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Phylogenetic relationships of the Lake Tanganyika cichlid tribe Lamprologini: The story from mitochondrial DNA

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Abstract

The Lamprologini are the most species-rich and diverse tribe of Lake Tanganyika cichlids, comprising around 90 described species. We reconstruct the most complete (~70 species) mtDNA phylogeny to date for this tribe, based on NADH dehydrogenase subunit 2 (ND2 ~ 1047 bp) and the non-coding control region (~874 bp) and examine the degree to which mtDNA trees are good proxies for species trees. Phylogenetic relationships are assessed using Bayesian inference, maximum likelihood and maximum parsimony to determine the robustness of relationships. The resulting topologies are largely congruent and only the tree produced by an unpartitioned BI analysis is rejected using the non-parametric likelihood-based AU test. The trees are remarkably balanced, with two major clades consistently recovered in all analyses and with reasonable support. A smaller clade of deep-water species is also recovered. Overall support is good, when compared to some groups that have undergone adaptive radiation and rapid lineage formation. The much-expanded phylogeny of the group helps resolve the placement of some previously problematic taxa, such as *Neolamprologus moori*, highlighting the importance of greater taxonomic sampling. The results include a number of divergent placements of closely related species, and the following genera *Neolamprologus*, *Lamprologus*, *Julidiochromis*, *Telmatochromis* are not monophyletic, with alternative hypotheses consistent with traditional taxonomy providing a significantly worse fit to the data. We find several examples of divergent mtDNA taxa sequences of presumed closely related species. This could be due to incorrect taxonomy or to the failure of the mtDNA to reflect species relationships and may support the hypothesis that speciation within this group has been facilitated by introgressive hybridisation.

Keywords: Cichlidae; Taxonomy; Molecular systematics; Adaptive radiation; Introgressive hybridization

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1. Introduction

Unlike in Lakes Victoria and Malawi, where haplochromine cichlids are the most dominant fish lineage, by far the most speciose tribe within Lake Tanganyika (LT) is the Lamprologini, including approximately 90 described species in seven genera. The majority of lamprologine species are endemic to LT, although around 10% occur in associated river systems (Schelly et al., 2003; Schelly and Stiassny, 2004). It is clear from the description of new lamprologine species since Poll's (1986) classification of LT cichlids that the number of species will rise, particularly in the relatively unexplored deeper waters of LT and fluviatile habitats. If cichlids from LT are morphologically, ecologically and behaviourally the most complex flock (Fryer and Iles, 1972), then lamprologines epitomise this complexity more than any other tribe. As such they represent an important radiation in which to investigate the evolutionary causes of their remarkable species diversity for which a robust comprehensive phylogeny is needed.

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LT, estimated to be 9–12 Myr (Cohen et al., 1993), is considerably older than both Lakes Victoria and Malawi. Studies investigating the phylogenetic relationships of the LT cichlid flock therefore potentially avoid the problems associated with the extremely young ages and fast rates of evolution associated with Malawi and Victoria species flocks (e.g., Albertson et al., 1999; Kocher, 2003), However, resolving phylogenies of Tanganyikan cichlids is not without some problems, such as incomplete lineage sorting (Takahashi et al., 2001) and introgressive hybridisation (e.g., Rüber et al., 2001; Salzburger et al., 2002a; Schelly et al., 2006). Previous studies of Tanganyikan cichlid relationships, using various molecular markers (e.g., Kocher et al., 1995; Salzburger et al., 2002b; Clabaut et al., 2005) and morphology (e.g., Stiassny, 1997; Takahashi, 2003) have shown that Lamprologini is undoubtedly monophyletic. Yet unlike the plethora of work directed towards the haplochromine radiations of the younger African lakes, lamprologine intrarelationships have remained largely ignored. As a consequence of their presumably longer evolutionary history, lamprologines exhibit a reasonable level of morphological disparity distinct enough for Stiassny (1997) to establish a set of discrete characters. One of which, the presence of an ossified labial cartilage (a discrete bone within the dentary, suspended in connective tissues of the labial ligament), supports a seemingly natural assemblage, the ossified group (Stiassny, 1997) within lamprologines, that is also supported by molecular phylogenetics (Schelly et al., 2006).

The last major overhaul of lamprologine taxonomy is Poll's (1986) classification, recognising the seven genera: *Altolamprologus* (Poll, 1986), *Chalinochromis* (1974), *Julidochromis* (Boulenger, 1898), *Lamprologus* (Schilthuis, 1891), *Lepidolamprologus* (Pellegrin, 1904), *Neolamprologus* (Colombe and Allgayer, 1985) and *Telmatochromis* (Boulenger, 1898). Poll (1986) rejected the monotypic genera *Variabilchromis* (*V. moori*) and *Paleolamprologus* (*P. toae*) (Colombe and Allgayer, 1985), instead placing their species within *Neolamprologus*, with the understanding that this genus would be further partitioned in future studies. Despite previous molecular studies indicating the non-monophyly of *Neolamprologus* and of *Lamprologus* (e.g., Schelly et al., 2006), the former continues to provide a repository in which many new lamprologine species have been placed (see Schelly et al., 2003) pending revision of the tribe.

Previous molecular phylogenies of lamprologines (Sturmbauer et al., 1994; Schelly et al., 2006) have included only a subset of species (25 and 40 species, respectively), representing less than half the known species. The latter study was primarily concerned with resolving relationships within the genus *Lepidolamprologus* using mtDNA (ND2 and partial control region) and nuclear (nc)DNA (S7 intron and microsatellite loci) data. Perhaps the most striking result of Schelly et al.'s (2006) study is the divergent placement of *Lepidolamprologus nkambae* and *L. kendalli* within the mtDNA tree, which is incongruent with both morphology as well as the tree inferred from ncDNA data. Their finding supports the hypothesis that introgression may have played an important role in the evolution of this group (Salzburger et al., 2002a).

The lamprologines are a potentially important group for investigating factors influencing adaptive radiation, and for testing generalities about radiations in East African lakes. The major obstacle is the lack of a comprehensive phylogeny. Problems of introgression not withstanding, most studies of intra-tribal relationships of cichlids have relied exclusively on mtDNA (e.g., Brandstätter et al., 2005; Duftner et al., 2005; Koblmüller et al., 2004, 2005). Here, we present the most inclusive mtDNA phylogeny of the Lamprologini based on new sequences for fifty-two species and previously published data, expanding sampling of taxa beyond all previous analyses. This study aims to establish the extent to which routinely used mtDNA may resolve species level relationships and higher order relationships within this radiation.

2. Material and methods

2.1. Species and taxon sampling

Approximately 70 species (107 terminal taxa) representing nearly 80% of the known species and all seven lamprologine genera are included in this study. New sequence data is generated for fifty-two species (68 taxa) for the purposes of this study, while data for additional species and taxa were obtained from Genbank (see Table 1 for taxa sequenced in this work and those from Genbank). Taxonomic sampling is particularly important when examining species with broad distributions. We use the generic names assigned by Poll (1986), but follow the reassignment of taxa within *Lepidolamprologus* (excluding *L. cunningtoni*) after Schelly et al. (2006).

Members of the tribe Eretmodini, the inferred sister group based on molecular phylogenetic analyses of LT cichlids, and the more distant *Oreochromis tanganicae* (Salzburger et al., 2002b; Clabaut et al., 2005) were selected as outgroup taxa. Specimens were collected using SCUBA equipment and nets from a number of sites (see Table 1). Additional samples were obtained through collectors and aquarists. All samples were preserved in 70–100% ethanol. Voucher specimens are deposited in the Natural History Museum, London (see Table 1 for voucher numbers, localities and corresponding Genbank accession numbers).

2.2. Genetic markers

An important consideration for building species-level phylogenies of a relatively young group such as the Lamprologini, is choice of genetic markers and their subsequent phylogenetic analysis. The control region (CR) and NADH dehydrogenase subunit 2 (ND2) are proven mitochondrial genes useful for elucidating species-level cichlid relationships in LT (e.g., Brandstätter et al., 2005; Duftner et al., 2005; Koblmüller et al., 2004, 2005). The rapidly evolving CR is particularly useful in resolving species-level relation-