

THE BIODIVERSITY, BIOGEOGRAPHY AND EVOLUTIONARY HISTORY OF THE NORTHERN BASINS OF THE GREAT AFRICAN LAKES: THE ENIGMATIC FISH FAUNAS OF LAKES KIVU, EDWARD AND ALBERT REVISITED

SUMMARY

Context

The ichthyofauna of the region of the northern East African rift-valley lakes Kivu, Edward and Albert (KEA) is poorly known. At the same time, it is one of the most enigmatic regions because of its complex ichthyo-geography as a result of its turbulent tectonic history and fluctuating climatic cycles. The three lakes each harbour an endemic assemblage of haplochromine cichlids, a major part of which needs to be (re)described. Even less attention has been paid to the non cichlids of the region.

Objectives

With as premises two bio-geographic scenarios from the literature - the (partial) out-of-Kivu origin for haplochromine cichlids and the possible existence of refuges in the region during the mega-drought, some 15.000 yrs BP ago – we wanted to evaluate to which extent the ichthyo-diversity of the region has been shaped by past geological and climatological events. Therefore, we provided a comprehensive baseline study of the ichthyofauna of the region. This was done with a multidisciplinary approach, including fieldwork, a review of literature and collections, morphometric studies of some key groups, the establishment of a large COI barcoding database of the ichthyofauna, and complementary whole-genome sequencing study of some key groups. On the basis of these data, inferences were made of evolutionary and bio-geographic scenarios for the fishes of the region.

Conclusions

In terms of fish diversity studies, we published an article on the ichthyofauna of the region of the Nyungwe Forest in Rwanda and have prepared an annotated checklist of the fish fauna of the Lake Albert system. An annotated checklist to the fishes of the Lake Edward system had already been published. Producing annotated checklists may look as a trivial exercise, but it is not. It requires a detailed scanning of literature, databases and collections. The breakdown of numbers for the Lake Albert system mentioned in the report give an idea about the complexity of this work.

With a combined morphometric/genetic approach, we continued to discover a large unrecognized diversity within *Enteromius*, with four species in each of the three complexes studied (*E. apleurogramma*, *E. kerstenii*, *E. pellegrini*) in the region.

The total number of endemic haplochromine cichlids of the Edward system is now at 56, 14 of which have been (re)described. For some ten species, the descriptions are being prepared. Furthermore, we found a total of 12 haplochromine species in the Lake Albert system, seven of which are undescribed.

We published a barcoding paper on the Lake Edward system, the strength of which was the nearly complete coverage of its ichthyofauna. We then we extended the barcoding component and

produced 15 COI ML trees (family, subfamily or genus level) for the fish fauna of the KEA region (excluding haplochromines and *Enteromius*), on a Pan-African level, including all other African representatives found in public databases (GenBank and Bold). This barcoding effort pointed at additional new species and new records for the region in several groups. It also brought up taxonomic issues in almost every group examined, but foremost, it underscored the problematic quality of the identifications on the public databases (Genbank and Bold). This was an eye-opener and points to a potential problem for the scientific community studying African fishes. These data are frequently and increasingly used and accepted at face value in comparative analyses, and not only in barcoding studies.

The genus *Enteromius* was targeted via a multidisciplinary approach. We published on the undiscovered species richness of the sawfin species in the region and their complex evolutionary history. This confirmed our initial results that what are regarded as species actually are species complexes each including several well-diverged lineages. These lineages, which we consider species, mostly have an allopatric distribution, are genetically very divergent (long-time separation) but display morphologically a near-stasis with no eco-morphological adaptive features. This is quite a unique situation in freshwater fishes. One of the interesting but puzzling findings is the presence, in all three complexes studied, of a lowland and highland species within the Edward drainage system. We are currently applying biogeographic and genomic tools to find out more about the evolutionary scenario behind this. For the large-scale phylogenetic and biogeographic framework, a pan-African database of more than 1000 COI barcodes has been assembled.

Lakes Albert, Edward, Kivu, and Victoria are inhabited by some 700 closely related species of haplochromine cichlids that radiated explosively in a very short time. Each of these species inhabits a single lake, and many species look very similar. Because of the large species coverage we obtained of the haplochromines of the KEA area, we could infer many instances of strong eco-morphological similarity between species from the different lakes, including the poorly known Lake Albert. Our whole-genome analyses showed strong signals of convergent evolution between flocks and rapid divergence within flocks, in addition to a weaker signal of convergence within flocks. We found the scenario of a hybrid Congo-Nile origin of the Lake Victoria Super Flock to be much more complex than previously thought, in accordance with a recent publication. We added important new elements and refined the scenario.

In a first step of the whole genome approach for *Enteromius*, we analysed the mitochondrial genome. We detected signatures of at least two independent events involving the duplication of the control region, tRNA and ribosomal gene(s). Given the limited number of specimens, these results suggest a more wide-spread occurrence of such phenomena. We are currently analysing the whole genomes of some 108 specimens to unravel the evolutionary history of the taxa in the KEA region and neighbouring regions. The mitochondrial lineages and their large diverges are confirmed by the genomic analyses.

The genomic approach on *Clarias gariepinus* confirmed the existence of a clustering pattern that aligns with major biogeographic regions throughout Africa. There is a clear Kivu/Edward clade while the Lake Albert specimens are part of a Nilotic clade. Specimens from the Lake Victoria region form a separate clade with those from the Tanganyika basin. These new data suggest that *C. gariepinus* originated in eastern Africa, but not really within the KEA region.

The results of a whole-genome approach for *Oreochromis niloticus* were in strong contrast with those of *C. gariepinus*. No correlation was found between phylogeny and geographic region. Consequently, no evolutionary scenario could not be inferred.

We collaborated in a more applied study on the commercially important fishes in the region. Overfishing in the region is growing and omni-present. Specifically for the Lake Edward system, important information gaps were found that hamper the sustainable management of its resources. Furthermore, we confirmed the poor status of 22 of the 24 stocks studied from Lakes Edward, George, Albert, Kyoga and Victoria. These results are in line with the dwindling catches reported in many parts of Africa, as part of what we call 'the quiet crisis'.

Introductions and translocations are becoming more numerous and hence an increasing threat to the native fauna. This was highlighted in our Nyungwe study, but is symptomatic for the whole KEA region. Most of these appear to be the result of ill-considered or hit-or-miss attempts rather than of careful considerations.

Biogeographic and evolutionary scenarios for the KEA region appear to be very complicated with discrepancies between the various fish groups (see comments above). We did not find further evidence for a general Out-of-Kivu hypothesis. Detailed analyses, especially for *Enteromius*, did not allow us to find traces of the region acting like a refuge during megadroughts. What has become clear is the strong ichthyo-faunal link between the Lakes Kivu and Edward systems, while the links between Lakes Edward and Albert that were connected during the Pliocene in one paleolake, are at present much more diffuse. In contrast, significant signals of the ancient connection (into the Pleistocene) of the river systems in the area (flowing westwards at that time) with the Congo basin have been found in the distribution of fish taxa, especially in *Enteromius*.

Keywords

East Africa, fish diversity, barcoding, Lake Edward, biogeography