Morphological Divergence in Endemic Gastropods from Lake Tanganyika: Implications for Models of Species Flock Formation

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Patterns of variability in gastropod shell morphology were used to examine modes of morphological divergence and their implications for intra-lacustrine divergence. Two thiarid gastropods endemic to Lake Tanganyika, that are both stenotopic and rock-dwelling, were investigated because they are believed to be equally subject to environmental barriers to dispersal. A model of allopatric divergence, facilitated by habitat fragmentation, predicts that variation among populations should be large relative to the variation within them, and that organisms equally subject to environmental barriers to dispersal should exhibit similar magnitude and character of morphological divergence. Spekia and members of the Lavigeria species flock appear only in rocky, wave-battered shoals and neither gastropod is known to exhibit wide dispersal. Intervening reaches of sandy and muddy substrates are thought to be barriers to gene flow. Analyses of variance of factor scores reveal that interpopulation morphological variance is greater than intrapopulation variance for both genera, suggesting that divergence is allopatric. However, Spekia shows little morphological variability compared to shallow-water Lavigeria. In graphical analyses of factor scores, Lavigeria forms discrete clusters of morphology related to differences in environment, geographic distribution, and timing of larval broods, all indicative of speciation. The model of allopatric divergence controlled by environmental barriers to dispersal must be reviewed because of two incongruent results: sympatry of divergent morphs of Lavigeria, and the observation that members of Lavigeria show much greater endemic divergence than members of Spekia, even though they are thought to be equally poor dispersers.

INTRODUCTION

Islands, caves (Mayr, 1970), mountains (Sullivan, 1985), and lakes (Fryer and Iles, 1972) may serve as evolutionary microcosms as a consequence of their geographical, physiographical, and environmental isolation from the provinces that surround them. In these settings good experimental control is possible, because their ecology and biogeography are relatively less complex than that of open marine or terrestrial settings. The rift lakes of tropical Africa exemplify such systems, and, interestingly, contain some of the most diverse lacustrine faunas. Characterized by high endemism, these lakes are relatively closed environments that allow the study of evolution over significant amounts of time (Beadle, 1982; Fryer and Iles, 1972; Greenwood, 1974, 1984b; Mayr, 1970). Lake Tanganyika, located in the western arm of the Great African Rift (Fig. 1), has been chosen as a natural laboratory for the investigation of morphological divergence among endemic gastropods.

Lake Tanganyika is of great size and antiquity. It is over 650 kilometers in length and over 1400 meters deep, and estimates of the lake's age, based on sediment accumulation rates, range from 2 to 20 million years (Beadle, 1982). Because of its tropical setting and great depth, Lake Tanganyika does not overturn seasonally, and well-circulated and oxygenated waters exist to only 200 meters in depth (Beadle, 1982; Degens, 1971). Consequently, benthic habitats for invertebrates are restricted to the lake's perimeter.

To understand the development of endemic species complexes among gastropods in the paleontological record, where only the shell is preserved, this study examines the inter- and intraspecific variability of shell morphology of two endemic gastropods with sympatric distribution. One genus, *Lavigeria*, is of particular interest because it may constitute a species flock (see Greenwood, 1984a). Since the other genus, *Spekia*, is represented by single species (Brown, 1981), characterizations of the patterns of morphological variation in these closely related endemic gastropods may provide relevant information about intralacustrine divergence and the formation of species flocks.

DIVERGENCE IN RIFT LAKE FAUNAS

Previous studies of intralacustrine evolution within Lake Tanganyika have supported allopatric divergence hypotheses, most notably for the remarkable cichlid fishes of which there are some 170 endemic species (Fryer and Iles, 1972). Greenwood (1974) and Beadle (1982) have favored models of
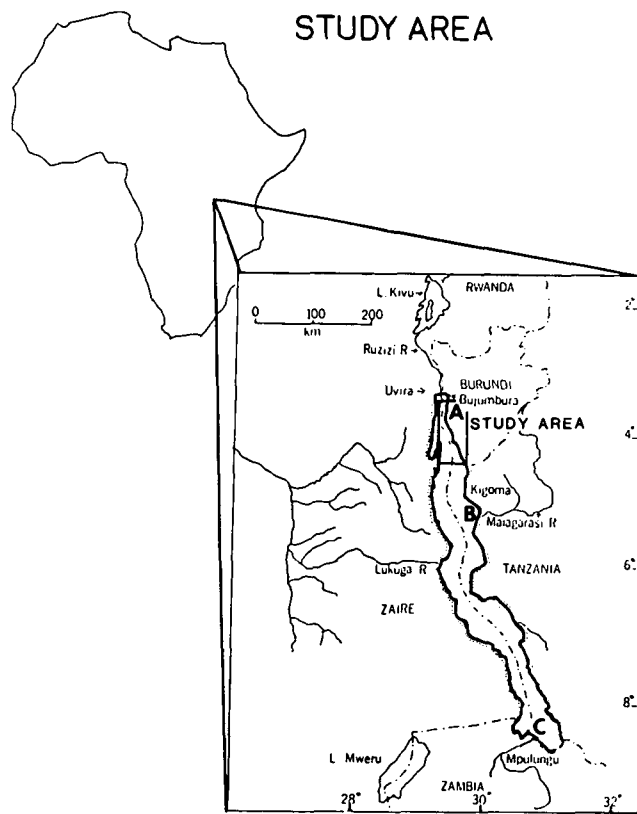
STUDY AREA

FIGURE 1—Lake Tanganyika in central Africa and the study area in Burundi.

allopatric divergence and speciation driven by fluctuations in lake level that may have stranded founder populations in separate lake basins. This seems an unlikely mechanism for Lake Tanganyika, where fluctuations would have had to have been frequent and over 500 meters—conditions more likely to delete species than create them.

Fryer and Iles (1972) and Fryer (1969) have argued that the invocation of separate basins to explain speciation is unnecessary. They have suggested that populations of habitat-restricted fish may have become isolated and morphologically divergent as once-continuous habitats became fragmented. This hypothesis is supported theoretically (Bush, 1975; Mayr, 1970, 1982; Endler, 1977) and empirically, to some extent, by McKaye and Gray (1984). This model may be particularly applicable for speciation in gastropods, since they are considerably less vagile than fish. Because a model of divergence based solely on physical and environmental parameters of the lake seems insufficient to account for the presence of sympatric sibling species, McKaye et al. (1982, 1984a, 1984b) and Dominey (1984) have suggested that, in addition to habitat barriers to dispersal, selective mating behavior in cichlids could maintain diverging species even if they are sympatric. These authors also believe that the brooding and maintenance of young is partially responsible for the development of preferences in this mate-selection process.

Other theories of speciation may also be important in explaining intralacustrine divergence. Divergence and speciation could be parapatric as populations become separated clinally by environmental gradients (Endler, 1973, 1977). Allochronic speciation models posit that population divergence is derived from divergence in the timing of breeding (Bush, 1975; Endler, 1977; Smith and Todd, 1984). Some of these models, developed to explain speciation in endemic cichlids, have been applied to the invertebrate faunas as well (e.g., Boss, 1978).

HYPOTHESES AND ASSUMPTIONS

The specific hypothesis of divergence we will examine, using intra- and interpopulation morphological variability of gastropod shells, is allopatric divergence facilitated by poor dispersal between habitats with patchy distribution.

Our first assumption is that the two gastropods have similar dispersal potentials. Dispersal strategies are thought to have an important effect on speciation processes (Jablonski and Lutz, 1983; Cohen and Johnston, this volume; Calow, 1978; Dominey, 1984). Especially where environmental factors are invoked as barriers to adult dispersal, strategies leading to wide dispersal can maintain gene flow and prevent divergence and speciation. Tanganyikan prosobranch gastropods lack long-distance larval dispersal mechanisms (Hubendick, 1952); indeed, no veliger larvae are known to exist in freshwater prosobranchs. Of the two gastropods investigated, *Lavigeria* is a brooder, but *Spekia zonata*'s larval development is not well known. *S. zonata* is certainly not a brooder and probably deposits eggs directly on the surface of rocks (Brown, 1980; Kat, pers. comm.). As a consequence of poor dispersal strategies among these gastropods, environmental and geographic barriers to post-larval dispersal may be expected to have a large net effect on the amount of gene flow between populations.

The second assumption of our study is that roughly the same barriers to adult dispersal exist for both gastropods—that is, both gastropods are similarly restricted to specific patches of habitat. Both organisms in the present study inhabit laterally discontinuous, rocky, wave-swept coastlines in shallow water. The organisms are not encountered on other substrates, except for one instance in *Lavigeria* (see below).

Lavigeria and *Spekia* are both thiarid gastropods, endemic to Lake Tanganyika (Brown, 1980; Leloup, 1953; Bourguignat, 1890). Figure 2 shows representative populations from three collection localities that span much of the lake. The different forms of *Lavigeria* are found at different depths but have broad sympatric overlap among adjacent forms. The systematic relationships of these forms are obscure, but recently collected electrophoretic data show that such sympatric but phenotypically distinct morphs are electrophoretically distinct, with fixed differences at a number of loci (Kat, pers. comm.). The morphology of marginal radular teeth also sorts with shell morphology (Kat, pers. comm.). Differences in the timing of brood formation among phenotypically distinct sympatric morphs suggest a lack of interbreeding among them (pers. obs.). *Spekia* is considered to have a single species (Leloup, 1953; Brown, 1980), and there is no morphological or electrophoretic evidence of speciation (Kat, pers. comm.).
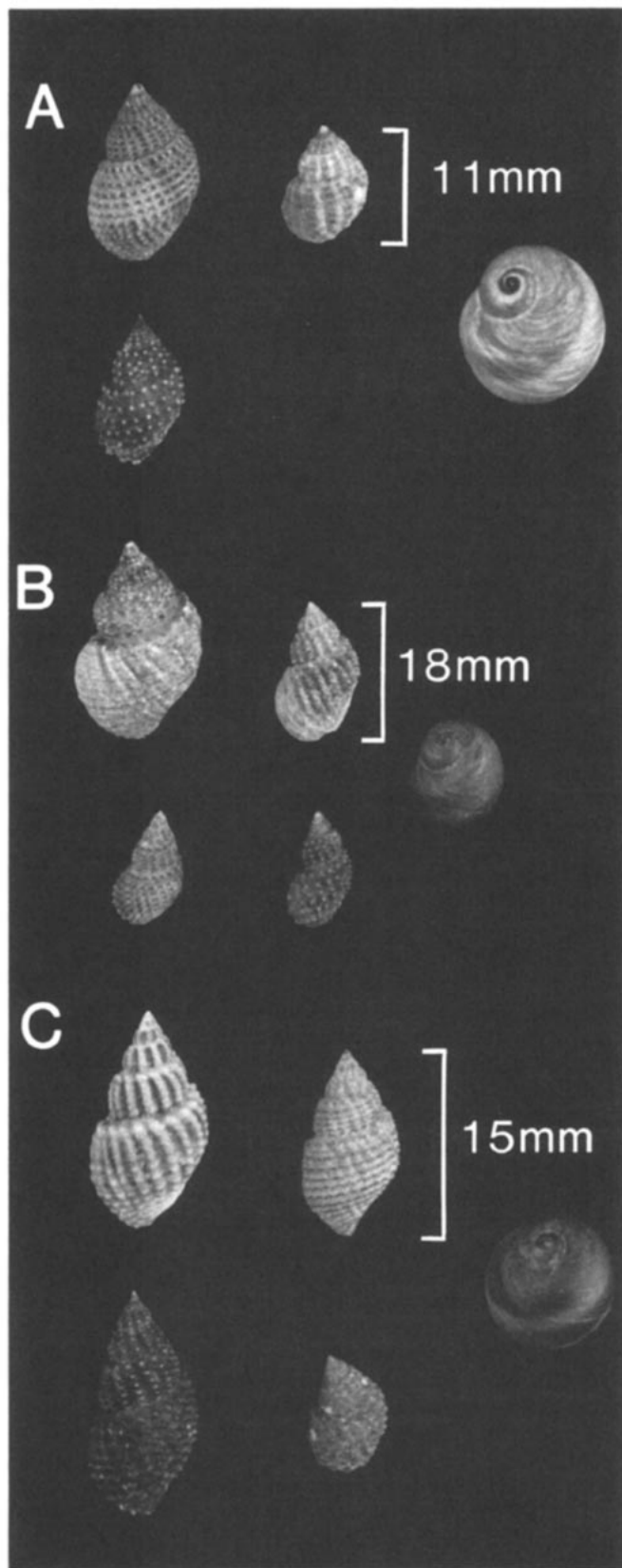
FIGURE 2—Three representative populations of *Lavigeria* and *Spekia zonata* from locations in Burundi (A), Tanzania (B), and Zambia (C). See locations in Figure 1. *Lavigeria* from right to left and top to bottom are from progressively deeper habitats at a given locale.

The question we are asking is not how many "good" species there are, but whether different patterns of endemic diversification exist among genera within the shallow-water habitat. This study focuses on shallow-water forms of *Lavigeria* that, based on the discussion above, are members of two species. It might be argued that the best test case would be made by comparing single species of *Lavigeria* and *Spekia* that are "incipiently" diverging. We have compared instead the pattern of morphological variation in a species that has split to one that has not. The comparison of these two genera is appropriate, as they are phylogenetically related, relatively stenotopic, and poor dispersers. We are assuming that the present distribution of variation in morphology may provide information about the mechanics of divergence. Morphological evidence suggests that the shallow-water species in Burundi are more closely related to each other than to other members of the *Lavigeria* species complex. Therefore, post-speciation data on morphology will apply to the question of divergence.

Finally, we are assuming that hard-part morphological data captures significant evolutionary divergence. In studies of speciation two kinds of data are generally important. Development of reproductive isolation is the criterion by which speciation should be judged (Mayr, 1972) and this requires data from breeding and behavioral experiments. However, differences in morphology are the most common indicator of species divergence. Hard-part, anatomical, and molecular morphology are all useful in assessing divergence. Neither morphological nor breeding data should be used to infer the other since cases of both sibling species and monospecific polymorphism are well documented (Mayr, 1972). The analysis of distribution and variation of morphological data in time and space is critical for inferring the pathways of divergence.

It is clear that the relationship between shell morphology, soft anatomy, and molecular data is not a simple one. A number of studies on gastropods (Dillon, 1984; Dillon and Davis, 1980; Gould et al., 1975; Gould and Woodruff, 1986) reveal that shell/anatomical morphometric and electrophoretic methods may or may not capture comparable information. Ecophenotypic divergence in shell form is a frequently cited problem in using shell morphology to assess evolutionary morphological divergence. Hubendick (1952) cites an example in which African planorbid snails, when bred and reared under different environmental conditions, produce morphologies that had previously been regarded as distinct species. The discussions of Williamson (1981, 1983, 1985) and his critics (Kat and Davis, 1983; Fryer et al., 1983; Palmer, 1985) illustrate many of the problems of ecophenotypic variability especially in paleontological studies. It is also true that strong ecological control of shell form may mimic the variability pattern expected from allopatric divergence. These concerns will have limited bearing on the present study because the study localities were chosen to be physiographically and environmentally similar.

Furthermore, water chemistry is nearly uniform throughout the lake's littoral zone (Degens et al., 1971; Beadle, 1982; Wombwell, 1986), and both *Lavigeria* and *Spekia* were collected from the same localities and experience quite similar environmental conditions.

On the other hand, important sculptural elements of gastropod shell form may be under rather simple Mendelian control (Palmer, 1985), suggesting that rather large changes in hard part morphology need not reflect speciation. In the case of the *Lavigeria* species complex, however, distinct shell morphologies correspond to electromorphically distinct species as regarded by P. Kat (pers. comm.).

While ecophenotypy may be expected to increase variance in shell morphology, selective pressure on certain shell morphologies can result in different species possessing shells that cannot be distinguished (Davis, 1979). This observation may have relevance for *Spekia* since it exhibits a rather invariant morphology. Recently completed electrophoretic investigations, however, have not uncovered cryptic species of *Spekia* (Kat, pers. comm.). The amount of morphological variability in *Spekia* is comparable to that of electrophoretic variability. Predation on gastropods by shell-cracking crabs and fish in Lake Tanganyika may lead to morphological adaptations that reduce the effectiveness of the predators (Vermeij and Covich, 1978; Cohen, 1985; West and Cohen, 1987). This too could result in convergence of shell form, but because members of the *Lavigeria* species complex are frequently subject to crab predation and have nonetheless diverged, this potential for convergence is not manifest.

The allopatric model of morphological divergence, facilitated by poor dispersal among populations residing in isolated habitats, predicts that interpopulation variance in morphology will be much greater than intrapopulation variance (Fryer and Iles, 1972; Fryer, 1969; Greenwood, 1984b; McKaye and Gray, 1984). Given the assumptions that the two study animals are: 1) similarly stenotopic to rocky, shallow-water habitats, 2) are equally subject to environmental barriers to dispersal, and 3) are phylogenetically related and endemic to the lake, a corollary prediction can be made. To the extent that environmental barriers and fragmented habitats control divergence, these two gastropods should exhibit similar magnitude and character of morphological variation and divergence. Large differences in the character of endemic divergence between these two gastropods could point out potential inadequacies of a simple allopatric model of intralacustrine divergence based solely on the extrinsic factors of the physical and geographic environment.

Collections and Morphometrics

The thiarid gastropods, *Spekia zonata* (Woodward) and members of the *Lavigeria* species complex (Woodward), were chosen for this study because of similarities in their habitat tolerance and dispersal ability. They were collected from the littoral zone in Lake Tanganyika from rocky, wave-swept coasts where they graze on algae.

Spekia zonata were collected from 12 collection sites, located respectively at 19.5, 28.9, 29.0, 32.6, 36.0, 39.5, 55.0, 104.9, 109.0, 109.1, and 114.2 km south of Bujumbura,

Burundi (Fig. 3). All collection localities will be referred to by km south of Bujumbura. Collection quadrats were between 20 to 30 m in length along shore and 20 m wide offshore. Individuals of *Lavigeria* were collected from the same localities as *Spekia* except for an additional locality, inserted at 22.0 km, and a collection at 115.0 instead of 114.2 km. For sites in which both species were found, the same collection quadrat was used. Collection localities were chosen to maximize the geographical separation of sites, the number of reaches of inhospitable habitats between sites (Fig. 3) and, the gross similarity of habitat among sites. Individuals of *S. zonata* were found only on rocky areas of the shoreline in less than 1 m of water and were often associated with large rocks and boulders up to 3 m in diameter. Individuals of the *Lavigeria* species complex were usually found on rocks, adjacent to *S. zonata* with less than 0.5 m of vertical sympatric overlap. In one instance, *Lavigeria* were found living on sublacustrine plants (*Chara* sp., *Potamogeton* sp.) in a calm bay, suggesting that *Lavigeria* has greater substrate tolerance than does *S. zonata*. However, despite an exhaustive survey of the Burundi coast, neither species was encountered on the wave-swept, sandy substrates that separate most collection localities, and such substrates probably represent environmental barriers to adult dispersal. Incurrent rivers, which separate many collection sites (Fig. 3), may also isolate populations of gastropods by establishing thermal and chemical barriers to dispersal (Beadle, 1982; Wombwell, 1986).

A series of mensural characters were selected based on their suspected morphological information content and result replicability and were made using vernier calipers and an optical micrometer fitted to a binocular microscope. R-mode factor analysis was made on the correlation matrix of measurement values for each gastropod. (These techniques have been used successfully in both neontological and paleontological studies [e.g., Gould and Woodruff, 1975, 1986; Dillon, 1984; Dillon and Davis, 1980].) Principal components were first extracted, and the Varimax criterion used to rotate axes orthogonally in order to associate axes more strongly with their attendant variables. The procedure does not affect the position of the cases relative to each other in the multidimensional space but reorients the axes to positions of "easier" interpretation (Norusis, 1985). Regression factor scores were then calculated for each specimen along each axis.

RESULTS

Spekia zonata

Factor analysis of the nine characters revealed a discernable degree of inter- and intrapopulation morphological variation. The analysis produced a four-factor solution that encompasses 92.6% of the variability present in the original data set (Table 1). The first axis, explaining 56.5% of data variance, has loadings of >0.85 for the following variables: apertural height, apertural width, maximum apertural dimension, opercular height, and opercular width (Fig. 4). These measures as a group are greatly dependent on the overall shell size. This first axis also has small negative loadings of cross-whorl width and sutural angle, two characters that are independent of size. The
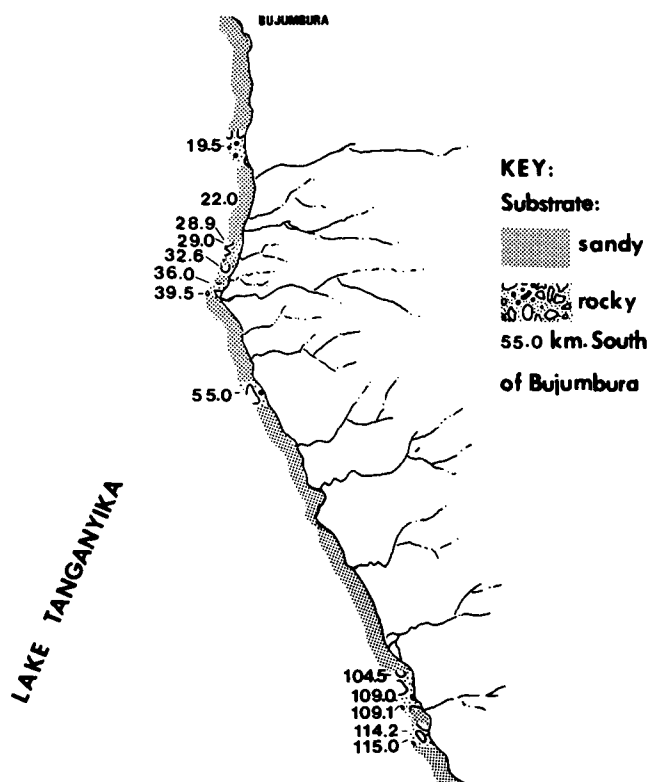
COLLECTION SITES

KEY:

Substrate:

[shaded] sandy

[shaded] rocky

55.0 km. South

of Bujumbura

FIGURE 3—*Lavigeria* and *Spekia zonata* collection sites in Burundi. All sites denoted by number of kilometers south of Bujumbura.

Morphometric Measures

Lavigeria nassa

1 HT 2 WD 3 APERHT 4 APERWD 5 WD15
6 WD20 7 HT15 8 HT20

Spekia zonata

1 LIP 2 MAXHT 3 APERHT 4 APERWD
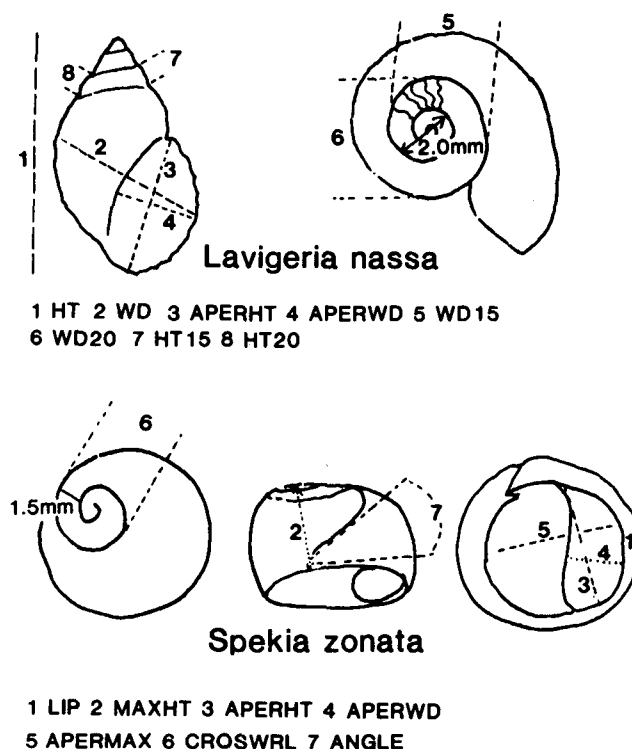5 APERMAX 6 CROSWRL 7 ANGLE

FIGURE 4—Morphometric Measures for *Lavigeria*. 1. Height of shell (HT). 2. Maximum width of shell perpendicular to the axis of coiling (WD). 3. Apertural height (APERHT). 4. Apertural width perpendicular to apertural height (APERWD). 5. Width of the whorl at the 15th axial rib as counted from a standardized whorl of width 2.0 mm (WD15). 6. Width of the whorl at the 20th axial rib (WD20). 7. Height of the whorl parallel to the axis of coiling at the fifteenth rib (HT15). 8. Height of the whorl at the 20th rib (HT20). Morphometric Measures for *S. zonata*. 1. Apertural lip thickness at thinnest point (LIP). 2. Height from final suture to top of protoconch (MAXHT). 3. Apertural height (APERHT). 4. Apertural width (APERWD). 5. Maximum apertural dimension (APERMAX). 6. Whorl width at standardized width (CROSWRL). 7. Angle of suture and base (ANGLE). 8. Operculum height (OPERHT). 9. Operculum width (OPERWD).

second factor axis shows high loadings for lip thickness and maximum height and moderate loadings on maximum apertural dimension and sutural angle. The third factor axis, accounting for 10.2% of the variance, shows high loadings only on sutural angle with low negative loadings for the apertural measures. The fourth axis, accounting for an additional 4.7% of the variance, has high loading only on cross-whorl width.

Reliable interpretation of factor axes requires that samples exhibit multivariate normality. Inspection of histograms and normal plots indicates that univariate normality is approximated by each variable (Johnston, 1986). This, however, is not a confirmation of multivariate normality. Factor analysis is a reasonably robust statistical technique (Reyment et al., 1984), and there are some salient relationships between the factors and their associated variables.

Plots of mean factor scores for each *Spekia* collection site reveal that collection sites 28.9, 29.0, and 32.6 km have the highest mean scores on factor axis one (Fig. 6), and they also contain the largest specimens in the data set (Fig. 5). This, together with the size-dependent nature of the first factor's attendant variables, is a strong indication that this axis may be regarded as a "size" factor. It is quite common for the primary axis to be size-dependent (e.g. Reyment et al., 1984).

The measure of apertural lip thickness, which indicates the degree of "adult" morphology in some gastropods (Gould et al., 1975; Gould, 1984), is most strongly associated with the second factor axis. In this case, apertural lip thickness is related to allometric thickening after a "standard" adult size has been reached. The other measure associated with this axis is maximum height, which records not only the overall height and size of the shell but also indicates the relationship of the shell's apertural base to the axis of coiling. This measurement is made from the suture to the top of the protoconch and often records

TABLE 1—Rotated factor loadings matrix for the four factor solution in *S. zonata*[1]

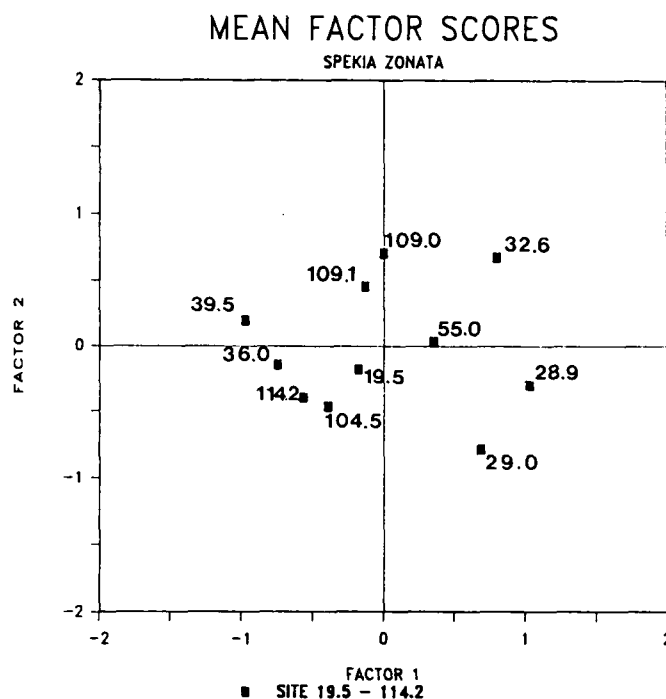| VARIABLES | % VARIATION | SPEKIA ZONATA | | | |
		FACTOR 1 56.5%	FACTOR 2 21.2%	FACTOR 3 10.2%	FACTOR 4 4.7%
LIP		.14	.92*	.26	.03
MAXHT		.56	.73*	.17	.03
APERHT		.93*	.02	−.22	−.08
APERWD		.91*	.14	−.04	−.01
APERMAX		.87*	.41	.05	−.01
CROSWRL		−.05	.05	.07	.99*
ANGLE		−.10	.31	.93*	.08
OPERHT		.93*	.17	−.01	−.01
OPERWD		.91*	.18	.03	−.02

[1]Variable definitions shown in Figure 4.
*High loadings on a given factor.
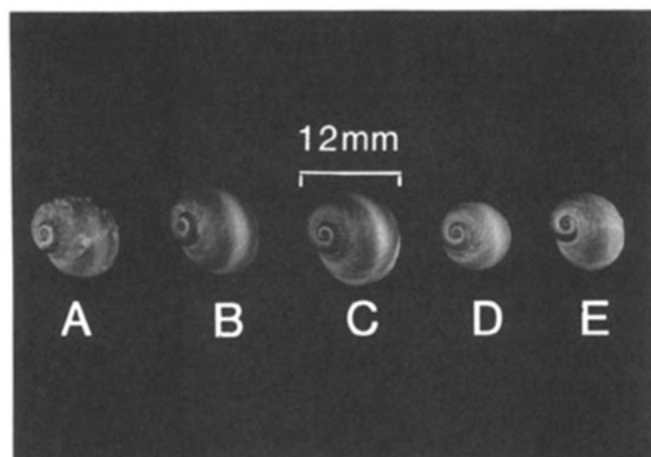
FIGURE 5—Representative samples of *Spekia zonata* from Burundi at
A) 19.5 km south of Bujumbura, **B)** 29.0 km, **C)** 32.6 km, **D)** 109.1
km, **E)** 114.2 km, and other sites. Note the overall similarity of the
snails. Factor score plot positions of snails A-E are shown in Figure 6.

FIGURE 6—Plot of site mean factor scores for all samples against the
first and second axes. Note the separation of 32.6, 28.9, and 29.0
km from other samples along the first axis.

a measure of the "uprightness" of the coiling axis rather than
gross size (Fig. 4). Such a variable in conjunction with apertural
lip thickness makes the second axis more difficult to interpret,
but may represent an allometric relationship between adult-
hood and uprightness.

As the third and fourth factor axes are strongly related to
single variables, their interpretation is straightforward. The
third factor axis, on which sutural angle loads strongly, can
likewise be regarded as a coiling factor and may represent the
amount of downward translation involved in the coiling. Cross-
whorl width, which is the measure of whorl width at a fixed
semi-whorl width, is related to the rapidity of whorl expansion,
and the fourth axis may represent a whorl expansion criterion.

Small values for this variable imply that the whorl began with a
small width and expanded more rapidly than those whorls that
score a large value on this measure (Fig. 4). Consequently, the
third and fourth factors are related to Raup's w and t parame-
ters, respectively (Raup, 1966).

TABLE 2—OneWay ANOVA of *Spekia* factor scores

SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARE	F RATIO	F PROB.
Factor 1					
between sites	10	284.7108	28.4711	51.3880	.0000
within sites	616	341.2892	.5540		
Factor 2					
between sites	10	128.2711	12.8271	15.8751	.0000
within sites	616	497.7289	.8080		
Factor 3					
between sites	10	139.1536	13.9154	17. 6069	.0000
within sites	616	486.8464	.7903		
Factor 4					
between sites	10	118.0899	11.8090	14.3221	.0000
within sites	616	507.9101	.8245		

FACTOR SCORE PLOT

Spekia zonata

FACTOR 2

19.5 □   29.0 △

39.5 ▼   114.2 ●
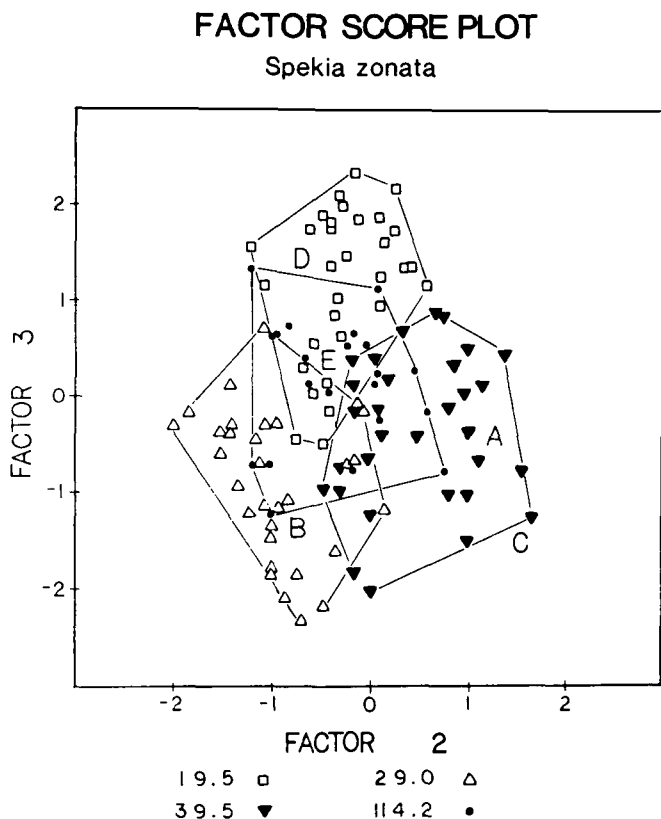
FIGURE 7—Factor score plot of individual *Spekia zonata* from four sites against the second and third (shape) axes. Note the morphological overlap of geographically separated samples.

One-way analysis of variance was used to test the hypothesis that interpopulation variance in *Spekia* morphology is greater than intrapopulation variance. The results of the tests (Table 2) show that for each factor the null hypothesis, that inter- and intrapopulation variance are equal, is rejected (p < .0001). For the given degrees of freedom, the F ratios are too large to have come from samples in which inter- and intrapopulation variance are equivalent. Therefore, between-site variance is significantly greater than that within sites for the size and the shape factors.

Although this test answers the question of where the greatest variability is housed, it offers no description of how variability is partitioned among populations. Therefore, a graphic exploration of variability was undertaken. Plots of mean factor scores of sites (Fig. 6) show that the largest individuals are found near 30 km, a site where unique morphs of *Lavigeria* were collected. Surprisingly, the smallest *S. zonata* are found in an adjacent site at 39.5 km. Figure 6 also shows that no geographic trend is indicated along either the first and second axes, which encompass most of the variation.

The analysis of the individual cases rather than sites in Figure 7 also illustrates the lack of correspondence between geographical separation and morphological variability. Along the first, second, and third axes, the morphological divergence between sites 19.5, 29.0, and 39.5 km are about the same. Site 114.2 km, the most geographically isolated, plots squarely within the distribution of the other sites. This illustrates that shape does not necessarily diverge with geographic separation. Indeed, large morphological overlap on all axes are found between geographic extremes (Fig. 7). On no axis is any incremental geographic trend indicated.

In summary the ANOVA shows that most existing morphological variability occurs among populations. Size is the dominant source of variation; shape is more homogeneously
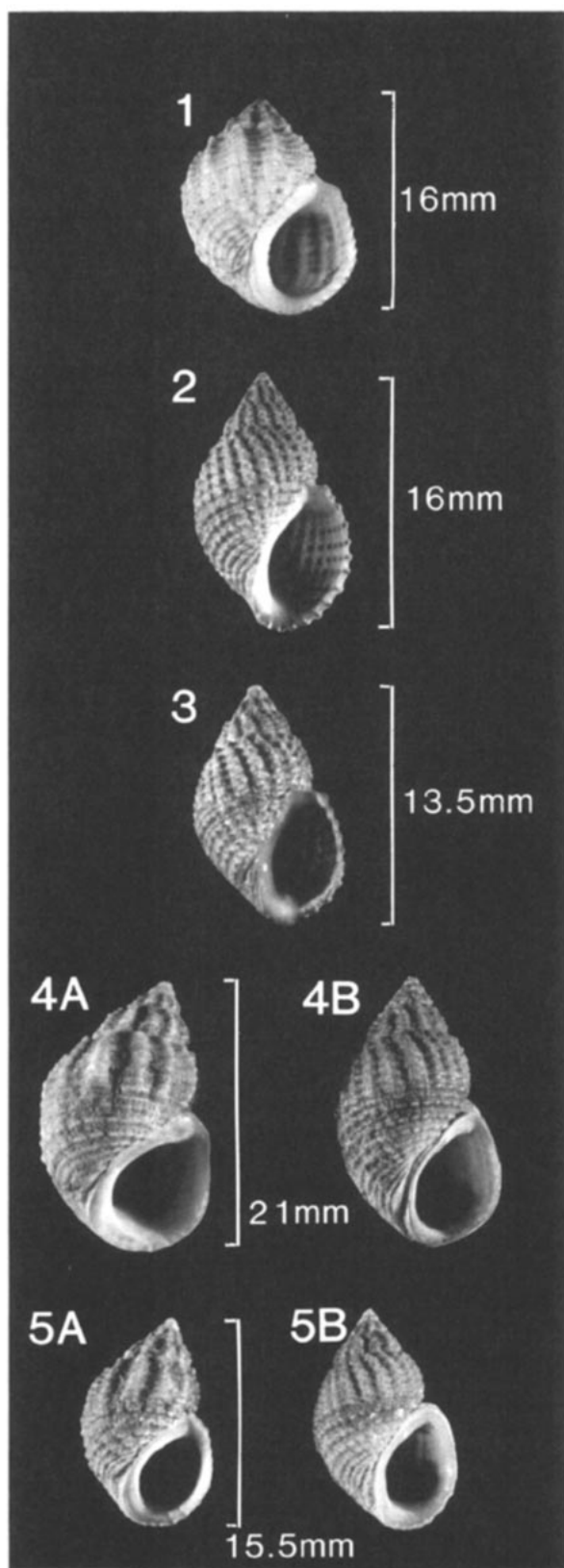
FIGURE 8—Representative samples of *Lavigeria* from Burundi. Note the variation in shape and size of these gastropods. Numerals 1-5 correspond to collection locations and factor score positions in Fig. 9: 1) 19.5 km south of Bujumbura, 2) 29.0 km, 3) 36.0 km, 4) 104.5 km, 5) 109.1 km.

distributed. Plots of individual cases (Fig. 7) suggest that there is often a large degree of morphological overlap between geographically remote sites. In general, *Spekia zonata* shows little morphological variation either between or within populations.

Lavigeria

Lavigeria displays much greater phenetic diversity (Figs. 2 and 8). Visual inspection suggests that ribbing, elongation, and size are all quite variable between sites and, in some instances, within sites (e.g., site 109.1 in Fig. 8). Data from *Lavigeria* were initially analyzed without regard to collection sites. Four factors accounted for 95.4% of the variance found in the original data (Table 3). The first factor however, explains only a modest 46.4% of the variance, and has high loadings on whorl width of the 15th rib (WD15) (see Figure 4 for explanation of characters) and whorl width of the 20th rib (WD20), and whorl height of the 15th rib (HT15) and whorl height of the 20th rib (HT20). All of the remaining variables have loadings near zero except height, which shows a low negative loading. The second axis, accounting for 41.0% of the variance, has high loadings for height, width, apertural height, and apertural width, and has low negative loadings for WD15 and WD20. The third axis, accounting for only 4.6% of the variance, has a moderately high loading for apertural height and an attendant low loading of height. The fourth factor accounts for 3.4% of the variance and has moderate to low loadings of HT15 and height with negative loadings for apertural width, WD15 and WD20. Graphical diagnostics show the data to approximate normal distribution for each variable (Johnston, 1986).

The first factor has high loadings of upper whorl measures (WD15, WD20, HT15 and HT20), as standardized by axial rib counts, and is clearly a ribbing criterion. A further indication of this axis' value as a ribbing criterion is suggested by factor score comparisons from the collection site 109.1 km. While measuring the individuals, we noticed that this sample comprised coarsely and finely ribbed morphologies (Fig. 8-5). There is a one-to-one correspondence between positive scores on the first axis and these coarse ribbing observations (Johnston, 1986). Comparisons of observed axial ribbing and first axis factor scores further confirm the axis to be a ribbing discriminator (compare Figures 8 and 9-5). The resolution of this ribbing factor is in itself important because it captures an aspect of morphology not resolvable using the parameters of Raup (1966).

Interpretations of the second axis are based on high loadings of all size-dependent variables. Moreover, since width measures dominate, this axis may represent an overall shell size/width criterion. Because of loadings of many different

TABLE 3—Rotated factor matrix [1]

		LAVIGERIA			
VARIABLES	% VARIATION	FACTOR 1 46.4%	FACTOR 2 41.0%	FACTOR 3 4.6%	FACTOR 4 3.4%
HT		−.24	.85*	.29*	.25*
WD		.00	.97*	.11	−.03**
APERHT		.01	.68*	.72*	−.01
APERWD		.09	.96*	.02	−.06**
WD15		.95*	−.05	.02	−.10
WD20		.95*	−.05	.06	−.20**
HT15		.89*	.02	−.06	.40*
HT20		.95*	.01	−.06	.06

[1]Variable definitions shown in Figure 4.
 * = high loadings on a given factor.
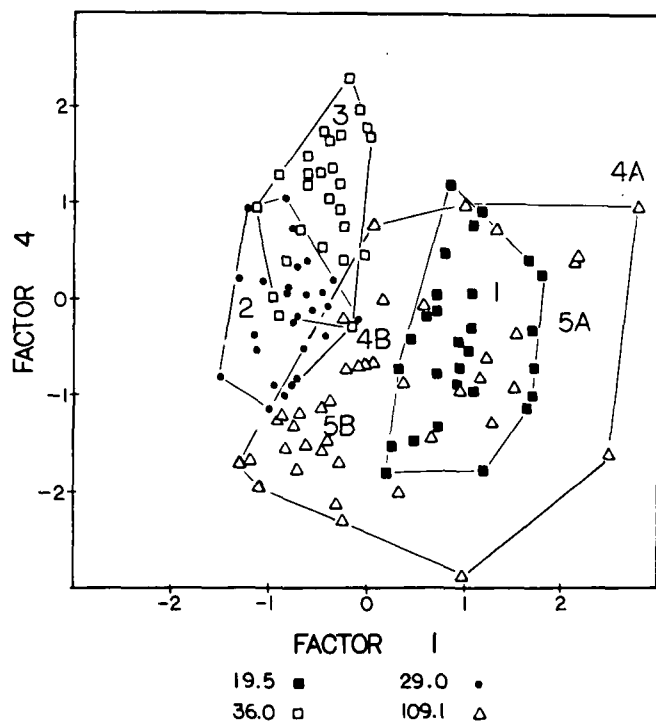** = inversely covarying variables on factor four.

FACTOR SCORE PLOT
Lavigeria nassa

FACTOR 1

19.5 ■   29.0 •
36.0 □   109.1 △

FIGURE 9—Plot of factor scores of individual cases from representative sites. Note the tight clustering of northern samples 19.5, 29.0, and 36.0 km, and the greater variability found in the southern sites such as 109.1 km. Note also the position of Lavigeria from Figure 8, numerals 1-5.

variables, the third axis is difficult to interpret. The fourth axis accounts for a small amount of the variance. It contrasts whorl heights with whorl widths and may represent a "squatness" criterion.

A one-way ANOVA was run to test the null hypothesis that inter- and intrapopulation variances are equivalent. The results of this test unequivocally demonstrate that interpopulation variance is larger (Table 4). Unlike the results for S. zonata, where F ratios were large on the size or first axis, the Lavigeria results show high F ratios for the first and fourth factor axis, interpreted as ribbing and squatness criteria, respectively. For the given degrees of freedom, shape factors show as great if not greater interpopulation variance than the size factor. Hence, the morphology of Lavigeria is highly site distinctive, as shown graphically in Figure 9.

To better understand how morphology is partitioned among individuals and populations, a graphical examination of factor scores was carried out. Plots of site mean factor scores among different combinations of the factor axes were constructed (Fig. 10). The first axis markedly separates sites at 19.5 and 22.0 km from those at 28.9–39.5 km. First axis factor scores for individuals are exclusively positive at sites 19.5, 22.0, and 55.7 km, and are exclusively negative for sites 28.9 through 39.7 km. This is shown by representative sites in Figure 9. Interestingly, sites 104.9, 109.0, 109.1, and 115 km have first axis factor scores that are both positive and negative.

A qualitative but significant physiographic difference among sites seems to correspond directly to observed morphological divergence along the first and fourth axes. Sites 28.9–39.5 km all have the shared characteristic that, 30–40 m offshore from the collection quadrates, the lake bottom plunges steeply. At all other sites, the slope is gradual for up to 1 km offshore. At the steep-sloped sites, the wave base is not encountered until shoreline, and benthic gastropods thereby experience explosive wave energy during storms and diurnal windy periods.

TABLE 4—OneWay ANOVA of *Lavigeria* factor scores

SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	F RATIO	F PROB.
Factor 1					
between sites	11	330.7433	30.0676	58.1573	.0000
within sites	662	342.2567	.5170		
Factor 2					
between sites	11	206.8087	18.8008	26.6975	.0000
within sites	662	466.1913	.7042		
Factor 3					
between sites	11	98.1369	8.9215	10.2738	.0000
within sites	662	574.8631	.8684		
Factor 4					
between sites	11	194.7403	17.7037	24.5052	.0000
within sites	662	478.2597	.7224		
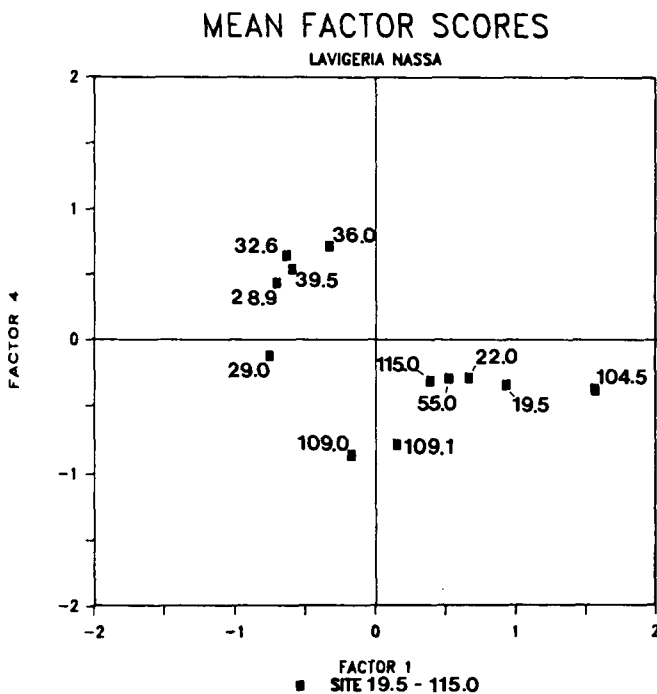
FIGURE 10—Mean factor for scores for *Lavigeria* from each collection site along the first and fourth axis. Note the distinct clustering of sites 28.9-39.5 km and the lack of a geographical cline from northern to southern sites.

Figures 9 and 10 reveal that collection sites 28.9–39.5 km are distinguished from all other sites along the first and fourth axes. Hence, the divergence of this *Lavigeria* morph may be related to adaptation to high wave energy.

Corroboration of the uniqueness of *Lavigeria* from 28.9 to 39.5 km comes from the observation that only at these particular localities were brooding young found in the female gastropods, during two months of sampling (July and August, 1985). This suggests that the breeding and rearing cycle of *Lavigeria* at these sites is out of phase with members of *Lavigeria* inhabiting the other sites to the north and south. This is also a strong piece of evidence that the fine-ribbed morphology is not merely an ecophenotypic effect of high energy environments.

The pattern of variation displayed in Figure 9 is characteristic of the data set as a whole. In the northern sites, ribbing, as delineated by the first axis, is relatively invariant within sites. The variation at 19.5, 29.0, and 36.0 km is strikingly small, as depicted by tight clusters, when compared to 109.1 km. Along the first axis, site 109.1 has a greater range than the other three sites combined and exhibits both coarse- and fine-ribbed specimens (Fig. 8). Northern sites are homogeneous within sites but they show marked morphological divergence from other sites (e.g., Figs. 8-1 and 9-3). Southern sites, as a group, are clearly distinguished from one another (Fig. 10), but show large degrees of within-site variation (109.1 in Fig. 9). The factor scores define three population types for *Lavigeria:* distinct northern fine- and coarse-ribbed populations with low intrapopulation variability, southern populations of high variability and a combined coarse- and fine-ribbed population.

To summarize, the ANOVA for *Lavigeria* populations shows that interpopulation variance is larger than intrapopulation variance for each factor axis. But unlike *Spekia*, *Lavigeria* has high F ratios on the first and fourth shape axes, implying that shape has greater interpopulation variance than size. Morphologies in members of the *Lavigeria* species complex are characterized by discrete clusters which are probably species, whereas *S. zonata* exhibits large morphological overlaps from

all localities. There also seems to be a relationship between the steep-sloped rocky coasts of sites 28.9 through 39.5 km and the unique morphology of *Lavigeria* individuals at those sites. The northern, fine-ribbed populations are further distinguished by their breeding cycle, being out of phase with other populations of *Lavigeria*. Graphic analysis of the factor scores reveals that three discrete population types exist within *Lavigeria:* low variability northern populations of distinct (1) fine- and (2) coarse-ribbed morphologies and (3) high variability southern populations where both fine- and coarse-ribbed morphs coexist.

DISCUSSION

Results of the morphometric analysis suggest that interpopulation variance is much greater than intrapopulation variance in both gastropod genera. This result agrees with a model of allopatric divergence. Given, however, our assumptions that the two gastropods are sympatrically distributed in similar shallow-water habitats and are similarly subject to environmental barriers to adult dispersal, our expectation of similar character and magnitude of variability and divergence is not met. *Lavigeria* exhibits a wider range of morphologies than *Spekia* and, at least in the northern sites, is characterized by discrete morphological clusters. Differences in shell morphology, radular morphology, electrophoretic data, and timing of brood development suggest that *Lavigeria* has speciated. There is little morphological evidence of divergence within *Spekia,* for which all sites show overlapping morphologies.

The failure to find equal divergence could arise from failure in our assumptions. Confusing patterns of morphological variation could be caused if shell morphology was not capturing evidence of significant evolutionary divergence. Ecophenotypic control of shell form may mimic the pattern of allopatric divergence. However, considerable evidence suggests that distinct morphs of *Lavigeria* are different species. In addition, if ecophenotypic effects were mimicking divergence, one might also expect some noticeable effect in *S. zonata,* as both genera share habitats. No such effect is observed. The evidence of speciation in shallow-water *Lavigeria* also rules out the possibility that variations in shell form are the result of genetic polymorphism within a single species. Selective convergence of shell form in *S. zonata* could be responsible for making the variability of *Lavigeria* appear larger. Again, the fact that the animals share adjacent habitats suggests that a tendency towards shell convergence would be exhibited in both species. Furthermore, preliminary electrophoretic studies provide no evidence of cryptic speciation in *Spekia*. Shell morphology appears to capture the relevant evidence of divergence.

Perhaps our most poorly constrained assumption is that present-day distributions of morphology contribute information about processes of divergence occurring in the past. Included in this broad assumption is a more specific assumption about phylogeny. We are assuming that the shallow-water species of *Lavigeria* in Burundi diverged from one another in their present habitat and that they are more closely related to each other than any other members of the *Lavigeria* species complex. In support of this assumption we know that the shallow-water forms share the same habitat and are morphologically more

similar to one another than to other forms of *Lavigeria.* Further systematic work is essential to support this contention.

Most models of speciation assume that divergence must be fixed between isolated populations. The highly variable populations in southern Burundi, if they are exhibiting evolutionary divergence, are not predicted by models of allopatric divergence. Assortative mating and sexual selection are potentially capable of maintaining divergent populations that are in sympatry (Dominey, 1984). The analyses of variance suggest that, overall, *Lavigeria* has greater morphological variance between than within populations. Nonetheless, breeding, behavioral, and other morphological data should be investigated, since there is evidence that sympatric divergence is important in the formation of fish species flocks (McKaye et al., 1984; McKaye and Gray, 1984).

The fact that different species of *Lavigeria* brood at different times of year indirectly raises the issue of whether morphological data are sufficient to assess divergence. Differences in timing of broods imply differences in the timing of breeding. We have no evidence on whether the change in the timing of breeding is a potential cause of speciation or a result of it. However, if allochronic divergence had occurred in *Lavigeria* prior to speciation it may be that this behavioral aspect— flexibility of breeding—could be more important in speciation than morphological differences. In this way, the development of reproductive isolation could have been decoupled from morphological divergence. Once again behavioral data are necessary to assess this concern.

Finally, if our assumption of equal environmental inhibition of dispersal is incorrect, we would expect different patterns of divergence between our two gastropods. If *Spekia* were a better disperser than *Lavigeria,* one would expect the pattern that our analyses reveal. The dispersal strategy of *S. zonata* is not well known; it lacks a brood pouch and probably lays egg masses on rocks (Brown, 1980). Because swimming veligers are unknown among non-marine prosobranchs, the only means of wide-dispersal for *S. zonata* are egg case detachment, rafting on wood or weeds, or hitchhiking on birds or fish. These behaviors have not been reported, but they cannot be ruled out.

One striking difference between the two gastropods is that *Lavigeria* broods its young. Perhaps, rather than *S. zonata* being a better disperser than expected, *Lavigeria* is a much poorer disperser than expected. The brooding of small clutches of young could confuse patterns of dispersal. First, the time from fertilization to offspring release is much longer in *Lavigeria* than in *S. zonata,* since the latter does not brood its young. This could allow more time for a single female gravid female to colonize a new patch of habitat and found a population, especially by unusual transportation. This may result in many small, isolated demes that might be expected to undergo fairly rapid divergence (Wright, 1940), since dispersal between patches of habitat is infrequent. Data on the behavior and colonization potential of these gastropods has yet to be collected but is an important area of future investigation.

There are some important implications from our finding that divergence has not been equal in *Spekia* and *Lavigeria*. For related, stenotopic organisms that are equally subject to environmental barriers to dispersal, simple fragmentation of

habitat is insufficient to explain differential degrees of morphological divergence. This further suggests that some intrinsic characteristics of the gastropods themselves render them more or less likely to diverge, because their physical environments are so similar. Therefore, it becomes important to ask what characteristics of the organisms themselves could affect potential for divergence.

CONCLUSIONS

While the distribution of morphs suggests allopatric divergence among *Lavigeria* and *S. zonata*, the fact that one genus shows great divergence and speciation and the other shows little suggests that the physical parameters of the lake environment are insufficient to explain these patterns of morphological distribution. The investigation of possible differences in behavior, flexibility of reproductive timing, and larval strategy, especially brooding versus non-brooding, will be necessary before this problem of differential endemic diversification will be solved.

ACKNOWLEDGMENTS

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Suess effected a change in geological methods that was certainly as momentous as his substantive contributions to theory: Suess made "working by the book" respectable. Suess's synthesis was a monument to the extraordinary value of sifting and mastering the geological literature already accumulated, rather than rushing off to some crucial locale to gain eyewitness verification or to produce one more field report. In the enlarged scope of Suess's synthesis of geology *all* locales became crucial—there is no analogue in Suess's theory to the Temple of Serapis or the Baltic tidemarks. The spectacular results of his method of work put a new pressure on the literature of geology and on the abilities of geologists; they marked the end of the age in which geology was a popular science and the observations of any literate amateur were gladly welcomed by a geological survey or journal. The literature was now too important to be entrusted to the tyro, and geology became a truly professional activity.

—Mott Greene