



## Research

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# Arrival order and release from competition does not explain why haplochromine cichlids radiated in Lake Victoria

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The frequent occurrence of adaptive radiations on oceanic islands and in lakes is often attributed to ecological opportunity resulting from release from competition where arrival order among lineages predicts which lineage radiates. This *priority effect* occurs when the lineage that arrives first expands its niche breadth and diversifies into a set of ecological specialists with associated monopolization of the resources. Later-arriving species do not experience ecological opportunity and do not radiate. While theoretical support and evidence from microbial experiments for priority effects are strong, empirical evidence in nature is difficult to obtain. Lake Victoria (LV) is home to an exceptional adaptive radiation of haplochromine cichlid fishes, where 20 trophic guilds and several hundred species emerged in just 15 000 years, the age of the modern lake that was preceded by a complete desiccation lasting several thousand years. However, while about 50 other lineages of teleost fish also have established populations in the lake, none of them has produced more than two species and most of them did not speciate at all. Here, we test if the ancestors of the haplochromine radiation indeed arrived prior to the most competent potential competitors, 'tilapias' and cyprinids, both of which have made rapid radiations in other African lakes. We assess LV sediment core intervals from just before the desiccation and just after refilling for the presence of fossil fish teeth. We show that all three lineages were present when modern LV began to fill with water. We conclude that the haplochromines' extraordinary radiation unfolded in the presence of potentially competing lineages and cannot be attributed to a simple priority effect.

## 1. Introduction

A major challenge in evolutionary biology is to explain the enormous variation in the rates at which new species arise and accumulate among lineages and among geographical locations. Chance, contingency and ecological determinism undoubtedly all play important roles, but which of them dominates when, and

how they interact, are big open questions. The process of adaptive radiation whereby many new species with different ecological functions emerge from an ancestral species in short time has attracted much attention [1–3]. Ever since Simpson's 1953 book [4], the concept of ecological opportunity has been central in explaining adaptive radiation [5]. A species experiences ecological opportunity when it finds itself in an environment with a diversity of accessible resources that no other species is competing for.

While intuitive in concept and quite well understood in theory, ecological opportunity is hard to quantify empirically, and many approaches are at least partly circular. Demonstration of resource competition in a given case requires detailed evidence of niche overlap and resource limitation, which is challenging to generate, especially for extended periods of time. Circumstantial support for the importance of competitive release from incumbent lineages can be inferred from the observation that most known adaptive radiations occur on oceanic islands and in isolated lakes [6]. Upon formation, these island-like environments are often assumed to have very simple biotic assemblages, such that early colonists do not experience interspecific competition and can seize ecological opportunities, monopolize them through adaptive diversification and thereby gain an evolutionary head start. Late-arriving species of a particular taxonomic group are likely to be excluded from resources to which early colonizing species and their descendants have already had time to adapt. Typically, only one lineage per major taxonomic group radiates on each island or lake, and this has been attributed to arrival order and priority effects [7,8]. While theoretical support is strong [8,9] and evidence from microbial experiments supports theoretical predictions [10], empirical evidence for an importance of priority effects in nature is scarce and difficult to obtain, as the circumstances in the early phases of well-known adaptive radiations are rarely known [7]. Theory and microbial evolution experiments suggest that evolutionary priority effects can be strong even when successive colonization events are separated just by tens to hundreds of generations [9,10]. Therefore, time-of-arrival data have to be resolved at a fine scale to test the hypothesis.

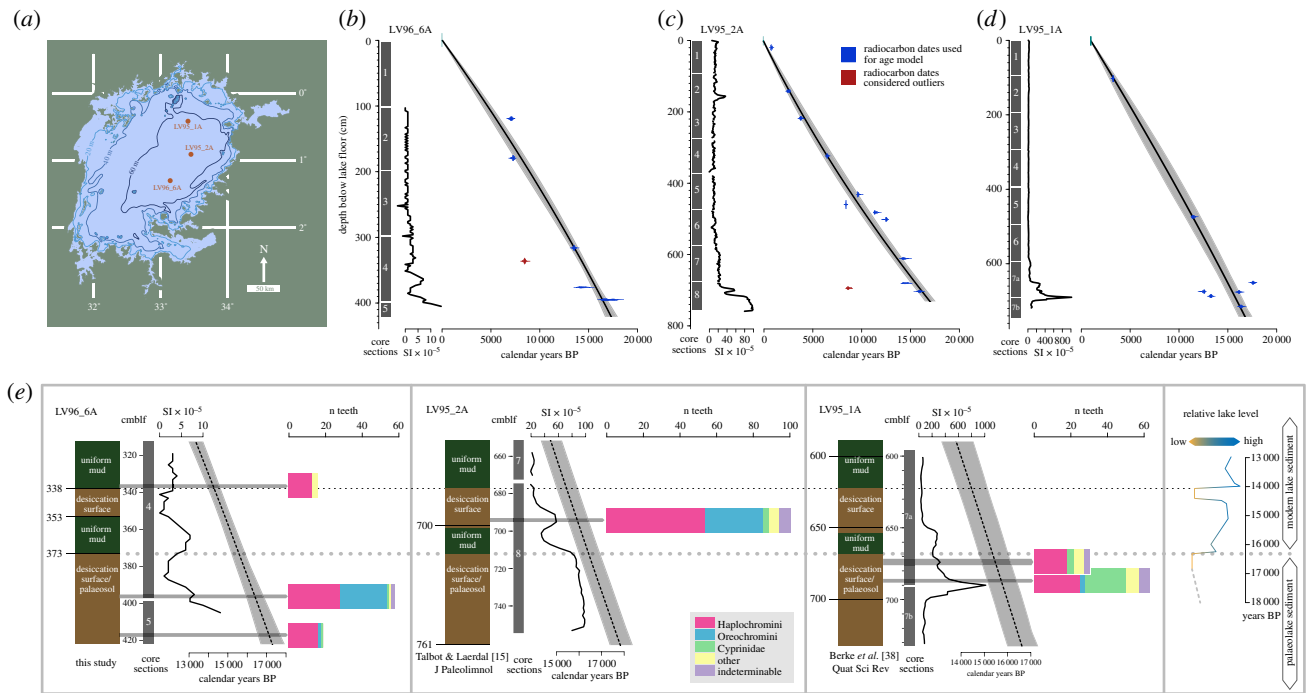
Islands and lakes that host a radiation were often colonized by several lineages in quick succession early in their history, but this makes it difficult to resolve the arrival order using phylogenetic methods. Consequently, this approach has only rarely been applied successfully [11] and to systems where successive colonization events are chronologically widely separated (e.g. [12]). Fossil data may also provide evidence of colonization history; however, few systems have a sufficiently rich fossil record and no case is known to us in which the priority effect was directly tested with fossils at a resolution better than what can be achieved phylogenetically.

The haplochromine cichlid fish of Lake Victoria (LV) represent the fastest known species radiation of any contemporary animals [13]. After several thousand years of desiccation, including a long phase of complete desiccation prior to 16 000 years before present (BP; i.e. before AD 1950; hereafter ka), LV refilled rapidly, starting approximately 15.2 [14,15] or 16.2 ka [16]. The several hundred species of endemic cichlid fish, belonging to 22 morphologically distinct genera and a similar number of trophic guilds appear to have evolved within the lake since its refilling, necessitating an astonishing diversification rate [14,17–19]. This has aptly been likened to Simpsonian quantum

evolution, the origin of major new adaptive types in an extremely short period of time [4,20]. The rapid diversification of cichlid clades has been the subject of extensive study (e.g. [13,21–23]), revealing that intrinsic properties such as sexually selected nuptial colouration [24], a highly adaptable and/or plastic trophic apparatus [25,26] and the potential to generate genetic variation through hybridization of even distantly related lineages [27–29] are all probably implicated in the evolutionary success of cichlids in general, and haplochromines in particular. The environmental and biotic conditions that allowed such remarkable diversification in little time are of major interest to ecologists and evolutionary biologists alike.

Spectacular adaptive radiations of cichlids took place in some but not in all the large lakes of Africa, and in some but by far not all the cichlid lineages. Environmental- and lineage-specific factors explain some of this variation [30,31], but they do not explain why typically only one of several lineages with similar traits radiated in each lake. The biotic conditions (i.e. the matrix of other species present at the time radiations are initiated), while of major interest, are largely unknown. Using comparative analyses of patterns in phylogenetic trees, Wagner and colleagues found some evidence for a negative effect of the presence of larger predators [30,32] and for negative effects of cichlid lineages on each other [31,32] indicative of an inhibitory effect of the presence of competitors. Specifically, Seehausen [32] observed that of three lineages of cichlids with identical mating system and similar opportunity for sexual selection, typically only one radiated in any one lake, even though multiple lineages have colonised and become established in many lakes [32]. Notably, these studies are based on the diversity and distribution of the extant fauna but cannot determine whether the ancestors of radiations were colonizing the new habitat prior to, or simultaneously with, potentially competing taxa that did not form radiations. Priority effects might explain these very uneven rates of diversification among lineages within each African Great Lake [1,2,5,10,33], but the relative timing of colonizations that are not separated by thousands of years is difficult to infer using phylogenetic methods with their sometimes substantial margin of error [34]. East African lakes nonetheless provide unique opportunities to investigate the role priority effects and release from competition played in adaptive radiations. The lakes accumulate sediment that incorporates fish remains (e.g. [35–37]), building a rich record of fossils - a rare situation among study systems in diversification research. Although typically disarticulated, fossil bones and especially teeth yield important information about ecological adaptations and the taxonomic composition of past communities.

To test the hypothesis that priority effects and (lack of) competition from other lineages were essential in allowing haplochromine cichlids to undergo their exceptional adaptive radiation in LV, and curtail diversification in other fish lineages, we gathered fish fossils from sediment layers deposited at the very beginning of modern LV, between 16 and 15 ka. In addition, we also collected older fossils from sediments deposited in palaeolake Victoria, which were later transformed to palaeosol, representing the final period of palaeolake Victoria shortly before complete desiccation. In total, we analysed 29 subsamples of three sediment cores, taken at different deep-water, offshore sites in LV [14] (figure 1*a–d*).



**Figure 1.** (a) Bathymetric map of LV with coring sites indicated. (b) Sections, depth below lake floor, magnetic susceptibility and age model of core LV96\_6A. One dated sample (red) was considered to be an outlier (see Material and methods). (c) Sections, depth below lake floor, magnetic susceptibility and age model of core LV95\_2A. One dated sample (red) was considered to be an outlier (see Material and methods). Note that the age model interpolation estimates an older age for the 680 cm depth below lake floor than given by radiocarbon-dated charcoal from that interval. The direct date is likely to be correct here and places the start of the final refilling at  $12\,400 (\pm 71)$   $^{14}\text{C}$  years. (d) Sections, depth below lake floor, magnetic susceptibility and age model of core LV95\_1A. The sediment–water interface was not recovered due to over-penetration and the top of the core was assumed to be 1 ka [38] (see Material and methods). The age model was built using three additional dates further down-core, not shown in the plot (table 2). (e) Cores zoomed in on intervals that contain the transition from the palaeolake to the modern lake. Stratigraphy was visually assessed for this study (LV96\_6A), or had been previously published (LV95\_2A [15]; LV95\_1A [38]). The depth below lake floor is indicated in centimetres and core sections shown as grey bars. The magnetic susceptibility is shown as a solid black line, the age model as a dotted line with error in grey (calibrated calendar years). Grey horizontal bars indicate the location and width of sampled intervals that yielded numerous fish teeth fossils. They point to bar diagrams illustrating the taxonomic composition of the respective fish teeth. The rightmost panel shows the interpretation from [16] with estimates of past lake levels through time. One complete desiccation event is assumed by most authors. A second lake-level low stand is interpreted as not having been a complete desiccation, but rather led to swamp-like conditions. Nevertheless, the corresponding sediment layer is termed *desiccation surface*. Dotted lines indicate the topmost layers of the complete desiccation period (thick, grey line) and the brief lake-level low-stand period (thin, black line), with the three cores being scaled for alignment. Misalignment between descriptions of core LV95\_2A ([15] and this study) by 6.5 cm results from a reassessment of core section photos. Resulting discrepancies in age models are probably due to several factors, including differences in erosion and sedimentation between sites, as well as bioturbation affecting the age–depth correlation.

## 2. Results

In total, we recovered 290 fossil fish teeth from all three cores analysed. The density of teeth across core intervals was uneven and appears to be dependent on lithofacies. The core record shows a thick desiccation surface consisting of a hard, crumbly palaeosol, as a result of a major desiccation event that ended approximately 16 ka (figure 1). This palaeosol layer is overlain by fine-grained, wet lake sediment, indicating a first lake high stand. This wet phase seems to have been brief, on the order of less than 1000 years, and deep-water conditions were soon interrupted by a low stand with swamp-like conditions, as indicated by a second desiccation surface, approximately 14–15 ka (figure 1e). This layer does not show indications of soil development, but rather consists of peat, suggesting the presence of an extensive cattail (*Typha* spp.) swamp. The presence of desiccation intervals and the intermittent high stand can also be seen in the magnetic susceptibility profiles, as desiccation forms and concentrates magnetic minerals (figure 1b–d) [39]. Following the second low stand, modern LV attained permanent open water conditions. We consider the fossil fauna of the first high-stand phase in our data as representing the earliest possible snapshot of the

newly assembling community of colonizing fish lineages in modern LV.

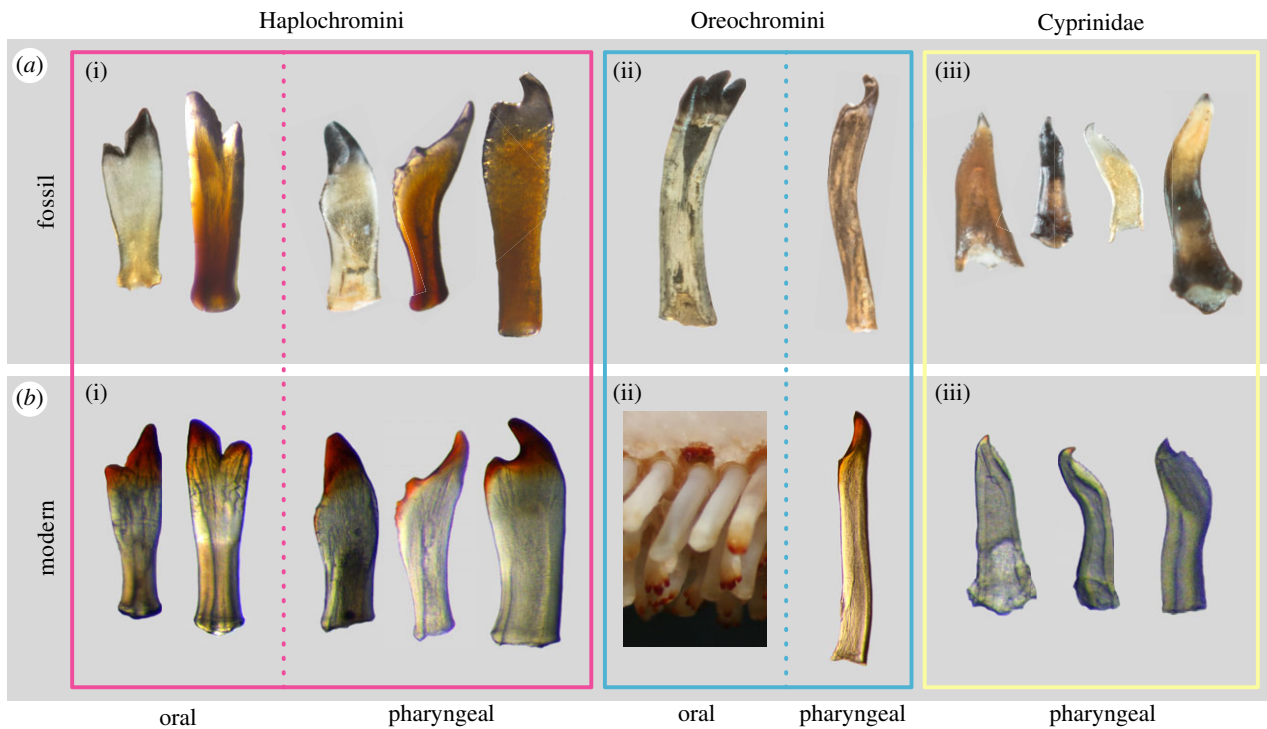
We observed that intervals close to desiccation surfaces often but not always contained higher densities of fossils than intervals of unaltered, uniform mud deposited during fully lacustrine conditions in the modern lake (figure 1e and table 1). The highest fossil density was found in the interval 20–22 cm in section 8 of core LV95\_2A, from the first high stand, with 47 teeth per  $\text{cm}^3$  sediment (figure 1e, panel 2). Intervals further up-core (i.e. younger) that were sampled in cores LV96\_6A and LV95\_1A were largely devoid of fossil fish teeth (figure 1e and table 1), with the exception of one interval in core LV96\_6A that was situated directly above the last lake-level low stand and contained several teeth. Four intervals from the palaeosol of cores LV96\_6A and LV95\_1A also yielded numerous fossils, which represent the palaeolake fauna.

We recovered teeth from all three major fish taxa, namely the cichlid tribes Haplochromini and Oreochromini, and the family Cyprinidae (figure 2), from the palaeolake and, crucially, also from the earliest refilling phase (the intermittently high lake level). The sediments deposited when the lake transitioned from its last lowstand with swamp-like conditions to the modern lake with persistent, widespread

**Table 1.** Numbers of fossil teeth extracted from core intervals. Given are the total number, numbers by fish groups and density considering the sampled sediment volume. Total depth is the depth in the core from the top of the core.

core	section	top (cm)	bottom (cm)	total depth top (cm)	total depth bottom (cm)	sediment volume (ccm)	n teeth	density (n/ccm)	Haplochromini	Oreochromini	Cyprinidae	other	indet
LV95_1A	6	84	87	579.5	582.5	8	0	0	0	0	0	0	0
	7a	6	7	602	603	1	0	0	0	0	0	0	0
	7a	14	16	610	612	4	0	0	0	0	0	0	0
	7a	57	60	653	656	3	0	0	0	0	0	0	0
	7a	71.5	72.5	667.5	668.5	1	0	0	0	0	0	0	0
	7a	76	80	672	676	8	30	3.8	18	0	4	5	3
	7a	76.5	78.5	672.5	674.5	3	0	0	0	0	0	0	0
	7a	89	90.5	685	686.5	2	0	0	0	0	0	0	0
	7a	89	91.5	685	687.5	6	63	10.5	25	3	22	7	6
	8	20	22	693	695	2	101	47	54	32	3	5	7
LV95_2A	8	30	31	703	704	2	1	0.5	1	0	0	0	0
	8	54	56	727	729	4	0	0	0	0	0	0	0
	2	18	20	119	121	14	0	0	0	0	0	0	0
LV96_6A	2	38	40	139	141	14	0	0	0	0	0	0	0
	2	58	60	159	161	14	0	0	0	0	0	0	0
	2	78	80	179	181	14	0	0	0	0	0	0	0
	2	98	100	199	201	14	0	0	0	0	0	0	0
	3	18	20	216	218	14	0	0	0	0	0	0	0
	3	38	40	236	238	14	0	0	0	0	0	0	0
	3	58	60	256	258	14	0	0	0	0	0	0	0
	3	78	80	276	278	14	0	0	0	0	0	0	0
	3	98	100	296	298	14	0	0	0	0	0	0	0
	4	18	20	316	318	14	1	0.1	1	0	0	0	0
LV96_6A	4	38	40	336	338	14	16	1.2	13	0	0	3	0
	4	58	60	356	358	14	0	0	0	0	0	0	0
	4	78	80	376	378	14	1	0.1	1	0	0	0	0
	4	97	99	395	397	14	58	4.6	28	26	1	1	2
	5	18	20	416	418	14	19	1.5	16	2	1	0	0





**Figure 2.** Examples of fossil and modern fish teeth from Lake Victoria. (a) Fossil teeth from LV sediment. (b) Teeth of extant, modern-day fish. The box on the left (pink outline) contains oral and pharyngeal teeth of haplochromines. The middle box (blue outline) shows oral and pharyngeal teeth of oreochromines; the modern pharyngeal tooth is *O. hunteri*, a non-LV species (courtesy of J. Dieleman); the modern oral teeth are attached to a piece of jaw bone. The box on the right (yellow outline) contains cyprinid pharyngeal teeth; modern specimens are from the pelagic zooplankton feeder *Rastrineobola argentea*. Images not to scale.

open-water conditions also yielded a small number of fossils (figure 1e). The composition varied widely between intervals, with more cyprinid teeth, in both absolute and relative terms, in intervals from the palaeolake. Haplochromini teeth are relatively numerous in all intervals. Oreochromini teeth are present in the palaeolake and in the earliest refilling phase but are not found among the 16 teeth from final return to open water conditions. A few teeth from the earliest refilling phase and the final return to open water conditions belong to other taxonomic groups (figure 1e, 'other'), such as *Synodontis* catfish.

Among the intervals from palaeolake sediment, taxon composition differed more strongly between cores than between intervals within cores, with LV96\_6A containing proportionately very few cyprinid teeth (3%), whereas LV95\_1A contained many (28%), a pattern that was reversed for Oreochromini teeth (36% and 3%, respectively).

### 3. Discussion

The fish fauna of modern LV, prior to the invasion of Nile perch, was dominated by haplochromine and oreochromine cichlid fish and carp-like fish (cyprinids) in terms of biomass [40]. Whereas haplochromines have radiated into hundreds of endemic species [41], there is no evidence for *in situ* speciation in *Oreochromis* and very little, if any, in cyprinids, or indeed in catfish or any other fish taxa in the lake [19]. Our analysis of 290 fossil fish teeth from three offshore cores clearly shows that all three dominant taxa were present in the nascent modern LV when it first filled with water. This implies that the large radiation of haplochromine cichlids cannot be attributed to the fortune of an early arrival into an environment free of presumed competitors.

Ancestral-type haplochromines, as can be found in streams and swamps in the LV basin even today, are diet generalists that

feed predominantly on bottom-dwelling invertebrates [20]. Representatives of the other major taxa are ecologically more strongly specialized. Cichlids of the genus *Oreochromis* are physiologically and morphologically highly specialized phytoplankton and detritus feeders, and their presence could have restricted access to such niches for haplochromines. Yet more than 20 species of phytoplankton- and detritus-eating haplochromines, and at least 30 species of benthic algivores, have evolved [42,43]. The presence of cyprinids, probably including the silver cyprinid (*Rastrineobola argentea*) (figure 2), could have constricted ecological opportunity for haplochromines through interspecific competition for zooplankton in the pelagic zone, yet at least 15 species of pelagic zooplankton feeding haplochromines have evolved. Finally, the presence of catfish, including the molluscivorous *Synodontis*, did not prevent the evolution of a wide range of mollusc-eating haplochromines.

Interestingly, these other taxa did undergo rapid radiations in other African lakes in the absence of haplochromines: cyprinids radiated into some 20 species within 15 000 years in Lake Tana, Ethiopia [44], and also radiated in Lake Lanao, Philippines [45]; *Oreochromis* radiated into three species in a few thousand years in Lake Natron, Tanzania [46]; and *Synodontis* catfish radiated into 13 species in Lake Tanganyika, albeit over a much longer timescale [47,48]. Despite their potential to commence evolutionary radiations, and despite colonization simultaneously with haplochromines, none of these other groups diversified in modern LV.

Future research should address the possibility that haplochromines differ from the other taxa in evolvability and/or the propensity to speciate. It is possible that diversification in the other taxa was curtailed by competition with haplochromines, and this could be interpreted as an evolutionary priority effect, but one due to heterogeneity in rates of evolution rather than the fortunes of arrival order. Perhaps a

**Table 2.** Dating of core intervals. Shown are estimated core surface ages and radiocarbon dates of intervals that were either available from the literature or were generated for this study. Radiocarbon dates were calibrated (see Material and methods) and the 95% confidence interval range in calendar years is given. Some previous studies corrected a subset of dates for a reservoir effect. Such correction was then also used here, and the number of years subtracted from the radiocarbon dates before calibration is indicated. Total depths of some intervals in core LV95\_2A calculated in this study did not align with those stated in some earlier publications. Here, we calculated the total depths by summing up the respective core sections lengths measured on the core photographs and added the depths in the respective section. Other publications used the initially assigned names for the same cores we referred to by their revised names. The original names are given for comparison.  $^{14}\text{C}$  dating was performed in two laboratories, at the University of Bern and the ETH Zürich.

core	section	total depth in core (cm)	$^{14}\text{C}$ years BP	error	correction for reservoir effect	included in age model	reference	depth-in-core diff. to ref. (cm)	max. calibrated calendar yrs BP	min. calibrated calendar yrs BP	initial core name	material	laboratory	laboratory reference number
LV96_6A	1	0	–45	1	0	yes	this study		–44	–46	V96-6P	charcoal	University of Bern	81442.1.1
	2	120	6160	100	0	yes	this study		7265	6797		charcoal	University of Bern	81442.1.1
	2	180	6320	90	0	yes	this study		7424	7013		charcoal	University of Bern	81443.1.1
	4	317	11 669	106	0	yes	this study		13 729	13 305		charcoal	ETH Zürich	83157.1.1
	4	337	7616	105	0	no	this study		8595	8200		fish fossils	ETH Zürich	83160.1.1
	4	377	12 290	180	0	yes	this study		15 024	13 786		charcoal	University of Bern	81439.1.1
	4	396	13 790	140	0	yes	this study		17 101	16 259		wood	University of Bern	81440.1.1
	4	396	14 350	240	0	yes	this study		18 047	16 807		charcoal	University of Bern	81441.1.1
LV95_1A	1	0	–1000	1	0	yes	Berke <i>et al.</i> [38]		1001	999	V95-1P			
	2	101.5	3060	35	0	yes	Berke <i>et al.</i> [38]		3359	3179				
	5	473	10 000	40	0	yes	Berke <i>et al.</i> [38]		11 700	11 275				
	7a	650	14 450	65	0	yes	Berke <i>et al.</i> [38]		17 858	17 419				
	7b	714	13 600	55	0	yes	Berke <i>et al.</i> [38]		16 621	16 191				
	7a	674	10 612	96	0	yes	this study		12 730	12 238				
	7a	675	13 440	71	0	yes	DeMaster [58]		16 410	15 929				
	7a	686	11 449	100	0	yes	this study		13 461	13 104				
	12	772	17 300	75	0	yes	Berke <i>et al.</i> [38]		21 107	20 628				
	13	831	16 800	140	0	yes	DeMaster [58]		20 614	19 930				
LV95_2A	13	883	14 600	60	0	yes	Berke <i>et al.</i> [38]		17 965	17 597				
	1	0	–45	1	0	yes			–44	–46	V95-2P	charcoal	ETH Zürich, CH	83158.1.1
	1	19	1450	61	–600	yes	Beuning <i>et al.</i> [55]		909	681				
	2	141	3050	51	–600	yes	Beuning <i>et al.</i> [55]		2707	2359				

(Continued.)

Table 2. (Continued.)

core	section	total depth in core (cm)	<sup>14</sup> C years BP	error	correction for reservoir effect	included in age model	reference	depth-in-core diff. to ref. (cm)	max. calibrated calendar yrs BP	min. calibrated calendar yrs BP	initial core name	material	laboratory	laboratory reference number
	3	217	4110	61	-600	yes	Beuning <i>et al.</i> [55]		3962	3637				
	4	323	6290	61	-600	yes	Beuning <i>et al.</i> [55]	-7	6637	6322				
	5	431	9260	60	-600	yes	Beuning <i>et al.</i> [55]	-7	9883	9528				
	5	459	8180	51	-600	yes	Beuning <i>et al.</i> [55]	-7	8515	8222				
	6	480	10 540	61	-600	yes	Beuning <i>et al.</i> [55]	-7	11 688	11 230				
	6	501	11 140	61	-600	yes	Beuning <i>et al.</i> [55]	-7	12 687	12 238				
	7	611	12 910	71	-600	yes	Beuning <i>et al.</i> [55]	-7	14 703	14 044				
	8	680	12 400	71	0	yes	Beuning <i>et al.</i> [55]	-7	14 895	14 138				
	8	694	7822	82	0	no	this study		8975	8427		wood, charcoal	ETH Zurich	83 156.1.1
	8	702	13 240	82	0	yes	Beuning <i>et al.</i> [55]	-7	16 174	15 669				

combination of high dispersal capability (as evidenced by the early arrival in young LV), ecological versatility and intrinsic mechanisms to generate reproductive isolation and form genetically isolated populations in proximity is the basis for the haplochromines' evolutionary success (see, e.g. [49]).

We observed very low densities of fish remains in the younger core intervals representing the later stages of the modern lake. This could be a consequence of the position of coring sites. All three cores were taken in deep offshore locations that provide less disturbed sedimentation conditions and better stratigraphic resolution than shallow-water settings. However, most of the fish biomass in LV today, as in most great lakes of the world [50], is concentrated in the littoral zone and the input of fossils is probably higher in nearshore locations. The high fish fossil density at the base of the lake sediment sequence could be a consequence of the position of the littoral zone being located close to the coring sites only shortly before desiccations and even more briefly after the start of rapid refilling. Slowed sedimentation during the transgressive phase could also lead to higher concentration of fish remains, even at the same fossil influx rate, forming a transgressive lag deposit rich in fish fossils. Additionally, at shallower depth, wind-induced water movement keeps fine particles in suspension, leading to a higher concentration of larger grain sizes in the sediment. At deep sites, also fine particles settle and thereby further dilute fish teeth fossils [51]. While some taphonomic biases can affect fossil density and species composition [52], this is very unlikely to have had an effect on the findings presented here. The stark delimitation of palaeolake and modern lake sediments by a crumbled palaeosol associated with the extended period of complete desiccation facilitates the assignment of core intervals to the palaeolake versus the modern lake.

## 4. Conclusion

This study highlights the value of fossil assemblages from environments that hosted early stages of extant species radiations for testing classical hypotheses about the role of biotic interactions during adaptive radiation and evolutionary community assembly. Lake sediments provide an especially good record as it is possible to collect sufficient numbers of fossils and place them into a chronological order using the often highly resolved stratigraphic layering of the sediment [53]. Leveraging this approach allowed us to investigate the circumstances during the initial phase of one of the largest recent adaptive radiations on Earth and to directly test a long-standing hypothesis for its evolutionary success. Release from competitors cannot explain why a benthic insectivorous cichlid ancestor radiated into niches as different and difficult as pelagic zooplankton feeding, herbivory and snail eating. Other taxa that were already specialized for each of these niches were present from the very beginnings of the lake. In the haplochromine radiation, these adaptations, and probably others too, evolved in the presence of already well-adapted specialists from other lineages.

## 5. Material and methods

We subsampled 29 intervals from three sediment cores from LV, which were taken as part of the International Decade of East African Lakes (IDEAL) project in 1995 and 1996 (figure 1 and table 1). Cores LV95\_1A and LV95\_2A have been used in several

previous studies and are well described [14–16,38,54–57]. Core LV96\_6A was opened and described for this study. Samples were wet-sieved at a 100  $\mu\text{m}$  mesh size using demineralized water, and remaining fractions were examined using a Zeiss Stemi 508 stereomicroscope. Fish teeth were photographed and identified to family or tribus level using reference collections, or photographs thereof, at the EAWAG, the University of Alberta, and the Canadian Museum of Nature in Ottawa. Teeth of haplochromines are uni-, bi- or tricuspid, comparatively short and can derive from either oral jaws or pharyngeal jaws, with each jaw apparatus bearing distinctive tooth shapes (figure 2). Oreochromine teeth are less varied in shape and typically more elongate than haplochromine teeth. Both oral and pharyngeal jaws bear many more teeth than in any LV haplochromine. Cyprinids do not have oral teeth, but a small number of rather robust pharyngeal teeth, often with a distinctive curvature and two parallel rows of minute protuberances towards the cusp.

For the construction of age models, we used previously published dates from cores LV95\_1A [38,58] and LV95\_2A [55], with the addition of two dates for LV95\_1A and one for LV95\_2A generated in this study. The age model for core LV96\_6A was based on seven dates generated in this study. The sediment surface was assumed to be contemporary at the time of sampling (i.e.  $-45$  calendar years BP). Core LV95\_1A does not include the sediment surface because the corer over-penetrated. The top of the core is assumed to be 1 ka [38]. Materials used for dating in this study were fish fossil fragments in one case, a wood fragment in another case and charcoal pieces in all other cases (table 2 for details). Some previously published dates were generated from organic carbon extracted from bulk sediment from core LV95\_2A and have been assumed to show a reservoir effect, leading to older radiocarbon dates than the actual ages of samples. In some previous studies, the respective radiocarbon dates were corrected by subtracting 330 [16], 500 [55] or 600 years [56]. Here, we subtracted 600 years from the respective dates from core LV95\_2A (table 2).

Our additional radiocarbon dates generated in this study for cores LV95\_1A and LV95\_2A in a few cases differed widely from the age model constructed from available dates. This might have resulted from contamination with younger carbon during sampling or through fungal growth on these much-handled cores [18]. Contamination was less likely to have been introduced this way for core LV96\_6A, as it was opened for this study more than 20 years after the other cores. The single outlier in this core was measured from fossil fragments that had been stored in

ethanol. Despite drying samples at 60°C for several hours, some ethanol might not have evaporated completely and might have introduced modern carbon into that sample. Outliers were excluded from the calculation of age models.

We used  $^{14}\text{C}$  dates, their associated errors, in some cases a correction for a reservoir effect and age estimates of the cores' top layer to construct age-depth models with the R function 'clam' v. 2.2 [59], second-order polynomial regression and the IntCal13 calibration curve [60].

Magnetic susceptibility data for cores LV95\_1A and LV95\_2A had previously been published [61] and are available from NOAA (see Data accessibility). Data for core LV96\_6A (sections 2–5) were generated for this study (electronic supplementary material, table S1).

**Ethics.** All samples were collected with the permission of the respective authorities in countries of sample origin. Sampling of Lake Victoria fish specimens used to prepare a reference collection of fish teeth was conducted with permission of the Tanzania Commission for Science and Technology (COSTECH) and support by Tanzania Fisheries Research Institute (TAFIRI). Sediment cores had been taken as part of the IDEAL research programme in 1995 and 1996 with permissions of the Republic of Uganda and the United Republic of Tanzania.

**Data accessibility.** All relevant data generated for this manuscript are contained within the tables of this manuscript or in electronic supplementary material. Magnetic susceptibility data for cores LV95\_1A and LV95\_2A are available from NOAA (<https://www.ngdc.noaa.gov/mgg/curator/data/ibis/vic95/data/>).

**Authors' contributions.** M.M. and O.S. designed the study. M.M. and E.J. collected fossils. J.W., K.M.S. and A.M.M. contributed reference images. M.M. and O.S. interpreted fossil data. J.M.R., J.C.S. and T.C.J. interpreted stratigraphy. N.D. contributed radiocarbon dates. M.M. and O.S. wrote the paper, with help of all the co-authors.

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