Lake Victoria region: *Large lakes and their surrounding minor water bodies as natural laboratories for speciation and evolution*

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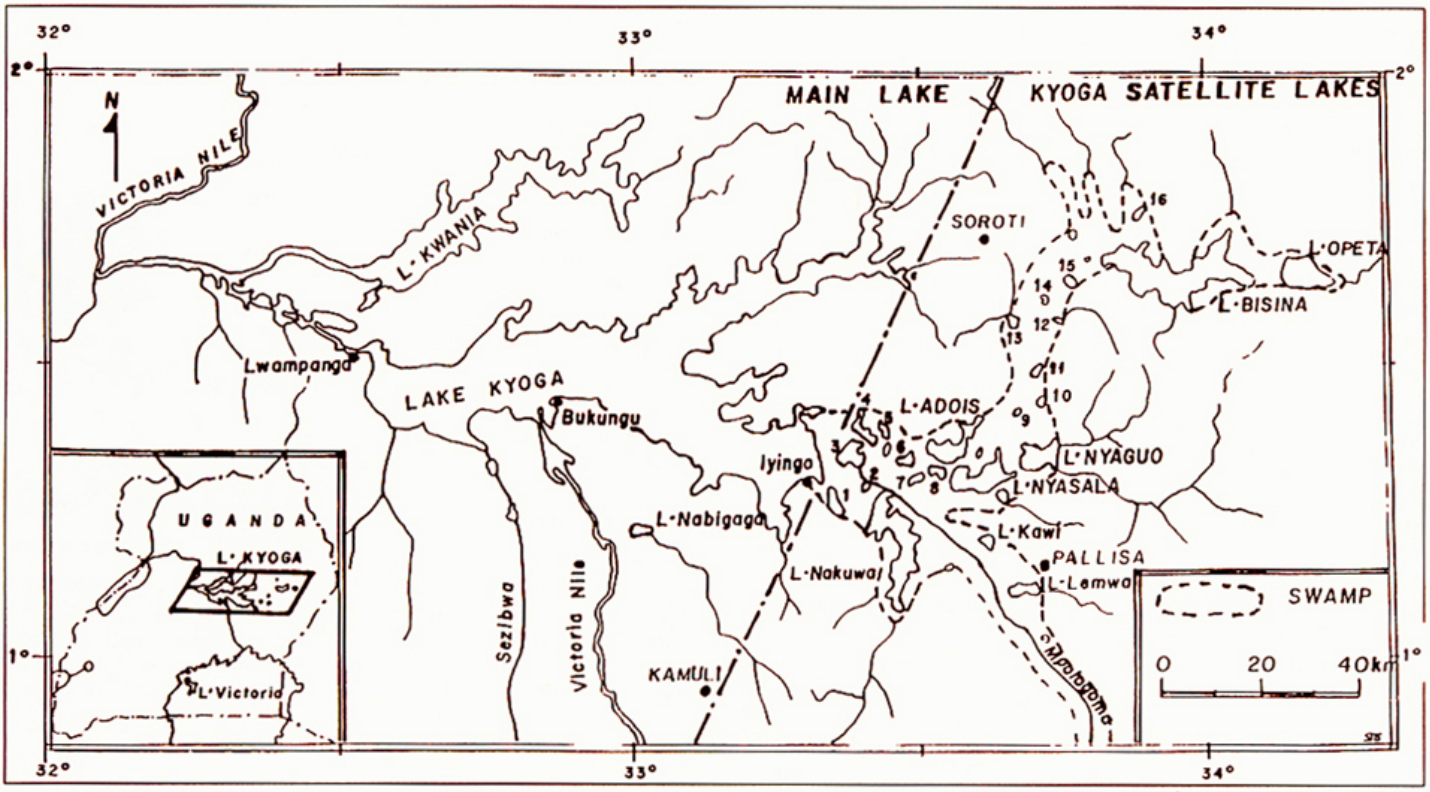
What is the Lake Victoria Region?

Lake Victoria Region (LVR) traverses and is centered around the equator in East Africa. It contains five large lakes with numerous minor satellite lakes around each of the large lakes. These lakes are zoogeographically connected and arose basically out of tectonic earth movements and volcanic activity not more than a million years ago. The large lakes include Victoria, Kyoga, Edward, George and Kivu.

The Lake Victoria basin was crossed by several rivers that ran in an east-west direction prior to the formation of the lake. With the down warping of the basin by the tectonic earth movements, the shallow trough that was created was filled by the backed up flow of these east-west running rivers about 750,000 years ago. This created Lake Victoria. The lake currently has a mean depth of only 40 meters but a surface area of about 68,000 km², making it the second largest freshwater lake in the world (in terms of surface area) next to Lake Superior in North America.

Connected to Lake Victoria is Lake Kyoga which has a mean depth of about 3 m and a much smaller surface area. Lake Kyoga is located within a massive swampy area in central Uganda. This area is similar to the Sudd swamps of southern Sudan, only less extensive and largely non-mobile. Lake Kyoga should



A map of Lake Kyoga and the satellite lakes with an inset location map of Uganda. Names of numbered lakes are: 1 – Nawampasa; 2 – Murlu; 3 – Namasajeri; 4 – Kiondo; 5 – Naragaga; 6 – Pachoto; 7 – Kadiko; 8 – Meito; 9 – Kodiki; 10 – Gawe; 11 – Kasago; 13 – Opare; 14 – Ajama; 15 – Semere; 16 – Owapet.

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have been formed by entrapment of the River Nile waters as they flowed north through a very shallow trough. This created a lake surrounded with a swamp containing numerous satellite lakes that may have been left behind during the recession of the original, expansive lake formed after the initial filling. Alternatively, the satellite lakes in Lake Kyoga basin may be as a result of the several drying and reflooding episodes that characterized much of the LVR.

On the western side of the LVR are Lakes Edward, George and Kivu which are currently situated within the western Rift Valley of East Africa. These lakes are thought to have been part of a single extensive lake that covered much of western Uganda until separated by volcanic activity and the formation of the Rift Valley during the Pleistocene epoch. Lake Edward system is believed to have been one of the possible sources of the progenitors of the fish species that entered Lake Victoria during its several episodes of drying and refilling.

Thus, in this way, the lakes of the LVR were connected, and, for this reason, have similar characteristic fish faunal groups. This is especially true among the cichlid fishes, and contributes to making the LVR lakes a single zoogeographic region.

Lake Victoria region satellite lakes

The LVR has a variety of minor water bodies that surround and are disjointed from the large lakes; hence, the name "satellite" lakes. Some are as close to the large lakes as a few tens of meters, while others are as distant as tens of kilometers. Some are connected to the large lakes by small streams or by occasional flooding through the surrounding swamps. Others are completely cut off from the main lakes. Satellite lakes differ in their modes of formation, hydrological regimes, limnological conditions, and occupant biodiversity. Examples include the swamp valley lakes, cut off lakes, saline rift lakes, crater lakes, and many other unique types such as Lake Wamala in central Uganda, Lake Eyasi in eastern Rift Valley in Tanzania, and Lake Bunyoni in Uganda. Our postulate with respect to these lakes is that there are three main modes of formation:

1. fragmentation from the larger lakes due to a drop in lake level, followed by swamp encroachment such as in Lake Victoria and Lake Kyoga basins;

2. desiccation, whereby one large lake turns into one or more smaller lakes such as in the case of the rift valley soda lakes;

3. volcanism, as a result of which a lake is formed either through the creation and subsequent filling with water as in the case of the crater lakes in western Uganda, or insertion of a volcanic lava/ash dike into a drainage as we believe to be the case for Lake Bunyonyi in southwestern Uganda.

As we begin to unravel the limnological history of these satellite lakes, and the process of evolution of their associated biological diversity, we are beginning to understand the role of the satellite lakes in species multiplication and/or adaptive diversification. Our team has initiated paleolimnological work that will include coring of representative types of these minor lakes so as to compare the results with the known hydrological

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history of the large lakes. Such studies, combined with ecological and evolutionary studies, will illuminate the exact role of the satellite lakes in the evolution and enormous radiation of cichlid fishes that characterises this extensive but geologically and zoogeographically young LVR system. Ultimately, these studies will determine whether the LVR satellite lakes are models of the greater system.

The author's wife, Deborah Talifuna, is holding a cat fish (*Bagrus docmac*).

Species radiation and extinction

The Lake Victoria Region, like Africa's other great lake regions around Lakes Malawi and Tanganyika, is known for the rapid radiation and enormous species diversity of cichlid fishes.

What makes the LVR even more interesting than the other lake regions is its much younger age. Lake Victoria appeared no more than 750,000 years ago, and is known to have last dried up completely only 12,000 years ago (see Johnson et al., 1996). Despite its young age, Lake Victoria is estimated to have contained over 500 cichlid fish species prior to the human induced changes that have taken place during this century. These changes have resulted in nearly two hundred species becoming extinct, with many more being found to be at great risk of extinction by each successive expedition to the lake.

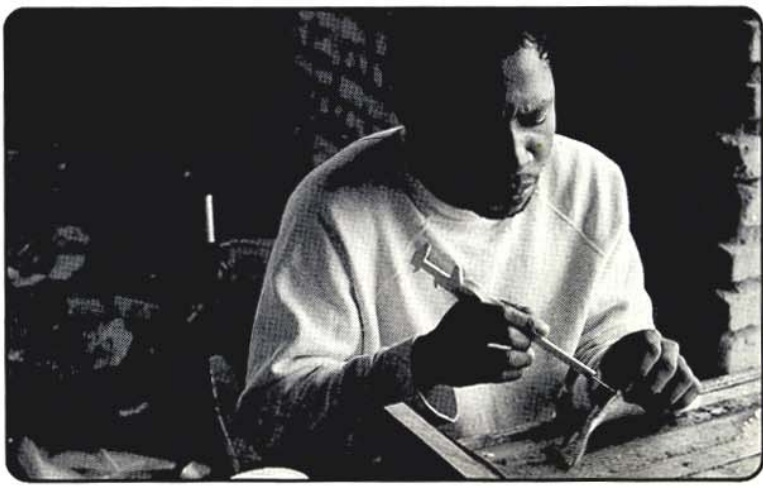
Unfortunately, large portions of the extant cichlid fauna in the LVR remain undescribed, as was the case with the largest portion of the now extinct taxa. This situation has placed increased urgency on the need for studies to assess what is left in the wild. This knowledge may not grant the threatened species a reprieve, but it may at least help to document the invaluable evolutionary knowledge trapped in these species that are going extinct at a faster rate than we can currently study them. Our exploratory survey so far has revealed that significant portions of the cichlid fauna previously considered extinct in the large lakes may still be surviving in several of the satellite lakes. Some of the satellite lakes, such as the Nabugabo lakes on the northwestern side of Lake Victoria, have a small number of species found nowhere else. Other satellite lakes, such as the Kyoga lakes in central Uganda, have a wide variety that include both known species and several undescribed species that are equivalent to species found in the large lake.

Although previous studies (Meyer et al., 1990) revealed no marked genetic differences among various Lake Victoria haplochromine species, new sets of molecular markers (microsatellite DNA markers), developed specifically for LVR haplochromine species in our laboratory, can differentiate populations and species even at a very fine scale. These techniques are currently being used to analyse the haplochromine species and provide insight into phylogenetic and macroevolutionary questions. Whether the fauna of these small water bodies is of recent origin or is simply reflective of the historical changes in the LVR is of great importance in elucidating the evolutionary and hydrological processes that have shaped the LVR system.

Among the tilapiines, the sister group to the haplochromine species, we have found significant populations, in several of the satellite lakes, of the two native forms that were displaced completely from the main lake. Molecular analyses has revealed strong population structuring and differentiation among the remnant populations, and the studies have revealed ample evidence of genetic interaction among the native and introduced species (Mwanja et al., 1996; Mwanja, 1996).

Satellite lakes versus large lakes

On the macroevolutionary level, a question of major interest to us is the historical nature of satellite lakes. Are the satellite lakes residual ponds left behind, isolating large portions of the biological diversity of the original large lakes, as the large lakes receded during extensive desiccation periods? Or, are the satellite lakes nursery beds for cichlid species that act as "lifeboats" for these



Author, Wilson W. Mwanja, examines a *Nile tilapia* fish.

species during periods of desiccation that later feed their trapped fauna back into the large lakes? There is no doubt about the role that these minor lakes are currently playing as refugia for endemic species ravaged by the dramatic human impacts in the LVR since the turn of this century. The bounty of cichlid fishes in these minor lakes was first documented by Greenwood (1981); some of the lakes on which Greenwood worked included the Nabugabo lakes west of Lake Victoria. He found these minor lakes to be not as speciose as Lake Victoria but markedly different in species composition. Much of this difference was comprised of species thought to be basal in evolution to those species in the larger lakes. Greenwood concluded that the minor lakes acted as nursery beds, spewing out new prototypes that move into the larger systems. These prototypes act as factories that radiate into the multitude of species in the greater systems.

Our recent discovery of cichlid fauna in satellite lakes in the LVR, that equate to large portions of the extinct species of the large Lakes Kyoga and Victoria, has led us to speculate about a broader role for these satellite lakes than Greenwood had envisioned. We have found that the minor satellite lakes act not only as nursery beds for the prototype fishes that inoculate the large lakes, but as factories and refugia of the equivalent species to those found in the large lakes. In our scheme, satellite lakes generate species at the same pace as, but on a smaller scale than, the large lakes. In addition, their sheltered habitats offer protection (to species equivalent to those in the greater systems) from the drastic changes that the large lakes have been experiencing. We think small lakes have often been part of the ontogenetic speciation cycles of large lakes. Remembering that this is so may help explain some of the faunal peculiarities of these systems. We are currently doing evolutionary analyses of these recent discoveries, using both morphological and molecular tools, to elucidate the evolutionary history of these interconnected systems (satellite lakes versus large lakes).

LVR as a natural experiment

The introduction of Nile perch and non-indigenous tilapiine fishes into the LVR lakes left little room for the native species, especially in the larger lakes. However, in only a few of the minor lakes (such as Lake Nabugabo in the Lake Victoria Basin and Lake Nyasala in Lake Kyoga Basin) has the Nile perch been able to take over and exert its "extinction machinery" on the endemic species. In some of the minor lakes, such as Lake Bisina in Lake Kyoga Basin, the Nile perch flourished early following its introduction, but has since been knocked down by selective fishing mortality. In such waters where the Nile perch fishery has collapsed we have begun to see an upsurge in the numbers of original native cichlid species. Such situations provide us with a natural experiment on speciation and/or those other factors that have been thought to lead to the resurgence of fish species in the LVR as a whole. From this, we can begin to piece together the evolutionary history, limnology, and the hydrological history of the region, and may well begin to understand some contentious issues pertaining to evolutionary theories and how species arise from other species. The numerous satellite lakes surrounding the large lakes, the vast number of species, the degree of human influence, and the recent history of the LVR provide us with great opportunity and challenge to scientifically unravel the hidden knowledge presented to us by nature. It took Darwin a trip to the Galapagos Islands to concretise his theory of natural selection as mechanism of evolution – it may well take LVR studies to answer the contentious questions on the general mechanism of speciation, including that most basic question of what a species really is.

For further reading

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