

# Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14 600 year history for its cichlid species flock

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Geophysical data are currently being interpreted as evidence for a late Pleistocene desiccation of Lake Victoria and its refilling 14 600 years ago. This implies that between 500 and 1000 endemic cichlid fish species must have evolved in 14 600 years, the fastest large-scale species radiation known. A recent review concludes that biological evidence clearly rejects the postulated Pleistocene desiccation of the lake: a 14 600 year history would imply exceptionally high speciation rates across a range of unrelated fish taxa. To test this suggestion, I calculated speciation rates for all 41 phylogenetic lineages of fish in the lake. Except for one cichlid lineage, accepting a 14 600 year history does not require any speciation rates that fall outside the range observed in fishes in other young lakes around the world. The exceptional taxon is a lineage of haplochromine cichlids that is also known for its rapid speciation elsewhere. Moreover, since it is unknown how many founding species it has, it is not certain that its speciation rates are really outside the range observed in fishes in other young lakes. Fish speciation rates are generally faster in younger than in older lakes, and those in Lake Victoria, by far the largest of the young lakes of the world, are no exception. From the speciation rates and from biogeographical observations that Lake Victoria endemics, which lack close relatives within the lake basin, have such relatives in adjacent drainage systems that may have had Holocene connections to Lake Victoria, I conclude that the composition of the fish assemblage does not provide biological evidence against Pleistocene desiccation. It supports a hypothesis of recent colonization from outside the lake basin rather than survival of a diverse assemblage within the basin.

**Keywords:** Lake Victoria; Pleistocene desiccation; speciation rates; cichlid fishes; adaptive radiation

## 1. INTRODUCTION

Lake Victoria in East Africa has an unusually species-rich flock of endemic cichlid fishes, the origin of which has recently emerged as one of the most debated issues in evolutionary biology (e.g. Kaufman *et al.* 1997; McCune 1997; Seehausen *et al.* 1997) because geophysical evidence suggests that the lake was entirely dry only 13 200 to 12 400 <sup>14</sup>C-years BP (Johnson *et al.* 1996, 2000; Beuning *et al.* 1997; Scholz *et al.* 1998). Yet, it contains between 500 and 1000 endemic species, rendering the fishes of Lake Victoria the world's most rapidly evolved (known) assemblage of animal species. Recently, arguments have been put forward that challenge the geological evidence and question the young age and correspondingly high rate of speciation in Lake Victoria (Fryer 2001).

In a review of geophysical and biological evidence, Fryer (2001) concludes that biological evidence, derived from the fish assemblage, rules out the postulated Pleistocene desiccation of the lake. Fryer (2001) acknowledges scenarios that may partly account for extraordinarily fast speciation of haplochromine cichlids (e.g. Galis & Drucker 1996; Kaufman *et al.* 1997; Seehausen *et al.* 1997; Turner 1999; Seehausen 2000; Fryer 2001). The biological evidence that he believes argues strongly against desiccation, however, is that various groups of non-cichlid fishes would also have undergone speciation at a pace unprecedented in fishes elsewhere in the world. Explanations given for

unusually rapid speciation in haplochromine cichlids (e.g. disruptive sexual selection, polymorphic coloration and anatomical adaptability) do not apply to other fish taxa of Lake Victoria. In the face of what Fryer (2001) considers uncertainties in the geophysical data, he therefore concludes that, before the desiccation hypothesis can be taken seriously, explanations have to be sought for why several unrelated groups of fishes speciated more rapidly in Lake Victoria than anywhere else in the world. This would render biological evidence against a Pleistocene desiccation because bursts of speciation, correlated across a large number of unrelated lineages, are an unusual phenomenon. Although there is good evidence for correlated bursts of speciation from palaeontological work (e.g. Willi- amson 1981; Ivany 1996; Brett *et al.* 1996; Brett 1998), bursts of speciation, correlated across fish families on the temporal scale implied by the desiccation of Lake Victoria, would appear to be unparalleled among extant taxa.

To investigate whether several independent fish lineages have undergone unusually rapid speciation, I have calculated the reciprocal of speciation rates (speciation intervals; McCune 1997) that would be required to explain the species assemblages presently observed, assuming 12 400 <sup>14</sup>C-years (= 14 600 years, used henceforth in this article) history of Lake Victoria. My calculations show that speciation intervals in all of the fishes of Lake Victoria, except one group of haplochromine cichlids, are well within the range observed in fish radiations in other young

lakes elsewhere in the world. Except for one group of haplochromine cichlids, the suggested 14 600 year history does not demand an explanation of unusually fast speciation in any of the at least 40 other evolutionary lineages of fishes inhabiting Lake Victoria. Rates of diversification in fishes, therefore, do not provide evidence against Pleistocene desiccation of Lake Victoria. Rather they emphasize the need to further study evolutionary processes affecting differences in rates of diversification between taxa.

## 2. MATERIAL AND METHODS

Net speciation intervals (SI, where net speciation = gross speciation – extinction) in thousands of years are calculated as the mean doubling time of species number, assuming two disparate models of diversification (McCune 1997): (i) a model of linear diversification, assuming a completely unbalanced tree shape, where bifurcations occur only in one of the two branches of the preceding bifurcation:

$$SI_{\text{lin}} = \frac{t}{N_t - N_0},$$

where  $N_t$  equals number of extant species,  $N_0$  equals number of founding species, and  $t$  equals age of radiation. (ii) A logarithmic model assuming a completely balanced tree shape where both branches resulting from a bifurcation always continue to bifurcate further:

$$SI_{\text{log}} = \frac{t \log_e(2)}{(\log_e N_t - \log_e N_0)},$$

$SI_{\text{lin}}$  and  $SI_{\text{log}}$  (=  $L$  of Turner 1999) are modifications of  $TFS_{\text{lin}}$  and  $TFS_{\text{in}}$  (Time For Speciation, McCune 1997) that allow accommodation of uncertainty over which species in a 'flock' are to be assigned to which of more than 1 potential founders by averaging SI over all potential founders.  $N_t$  is taken from two sources (Witte & van Densen 1995; Froese & Pauly 2000) for the non-haplochromine cichlids, and from Seehausen (1996) for the haplochromine cichlids.  $N_0$  is the number of evolutionary lineages (species or species complexes) within each genus occurring in Lake Victoria but also outside the Lake Victoria basin. Hence,  $N_0 = N_t - N_e$ , where  $N_e$  is the number of Lake Victoria endemics; except in the case  $N_t = N_e$ , where the founding species has transformed into a new endemic species or has gone extinct. In this case  $N_t$  is replaced by  $N_t + 1$  and  $N_0$  is conservatively (downwards-biased estimate of speciation intervals) assumed to be 1 unless actually known. In general, where no information was available about the number of evolutionary lineages that also occur outside the Lake Victoria basin, the conservative assumption was made that all endemics are products of *in situ* diversification (e.g. in small *Barbus* and in *Marcusenius*).  $t = 14\ 600$  yr for lineages that, within the Lake Victoria region, occur exclusively in Lake Victoria, including adjacent water bodies that would have been dry when Lake Victoria was dry (e.g. Lake Kyoga, Lake Nabugabo, Victoria Nile).  $t = 200\ 000$  yr for lineages that also occur in Lake Edward which is *ca.* 30–40 m deeper than Lake Victoria, may not have dried up even if Lake Victoria was dry, and is a probable source of recolonization of the refilling Lake Victoria. The palaeoclimate of the Great Lakes region makes it probable that Lake Edward was dry 200 000 years BP (Greenwood 1994).  $t = 14\ 600$ –200 000 yr for lineages that are a mixture of Lake Victoria endemics and taxa that also occur in Lake Edward. The range of  $t$  in such cases

accounts for the uncertainty about whether, and how many, species from Lake Edward have contributed to the colonists that subsequently radiated in Lake Victoria. Generic taxonomy follows Froese & Pauly (2000, and references therein). The cyprinid genus *Rastrineobola*, described only from Lake Victoria, is not derived from other Lake Victoria cyprinids but is closely related to *Neobola*, which occurs to the north of Lake Victoria. The catfish *Xenoclaris*, also described only from Lake Victoria, is either derived from a *Clarias* lineage that went extinct elsewhere or from one of the *Clarias* species that occur within the lake basin (Teugels & Adriaens 2002). Distribution data are taken from Froese & Pauly (2000), with additional data from Seegers (1996) and De Vos & Snoeks (1994).

## 3. RESULTS

Except in one lineage of haplochromine cichlids (see below), speciation intervals in all other fish lineages of Lake Victoria (table 1:  $SI_{\text{lin}}$  2900 to more than 200 000 years,  $SI_{\text{log}}$  9200 to more than 200 000 years) are entirely within the range of fish speciation intervals observed in young ( $\leq 200\ 000$  years) lakes elsewhere in the world (table 2). This is true independently of whether a linear model (minimizing SI) or a logarithmic model (maximizing SI) is applied to calculate mean net speciation intervals (table 2, radiations of  $\leq 200\ 000$  years of age:  $SI_{\text{lin}}$  1500–7100 years,  $SI_{\text{log}}$  1900–46 000 years).

The large number of 18 endemic species of fishes (other than members of the cichlid species flock) may suggest that Lake Victoria has experienced more speciation events than other lakes of comparable age (e.g. postglacial lakes in the Northern Hemisphere). However, this does not imply that these fishes have speciated faster in Lake Victoria than in other lakes. The rate of faunal diversification is measured as the mean doubling time of species numbers (net SI), which is a function of both the number of extant endemic species, as well as the number of founders (McCune 1997; Turner 1999). The fish biota of Lake Victoria was founded by at least 41 different lineages (table 1:  $n$  founders), which accounts for the high number of endemics among non-cichlids. Indeed, most of the 18 endemics of Lake Victoria that do not belong to the cichlid flock, are not products of diversification within the lake, but merely became specifically distinct from the ancestral populations in adjacent river systems. At least in some cases specific distinctiveness rests on the unproven assumptions of taxonomists.

If these assumptions are usually correct, the proportion of colonizing lineages that have transformed into new species (13 of 42) is also not higher than in other lakes of similar age. Postglacial Northern Hemisphere lakes often contain just a very few species, one or several of which often transform into one, or radiate into several, new species, e.g. smelt and whitefish in the St Lawrence River basin (Taylor & Bentzen 1993; Lu *et al.* 2001) or charr and stickleback in Icelandic lakes (S. Skulason & S. S. Snorrason, personal communication). What sets Lake Victoria apart from these lakes is its large size and equatorial location, and consequently its larger number of colonizing species. There are not many other large equatorial lakes of similarly recent age. Lake Rukwa is one such lake where little time was required to produce a comparable number of endemic species from the same genera found in Lake

Table 1. Species numbers and speciation rates in all evolutionary lineages of fishes inhabiting the Lake Victoria basin.

phylogenetic lineage	age (1000 yr)	<i>n</i> extant species	<i>n</i> of founders	net speciation interval linear model (1000 yr)	net speciation interval log model (1000 yr)	<i>n</i> speciation events = <i>n</i> endemic species <sup>a</sup>
cichlids						
<i>Astatotilapia</i> derived cichlids	14.6–200	500–1000	1	0.01–0.40	1.5–22 <sup>b</sup>	499–999
<i>Astatoreochromis</i>	200	1	1	> 200	> 200	1
<i>Pseudocrenilabrus</i>	200	1	1	> 200	> 200	0
<i>Oreochromis</i> ( <i>Oreochromis</i> )	14.6	1	1	14.6	14.6	1
<i>Oreochromis</i> ( <i>Nyasalapia</i> )	14.6	1	1	14.6	14.6	1
anabantids						
<i>Ctenopoma</i>	200	2	1?	200?	200?	1? <sup>c</sup>
cyprinodonts						
<i>Aplocheilichthys</i>	14.6	5	4	14.6	45	1
cyprinids						
<i>Barbus</i> large barbs	200	1	1	> 200	> 200	0
<i>Barbus</i> small barbs	14.6	13	8	2.9	20.8	5
<i>Labeo</i>	14.6	1	1	14.6	14.6	1? <sup>d</sup>
<i>Garra</i>	200	1	1	> 200	> 200	0
<i>Rastrineobola</i>	14.6	1	1	14.6	14.6	1
characids						
<i>Alestes</i>	14.6	2	2 <sup>e</sup>	14.6	14.6	1 <sup>e</sup>
catfish						
<i>Bagrus</i>	200	1	1	> 200	> 200	0
<i>Clariallabes</i>	200	1	1	> 200	> 200	0
<i>Clarias/Xenoclaris</i> <sup>f</sup>	14.6	5	4	14.6	45	1
<i>Schilbe</i>	200	1	1	> 200	> 200	0
<i>Synodontis</i>	200	2	2 <sup>e</sup>	> 200	> 200	0 <sup>e</sup>
elephant fish						
<i>Marcusenius</i>	14.6	2	1	7.3	9.2	2
<i>Mormyrus</i>	200	1	1	> 200	> 200	0
<i>Hippopotamyrus</i>	14.6	1	1	14.6	14.6	1
<i>Gnathonemus</i>	14.6	1	1	> 14.6	> 14.6	0
<i>Petrocephalus</i>	200	1	1	> 200	> 200	0
<i>Pollimyrus</i>	14.6	1	1	> 14.6	> 14.6	0
spiny eels						
<i>Caecomastacembelus</i>	200	1	1	> 200	> 200	0
lungfish						
<i>Protopterus</i>	200	1	1	> 200	> 200	0

<sup>a</sup> If  $\neq 0$  although *n* extant species = *n* founders, 'speciation events' are transformations of a more widely distributed ancestral species into a local endemic without *in situ* diversification.

<sup>b</sup> Note that this maximum figure lies above the age of Lake Victoria because it is calculated over the age of Lake Edward. It implies the hypothesis that most speciation has occurred in Lake Edward and a fully differentiated species flock invaded the refilling Lake Victoria from Lake Edward followed by subsequent extinction of most of the species in Lake Edward. This is a highly unlikely scenario, and the mean SI is very probably shorter.

<sup>c</sup> Not in Lake Victoria but around Lake Edward.

<sup>d</sup> There are unconfirmed reports of *Labeo* in Lakes Edward and George (Seegers 1996).

<sup>e</sup> *Alestes sadleri*, *Synodontis afrofisheri* and *S. victoriana*, previously believed to be endemic, have recently been recorded from the Malagarasi river basin (De Vos & Snoeks 1994) and Lake Rukwa (Seegers 1996) and the second species of *Alestes* is endemic but has its closest relatives outside the Lake Victoria basin.

<sup>f</sup> *Xenoclaris* is considered a junior synonym of *Clarias* (*Anguilloclarias*) and is closely related to *C. (A.) alluaudi* (Teugels & Adriaens 2002).

Age is the maximum age of the Lake Victoria (14 600 years) or Lake Victoria/Edward (200 000 years) population (in case of non-endemic species), species or larger lineage (endemics). Note that mean SI exceeds age when a genus had fewer speciation events than founding species (e.g. *Barbus*).

Victoria. Lake Rukwa has 12 endemic non-haplochromine fish species, including one species each of the genera *Oreochromis*, *Aplocheilichthys* and *Chelaethiops* (closely related to *Rastrineobola*), and two species of *Synodontis* (Seegers 1996), and is believed to be even younger (and much smaller) than Lake Victoria (Seegers 1996).

#### 4. DISCUSSION

These data and observations from other lakes only allow the conclusion that acceptance of the 14 600 year hypothesis for the origin of the Lake Victoria fish assemblage does, with the possible exception of one lineage of cichlids,

Table 2. Species numbers and speciation rates in fishes of other lakes of comparable age and in lineages related to those in Lake Victoria but from older lakes. Note that the negative relationship between age of lake and speciation interval is a general trend (McCune 1997).

phylogenetic lineage	age (1000 yr)	<i>n</i> extant species	<i>n</i> of founders	net speciation interval linear model (1000 yr)	net speciation interval log model (1000 yr)	<i>n</i> speciation events
pupfish (cyprinodont)	3–5	3	1	1.5–2.5	1.9–3.2	2
pupfish (cyprinodont)	8	5	1	2	3	4
Great Lake ciscoes (coregonid)	12	8	2	2	6	6
sticklebacks	12	2	1 or 2	12	12	2 <sup>a</sup>
lake whitefish (coregonid)	12	2	1	12	12	1 <sup>b</sup>
smelt (salmonid-like)	12	2	1	12	12	1 <sup>c</sup>
brown trout (salmonid)	15	2	1	15	15	1
Arctic charr (salmonid)	15	2–4	1	5–15	7.5–15	3 <sup>d</sup>
<i>Orestias</i> (cyprinodont)	60–150	~22	1	2.9–7.1	13–34	~21
haplochromine cichlids	200	40+	2	5.3	46	38+
small barbs (cyprinid)	90–2000	~17	1	5.6–125	22–490	~16
haplochromine cichlids	600–2000	600–1000	1	0.6–3.3	60–217	599–999
tilapiine cichlids	600–2000	3	1	300–1000	379–1262	2
tilapiine cichlids	1000–2000	11	1	100–200	289–578	10
clariid catfish	1000–2000	10	1	111–200	301–602	9
large barbs (cyprinid)	~2000	~13	1	167	540	~12
sculpins	2500	29	1 or 2	89 or 93	515 or 648	27 or 28

<sup>a</sup> Species pairs evolved independently in four different lakes. Single endemic species evolved in many more lakes.

<sup>b</sup> Species pairs (dwarf and normal) evolved from a single ancestral population at least three times independently in several lakes in Alaska, East Canada and Maine.

<sup>c</sup> Species pairs (dwarf and normal) evolved from a single ancestral population several times independently in several lakes in East Canada and Maine.

<sup>d</sup> A species flock of four ecotypes has evolved in Iceland and species pairs have evolved in a number of lakes in Iceland, Scotland, Norway and Sweden.

(Lake/region and published source in sequence: Lagoons on San Salvador Island: Holtmeier (2001), B. J. Turner (personal communication); Lake Chichancanab: Humphries (1984), Strecker *et al.* (1996); Laurentian Great lakes: Smith & Todd (1984); lakes on Texada Island and Vancouver Island: Taylor *et al.* (1997), Taylor & McPhail (1999); single species lakes on the Queen Charlottes: Reimchen *et al.* (1985); lakes in East Canada and Maine: Lu *et al.* (2001); lakes in Alaska: Bernatchez *et al.* (1996); lakes in East Canada and Maine: Taylor & Bentzen (1993); Lake Bunnarsjoarna/Sweden: Ryman *et al.* (1979), Schluter (1996); Lake Thingvallavatn/Island: Skulason & Smith (1995), Skulason *et al.* (1999); Norway and Scotland: Hindar *et al.* (1986), Hartley *et al.* (1992); Sweden: Svedaeng (1990); Lake Titicaca: Parker in McCune (1997); Lake Edward: Greenwood (1973, 1994); Lake Lanao: Kornfield & Carpenter (1984); Lake Malawi: Sodsuk *et al.* (1995); Lake Barombi Mbo: Schlieven *et al.* (1994); Lake Malawi: Lowe-McConnell (1987), Agnese & Teugels (2001); Lake Tana: Nagelkerke *et al.* (1995); Lake Baikal: Slobodyanyuk *et al.* (1995)).

not require higher speciation rates than those documented in other fishes in young lakes around the world (Schluter 1996; McCune 1996, 1997; McCune & Lovejoy 1998; Bernatchez & Wilson 1998; Skulason *et al.* 1999). Note that net speciation intervals of fishes seem generally shorter in geologically younger than in older lakes (McCune 1997), and Lake Victoria is well within the range observed for other lakes (figure 1).

Speciation rates are one thing but rates of ecological and morphological adaptations are quite another problem. However, it is not apparent that the endemic Lake Victoria fishes are exceptional in regard to the latter either. Similar to their relatives in Lake Victoria, several of the Lake Rukwa endemics appear to be adapted to lacustrine conditions and shun the adjacent rivers. In adaptation to deep water, the Lake Victoria endemic catfish *Xenoclarias* has lost a suprabranchial air-breathing organ typical for clariid catfish, but is otherwise very similar to the non-endemic species *Clarias* (*Anguilloclarias*) *alluaudi* (Teugels 1986). In fact, it is believed to be derived from that species, and the genus *Xenoclarias* is now considered a synonym of *Clarias* because no derived unique characters

could be found to support its genus status (Teugels & Adriaens 2002). Morphological and physiological adaptations of comparable magnitude to deep-water dwelling have also evolved in several salmonid and coregonid species in post-glacial lakes (Skulason & Smith 1995).

Other Lake Victoria endemics adapted to life in large water bodies, that have no more widely-distributed relatives within the lake basin, also do not provide evidence against a late Pleistocene desiccation if they have close relatives in either the Lake Edward system or in the Malagarasi River system to the south of Lake Victoria. These drainage systems may have been connected to the Lake Victoria drainage within the Holocene. Lake Edward is connected to Lake Victoria to the present day by the Katonga river that undergoes flow reversal in a swamp (Greenwood 1973). A connection to the Malagarasi may have existed during a lake-level high stand 8000 years BP, when Lake Victoria may have been overflowing to the south (Stager *et al.* 1986). An example of such a distribution pattern is two endemic, but unrelated *Oreochromis* species. *Oreochromis variabilis* of the subgenus *Nyasalapia* is very closely related to *Oreochromis* (*N.*) *malagarasi* from

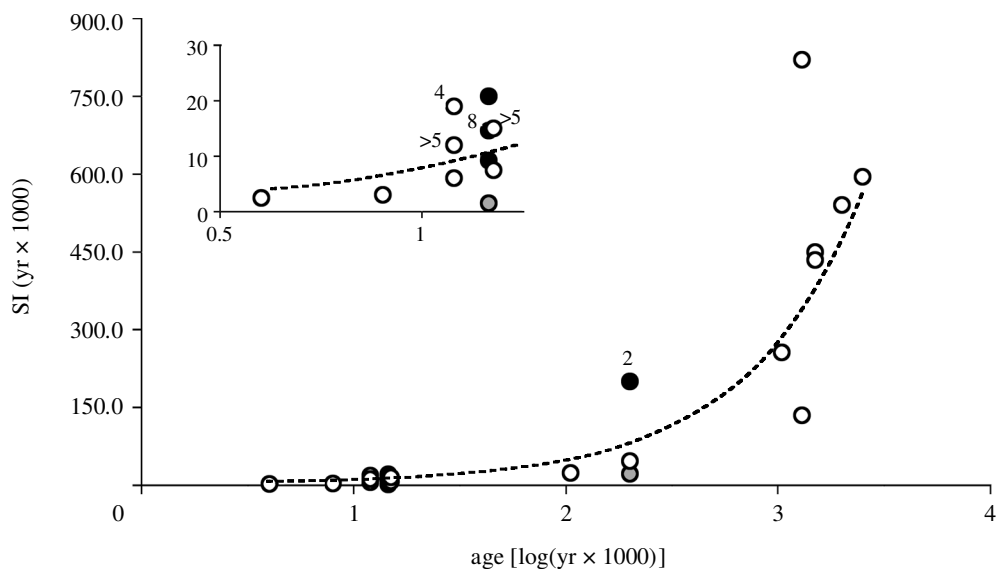


Figure 1. Net speciation intervals (logarithmic model) in fish radiations plotted against age of radiations (logarithmic scale). Data from tables 1 and 2. The line is the best fit to the data and is calculated excluding the Lake Victoria taxa. The inset is a magnification of the cluster of extremely recent radiations. Points that represent multiple observations have the number of independent observations attached. Filled points represent taxa from Lake Victoria. *Aplocheilichthys* and *Clarias/Xenoclaris* have been scored with  $SI_{log}$  of 14 600 yr for the one in four lineages that must have given rise to the one endemic species in each of these two genera. Grey circles are the two extreme alternative placements of the haplochromine species flock of Lake Victoria obtained under the alternative assumptions of monophyly and polyphyly (see table 1). Except for the haplochromine species flock, all Lake Victoria taxa have speciation intervals on or above the line of best fit for other fish radiations.

the Malagarasi River (Trewavas 1983), whereas *Oreochromis esculentus* belongs to the subgenus *Oreochromis* and is probably a close relative of *Oreochromis niloticus* that is native to Lake Edward (Trewavas 1983). After the introduction of the latter into Lake Victoria, the two forms appear to have introgressed (Mwanja & Kaufman 1995).

The mean net speciation interval in the haplochromine cichlid flock in Lake Victoria is shorter than that of all other teleost lineages in the same basin, including two other haplochromine and two tilapiine cichlid lineages. This demonstrates clearly that the unusually fast speciation does not distinguish cichlids from other fishes, but one particular cichlid lineage from other cichlids and non-cichlids. It had been shown before that cichlids of Lakes Victoria and Malawi have speciated faster than other African lake cichlids (McCune 1997; Turner 1999; Seehausen 2000, 2002). However, this was by comparison of lakes of different ages. Evolutionary rates, when calculated over disparate age, are not adequately comparable (Gingerich 1983; Gould 1984). The data from Lake Victoria presented here demonstrate enormous differences in rates between cichlid lineages calculated over the same lake age.

Nevertheless, if the unresolved phylogeny of the species flock resembles a fully balanced tree (as assumed by the logarithmic model), the net speciation interval may not deviate greatly from what is observed among fish radiations in young lakes elsewhere (McCune 1997; McCune & Lovejoy 1998; table 2). Moreover, it is still unknown whether the modern cichlid species flock of Lake Victoria is strictly monophyletic. There are strong indications that it includes lineages from Lake Edward (Booton *et al.* 1999; Nagl *et al.* 2000). If the Lake Victoria cichlid tree is well balanced and the flock turns out to be

derived from more than one colonizing lineage from Lake Edward, speciation intervals even in the cichlid flock (table 1), though doubtlessly exceptionally fast, may still fall within the tail of the distribution of speciation intervals observed in fishes across young lakes of the world (table 2). Lineages of haplochromine cichlids have also shown an unusual potential for multiple rapid speciation in other lakes (Owen *et al.* 1990). The result underlines the challenge to understand why these lineages appear to speciate faster than most other fishes. In this context it is important to note that the origin of species diversity does not have to coincide with the origin of the underlying genetic variation. I agree with other authors (Fryer 2001; Kaufman *et al.* 1997; Nagl *et al.* 2000) that the functional genetic variation observed in the Lake Victoria species flock is unlikely to have arisen within the Holocene; however, that is not to say that much of the sorting into species may not have happened much faster under strong selection (cf. Kaufman *et al.* 1997; Nagl *et al.* 2000).

I conclude that the fish species assemblage of Lake Victoria does not provide biological evidence against a Pleistocene desiccation of the lake. The results obtained from a combination of rates of diversification, biogeographic relationships of endemic species, and the composition of the non-endemic elements, which include species adapted to life in streams and lakes, imply recent major colonization events (Lake Edward and the Malagarasi river basin being the most likely sources) followed by rapid radiation in one group, rather than survival of a diverse assemblage inside the Lake Victoria basin.

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## REFERENCES

- Agnese, J. F. & Teugels, G. G. 2001 The *Bathyclarias*–*Clarias* species flock. A new model to understand rapid speciation in African great lakes. *C. R. Acad. Sci. ser. III—Life Sci.* **324**, 683–688.
- Bernatchez, L. & Wilson, C. C. 1998 Comparative phylogeography of nearctic and palearctic fishes. *Mol. Ecol.* **7**, 431–452.
- Bernatchez, L., Vuorinen, J. A., Bodaly, R. A. & Dodson, J. J. 1996 Genetic evidence for reproductive isolation and multiple origins of sympatric trophic ecotypes of whitefish (*Coregonus*). *Evolution* **50**, 624–635.
- Beuning, K. R. M., Kelts, K. & Ito, E. 1997 Palaeohydrology of Lake Victoria, East Africa, inferred from  $^{18}\text{O}/^{16}\text{O}$  ratios in sediment cellulose. *Geology* **25**, 1083–1086.
- Booton, G. C., Kaufman, L., Chandler, M., Oguto-Ohwayo, R., Duan, W. & Fuerst, P. A. 1999 Evolution of the ribosomal RNA internal transcribed spacer one (ITS-1) in cichlid fishes of the Lake Victoria region. *Mol. Phyl. Evol.* **11**, 273–282.
- Brett, C. E. 1998 Sequence stratigraphy, paleoecology, and evolution: biotic clues and responses to sea-level fluctuations. *Palaios* **13**, 241–262.
- Brett, C. E., Ivany, L. C. & Schopf, K. M. 1996 Coordinated stasis: an overview. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 1–20.
- De Vos, L. & Snoeks, J. 1994 The non-cichlid fishes of Lake Tanganyika. *Adv. Limnol.* **44**, 391–405.
- Froese, R. & Pauly, D. (eds) 2000 *Fishbase 2000*. Makati City, Philippines: International Center for Living Aquatic Resources Management. See <http://www.fishbase.org/home.htm>.
- Fryer, G. 2001 On the age and origin of the species flock of haplochromine cichlid fishes of Lake Victoria. *Proc. R. Soc. Lond. B* **268**, 1147–1152.
- Galis, F. & Drucker, E. G. 1996 Pharyngeal biting mechanics in centrarchids and cichlids: insights into a key evolutionary innovation. *J. Evol. Biol.* **9**, 641–670.
- Gingerich, P. D. 1983 Rates of evolution: effects of time and temporal scaling. *Science* **222**, 159–161.
- Gould, S. J. 1984 Smooth curve of evolutionary rate: a psychological and mathematical artifact. *Science* **226**, 994–995.
- Greenwood, P. H. 1973 A revision of the *Haplochromis* and related species (Pisces, Cichlidae) from Lake George, Uganda. *Bull. Br. Mus. Nat. Hist. (Zool.)* **25**, 139–242.
- Greenwood, P. H. 1994 The species flock of cichlid fishes in Lake Victoria—and those of other African Great Lakes. *Arch. Hydrobiol. Adv. Limnol.* **44**, 347–354.
- Hartley, S. E., McGowan, C., Greer, R. B. & Walker, A. F. 1992 The genetics of sympatric Arctic charr (*Salvelinus alpinus* (L.)) populations from Loch Rannoch, Scotland. *J. Fish Biol.* **41**, 1021–1031.
- Hindar, K., Ryman, N. & Staahl, G. 1986 Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. *Biol. J. Linn. Soc.* **27**, 269–285.
- Holtmeier, C. L. 2001 Heterochrony, maternal effects, and phenotypic variation among sympatric pupfishes. *Evolution* **55**, 330–338.
- Humphries, J. M. 1984 Genetics of speciation in pupfishes from Laguna Chichancanab, Mexico. In *Evolution of fish species flocks* (ed. A. A. Echelle & I. Kornfield), pp. 129–139. Orono, ME, USA: University of Maine Press.
- Ivany, L. C. 1996 Coordinated stasis or coordinated turnover? Exploring intrinsic vs extrinsic controls on pattern. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 239–256.
- Johnson, T. C., Scholz, C. A., Talbot, M. R., Kelts, K., Ricketts, R. D., Ngobi, G., Beuning, K., Ssemmanda, I. & McGill, J. W. 1996 Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* **273**, 1091–1093.
- Johnson, T. C., Kelts, K. & Odada, E. 2000 The Holocene history of Lake Victoria. *Ambio* **29**, 2–11.
- Kaufman, L. S., Chapman, L. J. & Chapman, C. A. 1997 Evolution in fast forward: haplochromine fishes of the Lake Victoria region. *Endeavour* **21**, 23–30.
- Lowe-McConnell, R. H. 1987 *Ecological studies in tropical fish communities*. Cambridge University Press.
- Lu, G., Basley, D. J. & Bernatchez, L. 2001 Contrasting patterns of mitochondrial DNA and microsatellite introgressive hybridization between lineages of lake whitefish (*Coregonus clupeaformis*); relevance for speciation. *Mol. Ecol.* **10**, 965–985.
- McCune, A. 1996 Biogeographic and stratigraphic evidence for rapid speciation in semionotid fishes. *Paleobiology* **22**, 34–48.
- McCune, A. 1997 How fast is speciation? Molecular, geological, and phylogenetic evidence from adaptive radiations of fishes. In *Molecular evolution and adaptive radiation* (ed. T. J. Givnish & K. J. Sytsma), pp. 585–610. Cambridge University Press.
- McCune, A. & Lovejoy, N. R. 1998 The relative rate of sympatric and allopatric speciation in fishes. In *Endless forms: species and speciation* (ed. D. Howard & S. Berlocher), pp. 172–185. Oxford University Press.
- Mwanja, W. & Kaufman, L. 1995 A note on recent advances in the genetic characterization of tilapia stocks in Lake Victoria region. *Afr. J. Trop. Hydrobiol. Fisher.* **6**, 51–53.
- Nagelkerke, L. A. J., Mina, M. V., Wudneh, T., Sibbing, F. A. & Osse, J. W. M. 1995 In Lake Tana, a unique fish fauna needs protection. *BioScience* **45**, 772–775.
- Nagl, S., Tichy, H., Mayer, W. E., Takezaki, N., Takahata, N. & Klein, J. 2000 The origin and age of haplochromine fishes in Lake Victoria, East Africa. *Proc. R. Soc. Lond. B* **240**, 519–553.
- Owen, R. B., Crossley, R., Johnson, T. C., Tweddle, D., Kornfield, I., Davison, S., Eccles, D. H. & Engstrom, D. E. 1990 Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proc. R. Soc. Lond. B* **240**, 519–553.
- Reimchen, T. E., Stinson, E. M. & Nelson, J. S. 1985 Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. *Can. J. Zool.* **63**, 2944–2951.
- Ryman, N., Allendorf, F. W. & Staahl, G. 1979 Reproductive isolation with little genetic divergence in sympatric populations of brown trout (*Salmo trutta*). *Genetics* **92**, 247–262.
- Schliewen, U. K., Tautz, D. & Paabo, S. 1994 Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* **368**, 629–633.
- Schluter, D. 1996 Ecological speciation in postglacial fishes. *Phil. Trans. R. Soc. Lond. B* **351**, 807–814.
- Scholz, C. A., Johnson, T. C., Cattaneo, P., Malinga, H. & Shana, S. 1998 Initial results of 1995 IDEAL seismic reflection survey of Lake Victoria, Uganda and Tanzania. In *Environmental change and response in East African lakes* (ed. J. T. Lehman), pp. 47–57. Dordrecht, The Netherlands: Kluwer.
- Skulason, S. & Smith, T. B. 1995 Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* **10**, 366–370.
- Skulason, S., Snorrason, S. S. & Jonsson, B. 1999 Sympatric morphs, populations and speciation in freshwater fish with emphasis on Arctic charr. In *The evolution of biological diver-*

- sity (ed. A. E. Magurran & R. M. May), pp. 70–92. Oxford University Press.
- Seegers, L. 1996 *The fishes of the Lake Rukwa drainage*. Tervuren, Belgium: Africa Museum.
- Seehausen, O. 1996 *Lake Victoria rock cichlids—taxonomy, ecology and distribution*. Zevenhuizen, The Netherlands: Verdujn cichlids.
- Seehausen, O. 2000 Explosive speciation rates and unusual species richness in haplochromine cichlid fishes: effects of sexual selection. *Adv. Ecol. Res.* **31**, 237–274.
- Seehausen, O. 2002 The cichlid fish radiations of East Africa: a model for understanding origin and loss of biodiversity. In *freshwater ecoregions of Africa, a conservation assessment* (ed. M. Thiele). (In the press.)
- Seehausen, O., van Alphen, J. J. M. & Witte, F. 1997 Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–1811.
- Slobodyanyuk, S. J., Kirilchik, S. V., Pavlova, M. E., Belikov, S. I. & Novitsky, A. L. 1995 The evolutionary relationships of two families of cottoid fishes of Lake Baikal (East Siberia) as suggested by analysis of mitochondrial DNA. *J. Mol. Evol.* **40**, 392–399.
- Smith, G. R. & Todd, T. N. 1984 Evolution of species flocks of fishes in north temperate lakes. In *Evolution of fish species flocks* (ed. A. A. Echelle & I. Kornfield), pp. 45–68. Orono, ME, USA: University of Maine Press.
- Sodsuk, P. K., MacAndrew, B. A. & Turner, G. F. 1995 Evolutionary relationships of the Lake Malawi *Oreochromis* species: evidence from allozymes. *J. Fish Biol.* **47**, 321–333.
- Stager, J. C., Reinthal, P. N. & Livingstone, D. A. 1986 A 25 000-year history for Lake Victoria, East Africa, and some comments on its significance for the evolution of cichlid fishes. *Freshwat. Biol.* **16**, 15–19.
- Strecker, U., Meyer, C. G., Sturmbauer, C. & Wilkens, H. 1996 Genetic divergence and speciation in an extremely young species flock in Mexico formed by the genus *Cyprinodon* (Cyprinodontidae, Teleostei). *Mol. Phyl. Evol.* **6**, 143–149.
- Svedaeng, H. 1990 Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.) in Stora Rosjoen, central Sweden. *J. Fish Biol.* **36**, 917–932.
- Taylor, E. B. & Bentzen, P. 1993 Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in northeastern North America. *Evolution* **47**, 813–832.
- Taylor, E. B. & McPhail, J. D. 1999 Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus*): insights from mitochondrial DNA. *Biol. J. Linn. Soc.* **66**, 271–291.
- Taylor, E. B., McPhail, J. D. & Schluter, D. 1997 History of ecological selection in sticklebacks: uniting experimental and phylogenetic approaches. In *Molecular evolution and adaptive radiation* (ed. T. J. Givnish & K. J. Sytsma), pp. 511–534. Cambridge University Press.
- Teugels, G. G. 1986 A systematic revision of the African species of the genus *Clarias* (Pisces; Clariidae). *Ann. Mus. R. Afr. Centr.* **247**, 1–199.
- Teugels, G. G. & Adriaens, D. 2002 Taxonomy and phylogeny of Clariidae: an overview. In *Catfishes* (ed. B. G. Kapoor, G. Arratia, M. Chardon & R. Diogo). New Delhi: Oxford & IBH Publishing Co. Ltd.
- Trewavas, E. 1983 *Tilapiines fishes of the genera Sarotherodon, Oreochromis and Danakilia*. London: British Museum (Natural History).
- Turner, G. F. 1999 Explosive speciation of African cichlid fishes. In *The evolution of biological diversity* (ed. A. E. Magurran & R. M. May), pp. 217–229. Oxford University Press.
- Williamson, P. G. 1981 Paleontological documentation of speciation in cenozoic molluscs from Turkana basin. *Nature* **293**, 437–443.
- Witte, F. & Van Densen, L. T. (eds) 1995 *Fish stocks and fisheries of Lake Victoria*. Dyfed, UK: Samara Publishing.

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