



Molecular phylogeny and evidence for an adaptive radiation of geophagine cichlids from South America (Perciformes: Labroidei)

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Abstract

Nucleotide sequences from the mitochondrial ND4 gene and the nuclear RAG2 gene were used to derive the most extensive molecular phylogeny to date for the Neotropical cichlid subfamily Geophaginae. Previous hypotheses of relationships were tested in light of these new data and a synthesis of all existing molecular information was provided. Novel phylogenetic findings included support for: (1) a 'Big Clade' containing the genera *Geophagus sensu lato*, *Gymnogeophagus*, *Mikrogeophagus*, *Biotodoma*, *Crenicara*, and *Dicrossus*; (2) a clade including the genera *Satanoperca*, *Apistogramma*, *Apistogrammoides*, and *Taeniacara*; and (3) corroboration for Kullander's clade Acarichthyini. ND4 demonstrated saturation effects at the third code position and lineage-specific rate heterogeneity, both of which influenced phylogeny reconstruction when only equal weighted parsimony was employed. Both branch lengths and internal branch tests revealed extremely short basal nodes that add support to the idea that geophagine cichlids have experienced an adaptive radiation *sensu* Schluter that involved ecomorphological specializations and life history diversification. © 2004 Elsevier Inc. All rights reserved.

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1. Introduction

The Neotropical cichlid subfamily Geophaginae encompasses 18 genera and over 180 described species (Kullander, 2003), with many more in need of description (e.g., Kullander, 2003; López-Fernández and Taphorn, 2004). Although our knowledge of geophagine biology is limited, this group of fishes displays diverse ecology, morphology, and reproductive behavior. Their overall morphological and behavioral diversity suggests ecomorphological specialization for feeding and habitat use (e.g., Winemiller et al., 1995; López-Fernández, unpublished). For instance, some taxa share a common feeding mode based on sifting of benthic invertebrates (e.g., Lowe-McConnell, 1991; Winemiller et al., 1995),

while others are strict piscivores. Geophagines also exhibit a variety of reproductive modes, from typical substrate spawners to mouth-brooding, and are the only riverine cichlids approaching the reproductive versatility of lacustrine cichlids (e.g., Barlow, 2000; Weidner, 2000; Wimberger et al., 1998). Several genera and species of geophagines are syntopic in South American rivers (e.g., Arrington and Winemiller, 2003; Winemiller et al., 1995), thus ecomorphological and behavioral specialization may facilitate niche partitioning within species-rich ecological communities. Although this Neotropical fish assemblage offers many opportunities for those interested in evolutionary ecology and the processes responsible for ecomorphological diversification, such studies require an interpretive framework based on knowledge of phylogenetic relationships and the timing and duration of speciation events. As can be seen in the following paragraphs, considerable controversy still

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surrounds the phylogenetics and classification of the Geophaginae.

Recent phylogenetic analyses of the Cichlidae (Farias et al., 1999, 2000, 2001; Kullander, 1998) have improved understanding of higher-level relationships within the Neotropical clade (e.g., establishment of subfamilies), yet even here there are disagreements. Using a morphology-based phylogeny, Kullander (1998) subdivided the Neotropical Cichlidae and the African genus *Heterochromis* into six subfamilies. The Retroculinae (genus *Retroculus*) and Cichlinae (*Cichla*, *Crenicichla*, and *Teleocichla*) constituted the basal clades of the American assemblage. The African Heterochromidinae (*Heterochromis*) was nested between the latter two and Astronotinae (*Astronotus* and *Chateobranhus*), which were sister to the rest of the Neotropical assemblage, thus the Neotropical cichlids were rendered paraphyletic. The more derived subfamilies Cichlasomatinae and Geophaginae included all the remaining genera within the American cichlids. Cichlasomatinae included over 25 genera placed in the tribes Cichlasomini, Heroini, and Acaroniini. Geophaginae included 16 genera and was divided into three tribes: Acarichthyini (*Acarichthys* and *Guianacara*), Crenicaradini (*Biotocus*, *Crenicara*, *Dicrossus*, and *Mazarunia*), and Geophagini (*Geophagus*, *Mikrogeophagus*, '*Geophagus*' *brasiliensis*, '*Geophagus*' *steindachneri*, *Gymnogeophagus*, *Satanoperca*, *Biotodoma*, *Apistogramma*, *Apistogrammoides* and *Taeniacara*).

In disagreement with the definition of Kullander, molecular studies (Farias et al., 1998, 1999) and total evidence analyses (Farias et al., 2000, 2001), including Kullander's morphological data, supported a monophyletic Neotropical Cichlidae and the placement of *Heterochromis* as basal to the African clade. Farias et al. (1999, 2000, 2001) also found the genera *Crenicichla* and *Teleocichla* nested within the Geophaginae, expanding the subfamily to 18 genera, and challenging the previously proposed relationship between *Crenicichla*, *Teleocichla* and the basal genus *Cichla* (Stiassny, 1987, 1991; Kullander, 1998). Despite the contribution of these studies to the clarification of higher-level relationships, the lack of relevant taxa limits their phylogenetic resolution and leaves many questions of geophagine relationships unanswered. Although geophagine monophyly seems indisputable, there is considerable disagreement between morphological and molecular evidence when analyzed separately, and the relationships within the Geophaginae are not clear. Kullander's study included an extensive taxon sampling of cichlids, and his proposed geophagine relationships were based on the analysis of 13 genera of geophagines (*sensu* Kullander) plus *Crenicichla* and *Teleocichla*. The studies of Farias et al. (1999, 2000, 2001) are not suited for testing Kullander's hypothesis, because taxon sampling is insufficient in their combined analyses. Farias et al. (2000) included only 11 genera in their molecular total evidence

analysis and 9 in the combined analysis of molecular and morphological data. Their total molecular evidence analyses lacked the genera *Satanoperca*, *Biotocus*, *Crenicichla*, *Dicrossus*, and the '*Geophagus*' *steindachneri* group (Farias et al., 2000), and several additional genera were absent from their analyses of molecular and morphological data combined (Farias et al., 2000, 2001). Clearly, exclusion of these taxa makes it impossible to test the monophyly of Kullander's (1998) tribes Crenicaradini and Geophagini, and impedes further resolution of internal relationships within the subfamily. Better taxon sampling and incorporation of new data are needed to clarify relationships within the Geophaginae.

In this paper, we used newly obtained sequences from the mitochondrial ND4 gene and the nuclear RAG2 gene to derive a molecular phylogeny of the Geophaginae. We also performed a combined analysis of the new data with previously published sequences from Neotropical cichlids, thus integrating all available molecular evidence into the resolution of geophagine relationships. In addition, taxon sampling was largely expanded with respect to previous studies to include 16 of the 18 genera and 30 species of geophagines. We used these data to: (1) evaluate relationships among genera of Geophaginae, comparing our results to those from previous studies; (2) determine the extent of substitutional saturation and heterogeneity of molecular evolutionary rates within the subfamily and their effect on phylogenetic reconstruction; and (3) evaluate the phylogenetic evidence supporting an adaptive radiation of the group, as a necessary step in studying patterns of evolution of morphology, ecology, and behavior within the Geophaginae.

2. Materials and methods

2.1. Taxon sampling

DNA sequence data were collected for both the mitochondrial ND4 (NADH dehydrogenase subunit 4) gene and the nuclear RAG 2 gene (Recombination Activating Gene 2). Specimens examined included 21 genera and 38 species of Neotropical cichlids, and when possible, sequences were obtained from two individuals of each species. Ingroup samples included 16 of 18 genera and 30 species (Table 1) of Geophaginae *sensu* Farias et al. (1999, 2000, 2001), excluding only the genera *Teleocichla* and *Mazarunia*, for which tissue samples could not be obtained. The absence of these taxa from the dataset should not affect the resolution of the phylogeny, because *Teleocichla* has been clearly established as the sister group of *Crenicichla* (Farias et al., 1999, 2000, 2001; Stiassny, 1987), and *Mazarunia* is known to be related to *Crenicara* and *Dicrossus* (Kullander, 1990). The genus *Geophagus sensu lato* includes three distinct genera, of

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