Society of Systematic Biologists

VARIATION IN LAND-SNAIL SHELL FORM AND SIZE AND ITS CAUSES: A REVIEW

GLENN A. GOODFRIEND

Isotope Department, The Weizmann Institute of Science, 76100, Rehovot, Israel

Abstract.—Variation in land-snail shell form has been extensively documented, but its causes are poorly understood. For no character are there general rules relating shell form to environmental characteristics, although certain correlations are common. Size variation generally has a large genetic component. Larger snails are often associated with moister conditions; the effect may be inductive (direct) or selective, but the mechanism is not documented. Snails may attain smaller adult sizes at higher population densities, apparently through the effects of pheromones on growth rate. Relative aperture area tends to be smaller under drier conditions, probably because of selection for smaller whorl cross-sectional area to reduce water loss. Larger snails tend to have higher whorl expansion rates. This pattern is variously interpreted as relating to the maintenance of constant attachment area/weight, whether of foot surface area when the snail is active or when attached to a substrate or of aperture perimeter when attached. Apertural denticles are generally thought to represent adaptations to reduce predation. Relative shell height of snail species relates to the angle of the substrate on which activity occurs; this could be related to the mechanics of shell balance. For unknown reasons, helicid species in the Mediterranean area frequently have forms with keeled and with rounded shell peripheries. Snails living on calcareous substrates sometimes have thicker shells; the effect is not necessarily direct. Surprisingly, only a weak relationship exists between shell thickness and moisture conditions. Shell coiling sometimes occurs in the opposite direction between sympatric species, probably as a result of selection for reproductive isolation. A recurring problem in the explanation of shell form is the interpretation of covarying shell characters. Identification of nonadaptive variation which results from developmental dependence on another character is dependent on the study of the selective and direct-environmental causes of variation in land snail shell form. [Snail; gastropod; shell; form; shape; size; denticles; variation.]

Land snails are notoriously variable animals. Numerous studies have documented geographical variation in the form and coloration of their shells. Variation in color polymorphisms has not only been extensively documented (mostly in the Helicidae and especially in the helicid genus *Cepaea*), but their genetics and the selective forces acting upon them have also received considerable attention (see reviews by Jones et al., 1977; Clark et al., 1978; Cain, 1983). The state of affairs with respect to variation in land-snail shell form is not nearly so advanced. The literature in this area was last reviewed by Rensch (1932). At that time, most shell form variation was interpreted as being environmentally induced. However, a number of studies have since shown a significant genetic component to shell form variation (e.g., Rensch, 1937; Cook, 1965; Murray and Clarke, 1968; Cook and Cain, 1980; Burla,

1984). The last several years have seen a heightening of interest in the causes of shell form variation and especially in its adaptive significance.

Because of the low mobility of land snails, their populations tend to reflect geographical variation of the environment, with little blurring of this pattern. Their shells are often easily collected in numbers and present a number of precisely quantifiable features. Many land snails reach a definite adult size, marked by a reflected lip, and then grow no more. This enables comparisons to be made at a standard life-history stage (Gould et al., 1974). The ontogeny of adult shell differences can be readily studied since the shell preserves the record of ontogeny of an individual (Gould, 1969b; Goodfriend, 1983a). In some cases, there may be a fossil record which can be used to provide information on the history of geographic variation (e.g.,

Cain, 1971; Heller, 1979; Goodfriend, 1983b, 1986b; Magaritz and Goodfriend, 1986).

I attempt here to draw together the varied literature on variation in land-snail shell form, on the relation of shell form to environmental and genetic influences, and on the adaptive significance of shell form variation. The review is organized by shell form characteristics (size, relative height, etc.) and, within each section, by the environmental properties with which they are correlated. Since correlations exist among environmental characteristics as well as among shell characteristics, this organization is unavoidably somewhat unnatural.

SHELL SIZE

Variation in shell size, usually characterized by shell diameter, is the most-studied aspect of geographic variation in land snails. Breeding experiments on a number of land-snail species have shown that size differences among populations have a high heritability (typically 50–70%). However, since populations representing extremes of size are generally chosen, these heritability values probably overestimate the genetic component of differences among more typical populations (L. M. Cook, pers. comm.). The species studied include the helicids *Cepaea nemoralis* (Cook, 1967; Cook and Cain, 1980), *Arianta arbustorum* (Cook, 1965; Baur, 1984; Burla, 1984), and *Murella muralis* (Rensch, 1937), as well as species of *Partula* (Murray and Clarke, 1968).

Within-population size variation may also have a significant genetic component. For example, Oosterhoff (1977) found that, within populations, faster-growing individuals of *C. nemoralis* reach a larger adult size (despite earlier maturation). Her laboratory breeding experiments showed that growth rate has a high heritability. Within some populations of *C. nemoralis*, size may be correlated with shell color or banding (Cook and O'Donald, 1971; DeSmet and Van Rompu, 1984). However, the direction of the correlation is not consistent, and no correlations are found in some *C. nemoralis* populations (Cook and O'Don-

ald, 1971; Carter and Ashdown, unpubl. manuscript, as cited by Carter and Ashdown, 1984; DeSmet and Van Rompu, 1984). In one *C. hortensis* population (but not another) studied by Häkkinen and Kopenen (1982), five-banded morphs tended to be larger than unbanded morphs. A possible interpretation of these correlations is that there are genes affecting shell size that are linked with color or banding genes. Alternatively, these differences may be interpreted as pleiotropic effects of color or banding genes (Cook and O'Donald, 1971). This latter explanation perhaps accounts better for the inconsistency of the relationships. The pleiotropy may be strongly affected by environmental variation. For example, different morphs have been shown to sometimes display different patterns of activity, depending upon insolation (Tilling, 1983) and this could affect growth rate and consequently also size.

Other evidence of direct environmental influences on shell size comes from studies on the relationship between population density and shell size, reviewed below.

Moisture.—Moisture conditions are the best-documented environmental correlate of shell size (Table 1). In a large number of cases, larger snails are associated with moister conditions. However, this pattern does not seem to hold for minute forms, such as the tropical diplommatinid prosobranchs (Berry, 1963; Peake, 1973; Tillier, 1981). Another departure from the pattern of larger snails in wetter areas is seen in the diminution of various species at high elevations, which are in most cases wetter, but also cooler, and have more intense insolation. These cases are discussed in the following section.

The association of larger size with wetter conditions has usually been interpreted as resulting from direct environmental influence. Variations on two general scenarios have been proposed:

(1) Greater moisture produces a larger adult size by increasing the growth rate (e.g., Clessin, 1897; Brown, 1913; Rensch, 1932; Sacchi, 1965; Gould, 1984b). Wetter

TABLE 1.   Some environmental correlates of geographic variation in shell size of land snails.

Species	Area	Size correlation	Reference
Moisture			
Cepaea nemoralis (L.), *Chondrula tridens* (Müller)	Europe	Larger with higher rainfall	Rensch, 1932
Levantina spiriplana (Olivier)[a]	Israel	Larger with higher rainfall	Heller, 1979; Magaritz and Heller, 1980
Chloritis argillacea (Fér.)	Timor	Larger with higher rainfall	Rensch, 1931
Pleurodonte lucerna (Müller)	N-central Jamaica	Larger with higher rainfall	Goodfriend, 1983b
Diplommatina spp.	Malaya	Smaller with higher rainfall	Berry, 1963
Palaina spp.	New Caledonia	Smaller with higher rainfall	Tillier, 1981
Pleurodonte lucerna[b]	W-central Jamaica	Larger in moister habitats	Brown, 1911
Laciniaria biplicata (Mont.)	Germany	Larger in moister habitats	Schmid, 1919
Cerion uva (L.)	Aruba, Bonaire, Curaçao	Larger in moister habitats	Baker, 1924; Gould, 1984b
Clausilia bidentata (Ström), *Ena obscura* (Müller)	England	Larger in more sheltered (? moister) habitats	Boycott, 1920
Temperature and insolation			
Cepaea nemoralis, Perforatella incarnata (Müller), *Zebrina detrita* (Müller), *Helix cincta* (Müller)	Europe	Larger at higher temperature	Rensch, 1932
C. hortensis (Müller)	Iceland	Larger at higher minimum temperature	Bengtson et al., 1979
C. nemoralis	Pyrenees	Larger at higher elevations	Ramos, 1980
Chloritis argillacea	Timor	Smaller at higher elevations	Rensch, 1931
Achatinella spp.	Hawaii	Smaller at higher elevations	Welch, 1938, 1954
Diplommatina spp.	Solomon Islands	Smaller at higher elevations	Peake, 1973
Arianta arbustorum (L.)	Switzerland	Smaller at higher elevations	Baur, 1984; Burla and Strahel, 1983
Calcium			
Limicolaria martensiana (Smith)	Eastern Africa	Larger on high-Ca soil	Owen, 1965
Sphincterochila candidissima (Dr.)	Southern France	Larger on calcareous substrates	Altes, 1956
Eremina irregularis (Fér.)[c]	Egypt	Larger on calcareous substrates	Kaltenbach, 1942
Cerion uva (L.)	Aruba, Bonaire, Curaçao	Smaller on calcareous substrates	Gould, 1984b
Population density			
Cepaea nemoralis	England, Netherlands	Smaller at higher population density	Cook and O'Donald, 1971; Williamson et al., 1976; Oosterhoff, 1977
Arianta arbustorum	Switzerland	Smaller at higher population density	Burla, 1984
Helicella itala (L.), *Candidula intersecta* (Poiret), *Cochlicella acuta* (Müller)	England	Smaller at higher population density	Tattersfield, 1981

[a] =*L. caesareana* Parreyss.
[b] =*P. acuta* (Lam.).
[c] =*E. hasselquisti* Ehrenberg.

conditions provide more frequent and/or longer periods when activity is possible. Thus, food intake would be increased and a higher growth rate would result. As long as age at maturation is not negatively correlated with growth rate, faster-growing individuals would attain a larger adult size. There is some evidence linking growth rate and adult size. In *C. nemoralis* in the laboratory, faster-growing individuals reach a larger adult size. However, growth-rate differences among individuals have a strong genetic component (Oosterhoff, 1977).

(2) More favorable moisture regimes have been hypothesized to cause a larger adult size by increasing the rate of whorl expansion (e.g., Brown, 1911; Gould, 1984b). As long as whorl number at maturation is not negatively correlated with whorl expansion rate, the snails will reach a larger adult size. Evidence supporting a causal relationship between moisture and whorl expansion rate is presently lacking.

While direct environmental influences might play a significant role in moisture-correlated geographic variation in size, there is no study demonstrating such a role, despite the frequency with which the relationship is proposed. The importance of genetic influences in geographic variation in size, as revealed by breeding experiments (see above), suggests that selection may play a dominant role in moisture-related size variation.

Since surface area/volume ratio increases with decreasing size (if the decrease is isometric), it would be expected that conditions of greater moisture stress would favor larger snails (Nevo et al., 1983). Certainly this is not true at a faunal level: both dry and wet regions support both small and large snail species. However, the tendency for very small species to show within-species size variation that correlates negatively with rainfall may possibly be the result of selection for reduction of water loss in drier areas. Water balance should be of particular importance to small species because of their unfavorable surface area/volume ratio.

Advancement in our understanding of moisture-related size variation is likely to come from the study of life-history characteristics of populations under different moisture regimes. Snails may grow faster under wetter conditions and, thus, have the potential to reach a larger size in a given period of time. Under such conditions, selection may favor maturation at a larger size (if maturation is under genetic control), since this may confer a reproductive advantage (see below).

Temperature and insolation.—In a broad survey of geographic trends in European and Mediterranean land snails, Rensch (1932) showed that several species have a tendency to be larger in warmer regions (Table 1). Although the number of regions compared (two to seven, with a mean of four) was far too small for any definite conclusions to be reached, it is clear that there is no general rule concerning latitudinal trends in shell form. On a more local geographic scale, Bengtson et al. (1979) found larger *C. hortensis* associated with warmer sites (as measured by mean daily minimum temperature) in Iceland. High-elevation forms of land snails have been shown to be particularly small in a variety of different areas, although the opposite trend is clearly seen in *C. nemoralis* in the Pyrenees over a wide range of elevations (see Table 1; Ramos, 1980). This size variation may be associated with the lower temperature or higher insolation at high elevations, or with other correlates of elevation, such as rainfall.

In an outdoor cage experiment on *C. hortensis*, Knights (1979) found that under shaded conditions, larger snails had better survivorship than smaller snails, whereas the situation was reversed under unshaded conditions. The significance of these findings is difficult to evaluate, since it is not possible to separate the effects of insolation from those of temperature or moisture—the less-shaded cages would also be drier and warmer. In any case, the results are the opposite of what one would expect based on the field surveys of this and other species discussed above.

Calcium.—Evidence suggesting a relationship between shell sizes and the cal-

cium-carbonate content of the substrate comes from two studies in which the shell sizes of a series of populations on two different substrates were compared (Altes, 1956; Owen, 1965). In both cases, the calcareous substrate supported larger snails than the more siliceous one. In a study of Norwegian land snails, Økland (1925; as discussed by Rensch, 1932) noted that various helicids tended to be *smaller* in limestone areas. In contrast, surveys of *Helix pomatia* L. (Agócsy, 1963), *C. hortensis* in Iceland (Bengtson et al., 1979), *Theba pisana* (Sacchi, 1971) and a variety of other European and Mediterranean species (Rensch, 1932) have failed to reveal any relationship between shell size and the calcium-carbonate content of the substrate.

Experimental studies give similarly inconsistent results. Broods of *Arianta arbustorum* that were divided, with one-half raised with chalk and one-half without, showed differences in adult size in some cases (with individuals raised on chalk being larger), but no differences in others (Oldham, 1929; Cook, 1965). *Helix pomatia* and *H. aspersa* (Müller) attain a slightly larger size when raised with chalk (Oldham, 1934), whereas *Bradybaena fruticum* (Müller) does not (Frömming, 1954). The laboratory results for *H. pomatia* are discordant with the lack of correlation between size and substrate found in Agócsy's (1963) field study. Taken together, the laboratory and field results suggest that there are genetic differences, among species as well as among populations, in the response of shell size to calcium-carbonate content of the substrate.

Population density.—A trend of decreasing adult size with increasing population density has been firmly established for several European helicid species through a number of field and laboratory studies (Table 1). All available evidence points to a direct environmental influence of density on shell size, rather than a selective effect. It has been shown in the laboratory that the smaller adult size attained at higher densities is associated with a lower rate of growth (Oosterhoff, 1977; Cameron

and Carter, 1979; Charrier, 1981; Lazaridou-Dimitriadou and Daguzan, 1981; Lucarz, 1982). This lower growth rate is apparently a result of inhibition of activity at higher densities, which has been shown experimentally to be the result of an unidentified pheromone present in snail mucus (Cameron and Carter, 1979; Dan and Bailey, 1982).

In the one case where differential mortality with respect to size was examined in relation to population density (in *C. hortensis*; Knights, 1979), no consistent pattern was found, indicating that size differences among populations cannot be attributed to selective effects of differences in population density. The significant change in shell size observed by Cook and Cain (1980) over little more than one generation again suggests environmental rather than selective causes and may relate to the effect of population density.

Interactions between related species.—Two studies on minute diplommatinid land snails have proposed that species interactions may be important in determining shell size of coexisting populations. Peake (1973) showed that the size frequency distributions of sympatric *Diplommatina* species in Malaya and in the Solomon Islands were non-overlapping and regularly spaced, except where the direction of coiling differed. However, without statistical tests comparing the size distributions of sympatric populations to randomly selected allopatric populations, the significance of this pattern is unclear (Connor and Simberloff, 1979). The widespread dextral *D. nevilli* Cross shows considerable geographic variation but allopatric populations are not smaller on average than sympatric populations that occur with larger dextral species. Thus there is no indication of character displacement with respect to size.

Tillier (1981), studying New Caledonian diplommatinids, gave one example of two sympatric populations which showed less overlap in shell dimensions than the two species as a whole. This was taken as evidence of character displacement. However, the amount of overlap of a pair of

samples with some mean difference increases with increasing sample size. Even between randomly selected pairs of populations (one of each of two species), the overlap is expected to be smaller than the overlap between the two species as a whole, simply because the sample size of the populations is smaller. Comparison of the means of the sympatric populations of diplommatinids to the means for the two species as a whole shows that the sympatric population means are actually *closer* than the species means. Thus, if anything, convergent character displacement (Grant, 1972) was shown, although the statistical significance of this pattern cannot be evaluated from the data provided.

Predation.—In a few cases, predation has been found to differentially select land snails with respect to shell size (Table 1). Oosterhoff (1977) noted that smaller *C. nemoralis* were preferentially preyed upon by beetles. Reichholf (1979) found that thrushes differentially prey on larger individuals of *Arianta arbustorum*. However, since juveniles and adults were not distinguished, the data could also be interpreted as indicating a preference for adults over juveniles, possibly resulting from habitat differences. Such prey selection would not necessarily have any selective effect on adult size. In a field experiment on predation by the song thrush (*Turdus ericetorum*), Bantock and Bayley (1973) found that, in a mixed population of *C. nemoralis* and the generally smaller *C. hortensis*, *C. nemoralis* was preferentially preyed upon. These data suggest that the thrushes do not distinguish between the two species and that they preferentially prey upon snails of intermediate size, perhaps implying formation of a search image or greater efficiency of handling of snails of such size. A later study (Bantock et al., 1975) showed that selection for size by thrushes differs among the different morphs. Yellow five-banded *C. nemoralis* were subject to disruptive selection with respect to size, whereas yellow midbanded morphs were preyed upon randomly with respect to size. The cause of this pattern is entirely unclear.

Taken together, the studies on predation in relation to size present no consistent picture. No one case has been studied in sufficient detail to permit assessment of the role of predation in size variation in natural populations.

Parasitic castration.—An unusually large size, associated with a larger-than-normal whorl number, is attained in individuals whose gonads have been destroyed by parasitic trematodes (Boettger, 1952). The nonproduction of a hormone that induces shell maturation has been suggested as producing continued growth in such individuals (Boettger, 1952).

Reproduction.—In captive populations of land snails, reproductive output often shows a positive correlation with size (Table 2). This may express itself in any of a number of ways: larger clutch size or egg size; higher frequency of oviposition; or earlier time of first reproduction. Of particular interest is the laboratory study of Carter and Ashdown (1984), which showed that size-correlated reproductive characteristics may vary considerably among populations (Table 2). Higher reproductive output of larger snails, thus, is not a direct consequence of size, but results from the interaction of size with other (probably genetic) factors. Whether larger snails also have a reproductive advantage under natural conditions remains to be established. This advantage might disappear or turn to a disadvantage under certain ecological conditions (e.g., when food resources are scarce and distributed in small patches).

Problematic patterns.—In several surveys of variation in land snails, a regular geographic pattern was found, but with no clear correlation with environmental factors. The genus *Cerion* in the Bahamas displays a huge diversity of geographical variation, often involving size (Gould et al., 1974; Gould and Woodruff, 1978; Woodruff and Gould, 1980). A particularly clear pattern is seen on Grand Bahama, where small forms on the innerbank side of the island grade into large forms on the outer bank (Gould and Woodruff, 1978). It is unclear what environmental correlates, if any, are associated with this cline.

TABLE 2. Correlation of size with reproductive characteristics of land snails.[a,b]

Species	Clutch size	Egg size	Oviposition frequency	Reference
Cepaea nemoralis	+		+	Wolda, 1963
C. nemoralis	+	+		Oosterhoff, 1977
C. nemoralis	0	0	+	Carter and Ashdown, 1984 (pop. A)
C. nemoralis	+	+	0	Carter and Ashdown, 1984 (pop. B)
Theba pisana (Müller)	+			Cowie, 1984a
Achatina fulica Bowdich	(+)		0	Kekauoha, 1966
Archachatina marginata (Swain.)		+[c]		Plummer, 1975

[a] + = positive correlation; 0 = uncorrelated; parentheses indicate nonstatistically significant correlation.
[b] First study on artificial outdoor population; others on populations in laboratory.
[c] Snail size and egg size also positively correlated with age.

Transplant experiments performed earlier in the century by Bartsch indicate that most morphological variation in Cerion has a strong genetic component (Woodruff and Gould, 1980).

Sacchi (1957, 1961) has documented several cases of Mediterranean island populations of helicids in which the mean shell diameter is either unusually small or unusually large. No correlation with environmental factors was observed. Several cases of noncorrelated variation on a broad geographic scale are also seen in clinal trends in the east African snails Metachatina kraussi (Pfeiffer) (van Bruggen, 1969) and several Gulella species (van Bruggen, 1980). In the latter case, different species appear to show opposite trends in size. However, it is not clear in how many of the species the clinal trends are statistically significant.

Two experimental studies concerning shell size have produced data whose interpretation is problematic. Cook and O'Donald (1971) observed differential mortality with respect to size in some dormant laboratory populations of C. nemoralis over the winter. Whereas one population showed no differential mortality, another showed significantly higher mortality of smaller snails. Replicates of a third population gave inconsistent results: one showed no differential mortality whereas two others showed higher mortality of smaller snails. These experiments show that conditions of the environment might select for size in land snails through differential mortality. However, the cause of mortality and the environmental factors involved are unknown.

Wolda (1972) observed a trend of decreasing size at maturation over several years in a series of captive outdoor populations of C. nemoralis. This trend could not be explained by changes in population density. The very rapid rate of decrease in shell size strongly suggests an ecological cause rather than a genetic change resulting from selection. However, no temporal environmental trends that correlated with the size change could be identified.

WHORL NUMBER, WHORL EXPANSION RATE, APERTURE SIZE, AND APERTURE FORM

Adult shell size is a function of the number of whorls, the rate at which the whorls expand, and also the initial size of the whorls. A given size may be achieved by few whorls which expand rapidly or by numerous whorls that expand slowly. In the former case, the whorl cross-sectional area would be relatively smaller throughout ontogeny. This area represents the aperture area, at various stages of growth and also in the adult, although upon maturation of the shell the aperture may be further modified by flaring out or growing in. Thus, whorl number and expansion rate have important consequences for the degree to which a retracted snail is in contact with the outside world.

It is not clear to what degree whorl number and expansion rate show adaptive variation, independent of their effect on aperture area or cross-sectional area. Cain (1980) showed that more elongate species

of snails tend to have more numerous whorls and proposed that the larger number of whorls provides additional strutting to strengthen this inherently weak shape. Gould (1984a, b), on the other hand, saw no particular adaptive significance to variation in whorl number or expansion rate in *Cerion*. He interpreted them as representing environmentally-induced variation in one case (Gould, 1984b), but more generally as a consequence of selection for size, without adaptive significance by themselves (Gould, 1984a).

Variation in aperture area has generally been interpreted as representing either an adaptation for regulation of water loss or for reduction of predation, or both. Water loss from inactive snails occurs mainly through the aperture, although significant water loss may also occur through the shell (Gebhardt-Dunkel, 1953; Machin, 1967). Machin (1967), comparing inactive individuals of three species of snails, found that mean water loss through the aperture increased nonlinearly with mean aperture area both with and without the epiphragm present. Species with smaller apertures lost proportionately more water per unit aperture area (although this effect appears to be compensated for by increased epiphragm thickness in the smaller species). On the other hand, Goodfriend (1983b) found that in water-filled shells of a single highly-variable species of land snail, water-loss rate through the aperture was proportional to aperture area. These contradictory results may be resolved if one assumes that the nonproportionality found by Machin (1967) was a result of vital effects (i.e., physiological differences among the species compared). Clearly, further work to separate vital effects from effects of shell morphology is needed.

Several studies have shown a relationship between aperture area and moisture conditions. A survey by Gebhardt-Dunkel (1953) showed that xerophilous species tend to have relatively smaller apertures, apparently due to low whorl expansion rates rather than modification of the aperture at maturity. In *Buliminus* in Israel, species inhabiting drier areas tend to have

smaller apertures (Heller, 1975); in *Pleurodonte lucerna* in Jamaica, populations living in drier areas have lower whorl expansion rates and, thus, relatively smaller apertures (Goodfriend, 1983b).

Apertural denticles have been supposed to function in the reduction of water loss (Boettger, 1921, 1935). However, Paul (1974) doubted this, supposing that water loss should be a function of the surface area of the mantle collar in a retracted snail (i.e., the evaporative surface area, equal to the whorl cross-sectional area at the depth of retraction for a flat mantle collar surface). Experiments on water-loss rates from water-filled *Pleurodonte lucerna* shells with denticles and with the denticles removed support this hypothesis—denticles had no effect on water-loss rate (Goodfriend, 1983b). Whorl cross-sectional area, rather than aperture area, may be the critical shell feature affecting water loss. However, the two measures are highly correlated, except where the aperture is highly modified. Cain (1980) also attached adaptive significance to variation in whorl cross-sectional area. He found that very small species tend to have a relatively low whorl number (consequently, a higher whorl expansion rate) and suggested this might be adaptive in maintaining a sufficiently large whorl cross-sectional area for efficient circulation.

Although aperture area does not appear to limit water loss, experiments with water-filled shells indicate that the depth of the evaporating surface inside the shell (equivalent to depth of retraction) does have a major effect on water-loss rate (Goodfriend, 1983b). Snails producing shells with a larger whorl number relative to body size would be able to retract deeper and, thus, would be expected to lose water slower. This may explain the geographic variation in whorl number seen in the Jamaican land snail *Pleurodonte lucerna*: in drier areas, the shells have more whorls than the shells of snails in wetter areas; and the snails in drier areas are able to retract deeper into their shells (Goodfriend, 1983b).

In a study of British land snails, Cam-

eron (1981) considered the adaptive significance of variation of aperture area in relation to snail size. He showed that larger species have larger aperture areas (than would be expected from isometry) relative to small species. This is the result of higher whorl expansion rates and lower whorl numbers in larger species. He pointed out that, under isometry, loading on the aperture (snail weight/surface area of aperture) would increase with size. Thus, larger snails would have a greater risk of detachment when resting with the aperture pressed up against a substrate (when foot attachment area = aperture area). He suggested that this is compensated by a positive allometric increase of aperture area with larger size.

Goodfriend (1983b) also found that among populations of the highly-variable land snail *Pleurodonte lucerna*, larger snails had fewer whorls, a higher whorl expansion rate, and relatively larger apertures. Foot *surface area* of active snails showed isometric variation with snail mass, thus implying that foot *volume* must increase with positive allometry with respect to snail mass. It was hypothesized that larger snails must have higher whorl expansion rates and consequently higher relative whorl cross-sectional area in order to accommodate the larger foot when the snail is retracted into the shell.

Both Cameron's (1981) and Goodfriend's (1983b) hypotheses provide explanations for the observed size-whorl expansion rate relationship observed among and within species. There is at present no evidence to allow one to decide between these alternatives. Both may be correct in some situations, or one may apply to some situations and the other to others. There is yet a third explanation: for species that seal the aperture to a substrate, apertural circumference may be limiting to attachment strength. Larger snails may have higher whorl expansion rates to keep apertural circumference from decreasing relative to mass. Mazek-Fialla (1934) noted that snails that seal to substrates tend to have flared apertures, which would increase apertural circumference. Certainly the resting habits of land snails—whether they attach to a substrate, the curvature of the substrate they select, and the manner of attachment (by foot or by sealing)—must have profound consequences for the form of the aperture. Yet, no study has systematically and quantitatively examined these relationships.

Cook (1895) and Solem (1972) considered apertural denticles to serve as protection against predation by arthropods. Boettger (1921, 1935) also considered apertural denticles in *Otala* to serve an antipredator function. He observed geographic variation in the degree of development of apertural denticles which was positively correlated with the degree of elongation of the anterior end of a carabid beetle species preying on *Otala*. He interpreted the correlation as probably representing coevolution between the snails and beetles. But the beetles may have responded to an already existing pattern of denticle variation related to some other environmental factor. Boettger himself suggested the possibility that the denticles may have originated as structures for the reduction of water loss. Goodfriend (1983b) showed that geographic variation in denticle size in a Jamaican land snail was positively correlated with predation pressure by unidentified predators, apparently birds. Despite the prevalence of the view that denticles relate to predation (but see Paul [1974] for an opposing view), there are as yet no studies demonstrating that apertural denticles have any effect on predation.

Some species of land snails develop very small denticles which would seem to be totally ineffective against predators. In *Bulimulus* in the Galapagos, species occupying moister microhabitats tend to have small denticles, which are lacking in other species (Coppois and Glowacki, 1983). *Partula otaheitana* in areas of high rainfall and higher insolation also tends to develop small denticles (Emberton, 1982). The functional significance of these denticles is a mystery.

In many land snails which reach a final adult size, the aperture becomes deflected downward during the last phase of shell growth. This modification has been interpreted as representing an adaptation to re-

duce water loss from resting individuals, since it permits the aperture to be pressed against a flat substrate with only a small gap remaining (Mazek-Fialla, 1934). Aperture deflection has also been interpreted as an adaptation to lower the center of gravity to reduce the probability of dislodgement during inactivity (McNair et al., 1981). Such conjectures seem a bit premature, since no association between resting habits (whether the snails attach to a substrate), and aperture deflection has yet been established, although it seems likely to exist.

SHELL SHAPE

Two basic approaches have been taken to the study of variation in shell shape. One approach, following that of Raup (1966), involves the analysis of the distribution of shapes among taxa and hypothesizing the reasons for low or high frequencies of certain shapes. The second approach involves the study of correlations between variation in shape (within or among species) and environmental variation.

Rensch (1932) and Gould (1971a) have pointed out that shell shape variation may not necessarily be adaptive per se, but may be simply an inadvertent consequence of selection for other developmentally-correlated shell features. For example, Gould (1984a) interpreted the greater relative height of unusually small and unusually large *Cerion* as being a consequence of selection for size, with no adaptive significance per se. Smaller size is achieved by producing narrower whorls, which increases relative height, whereas larger size is produced by adding additional whorls, which also increases relative height.

Cain (1977, 1978a, b) has shown that the statistical distribution of the relative height of land-snail shells of many regions is bimodal—the shells tend to be either very elongate or slightly flattened, rarely globular or slightly elongate. Cain (1977) has proposed that this may be due to the mechanics of balancing the shell during locomotion. Considering the great weight of the shell and enclosed visceral mass, dif-

ferences in shape are likely to have a significant effect on the energy expended in holding the shell in a balanced position during locomotion (Cain, 1977). Field studies of activity sites of British land snails (Cain and Cowie, 1978; Cameron, 1978) show that differently-shaped species tend to differ in their sites of activity: high-spired species are generally active on high-angle or vertical surfaces, flat species on low-angle or horizontal surfaces, and intermediate species on a wide variety of angles (e.g., plants). A laboratory study (Cook and Jaffar, 1984) in which British snails were given a choice of vertical or horizontal surfaces produced results consistent with field observations—elongate species tend to associate themselves with vertical surfaces and flat ones with horizontal surfaces, whereas species of intermediate shape generally showed weaker preferences. It is not clear whether these observations represent resting or activity sites of the snails or a combination of these. Cameron (1978) suggested that species show weaker differences in resting sites than in activity sites. This would be expected if shell form were related to the problem of shell balance on different substrates, as suggested by Cain and Cowie (1978). The association of shell shape with substrate angle seems well established for British land snails, but these studies clearly need to be extended to other faunas (Cain and Cowie, 1978).

Within-species variation in relative shell height correlates with environmental variation in a number of species (Table 3). All examples of tropical snails and the European species *Discus rotundatus* show a negative correlation between relative height and rainfall, whereas the examples from Israel show the opposite pattern. A major problem in interpreting this variation is that in most land snails, relative height increases ontogenetically with whorl number (i.e., growth is allometric, with height increasing faster than width; e.g., see Gould, 1969a). In most cases, published data are not sufficient to determine to what degree geographic variation in relative height is a function of variation in whorl number. As discussed above, drier

TABLE 3. Correlation between relative shell height and environmental characteristics.

Species	Area	Relative height increased with:	Reference
Levantina spiriplana	Israel	Increasing rainfall	Heller, 1979
Buliminus spp.	Israel	Increasing rainfall	Heller, 1975
Cepaea nemoralis	Belgium	Increasing rainfall	De Smet and Van Rompu, 1984
Pleurodonte lucerna	Jamaica	Decreasing rainfall	Goodfriend, 1983b
Palaina spp.	New Caledonia	Decreasing rainfall	Tillier, 1981
Discus rotundatus (Müller)	Germany	Increasing humidity of habitat	Boettger, 1929
Partula otaheitana	Tahiti	Decreasing insolation, decreasing rainfall	Emberton, 1982
Achatinella mustelina Mighels	Hawaii	Decreasing elevation, decreasing rainfall	Welch, 1938
Miscellaneous helicid species	Europe	Increasing elevation	Knipper, 1939

conditions may select for more numerous, narrower whorls; such shells would also tend to be relatively higher and this could possibly account for the height-rainfall relationship seen in tropical snails and *Discus rotundatus*. Direct environmental influences on adult size might produce the opposite pattern (seen in the Israeli snails): with slower growth under drier conditions, a smaller adult size with fewer whorls may be attained. These shells will be relatively less high if height increases with positive allometry with respect to width during ontogeny. These explanations must remain conjectural until detailed ontogenetic information is available for the snails involved.

Character displacement involving shell shape has been shown in fossil *Poecilozonites* (Schindel and Gould, 1977). The nature of the interaction producing this effect is unknown, but competitive interactions or reproductive isolation might be involved.

PERIPHERAL ANGLE

Another aspect of shell morphology which shows considerable variation is the form of the periphery—whether rounded or angular. An ontogenetic change from an angular juvenile form to an adult with a rounded periphery is very common. In a large number of species, both rounded and keeled forms of adults occur (Table 4). The preponderance of this pattern in helicids around the Mediterranean area (the first 18 examples in Table 4) is particularly

striking. Rensch (1937) noted this pattern long ago and it has been further documented by subsequent studies (e.g., de Bartolomé, 1982). In most cases, the keeled forms are also characterized by being relatively flatter, having a stronger, more widely-spaced sculpture of ribs, and having an open (versus closed) umbilicus (Rensch, 1937). Rensch's (1937) laboratory breeding experiments showed that peripheral angle as well as correlated shell features are in large part hereditary. Gould (1969a, 1971a) interpreted a similar suite of character correlations in some *Poecilozonites* forms as representing paedomorphy. This interpretation may also apply to the Mediterranean helicids but detailed study of their ontogeny is needed to evaluate this possibility. Gould (1971a) hypothesized that paedomorphy in one species of *Poecilozonites* was the result of selection for thinner shells in low-calcium environments (see below); keeling was interpreted as an inadvertent consequence of this selection. The presence of a keel in adult *Pleurodonte lucerna* is characteristic of larger forms (Goodfriend, 1983b). This was hypothesized to represent an adaptation to compensate for the decrease of lung surface area (relative to snail mass) with increasing size under isometry. Neither explanation can apply to Mediterranean helicids, since keeled forms often live on limestone substrates and are not larger than rounded forms. Cook and Pettitt (1979) suggested that keeled shells may be more resistant to crushing than rounded

TABLE 4. Some species in which both rounded and keeled shell peripheries occur.

Species	Area	Environmental correlation	Reference
Discula polymorpha	Madeira	—	Cook and Pettitt, 1979
Iberus gualtierianus (L.)	Southeastern Spain	Keeled in karst areas	Alonso et al., 1985
I. rositai Fez	Southern Spain	—	Alonso and Ibáñez, 1978
Trochoidea ebusitana (Hidalgo)	Balearic Islands	—	Schröder, 1978
T. syrensis (Pfeiffer)	Cyprus	—	Haas, 1933
T. simulata (Ehrenberg)	Israel	Keeled near coast	H. K. Mienis, pers. comm.
T. gestroi (Gambetta)	Libya	—	Brandt, 1959
T. limbata (Philippi)	Libya	—	Brandt, 1959
Theba pisana (Müller)	Italy	—	Porpora and Sacchi, 1958
Marmorana (Tyrrheniberus) villi-ca (Paul.)	Sardinia	—	Rensch, 1937
M. (Murella) muralis (Müller)	Sicily	Keeled in drier areas	Rensch, 1937
Levantina gyrostoma (Fér.)[a]	Libya	—	Pfeiffer, 1947
L. spiriplana (Olivier)	Israel	—	Pfeiffer, 1949
Xeropicta ilanae Forcart	Israel	Keeled in drier areas	Goodfriend, unpubl. data
Eremina irregularis (Fér.)[b]	Egypt	—	Kaltenbach, 1934
Rossmaessleria subscabriuscala Bgt.	Morocco	—	Rensch, 1937
Sphincterochila candidissima (Dr.)[c]	Southern France	—	Altes, 1956
S. cariosula (Michaud)	Southern Spain	—	Alonso and Ibáñez, 1979
Poecilozonites spp.[d]	Bermuda	Keeled on low-car-bonate substrates	Gould, 1969a
Pleurodonte lucerna (Müller)	Jamaica	Keeled in wetter areas	Goodfriend, 1983b

[a] Also =keeled form *L. tripolitana* (Wood) (=*L. leachi* [Fér.]; Pfeiffer, 1948); H. K. Mienis, pers. comm.
[b] =*E. hasselquisti* Ehrenburg.
[c] Keeled form occurs at varying frequencies within populations of snails with rounded peripheries.
[d] Pleistocene fossils.

forms. This supposition has not been tested experimentally. Selection for flatter shells in populations that use narrow spaces in or under rocks as resting sites might also produce keeled shells, if this selection acted by favoring paedomorphy. Relative shell height typically increases during ontogeny (Gould, 1969a; Goodfriend, 1986a), along with an increase in the angle of the periphery. In *Xeropicta ilanae* in the Negev Desert of Israel, the keeled forms characteristic of drier areas tend to select the underside of small stones as resting sites, whereas the rounded forms in wetter areas usually rest on the stems of plants. In *Iberus gualtierianus*, keeled forms are associated with fissured karst limestone, whereas rounded forms occur on weaker karst (Alonso et al., 1985). Possibly the microkarst limestone which is frequent around the Mediterranean may provide local microenvironments that favor flat, keeled shells.

UMBILICUS

Most juvenile land-snail shells are umbilicate. The umbilicus often becomes covered at shell maturity in species reaching a final adult size or may close over later in ontogeny (e.g., *Sagda* spp.; Goodfriend, 1986a). In forms with narrower umbilici, the umbilicus is more frequently covered or closes over. As noted above, there is a tendency for keeled and/or flat shells to retain an open umbilicus throughout ontogeny. In some of these cases, the open umbilicus may represent one of a suite of paedomorphic characters. Covering of the umbilicus in adults also varies independently of shell shape within some species—for example, between subspecies of *Levantina spiriplana* in Israel (Heller, 1979) and Cyprus (H. K. Mienis, pers. comm.). Why umbilicus closure or covering commonly occurs in mature land snails is simply unknown. The prevalence of an

umbilicate shell in juveniles may have an adaptive explanation. This pattern of growth produces a tubular central axis which may serve to increase the resistance of the shell to crushing.

There is a tendency for umbilical width to show negative allometry through ontogeny. Thus, paedomorphs tend to be more widely umbilicate (Gould, 1969a) and shells that grow larger have relatively narrower umbilici (e.g., *Discus rotundatus*; Boettger, 1929). Among endodontid species, a smaller relative umbilical width is associated with larger diameter, more whorls, and greater relative height (Solem, 1976). This pattern may be an expression of differences among species in the length of the ontogenetic program expressed (i.e., smaller species may be paedomorphic). Temporal variation in umbilical width was documented by Gould (1969b, 1970) in some Bermudan land snails. Wider umbilici were associated with substrates poorer in carbonate and, except in one case, were not associated with paedomorphic features. The cause of this correlation is unknown. Ontogenetic changes in umbilical width have a special significance in endodontids: in some species, a brood chamber is formed by expansion of absolute umbilical width followed by reduction during ontogeny (Solem, 1969, 1976). Variation in umbilical width might also be related to shell balance during locomotion. The retractor muscles, which hold the shell up, wrap around the columella of the shell. As umbilical width increases, the point at which the force of the retractor muscle is exerted is displaced away from the axis of coiling. Thus, one might expect umbilical width would relate to shell shape and perhaps also the angle of the substrate on which activity occurs. No specific predictions can be made until some understanding of the mechanics of shell-carrying is achieved.

SHELL THICKNESS

A number of laboratory experiments have shown that thinner shells may be produced by depriving snails of a calcium-carbonate source (Oldham, 1929, 1934; Voelker, 1959; Crowell, 1973; Oosterhoff, 1977). But breeding experiments by Pollard (1975) have shown that among-population variation in shell thickness is in large part heritable in *Helix pomatia*.

Not surprisingly, the availability of calcium has been shown to be associated with thicker shells in a number of cases—various European helicid species (thicker in limestone areas; Taylor, 1881; Hoff, 1923; Agócsy, 1963), *Poecilozonites* spp. in Bermuda (thicker on calcareous soils; Gould, 1969a), and apparently also *Limicolaria* (thicker on calcareous soils; Owen, 1965). In no case is it known to what degree these represent genetic versus inductive differences.

Since water permeability of the shell decreases with increasing thickness (Gebhardt-Dunkel, 1953; Machin, 1967)—although not necessarily linearly (Gebhardt-Dunkel, 1953)—and since significant water loss occurs through the shell in dormant snails (Machin, 1967), it might be expected that drier areas would have snail populations or species with thicker shells (Sacchi, 1971). This expectation is only weakly supported by available evidence. Pollard (1975) established a negative correlation between shell thickness and mean annual rainfall for *H. pomatia* in England. *C. nemoralis* on Belgian dunes also seems to follow this pattern (DeSmet and Van Rompu, 1984). Gebhardt-Dunkel (1953) presented data on shell thickness for four species and noted that the more xerophilous ones tended to have thicker shells. But Rensch's (1932) data on nine helicid species fail to reveal average differences in shell thickness between xeric and mesic species. Bar (1978) reported a negative correlation between shell thickness and rainfall in *Theba pisana* in Israel. But a much more extensive survey of the same species by Cowie (1984b), which included the region studied by Bar, showed no such correlation. *Pleurodonte lucerna* does have a thicker shell (relative to shell diameter) in drier areas (Goodfriend, 1983b). However, predation is also higher in drier areas and

might account for the correlation. Also, the shells are smaller in drier areas, so a negative allometric relationship between shell thickness and shell size could also account for the pattern. In fact, shell thickness does indeed seem to show such an allometric pattern in land snails. Within two populations of *Theba pisana*, thickness increases with negative allometry with respect to linear dimensions of the shell (i.e., larger shells are relatively thinner; data in Cowie, 1984b). Negative allometry is also seen in among-populations comparisons in *Cepaea nemoralis* and among-species comparisons of helicid species (data in Rensch, 1932). Particularly noteworthy is the *lack* of a correlation between shell thickness and moisture conditions where it would most likely be expected: *Trochoidea simulata* (=*T. seetzeni*; J. Heller, pers. comm.) inhabits extremely arid to semiarid areas (50–500 mm mean annual rainfall) in Israel. But the thickest shells occur in areas with intermediate rainfall and very thin shells occur in the driest areas (<100 mm rainfall; Goodfriend, unpubl. data). The weak relationship between shell thickness and moisture conditions is surprising in view of the apparent relationship of shell thickness to water balance. A more thorough study of the relationships is needed.

Shell thickness might also be expected to be related to predation but data are lacking. Selection may favor thicker shells through two possible mechanisms. If potential predators are able to distinguish thicker and thinner shells, and if thicker shells are more costly in terms of the time or energy required to break them, then predators may avoid thicker shells and thus confer a selective advantage to them. Such a scenario could be assessed by comparisons of the shells of predated and living snails in the field but would be complicated by seasonal and/or ontogenetic changes in shell thickness (e.g., Heller, 1982; Cowie, 1984b). If predators are not able to assess shell thickness, then predation would still affect shell thickness if some individuals had sufficiently thick shells to survive attempted predation

(Vermeij et al., 1981). This is difficult to assess in the field but is amenable to laboratory studies (e.g., Vermeij [1982] on marine gastropods).

DIRECTION OF COILING

Most land-snail genera are composed exclusively of dextral (or more rarely, sinistral) species. However, a few genera contain both dextral and sinistral forms. In such genera, sympatric species may show opposite directions of coiling. Peake (1973) found that sympatric *Diplommatina* species of similar size always differed in the direction of coiling. Populations of *Partula suturalis* Pfeiffer sympatric with one or more other *Partula* spp. on Moorea usually differ from the most closely-related species in the direction of coiling (Murray and Clarke, 1980). Coiling direction is known to be maternally inherited in *Partula* (Murray and Clarke, 1966). Differences in direction of coiling may serve as a mechanism of partial reproductive isolation between species, since it serves as a partial barrier even within species (Lipton and Murray, 1979). These coiling differences between sympatric populations might represent an initial response to selection for reproductive isolation when two species come in contact. Since *Partula* are often polymorphic for coiling direction, the variability on which selection could act may be present from the time of contact. Over time, other more effective mechanisms may evolve but the differences in coiling direction might still be retained due to fixation of alleles controlling coiling.

DISCUSSION AND CONCLUSIONS

Our understanding of variation in the form of land-snail shells is noticeably meager compared to other animal groups, and indeed even to aquatic mollusks. However, there has been enough work to show that broad geographic patterns, relating to latitude or climate, are generally lacking. Thus, there are no overriding environmental factors to which shell form responds. Rather, shell form is responsive

to a variety of environmental factors, whose relative importance may vary geographically or among taxa. Shell form may also relate to a snail's way of dealing with the environment (niche).

A recurring problem in the explanation of land-snail shell form is the interpretation of the correlation of environmental factors with sets of covarying morphological features. Which characters are adaptive and which are nonadaptive correlates?

S. J. Gould, who has treated this question in a series of papers on shell form of land snails (e.g., see Gould, 1969a, 1971a, 1984b), has proposed a "test" of a nonadaptation involving multivariate morphometric analysis (Gould, 1984b). The method consists of: (1) identifying sets of covarying morphometric shell characters through multivariate analysis; (2) interpreting certain sets as developmental correlates; (3) hypothesizing an adaptive or environmental (inductive) cause for variation in one character; and (4) concluding that variation in other correlated characters is a nonadaptive consequence of variation in that character. However, this approach has at least three weaknesses.

First, by passing off some variation as nonadaptive, this approach overlooks the broader, possibly adaptive reasons for the existence of developmental programs involving character covariation. For example, even if changes in relative height might be a necessary consequence of selection for larger size (through increased whorl number), the fact that there exists a developmental pattern in which relative height increases with size is interesting and deserving of investigation. Cain (1981), for example, has suggested an adaptive significance for shape change during ontogeny in *Cerion*, a pattern that Gould (1984a) accepted simply as a historical fact.

Second, covariation among characters does not prove developmental dependence (acknowledged by Gould, 1984b: 235); this can only be firmly established by experimental studies. However, comparison of within-population and among-population covariance sets may be helpful in identifying possible developmental correlates. Developmentally-correlated characters should show similar covariance patterns within and among populations. For example, if populations differ by a covarying set of characters such as whorl number, diameter, and relative height as against relative umbilical width (a common pattern in land snails), then, if these covary due to a common pattern of ontogeny among populations, one should find the same covariance pattern among individuals within the populations. In *Pleurodonte lucerna*, relative shell height is strongly negatively correlated ($r = -0.96$) with diameter in *among-population* comparisons, as might be expected if these characters were developmental correlates (Goodfriend, 1983b). However, *within* 13 out of 15 populations, relative height and diameter are independent, thus implying that the among-population correlation is not simply developmental. A more rigorous evaluation of developmental relationships among characters can be obtained through among-population comparison of plots of shell form characteristics versus whorl number (from apex to lip; Goodfriend, 1983b). These show the ontogenetic pattern of change in form and provide a basis for evaluating among-population homologies and differences in shell ontogeny. For example, if a population has more whorls, a larger diameter, and a greater relative height than another, such an analysis could reveal whether the pattern of shell ontogeny is the same in both populations up to the whorl number of the smaller shells. If so, the larger shells could be interpreted as simply representing further growth.

Third, given developmental dependence between characters, the inference of nonadaptive variation in one character depends on demonstration of the cause of variation of the other character, whether due to selection or direct environmental influence. Where this latter causation is only hypothetical, then nonadaptive variation is only hypothetical. For example,

Gould (1969b) has interpreted paedomorphs (flat, thin, widely-umbilicate shells) as resulting from selection for thinner shells on low-calcium substrates; the other characters are considered nonadaptive developmental correlates. But an argument could also be made for selection acting, for example, on relative height, with flatter shells occurring under the wetter conditions temporally associated with low-calcium substrates; thinner shells could be a consequence of selection for flatter shells. No conclusion of nonadaptive variation in a character can be reached until the selective regime or environmental influences are known. It follows then that further understanding of variation in shell form must come from the study of adaptive and/or environmental (inductive) causes; even identification of nonadaptive variation is dependent on understanding of these causes. Nevertheless, nonadaptive developmentally-correlated traits very probably exist and may be common. The difficulty is to demonstrate that they are nonadaptive.

The shells of land snails are not unique among gastropods with respect to basic morphological characteristics such as relative height (Cain, 1977), translation rate, angle of elevation of coiling axis, or the shape of the generating curve (Vermeij, 1971). Nevertheless, anyone familiar with mollusks can usually distinguish readily between the shells of terrestrial and aquatic snails. Just what is unique about terrestrial snail shells has never been characterized quantitatively. Some features—such as apertural denticles, expansion of the lip of the adult, and a relatively thin shell—are more common among terrestrial snails, but none is unique to terrestrial snails; and even taken together, they do not permit terrestrial forms to be clearly distinguished from aquatic forms. I suspect that detailed morphometric analysis may show that terrestrial mollusks are characterized by distinctive allometric patterns of shell form ontogeny.

The morphological distinctiveness of terrestrial snail shells is almost certainly related to the unique ecological conditions of terrestrial environments. For example, in marine environments, predatory crabs may be important in selecting for thick shells and thickened lips formed at the end of growth periods (Zipser and Vermeij, 1978); whereas, in terrestrial environments, predatory insects may select for apertural denticles (Solem, 1972). In aquatic gastropods, aperture form may be related to respiratory requirements of water circulation into and out of the mantle cavity (Linsley, 1977). Terrestrial prosobranchs, on the other hand, may show apertural modifications to permit respiration during dormancy (e.g., breathing tubes in pomatiasids and cyclophorids, sensu lato [Rees, 1964], or lip notches in helicinids). Shell balance is certainly a particular problem for terrestrial snails because of the great weight of the shell and enclosed visceral mass (Cain, 1977). But it is not yet clear what modifications in shell form may be related to this problem. A quantitative understanding of the distinctiveness of land-snail shell form relative to aquatic shell form would probably go a long way in revealing these balance-related shell modifications.

REFERENCES

AGÓCSY, P. 1963. The examination of some edible snail (*Helix pomatia* L.) populations (Mollusca). Ann. Hist. Nat. Mus. Natl. Hung., 55:513–520.

ALONSO, M. R., AND M. IBÁÑEZ. 1978. El genero *Iberus* Montfort 1810 (Pulmonata: Helicidae). 1. *Iberus rositai* Fez 1950. Arch. Moll., 108:185–192.

ALONSO, M. R., AND M. IBÁÑEZ. 1979. Nuevos datos sobre la relacion sistematica entre *Sphincterochila hispanica* (Westerlund, 1886) y *Sphincterochila cariosula* (Michaud, 1833) (Pulmonata: Sphincterochilidae). Boll. Malacol., Milano, 15:1–18.

ALONSO, M. R., A. LÓPEZ ALCÁNTARA, P. RIVAS, AND M. IBÁÑEZ. 1985. A biogeographic study of *Iberus gualterianus* (L.) (Pulmonata: Helicidae). Soosiana, 13:1–10.

ALTES, J. 1956. Sur le polymorphisme de la coquille de *Leucochroa candidissima* modalités et déterminisme. Bull. Mus. Hist. Nat. Marseille, 16:53–67.

BAKER, H. B. 1924. Land and freshwater molluscs of the Dutch Leeward Islands. Occas. Pap. Mus. Zool. Univ. Mich., 152:1–159.

BANTOCK, C. R., AND J. A. BAYLEY. 1973. Visual selection for shell size in *Cepaea* (Held.). J. Anim. Ecol., 42:247–261.

BANTOCK, C. R., J. A. BAYLEY, AND P. H. HARVEY. 1975. Simultaneous selective predation on two features of a mixed sibling species population. Evolution, 29:636–649.

BAR, Z. 1978. Variation and natural selection in shell thickness of *Theba pisana* along climatic gradients in Israel. J. Moll. Stud., 44:322–326.

BAUR, B. 1984. Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata: Helicidae). Rev. Suisse Zool., 91: 37–46.

BENGTSON, S.-A., A. NILSSON, S. NORDSTRÖM, AND S. RUNDGREN. 1979. Selection for adult shell size in natural populations of the landsnail *Cepaea hortensis* (Müll.). Ann. Zool. Fennici, 16:187–194.

BERRY, A. J. 1963. Growth and variation of the shell in certain Malayan limestone hill snails. Proc. Malacol. Soc. Lond., 35:203–206.

BOETTGER, C. R. 1921. *Carabus morbillosus* Fabr. und *Otala tigri* Gerv., eine Studie gegenseitiger Anpassung. Abh. Senckenb. Naturforsch. Ges., 37:321–325.

BOETTGER, C. R. 1929. Beeinflussung des Schalenbaus der Landschnecke *Gonyodiscus rotundatus* Müller. Biol. Zentralbl., 49:559–568.

BOETTGER, C. R. 1935. Die Abwehr der Landschnecken gegen Käfer. Sber. Ges. Naturf. Freunde Berl., (1935):93–102.

BOETTGER, C. R. 1952. Grössenwachstum und Geschlechtsreife bei Schnecken und pathologischer Riesenwuchs als Folge einer gestörten Wechselwirking beider Faktoren. Zool. Anz., 17:468–487.

BOYCOTT, A. E. 1920. On the size variation of *Clausilia bidentata* and *Ena obscura* within a "locality." Proc. Malacol. Soc. Lond., 14:34–42.

BRANDT, R. A. 1959. Die Helicellinae der Cyrenaika. Arch. Moll., 88:81–162.

BROWN, A. P. 1911. Variation in some Jamaican species of *Pleurodonte*. Proc. Acad. Nat. Sci. Philad., 63:117–164.

BROWN, A. P. 1913. Variation in two species of *Lucidella* from Jamaica. Proc. Acad. Nat. Sci. Philad., 65:3–21.

BURLA, H. 1984. Induced environmental variation in *Arianta arbustorum* (L.). Genetica, 64:65–67.

BURLA, H., AND W. STAHEL. 1983. Altitudinal variation in *Arianta arbustorum* (Mollusca, Pulmonata) in the Swiss Alps. Genetica, 62:95–108.

CAIN, A. J. 1971. Colour and banding morphs in subfossil samples of the snail *Cepaea*. Pages 65–92 in Ecological genetics and evolution (R. Creed, ed.). Blackwell Scientific Publications, Oxford.

CAIN, A. J. 1977. Variation in the spire index of some coiled gastropod shells and its evolutionary

significance. Phil. Trans. R. Soc. Lond., B, 277:377–428.

CAIN, A. J. 1978a. Variation of terrestrial gastropods in the Philippines in relation to shell shape and size. J. Conchol., 29:239–245.

CAIN, A. J. 1978b. The deployment of operculate land snails in relation to shape and size of shell. Malacologia, 17:207–221.

CAIN, A. J. 1980. Whorl number, shape, and size of shell in some pulmonate faunas. J. Conchol., 30: 209–221.

CAIN, A. J. 1981. Possible ecological significance of variation in shape of *Cerion* shells with age. J. Conchol., 30:305–315.

CAIN, A. J. 1983. Ecology and ecogenetics of terrestrial molluscan populations. Pages 597–647 in The Mollusca. Volume 6. Ecology (W. D. Russell-Hunter, ed.). Academic Press, New York.

CAIN, A. J., AND R. H. COWIE. 1978. Activity of different species of land snail on surfaces of different inclinations. J. Conchol., 29:267–272.

CAMERON, R. A. D. 1978. Differences in the sites of activity of coexisting species of land mollusc. J. Conchol., 29:273–278.

CAMERON, R. A. D. 1981. Functional aspects of shell geometry in some British land snails. Biol. J. Linn. Soc., 16:157–167.

CAMERON, R. A. D., AND M. A. CARTER. 1979. Intra- and interspecific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). J. Anim. Ecol., 48:237–246.

CARTER, M. A., AND M. ASHDOWN. 1984. Experimental studies on the effects of density, size, and shell colour and banding phenotypes on the fecundity of *Cepaea nemoralis*. Malacologia, 25:291–302.

CHARRIER, M. 1981. Contribution à l'étude des effets du groupement sur la croissance de l'escargot "petit gris" *Helix aspersa* Müller (Gastéropode pulmoné stylommatophore). Archs. Zool. Exp. Gén., 122:29–38.

CLARKE, B., W. ARTHUR, D. T. HORSLEY, AND D. T. PARKIN. 1978. Genetic variation and natural selection in pulmonate molluscs. Pages 219–270 in Pulmonates. Volume 2A. Systematics, evolution and ecology (V. Fretter and J. Peake, eds.). Academic Press, London.

CLESSIN, S. 1897. Ueber den Einfluss der Umgebung auf die Gehäuse der Mollusken. Jh. Ver. Vaterl. Naturk. Württ., 53:68–86.

CONNER, E. F., AND D. SIMBERLOFF. 1979. The assembly of species communities: Chance or competition? Ecology, 60:1132–1140.

COOK, A. H. 1895. Molluscs. Pages 1–459 in The Cambridge natural history. Volume 3 (S. T. Harmer and A. E. Shipley, eds.). Macmillan and Co., New York.

COOK, L. M. 1965. Inheritance of shell size in the snail *Arianta arbustorum*. Evolution, 19:86–94.

COOK, L. M. 1967. The genetics of *Cepaea nemoralis*. Heredity, 22:397–410.

COOK, L. M., AND A. J. CAIN. 1980. Population dynamics, shell size and morph frequency in exper-

imental populations of the snail *Cepaea nemoralis* (L.). Biol. J. Linn. Soc., 14:259–292.

COOK, L. M., AND W. N. JAFFAR. 1984. Spire index and preferred surface orientation in some land snails. Biol. J. Linn. Soc., 21:307–313.

COOK, L. M., AND P. O'DONALD. 1971. Shell size and natural selection in *Cepaea nemoralis*. Pages 93–108 *in* Ecological genetics and evolution (R. Creed, ed.). Blackwell Scientific Publications, Oxford.

COOK, L. M., AND C. W. A. PETTITT. 1979. Shell form in *Discula polymorpha*. J. Moll. Stud., 45:45–51.

COPPOIS, G., AND C. GLOWACKI. 1983. Bulimulid land snails from the Galapagos: #1. Factor analysis of Santa Cruz Island species. Malacologia, 23:209–219.

COWIE, R. H. 1984a. The life-cycle and productivity of the land snail *Theba pisana* (Mollusca: Helicidae). J. Anim. Ecol., 53:311–325.

COWIE, R. H. 1984b. Shell thickness in the land snail *Theba pisana* (Pulmonata: Helicidae). Biol. J. Linn. Soc., 21:423–429.

CROWELL, H. H. 1973. Laboratory study of calcium requirements of the brown garden snail, *Helix aspersa* Müller. Proc. Malacol. Soc. Lond., 40:491–503.

DAN, N., AND S. E. R. BAILEY. 1982. Growth, mortality, and feeding rates of the snail *Helix aspersa* at different population densities in the laboratory, and the depression of activity of helicid snails by other individuals, or their mucus. J. Moll. Stud., 48:257–265.

DE BARTOLOMÉ, J. F. M. 1982. Comments on some Mediterranean rockdwelling helicids. J. Conchol., 31:1–6.

DE SMET, W. H. O., AND E. A. M. VAN ROMPU. 1984. Shell size and thickness in adult *Cepaea nemoralis* (L.) (Gastropoda) from the Belgian coastal dunes. Biol. Jb. Dodonaea, 52:26–34.

EMBERTON, K. C. 1982. Environment and shell shape in the Tahitian land snail *Partula otaheitana*. Malacologia, 23:23–35.

FRÖMMING, E. 1954. Biologie der mitteleuropäischen Landgastropoden. Duncker and Humblot, Berlin.

GEBHARDT-DUNKEL, E. 1953. Die Trockenresistenz bei Gehäuseschnecken. Zool. Jb., Abt. Allg. Zool., 64: 235–266.

GOODFRIEND, G. A. 1983a. Some new methods for morphometric analysis of gastropod shells. Malacol. Rev., 16:79–86.

GOODFRIEND, G. A. 1983b. Clinal variation and natural selection in the land snail *Pleurodonte lucerna* in western St. Ann Parish, Jamaica. Ph.D. Dissertation, Univ. Florida, Gainesville.

GOODFRIEND, G. A. 1986a. Radiation of the land snail genus *Sagda* (Pulmonata: Sagdidae): Comparative morphology, biogeography, and ecology of the species of north-central Jamaica. Zool. J. Linn. Soc. (in press).

GOODFRIEND, G. A. 1986b. Late Holocene morphological changes in a Jamaican land snail: Evidence for fluctuation in rainfall. Abstracts and reports from the Conference on Abrupt Climatic Change (W. H. Berger and L. Labeyrie, eds.). Scripps Inst. Oceanogr. Reference Ser., 86–8:125–127.

GOULD, S. J. 1969a. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P.* (*Poecilozonites*) in Bermuda. Bull. Mus. Comp. Zool., 138:407–532.

GOULD, S. J. 1969b. Character variation in two land snails from the Dutch Leeward Islands: Geography, environment and evolution. Syst. Zool., 18: 185–200.

GOULD, S. J. 1971a. Precise but fortuitous convergence in Pleistocene land snails from Bermuda. J. Paleontol., 45:409–418.

GOULD, S. J. 1971b. Environmental control of form in land snails a case of unusual precision. Nautilus, 84:86–93.

GOULD, S. J. 1984a. Morphological channeling by structural constraint: Convergence in styles of dwarfing and gigantism in *Cerion*, with a description of two new fossil species and a report on the discovery of the largest *Cerion*. Paleobiology, 10: 172–194.

GOULD, S. J. 1984b. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curaçao: A way of studying nonadaptation. Syst. Zool., 33:217–237.

GOULD, S. J., AND D. S. WOODRUFF. 1978. Natural history of *Cerion*. VIII. Little Bahama Bank—A revision based on genetics, morphometrics, and geographic distribution. Bull. Mus. Comp. Zool., 148: 371–415.

GOULD, S. J., D. S. WOODRUFF, AND J. P. MARTIN. 1974. Genetics and morphometrics of *Cerion* at Pongo Carpet: A new systematic approach to this enigmatic land snail. Syst. Zool., 23:518–535.

GRANT, P. R. 1972. Convergent and divergent character displacement. Biol. J. Linn. Soc., 4:39–68.

HAAS, F. 1933. Bemerkungen über und Neubeschreibungen von Heliciden aus Zypern und Palästina. Senckenbergiana, 15:25–31.

HÄKKINEN, I., AND S. KOPENEN. 1982. Two marginal populations of *Cepaea hortensis*: Morph frequency, shell size and predation. Hereditas, 97:163–166.

HELLER, J. 1975. The taxonomy, distribution and faunal succession of *Buliminus* (Pulmonata: Enidae) in Israel. Zool. J. Linn. Soc., 57:1–57.

HELLER, J. 1979. Distribution, hybridization and variation in the Israeli landsnail *Levantina* (Pulmonata: Helicidae). Zool. J. Linn. Soc., 67:115–148.

HELLER, J. 1982. Natural history of *Theba pisana* in Israel (Pulmonata: Helicidae). J. Zool., Lond., 196: 475–487.

HOFF, A. 1923. Zur Variabilität von *Arianta* (*Helix*) *arbustorum* Leach. Z. Indukt. Abstammungs-Vererbungsl., 30:99–129.

JONES, J. S., B. H. LEITH, AND P. RAWLINGS. 1977. Polymorphism in *Cepaea*: A problem with too many solutions? Annu. Rev. Ecol. Syst., 8:109–143.

KALTENBACH, H. 1934. Die individuelle, ökologische und geographische Variabilität der Wüstenschnecken *Eremina desertorum, hasselquisti* und *zitteli*. Arch. Naturgesch., n.f., 3:383–404.

KALTENBACH, H. 1942. Beitrag zur Kenntnis der Wüstenschnecken *Eremina desertorum, kobelti* und *hasselquisti* mit ihren individuellen, ökologischen

und geographischen Rassen. Arch. Naturgesch., n.f., 11:350–386.

KEKAUOHA, W. 1966. Life history and population studies of *Achatina fulica*. Nautilus, 80:3–10.

KNIGHTS, R. W. 1979. Experimental evidence for selection on shell size in *Cepaea hortensis* (Müll.). Genetica, 50:51–60.

KNIPPER, H. 1939. Systematische, anatomische, ökologische und tiergeographische Studien an südosteuropäischen Heliciden (Moll. Pulm.). Arch. Naturgesch., 8:327–517.

LAZARIDOU-DIMITRIADOU, M., AND J. DAGUZAN. 1981. Etude de l'effet du "groupement"des individus chez *Theba pisana* (mollusque gastéropode pulmoné stylommatophore). Malacologia, 20:195–204.

LINSLEY, R. M. 1977. Some "laws" of gastropod shell form. Paleobiology, 3:196–206.

LIPTON, C. S., AND J. MURRAY. 1979. Courtship of land snails of the genus *Partula*. Malacologia, 19: 129–146.

LUCARZ, A. 1982. Effet du groupement sur la croissance pondérale d'escargots *Helix aspersa* Müller. C. R. Acad. Sci. Paris, 294:753–756.

MACHIN, J. 1967. Structural adaptations for reducing water-loss in three species of terrestrial snail. J. Zool., Lond., 152:55–65.

MAGARITZ, M., AND G. A. GOODFRIEND. 1986. Movement of the desert boundary in the Levant from Late Pleistocene to Early Holocene. *In* Proceedings of the Conference on Abrupt Climatic Change (W. H. Berger and L. Laberyrie, eds.). D. Reidel Publishing Co., Dordrecht (in press).

MAGARITZ, M., AND J. HELLER. 1980. A desert migration indicator—Oxygen isotopic composition of land snail shells. Palaeogeogr., Palaeoclim., Palaeoecol., 32:153–162.

MAZEK-FIALLA, K. 1934. Die Lebensweise xerophiler Schnecken Syriens, Griechlands, Dalmatiens und der Türkei und die Beschaffenheit ihrer subepithelialen Drüsen. Z. Morph. Ökol. Tiere, 28:445–468.

McNAIR, C., W. M. KIER, P. D. LA CROIX, AND R. M. LINSLEY. 1981. The functional significance of aperture form in gastropods. Lethaia, 14:63–70.

MURRAY, J., AND B. CLARKE. 1966. The inheritance of polymorphic shell characters in *Partula* (Gastropoda). Genetics, 54:1261–1277.

MURRAY, J., AND B. CLARKE. 1968. Inheritance of shell size in *Partula*. Heredity, 23:189–198.

MURRAY, J., AND B. CLARKE. 1980. The genus *Partula* on Moorea: Speciation in progress. Proc. R. Soc. Lond., 211:83–117.

NEVO, E., C. BAR-EL, AND Z. BAR. 1983. Genetic diversity, climatic selection and speciation of *Sphincterochila* landsnails in Israel. Biol. J. Linn. Soc., 19: 339–373.

ØKLAND, F. 1925. Die Verbreitung der Landgastropoden Norwegens. Skr. Nor. Vidensk. Akad. Oslo Mat. Naturvidensk. Kl., 8:1–168.

OLDHAM, C. 1929. The influence of lime on the shell of *Arianta arbustorum* (L.). Proc. Malacol. Soc. Lond., 18:143–144.

OLDHAM, C. 1934. Further observations on the in-

fluence of lime on the shells of snails. Proc. Malacol. Soc. Lond., 21:131–138.

OOSTERHOFF, L. M. 1977. Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). Netherl. J. Zool., 27:1–132.

OWEN, D. T. 1965. A population study of an equatorial land snail, *Limicolaria martensiana* (Achatinidae). Proc. Zool. Soc. Lond., 144:361–382.

PAUL, C. R. C. 1974. *Azeca* in Britain. J. Conchol., 28:155–172.

PEAKE, J. F. 1973. Species isolation in sympatric populations of the genus *Diplommatina* (Gastropoda, Prosobranchia, Cyclophoridae, Diplommatininae). Malacologia, 14:303–312.

PFEIFFER, K. L. 1947. Die Gyrostomellen N-Afrikas. Arch. Moll., 76:9–35.

PFEIFFER, K. L. 1948. Die Gyrostomellen N-Afrikas (Berichtigung). Arch. Moll., 76:192.

PFEIFFER, K. L. 1949. *Levantina spiriplana* (Olivier). Arch. Moll., 77:1–51.

PLUMMER, J. M. 1975. Observations on the reproduction, growth and longevity of a laboratory colony of *Archachatina* (*Calachatina*) *marginata* (Swainson) subspecies *ovum*. Proc. Malacol. Soc. Lond., 41: 395–413.

POLLARD, E. 1975. Differences in shell thickness in adult *Helix pomatia* L. from a number of localities in southern England. Oecologia, 21:85–92.

PORPORA, L., AND C. F. SACCHI. 1958. Ricerche su *Euparypha arietina* (Rossmaessler). II—Dati biometrici. Ann. Ist. Mus. Zool. Univ. Napoli, 10:1–44.

RAMOS, M. A. 1980. Estudio del tamaño de la concha de *Cepaea nemoralis* (L.) en tres valles del Pirineo Español. Com. Prim. Congr. Nac. Malacol., pages 47–49.

RAUP, D. M. 1966. Geometric analysis of shell coiling: General problems. J. Paleontol., 40:1178–1190.

REES, W. J. 1964. A review of breathing devices in land operculate snails. Proc. Malacol. Soc. Lond., 36:55–67.

REICHHOLF, J. 1979. Gefleckte Schnirkelschnecken, *Arianta arbustorum*, als Nahrung der Singdrossel, *Turdus philomelos*, im Auwald: Selektive Grössen- and Typenwahl. Bonn. Zool. Beitr., 30:404–409.

RENSCH, B. 1931. Zur Kenntnis der Molluskenfauna Timors. Zool. Jb., Abt. Syst. Ökol. Geogr. Tiere, 60: 429–456.

RENSCH, B. 1932. Über die Abhängigkeit der Grösse, des relativen Gewichtes und der Oberflächenstruktur der Landschneckenschalen von Umweltsfaktoren (Ökologische Molluskenstudien I.). Z. Morphol. Ökol. Tiere, 25:757–807.

RENSCH, B. 1937. Untersuchungen über Rassenbildung und Erblichkeit von Rassenmerkmalen bei sizilischen Landschnecken. Z. Indukt. Abstammungs-Vererbungsl., 72:564–588.

SACCHI, C. F. 1957. Un caso di "gigantisme insulare" *Helicella profuga* (A. Schm.) ssp. *Torcellensis* n. Atti Ist. Veneto Sci. Lett. Arti, 105:285–298.

SACCHI, C. F. 1961. Considérations sur les phénomènes microévolutifs animaux des petites îles méditerranéennes. Pages 321–337 *in* Le peuple-

ment des Iles Méditerranéennes et le problème de l'insularité. Colloq. Int. Cent. Natl. Rech. Sci.

SACCHI, C. F. 1965. Ecological and historical bases for a study of the Iberian terrestrial Mollusca. Proc. 1st Europ. Malacol. Congr., (1962):243–257.

SACCHI, C. F. 1971. Écologie comparée des gastéropodes pulmonés des dunes Méditerranéennes et Atlantiques. Natura, Milano, 62:277–358.

SCHINDEL, D. E., AND S. J. GOULD. 1977. Biological interaction between fossil species: Character displacement in Bermudian land snails. Paleobiology, 3:259–269.

SCHMID, G. 1919. Zur Variabilität der *Clausilia* (*Alinda*) *biplicata* Mont. Nachrichtenbl. dt. Malakozool. Ges., 51:24–44.

SCHRÖDER, F. 1978. *Trochoidea* (*Xerocrassa*) *ebusitana* (Hidalgo 1869) und ihre Rassen auf den Pityusen/ Spanien. Veröff. Überseemuseum Bremen, Reihe A, 5:83–120.

SOLEM, A. 1969. Abundance, local variation and brood pouch formation in *Libera fratercula* from Rarotonga, Cook Islands. Annu. Rep. Am. Malacol. Union, (1968):10–12.

SOLEM, A. 1972. Microarmature and barriers in the apertures of land snails. Veliger, 15:81–87.

SOLEM, A. 1976. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part I. Family Endodontidae. Field Museum of Natural History, Chicago.

TATTERSFIELD, P. 1981. Density and environmental effects on shell size in some sand dune snail populations. Biol. J. Linn. Soc., 16:71–81.

TAYLOR, J. W. 1881. Life histories of British helices. J. Conchol., 3:241–259.

TILLIER, S. 1981. Clines, convergence and character displacement in New Caledonian diplommatinids (land prosobranchs). Malacologia, 21:177–208.

TILLING, S. M. 1983. An experimental investigation of the behaviour and mortality of artificial and natural morphs of *Cepaea nemoralis* (L.). Biol. J. Linn. Soc., 19:35–50.

VAN BRUGGEN, A. C. 1969. Studies on the land molluscs of Zululand, with notes on the distribution of land molluscs in Southern Africa. Zool. Verh., Leiden, 103:1–16.

VAN BRUGGEN, A. C. 1980. Size clines and subspecies in the streptaxid genus *Gulella*-Pfr. (Mollusca, Gastropoda, Pulmonata) in southern Africa. Zool. Verh., Leiden (180):3–62.

VERMEIJ, G. J. 1971. Gastropod evolution and morphological diversity in relation to shell geometry. J. Zool., Lond., 163:15–23.

VERMEIJ, G. J. 1982. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. Malacologia, 23:1–12.

VERMEIJ, G. J., D. E. SCHINDEL, AND E. ZIPSER. 1981. Predation through geological time: Evidence from gastropod shell repair. Science, 214:1024–1026.

VOELKER, J. 1959. Der chemische Einfluss von Kalziumkarbonat auf Wachstum, Entwicklung und Gehäusebau von *Achatina fulica* Bowdich (Pulmonata). Mitt. Hamb. Zool. Mus. Inst., 57:37–78.

WELCH, D'A. A. 1938. Distribution and variation of *Achatinella mustelina* Mighels in the Waianae Mountains, Oahu. Bull. Bishop Mus., 152:1–164.

WELCH, D'A. A. 1954. Distribution and variation of Hawaiian tree snail *Achatinella bulimoides* Swainson on the leeward and northern slopes of the Koolau Range, Oahu. Proc. Acad. Nat. Sci. Philad., 106:63–107.

WILLIAMSON, P., R. A. D. CAMERON, AND M. A. CARTER. 1976. Population density affecting adult shell size of snail *Cepaea nemoralis* L. Nature, 263:496–497.

WOLDA, H. 1963. Natural populations of the polymorphic landsnail *Cepaea nemoralis* (L.). Factors affecting their size and their genetic constitution. Archs. Neerl. Zool., 15:381–471.

WOLDA, H. 1972. Changes in shell size in some experimental populations of the landsnail *Cepaea nemoralis* (Linnaeus). Argamon, Israel J. Malacol., 3:63–71.

WOODRUFF, D. S., AND S. J. GOULD. 1980. Geographic differentiation and speciation in *Cerion*—A preliminary discussion of patterns and process. Biol. J. Linn. Soc., 14:389–416.

ZIPSER, E., AND G. J. VERMEIJ. 1978. Crushing behavior of tropical and temperate crabs. J. Exp. Mar. Biol. Ecol., 31:155–172.