many interglacial habitats.

No. 4: *Carychium* assemblage: required limey substrates and warmth, but also tolerated greater dryness than other assemblages.

5). Additional evidence provided for this interpretation by multivariate studies includes:

a). Projections for mean samples of each time period upon Q-mode axes representing assemblages fluctuate in sympathy with inferred climates. Mean samples of interglacial times have high projections on axes for assemblages that required lime and low projections on the axis of glacial assemblage 1; red soil averages project strongly upon the axis of assemblage 1, weakly upon the others.

b). Discriminant function analysis establishes a strong separation between all red soil and all eolianite localities; very few localities were misclassified and these have anomalously high percentages of species that usually characterize the opposite habitat.

6). The utility of this interpretation is apparent in the solution it provides for a major problem in the distribution of *P. (Poecilozonites)*, a subgenus of Bermuda's outstanding, large, endemic pulmonate. Two of its species, *P. cupula* and *P. nelsoni*, often occur together and both were strongly affected by the rise of the Spencer's Point interglacial sea to plus 60 m (extinction for *P. cupula*; marked limitation of range for *P. nelsoni*). *P. bermudensis* is not found with these species and was not influenced by the high sea. *P. bermudensis* occurs with microgastropods of assemblage 4, *P. cupula* and *P. nelsoni* with assemblages 2 and 3. This correlation is evident both when samples are represented by microgastropod percentage abundances (factor analysis) and when *Poecilozonites* data are included, but only presence-absence is recorded for each species (clustering by Jaccard coefficient). Relatively dry conditions that favored assemblage 4 probably prevailed over all of Bermuda during the Spencer's Point interval.

7). The hypothesis of climatic influence is further affirmed by the discovery that form, as well as diversity, varies systematically with climate. *Carychium* is higher in both red soils than in both eolianites; *Thysanophora* is more broadly umbilicate in both red soils. The precision of climatic control is often striking. For five helicoid species, that is, for five separate evolutionary events, in three size ranges (from *Thysanophora* at 1.9 mm to *Poecilozonites bermudensis* at 30 mm), umbilici in the Tom Moore's Cave sample are broader than those in any other Shore Hills sample.

8). A tabulation of environmental influence upon form and diversity in different size ranges forms the epitome of Fig. 10. The most important factor is probably the abundance of calcium carbonate for shell construction.

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APPENDIX: A

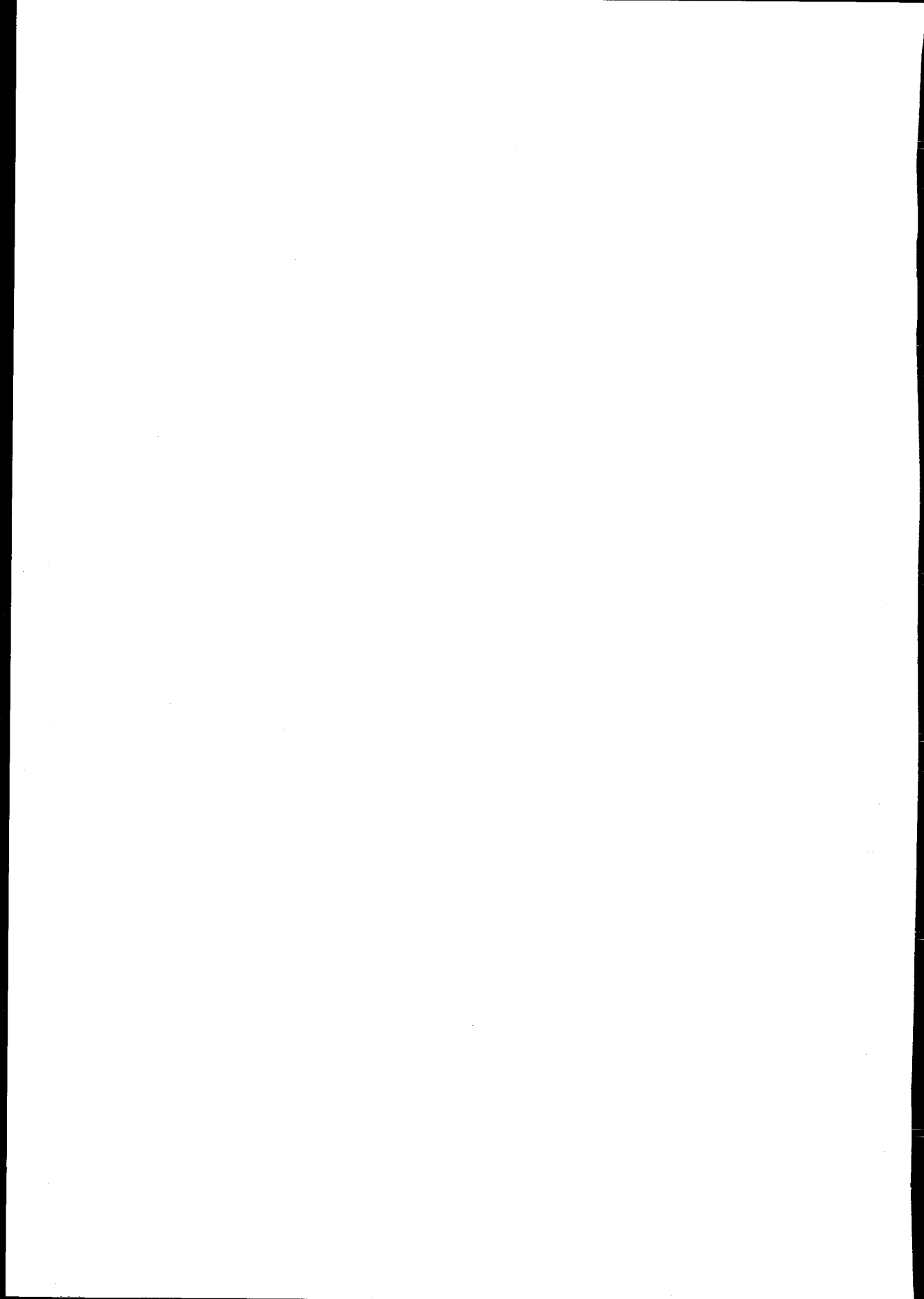
Basic Data Matrix of Relative Abundances for all Species in all Samples.

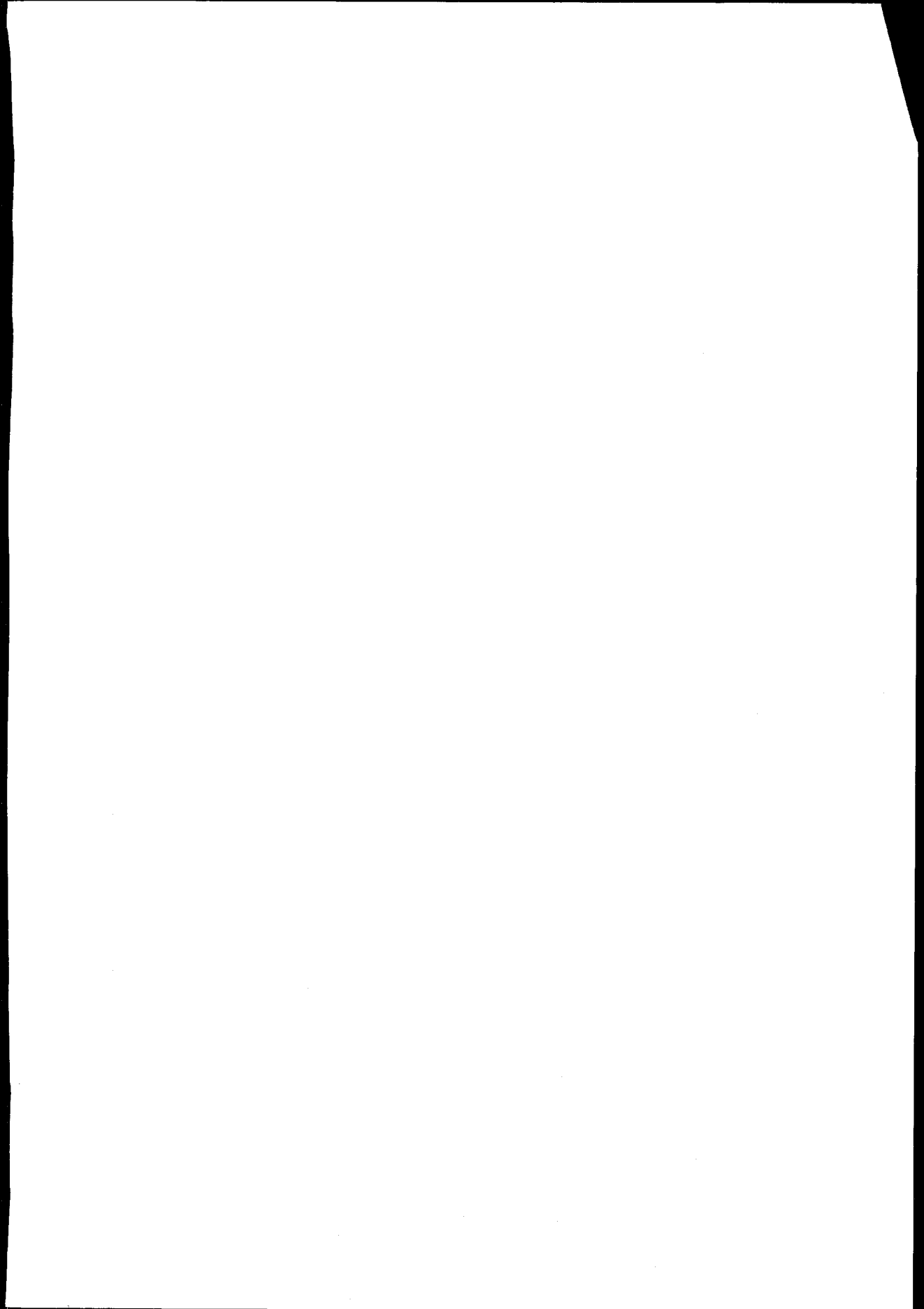
Line Number	Formation	Locality Number from Gould (1969)	Number of specimens in sample	<i>Trysanophora hypolepta</i>	<i>Corychium bernardense</i>	<i>Vertigo numellata</i>	<i>Gastropocopta ruficollis</i>	<i>Gastropocopta pellucida hordeacella</i>	<i>Pupoides abillabris</i>	<i>Strobilopsis hubbardi</i>	<i>Punctum bristolii</i>	Species A	<i>Pupoides</i> sp.	<i>Vertigo markii</i>	<i>Eucomidus turbinatus</i>
1	Walsingham	9	61	.459	.328	.098	.082				.033				
2	Shore Hills	5(main)	253	.387	.581	.012	.016								
3		5(bird)	237	.384	.473	.084	.038								.004
4		53	513	.193	.435	.127	.224			.004	.013		.004		
5		48	45	.089	.422	.267	.133			.010	.004	.008			
6		30	276	.297	.149	.076	.457			.022	.022	.044	.022		
7	Shore Hills(?)	13	225	.040	.266	.169	.120	.382		.022					
8	Harrington-Pembroke	1	56	.054	.054	.268	.536			.018	.004			.009	
9		42	74	.243	.351	.122	.270			.071					.018
10		82	283	.106	.792	.088	.014			.014					
11		55	249	.161	.586	.024	.193								
12		84	61	.180	.344	.148	.279				.024		.012		
13		41(west)	150	.060	.167	.473	.180			.049					
14		41(middle)	137	.073	.073	.350	.394			.033	.040	.007	.007		.033
15		41(east)	283	.028	.127	.303	.254	.134		.036	.058	.015			
16		2	64	.515	.156	.078	.219			.011	.131		.007		.004
17		47	55	.364	.345	.091	.182			.016	.016				
18		44	112	.125	.589	.080	.179			.018					
19		63(lower)	114	.088		.053	.096	.667	.044	.009	.018				
20		63(upper)	279	.276	.416	.104	.183		.004	.004	.004			.011	
21		45	150	.226			.693	.047		.033					
22		86	101	.238			.149	.594		.020					
23		85	66	.121		.091	.015	.697	.061	.015					
24		46	89	.247	.180	.213	.258			.056	.034		.011		
25		4	94	.160		.447	.032	.149		.021	.096	.043	.021	.032	
26		106	215	.126	.651	.070	.107			.037	.005	.005			
27		49	63	.190	.507	.175	.095			.032					
28		51	130	.308	.439	.100	.139			.015					
29		92	226	.181	.181	.248	.353			.026			.004	.008	
30		61	352	.068	.668	.057	.119			.006	.037	.009	.037		
31		62(middle)	349	.046	.811	.046	.083			.014					
32	St. George's	23	89	.270	.371	.056	.292			.011					
33		11	65	.215	.215	.185	.369						.015		
34		17	300	.217	.510	.123	.133			.013	.003				
35		18	108	.407	.343	.213	.037								
36		33	57	.404	.404	.018	.175								
37		41(east)	113	.248	.469	.035	.204	.018		.009	.018				
38		41(middle)	210	.129	.491	.167	.210			.005					
39	Southampton	21(lower)	73	.164	.233	.082	.479				.041				
40		21(middle)	200	.190	.335	.160	.295			.015	.005				
41		27	96	.115	.292	.156	.396	.010		.021			.010		
42		104	115	.104	.470	.148	.261			.017					
43		36	259	.035	.521	.127	.158	.004		.019	.070		.019	.031	.015
44		41(west)	390	.159	.613	.054	.141			.010	.023				
45		41(middle)	398	.048	.460	.060	.289			.010	.106	.005	.023		
46		57	117	.034	.009	.077	.462	.308	.017	.060			.034		
47		81	71	.028	.563	.113	.282			.014					
48		73	67	.104		.030	.015	.687	.149				.015		
49	Shore Hills Average*			.270	.412	.113	.174	.000	.000	.007	.008	.010	.005	.000	.001
50	Harrington-Pembroke Average			.176	.393	.160	.213	.001	.000	.014	.030	.002	.004	.002	.003
51	St. George's Average			.270	.400	.114	.203	.003	.000	.005	.003	.000	.002	.000	.002
52	Southampton Average			.105	.436	.113	.288	.002	.000	.011	.033	.001	.007	.004	.002
53	Grand Average All Samples			.190	.406	.136	.222	.001	.000	.011	.023	.002	.004	.002	.002
54	Number of samples containing species			48	42	46	48	12	5	32	29	9	16	5	5

* As explained in the text, these averages exclude samples dominated by *G. pellucida hordeacella*.

APPENDIX: B
Varimax Factor Matrix for All Samples.

Sample Number	Age of Localities	Projection on Axis 1	Projection on Axis 2	Projection on Axis 3	Projection on Axis 4	Species of <i>P. (Poecilonites)</i> Present
1	Walsingham Fm. Red Soil	0.573	0.198	0.118	0.767	c
2	Shore Hills Fm. Red Soil	0.819	-0.010	0.077	0.567	b
3		0.769	0.090	0.097	0.613	n
4		0.825	0.430	0.061	0.361	p
5		0.856	0.418	0.074	0.117	c
6		0.277	0.760	0.052	0.543	c, n
7		0.543	0.297	0.776	-0.026	c
8	Harrington-Pembroke Fm.	0.152	0.983	0.027	0.061	b
9	Eolian Carbonates	0.696	0.534	0.070	0.471	b
10		0.988	0.003	0.035	0.145	b
11		0.916	0.228	0.032	0.287	b
12		0.717	0.596	0.062	0.350	c, n
13		0.413	0.703	0.101	-0.016	c
14		0.219	0.950	0.063	0.063	c
15		0.363	0.804	0.353	-0.061	c
16		0.271	0.404	0.114	0.863	b
17		0.647	0.355	0.095	0.667	p
18		0.939	0.251	0.035	0.219	b
19		-0.009	0.142	0.983	0.019	n
20		0.781	0.350	0.079	0.511	c
21		0.006	0.833	0.067	0.353	n
22		-0.019	0.188	0.925	0.274	n
23		-0.006	0.061	0.997	0.044	c
24		0.445	0.717	0.104	0.489	c
25		0.098	0.500	0.423	0.114	c
26		0.968	0.131	0.036	0.203	b
27		0.903	0.241	0.076	0.310	b
28		0.789	0.266	0.085	0.545	b
29		0.418	0.837	0.076	0.323	p
30		0.978	0.132	0.024	0.122	b
31		0.991	0.049	0.017	0.085	b
32	St. George's Fm. Red Soil	0.684	0.483	0.058	0.521	p
33		0.461	0.783	0.068	0.406	p
34		0.889	0.253	0.068	0.371	b
35		0.625	0.218	0.131	0.652	n
36		0.667	0.245	0.082	0.695	b
37		0.822	0.300	0.085	0.459	b
38		0.883	0.405	0.052	0.222	b
39	Southampton Fm. Eolian	0.435	0.793	0.024	0.320	p
40	Carbonates	0.688	0.620	0.064	0.367	p
41		0.589	0.762	0.054	0.222	p
42		0.855	0.474	0.040	0.192	p
43		0.946	0.301	0.038	0.060	b
44		0.943	0.174	0.039	0.267	b
45		0.840	0.464	0.012	0.111	b
46		0.032	0.765	0.531	0.029	b
47		0.898	0.407	0.015	0.071	b
48		-0.015	0.018	0.986	0.037	b
49	Shore Hills Average	0.786	0.350	0.080	0.502	
50	Harrington-Pembroke Average	0.807	0.480	0.071	0.333	
51	St. George's Average	0.762	0.397	0.083	0.503	
52	Southampton Average	0.822	0.514	0.037	0.208	





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