

## **The Structure of Endemic Variation: Genetic and Morphologic Variation in Littoral Snails and Fishes**

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### *Introduction*

Lake Tanganyika is renowned for the diversity of its endemic fauna. Its hundreds of species of endemic cichlid fishes are the most diverse among the East African rift lake cichlids in terms of morphology, ecology and behavior, and its invertebrate radiations are unparalleled in the other East African rift lakes (Coulter, 1991). The processes creating this biological diversity are inextricably connected with the lake's geologic and limnologic history. Heterogeneity in substrate type in Lake Tanganyika's littoral zone creates the opportunity for biological specialization tied to feeding, habitat use, and reproduction. Substrate specialization may, in turn, play a role in speciation. For organisms that are substrate-specific and do not widely disperse, patches of appropriate habitat function as islands. The potential for isolation and allopatric separation of populations thus created may play a major role in creating the conditions necessary for speciation.

If isolation of populations through substrate specificity and limited dispersal has historically played a prominent role in speciation within Lake Tanganyika, these processes should be detectable in modern patterns of variation within the lake's fauna. In this framework, organisms from groups with high endemic diversity are expected to show evidence of isolation between populations. Populations separated by stretches of substrate inappropriate for their own use should show stronger evidence of restricted contact than populations separated by stretches of appropriate substrate. Rocky littoral habitats are home to the most diverse assemblages of both fish and gastropod mollusc taxa within the lake. Benthic herbivores in these rocky environments are particularly tied to the substrate through their means of feeding.

This study examines patterns of variation in three species of cichlid fishes of the tribe Tropheini and four species of *Lavigeria* gastropods. Both *Lavigeria* gastropods and Tropheine cichlids are monophyletic endemic radiations within Lake Tanganyika, and both groups are composed primarily of benthic herbivores on rocky substrate. Two questions are primary in this study:

1. Do patterns of morphological variation coincide with patterns of population genetic structure? Through quantifying both genetic and morphologic patterns of variation among populations, I will be able to examine the morphological effects of restricted gene flow. If species with more localized gene pools are also morphologically divergent, phenotypic traits will be supported as indicators of the underlying population genetic structure. Alternatively, if morphology and molecular data are discordant, phenotypic plasticity may play a more important role in shaping patterns of morphological variation.

2. Is there evidence that shared extrinsic ecological factors are important in driving diversification in both snails and fishes? It is possible that taxa with shared specialization for particular substrates will have similarities in population genetic structure and morphological diversification, due to similarities in dispersal limitations among habitat patches. If this is true, parallel geographic patterns in diversity should exist across taxa: more isolated patches will contain both snails and fishes with more population genetic structure and/or morphological differentiation than less isolated patches. Differences between fishes and snails in the effects of isolation would indicate that these taxa differ in the degree of habitat patchiness necessary to provide a barrier to gene flow.

### *Methods, Results and Discussion*

Fieldwork completed during Nyanza 2005 constituted the main sample collection period for this project, which will be the subject of my Ph.D. dissertation. Genetic and fish morphological work will be completed at Cornell University using samples that I have brought back to the United States. Results of the snail morphological work are reported in Callier (this volume).

I collected fishes and snails at five sites along the coastline bordering the region of Kigoma, Tanzania (Figure 1). Snails were collected by hand along transects while snorkeling, and fish were collected with the aid of a gill net while snorkeling. All snails and fish are from 1-10 meters water depth. Numbers of individuals collected per species per site are given in Table 2. Upon collection, snails were photographed (see Callier, this volume), and subsequently cracked in order to preserve tissues in DMSO-EDTA buffer for later genetic analysis. Shell fragments were retained as species identity vouchers. All fish were sacrificed according to protocols approved by the Cornell Animal Care and Use Committee, photographed, sampled for genetic vouchering, and preserved. The preserved fish have been deposited in the Cornell University Museum of Vertebrates, where I will conduct morphological analyses and where they will subsequently be available to future researchers.

Sites were selected due to the presence of appropriate habitat for the focal organisms and due to their proximity to each other. In addition, these sites were explicitly chosen in order to sample on either side of two substantial potential barriers to dispersal: Kigoma Bay and the Luiche River Delta. Both of these locations contain broad stretches of sandy and muddy shoreline inappropriate for *Lavigeria* gastropods and for *Petrochromis* and *Simochromis* cichlids.

The sample sizes of individuals collected (Table 2) will be sufficiently large to allow the discrimination of population genetic patterns with high resolution. I will use both mitochondrial DNA (mtDNA) sequence and microsatellite DNA data to analyze patterns of gene flow within and among populations, and will compare these patterns across taxa. In addition to genetic analysis, I will quantify morphological variation within and among populations of focal taxa in order to document the potential phenotypic effects of localization of gene pools. Using multivariate geometric morphometric techniques, (e.g. Bookstein et al, 1995) I will analyze the degree of covariation between morphological and genetic variation among populations in both snails and fishes (e.g. Strauss, 1991).

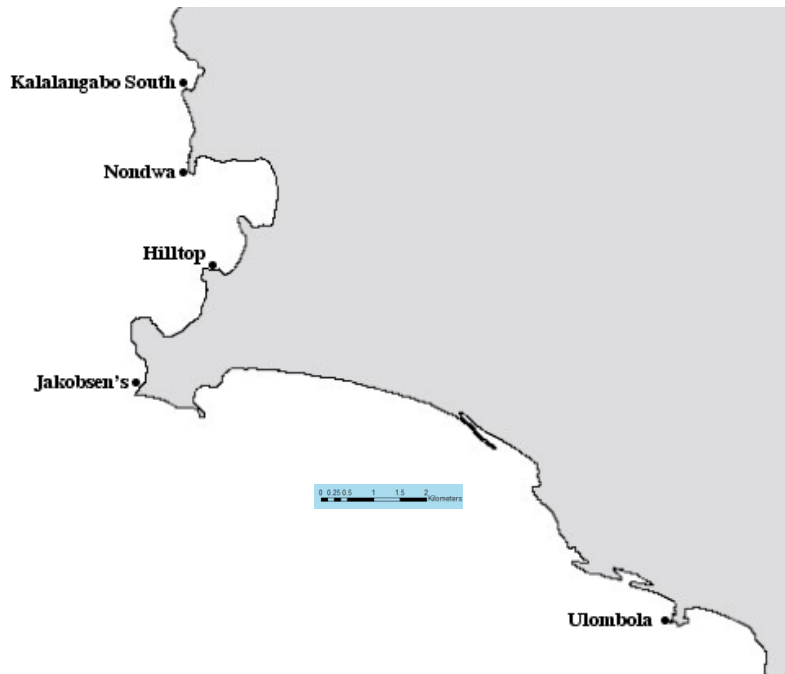
While cichlids have long remained the focal research taxon in studies of speciation in the East African rift lakes, the cross-taxonomic approach of this study will offer new perspectives on the patterns and processes of evolution at work in these ecosystems. This work is the first to directly explore population genetic structuring and its effects on phenotypic diversity among multiple major taxonomic groups in the East African rift lakes, a first step toward achieving a unified framework for understanding cross-taxonomic speciation and diversification processes in these remarkable ecosystems.

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**Figure 1.** Five study sites where fishes and snails were collected.

**Table 1.** Number of focal species collected per site.

<b>Species</b>	<b>Site</b>	<b>Sample Size</b>
<i>Petrochromis sp. "kazumbe"</i>	Kalalangabo	19
	Nondwa	26
	Hilltop	29
	Jakobsen's	23
	Ulambolo	29
<i>Petrochromis sp. "moshi"</i>	Kalalangabo	11
	Nondwa	14
	Hilltop	25
	Jakobsen's	20
	Ulambolo	22
<i>Simochromis diagramma</i>	Kalalangabo	20
	Nondwa	21
	Hilltop	20
	Jakobsen's	21
	Ulambolo	26
<i>Lavigeria nassa</i>	Kalalangabo	50
	Nondwa	30
	Hilltop	50
	Jakobsen's	50
	Ulambolo	50
<i>Lavigeria grandis</i>	Kalalangabo	50
	Nondwa	51
	Hilltop	50
	Jakobsen's	50
	Ulambolo	50
<i>Lavigeria sp. J</i>	Nondwa	62
	Hilltop	50
<i>Lavigeria sp. W</i>	Kalalangabo	50