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The impact of paleoclimate, geologic history, and human influence on the evolution of East African cichlids

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ABSTRACT

The cichlid fishes of the East African Great Lakes are the largest extant vertebrate radiation identified to date. These lakes and their watersheds support over 2000 species of cichlid fish, many of which are descended from single common ancestor within the past 25 Ma–10 Ma. The extraordinary East African cichlid diversity is linked to the highly variable geologic and paleoclimatic history of this region. The East Africa rift system (EARS) is the roughly north–south alignment of rift basins in East Africa that defines the boundary between the Somalian and African plates. The EARS is divided into two structural branches that are also oriented roughly north–south. Rifting in the eastern branch began 30–35 Ma in the Afar and Ethiopian Plateau and propagated north–south until it impinged on the strong Precambrian Tanzanian cratonic block, which is in the center of the East Africa Plateau. The timing of the initiation of the western branch of the EARS is uncertain and has been suggested to have begun as early as 25 Ma to as recently as 12–10 Ma. Uplifting associated with this rifting backponded many rivers and created Lake Victoria. Since their creation, these lakes have changed dramatically which has, in turn, significantly influenced the evolutionary history of the lakes' cichlids. This paper examines the geologic history, paleoclimate of the East African Great Lakes, and human influence and the impact of these forces on the region's endemic cichlid fishes using evidence from geologic and molecular data. A drastic decline has occurred in the size of cichlid fishes populations since the beginning of the 20th century, exacerbated by two main factors; an increase in the size of the human population and increased fishing pressure and fish introductions. One of the attendant consequences of such a decline is a reduction in the amount of genetic diversity in the surviving populations due to increased effects of random genetic drift. Information about the amount of genetic variation within and between the remaining populations is vital for their future conservation and management. The genetic structure of a cichlid fish, the Nile tilapia, was examined using nucleotide variation of mitochondrial control region sequences and four nuclear microsatellite loci in 128 individuals from seven localities. Forty three mitochondrial DNA (mtDNA) haplotypes were observed, fourteen of which were geographically localized. We found significant genetic differentiation between the five populations at the mitochondrial locus while three out of the four microsatellite loci differentiated five populations. The possible contributions from human activities such as water pollution, overfishing and fish introductions are also discussed.

1. Introduction

The East African Great Lakes Region had a highly dynamic geological and ecological history. Over the past 35 million years (Ma), tectonic plates have shifted, rifts in the landscape have opened, rivers have reversed course, and lakes have formed and desiccated. It is within this environment that the African Cichlid fishes originated. A total of more than 2000 species of cichlid fishes have diversified to fill nearly every niche available to a freshwater fish. All of these cichlids are endemic to East Africa, many are single lake endemics, and several are microendemics found only at isolated areas within a given lake (Danley et al., 2012). This paper examines the geological and ecological history of East Africa and discusses how these forces have influenced this spectacular vertebrate radiation, using molecular data from one of the most widespread cichlid fish, the Nile tilapia (*Oreochromis niloticus*, Linnaeus, 1758).

The Nile tilapia (*O. niloticus*, Linnaeus, 1758) is one of the cichlid fishes which have received much attention from evolutionary biologists because of their extremely diverse morphology, behavior, and ecology (Fryer and Iles, 1972; Trewavas, 1983; Stiassny and

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Meyer, 1999). The cichlid family has over 220 recognized genera with approximately 2000 species (Kullander, 1998). Members of this family are found mainly in the fresh waters of Africa. The African cichlids are divided into two major groups: haplochromines and the tilapiine cichlids, which have also repeatedly formed smaller species flocks of typically less than 10 species, for example, in some crater lakes in Cameroon, but they have not produced many species like the cichlids of their putative sister group, the haplochromines.

In contrast to the highly specialized species of the famous haplochromine cichlid species flocks of Lakes Malawi and Victoria, the tilapiines have a more general body plan and are often river inhabitants, whereas most haplochromines live in lakes (Trewavas, 1983). Evolutionary biologists dealing with the relationships of cichlids have often assumed a basal position of the tilapiines within the African clade because of their generalized morphology and ecological diversity (Fryer and Iles, 1972; Stiassny, 1991). Because of this less specialized morphology, tilapiines are highly adaptable to diverse ecological habitats and are presumably less prone to extinction (Trewavas, 1983). The Tanganyikan cichlid species flock is the most complex assemblage of cichlids with respect to morphology, ecology, and behavior in the world (Brichard, 1989).

1.1. Phylogeny of African cichlids

The Great Lakes of East Africa are home to an exceptionally diverse ichthyofauna (Fryer and Iles, 1972). The most famous elements of the lakes' faunas are the cichlid fishes that have formed species flocks of an unparalleled species-richness and degree of eco-morphological and behavioral complexity (Stiassny and Meyer, 1999; Kocher, 2004; Koblmüller et al., 2006). It has been estimated that almost 2000 cichlid species inhabit Lakes Tanganyika, Malawi and Victoria (Snoeks, 1994; Turner et al., 2001) and that these lake endemic species are likely to have evolved in the last few millions or as recently as the last thousands of years only (Salzburger et al., 2002, 2005). It is thus not surprising that the cichlid species flocks from the East African Great Lakes have received considerable attention as model systems for the study of adaptive radiation and explosive speciation (Kornfield and Smith, 2000; Salzburger and Meyer, 2004). Cichlid fishes are the only freshwater representatives of the suborder Labroidei and are naturally distributed across Africa, Madagascar, South and Central America, the Middle East, and the Indian subcontinent (Fig. 1).

1.2. The geology and East African climate

The East Africa rift system (EARS) is the roughly north–south alignment of rift basins in East Africa that defines the boundary between the Somalian and African plates (Chorowicz, 2005). The EARS is divided into two structural branches that are also oriented roughly north–south. Rifting in the eastern branch began about 30–35 Ma in the Afar and Ethiopian Plateau and propagated north–south until it impinged on the strong Precambrian Tanzanian cratonic block, which is in the center of the East Africa Plateau (Nyblade and Brazier, 2002). The extensional stress associated with the rifting or with widespread plume-related uplift was then transported westward across the craton to weaker mobile crust on the craton's western edge creating the western branch of the rift. The timing of the initiation of the western branch of the EARS is uncertain and has been suggested to have begun as early as 25 Ma to as recently as 12–10 Ma (Roberts, 2012). After its onset, rifting then continued to propagate in the western branch of the EARS forming the rift basins that encompass Lakes Tanganyika and Malawi (Bishop and Trendall, 1967). Extension and uplift associated with rifting created a reversal in rivers flowing westward across the East African Plateau and caused backponding into a topographic low in between the two branches of the rift, forming Lake Victoria (Fig. 2).

1.3. East African paleoclimate (10 Ma–present)

The East African climate has been and continues to be dynamic (Nicholson, 1996). Late Miocene (8–10 Ma) climate in East Africa was humid and supported a variety of savanna and forest habitats, including rain forests. Following this humid period, from 7–5 Ma, the ice volume of the Antarctic ice sheet expanded, and global temperatures fell (Kennett, 1980). This time period is also associated with aridification across East Africa (Cerling, 2011), as well as the uplift of the Himalayas and the resulting intensification of the Indian Monsoon, which may also have contributed to increased aridity. The early Pliocene (5–3 Ma) is characterized by warmer and wetter conditions globally and across Africa (Haywood et al., 2000). During this global warm, wet period, East Africa was also very humid (Pickford, 1990), perhaps driving the expansion of Lake Tanganyika during the middle Pliocene (Cohen et al., 1997). Significant Northern Hemisphere Glaciation began and intensified between 3.2 and 2.6 Ma (Shackleton, 1995; Ravelo et al., 2004) and beginning at 2.0 Ma, Southern Hemisphere Glaciation expanded (Meyer, 1993). The interval beginning at 2.8 Ma represents the onset of the glacial–interglacial cycles that characterizes the Pleistocene (deMenocal, 1995).

In particular, the climate in East Africa during the last 500 ka has been extremely variable, transitioning between wet and dry intervals that have caused significant fluctuations in the lake levels of the African Great Lakes (Fig. 3) (Johnson et al. 1996; Cohen et al.

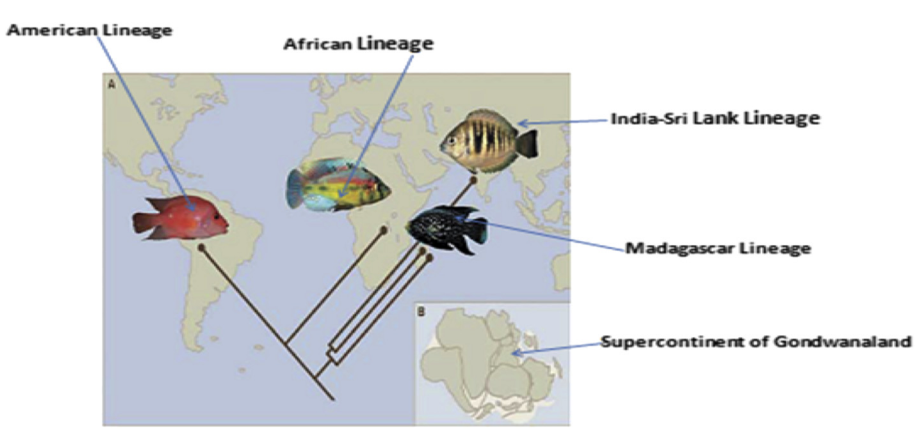

Fig. 1. A, The distributional pattern of the cichlids, with the representatives from India, Sri Lanka, and Madagascar forming the most basal lineages and the reciprocally monophyletic African and American lineages as sister-groups. B, Inset of the supercontinent of Gondwanaland some 200 million years ago (Salzburger and Meyer, 2004).