

## Large African Lakes as natural laboratories for evolution: Examples from the endemic gastropod fauna of Lake Tanganyika

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Lake Tanganyika is justifiably famous for an aquatic fauna that exceeds most other lakes in ecological complexity and evolutionary derivation. Endemics outnumber non-endemics in many taxa. Only four of the 171 species of cichlid fish are not endemic. All seven species of crab are endemic. Eighty percent of the molluscs are unique to this lake. All of these groups are morphologically highly divergent, with associated behavioral diversity and trophic complexity. A biologist diving on the steep rocky shore is left with an impression of a coral reef rather than a standard lake ecosystem. This unique fauna is probably the result of a long period of isolation and phylogenetic lability of the colonizing organisms. The lake is approximately six million years old (SCHOLZ & ROSENDAHL 1987) and the dominant taxa form species flocks in other ancient lakes (GREENWOOD 1964, BOSS 1978). Lake Tanganyika is a natural laboratory for addressing the question of lacustrine speciation. Conservation of this lake will be rewarded not only by the beauty and uniqueness of the habitats, but by the wealth of information that can be gained from studying the interplay of organisms and environments here.

The gastropods of Lake Tanganyika are one of the most spectacular examples of the endemic radiations in this lake. Their heavily calcified and ornately sculptured shells have excited the interest of evolutionary biologists since they were first described in the last century. Because their shells strongly resemble those of marine molluscs, early workers proposed that the lake is a remnant body of the Indian ocean, complete with a relict marine fauna. Taxonomic work on soft-part anatomy, however, revealed that they are derived from fresh water ancestors.

The gastropods that radiated in this lake are in the freshwater family Thiaridae of the mesogastropod superfamily Cerithioidea (Prosobranchia) (BROWN 1980, HOUBRICK 1988). In an effort to address the question of lacustrine speciation, we have investigated several aspects of the thiarid radiation, concentrating on the genus *Lavigeria*. This paper is a review of our work over the past four years.

### Taxonomic status

The first work on the gastropods of Lake Tanganyika was done by the renowned taxonomic

splitter BOURGIGNAT (1890) who named about 75 species of *Lavigeria* from shell material of the shallow water morphospecies alone. Many of these were based on a single, beach collected shell. LÉLOUP reclassified the *Lavigeria* group into two hyper-variable species, *L. nassa* with 6 'formes' and *L. grandis*, a giant with one 'forme' (LÉLOUP 1953). LÉLOUP's work was also based almost exclusively on shell material. His classification was followed by BROWN without revision (BROWN 1980 and pers. comm.). Our research shows that LÉLOUP's classification severely underestimates the true diversity of *Lavigeria* based on several lines of evidence: 1. Morphospecies often differ in habitat and timing of reproduction. 2. The distributions of some morphospecies are sympatric, yet the morphospecies are statistically distinct in shell morphology (JOHNSTON 1987, MICHEL & COHEN 1988). 3. The internal anatomy differs between some morphospecies (MICHEL in prep.). 4. Electrophoretic data indicate that the morphospecies are non-interbreeding units. These data imply that shell morphology underestimates species diversity because they point to instances of convergence in shell morphology.

### Biochemical studies

Electrophoretic analyses of *Lavigeria* reveal fixed allele differences between morphospecies, indicating that they do not interbreed (KAT 1988, MICHEL 1991). There is considerable genetic divergence within the genus, and this coincides with habitat and morphological variation. KAT's study examined 26 loci, of which 17 were polymorphic among taxa. Within taxa a minimum of two and maximum of four loci were polymorphic (Table 1). Nei's genetic distance and similarity values are presented in Table 2; the distances are moderate. The genetic distances and our proposed evolutionary relationships between these eight

0538-4680/92/0023-0085 \$ 3.75

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Table 1. Genetic variability at 26 loci in all populations (Standard errors in parentheses).

Population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
				Direct count	HdyWbg expected**
1. LTYE TAN	10.0 (0.0)	1.2 (0.1)	15.4	0.027 (0.016)	0.067 (0.036)
2. LTBR TAN	10.0 (0.0)	1.2 (0.1)	11.5	0.023 (0.017)	0.053 (0.032)
3. LGRA TAN	12.0 (0.0)	1.3 (0.2)	15.4	0.051 (0.028)	0.078 (0.041)
4. LNAS TAN	12.0 (0.0)	1.3 (0.1)	19.2	0.045 (0.020)	0.078 (0.034)
5. LSPA MWI	6.0 (0.0)	1.0 (0.0)	0.0	0.000 (0.000)	0.000 (0.000)
6. LNAS BUR	11.0 (0.0)	1.1 (0.1)	7.7	0.017 (0.014)	0.033 (0.025)
7. LTDA TAN	10.0 (0.0)	1.2 (0.1)	15.4	0.031 (0.020)	0.054 (0.026)
8. LSDA TAN	10.0 (0.0)	1.2 (0.1)	15.4	0.015 (0.009)	0.065 (0.032)

\* A locus is considered polymorphic if more than one allele was detected.

\*\* Unbiased estimate (see Nei 1978). Population names are keyed to morphologies on Fig. 1.

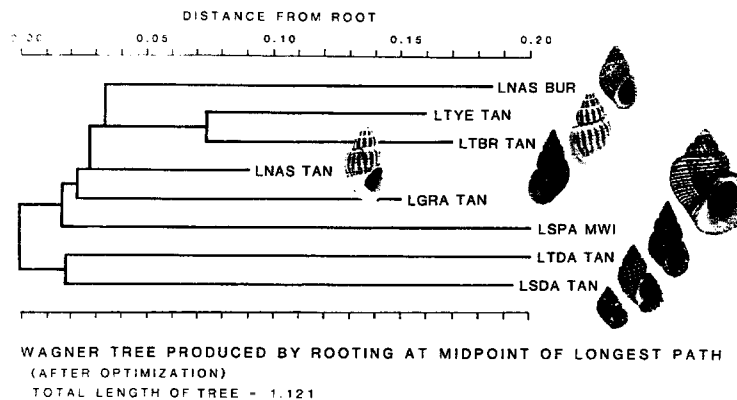


Fig. 1. Wagner Tree, generated for 8 *Lavigeria* species, using Nei's (1978) distance data from Table 1. The Wagner Tree was produced by rooting it at the midpoint of the longest path. Wagner and UPGMA Trees produced highly congruent results in this initial study. Representative individuals of each population are shown to the right of each branch.

taxa are presented in Fig. 1. This diagram provides evidence for convergence in shell characters. The high-spined, fine-ribbed morphospecies coded LTYE TAN is not closely related to a similar looking morphospecies, LSPA MWI.

### Morphometric studies

#### Speciation potential

The formation of species flocks such as the gastropods or cichlid fish of Lake Tanganyika pre-

Table 2. Matrix of genetic similarity and/or distance coefficients.

Population	1	2	3	4	5	6	7	8
1 LTYE TAN	-	0.813	0.731	0.778	0.645	0.756	0.637	0.612
2 LTBR TAN	0.207	-	0.689	0.804	0.640	0.672	0.688	0.615
3 LGRA TAN	0.314	0.372	-	0.798	0.691	0.706	0.601	0.661
4 LNAS TAN	0.251	0.218	0.226	-	0.785	0.782	0.644	0.683
5 LSPA MWI	0.438	0.446	0.370	0.243	-	0.647	0.595	0.613
6 LNAS BUR	0.279	0.398	0.348	0.246	0.435	-	0.604	0.621
7 LTDA TAN	0.450	0.375	0.509	0.409	0.519	0.505	-	0.632
8 LSDA TAN	0.491	0.487	0.414	0.381	0.490	0.477	0.460	-

Below diagonal: Nei (1978) unbiased genetic distance.  
 Above diagonal: Nei (1978) unbiased genetic identity.  
 Population names are keyed to morphologies in Fig. 1.

COLLECTION SITES

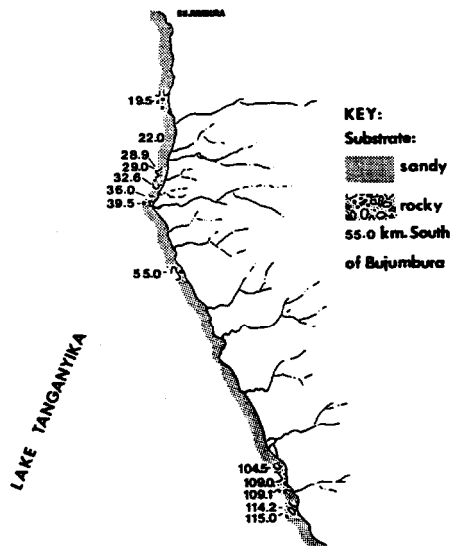
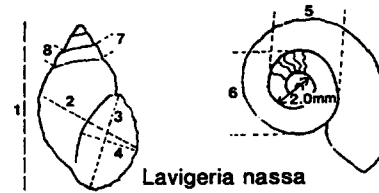


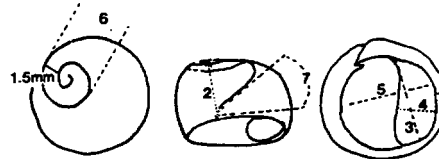
Fig. 2. *Lavigeria* and *Spekia zonata* collection sites in Burundi. All sites denoted by number of kilometers south of Bujumbura.

sents challenges to standard evolutionary theory. It is difficult to explain why some taxa speciate extensively while others in the same habitat do not. To test the idea that allopatric separation is the only requisite for evolution of large groups of closely related endemics, we compared the pattern of morphological divergence between two genera of endemic Thiarid gastropods that both live on the rocks of littoral zone (JOHNSTON 1986, JOHNSTON & COHEN 1987). Presumably since

Morphometric Measures



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



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

Fig. 3. 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 2.0mm (WD 15). 6. Width of the whorl at the 20th axial rib (WD 20). 7. Height of the whorl parallel to the axis of coiling at the fifteenth rib (HT 15). 8. Height of the whorl at the 20th rib (HT 20). 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. Oberculum height (OPERHT). 9. Oberculum width (OPERWD).

*Spekia zonata* and the *Lavigeria* morphospecies studied have similar habitat tolerances and dispersal abilities they are subject to the same allopatric barriers. Both are shallow water rock dwellers though *Spekia* is more restricted to the swash zone. *Lavigeria* is a brooder while *Spekia* desposits its eggs on rocks, but both are considered poor dispersers (KAT pers. comm.). The prediction is that the two genera should be comparable in magnitude and character of mor-

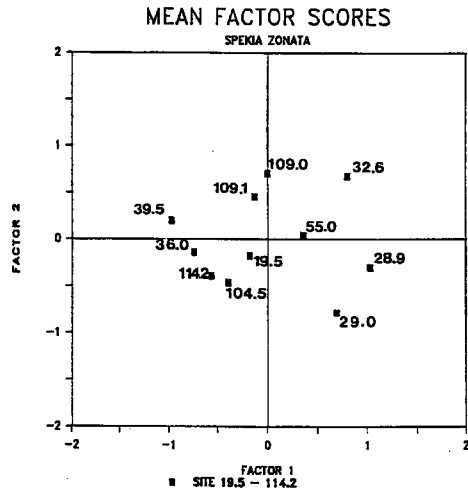


Fig. 4. Plot of site mean factor scores for all samples against the first and second axes. Note the separation of 32.6, 28.9, and 29.0 km from other samples along the first axis.

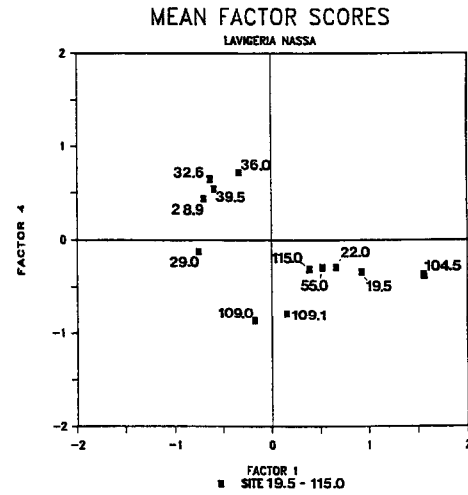


Fig. 6. Mean factor for scores for *Lavigeria* from each collection site along the first and fourth axis. Note the distinct clustering of sites. 28.9–39.5 km and the lack of a geographical cline from northern to southern sites.

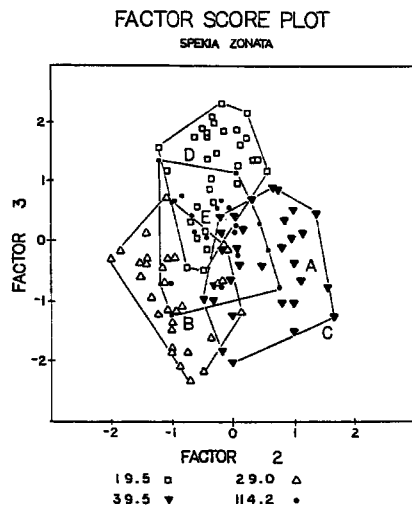


Fig. 5. Factor score plot of individual *Spekia zonata* from four sites against the second and third (shape) axes. Note the morphological overlap of geographically separated samples.

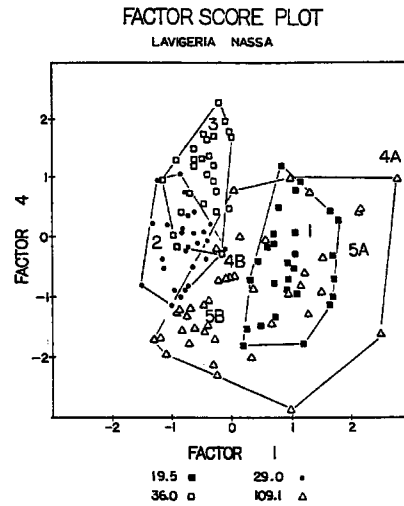


Fig. 7. Plot of factor scores of individual cases from representative sites. Note the tight clustering of northern samples 19.5, 29.0, and 36.0 km, and the greater variability found in the southern sites such as 109.1 km. Note also the position of *Lavigeria* from Fig. 8, numerals 1–5.

phological variation if environmental barriers control divergence.

Representatives of each morphospecies were collected from each of twelve sites along the Bu-

Table 3. 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		

OneWay ANOVA of *Lavigeria* factor scores.

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		

rundi shoreline (Fig. 2). Morphometric characters shown in Fig. 3 were analyzed with R-mode factor analysis. Principle components were extracted and rotated with the Varimax criterion to determine the most important descriptors of variation, then regression factor scores were calculated for each specimen along each axis. A one-way Analysis of Variance (ANOVA) was used to test whether within population variation exceeds between population variation.

The results from the analyses of *Spekia* and *Lavigeria* morphometrics are presented in Figs. 4–7. Both genera vary significantly more between populations than within populations, which is the prediction of an allopatric separation model (Table 3). However, the two genera differ in their patterns of variation. The bulk of variation between populations in *Spekia* is in factor 1 which describes size differences. The mean factor scores for each population are plotted in Fig. 4. Notice that most of the separation is along factor 1, the size factor. For the other factors, which are shape dependent, interpopulation variation exceeds intrapopulation

variation as well, although the variation between populations is largely overlapping, as shown in Fig. 5. This is in contrast to the pattern of variation in *Lavigeria* where the first factor is a descriptor of the number of ribs, not size. The size dependent factor is important in separating populations, but the fourth factor describing shape of the shell is of almost equal importance. A plot of the mean factor scores for factors 1 and 4, both shape descriptors, shows the distribution of variation between sites (Fig. 6). As with *Spekia* variation is not clinal, but there is clustering of sites 28.9–39.5. These populations have a unique morphology. A factor plot of the individuals in a representative sample of several populations of *Lavigeria* shows that these sites cluster tightly and distinctly in comparison to the other sites (Fig. 7). Notice the large variation in site 109.1. This site, as well as the other southernmost sites, contains snails of both the fine and coarse ribbed morphospecies (Fig. 8). We know from electrophoretic data that these are reproductively as well as morphologically separate. The coarse

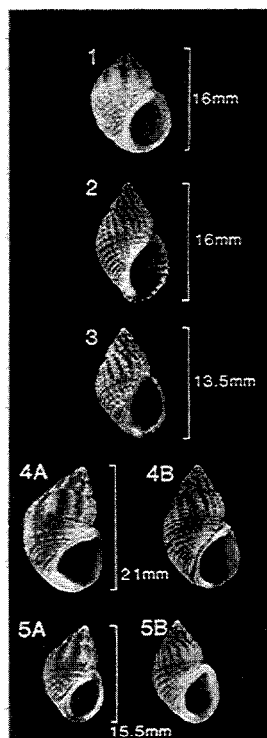


Fig. 8. Representative samples of *Lavigeria* from Burundi. Note the variation in shape and size of these gastropods. Numerals 1–5 correspond to collection locations and factor score positions in Fig. 9: 1) 19.5 km south of Bujumbura, 2) 29.0 km, 3) 36.0 km, 4) 104.5 km, 5) 109.1 km.

ribbed morphospecies is genetically identical to the northern coarse ribbed morphospecies while the southern fine ribbed morphospecies is distinct from both the northern fine ribbed morphospecies and the sympatric coarse ribbed morphospecies.

Discrete clusters of morphology, fixed allele differences and geographical disjunctions all point to the fact that *Lavigeria* has speciated while at the same sites *Spekia* has remained relatively undifferentiated. These results are unlikely to be the result of ecophenotypy because the specimens were collected from the same sites. The two genera are probably comparable in dispersal ability; for both genera the populations form morphological clus-

ters (within population variation is less than between population variation) indicating isolation and neither has a dispersing larval stage. If the present-day distributions of these genera are indicators of their history of divergence, we must conclude that physical separation is not a sufficient explanation for morphological divergence. A similar result is seen in Tanganyikan ostracods, in which a brooding species has morphological discontinuities while a sympatric non-brooding species is morphologically continuous (COHEN & JOHNSTON 1987). We must look to differences in breeding behaviour, larval strategy and reproductive times to explain mechanisms of separation and we must look further into the phylogenetic constraints of the *Lavigeria* group to understand its propensity to form distinct morphospecies.

### Biogeography of *Lavigeria*

Because *Lavigeria* is the most speciose gastropod genus in Lake Tanganyika based on morphological diversity, it is an ideal group with which to test hypotheses of lacustrine speciation (MICHEL & COHEN 1988). There are two extrinsic driving mechanisms that have commonly been proposed for African Rift Lake faunas. FRYER & ILES (1972) propose that local habitat fragmentation is sufficient to allow speciation *in situ*. In their theory major discontinuities in habitat are responsible for isolating populations. Alternatively, GREENWOOD (1964) suggests that rift lake faunas have speciated as a result of changes in lake level. Populations are divided into separate lakes as water levels drop. They evolve quickly and become genetically isolated and thus evolutionarily independent when water levels rise and populations are re-joined. The first model predicts coincidence of distributions with existing boundaries. The second model predicts 'ghosts' of separation mechanisms, that is, the boundaries between species today reflect historical allopatric divisions rather than existing physical barriers. These mechanisms are most effective for organisms with limited dispersal ability, such as brooding gastropods. Clearly these models are not mutually exclusive, but this study may provide information as to the importance of one mechanism over another in the diversification of this clade.

The specific predictions for Lake Tanganyika are illustrated in Fig. 9 and 10. Habitat barriers to dispersal will occur at large scale changes in substrate, such as the division of rocky shoreline by

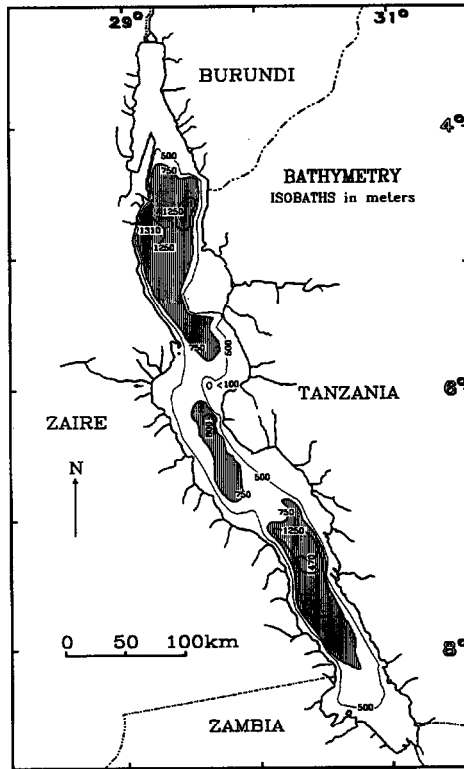


Fig. 9. Bathymetric map of Lake Tanganyika. Shaded areas are below the 750 m isobath. SHOLTZ & ROSENDAHL (1987) proposed a division of the basin into 3 separate lakes during a Pleistocene lake level decline of as much as 700 m below present lake level.

the Ruzizi or Malagarasi River deltas (Fig. 10). If the habitat fragmentation model is valid, both genetic and morphologic disjunctions in *Lavigeria* distribution will occur at points such as these. The changing lake basin model originally invoked small peripheral isolates, but in a steep-sided basin such as Tanganyika, these are unlikely. We do know from seismic reflection data that the lake was divided into three separate basins between 50,000–100,000 years ago when lake levels dropped approximately 700 m (SCHOLZ & ROSENDAHL 1987). If the separate basins shown in Fig. 9 were the mechanism of speciation for the tremendous diversity of organisms, the fauna would show distinct remnants of the three basin division

in both their genetic and morphologic relationships.

To test these two models, we plotted the distributions of eleven morphospecies of *Lavigeria* that were collected alive using SCUBA along the Tanganyikan shore of Northern Zaire, Burundi, Tanzania and Zambia. Distinctions between morphospecies were made on the basis of visual differences in shape, sculpture, colour and adult size. Decisions on morphologic groups were made by considering how they cluster as discrete morphological units in the field. Some morphospecies are highly variable, others distinguished on fine scale differences.

The results show that two major disjunctions in distribution of *Lavigeria* coincide with the inflows of the Ruzizi and Malagarasi Rivers. The distributions for the nine morphospecies are plotted in Fig. 11 (there are other morphospecies with more limited occurrences not discussed here). There is no evidence of disjunctions with smaller rivers. At the level of resolution used for this survey, there is little evidence of a three basin division of the *Lavigeria* morphospecies. There are two morphospecies that may have used the ridge at the northern basin boundary as an avenue for dispersal from Tanzania to Zaire; they are not found in Burundi. But divisions between morphospecies fall at major habitat barriers, not basin boundaries. The six morphospecies that have distribution boundaries near the river deltas are all limited to living on hard substrate. The two that are continuous across these barriers are either tolerant of soft substrate, in the case of the coarse ribbed morphospecies, or living in deep water like the small dark morphospecies, and able to negotiate the deep water shell lags that span the front of the river deltas.

In conclusion, this rough division of *Lavigeria* morphospecies shows us:

1. There is morphological congruence with substrate types. Fine and medium ribbed morphospecies are confined to rocks, coarse ribbed morphospecies can be found on sand, and deep water morphospecies may be found on shell lags as well as rocks and stromatolites.
2. Substrate limitations are translated into distribution limitations. Rock dwellers are more subject to barriers to dispersal. We predict they will be most variable genetically and fine scale morphometrically. Because their effective population sizes are smaller, they may show the most rapid rates of evolution, thus a larger number of phenotypic variants which are more likely to exhibit convergence. This prediction has already been upheld in that in this discussion there have been

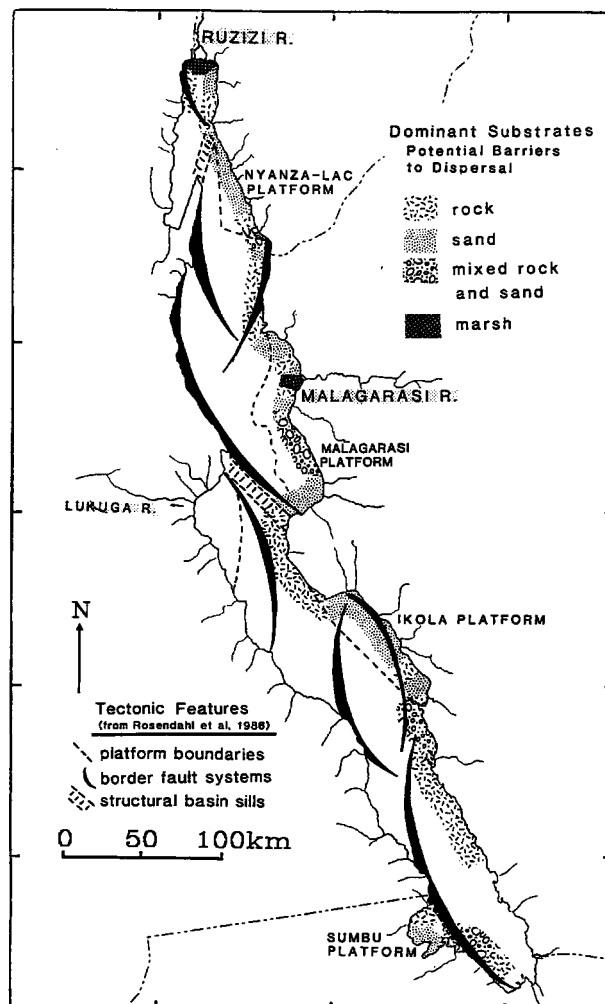


Fig. 10. Map illustrating potential physical barriers to dispersal in Lake Tanganyika. Simplified tectonic features of the Tanganyikan basin show dateable geological features which have historically regulated the positions of major substrate boundaries. Border faults are dominated by rocky substrates whereas platform margins are predominantly sandy. Substrate types are indicated in patterns for the areas where we have worked.

six morphospecies limited to rock and three not limited to rock. In addition, the example of convergence shown by KAT, Fig. 1, is a rock limited morphospecies.

3. The habitat fragmentation model is more effective at explaining current distributions of morphospecies than

the changing lake level model. Lowered lake level does not appear to be the driving mechanism for endemic radiation in *Lavigeria*, though it may have influenced dispersal. Large scale differences in substrate and ancient rivers correlate with disjunctions in morphospecies assemblages.

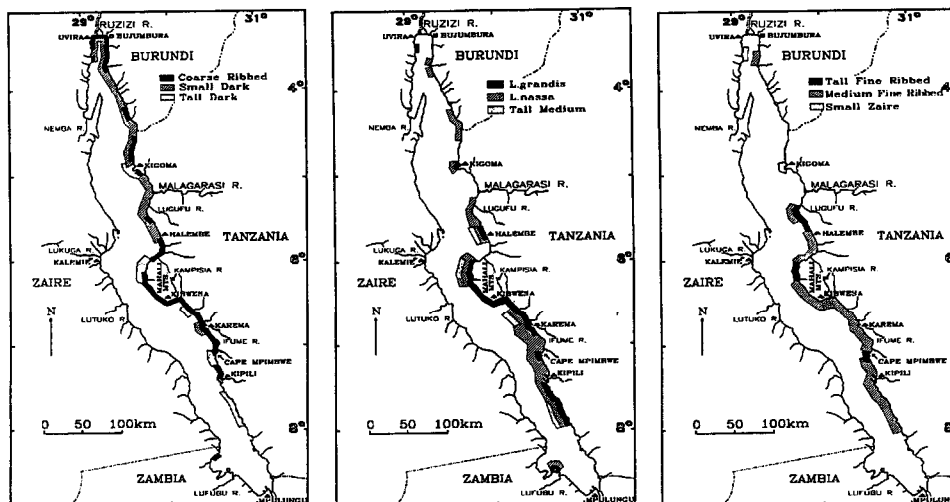


Fig. 11. Known distributions of nine *Lavigeria* morphospecies. No association is implied between morphospecies on the same map.

#### Morphometric test of a habitat barrier

To test the habitat barrier model on a finer scale, we investigated the fine scale morphometric divergence across a major habitat barrier, the Ruzizi River (MICHEL 1988). This river has separated the rocky coasts of present day Zaire and Burundi with a large sandy delta and extensive marshes since the Pliocene (EBBINGER 1984). The habitat fragmentation model predicts that populations on either side of the Ruzizi should be more similar to each other than to the populations on the opposite side. Rephrasing this prediction in the form of a hypothesis test, the null model says that the Ruzizi is not a barrier to *Lavigeria* populations. Furthermore, substrate specificity will not influence morphospecies response to this barrier.

This study focused on three morphospecies that differ markedly in morphology and habitat tolerances. The small dark morphospecies occurs on hard substrates like rocks, stromatolites and shell lags in deep water (10–50 m). The fine ribbed morphospecies occurs on rocky substrate in the littoral and sublittoral zone to 10 m, whereas the coarse ribbed morphospecies is the only one found occasionally on sand as well as rocks in the littoral and sublittoral zone. None of these animals are found in mud or in marshes; they do not live in the littoral zone of the delta. An

ANOVA comparing all the morphospecies to each other shows that they are irrefutably distinct. Twenty specimens of each morphospecies from each site were taken from either side of the Ruzizi (Fig. 12). Morphometric variables (Fig. 13) were chosen to describe changes in morphology during growth (e.g. cross-whorl distances) and variation in development (e.g. sculptural replicates). These data were taken with a camera lucida and then digitized. The variables were analyzed with a principle components analysis to decompose the variance, then tested with a non-parametric ANOVA and a MANOVA (multivariate analysis of variance) for the effects of the barrier.

The principle components analyses show that sculpture variables are most useful in separating morphospecies from each other while shape variables distinguish populations from each other (Fig. 14). The first two factors in the sculpture analysis describe axial and spiral sculpture variables respectively. The shape factors are a size factor and a combined variable describing shape of the spire and tilt of the aperture. The ANOVA compares variation within sites on the same side of the barrier to variation between sites across the Ruzizi (Table 4). We found that hard substrate gastropods are morphologically divergent across the barrier, but the soft substrate morphospecies is not. Significant differences are shown as  $p < 0.05$ ,

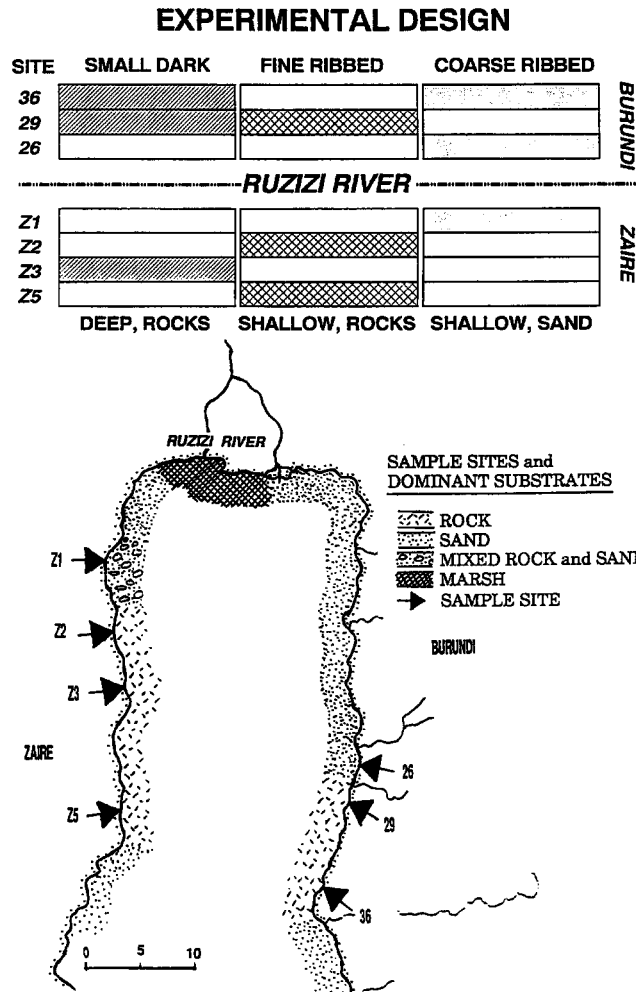


Fig. 12. Sampling design and site locations for morphometric test of the effects of the Ruzizi as a major habitat barrier.

$p < 0.01$  and  $p < 0.001$ . The small dark morphospecies varies significantly in the variables of shape and number of ribs in the final whorl across the Ruzizi but not within Burundi sites. The fine ribbed morphospecies shows this pattern even more strongly. There is significant variation in ribs, size, shape and axial sculpture across the Ruzizi. The MANOVAs for both groups support the conclusion that there is morphological di-

vergence across the Ruzizi for both hard substrate morphospecies. In contrast, the morphospecies that can tolerate soft substrate does not exhibit these patterns. The coarse ribbed morphospecies does not vary significantly across the Ruzizi. This suggests that the river delta is not a barrier to gene flow for this morphospecies. The small dark and coarse ribbed morphospecies both have significant variance in one character between populations on

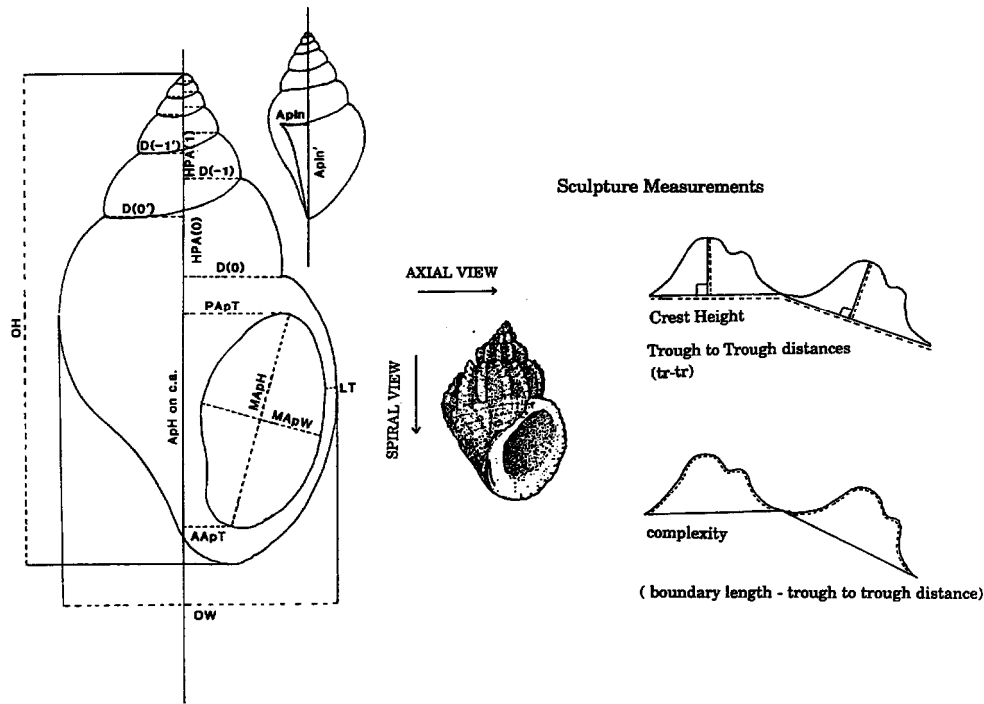


Fig. 13. Detailed morphometric descriptors for gastropods measured in the laboratory.

Left: Measures taken in axial plane view on complete shells: OH – overall height; OW – overall width; MApH – maximum apertural width perpendicular to height; LT – lip thickness at periphery; AApT – anterior measure of apertural tilt; PApT – posterior measure of apertural tilt; D(-n) and D(-n) – distance of point of adherence to coiling axis (these are summed to give a diameter measure of each whorl); HPA(-n) – height of point of attachment for whorl n from aperture; ApIn and ApIn' – measures of apertural inclination.

Right: Sculptural measures seen in axial and apical cross-sections' measures taken  $\frac{1}{4}$  whorl back from aperture; I) complexity measure, compares straight line distance between troughs with boundary distance between troughs; II) trough-crest distances and crest heights.

the same side of the barrier. These may be real biological differences or statistical artifacts. With forty-two different F-statistics there may be two that are significant at the 0.05 level due to random variation alone.

In conclusion, we can refute the null hypothesis. The Ruzizi is a demonstrable barrier to the hard substrate gastropods whether they inhabit shallow or deep water. The morphospecies that is tolerant to soft substrate is not divergent across this barrier. So not only can we say that habitat fragmentation has been important in the diversification of this clades, but substrate specificity creates different responses to habitat barriers.

### Functional morphology studies

Not only is there an unusual number of gastropod species in Lake Tanganyika, but their shells are highly sculptured and heavily calcified which is an anomaly for fresh water molluscs. The molluscivorous fish and decapod crustaceans are also remarkably well-equipped for eating their well-armoured prey. The fish have massive crushing teeth and the crabs have large, heavily calcified chelae. Because this is suggestive of a coevolutionary relationship between the predators and prey (VERMEIJ 1978, COHEN 1985), WEST (1987) compared the functional effectiveness of the gastropod shells for

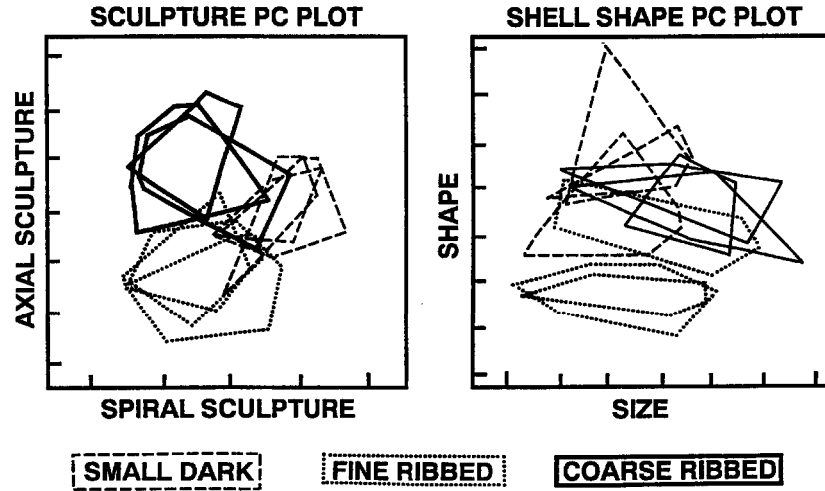


Fig. 14. Plot of factors describing shell sculpture and shape from principal components analysis on *Lavigeria* shell morphometrics. Sculpture factors, shown on the left, separate morphospecies from each other. Shape factors, shown on the right, separate populations within a morphospecies.

Table 4. F-Statistics for *Lavigeria* morphospecies.

Site Comparisons	Axial Sculpture (factor)	Spiral Sculpture (factor)	Ribs (variable)	Size (factor)	Shape (factor)	Lip Thickness (variable)	MANOVA
<b>Small Dark</b>							
Across Barrier	-	-	xxx	-	xxx	-	xxx
Within Sides	-	-	-	xx	-	-	x
<b>Fine Ribbed</b>							
Across Barrier	x	-	xxx	xxx	xxx	-	xxx
Within Sides	-	-	-	-	-	-	-
<b>Coarse Ribbed</b>							
Across Barrier	-	-	-	-	-	-	-
Within Sides	-	-	-	-	-	x	-

xxx =  $p < 0.001$ , xx =  $p < 0.01$ , x =  $p < 0.05$ , - = not significant.

several genera in aquarium studies of predation by the crab *Platytelphusa armata*. She also directly quantified shell strength by crushing shells from each species in a tensiometer at a constant load.

The aquarium studies were conducted with the species *Spekia zonata*, *Neothauma tanganyicense*, *Paramelania damoni*, and the three morphospecies of *Lavigeria* described by Johnston. Ten individuals of each species, spanning the range of growth stages, were measured and then added to a tank with a *P. armata*, which also had been pre-

viously measured. Mensural characters described shell size, lip thickness and degree of sculpture in the gastropods and chelae size for the crabs. The experiment was repeated forty-one times with forty-one different crabs. The results were plotted on histograms and verified with chi-square tests for statistical significance. There is a strong correlation of increased size, lip thickness, and sculpture and ability to deter the predator (Examples in Fig. 15). Likewise, smaller individuals with less sculpture were more heavily preyed upon. Small

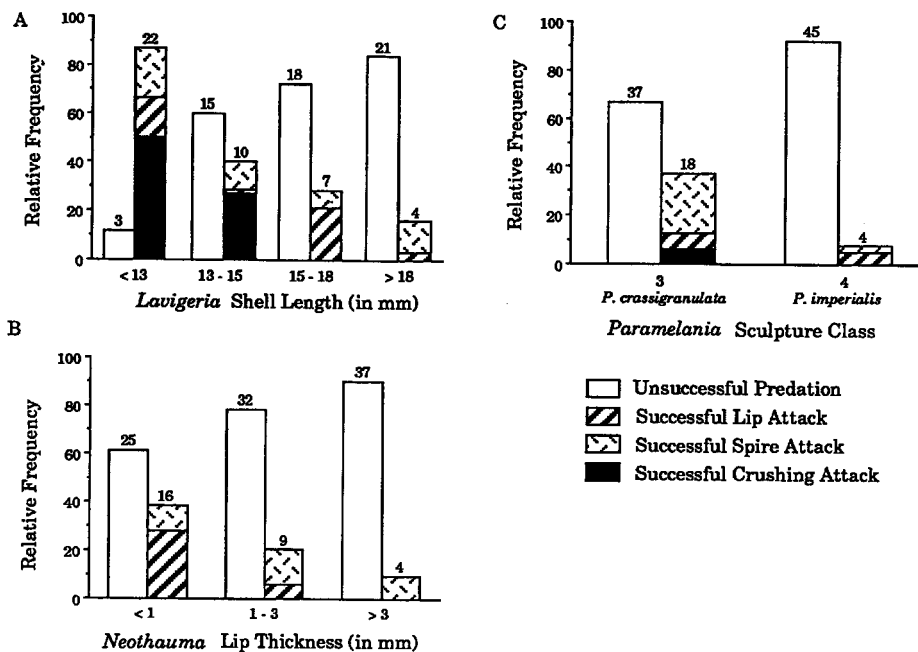


Fig. 15. The effects of gastropod shell architecture on predation results and methods of successful predation by the crab *Platyelphusa armata*. Numbers above the histogram bars are the absolute frequencies of unsuccessful and successful attacks for each size class. Crabs used in these experiments were pooled across size classes. (A) Successful predation on *Lavigeria paucicostata* (populations 19.5 and 105.6) by crabs drops markedly while unsuccessful encounters steadily increase with increased shell length. In successful attacks, smaller *Lavigeria* shells were more likely to be crushed whereas crabs employed the more time-consuming peeling and spire attacks on larger *Lavigeria*. (B) Cases of successful predation on *Neothauma tanganyicense* steadily drop off while cases of unsuccessful predation steadily increase with increased apertural lip thickness. As apertural lip thickness increases, successful peeling attacks at the aperture decline. In *N. tanganyicense* with the thickest apertural lips, there were no successful lip attacks. (C) *Paramelania crassigranulata* (noded ribbing, sculpture rating = 3) suffered significantly more cases of successful predation than *Paramelania imperialis* (spines and noded ribbing, sculpture rating = 4). All successful attacks on *P. imperialis* were at the shell spire or apertural lip, whereas some crabs were able to crush *P. crassigranulata*.

crabs were unable to attack larger gastropods, though they successfully consumed juveniles. Juvenile *Neothauma* and *Paramelania* may compensate for this with a behavioral refuge; they burrow in the sand until they grow larger. Predation methods change with gastropod and decapod size as well. Fig. 15 shows that smaller gastropods are more likely to be crushed while large ones are peeled or have their spires snapped.

Shell crushing experiments verify the robustness of Tanganyikan gastropods compared to other gastropods. VERMEIJ & CURREY (1980) showed that tropical thaidids have a higher load strength to mass relationship than temperate thaidids

probably due to strong predation pressure and carbonate availability (regression line in Fig. 16). WEST, COHEN & BARON (1991) showed that lacustrine gastropods in general plot very low on this graph; they are relatively very weak. This work demonstrates that not only are the Tanganyikan endemics stronger than other lacustrine gastropods, but they are of comparable strength to the tropical marine thaidids (Fig. 16).

Combining the results from these two studies presents a very strong argument that co-evolution between predator and prey has selected for the robust shells of the Tanganyikan endemic gastropods and crabs. Shell strength for each species is

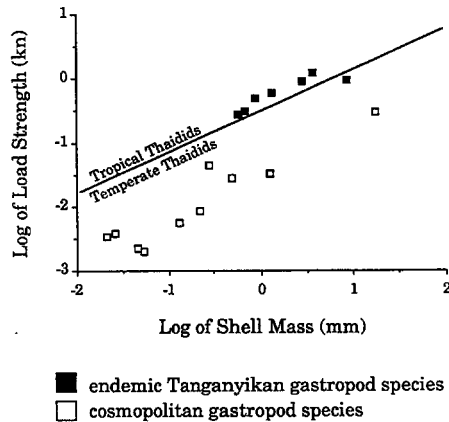


Fig. 16. Log-log plot of shell load strength versus shell mass for 17 varieties of lacustrine gastropods. Endemic Tanganyikan gastropods are denoted by shaded symbols, unshaded symbols represent closely-related cosmopolitan gastropods. Each symbol represents the mean shell mass and mean load strength of all individuals of a gastropod variety. The line "log of load strength =  $-0.3 + 0.67(\log \text{ of mass})$ " represents the demarcation of robust tropical-latitude marine thaidid gastropods and the weaker temperate-latitude marine thaidid gastropods, derived by VERMEIJ & CURREY (1980, their Fig. 1). Most of the mature endemic Tanganyikan gastropods cluster near this line, while other freshwater gastropods were considerably weaker.

negatively correlated with predation frequencies determined in the aquarium studies. Tanganyikan gastropods also exhibit shell scars, the remains of unsuccessful predation attempts, which are seldom seen in lacustrine gastropods and most often seen in tropical gastropods, which are highly co-evolved with their predators (VERMEIJ & CURREY 1980). Most lakes do not have specialized molluscivores, as does Lake Tanganyika.

### Summary

By combining several methods we have set the groundwork to uncover the mechanisms behind the diversification of the endemic Tanganyikan gastropods. Genetic studies have shown that the number of species of these gastropods is greatly underestimated by previous taxonomists and convergence in shell characters makes even current estimates, which are based on shell form, likely to be conservative. Morphometric studies demonstrated that some gastropod taxa like *Lavigeria* are speciation prone. Biogeographic work showed that the habitat

barriers have had a more significant evolutionary effect on species distributions than changes in lake level. Rock-dwelling *Lavigeria* morphospecies are currently diverging across one of those barriers, the Ruzizi River. The unusual shell morphologies of many of the endemic molluscs are explained as the result of predator-prey co-evolution. Clearly, this Tanganyikan molluscan fauna has tremendous potential for exposing the causes and rates of rift lake evolution.

### Acknowledgements

This work has only been possible through the unflagging support of the University of Burundi with special thanks to PONTIEN NDABANEZE, GASPARD NTAKIMAZI and LAURANT NTAHUGA. Field work and manuscript preparation benefitted immeasurably from the efforts of PIERRE VERHOYEN, BOUDOIN HUSSEIN, and PIERRE NDAMAMA. The Centre de Recherche en Sciences Naturelles in Uvira, Zaire, The Tanzania National Scientific Research Council (UTAFITI, permit # NRS/RA47), The Geological Survey of the Republic of Zambia have all supported work on their respective Tanganyikan coasts. This work has been supported by N.S.F. grants # BSR 8415289 and # BSR 83-15195.

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