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Source: *Journal of Paleontology*, Vol. 45, No. 3 (May, 1971), pp. 409-418

Published by: [SEPM Society for Sedimentary Geology](#)

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JOURNAL OF PALEONTOLOGY

A publication of THE SOCIETY OF ECONOMIC PALEONTOLOGISTS
AND MINERALOGISTS and THE PALEONTOLOGICAL SOCIETY

VOLUME 45

MAY 1971

NUMBER 3

JOURNAL OF PALEONTOLOGY, v. 45, no. 3, p. 409-418, 4 TEXT-FIGS., MAY 1971

PRECISE BUT FORTUITOUS CONVERGENCE IN PLEISTOCENE LAND SNAILS FROM BERMUDA

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ABSTRACT—Two convergences between subgenera of Bermudian land snails [*P. (Poecilozonites)* and *P. (Gastrelasmus)*] were initiated when a taxon of one subgenus evolved to the very different size range of the other. Entrance into this new size range produced or required a set of correlated changes in shape, color, and thickness that resulted in very precise convergences. Some of these ancillary changes were direct adaptations to the new size range: the large taxon of the generally small subgenus evolved a triangular dome; the rapid increase of height/width that produced a strong dome at the usual small sizes could not be maintained to this large size. Other changes were fortuitous consequences of growth and its interaction with the developmental rate: the small taxon of the generally large subgenus retained its color bands; the small subgenus does not usually produce bands—adult shells display the blotched pattern of an earlier ontogenetic stage common to the whole genus; but one taxon of the small subgenus grew more than the usual number of whorls, forming thereby both the high dome and the color bands that produced convergence. Convergence would seem awesome if we recognized: a) how many characters can be modified together as mechanical or developmental consequences of a primary adaptation; b) how limited are the adaptive solutions to common problems—in particular to altered size.

INTRODUCTION

BASHFORD DEAN, Columbia's eminent ichthyologist, once wrote a "chapter in un-natural history" in which he catalogued a set of strictly fortuitous resemblances between, for examples, Japanese crab carapaces and oriental faces, or whale "earbones" beached in Norway and Scandinavian sailors (Dean, 1908). These examples are at one clear extreme of the continuum between "fortuitous" and "adaptive" convergences that Rudwick (1965) recognizes. Despite some disagreement,¹ I do not see what sense can be

¹ Although noble attempts have been made to resolve, or at least to categorize, the confusion (Haas and Simpson, 1946), this little corner of evolutionary theory is wallowing in a mire of terms used in different ways by various authors. George (1962, p. 22), for example, terms "accidental" all convergence that does not have genetic equivalence as its basis; practically every case of our adaptive—and therefore not fortuitous—convergence would be termed accidental by George. (Most authors would resolve this dilemma by definition—by designating as parallelism, rather than as convergence, all similar features evolved in

made of these terms unless "fortuitous" convergence covers all similarities that are evolved independently by different lineages, but are not the results of selection operating directly for their attainment. I will argue here that two very precise convergences in Bermudian land snails include fortuitous features evolved as the correlates of a primary adaptation—the encroachment by an unusual form upon the size range of a related subgenus. As Dean's examples show, our sense of wonder is inspired in direct proportion to the extent of fortuitous resemblance.

A convergence may be "explained" at various levels of satisfaction. Ideally, we know the significance of each adaptive feature and the cause of every fortuitous resemblance. Often, here in-

separate lineages by the selection of homologous genes). An event, of course, is "fortuitous" only in respect to the theory under which it is analyzed. The similarity of shells and faces—or of staurolite crystals and the true cross—was once awarded great significance as a sign of divine unity in the plan of creation.

cluded, we can only identify the adaptation, but can explain other resemblances as necessary correlates to it. Raup (1968) achieved this level of explanation when he rendered the form of some echinoid plates as a consequence of close packing (mechanical pressure), given an initial plate shape, rate of growth and rate of supply, but did not explain why one set of "givens" was selected over another.

ARGUMENT: TWO CONVERGENCES
AND THEIR CAUSES

I shall state the argument and then develop its points.

1. Shells of *Poecilozonites* (*Poecilozonites*) are generally large (up to 45 mm in width), while those of *Poecilozonites* (*Gastrelasmus*) are usually small (rarely more than 10 mm). Once during the Pleistocene history of each subgenus, a single form evolved to the size range of the other.

2. When it entered this new size range, each form converged in shape and color upon a taxon of the other subgenus.

3. For the large taxon of *P. (Gastrelasmus)*, convergence in shape was a necessary consequence of growth to an unusually large size. The small taxon of *P. (Poecilozonites)* evolved a shape that it could not have maintained when large and, thereby, converged upon a subspecies of *P. (Gastrelasmus)*. Size and shape are correlated in each case.

4. Each converging taxon retained, at its new and unusual size, the characteristic color pattern of its subgenus. The taxa converged upon had evolved these same patterns. Since color has the same ontogeny in all *Poecilozonites*, differences among taxa result from variation in size, whorl number and rate of growth. Convergences in color are the fortuitous results of similarities in these variables.

1. The genus *Poecilozonites* in Bermuda

The speciation of *Poecilozonites* on Bermuda provides a classic example of "island evolution." With the exception of *Succinea*, it is the only large pulmonate that reached this isolated island. It diversified remarkably and had split into three subgenera (with at least 10 species) when fossils are first found in the Pleistocene (see Pilsbry, 1924 and Gould, 1969 on *Poecilozonites*; Bretz, 1960 and Land, Mackenzie and Gould, 1967 on Bermudian geology; the volcanic base of Bermuda has recently been dated as Oligocene-Miocene in age). Each subgenus has its characteristic size, shape, and color.

a) *P. (Poecilozonites)*, the nominate sub-

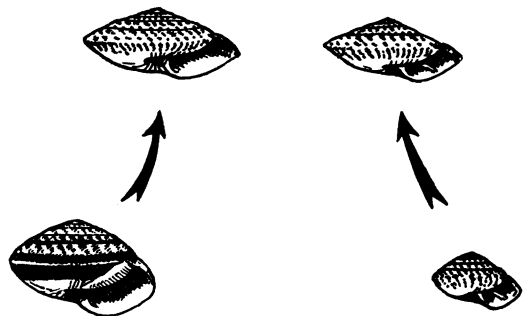
genus and only one recently studied (Gould, 1969), is generally large (20–40 mm in width), strongly domed, thick, and colored with chestnut-brown bands as an adult. (Band number, width and position vary among taxa—Gould, 1969, pp. 429–431). Subgeneric terminology was erected by Pilsbry (1924) who established the subfamily Poecilozonitinae (in the Zonitidae) for this genus alone.

b) *P. (Gastrelasmus)* is generally small (5–10 mm in width), strongly domed, narrowly umbilicate, thin, and colored with discontinuous blotches that become stronger and wider with growth but do not coalesce to form bands. It has one unique and defining feature: an internal palatal lamina that extends from the aperture to the termination of the protoconch (though it is often resorbed in the apical whorls). Were it not for this lamina, I would not have recognized the convergences reported here.

c) *P. (Discozonites)* is generally small (8–15 mm in width), flat to strongly domed, thin, colored with discontinuous blotches, and as defining features, has a rounded whorl periphery and wide umbilicus. Both convergences are between *P. (Poecilozonites)* and *P. (Gastrelasmus)*; *P. (Discozonites)* shall not be considered further, although it developed some equally outstanding convergences with *P. (Gastrelasmus)*. This paper reports only those convergences that result from the transgression of one subgenus upon the characteristic size of another.

2. Two convergences between *P. (Poecilozonites)* and *(P. Gastrelasmus)*

Case 1 (Text-fig. 1): In all Bermudian formations, the most common species of *P. (Gastrelasmus)* is *P. (G.) circumfirmatus* Redfield; it is depicted on the lower right of Text-figure



TEXT-FIG. 1—The convergence of *P. (P.) bermudensis* pedomorphs (upper left) and *P. (G.) acutissimus* (upper right). Convergence involves size, shape, color, and thickness. The internal palatal lamina of *P. (Gastrelasmus)* distinguishes the subgenera. Actual size.

1. Other taxa are larger, more widely umbilicate, or more triangular in cross-section but these variations are minor compared with that found in *P. (G.) acutissimus* Pilsbry, 1924. Pilsbry's types and paratypes do not stand out among the subgenus; for while they are more delicate, sharply keeled and triangular than any others, they are not distinct in size, the largest being 11 mm in width. In 1966, at an exposure of the Harrington-Pembroke Formations (east of Pink Beach on the south coast), I found a sample that shares all the characters of Pilsbry's *P. (G.) acutissimus* but contains specimens that are almost twice as large (up to 20.5 mm in width). Zonitoids grow throughout life; they have no recognizable adult stage. All but 3 of Pilsbry's specimens are broken; the others may be juveniles. The extremely delicate shell is rarely preserved intact. Thus, Pilsbry missed the outstanding characteristic of *P. (G.) acutissimus*—its large size. At widths greater than 20 mm, it lies well in the range of *P. (Poecilozonites)* where I would have placed it without hesitation had it not been for its palatal lamina. A specimen is shown in the upper right of Text-figure 1.

Even at its large size, *P. (G.) acutissimus* does not approach the characteristic form of *P. (Poecilozonites)*. Its rather triangular cross-section, wide umbilicus, thin shell and blotched coloration, contrast with the strong dome, narrow umbilicus, thicker shell and color bands of most *P. (Poecilozonites)*—lower left of Text-figure 1. Yet, four times during its Pleistocene history, *P. (P.) bermudensis zonatus* evolved paedomorphic subspecies that are scaled-up replicas of its juvenile shell (Gould, 1968, 1969, pp. 469–483). And these paedomorphic shells are:

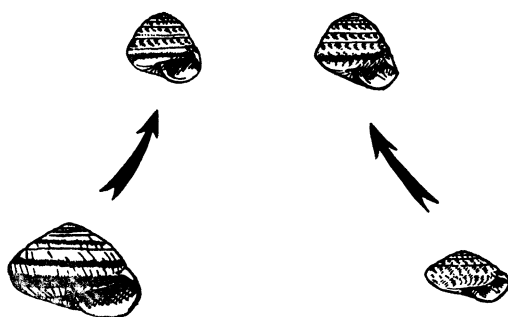
a) rather triangular in cross-section—since the dome develops gradually during growth.

b) widely umbilicate—since umbilical width is a mechanical correlate of the shell's relative width (Gould, 1968).

c) thin—since the shell increases in relative thickness during growth.

d) blotched in color—since the development of color progresses from juvenile blotches to adult bands. In other words, these paedomorphic subspecies of *P. (P.) bermudensis* share all major features of size, shape, color, and thickness with *P. (G.) acutissimus*, but lack a palatal lamina (upper left of Text-fig. 1).

Case 2 (Text-fig. 2): In 1904, Gulick described, as *P. dalli*, a peculiar shell from an unknown locality on Bermuda. It clearly belonged to *P. (Poecilozonites)* and stood in closest relation to *P. cupula*, the smallest species of this subgenus. Yet, it was a good deal smaller than

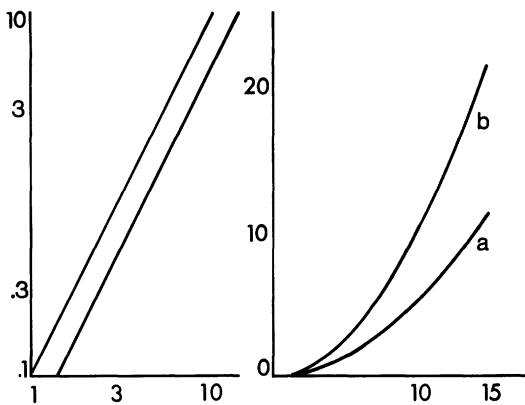


TEXT-FIG. 2—The convergence of *P. (P.) cupula dalli* (upper left) and *P. (G.) circumfirmatus cavespiram* (upper right). Convergence involves size, shape, color, and thickness. The internal palatal lamina of *P. (Gastrelasmus)* distinguishes the subgenera. Actual size.

any other *P. (Poecilozonites)* and had a remarkably high and strongly-domed spire. In the 1920's, Sayles collected a large sample from Harrington-Pembroke outcrops on Bermuda's south shore. I collected more specimens and demonstrated that this taxon is a subspecies of polytypic *P. (P.) cupula* (in Gould, 1966a, 1969).

P. (P.) cupula dalli is shown in the upper left of Text-figure 2; its progenitor *P. (P.) cupula cupuloides* occupies the lower left. The size difference is not as striking in two-dimensional representation as it is in actual specimens. This is a common psychological artifact. We intuitively judge size by volume when holding actual specimens. Size differences seem much smaller in figures—where we compare areas at best, and often only lengths. There is a large literature on the relationship between perceived and actual differences in sizes, sounds, light intensities, etc. (Stevens and Girao, 1963; Stevens, 1968, for example). The principle is well understood by map makers in their choice of symbols for relative sizes of cities or production of commodities; but it is rarely recognized by biologists or geologists. Likewise, in Text-fig. 1, *P. (G.) acutissimus* is not quite twice as long as *P. (G.) circumfirmatus*: yet its volume is almost eight times as great.

Although *P. (G.) cupula dalli* lies in the size range of *P. (Gastrelasmus)*, it is not close to the usual shape of that subgenus, for its spire is too high, its dome too strong, and it has retained the adult color bands of larger *P. (Poecilozonites)*. But in 1965, I collected from the Shore Hills soil of St. George's Island (Locality 48 of Gould, 1969), a sample that I labelled as *P. (P.) cupula dalli* until I noticed the well-developed palatal lamina of *P. (Gastrelasmus)*. The char-



TEXT-FIG. 3—Left. Log-log plots of spire height (ordinate) vs. spire width (abscissa) for two hypothetical individuals of the same doming intensity but different initial shapes. Lower equation: $y = .05x^2$. Equation of upper line: $y = .10x^2$. Right. The same two equations on arithmetic coordinates to show that intensity of doming and spire height are not synonymous. Line *a* (lower line of log-log plot) has the same doming intensity but lower initial shape than line *b*. The arithmetic curves represent actual spire geometry (of an inverted shell with its apex at the origin of the graph). Thus, the shell represented by curve *a* is relatively wider than that of curve *b* at any adult size.

acteristic Shore Hills *P. (Gastrelasmus)* is widely-umbilicate, thin-shelled *P. (G.) circumfirmatus caliban*. The shells at Locality 48 are not only thick and narrowly-umbilicate (in addition to the spire and color characters that converge on *P. (P.) cupula dalli*), but they also occupy a geographic area inhabited by no other *P. (Gastrelasmus)* at that time. They therefore merit recognition as a subspecies, which I name *P. (G.) circumfirmatus cavespiram* (Text-fig. 2, upper right), in reference to the deceptive configuration of the spire (formal description and figure in appendix).

3. The correlation of size and shape

The basic shape of a domed shell can be rendered by three factors:

a) the intensity of doming. To produce a dome, the shell spire must increase in height faster than it grows in width. If y and x represent, respectively, the height and width of the spire at each postprotoconch whorl, the rate of doming can often be represented by a standard power function of the form

$$y = bx^k \quad (1)$$

in which k is the ratio of specific growth rates of y vs. x (Goald, 1966a, 1969, pp. 426–428).

b) the initial shape upon which doming is

imposed. The embryonic shell, or protoconch, is deposited within the egg, essentially as a single unit. Although it differs in mode of growth from later shell and is subject to other selective and mechanical pressures, it nevertheless forms a nucleus about which the accretionary shell grows. Its initial shape has a great effect upon final form when growth of the dome follows a power function. Shells that differ only in initial shape and not in intensity of doming will plot as a series of parallel lines on log-log paper Text-fig. 3). On arithmetic coordinates, the same formulae yield curves that differ greatly in spire height at any given size. (Intensity or rate of doming is not equivalent to spire height, though the two are usually correlated.) These arithmetic curves are actual portrayals of spire geometry, as if the shell were placed upside down with its apex near the origin of the graph. [Here, for reasons outlined in Goald, 1969, p. 426, equation (1) was fit for each shell from whorl 2 to the end of growth and protoconch height was subtracted from each of the height measures. Thus, my measure of initial shape, as reported in Table 1, is spire height at whorl 2—protoconch spire/spire width at whorl 2].

c) the size at which doming begins. Since the height/width ratio of the spire increases continually during accretionary growth, a shell that begins doming at the same intensity and initial shape but at a smaller size than another will have a higher spire at any later common size. Since width at the end of the first whorl is a redundant measure of protoconch width in *Poecilozonites* (Goald, 1969, p. 443), protoconch width is an appropriate measure of initial size; it is recorded in Table 1.

When intensity of doming, initial shape and initial size are specified, height/width ratios and spire shape can be calculated for any later size. Their values, in fact, place constraints upon final size. The most important of these is imposed by intensity of doming, for the higher the k -value in (1), the faster height increases than width. High values of k cannot be maintained over a wide size range, lest the spire reach inadaptive heights. The negative correlation of final size and intensity of doming in *P. (Poecilozonites)* (Goald, 1966a) reflects this principle: *P. (P.) cupula* must remain small, for extrapolation of its high k -values to the shell width of *P. (P.) nelsoni* would produce spires up to twenty times higher than wide.

The shapes of our convergent forms are also related to their unusual sizes:

Case 1: For the small sizes that characterize all but one of its species, high k -values pose no

TABLE 1—Summary of doming factors in selected taxa of *Poecilozonites*

Taxon	<i>k</i> -value	Initial shape	Initial size (protoconch width)	Number of samples (20 shells per sample)
<i>P. (P.) bermudensis</i> paedomorphs				
<i>P. (P.) b. fasolti</i>	2.02	.160	2.00	1
<i>P. (P.) b. siegmundi</i>	1.99	.250	2.13	1
<i>P. (P.) b. sieglindae</i>	1.99	.209	2.18	2
<i>P. (P.) b. bermudensis</i>	1.92	.269	2.09	10
<i>P. (G.) acutissimus</i>				
Pink Beach Sample	1.92	.173	1.65	1
Type Sample	1.77	.241	1.51	1 (7 specimens)
<i>P. (P.) cupula dalli</i>	2.95	.418	1.52	1
<i>P. (P.) cupula cupuloides</i>	2.15	.266	1.85	6

problems for *P. (Gastrelasmus)*. Most of its taxa have *k*-values greater than 2.3, relatively high initial shapes, and small initial sizes; this combination is strongly size-limiting. To reach the size of *P. (G.) acutissimus*, some doming factor had to be modified. Table 1 shows that the initial size of *P. (G.) acutissimus* remained small; hence it needed a more triangular cross-section (= lower rate of doming) in order to reach its final size. The two samples of *P. (G.) acutissimus* display different strategies for attaining large sizes. The type sample has maintained a high initial shape, but reduced its *k*-value below that recorded for any *P. (Poecilozonites)*; the Pink Beach sample has a much wider initial shape and can maintain a greater rate of doming. The four paedomorphs of *P. (P.) bermudensis* have combinations of *k*-value and initial shape that should produce spires higher than those of *P. (G.) acutissimus*, but their initial sizes exceed those of *P. (G.) acutissimus* and near-identity of shape is maintained by any common adult size because this tendency towards higher spires began at a larger size. With its retention of small initial size, convergence by *P. (G.) acutissimus* upon the shape of *P. (P.) bermudensis* paedomorphs became an inevitable consequence of evolution towards the larger sizes of *P. (Poecilozonites)*.

Case 2: As the smallest taxon of its subgenus, *P. (P.) cupula dalli* stands at one extreme of a pervasive correlation between size and shape. Its mean *k*-value of 2.95 is the highest I have recorded for the genus; since this is imposed on a high initial shape and small initial size, all doming factors combine to produce the highest and most intensely-domed spire in *Poecilozonites*. In evolving to the small size of *P. (Gastrelasmus)*, *P. (P.) cupula dalli* did not cease growth at fewer whorls, but rather miniaturized its whorls, attaining a protoconch size well within

the range of *P. (Gastrelasmus)*; I cannot argue, as I did for Case 1, that the unusual shape of this convergent form was a prerequisite to its entrance into a new size range. The correlation of size and shape is weaker here. The small size of *P. (P.) cupula dalli* allowed it to attain a shape that no normal taxon of its subgenus could maintain at the usual large size.

P. (G.) circumfirmatus cavespiram produced its high spire both by increasing its *k*-value and, more importantly, by maintaining that intensity of doming over a greater than usual number of whorls.

In both cases, I suspect that new sizes and shapes were produced by active selection for them. Beyond this, we can only speculate on primary effects and secondary consequences. In *P. (G.) acutissimus*, the low, triangular dome might have evolved before size increased. Alternatively, selection pressure for this shape may have arisen only when the size that required it also became advantageous. At least, increase in size could not have preceded the modification of shape. We encounter the reverse situation in *P. (P.) cupula dalli*; here alteration of shape could not have preceded the diminution of size. In this case, either size and shape were selected in concert, or small size came first and permitted a positive selection for high *k*-values with intense domes at small initial sizes. I have no way of distinguishing these alternatives.

But there is also a fortuitous aspect to these convergences in shape. With its small initial size, *P. (G.) acutissimus* could only have grown large by evolving a weakly-domed, rather triangular spire. Yet, this shape produces no convergence with any normal taxon of *P. (Poecilozonites)*; these are all more intensely domed. The unusual *P. (P.) bermudensis* paedomorphs have a weakly-domed, triangular spire because selection for a retarded developmental rate pro-

longed juvenile shapes to adult sizes. Yet this retardation was selected to produce a thin shell in the calcium-poor environments of Bermuda's red soils (Gould, 1968, 1969). The weak color and triangular spires are secondary, and non-adaptive (though obviously not inadapative), consequences of this primary advantage. Thus, the weakly-domed triangular spire is directly adaptive in one taxon, but produced as a developmental consequence of another adaptation in the second. The similarity is fortuitous.

Likewise, in becoming small and high-spired, *P. (P.) cupula dalli* did not resemble any normal taxon of *P. (Gastrelasmus)*, for these are all lower-spired. If the unusual *P. (G.) circumfirmatus cavespiram* grew more whorls in order to attain a high spire, then the convergence is adaptive since high spires were selected directly in both taxa. If the high spire of *P. (G.) circumfirmatus cavespiram* is a by-product of strong allometry prolonged to an advantageously large number of whorls, then the convergence is fortuitous. Again, I can neither distinguish these alternatives nor assess a third—that both increased whorl number and a high dome were favored by selection, and that the mode of growth that links the two provided an easy mechanism for their mutual production.

4. Color and thickness

Although band numbers, widths, positions, and times of formation differ within and among taxa, the basic ontogeny of coloration is common to the entire genus. Deposition brings on the last half whorl of the protoconch as even-sided radial stripes. These continue for about one whorl of accretionary growth, but are gradually transformed to the characteristic zigzags (also called flames or blotches) that give the genus its name (*Poecilozonites* = variegated-banded). Next, constrictions form in those parts of the zigzag that will not form bands in the adult. Finally, the remaining parts of the zigzag strengthen and widen, interstitial color is deposited between zigzags and bands form. The sequence of flame-band transitions is also invariant, moving from bottom to top of the whorl. The subperipheral color band always forms first, followed by the supraperipheral (if present), and finally by the subsutural (if present). The subsutural band forms so late in ontogeny, that most taxa do not produce it at all, but maintain color blotches in this position as adults. There is enormous variation in whorl number of the flame-band transition among taxa. The subperipheral band, for example, may form by the second postprotoconch whorl (most *P. (P.) cupula* subspecies) or still be repre-

sented by precursor blotches at the sixth (paedomorphic *P. (P.) bermudensis* subspecies).

The processes of growth and development are partly correlated and partly independent. The ontogenetic color sequence, as an aspect of development, is obviously displayed through growth—its stages, in any single individual, appear sequentially as size increases. But development can be retarded or accelerated relative to growth, producing the phylogenetic phenomena of heterochrony. The paedomorphic subspecies of *P. (P.) bermudensis* are greatly retarded in development; the colors and shapes that characterize small ancestral juveniles do not appear until adult sizes in these taxa. Our color convergences are fortuitous results of the influence of developmental heterochrony upon a universal ontogeny of color.

Case 1: Because they are small, shells of *P. (Gastrelasmus)* rarely advance beyond the flame stage to the formation of bands. *P. (G.) acutissimus* reaches its abnormally large size not by growing more whorls (with consequent intensification of development), but by enlarging the size of late whorls. All three subgenera of *Poecilozonites* have approximately the same number of adult postprotoconch whorls (5–6). Color differences among subgenera are correlated with size—the two small subgenera rarely form bands, but only the developmentally-retarded *P. (Poecilozonites)* lack them. However, within any subgenus, given stages in the ontogeny of color tend to occur at the same whorl number regardless of size at that whorl. Since *P. (G.) acutissimus* does not have an unusually large number of whorls, it remains in the flame stage as an adult. In addition, there is a pervasive, though unexplained, correlation between high spires and strong coloration in *Poecilozonites* (Gould, 1969, p. 441 and p. 501). As the relatively widest taxon of its subgenus, we might expect *P. (G.) acutissimus* to retain weak color even if it possessed more than the usual number of whorls.

The retention of flames in adult *P. (G.) acutissimus* is a consequence of normal growth patterns for the subgenus. *P. (P.) bermudensis* paedomorphs, on the other hand, form no bands because their developmental rates are retarded relative to size. The adaptive significance of this retardation lies in the thin shell it produces in calcium-poor habitats; weak coloration is an accidental by-product of an evolutionary mechanism utilized to produce a thin shell rapidly. In neither case does the retention of flames have adaptive significance for its own sake. The same result is reached in a different way in each case. The resemblance is fortuitous.

Case 2: If *P. (P.) cupula dalli* had become small by reducing its number of whorls, shell coloration would not have progressed beyond the flame stage. But since miniaturization of whorls formed its path to small size, *P. (P.) cupula dalli* retains the banded adult coloration of its ancestors. Its color does not correspond to the normal, flammulated pattern of *P. (Gastrelasmus)*. But *P. (G.) circumfirmatus cavespiram* does develop bands for two reasons: 1) It has an unusually large number of postprotoconch whorls (6–7) and thereby reaches stages of the universal color ontogeny that normal taxa of its subgenus do not attain. 2) It partakes of the common correlation between high spires and strong coloration.

In both taxa, color bands are developed as a simple consequence of growth. I have no evidence that these modes of growth were selected to produce a favored color rather than for their own sake and suspect, therefore, that similarities in color are fortuitous.

Other allometric features of growth are common throughout the genus; they produce additional fortuitous convergences that are visually less striking than that involving color:

1. umbilical width. In *Poecilozonites*, umbilical width increases regularly until the shell reaches its maximum relative width; thereafter it remains constant (Gould, 1969, fig. 6, p. 432). The few relatively high-spired taxa of *Poecilozonites* are exceptional. In these, umbilical width, after reaching its maximum in the normal way, becomes progressively constricted as rapidly increasing height/width ratios form a high dome (Gould, 1969, photo on frontispiece). In accordance with these patterns, both *P. (G.) acutissimus* and *P. (P.) bermudensis* paedomorphs have equally wide umbilici, while both *P. (G.) circumfirmatus cavespiram* and *P. (P.) cupula dalli* have narrowly constricted ones. These resemblances are mechanical consequences of similar shell shapes; we need not postulate any direct selection for their presence.

2. shell thickness. Relative shell thickness increases constantly during the ontogeny of all *Poecilozonites*, but the rate of increase varies greatly. The thin shells of *P. (P.) bermudensis* paedomorphs are produced by relative retardation of the developmental rate; this, as I argued before, is an adaptation to the low lime content of Bermuda's red soils. *P. (G.) acutissimus* retains, at its increased size, the thin shell that characterizes its subgenus because it reaches this size at a normal number of whorls and shows no sign of any prolongation of development. Since *P. (G.) acutissimus* lived only in carbonate dunes, the thin shell is not likely to

have had the same significance that it did in *P. (P.) bermudensis* paedomorphs. *P. (P.) cupula dalli* retains its relatively thick shell because it decreased in size by miniaturizing its whorls without altering its rate of development. *P. (G.) circumfirmatus cavespiram* has an unusually thick shell for its subgenus because it grew more whorls and thereby prolonged its period of development to a stage of shell thickness attained by no other taxon of its subgenus. I have no reason to believe that retention or acquisition of a thick shell played a direct part in the adaptation of these forms.

A CONCLUSION AND MODEST PROPOSAL

The preceding examples remain trivial in themselves and even a bit whimsical for their fortuitous precision. Yet, I detect a larger significance for these cases because they exemplify, so very well, two general aspects of convergence that rarely receive the emphasis they deserve.

1. Forms of apparent complexity are often generated by few factors. We doubt (or wonder inordinately at) many precise convergences because we view each of their attributes as a separate event. Yet, as Raup has shown in his computer simulations (1966, 1968, 1969), the interaction of simple rates and gradients upon initial shapes during growth can produce such remarkably intricate structures as the echinoid ambulacrum. In most fields that deal with complex situations, progress from near-blind empiricism to general theory comes when that complexity is displayed as a result of few causal factors. (We are, I believe, not witnessing this progression in the ideas of mathematical population ecology—what Wilson (1969) has so aptly termed “post-Darwinism”). Morphology, another field that deals in complexity, has long been hampered by a tradition that exalts detailed, part-by-part description as virtuous because it is “pure fact” and not theory-loaded—without realizing that such a procedure subtly nudges us to a theory that complexity is irreducible. I have argued elsewhere (chapter 3 of Gould, 1970) that the reduction of complexity to fewer generating factors would provide an essential component to a causal morphology.

We meet, in our convergences, two types of character-groupings that can be reduced to simpler casual factors:

a) mechanical correlates. It has long been recognized that the exuberant diversity of molluscan shells can be rendered by varying the few factors that must be specified to generate a spiral. D'Arcy Thompson (1942, p. 785) notes that Swammerdam had stated this as early as

1737: "Omnis enim quae inter eas animadvertitur differentia ex sola nascitur diversitate gyrationum"—for all difference that is noted among them originates only from the diversity of spirals. Since we are used to expressing our observations in widths, lengths and ratios (the products, not the causes), we rarely apprehend the redundancy. In this study, for example, convergence in umbilical width is only the necessary consequence of convergence in spire shape. "Even strong and apparently complex resemblances in form . . . may sometimes signify no more than the . . . numerical coincidences which are manifested in identity of length or weight or any other simple magnitude" (Thompson, 1942, p. 808).

b) developmental correlates. In land snails, the changes that mark adulthood are widespread and varied. Land snails often change color, shell thickness and coiling direction at this stage and these features arise in concert, presumably under the influence of a single sex or growth hormone. In *Poecilozonites*, development is often accelerated or retarded relative to the rate of size increase. In paedomorphosis, characters of spire shape, color and thickness are delayed to an equal degree in size of appearance (Gould, 1968). Their correlated modification probably marks a change in a single factor that monitors the rate of development.

2. Change in size requires correlated modifications of shape; these are often so rigidly specified that convergence is inevitable.

With these two statements, I am arguing that close convergence is less surprising and improbable than it appears under our usual views of phylogeny. The first statement, discussed above, argues that the mechanism of a precise convergence in many characters may be simple because it involves the modification of a single factor with many correlated effects. This second statement contends that a close convergence may be inevitable because it represents the only adaptive solution to a problem faced in common by several lineages. In this realm of biomechanics, no factor imposes more serious constraints upon form than large changes in size itself. Best documented are the relative increases in surface area that large animals require to maintain the processes of respiration, digestion and support; the geometric pathways to this increase—flattening, elongation and convolution—are strictly limited (Thompson, 1942; Gould, 1966b; Alexander, 1968). The fossil record provides many examples of size-imposed similarities among lineages increasing in size. The brachiopod lophophore gathers food through its surfaces and must be multi-lobed or spirally

coiled in large forms (Gould, 1966b, p. 591). Several authors have documented similar features evolved independently by many larger foraminifers to meet structural problems of their size (Dunbar, 1963 for fusulines; Drooger, 1956 and Rat, 1963 for orbitoids). And a major event in the history of life, the evolution of internal organs as concentrations of surfaces (lungs, intestine, circulatory tubes), was so necessary for the existence of large organisms rounder than a tapeworm that the presence of similar structures need not imply their presence in a common ancestor. The precision of size-imposed convergence is often striking. *Andrewsarchus*, the enormous terminal member of mesonychid lineage that passed from cursorial carnivorous to carrion feeding to omnivorous life at increased sizes, evolved a remarkable likeness to the later omnivorous entelodonts (Szalay and Gould, 1966).

Both convergences reported in this paper were initiated by the entrance of one taxon into the size range of another subgenus. In one case, the new and larger size required an altered shape that ensured convergence upon a taxon of the large subgenus. The mechanical correlates of these size-required changes then intensified the extent of an already precise convergence.

If the principles embodied in my two statements were more widely applied, we would have to accept the unpleasant truth that convergence is a more fundamental phenomenon than we have allowed. I label this unpleasant for two reasons. First, it confounds the efforts of taxonomists working on fossils with simple hard parts (where the tired argument that all convergences can be recognized if enough characters are studied does not apply). The enormous taxonomic frustrations of homeomorphy have been well expressed by Ager (1965) for Jurassic brachiopods. But I think we have finally reached an age in which increased difficulties in ordering will no longer argue against a biological principle. Secondly, convergence does not fit well on the traditional tree that we choose for our phylogenetic representations. Most of the quantitative phyletics of modern numerical taxonomy presuppose a continuing divergence, while other recommendations for a phylogenetic classification (Hennig, 1966) would consider only the branching points of a diverging system. What we need, I expect, are new pictures of phylogeny (strawberry runners or combs), and perhaps a new vocabulary like that proposed by Huxley (1958).

The case of convergence will, perhaps, best be made not by a theoretical assault, but by the documentation of such harmless, trivial, and

whimsical examples that can propel this unpleasant truth through a back door of our evolutionary literature. For as Gilbert's jester, Jack Point, once remarked:

When they're offered to the world in merry guise,
Unpleasant truths are swallowed with a will—
For he who's make his fellow-creatures wise
Should always gild the philosophic pill!

SYSTEMATIC PALEONTOLOGY

Family ZONITIDAE

Subfamily POECILOZONITINAE

Pilsbry, 1924

Genus POECILOZONITES O. Boettger, 1884

Subgenus POECILOZONITES (GASTRELASMUS)

Pilsbry, 1924

Species *P. CIRCUMFIRMATUS* (Redfield)

Poecilozonites (Gastrelasmus) circumfirmatus
cavespiram, n. subsp.

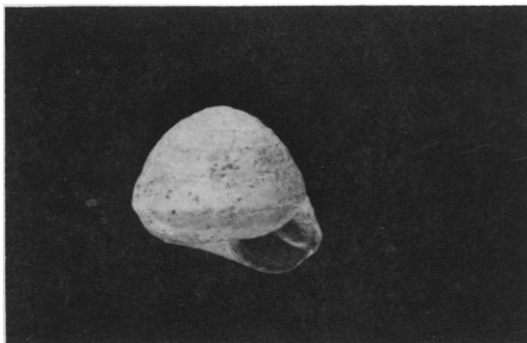
Text-figure 4

Description.—Adult with $5\frac{1}{2}$ –7 postprotoconch whorls (6 in holotype); holotype is 9.8 mm in width, 8.6 in height; spire tall and intensely domed; whorl periphery only slightly angulate; aperture rounded; umbilicus constricted; strong palatal lamella terminating just inside aperture at whorl periphery; subperipheral color band present in adult; flames still present in subsutural band position; supraperipheral band sometimes present, sometimes as flames.

Comparison.—Highest spired, most intensely domed, most narrowly umbilicate and most strongly colored taxon of its subgenus: all these features are correlated in development or the mechanics of spiral growth.

Occurrence.—Shore Hills Soil, western part of St. George's Island, Bermuda. Locality 48 of Gould, 1969. More than 50 specimens found with *P. (P.) cupula cupuloides*.

Etymology.—The subspecies name (*cavespi-*



TEXT-FIG. 4—Holotype of *P. (G.) circumfirmatus cavespiram*. Actual width of specimen is 9.8 mm.

ram = beware the spire) is given to warn of possible confusion between this taxon and the more common, equally small and high spired *P. cupula dalli*.

Repository.—Holotype MCZ29021 (Invertebrate Paleontology: Gastropoda), Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

ACKNOWLEDGMENTS

Supported in part by NSF Grant GA-901. This paper is a contribution from the Bermuda Biological Station for Research. I thank C. Jones, H. Holland, and R. Adlington for figures and photography.

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MANUSCRIPT RECEIVED MARCH 31, 1970