

Evolution in fast forward: haplochromine fishes of the Lake Victoria region

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The explosive speciation and adaptive radiation of haplochromine cichlid fishes in Lake Victoria is unrivalled among vertebrates. It holds answers to many intriguing questions about the origins and maintenance of biological diversity. Unfortunately, Lake Victoria is also a case-study in anthropogenic mass extinction. Over 50 per cent of its endemic fishes disappeared between 1980 and 1986. Hundreds of species abruptly became extinct or vanished, disappearing an order of magnitude faster than they could be described. This article examines the dynamics that underlie this fauna's extraordinary volatility, and hence points the way towards its conservation.

The Great Lakes of East Africa are among the largest and deepest in the world, and are without equal for their biological diversity. Most are dominated by small, brightly coloured perch-like fishes called cichlids, which have differentiated time and again in different lakes. Specializations for specific feeding modes are striking and strikingly convergent among these lake assemblages [1,2]. Scientists are fascinated with East African great lake cichlids, but they are not the only ones that view these fishes as important. The great lakes fishes represent food to local peoples. They are also an integral part of the global economy and lore:

they appear on airline and fine-restaurant menus; they are cultured worldwide and available in many neighbourhood supermarkets; they are frequently highlighted on nature shows; and aquarists prize them and pay large sums for new varieties.

The fish communities of Lake Victoria (Figure 1) are superficially similar to those of Lakes Malawi and Tanganyika, but Lake Victoria itself is profoundly different in many ways. Lakes Malawi and Tanganyika lie in ancient rifts with precipitous shorelines, and have deep, anoxic hypolimnia. In contrast, Lake Victoria is vast, but shallow, and prior to 1989 was well mixed for most of the year, although anoxia is now widespread in deeper waters [3,4]. The deep rift lakes are old and their histories complex. For example, the Tanganyikan fish fauna is an amalgam of ancient lineages, multiple invasions, and intralacustrine speciation, some surprisingly long ago [5,6]. In contrast, the great shallow pan of the Victoria Basin has flooded and dried out several times since its creation. The Lake Victoria that we see today is astonishingly young. Johnson *et al.* [7] have finally confirmed what was long suspected [8,9]. It has been only about 12,000 years since the lake basin last reflooded, after drying up completely during the late Pleistocene. Despite its young age, Lake Victoria has hundreds of endemic species and six endemic genera. The presumption is that all of the fishes endemic to the lake evolved *in situ* within this very brief time. The fishes of Lake Victoria are part of a larger Lake Victoria region superfluous, a monophyletic assemblage spread across the watersheds of the region [1,10,11–13]. There are close biogeographical links between Lakes Victoria and Kyoga, Edward and George, and between Edward-George and Kivu. Nonetheless, endemic species occur in every one of these five lakes.

The East African great lakes and their fishes are now critically threatened by human impacts [14–18]. The Lake Victoria system was the first to show severe, lakewide environmental degradation, collapsing fisheries, and wholesale loss of fish species [3,4,19–21]. These dramatic changes in the limnology and native fishery stocks have been attributed to overfishing, the introduction of non-native species, deleterious land-use practices, and pollution from various sources. The rate of change and degree of impact has spurred a flurry of new information about Lake Victoria over the past five years. The destruction of Lake Victoria's cichlid fauna was bemoaned by scientists who saw it as a model for the study of speciation dynamics [22]. Now it is also a case study in anthropogenic mass extinction [23,24]. Over 50 per cent of the endemic fishes disappeared from Lake Victoria between 1980 and 1986, and many are presumed extinct [21,23,25]. The introduced Nile perch (*Lates niloticus*) population is proposed to have been a major contributor to the mass extinction; the decline in endemic haplochromines is almost reciprocal with the increase in Nile perch [19,23]. As recently as 1978, the haplochromine fauna was intact; haplochromines contributed about 80 per cent of the biomass and Nile perch less than 2 per cent, with the remainder consisting of the introduced *Oreochromis niloticus* and native non-cichlids [21]. By 1983 in Kenya and by 1986 in Tanzania, the Nile perch comprised greater than 80 per cent of the catch [21]. The situation in Lake Victoria has been followed most closely by the international community, because of its economic importance and extremely high endemism. But similar changes have occurred with the introduction of Nile perch into other lakes in the region (for example, Kyoga, Nabugabo).

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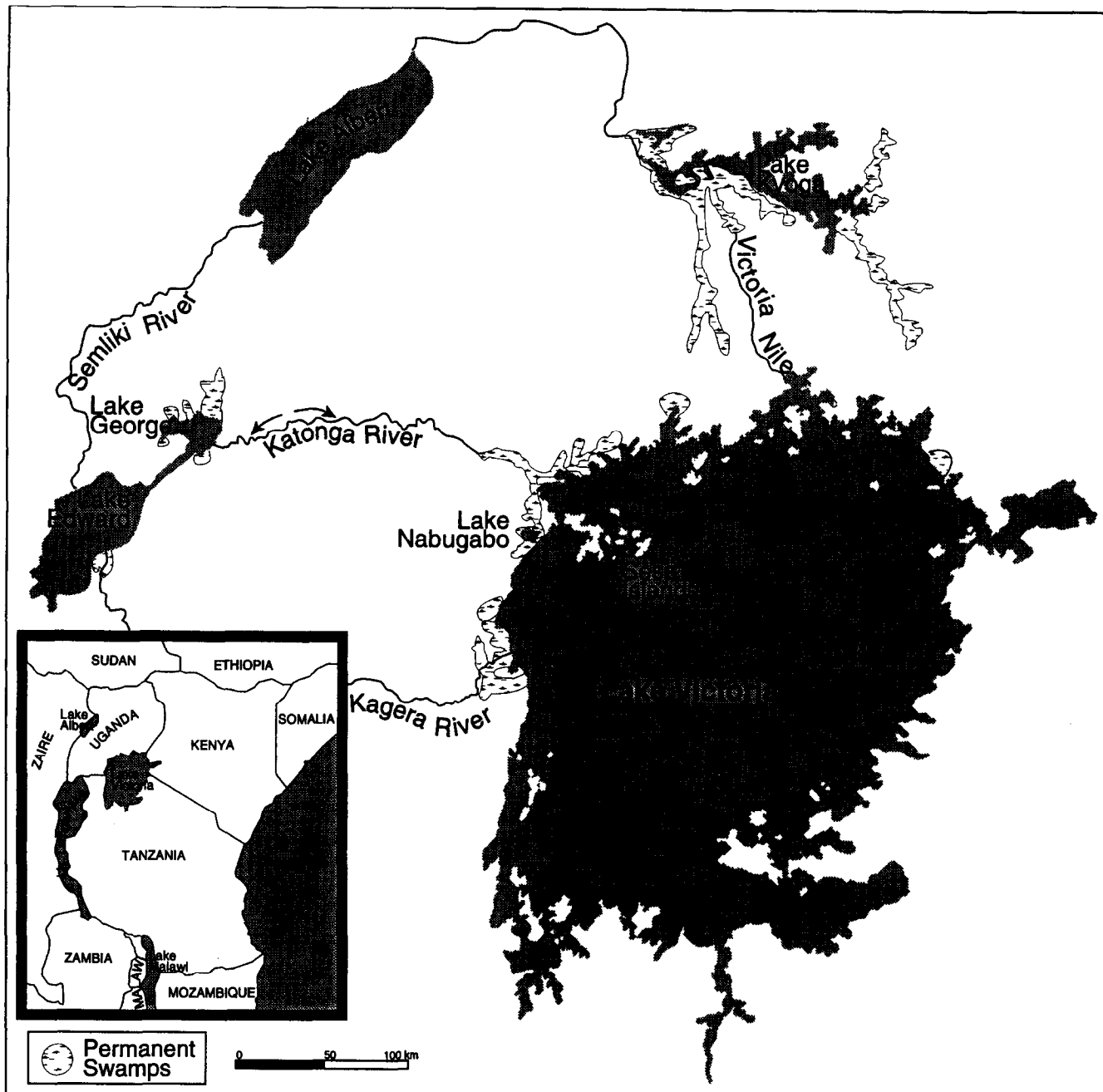


Figure 1 Map of lakes and major rivers in the Lake Victoria Basin of East Africa.

The three nations that border Lake Victoria – Tanzania, Uganda and Kenya – have embarked upon the Lake Victoria Environmental Management Programme [21]. This programme is a co-operative effort designed to (1) address the environmental problems afflicting Lake Victoria and its catchment; (2) promote the sustainability of lake resources, especially fisheries; and (3) arrest the anthropogenic extinctions. One of the basic tenets of the programme is that indigenous species like the haplochromines provide a wealth of essential information about system status, information highly relevant to human needs.

If the interest in the indigenous species is serious, then there is a critical handicap to overcome. The fish fauna of Lake Victoria (not to mention Lakes Kyoga or Edward) is very poorly known. Only about one-fifth of

the species have been described [25,26], and surviving taxa may be disappearing an order of magnitude faster than they can be described.

Taxonomy: finding and identifying the pieces

East Africa boasts the greatest geographical concentration of freshwater fishes on earth. When taxonomic work is completed for Lakes Victoria and Kyoga the number of haplochromine species could level off somewhere around 700 [13]. Total fish diversity in the East African lakes will probably top 2000 species, or about 8 per cent of the fish species in the world.

Some of this diversity is disputed, particularly the number of fish species in Lakes Victoria and Malawi. Figure 2 illustrates changes in estimates of species richness for

Lake Victoria haplochromines since the first specimens collected for Western science were published in 1888 [26]. The exponential upturn in this figure in recent years is part of a broader realization that alpha diversity has been grossly underestimated for most of life on earth, even for things like birds that we once thought we knew a lot about [27]. As for Lake Victoria haplochromines, there are many doubters. Though they converge in appearance when dead in a jar, in life the haplochromines look, act, and are distributed differently from one another. The evidence for the existence of hundreds of quite distinct species is incontrovertible. This is not to imply that the taxonomic situation is clean, simple, or unexciting.

More interesting are disputes over the number of genera of fishes in Lake Victoria.

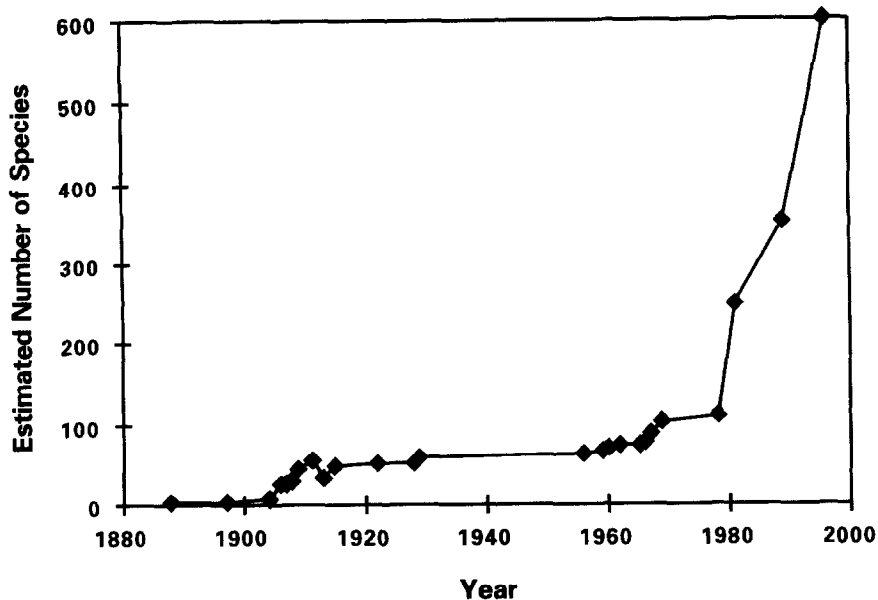


Figure 2 Changes in the estimates of species richness of Lake Victoria's haplochromine cichlids since the first publication on the group in 1888.

When Greenwood [11] revised the haplochromines, he broke up the genus *Haplochromis* into 20 genera, admitting in the process that many ambiguities remained (see [26]). The defining characters include some that are ecologically and ontogenetically labile, such as dentition (Figure 3) [23,25]. The genera grade into each other around the edges, a phenomenon that Greenwood attributed to very rapid differentiation of only marginally dissimilar species accompanied by low extinction rates [11]. Recently, van Oijen [26] rejected Greenwood's revision and returned all haplochromines in the region to the genus *Haplochromis*, while also sinking three genera endemic to Lake Victoria that predated Greenwood's revision. Response to this proposal has been mixed.

At the heart of the matter is the question of why we have a taxonomic system at all. The situation is precisely analogous to a comparison of ostracod nomenclature in Lake Baikal versus Lake Tanganyika [28]. Faced with a diverse fauna rich in functional intermediates, should a taxonomic system advocate prudence and stability (few, robust genera, as in van Oijen [26])? Or should it instead capture and organize as much information as possible about supraspecific evolution [11,12]?

A great irony of the taxonomic 'problem' in Lake Victoria is that fishes that 'all look the same' are difficult to resolve for the very reason that they are so interesting: they are evolution's smoking gun. Greenwood [11] expressed this most eloquently: 'It is the elements of temporal and spatial condensation [of evolutionary processes] coupled with the persistence of all or nearly all stages in the development of different anatomical specializations, that make species flocks and explosive speciation so conspicuous: on studying a species flock one experiences the feeling of looking into a

factory where prototypes are still in production alongside the latest models.' All students of haplochromines agree that we need to know more, especially regarding evolutionary history. We can, and most likely will, argue about the book-keeping for some time to come.

Reconstructing history

Origins of the recent haplochrome fauna

A lake of some sort has existed on and off in the Lake Victoria Basin since its formation in the early to mid Pleistocene about 750,000 years ago [24]. The haplochromines of the Lake Victoria region are presumed to have diverged from a riverine ancestor that inhabited the Kagera and Katonga rivers before Lake Victoria formed. Meyer *et al.* [29] dated the initial divergence at about 200,000 BP, based on a mitochondrial DNA clock. This date agrees well with a regional desiccation event that could have dried up Lake Victoria [24]. We have no idea what went on during the half million plus years that existed between the onset of basin formation and the clock date for the haplochromine radiation. Equally mysterious are the 188,000 or so years that separate the initial radiation and subsequent formation of the modern Victoria flock *sensu stricto*, following the last refilling of the lake basin. More importantly, where could 600 plus endemic fishes of such broad trophic diversity come from in 12,000 years? There are two logical possibilities: reinvasion of congenics from outside the lake basin, or intralacustrine radiation. If reinvasion came from outside the basin, then stock representing morphologically derived lineages could have given the Victoria radiation a head start on adaptive differentiation. If the source was evolution from ancestral stock still present in the lake basin, the entire panoply of trophic morphs would have to be re-evolved from scratch. Of

course, the two scenarios are not mutually exclusive. The problem is that a likely scenario for either process is difficult to envision within the very narrow time constraints imposed by a 12,400 BP desiccation event.

Interlake dispersal: was Lake Victoria rescued?

Any desiccation event intense and prolonged enough to completely dry up Lake Victoria is unlikely to have left nearby satellite lakes or rivers capable of sheltering many species of lacustrine haplochromines. Thus, if the lake was rescued through recolonization, it would most likely have been from the Lake Edward-George system, through the Katonga and Kagera River corridors. Faulting of the Western Rift Valley beginning in the Miocene led to uplifting of land to the west of the basin. This eventually led to reversed flow of the upper sections of previously west-flowing rivers, including the Kagera and Katonga, during the Pleistocene and to the formation of Lake Victoria [24,30,31]. It is thought that the uplifting process was slow and that Lake Victoria may have drained into Lake George until as late as 25,000–35,000 years ago; this would have been the last unidirectional connection between the systems [31]. Today the rivers are characterized by divides marked by a dense swampy watershed from which water flows in both directions [30,31]. They could be penetrated by lacustrine fishes only if it was much wetter during reflooding than today; this may have occurred about 8000 BP, the lake's last high stand. Current distribution patterns offer evidence that interlake dispersal along riverine corridors is at least a possibility. First, a few lacustrine haplochromines exist through most or all of the Victoria Nile, which joins Lake Victoria to Lake Kyoga. Secondly, species common to both Lake George and Lake Edward abound in the 23 km-long Kazinga Channel that joins the two lakes [11]. Thirdly, *Thoracochromis* spp. occur in Lake Albert, Lake Edward, and in the Semliki River by which they are linked. Lastly, *Astatotilapia aenocolor* of Edward-George occurs in Lake Kabaleka, several kilometres north of Lake George and joined by an extensive swampy divide. The extant Lake Victoria haplochromines have congeners in the Lake George-Edward system. Furthermore, some morphological types that occur in both the Victoria-Kyoga and the Edward-George systems are so idiosyncratic that it seems unlikely they would have evolved twice. In both systems there are two types of paedophagous (baby-sucker) haplochromines: one with a U-shaped lower jaw and the other a sharply V-shaped lower jaw. Both systems harbour representatives of Greenwood's genus *Pyxichromis*, distinguished by a seemingly deformed head profile and close-set teeth curved medially, giving the appearance of wire coils [13].

Even so, until there is solid evidence to the contrary, we remain sceptical about the

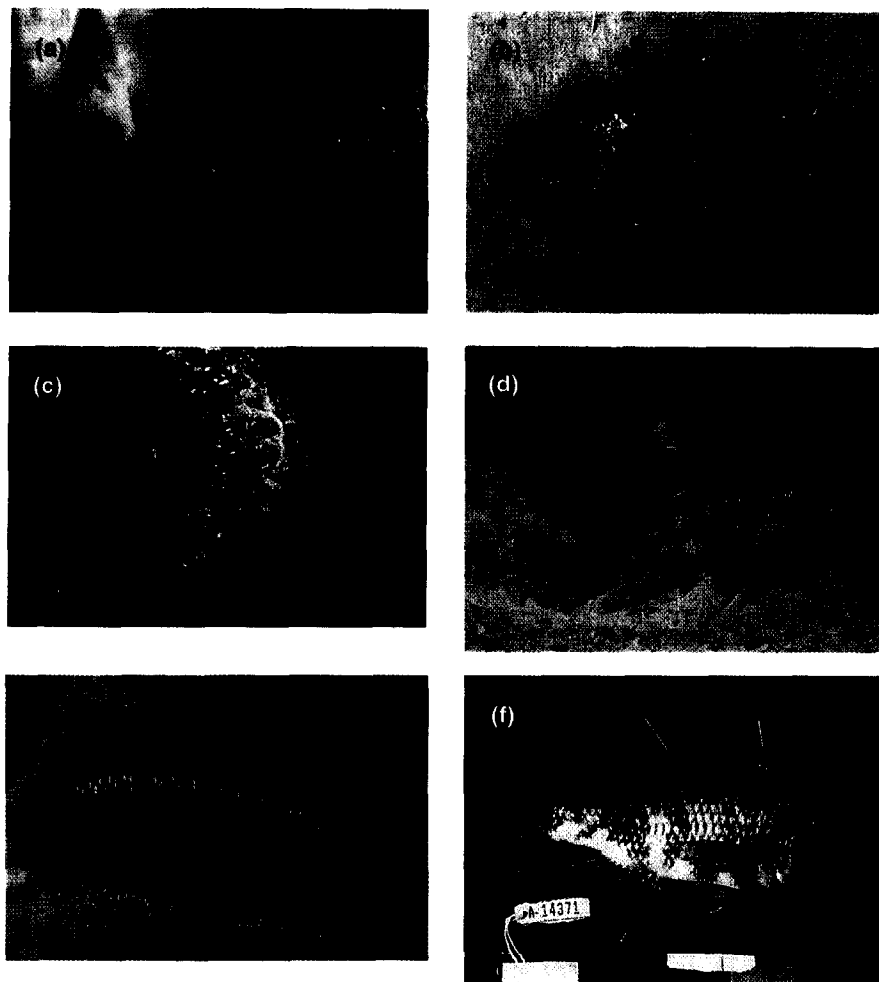


Figure 3 Examples of buccal tooth form variation in Lake Victoria Region haplochromines: (a) outward-pointing lower jaw teeth in the paedophagous (baby-eating) *Lipochromis maxillaris* of Lake Kanyaboli; (b) a related, undescribed *Lipochromis* sp. from Lake Nawampasa, Uganda. It is believed that this dentition aids in grabbing and subsequently releasing the head of mouthbrooding cichlid females; the paedophage removes the young and releases the mother fish; (c) robust, slightly procumbent teeth of an insect-picker, *Paralabidochromis* 'rock kribensis' of Lake Victoria (Ugandan form), and (d) photo of a quiescent male; (e) strongly procumbent, hooked oral teeth of a snail-sheller, *Ptyochromis* 'Rusinga oral sheller' of Lake Victoria (Kenya), and (f) the piebald morph; mottled morphs are common among the littoral cichlids of the Lake Victoria and Lake Malawi regions.

notion of flooding sufficient to permit species exchanges between two highly specialized lacustrine faunas across a basin divide – essentially, a biogeographical 'reversing falls'. For, if Lake Victoria was rescued by fishes from the Edward-George system, then it must also be proposed that the rescue effect proceeded in the opposite direction a few thousand years later, after the Lake Edward-George fauna of that time was dramatically reduced by a massive volcanic explosion in the region [31].

Explosive adaptive radiation

Even if Lake Victoria was reseeded by lineages born in an earlier regional radiation event, the high rate of both species and functional type endemism still demands explanation. Rapid biological change may be expected in a landscape and/or climate that is frequently changing [32], and one need not look far for physical driving forces in a highly volatile lake like Victoria. The recent history of the region has been pep-

pered by volcanic explosions and changing lake levels [7,9,31]. Such tumult can sweep a system free of incumbent taxa, while also creating extensive regions of brand new habitat. The population of new or newly vacated habitat space is strongly associated with macroevolutionary pulses in the fossil record [33,34]. This situation can arise in aquatic ecosystems during: reinvasion of an adaptive zone following mass extinction; transgression events; and periods of intense geological activity that disturb population and habitat structure [32,35]. Lake Victoria and the larger Lake Victoria region could well have experienced several radiation/extinction cycles in the course of basin morphogenesis and climatic shifts over the last couple of hundred thousand years. To be relevant, however, these mechanisms must assist in explaining both the speed of speciation, and the speed of adaptive divergence.

With its shallow basin, myriad islands, and vast valley swamps and swampy margins, Lake Victoria is highly vulnerable to

changes in water level [9,36]. The speciation engine most closely associated with Lake Victoria in the literature is the formation of peripheral isolates in satellite lakes. Are the temporal and spatial scales of marginal flux in the Lake Victoria Basin consistent with this hypothesis? On a time-scale of centuries, the level of Lake Victoria has risen and fallen within a range of about three to tens of metres. Rising levels turn peninsulas into islands and create new habitat mosaics in nearshore waters, while also merging the faunas of satellite lakes. Falling levels reunite islands with the mainland, but also fragment marginal populations in satellite lakes. On a decadal time-scale, lake level has fluctuated from 2–5 m, a disturbance capable of turning seasonal wetlands into standing water with flood events, or creating myriad backwaters and lagoons [37]. Where over this range of scales should evolutionary processes be concentrated?

The smallest semi-permanent water bodies around Lake Victoria are lagoons in marginal wetlands (Figure 4) [37]. The lagoons are small shallow ponds (mean depth less than 2 m) that are situated in low-lying depressions behind or within the fringing wetlands. Studies of the fish faunas of marginal lagoons in Lake Victoria and Lake Nabugabo indicate that species decay curves in these lagoons are quite rapid. The lagoons are generally very hostile to specialized lacustrine taxa because of their extreme physicochemical conditions; most experience chronic hypoxia (oxygen scarcity) or diel shifts in dissolved oxygen with severe nocturnal hypoxia [37,38]. Thus, marginal lagoons are unlikely places to produce either new species or new functional types.

In his classic paper on Lake Nabugabo, Greenwood [36] proposed that marginal satellite lakes could act, literally, as boiler plates for speciation and thus play a major role in the rapid multiplication and adaptive radiation of haplochromine cichlids. Lake Nabugabo has been isolated from the main waters of Lake Victoria for about 4500 years [36]; and multiple strand lines near Sango Bay, Uganda (just south of Lake Nabugabo) suggest that satellite lakes could be formed and destroyed all around the basin on a 0.1–1.0 millennial time-scale. Despite the obvious potential, however, several arguments weigh strongly against a major role for satellite lakes in species multiplication. Species diversity in satellite lakes is generally low [20,25]. Even Lake Nabugabo harboured only five endemic haplochromine taxa, none of which represented new or unique adaptive types [36]. By comparison, an average bay of Lake Victoria the size of Nabugabo could harbour between 100 and 200 species of haplochromines [23]. Similar situations were observed in the Kooki Lakes of Uganda, and the Yala Lakes of Kenya. Thus, satellite lakes act like large lagoons. They certainly afford a greater opportunity than do lagoons for new species to form. Yet this hardly

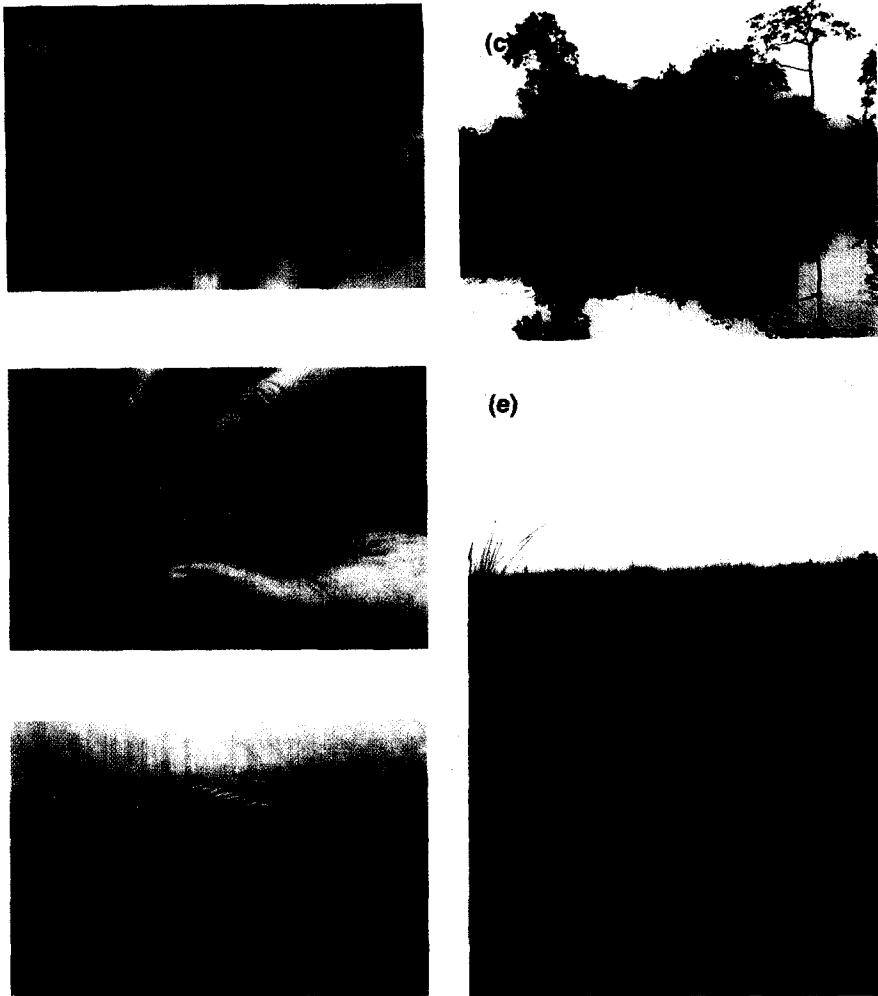


Figure 4 Wetland refugia and haplochromine cichlids: (a) *Prognathochromis venator*, a piscivorous haplochromine, disappeared from Lake Nabugabo coincident with the increase in introduced Nile perch, but survives in nearby satellite lakes (Lakes Kanyanja, Kayugi and Manywa); (b) *Astatoreochromis alluaudi*, a widespread haplochromine cichlid can be found inhabiting some (c) ecotonal wetlands of Lake Nabugabo; (d) *Pseudocrenilabrus multicolor victoriae*, a widespread haplochromine, dominates (e) the lagoons of the extensive Lwamunda Swamp that surrounds Lake Nabugabo. (Photos (c) and (e) by Amanda E. Keiter.)

seems an adequate mechanism to explain the extraordinary radiation in Lake Victoria in 12,000 years or less.

Islands and marginal lakes are conspicuous features of Lake Victoria, but there are not all that many of significant size. Lake Nawampasa, a glaring exception to these observations, is discussed below. The major insight here is that models for allopatric speciation based on marginal dynamics can account in part for the speed of speciation in the Lake Victoria basin, but it is difficult for the allopatric model, as manifested in the region, to account for the remarkable extent of adaptive diversification in this fauna.

As Lake Victoria refilled, littoral habitats would have expanded outwards from the lowest points in the basin. Given the morphometry of the basin, the submergence of the landscape should have evolved through three phases. First, there would be shallow flooding of the two old east-west river valleys to form either one broad or two narrow

swampy, Kyoga-like lakes, and filling of the lake basin's eastern deep zone. Although it was originally thought that there might have been several proto-lakes that eventually merged (thus creating early opportunities for isolation on a very coarse geographical scale), it now seems more likely that there was one proto-lake with a deep pocket and extensive swamplands [7]. From here, the waters would rise to the lake's high stand (8000 BP), inundating portions of all of the basin tributaries. This is also a time when there could have been some faunal exchange with the Edward-George system. Finally, lake level would recede to just below the current level, leaving behind satellite lakes and extensive swamp systems along the Katonga, Kagera, Nzoia, Mara, and other river valleys, such as we see today.

As the water level rose in Lake Victoria, littoral fish communities would have been forced inland to keep pace with appropriate

habitat. Taxa faithful to patchy habitats (for example, rock or sand exposures) would trace the snaking paths of those habitats up the sides of the basin, experiencing unification and isolation, mostly the latter, as they spread away from each other [39]. While this was happening, local populations would also be adapting to the new and much wider range of habitats formed as a consequence of the reflooding. The combination of population fragmentation around an expanding ring of littoral habitat, and increasing diversity of habitat patches, could have precipitated explosive speciation. Because population sizes would be smallest during the earliest phases of this process, the speed of evolution (both speciation and adaptive divergence) should have been highest early in the reflooding event [40,41]. According to this view, as both the new lake and its habitats stabilized, rates of speciation would slow, but the origination rate for higher taxa (that is, new body plans) would slow even faster, leading to a build-up of clusters of species – generally similar in morphology and ecology but with different male breeding colours – within each functional modality. This is the pattern of 'Easter egg species' exhibited by the Victorian haplochromine assemblage. Decline in speciation rates in maturing radiations is also predicted by diversity-dependent diversification models based in biotic interaction as a prime forcing function. Ironically, it seems that density-dependence scales up to the level of macroevolutionary dynamics only for narrowly delimited faunas like lacustrine haplochromines [42].

Radiation, adaptation, and the memory of the clade

Early stages in the above scenario are supported by numerous accounts of trophic differentiation among fishes, especially cases where populations are trapped in new, isolated, or species-poor lakes [43–47]. Clearly, it is not unlikely that haplochromines trapped in a new, expanding lake (and in the company of few other species) could produce a range of new ecophenotypes [45,48]. However, this alone would not constitute a 12,000-year adaptive radiation. Two additional factors are necessary: information capture through speciation, and extreme speed. Speciation mechanisms involving various forms of sexual selection and mate recognition systems are integral to haplochromine biology, so the capacity for rapid speciation is there even though case-specific data are still quite lacking [28,35,49,50].

But what about the speed of ecological diversification? The family Cichlidae has probably exhibited adaptive radiation in lacustrine waters many times over in its history. The distinctive patterns of morphological adaptation to different diets and habitats are mirrored over and over again, both within [46] and among species, in both Africa and tropical America. At larger scales, there are strong functional parallels

among a great variety of teleostean radiations, both freshwater and marine, united by their evolution on structurally diverse submerged landscapes [1,44,51,52]. It was this transcendent convergence that led the European explorer-biologists to assert that the Lake Tanganyika fauna was directly descended from nearshore marine ancestors (see, for example, [53]). Kaufman and Liem [51] attributed such parallels in part to domination by labroid fishes, all of which share a key adaptive complex (a particular set-up in the pharyngeal jaws). Key innovations are typically thought to expand the fundamental niche and increase evolutionary potential [21]. But what if they also constrain subsequent patterns of evolution even while expanding the overall range of patterns that can be assumed?

The constraint in question could be genetic, not kinematic. Stiasny [54] proposed that the impressive evolutionary potential of cichlids can be partly explained by 'taxic atavism', or the preservation of adaptive information in suppressed form, whose expression could be re-invoked at some later date by appropriate selective regimes. The retention of multiple body plans within a common genome could result in a clade capable of undergoing repeated, almost perfectly reiterative adaptive radiation in a divergent selection milieu. This would be especially likely if the 'experienced' clade was exposed anew to a selective regime very similar to the ones that originally shaped its genomic characteristics. The recreation of a lake in a previously flooded basin is a mechanism that can replicate a spatially explicit set of selective pressures and microenvironments.

Clades that experience repeated episodes of strong divergent selection could accumulate capacity to respond to similar situations in the future. Clades that start out with versatile body plans always have the potential for adaptive radiation, given time. However, they may gain the capacity for explosive radiation only after they are subjected to harlequin selection regimes multiple times in the course of their histories. With each subsequent radiation event, less and less new information is incorporated, as greater reliance can be placed on the legacy of solutions inherited through the ancestral genome. The invocation of taxic atavism as an *ad hoc* explanation for rapid radiation may seem extreme, but it does help to explain another puzzling aspect of haplochromine radiations: they involve very low levels of genetic variability. The levels of variability found among haplochromines in the Lake Victoria region are low, often within the range we are accustomed to seeing within a single species – *Homo sapiens*, for example [55–57]. By comparison, the levels of between-population variation in certain Tanganyikan cichlids [58], or that we have found within tilapiine and cyprinid fishes in the region, are as large as those typically found among different species [59]. One possible interpretation of these

data is that the haplochromines in the Lake Victoria region are indeed one highly variable species. This is completely inconsistent with field observations. The alternative interpretation, and the one that we strongly favour, is the empirical one: the haplochromines in the Lake Victoria region by and large share a common genome. It is a genome capable of producing a range of quite distinct adaptive types with very little readjustment [29,56]. In other words, any one of the species in the superflock may contain most of the information required to produce all of the others. Conversely, the phenotype that it expresses may be only one of many that are possible, but suppressed within the genome.

Levinton [60] objected adamantly to the notion that taxic atavisms were of macroevolutionary importance, on the grounds that nothing new is brought to light by hopeful monsters. In attempts to explain the appearance of Lake Victoria's geologically 'instant' fish fauna, Levinton's criticism is exactly the point: not much new has to be added. The radiation proceeds just as quickly as speciation can select, bind, and shelve new excerpts from the old genomic library that is the clade's common heritage. This phenomenon is not that much more remarkable than complete metamorphosis and seasonal morphs in insects and amphibians, or the fact that every organism produces a great diversity of cell types through differential expression of its singular genome.

Species hybridization provides another mechanism of almost instantaneous cladogenetic potential [61,62]. The concentration of many species in small areas that characterizes several phases in lake ontogeny would only accelerate this process. Perhaps the greatest significance of a hybrid origin of species is the replicability that it offers for reiterative evolution from a common pool of ancestral taxa [62].

Extinction dynamics and conservation biology

Extinction mechanisms

Not surprisingly, the macabre spectacle of watching several hundred fish species disappear has begun to generate some interesting empirical notions about the mechanism and dynamics of mass extinction. Kaufman and Ochumba [25] proposed that in Lake Victoria, the speed and ecological breadth of the anthropogenic extinction event was the result, in part, of simultaneous selection for mutually exclusive refugia (the 'crossed forces' hypothesis). Deep-water anoxia forced a component of the open-water haplochromine fauna (some detritivores, zooplanktivores, planktivores, and insectivores) up and out of the hypolimnion, while Nile perch predation pressure forced them down, into the anoxic zone. The result was the loss of refugia for some of these open-water species and, consequently, extinction.

The haplochromines in the Lake Victoria region also make it possible to assess the concept that biota repeatedly exposed to extinction filters could prove increasingly resistant to extinction in the future [63]. It would be very good news if this is true for Lake Victoria haplochromines. Presuming that the extinction wave of the mid 1980s has crested, the remaining taxa may have a solid lease on life after all. They may, in fact, be the seeds of a new radiation [24]. Indeed, the post-disturbance, or 'resurgence' assemblage of haplochromines in Lake Victoria today includes hypervariable, species-rich taxa ('explosive' taxa) suspected to be capable of seeding new radiations [13,25].

Satellite lakes and wetlands as species refugia

The extraordinary loss of biodiversity in the Lake Victoria Basin has led to a series of studies directed at the identification of faunal refugia. Rocky crevices appear to be important refugia for rock-dwelling haplochromine cichlids in the Mwanza Gulf area of Lake Victoria [23]. In Lakes Victoria, Kyoga and Nabugabo, wetlands may also protect some indigenous fishes from Nile perch predation by providing both structural and low-oxygen refugia for prey species that can tolerate the hypoxic conditions that prevail in their dense interior. In addition, they may serve as barriers to the dispersal of Nile perch. There are two major kinds of wetlands: marginal wetlands, and valley swamps. Both are usually dominated by papyrus (*Cyperus papyrus*) which forms a dense canopy 4–5 m in height or by dense stands of the grass *Miscanthidium violaceum*. Little light or wind penetrates the swamp canopy, and both growth and decomposition proceed at high rates. This results in extremely low levels of oxygen in the swamp waters, and creates a gradient of habitats with increasing oxygen availability from the dense wetland interior to the open water of the adjacent river or lake.

Remnant populations of indigenous fishes (both cichlid and non-cichlid) persist in the lagoons and satellite lakes that are separated from the main lakes by extensive areas of swamp, while other indigenous species find refuge in ecotonal areas at the edges of marginal swamps in the main lakes (Figure 4) [20,38,64]. Use of these areas depends to some degree on the capacity of species to tolerate low oxygen levels. Fish kills associated with upwellings of anoxic water suggest that deeper waters of Lake Victoria impose a high risk for some species [25]. However, laboratory experiments have demonstrated a relatively high tolerance to hypoxia in some haplochromines. This may permit use of marginal wetlands, particularly ecotonal wetlands where hypoxia is moderated by interaction with the main lake waters [65]. Having evolved in a shallow, swampy basin, it is not surprising that the Lake Victoria haplochromines may be, as a group, relatively hypoxia-tolerant, nor that

such tolerance is higher among widely distributed swamp specialists than in more stenotypic lacustrine forms [65]. Physiological studies suggest that Nile perch are relatively intolerant of low oxygen conditions. Fish [66] found that Nile perch require water with high dissolved oxygen (>5 mg/l) since their blood has a low affinity for oxygen. Both their metabolic rate and critical oxygen tension (physiological measurements that relate to oxygen demand and low oxygen tolerance) are higher than for several haplochromine cichlids and tilapiines from the region (Chapman, Chapman and Keiter, unpublished data). In addition, in a comparison of ecotone areas of Lake Nabugabo, Chapman *et al.* [64] found that Nile perch were less abundant in wetland ecotones relative to exposed inshore areas and less abundant in areas of low dissolved oxygen concentration. Although it is difficult to separate the effects of structure and low oxygen on habitat use of Nile perch, it is clear that tolerance to low oxygen may permit indigenous species to use structured inshore areas which would offer some measure of protection against predation by introduced Nile perch. Further, the expansion of Nile perch from lakes into river systems and wetlands in the Lake Victoria region may be limited by river mouths and valley swamps choked with papyrus [38].

Nile perch were introduced into Lake Nabugabo about the same time as they were introduced into Lake Victoria [20]. Lake Nabugabo is surrounded by an extensive peat, sedge and papyrus swamp riddled with passageways and lagoons. It thus affords a wonderful model system for testing the wetland refugium hypothesis [38,64]. In Lake Nabugabo swamp lagoons, papyrus 'plugs' in river inlets, and marginal wetland ecotones harboured nine of the 16 species reported extinct or rare in previous main lake re-surveys (Figure 4) [20,25,38,64]. Wetland ecotones harboured the most species, probably because only the most hypoxia-tolerant taxa can survive under the more extreme conditions of the lagoons and river mouth swamps.

Some of the survivors in the wetland lagoons and tributaries were totally unexpected. The tiny electric mormyrid fish *Petrocephalus catostoma* is not an air-breather, and is extinct in Lake Nabugabo proper. Yet it has persisted in deep swamp refugia, by virtue of a low metabolism, a low critical oxygen tension, and a large gill surface area. In addition, when it finds itself in water that is too low in oxygen *Petrocephalus* flips upside down, thus rolling its tiny, underslung mouth up from beneath its body, and into close proximity with the oxygen-saturated surface film. We had seen this before: the central African catfish *Synodontis nigriventris* spends so much time in this odd position that aquarists call it the 'upside-down catfish' [67].

Lakes Victoria and Kyoga are now both so severely eutrophied that it is unlikely that

marginal submerged vegetation will soon recover to the levels that existed prior to the floods of the early 1960s [21,36]. The extreme importance of these beds for the haplochromine fauna never really hit home until we went to a remarkable satellite lake in the Lake Kyoga system, called Lake Nawampasa. Lake Nawampasa is a fragile, minute, and now gravely endangered refugium of the former Lake Victoria-Kyoga fauna. Only 1 km by 5 km in size, Nawampasa houses more than three dozen haplochromine taxa representing most of the described genera of the Lake Victoria regions [Kaufman, Wandera and Armoudlian, unpublished data]. Many of the Lake Nawampasa fishes are closely associated with dense, reef-like mounds of the aquatic macrophyte *Ceratophyllum demersum*. *Allochromis welcommei*, a scale-eating haplochrome, survives only in this tiny refugium, as far as we know [13]. Satellite lakes like Nawampasa and Nabugabo may be less important to speciation or adaptive divergence than Greenwood [36] thought, but they play a crucial role in modulating extinction today [25].

The fish fauna of the Lake Victoria region offers wonderfully tractable grist for the mill of 'ecological biogeography' [32]. Indeed, hidden *en masse* in the Lake Victoria fish species flock are the answers to many evolutionary questions for which scientists have groped in the dark for a hundred years. With current progress in the genetics, physiological ecology, and systematics of these fishes, an exciting turning point in the intellectual game is close at hand. For any taxa the fossil record is largely a record of stasis. Fossils form slowly, and so can shed only faint light on the brief outbursts of invention and catastrophe that fuel macroevolution [68]. To understand the works of Shiva, you must bear witness at first hand to both the destruction and the birth of worlds. In Lake Victoria, there is still that chance.

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