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Phylogenetic relationships of the lamprologine cichlid genus *Lepidiolamprologus* (Teleostei: Perciformes) based on mitochondrial and nuclear sequences, suggesting introgressive hybridization

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Abstract

Using sequences of the mitochondrial NADH dehydrogenase subunit 2 gene (ND2, 1047 bp) and a segment of the non-coding mitochondrial control region, as well as nuclear sequences including two introns from the S7 ribosomal protein and the loci TmoM25, TmoM27, and UME002, we explore the phylogenetic relationships of *Lepidiolamprologus*, one of seven lamprologine cichlid genera in Lake Tanganyika, East Africa. Analyses consisted of direct optimization using POY, including a parsimony sensitivity analysis, and maximum likelihood and Bayesian inference for comparison. With respect to *Lepidiolamprologus*, the results based on the mitochondrial dataset were robust to parameter variation in POY. *Lepidiolamprologus cunningtoni* was resolved in a large clade sister to ossified group lamprologines, among which the remaining *Lepidiolamprologus* were nested. In addition to *L. attenuatus*, *L. elongatus*, *L. kendalli*, and *L. profundicola*, *Neolamprologus meeli*, *N. hecqui*, *N. boulengeri*, *N. variostigma*, and two undescribed species were resolved in a two-pore *Lepidiolamprologus* clade sister to *Lamprologus callipterus* and two species of *Altolamprologus*. *Lepidiolamprologus nkambae*, in marked conflict with morphological and nuclear DNA evidence, nested outside of the two-pore *Lepidiolamprologus* clade, suggesting that the mtDNA signal has been convoluted by introgressive hybridization.

Keywords: Cichlidae; Lamprologini; *Lepidiolamprologus*; Lake Tanganyika; Introgressive hybridization

1. Introduction

Among the 12 cichlid tribes recognized by Poll (1986) in Lake Tanganyika, East Africa, the substrate-brooding lamprologines are the most diverse, with about 80 species. Additionally, eight lamprologine species are found in the Congo River (Schelly and Stiassny, 2004), and at least one species occurs in the Malagarasi River (De Vos et al., 2001; Schelly et al., 2003). While the monophyly of Poll's tribe Lamprologini has withstood scrutiny (Salzburger et al., 2002a; Stiassny, 1997; Sturmbauer et al., 1994; Takahashi et al., 1998), most genera within the tribe are unquestionably polyphyletic. For instance, members of the "ossified group," identified by Stiassny (1997) and distinguished by a labial bone suspended within the labial ligament, are scattered among four of seven lamprologine genera potentially rendering

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Lamprologus, *Neolamprologus*, and *Lepidiolamprologus* non-monophyletic.

Pellegrin (1904) originally erected the genus *Lepidiolamprologus* for *Lamprologus elongatus*, defining the new genus, closely allied with *Lamprologus*, as somewhat more elongate, with teeth-like *Lamprologus*; rather long gill rakers (12); small ctenoid scales numbering 90–95 in longitudinal series; 18 dorsal spines; and 5 anal spines. Boulenger (1915) synonymized *Lepidiolamprologus* with *Lamprologus*, and arrayed lamprologines in the genera *Lamprologus*, *Julidochromis*, and *Telmatochromis*, with no statement as to their being part of a natural group. Subsequently, Regan (1920) recognized affinities between the lamprologines known at the time, *Telmatochromis*, *Julidochromis*, and *Lamprologus*, based on their strong conical teeth and 4–10 anal spines. Regan (1920, 1922) argued that the diversity of *Lamprologus* species in the lake implied that the group originated in Lake Tanganyika, despite the existence of Congo River representatives, which he believed were a single lineage. The first significant effort to use osteology to guide lamprologine classification was that of Colombe and Allgayer (1985). In that study, the genus *Lamprologus* was subdivided into five genera based on characters of the infraorbital series, with only the Congo River species retained in the genus *Lamprologus*. Pellegrin's genus *Lepidiolamprologus* was rehabilitated for six species (*L. attenuatus*, *L. cunningtoni*, *L. elongatus*, *L. kendalli*, *L. nkambae*, and *L. profundicola*), and three new genera were created: the monotypic *Variabilichromis* for *V. moorii*, the monotypic *Paleolamprologus* for *P. toae*, and *Neolamprologus* for 38 species.

Poll (1986) retained the resurrected *Lepidiolamprologus*, but criticized the sufficiency of Pellegrin's original characters for the genus. Instead, he listed 61–73 lateral line scales, vs. 30–40 in other genera, plus a unique structure of pelvic fin rays and numerous scales in the occipital, thoracic, and abdominal regions as supporting the group. Poll (1986) criticized the infraorbital characters of Colombe and Allgayer because of their variability within species and even individuals. On these grounds, he altered their generic allocation in his new classification. In addition to re-assigning several lake endemics to the genus *Lamprologus*, Poll (1986) rejected the monotypic genera *Variabilichromis* and *Paleolamprologus*, and additionally proposed *Altolamprologus* as a new genus, for the highly distinctive *A. compressiceps* and *A. calvus*. Finally, Poll accepted *Neolamprologus* for most remaining Lake Tanganyika lamprologine species, with the caveat that *Neolamprologus* would likely be further partitioned in the future.

The most thorough morphology-based treatment of lamprologines was carried out by Stiassny (1997), who listed a suite of osteological characters supporting lamprologine monophyly, in accord with numerous molecular studies (e.g., Salzburger et al., 2002a; Sturmbauer et al., 1994; Thompson et al., 1994). Unlike Poll (1986), Stiassny (1997) supported the creation of the genus *Variabilichromis* for *V. moorii*. Regarding the genus *Lepidiolamprologus*, she suggested that *L. cunningtoni* should be excluded, and *N. pleuromaculatus*, *N. boulengeri*, *N. hecqui*, *N. meeli*, and *N. lemairii* should be included to render the genus monophyletic. Stiassny highlighted the inadequacy of current lamprologine classification by defining an "ossified group" of lamprologines, with representatives scattered among the genera *Lamprologus*, *Neolamprologus*, *Lepidiolamprologus*, and *Altolamprologus*. Ossified group lamprologines posses a sesamoid bone within the labial ligament, a condition mirrored in certain atherinomorphs, but unique among cichlids and perhaps even Perciformes. More recently, Takahashi (2003) used morphological characters to examine relationships among Tanganyikan cichlids, but did not recover the ossified group as a monophyletic assemblage in his lamprologine clade, consisting of 10 species only.

Utilizing two mtDNA loci and five nuclear loci for a subset of taxa, this study focuses on resolution of the phylogenetic relationships of species assigned to the genus *Lepidiolamprologus*, one of the most distinctive genera of the ossified group of lamprologines. The mtDNA phylogeny is then used to trace the evolution of two distinctive morphological characters. We follow Poll's (1996) classification, in which lamprologines comprise seven genera: *Altolamprologus* Poll, 1986; *Chalinochromis* Poll, 1974; *Julidochromis* Boulenger, 1898, *Lamprologus* Schilthuis, 1891, *Lepidiolamprologus* Pellegrin, 1904; *Neolamprologus* Colombe and Allgayer, 1985; and *Telmatochromis* Boulenger, 1898.

2. Materials and methods

2.1. Taxon sampling

In addition to 36 lamprologines, we included three eretmodines (*Spathodus erythrodon*, *Tanganicodus irsacae*, and *Eretmodus cyanostictus*) and one perissodine (*Perissodus microlepis*), representatives of lineages nested close to lamprologines in the analysis of Salzburger et al. (2002a), as outgroups. Since the focus of this study was the genus *Lepidiolamprologus*, we included all but one species that has ever been placed in that genus or suggested to be closely allied with it (only *N. pleuromaculatus* was unavailable), and two undescribed species, one with a flank pigmentation pattern similar to that of *L. profundicola*, fresh material of which was collected in Zambia in March, 2004, and the other morphologically similar to *N. boulengeri* and *N. meeli*, collected in Zambia in October, 2001, and March, 2003. In addition, we thoroughly sampled from the ossified group of Stiassny (1997), including 20 out