

Thomas Wilke
Risto Väinölä
Frank Riedel
Editors

Developments in Hydrobiology 205

Patterns and Processes of Speciation in Ancient Lakes



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Developments in Hydrobiology 205

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K. Martens

Patterns and Processes of Speciation in Ancient Lakes

Proceedings of the Fourth Symposium on Speciation in Ancient Lakes, Berlin, Germany, September 4–8, 2006

Editors

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Cover illustration: Eastern shore of Lake Ohrid near Veli Dab – one of the lake's major hotspots of endemic biodiversity. Photograph: Thomas Wilke, 2004.

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Preface

Thomas Wilke · Risto Väinölä · Frank Riedel

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Ancient lakes, that is, extant lakes that typically have continuously existed since before the Pleistocene, for more than two million years—such as lakes Baikal, Tanganyika, Malawi, Biwa, and Ohrid, have long been recognized as centres of biodiversity. Moreover, during the past years, speciation in ancient lakes has emerged as an important and fruitful topic in studies of evolutionary biology. The current understanding of a number of key evolutionary concepts, such as sympatric speciation, sexual selection, adaptive radiation, hybridization, and punctuated equilibrium, is in part based on insights from speciation studies in these lakes, and this is evident in the increasing number of citations of articles pertaining to speciation in ancient

lakes. Thomson Reuter's Web of Science[®], for example, lists under this topic, only one cited paper in 1996, but 190 for the year 2007.

This volume represents the outcome of a fourth meeting in a series of conferences on speciation in ancient lakes (SIAL). The series was started by a meeting that took place in 1993 in Mont-Rigi, Belgium, and was brought together to review the state of art in the field for the first time since the classical seminal review of Brooks (1950). The proceedings of that meeting were published as a special volume of *Archiv für Hydrobiologie* (Martens et al., 1994); apart from summarizing both theoretical concepts of evolution in ancient lakes and practical activities in these systems, it also initiated a wealth of renewed interest in ancient lake issues.

The second SIAL meeting entitled “International Conference on Ancient Lakes: their Biological and Cultural Diversities” was held in 1997 near Lake Biwa in Japan. It focused on the cultural diversity of ancient lakes (Kawanabe et al., 1999) as well as on their biodiversity, ecology, and evolution (Rossiter & Kawanabe, 2000).

The third conference, SIAL-3, took place in Irkutsk. Naturally, the focus of that conference was the oldest and arguably most famous of the ancient lakes—Lake Baikal. The conference proceedings were published in two special issues (Ivanov et al., 2003; Coulter et al., 2006), adding to the reputation of Baikal as one of the best-studied lakes in the world.

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Finally, the latest meeting SIAL-4 was held on September 4–8, 2006, at the Freie Universität Berlin, Germany, organized by Frank Riedel (Germany) together with George Coulter (New Zealand), Matthias Glaubrecht (Germany), Doug Haffner (Canada), Hiroya Kawanabe (Japan), Koen Martens (Belgium), Oleg Timoshkin (Russia), Risto Väinölä (Finland), and Thomas Wilke (Germany); 67 scientists from 16 different countries contributed to the scientific program. While the abstracts of SIAL-4 were published in a special issue of *Berliner Paläobiologische Abhandlungen* (Kossler et al., 2006), selected full papers are subject of the present special issue “Patterns and processes of Speciation in Ancient Lakes.” The contributions in this issue deal with three ancient lakes systems. One system is the famous East African Great Lakes, which have been studied extensively over the past decades, resulting in significant new findings about evolutionary processes in general. On the other hand, we include a set of papers on two other prominent lake systems that have so far received much less attention, the European ancient sister lakes Ohrid and Prespa, which have long been recognized as hotspots of biodiversity but were largely neglected in the international scientific literature until recently, and the two central lake systems on the Indonesian island of Sulawesi, the rich biodiversity and interesting evolutionary patterns of which only very recently have started to draw the attention of evolutionary biologists.

East African Great Lakes

The African Great Lakes—a series of lakes in or near the Great Rift Valley, for example Lake Victoria, Lake Tanganyika, and Lake Malawi—are major hotspots of freshwater biodiversity, with splendid examples of large radiations of cichlid fishes. While not all of the African Great Lakes qualify as ancient (e.g., the relatively young Lake Victoria), these lakes have long been a “playground” for evolutionary biologists.

In the current issue, Koblmüller et al. give an account of the higher taxonomy and phylogeny of the Lake Tanganyika cichlid species assemblage, its relationship to the African cichlid fauna, and key factors leading to the astonishing diversity of cichlids in the lake. Several other workers report on the emerging field of sexual selection and reproductive

strategies of cichlid fish species in Lake Tanganyika (Sefc, Egger et al. and Sturmbauer et al.) and Lake Malawi (Anseeuw et al.). An endemic radiation of freshwater crabs in Lake Tanganyika is the subject of the study of Marijnissen et al., who discuss data on interspecific spatial and ecological segregation in the framework of adaptive radiation theory. Finally, Sturmbauer reviews and discusses conservation strategies for aquatic biota and their biological impact on species flocks in the East African Great Lakes.

The Balkan lakes Ohrid and Prespa

One of the most outstanding European ancient lakes is the oligotrophic and karstic Lake Ohrid situated in the central Balkans. Together with its sister lake, Lake Prespa, it represents one of the most significant hotspots of endemic biodiversity in the world. Although the recognition of Lake Ohrid as a peculiar lake with an outstanding biodiversity began in the late 19th century, and basic taxonomical and evolutionary studies were carried out prior to and after World War II, the political instabilities in the Balkans in the 1980s and 1990s led to a sharp decline of projects carried out at these lakes. Only the last decade has seen a revival of scientific activity in lakes Ohrid and Prespa.

Here, Albrecht and Wilke summarize the current knowledge of the limnological and faunal history of Lake Ohrid, update the existing data on its biodiversity and endemism, and review patterns and processes of speciation in the lake. In primary research studies, several groups of endemic molluscs are investigated with regard to the sister-lake relationship of lakes Ohrid and Prespa (Albrecht et al.), patterns of endemic biodiversity (Hauswald et al.), and evolutionary patterns in inconspicuous (cryptic) taxa (Schultheiß et al.).

Sulawesi lake systems

While evolutionary studies in ancient lakes such as Lake Baikal and Lake Tanganyika have been ongoing for many decades, patterns of endemic diversity in the two central lake systems on the Indonesian island of Sulawesi, that is, Lake Poso and the lakes of the Malili lake system, have been largely neglected for a century. Recently, however, there has been a renewed

interest in these lakes and in their endemic species flocks.

In the present issue, Glaubrecht and Rintelen review and discuss the evolutionary and taxonomic implications of the *Tylomelania* gastropod species flocks and demonstrate that they provide instructive model cases for the study of speciation mechanisms, adaptive radiation, and niche exploitation. Schwarzer et al. utilized the adaptive radiation of sailfin silver-sides in Lake Matano (Malili lake system) to study the effect of gene flow on speciation processes. The data presented suggest that genetic exchange between lacustrine and riverine taxa takes place, potentially allowing introgression into Lake Matano from lower lakes and streams. The rich endemic diatom flora of the Malili lake system is the subject of the study of Bramburger et al. The workers reviewed the mechanisms contributing to the development and maintenance of community composition and relative abundance of taxa. Finally, Sabo et al. studied the phytoplankton and zooplankton communities of Lake Matano and substantiated the assumption that resource limitation plays an important role in shaping the unique endemic assemblages currently observed in the food web of the lake.

We hope that the present special issue can deepen the awareness of ancient lakes in the scientific community in general, and of their role as natural laboratories and prime hotspots of biodiversity in particular. It is also hoped that this issue stimulates further research that may lead to a better understanding of key evolutionary processes in these lakes and that ultimately may help in mitigating the decline of biodiversity seen today in many ancient lakes. These

topics will certainly continue to be focal points during the fifth conference, SIAL-5, which is scheduled to take place at Lake Ohrid in September 2009.

We would like to thank the other members of the organizing committee for their hard work. We also would like to thank Koen Martens, who kindly gave us the opportunity to publish this issue and who assisted us during preparation. Eugene Coan is gratefully acknowledged for improving a number of manuscripts as a native English speaker and biologist, and Claudia Wilke helped with proofreading.

The Guest Editors

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The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics

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Abstract Lake Tanganyika is not the most species-rich of the Great East African Lakes, but comprises the greatest diversity of cichlid fishes in terms of morphology, ecology, and breeding styles. The lake contains a polyphyletic assemblage of cichlid lineages, which evolved from several ancient species that colonized the emerging lake some 9–12 million years ago. Based on morphological characteristics, the Tanganyikan cichlids have been classified into 12, or, more recently, 16 tribes, which are largely supported by molecular data. The radiations of East African cichlids are believed to be driven by complex interactions between extrinsic factors, such as climatic changes and geological processes, and intrinsic biological characteristics of the involved organisms. Diversification within different lineages occurred simultaneously in response to drastic habitat changes such as the establishment of lacustrine deep-water

conditions 5–6 MYA and subsequent major lake-level fluctuations. This seems particularly true for the mouthbrooding lineages whereas the substrate breeders underwent a more gradual process of diversification. This review presents an account of the taxonomy and phylogeny of the Lake Tanganyika cichlid species assemblage, its relationship to the African cichlid fauna, key factors leading to the astonishing diversity and discusses recently proposed alternative age estimates for the Lake Tanganyika cichlid species assemblage.

Keywords Adaptive radiation · Cichlidae · Diversification · Phylogeny · Speciation

Introduction

With about 3,000 species, distributed from Central and South America, across Africa to Madagascar and southern India, the family Cichlidae represents the most species-rich family of vertebrates. Cichlids are outstanding in terms of variation of body shapes, color patterns and behavior, and their enormous diversity of trophic and ecological specializations (Fryer & Iles, 1972; Meyer, 1993; Kornfield & Smith, 2000; Kocher, 2004; Salzburger & Meyer, 2004). Throughout their range of distribution cichlids have repeatedly demonstrated their capacity for rapid speciation with niche partitioning, a process termed adaptive radiation (reviewed in Turner, 2007), but their greatest diversity

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counting almost 2,000 species arose within the three Great East African Lakes, Tanganyika, Malawi, and Victoria (Turner et al., 2001; Kocher, 2004).

Adaptive radiation is believed to be induced by extrinsic environmental factors such as geologic and climatic events, which create novel and vacant niches, and intrinsic traits of the organism, providing a key to the success over other organisms, termed key innovations. After its initiation, radiation is modulated by extrinsic factors interacting with biological characteristics of the involved species such as ecological specialization, site fidelity, territoriality, homing and mating behavior, and social organization (Fryer & Iles, 1972; McKaye & Gray, 1984; Rossiter, 1995; Sturmbauer, 1998). Extrinsic factors provide the opportunity and intrinsic factors the potential for radiation and both have to coincide to trigger a radiation (Martens et al., 1994; Sturmbauer, 1998).

Two key innovations are thought to be responsible for the evolutionary success of cichlids. The particular anatomy of the pharyngeal apophysis (Liem, 1973; Greenwood, 1973, 1978; Rice & Lobel, 2003) provides a second set of jaws decoupled from the oral jaws. This derived morphological trait is shared with the families Embiotocidae, Pomacentridae, and Labridae and allows for efficient processing of prey (Yamaoka, 1978; Liem & Greenwood, 1981; Liem, 1986; Liem & Sanderson, 1986; Stiassny & Jensen, 1987; Drucker & Jensen, 1991; Galis & Drucker, 1996; Koblmüller et al., 2003; Wainwright, 2005). The elements of the pharyngeal jaw apparatus were used as the primary taxonomic characters uniting the Cichlidae, Embiotocidae, Pomacentridae, and Labridae into the suborder Labroidei (Kaufman & Liem, 1982; Stiassny & Jensen, 1987). Molecular data, on the other hand, indicate that the Labroidei do not constitute a monophyletic assemblage, suggesting a repeated independent evolution of a specialized pharyngeal jaw apparatus (Streelman & Karl, 1997; Mabuchi et al., 2007). Minor structural modifications allow the utilization of novel food resources, so that new trophic niches can be rapidly occupied (Stiassny, 1991; Sturmbauer, 1998; Albertson et al., 1999). Moreover, the pharyngeal jaws are involved in sound production and are thus important for communication (Lobel, 2001; Kaatz, 2002; Rice & Lobel, 2002, 2003).

The second key factor believed to be associated with the diversification of cichlids is their highly specialized reproductive behavior (Crapon de Crapona,

1986), in particular, the various modes of brood-care behavior found in the East African cichlids (Fryer & Iles, 1972; Goodwin et al., 1998; Barlow, 2000; Kornfield & Smith, 2000; Klett & Meyer, 2002). Especially in polygamous mouthbrooding lineages, sexual selection via female choice of nuptial male coloration seems to play an important role in species diversification (McKaye et al., 1993; Turner & Burrows, 1995; Deutsch, 1997; Seehausen et al., 1997, 1998, 1999; Knight et al., 1998; Seehausen & van Alphen, 1999; Allender et al., 2003; Knight & Turner, 1999, 2004). However, a recent simulation study (Sefc, 2008) demonstrated that a mating system such as that of the sexually monomorphic, sequential monogamous, mouthbrooding cichlid genus *Tropheus* can also provide a considerable opportunity for sexual selection.

Due to their enormous species number and the complex behavioral and morphological characteristics, enabling the utilization of specific niches within a species-rich assemblage, the family Cichlidae has become a popular and well-known model system in various disciplines of biological sciences (Fryer & Iles, 1972; Sturmbauer, 1998; Kornfield & Smith, 2000; Kocher, 2004). Currently, 200 cichlid species are described for Lake Tanganyika, with several more awaiting scientific description. By recent estimates, the total number is expected to amount to 250 endemic cichlid species in Lake Tanganyika, and represents the morphologically, behaviorally, and ecologically most diverse species assemblage (Snoeks, 2000; Turner et al., 2001), even though the number of endemic cichlids is much higher for Lake Malawi (500–1,000) and Lake Victoria (>500; Turner et al., 2001). In contrast to the mono- or di-phyletic origin of the haplochromine cichlids in the species flock of Lake Malawi and the “superflock” of Lake Victoria, which includes the cichlid fauna of neighboring rivers and lakes such as Lake Albert, Edward, George, Kyoga, and Kivu (Meyer et al., 1990; Moran et al., 1994; Nagl et al., 2000; Seehausen, 2002; Verheyen et al., 2003; Takahashi et al., 2001a; Terai et al., 2004), the cichlids of Lake Tanganyika are of polyphyletic origin and comprise both substrate breeding and mouthbrooding lineages (Salzburger et al., 2002a; Koblmüller et al., 2005). While the cichlid species radiation in Lake Tanganyika enjoys a longstanding reputation among biologists, the lake’s small flocks of other organisms—catfish, spiny eels, Nile perches, as well as groups of

gastropods, crabs, and shrimps (Coulter, 1991)—have been less intensively studied. Only recently, studies explicitly focused on some of these less species-rich flocks of Lake Tanganyika: the squeaker catfishes of the genus *Synodontis* (Day & Wilkinson, 2006; Koblmüller et al., 2006), thiarid and thalassoid gastropods (e.g., West & Michel, 2000; Wilson et al., 2004), platythelphusid crabs (Marijnissen et al., 2006), and atyid prawns (Fryer, 2006). To date, however, the most comprehensive data exist for Lake Tanganyika's cichlids, and this article presents a synthesis of recent molecular phylogenetic work on the lake's cichlid species assemblage.

Classification of Lake Tanganyika cichlids into tribes and their phylogenetic relationships

Based on morphological characteristics, the Tanganyikan cichlids have been classified into 12 (Poll, 1986) or, more recently, 16 tribes (Takahashi, 2003),

which are largely supported by molecular data (see Table 1). However, some disagreement exists. Poll (1986) assigned the two species *Oreochromis tanganyicae* and *Boulengerochromis microlepis* to the tribe Tilapiini. In a mitochondrial phylogeny of the Tilapiini, *B. microlepis* clusters with *Tilapia sparrmanii*, a species widely distributed in southern African rivers (Klett & Meyer, 2002), but bootstrap support was very low. Takahashi (2003) erected a new tribe—Boulengerochromini—for the monotypic genus *Boulengerochromis*. The erection of a new tribe is indeed supported by nuclear genetic data, which place *B. microlepis* within the Lake Tanganyika cichlid species flock, albeit at different positions (Nishida, 1997; Terai et al., 2003; Clabaut et al., 2005; Sugawara et al., 2005). These studies, however, included only a few if any tilapiine species, and the systematic placement of *B. microlepis* in the context of other nonmouthbrooding tilapiine cichlids will require further phylogenetic analyses with representative taxon sampling of both tilapiine and Lake Tanganyika lineages.

Table 1 Classification of Lake Tanganyika cichlids into tribes according to Poll (1986), Takahashi (2003), and as suggested by molecular data

Poll, 1986	Takahashi, 2003	Molecular classification ^a	
Tylochromini	Tylochromini	Tylochromini	
Tilapiini	Tilapiini	Tilapiini	
	Boulengerochromini	Boulengerochromini	
Bathybatini	Bathybatini	Bathybatini	Bathybatini
			Hemibatini
Trematocarini			Trematocarini
Eretmodini	Eretmodini	Eretmodini	
Lamprologini	Lamprologini	Lamprologini	
Ectodini	Ectodini	Ectodini	
Cyprichromini	Cyprichromini	Cyprichromini	
Perissodini	Perissodini	Perissodini	
Limnochromini	Limnochromini	Limnochromini	
	Greenwoodochromini		
	Benthochromini	Benthochromini	
Haplochromini	Haplochromini	Haplochromini	
	New tribe ^b	?	
Tropheini	Tropheini	Tropheini form monophyletic sub-group within the Haplochromini	
	Cyphotilapiini	Cyphotilapiini	

^a References for molecular data: Nishida, 1997 (note that in this study based on allozyme data *Gnathochromis permaxillaris* was not resolved within the Limnochromini); Salzburger et al., 2002a, 2005; Clabaut et al., 2005; Koblmüller et al., 2005

^b Takahashi (2003) erected a new tribe for '*Ctenochromis benthicola*'. Since its genus name is unlikely to remain valid in future, Takahashi (2003) refrained from assigning a name to this new tribe

According to Poll's (1986) classification, the Bathybatini include the genera *Bathybates* and *Hemibates*, and the Trematocarini comprise *Trematocara* and *Telotrematocara*, whereas Takahashi (2003) joins all four genera into a single tribe, the Bathybatini. In contrast, mitochondrial data (Koblmüller et al., 2005) indicate that Poll's Trematocarini and the genera *Bathybates* and *Hemibates* constitute three equally divergent lineages. Hence, the molecular data support Takahashi's comprehensive Bathybatini, or, alternatively, suggest a split of Poll's (1986) Bathybatini into the Bathybatini and a new tribe, Hemibatini.

Among the remaining tribes, the Eretmodini, Lamprologini, Ectodini, Cyprichromini, and Perissodini are identical in both Poll's and Takahashi's classification. Their respective monophyly is also well supported by molecular data (Sturmbauer & Meyer, 1993; Sturmbauer et al., 1994; Takahashi et al., 1998; Salzburger et al., 2002a; Koblmüller et al., 2004, 2007b; Brandstätter et al., 2005; Duftner et al., 2005). In Takahashi's classification, Poll's Limnochromini were split into the tribes Limnochromini, Greenwoodochromini (comprising *Greenwoodochromis bellcrossi* and *G. christyi*), and Benthochromini (including *Benthochromis melanoides* and *B. tricoti*), of which the Greenwoodochromini are not supported by molecular data. While, based on mitochondrial DNA sequences, the genus *Benthochromis* constitutes a distinct lineage, the genus *Greenwoodochromis* is clearly nested within the Limnochromini (Duftner et al., 2005).

The Haplochromini, which comprise the major cichlid species flocks in the remaining East African rift lakes and the vast majority of the African riverine cichlid fauna (except for western Africa), are the most species rich cichlid tribe in Africa. Nevertheless, only a few haplochromine cichlids occur in the Lake Tanganyika basin, and even these are usually found in river mouths of inflowing rivers rather than in the lake itself. Only two truly lacustrine species were originally assigned to the Haplochromini by Poll (1986), *Ctenochromis benthicola* and *C. horei*. Takahashi (2003) erected a new tribe for *C. benthicola*, but as the genus name will not remain valid, he did not suggest a name for the new tribe. Molecular work on the phylogenetic placement of *C. benthicola* is still needed. The second species, *Ctenochromis horei*, is currently assigned to the Tropheini (Takahashi, 2003), which is also confirmed by both

mitochondrial and nuclear molecular data (Sturmbauer et al., 2003; Koblmüller, Egger & Sefc, unpublished data). Takahashi split the Tropheini into two tribes, Tropheini and Cyphotilapiini, a hypothesis strongly supported by lepidological (Lippitsch, 1998) and molecular data (Nishida, 1997; Salzburger et al., 2002a; Clabaut et al., 2005; Duftner et al., 2005). Furthermore, a recent molecular study showed that the Tropheini constitute a monophyletic lineage within the Haplochromini (Salzburger et al., 2005).

Hypotheses regarding the molecular phylogenetic relationships between the distinct tribes differ slightly depending on whether nuclear or mitochondrial data are used. Nuclear data support, with the exception of *Tylochromis polylepis* and *Oreochromis tanganyicae*, a monophyletic group including the whole Lake Tanganyika cichlid species flock (including the Orthochromini from the Malagarazi system and the Haplochromini, which are distributed from northern to southern Africa, but are supposed to have their origin in Lake Tanganyika). One should note, however, that all nuclear phylogenies available to date are based on a rather incomplete taxon sampling concerning riverine species that might potentially cluster within the Lake Tanganyika cichlid species flock. Thus, the available nuclear data allow only limited conclusions concerning the phylogenetic inter-relationships among the major ancestral Tanganyikan lineages and riverine tilapiine lineages. Both mitochondrial (Klett & Meyer, 2002; Salzburger et al., 2002a; Koblmüller et al., 2005) and nuclear data (Takahashi & Okada, 2002; Terai et al., 2003) suggest that the Trematocarini, Bathybatini, and *Hemibates* are ancestral to the so-called MVhL-clade (Takahashi et al., 2001b), which includes the species flocks of Lake Malawi and Victoria, the H-lineage (comprising the Eretmodini, Limnochromini, Benthochromini, Ectodini, Perissodini, Tropheini, Cyphotilapiini, and Haplochromini; Nishida, 1991), and the Lamprologini. The H-lineage was defined by Nishida (1991) based on allozyme data. However, mitochondrial data rejected the H-lineage in its original composition, since the Eretmodini were placed either as most ancestral lineage within the MVhL-clade or as sister group to the Lamprologini (Salzburger et al., 2002a, 2005; Clabaut et al., 2005; Koblmüller et al., 2005). This led Clabaut et al. (2005) to define the C-lineage, which is equivalent to the H-lineage except for the exclusion of the

Eretmodini (Fig. 1). All phylogenetic hypotheses suggest, regardless of the markers used, a period of extremely rapid cladogenesis at the base of the radiation of the C-lineage, leading to the formation of

several tribes, whose inter-tribal phylogenetic relationships could not be resolved with confidence so far (Sturmbauer & Meyer, 1993; Streebman et al., 1998; Takahashi et al., 2001b; Salzburger et al., 2002a,

Fig. 1 Schematic molecular phylogeny of the Lake Tanganyika cichlid species assemblage based on combined evidence from several studies. No molecular data exist for *Ctenochromis benthicola*, and this species was placed as a distinct tribe within the Lake Tanganyika cichlid species assemblage according to Takahashi's (2003) morphological classification. Lineages that underwent radiation are indicated by triangles, whose size corresponds to the species number within the lineage (except for the very species-rich nonTanganyika haplochromines). Gray triangles indicate lineages that do not occur in Lake Tanganyika. The "primary lacustrine radiation" is assumed to have coincided with the establishment of a true lacustrine habitat with deep-water conditions about 5–6 MYA. Bars to the right indicate taxonomic groups that have been proposed based on combined mitochondrial and nuclear DNA sequence data (C-lineage; Clabaut et al., 2005), allozyme data (H-lineage; Nishida, 1991), and SINEs (MVhL-lineage; Takahashi et al., 2001b). Note that the phylogenetic history of most tribes is much better resolved than illustrated and that branch lengths and proportional times of radiation are not to be taken as accurate

