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NEWS AND COMMENTARY

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Cichlid species flocks of the past and present

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A recent phylogeographical examination of east African river cichlid fish species has pinpointed the area of speciation to a now extinct lake in Botswana.

The east African Great Lakes contain the most species-rich adaptive radiations known (recently reviewed in Salzburger and Meyer, 2004). Particularly noteworthy is a distinct group of cichlid fishes, the haplochromines, of which single ancestral colonizers formed species flocks of hundreds of species. This happened in the record-breaking time of less than 100 000 in Lake Victoria (Meyer *et al*, 1990; Verheyen *et al*, 2003); the 500–1000 species that are endemic to Lake Malawi took a few hundred thousand years longer. Lake Tanganyika hosts the genetically oldest lineages of cichlids (eg, Nishida, 1991); the haplochromines originated there and later dispersed through the rivers of eastern Africa to colonize the younger lake basins of, among others, Lakes Malawi and Victoria (Meyer *et al*, 1994; Salzburger *et al*, 2002).

The turbid rivers of Africa typically contain relatively few, and morphologically similar, species of cichlids compared to the large lakes. This is possibly because of a combination of greater ecological opportunities and greater water clarity in lakes, which might permit speciation through sexual selection due to color variation among males. This potential mechanism of species formation is presumably much less prevalent in turbid riverine habitats, whereas other geographic mechanisms of speciation would surely be expected to work in rivers too. However, generally speaking, the cichlid species diversity in rivers is much smaller than that found in lakes.

A more complete understanding of the haplochromine phylogeny, phylogeography and colonization history of the rivers and lakes of subequatorial Africa has only recently emerged (Verheyen *et al*, 2003; Salzburger *et al*, 2005). Salzburger *et al* (2005) phylogenetically defined the exceedingly species-rich (>1800 species are known) 'modern haplochromines', which can be distinguished from the more basal and less diverse haplochromine lineages by derived maternal mouthbrooding behavior and special markings on the anal fin of males, termed 'egg-spots'. These markings play an important role in species recognition, courtship and spawning behavior and might be one reason for the extraordinary evolutionary success of the modern haplochromines cichlids (Salzburger *et al*, 2005).

Now, Joyce *et al* (2005) suggest that a new, but extinct, cichlid species flock existed until about 2000 years ago in the paleo-Lake Makgadikgadi. This recent DNA-based phylogeographic study focused on the basal haplochrome cichlids and suggests that some of the southern African riverine cichlids are surprisingly diverse, as determined by morphometric comparisons. These basal haplochromines are maternal mouthbrooders but lacking the egg spots, are postulated to be remnants of a heretofore unrecognized, and now extinct, species flock from a lake located in Botswana, which dried up in the Holocene. This last point was inferred from a comparison of the geographic distribution of the studied cichlids with data from geology and paleo-limnology. Joyce *et al* (2005) combined analyses of genetic, morphological and biogeographical data that show that species richness is highest in the area for which geological data reveal the historical existence of the paleo-Lake Makgadikgadi. The center of this extinct lake is now a saltpan in the Middle Kalahari Desert of northern Botswana, not a habitat that one would describe as very hospitable, particularly to a fish. Joyce's group's results (2005) agree with the hypothesis that some of the largely southern African riverine cichlids that are now found in the Congo, Zambesi, Okavango and Limpopo are remnant products of an adaptive radiation in this paleo-lake. This ancient cichlid radiation of Lake Makgadikgadi might have included ecologically diverse lineages of cichlids and their morphological diversity, Joyce *et al* (2005) suggest, might have even approached that of the extant large east African Lakes, Victoria and Malawi. That lake-adapted cichlids can—although they probably rarely do—also thrive in rivers had been suggested before (Salzburger *et al*, 2002, 2005; Verheyen *et al*, 2003). More modern haplochromine lineages, some of which also live in the rivers of eastern Africa, derive their origin from the endemic Tropheini of Lake Tanganyika (Salzburger *et al*, 2005), and some of those were the seeds for the lineages that now form the exceedingly diverse species flocks of Lakes Malawi and Victoria (Verheyen *et al*, 2003; Salzburger *et al*, 2005).

The proposal for an extinct species radiation of paleo-Lake Makgadikgadi cichlids is highly interesting and points, again, to the propensity of cichlids for speciation. Only through the geographic analysis of extant riverine species were Joyce *et al* (2005) able to place the presumed flock to Botswana. The highest diversity (25 species) of riverine cichlids was located in this region, but, sadly, without a fossil record, we will never know how diverse the Makgadikgadi species flock ever was. It is particularly noteworthy that Joyce *et al* (2005) suggest that this flock of the past did not perish with its lake, but has some recent survivors in several African rivers. Yet, it remains to be seen if additional molecular clock and genetic diversity analyses confirm the presumed timing of this radiation with the existence of this paleo-lake or whether, as recent phylogenetic data suggest (Salzburger *et al*, 2005), the extant basal haplochromine lineages are older than Lake Makgadikgadi and therefore had much more time to diversify than the intermittent existence of this paleo-lake would have permitted.

More generally, Joyce's group's study (2005) further demonstrates the effects of the earth's constantly changing climate on the distribution and diversity of earth's biota. Climate changes also especially affected the lake-level stands of many of Africa's shallow lakes such as Lake Victoria (Johnson *et al*, 1996), with a maximum depth of less than 100 m and nearly, but probably not completely, wiped out all its diversity about 14 000 years ago (Verheyen *et al*, 2003). After this period, it recovered in less than 14 000 generations to its current diversity of 300–500 species. Long periods of drought also had a pronounced effect, through lake level changes, on speciation and the geographic distribution of genetic variation in the almost 1 500 m deep Rift Valley lakes such as Lake Tanganyika (Sturmbauer *et al*, 2001). The recent discoveries of Joyce *et al* (2005) demonstrate the power of molecular phylogeographic analyses and specifically show how geographically and temporally small-scaled evolutionary events combined with ecologically favorable conditions—in this case a paleo-lake—might sometimes have a major and enduring effect on large-scale patterns of biodiversity.

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