

AFRICAN CICHLID FISHES: Model Systems for Evolutionary Biology

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■ **Abstract** Cichlid fishes (Perciformes: Teleostei) found in the lakes of Africa have served as model systems for the study of evolution. The enormous number of species (1000 in Lake Malawi alone), the great diversity of trophic adaptations and behaviors, and the extreme rapidity of their divergence (<50,000 y for some faunas) single out these organisms as examples of evolution in progress. Because these fishes are confined to discrete lacustrine environments and their origination is bounded by geological features, these groups provide models with which to study evolution. We review theoretical studies and empirical research on the cichlid faunas of Africa to provide a synthetic overview of current knowledge of the evolutionary processes at work in this group. This view provides the critical information needed to formulate and test hypotheses that may permit discrimination among the diverse theories and models that have been advanced to explain the evolution of these fishes.

INTRODUCTION

Periods of explosive speciation and adaptive radiation have punctuated the history of metazoan evolution. The cichlid fish faunas of lakes in Africa present singular opportunities to study such events. Lineages within the Cichlidae have diversified extensively in both the New World and the Old World (26, 67), but it is in Africa where the most spectacular examples of radiation and speciation are found. Because of this, African cichlids have been incorporated into many basic evolutionary texts (e.g. 172).

The cichlid fishes of Lakes Malawi, Tanganyika, Victoria (38, 66, 104), and the other, much smaller, African lakes (34, 155, 159) provide unique opportunities with which to investigate evolutionary processes (25, 67, 146). Times associated with diversification for many of these complexes are extremely short (83) (<50 ky for some faunas), the extent of trophic differentiation is extensive

(34) (ranging from plankton grazers to egg predators), and the number of endemic taxa is enormous [1000 species in Lake Malawi is a reasonable estimate (185)]. Because of these factors, the cichlids of African lakes provide geologically bounded systems within which to explore fundamental processes of speciation and diversification.

There is an extremely rich, speculative literature concerning the mechanisms underlying the processes of cichlid divergence (35, 118, 171, 184). The rapidity of radiations has suggested to many that some exceptional mechanism(s), including special water characteristics (91), habitat complexity (180), lake age (91), lake level fluctuation (32, 183), predation (42), mutation (34), hybridization (19), reproductive characteristics (22, 88), and trophic polymorphism (152) are necessary to explain the extent of cichlid radiation. Similarly, allopatric (45, 112), microallopatric (32), and sympatric (88, 155, 162, 185) modes of speciation have been suggested. There is general consensus that almost all of the endemic cichlid species and genera of Lakes Malawi and Victoria originated within the lakes proper (106); intralacustrine speciation is extensive in Lake Tanganyika, though it was clearly seeded several times (176). However, despite a wealth of recent theoretical and modeling efforts, limited empirical progress has been made in determining the critical factors that have accelerated or retarded diversification.

The possibility of sexual selection has raised enormous interest (184), but there have been few critical examinations of more conventional models of diversification. That is, alternative population processes such as subdivision, isolation, and drift may be significant driving forces for speciation at the geographic level. The extent of panmixia is not known, and the possibility of geographic structuring on local or regional scales has received limited attention (see below). Similarly, tests of many hypotheses have been hampered by the absence of reliable phylogenies for closely related species within the lakes. It may be beneficial to seek to reject null hypotheses of spatial variation prior to proposing more elaborate explanations for diversification.

In this contribution we assemble and review basic data on the geological and biological attributes that make African cichlid species unique and useful systems in which to study evolution. These faunas challenge simple application of species concepts; clarification of and consensus on this topic is of central importance to resolve persistent questions in cichlid evolution. Geographical models of speciation in African cichlids are summarized and empirical studies that have been offered as support for specific models are critiqued. The effects of fluctuating lake levels as a promoter of allopatric divergence are presented and examined. We offer a critical evaluation of the mechanisms potentially contributing to this spectacular diversification, discuss classical evolutionary forces as they apply to these cichlid fish systems, and offer speculation on alternative processes such as hybridization and the emerging mechanism of favor, sexual selection.

GEOLOGICAL FRAMEWORK AND CICHLID RADIATIONS

One of the most compelling aspects of the African cichlid fauna is that geology indicates that diversification of species and entire faunas has occurred at rates that many biologists have found difficult to accept. Further, geophysical processes have also played a central role in the formulation of hypotheses about mechanisms of diversification.

Rates and ages of cichlid diversification have been inferred from three elements: geological history, topography, and comparative genetic analysis. Early estimates for the ages of the African great lakes were based on gross geological features external to the lakes (34); more recent age estimates and, particularly, dates for lake level variations have been based on evidence from coring, acoustic profiling, climatic data, and modeling (reviewed in 17, 58). Estimates of maximum ages for Lake Tanganyika range from 9 to 12 my, 4 to 9 my for Lake Malawi, and 0.5 to 1 my for Lake Victoria (104). Extensive sediments (>4 km) in the basins of Lakes Malawi and Tanganyika testify to an aquatic environment of long duration, though such sedimentation need not be continuous.

Ages of the cichlid faunas estimated indirectly from molecular data assume that the markers being used behave as reasonably constant molecular clocks. This assumption may not hold when dealing with very divergent cichlid lineages (26) and is subject to modifications associated with geography, population structure, and behavior (53). Relative levels of sequence divergence suggest that the endemic cichlid fauna of Lake Victoria is of extremely recent origin (120, 121, but see 126). In Lake Malawi, divergence between the two major clades of endemic haplochromines may be on the order of 1 my (125), while divergence among taxa within these lineages is extremely recent (123, 138) and comparable to that observed in Victoria. In Tanganyika, divergence between cichlid tribes is extensive (76), and some predate the estimated age of the lake (176). Many lineages within tribes are well differentiated (76, 130), but some diverse genera possess numerous species which are also of extremely recent origin (173, 175).

Historical Lake Level Fluctuations and the Age of Cichlid Faunas

The time during which a lake has been able to support teleost faunas depends on lake characteristics, particularly topography, maximum depth, and number of basins. Evidence of desiccation and geological structures associated with shallow water sedimentation provide evidence for the boundaries of such events. However, sedimentary profiles are complex and rates of sedimentation are variable in time and space (59). Lake Tanganyika is now composed of three discrete basins separated by shallow sills; lake level declines in excess of 550 m serve to isolate these regions, and desiccation occurs with declines in excess of 1000 m (173). Approximately

1.1–0.67 mya the northern basin itself may have contained multiple lakes (17). Though originally separated, the three basins of Lake Tanganyika have remained continuously connected as a single lake for >21 ky. By contrast, Lake Malawi is composed of one basin that could not have been fragmented into isolated sub-basins. With a maximum depth of 800 m in the northern rift, Malawi has probably never been subject to complete desiccation, but given shoaling topography in the southern regions, lake level decreases of ~100 m would result in desiccation and could eliminate many narrow endemics. Similarly, the form of Victoria is a single, shallow basin (maximum depth of ~80 m). Such topography makes much of the fauna vulnerable to the effects of drying events.

New data suggest that earlier estimates of recent lake level fluctuations (157) may have been inflated. A review of data for lake level declines suggests that Lake Tanganyika was depressed 600 m approximately 200–75 kya and 300 m approximately 21–13 kya (58). Depressions of ~250 m for 190–170 kya and ~160 m for 40–35 kya have also been estimated (17). In Lake Malawi, lake level was 200–300 m lower than present 40–28 kya, and 100–150 m lower than present 10–6 kya (29). Desiccation of Lake Victoria has been estimated to have occurred 12 kya (60). Approximations of the timings of past lake levels depend upon rates of sedimentation. However, extrapolation of sedimentary rates is subject to considerable uncertainty, especially because the rates are based on relatively few radiocarbon dates that are themselves subject to considerable error (T Johnson, personal communication).

Numerous lake level fluctuations have been documented for all studied African lakes, but there is no consensus regarding continental coordination. Lake Tanganyika and Lake Victoria appear to vary in concert with glaciation events (13, 37), while Lake Malawi appears out of phase with these more northern lakes (29, 58). In consequence, it is difficult to establish a single geohydrological mechanism driving these potentially biologically significant events.

The hypothesis of complete desiccation of Lake Victoria (60) has had a singular impact on models of rapid cichlid diversification, particularly if, as claimed, refugia for endemics were absent during such events. In the absence of refugia, virtually all of the current diversity in the lake would have been generated since the most recent desiccation, 12 kya. However, paleolake Natron/Magadi in an adjacent basin experienced a significant increase in water level (60 m) at almost precisely the same time as Lake Victoria dried (158). Further, presumed endemism of non-cichlid fishes and aquatic invertebrates challenges the idea that refugia were absent in this region (33). For example, at least 11 species of gastropods are endemic as well as two catfishes with deep water adaptations. Thus, the rates of diversification of the Victorian cichlid fauna are unclear. A similar situation exists for Lake Malawi where sediment analysis, hydrological modeling, and oral tradition suggest that the southern portion of the lake was dry approximately 200 ya (134). Because of the large number of endemic cichlids in this region (145), speciation rates would have to have been extremely rapid to generate the current diversity. However, a synthetic review of available information suggests only minor

lake level fluctuations in the last millennium (128). In general, resolution of the timing involved in abiotic processes will permit a fuller understanding of the biological impact of hydrological events.

BASIC BIOLOGY

Given the extremely large number of cichlid species, there is immense variation in virtually all aspects of their ecology, behavior, and reproductive biology (34). Comprehensive field studies have focused on pelagic and sand communities of Lakes Victoria (39) and Tanganyika (66), and particularly on rocky littoral faunas of Lakes Malawi (145), Tanganyika (149), and Victoria (160).

Ecological Diversity

Taxa in all of the African great lakes provide extensive examples of adaptive radiation, spanning trophic guilds that include benthic algae grazers, sand-dwelling planktivores, pelagic piscivores, ambush predators, and specialized pursuit predators (for summaries, see 24, 34, 44, 56). This diversification may have been facilitated by a key innovation associated with pharyngeal jaws (56a). The extent of trophic diversification (and associated behavioral adaptations) is similar among lakes, but reaches its most extreme in Lake Tanganyika where cichlids are represented by multiple tribes with long and distinct evolutionary histories (129, 173). In each lake, faunas may be divided into several basic ecological guilds on the basis of habitat preference and, in several cases, also by genealogy (125). One group typically inhabits shallow waters surrounding rocky outcrops, a second occurs over sandy sediments at a variety of depths, and a third is principally pelagic. In all lakes, additional specialization occurs within habitats, exemplified by species inhabiting swamps or abandoned gastropod shells (154). In the large lakes, some taxa change habitats during the reproductive season. In the deep rift lakes of Tanganyika and Malawi, cichlids are absent from anoxic waters at depths >100–200 m.

In several regions within the African great lakes, habitats are discontinuous: rocky islands may be isolated by surrounding sandy substrate, and many coastal areas are characterized by alternating patches of rocks and sand on scales of 1–10 s of km. In other regions, habitats are continuous for 10–100 s of km.

Within these habitat-defined groups, there may be gross similarities in trophic adaptations among taxa, but virtually all sympatrically occurring species examined to date differ in obvious or subtle aspects of resource exploitation (10, 142, 149). For example, differential exploitation of invertebrates and associated microfloras in sandy habitats may be realized either via diversity of oral dentitions or via specialized grazing behaviors (24); mutualistic interactions are also common cichlid resource utilization strategies (65). Though trophic differentiation may be inferred through morphology and behavior, in situ observations have revealed

food-switching with fluxes in prey abundance (115); this phenomenon may be particularly apparent during plankton blooms (11), suggesting that species-specific strategies and adaptations may be of greatest significance in the relatively leanest times. However, in a well-studied community in Victoria, niche differentiation was not obvious among some taxa (11). Comprehensive understanding of the importance of trophic specialization to generation and maintenance of species diversity may thus mandate long-term observation.

One ecological guild, the rockfishes, is of particular interest to speciation theorists; they include the mbuna in Lake Malawi, the mbipi in Lake Victoria, and multiple lineages in Lake Tanganyika. The mbuna, one of the most extensively studied groups (81, 145), is a useful example; species of *Tropheus* and other genera, such as *Simochromis* and *Petrochromis*, form an analogous group in Lake Tanganyika (82, 174). The mbuna constitutes a diverse monophyletic group of >300 species in 10 genera that feed and breed primarily on algae-covered rocks and cobbles in relatively shallow (<20 m) water. Some species are extremely abundant with >10⁶ individuals along continuous habitats (145), while other taxa are rare. Most mbuna have extremely restricted dispersal abilities (50, 115) and are generally absent from areas of sand, sediment, and deep water, which act as barriers to dispersal (103). Preliminary genetic study suggests that within rocky outcrops, male dispersal may be greater than that of females (74), but both fine-scale and long-term analyses have yet to be conducted. In a similar manner, rockfish in Lake Tanganyika show extremely weak dispersal (173). In all of these faunas, many common species are widely distributed, but typically have discontinuous distributions.

Reproduction

Modes of reproduction in African lake cichlids are extremely varied (34, 66, 67). Because of intense predation, diverse strategies for protection of eggs and fry have evolved. Oral incubation has independently arisen many times in cichlids (40) and is practiced by all Lake Malawi and Lake Victoria endemics; in Lake Tanganyika, several lineages also utilize this form of parental care. Microsatellite-based paternity analysis for a number of mbuna species has demonstrated multiple paternity with up to six males fertilizing a single clutch (68, 137); polygyny has also been observed in sand-dwelling Lake Malawi cichlids (113). The evolutionary significance of multiple mating by females is problematic (193a).

In Malawi, males of *Metriaclima*(= *Pseudotropheus*) *zebra* (167) and related mbuna defend small (~1-m²), permanent territories primarily against conspecific males. These areas serve as foci for breeding and male foraging. Territories are densely packed and often overlap those of other mbuna. In *M. zebra*, appropriate rocky substrate for such territories is limited; removal experiments demonstrate rapid species-specific colonization by non-territorial males (48; I Kornfield, unpublished data). In Lake Tanganyika, removal experiments for several species

show similar results (36, 55, 78). Because of this space limitation, only a fraction of males in a population can hold territories and thus potentially breed. Although sneaker males may occur in some taxa (149), none have been observed in *M. zebra*. Further, males may maintain territories for several (>2.5) years (48; I Kornfield, unpublished data). Thus, for some taxa, space per se is a major reproductive resource (194). In these and related species, territory acquisition and defense may be the most critical factors influencing male reproductive success.

By contrast, females in *M. zebra* are non-territorial, although they are markedly philopatric (50). Females forage on algae-covered substrates across the territories of many species. When reproductively active females swim over areas of densely packed territories of conspecific males, they are solicited by territorial males using behavioral displays such as side presentation and leading (108). Comparative behavioral analyses and extensive in situ observation of the mbuna have not demonstrated species-specific variation in these behaviors (108). Spawning occurs when a female follows a male down to his territory, where he continues to display; the female deposits one or several eggs that she immediately puts in her mouth. In *M. zebra*, fertilization may be achieved while the eggs are still on the substrate or after they are in the mouth of the female. Females leave the male territory following the reproductive bout, although they may return for subsequent matings. Clutch size in rockfish from all lakes is small, ranging from ~10 to 50 eggs; with determinate growth, buccal cavity size may limit reproductive output (132). Following oral incubation for several weeks, females deposit free-swimming fry in rocky crevices (182). There is thus no opportunity for behavioral imprinting in these taxa. However, in other mouth-brooders, females guard schools of foraging fry for extended periods and protect them from predation by gathering them back into the mouth (81). In these latter cases, post-hatching interactions between parent and offspring do represent an opportunity for cultural (i.e. extra-genetic) transmission of behavior to succeeding generations (153), although no such occurrence has been documented to date.

The reproductive behavior of many species of sand-dwelling fishes is similar to that of *M. zebra* (113, 149). In species that spawn on sandy substrates, males commonly build and defend nests or "bowers" (187, 193) in dense aggregations. Male-male interactions on such leks are extensive, and sneaking is a common strategy (67). Females mate with multiple males that, as for male mbuna, provide no resources other than fertilization.

In some of the substrate-guarding endemic Tanganyikan lamprologines, familial communities are established where young act as helpers at the nest (36, 154). Because of space limitations, some sub-adults cannot find a place to breed and help their parents instead. In these taxa, many of which are shell-brooders, mating systems are extremely polygynous, nest-brooding females adopt gregarious behaviors, and opportunities for social interactions are extensive. There may be great advantage in numbers to avoid predation.

In summary, there is a premium on available substrate for reproduction in all these systems. This is nearly universal for males, but extends to females in the case of substrate guarders. The intense predation on early life-history stages in these fishes has promoted the development of diverse protection strategies. In turn, these strategies have influenced the development of community-wide behaviors.

Sensory Modalities

In general, cichlids perceive chemical stimuli and differentiate species or reproductive condition on the basis of olfaction/taste (127). While little is known about specificity of odor production among closely related species, the dynamics of odor transmission in aquatic environments (28) suggests that this modality would be expected to be of limited value in rapid interactions among conspecifics. Similarly, acoustical communication has been demonstrated in a variety of cichlid species (127). Extensive ambient sound is associated with feeding activities and with some other behaviors. In situ measurement of sound production in Lake Malawi demonstrated the potential for conspecific recognition using auditory cues; significantly different pulse rates within calls were associated with courtship in two sand-dwelling species (99). Whether this sensory modality has played a role in evolutionary differentiation is unclear.

Males of most rockfishes in Lakes Malawi (81, 45), Tanganyika (79, 82), and Victoria (160) have dramatic breeding coloration in which there is tremendous variation. Female coloration is generally so drab that specific identification can be taxonomically challenging (e.g. 190). Variation in coloration is extensive within species complexes; the colors of males in Malawi mbuna have been analyzed qualitatively (21, 110), and certain hues are more common than others. In *M. zebra* and other taxa, quantitative reflective scanning demonstrated intense coloration ranging from UV through long wavelengths (84). Analysis of visual systems in a number of African species has demonstrated multiple absorption maxima across the visible spectrum (27, 188). Vision in the UV portion of the spectrum has been convincingly demonstrated for mbuna species based on microspectrophotometry, analysis of opsin genes (15), and electroretinograms of retinal bipolar cells (9). Thus UV colors, unperceived by human observers, could play diverse roles in cichlids, as they may in other fishes (100).

While the bulk of intraspecific phenotypic differentiation of males occurs among allopatric populations (79, 145), extensive variation may be present within populations. Variation in male coloration within populations has been documented in Lakes Malawi (81), Tanganyika (82), and Victoria (161). For example, in the *M. zebra* species complex, males in many populations exhibit continuous variation in colors and color patterns (Figure 1; see color insert). The relevance of color variation to taxonomic differentiation remains a central question in the evolution of the East African cichlid species flocks.

SPECIES CONCEPTS, DIVERSITY, AND TAXONOMY

Discussions about definitions of species have dominated the cichlid literature for many years. Although most research before 1980 assumed the Biological Species Concept (BSC) of Mayr, subsequent studies considered alternative definitions. While the BSC or “isolation concept” has been called the most useful species concept for the study of speciation, alternative approaches have been explicitly championed by some cichlid researchers. The recognition concept of Patterson (139), which defines species as groups that share common fertilization systems, and the cohesion concept (181) have been emphasized (46, 143, 144, 173, 185).

Understanding the speciation process may depend upon the species concept employed (181). For this reason, Ribbink (144), Sturmbauer (173), and Turner (185) have chosen non-relational species concepts in the study of cichlid evolution. However, the species concept debate can also be viewed as semantic. Indeed, regardless of the species concept used, the processes (genetic drift, natural selection, sexual selection, etc) involved in the early divergence of populations are the same, whether they are seen as divisive or cohesive. Confusing issues surrounding the use of the BSC may result from what has been observed as a tendency of biologists to create caricatures of one species concept in order to clarify the reasoning of another (47). Here we adhere to the reasoning of the BSC, but do not reject the incorporation of alternate views.

Species Definitions

How are species recognized? Because of their phenotypic similarity and patchy distribution, distinguishing species is problematic (173). When sympatric, biological species have been demonstrated by *in situ* observations of assortative mating by color morphs (e.g. 54, 166; P Reinthal, unpublished information; JA Stauffer, personal communication). More typically, species have been established (or their status confirmed) by studies that report significant differences in frequencies of molecular markers among sympatric morphs (83, 111, 116, 190) or by laboratory examination of mate discrimination (72, 73, 165).

In allopatry, differences in male breeding coloration have been uniformly employed to recognize species, while qualitative differences in dentition and osteology have been important in defining genera and species groups (96). It is nearly universally presumed that the existence of unique male breeding coloration is sufficient to delimit species (24, 45, 81, 96, 145, 185.). Though a few taxa have wide distributions, most species defined on the basis of color are “narrow endemics,” restricted to specific islands or rocky outcrops (81, 145). Note that under an ecological species concept, closely related allopatric populations differing only in color may be the same species if they all occupy the same ecological niche. Indeed, many geographic variants, strikingly different in coloration, possess indistinguishable trophic adaptations and foraging ecologies (174; I Kornfield, unpublished

information). Such geographical color variants may be of central importance to reproductive isolation and generation of diversity. Comparative studies of sympatric and allopatric populations in different stages of divergence may provide the most profound insights into geographic modes of speciation (30).

Taxonomic Diversity

Most species of African cichlids have yet to be formally described. The task of cataloging the diversity of the East African great lakes is particularly difficult both because of the large number of species (38) and because of the obscurity of species boundaries (173). In the case of allopatric populations showing geographic color variation, reproductive isolation may never be tested in nature. While allopatric populations are not necessarily biological species, the magnitude of novel coloration may merit taxonomic recognition. For example, newly discovered cichlids are given descriptive names in order to distinguish them from all other populations [e.g. "*Pseudotropheus* species tropheops mbenji blue" (see 81, p 53)]. With extremely few exceptions, allopatric variants have not been assigned subspecific epithets, although several such populations have recently been given specific status (167). However, because of the ubiquity of geographic variation, considerable care needs to be exercised in defining taxa and interpreting taxonomic definitions. In particular, we emphasize the need to examine adequate sample sizes of organisms and to make in situ observations of coloration; in the absence of such practices, artificial species may be created (Figure 1; cf 167). Additionally, it is important to recognize the subtle yet critical difference between population differentiation and speciation (102). The inability to distinguish between these two biological processes may confound evolutionary studies.

CENTRALITY OF PHYLOGENETIC RECONSTRUCTION

Differentiating alternative explanations for patterns of divergence and the processes that drive them requires robust hypotheses of relationships among species. Organismal phylogenies are essential for adjudication of the roles that special processes or characters may play in the speciation process. In the Cichlidae, there is extensive potential for convergence or parallelism in trophic or morphological domains (94). Among haplochromines, the most speciose lineage of African cichlids, morphological similarity and ecological equivalence are obvious among the three major lakes (34, 170). Within lakes, the magnitude of similarity is striking as well (24, 44). If convergence is real, the use of standard ichthyological characters for the construction of phylogenies, particularly those associated with dentition, can be misleading.

The study of lepidological variables (those derived from scale morphology and squamation pattern), pioneered by Lippitsch (97), has proved exceedingly valuable in establishing interrelationships among some groups of African cichlids. They have been used to demonstrate monophyly in the well-defined tribes in Lake

Tanganyika and to erect a phylogeny among some of these lineages (98); they also appear useful for defining lineages among some groups of more closely related haplochromines (160). While general application of this approach to some haplochromine taxa has been problematic (90), it shows promise for well-defined groups.

Given the potential for convergence, it is clear that phylogenies generated from characters independent of morphology are desirable. More specifically, findings from molecular studies are central to resolving debates involving such attributes as behavior and morphology. Molecular studies have clarified relationships for the Cichlidae in general (26) and among African great lake cichlids, and have begun to provide insights among taxa within lakes. The seminal paper by Meyer and coworkers (120) using mtDNA demonstrated monophyly of the faunas of Lakes Malawi and Victoria and established relationships of the cichlid faunas among lakes. The often cited convergence among the mbuna of Lake Malawi and the rockfishes of Lake Tanganyika was unambiguously confirmed by Kocher and colleagues (75) with comparative mtDNA sequence analysis; subsequent analyses established sister-group relationships between faunas of Lakes Malawi and Tanganyika (118). Relationships among tribes within Tanganyika and confirmation of multiple invasions of portions of this fauna were initially established with allozymes (129, 130) and have been extended and clarified using mtDNA data (76, 175, 176). SINES (Short Interspersed Nuclear Elements) have been exploited to support monophyly of several Tanganyikan tribes (179). The unique insertion events associated with SINES are compelling, but the sensitivity of this assay among very closely related cichlids may be limited (179).

Elucidating the relationships among more recently diverged taxa using molecular techniques has been problematic. While mtDNA proved useful to understand divergence within several lineages in Lake Tanganyika (174), it discriminates only major, divergent clades in the Lake Malawi fauna (125). The reason that mtDNA failed at lower levels is that many taxa retain ancestral polymorphisms (123, 124); comprehensive analysis of mtDNA revealed extensive retained polymorphism throughout the Lake Malawi fauna (138). The absence of lineage sorting of mtDNA compromises interpretation of molecular data in a phylogenetic context (12, 141) in which gene trees may masquerade as species trees (6). In Lake Victoria and surrounding waters, neutral nuclear polymorphisms have persisted in cichlids for extended periods of time (126). Extreme caution needs to be exercised in exploiting sequence data (70, 133, 178) for phylogenetic analyses in cichlid fishes, particularly where samples sizes are limited. Note, however, that molecular polymorphisms may be useful tools for examining other aspects of the evolutionary process (16, 71) such as effective population size.

Multilocus comparisons have demonstrated the utility of microsatellites to distinguish groups of closely related taxa (85). This class of markers appears to be sufficiently informative to erect statistically compelling phylogenies among some closely related species (PF Smith & I Kornfield, in preparation). In like manner, large numbers of AFLPs (Amplified Fragment Length Polymorphisms) have been used to examine phylogenetic relationships among several well-defined groups of

mbuna (1). In distance analyses, significant phylogenetic affinities among groups of congeners were demonstrated, but statistical support for intergeneric relationships was more limited (1).

In general, the difficulty in establishing phylogenies reflects the short intervals of time that must have transpired during generic-level divergence. If diversification is concentrated in short periods associated with major hydrological events such as lake expansions, speciation may effectively occur over wide geographic areas. In such cases of near simultaneity, resultant star phylogenies may reflect hard polytomies (52) rather than an inability to resolve underlying signals. Distinguishing such bursts of speciation from soft polytomies may be possible if there is resolution above and below the event in question (95). Because of the desirability of a phylogenetic framework for evaluating hypotheses of origination and their associated mechanisms (14), additional research should be vigorously pursued.

GEOGRAPHICAL MODELS OF SPECIATION IN CICHLID FISH

Monophyly of Lake Malawi and of Lake Victoria cichlids suggests intralacustrine speciation, but strictly speaking, this is different from sympatric speciation. Several authors have developed scenarios whereby intralacustrine speciation occurs in an allopatric mode. Macro-allopatric speciation results from differentiation between separate basins, and micro-allopatric speciation is caused by differentiation between patches of fragmented habitat or via isolation by distance (121, 148). Sympatric speciation is used in reference to divergence in the absence of geographical barriers to gene flow (O Seehausen & JJA van Alphen, submitted for publication; 162). Here we consider speciation from allopatric and sympatric perspectives.

Allopatry

One general model for allopatric speciation, the “Nabugabo scenario,” was articulated by Greenwood (42) for Lake Victoria. In this widely cited scheme, very minor fluctuations in lake level would serve to isolate fish in small, peripheral lakes over short periods of time (<4 ky); such lakes could generate endemics that might retain specific identity upon reunion with Victoria and thus contribute to cumulative diversity. Difficulties with the evaluation of this model based on the present condition of the lake (64) have included the inability to confirm that extant “peripheral endemics” are truly absent from Lake Victoria and the observation that some “peripheral endemics” have been found in multiple satellite lakes (31, 131). There has also been faunal interchange among other lakes in the region (63). Nevertheless, given that the extensive and exceedingly complex shoreline of Lake Victoria has not been systematically surveyed (63), the idea that novel assemblages of endemics might have persisted and reinvaded Lake Victoria remains appealing.

Fryer (32) presented a hypothesis of intralacustrine speciation that does not require fragmentation of a lake basin into separate bodies of water. In his scenario for Lake Malawi, allopatry is achieved by highly philopatric cichlids occupying isolated areas of habitat, allowing genetic divergence to take place over distance (see 83, 103). In Lake Tanganyika, secondary contact between divergent populations of *Tropheus* inferred from biogeography illustrate micro-allopatric divergence (34). Subsequent molecular studies of several Tanganyikan rockfish lineages (177) have revealed patterns ranging from localized differentiation to continuity. The extent of population structure is important to all allopatric models of cichlid speciation, regardless of the proposed mechanism, because greater population subdivision implies a greater number of discrete entities subject to genetic drift and selection. While divergence in allopatry (micro-allopatry) may provide some insight into the early stages of intralacustrine speciation, there is a great deal still unknown about why divergence of sexual characteristics in allopatry would be so rapid and how newly divergent populations could survive presumed repeated bouts of secondary contact to become new species.

Evolutionary Implications of Lake Level Fluctuations

Changes in habitat are associated with lake level fluctuations; these events could be central to understanding broader patterns of radiation and, perhaps, mechanisms controlling diversity and rates of speciation. Repetitive changes in lake level might continually create new opportunities for isolation in allopatry. Such potential effects were explicitly noted in early studies (32,42) and have been considered by many others (112, 173). For example, two hypotheses have been presented to explain the presence of many species endemic to small islands in the southern shallow areas of Lake Malawi. First, it may be that these taxa predate the most recent rise in lake level; in this scenario, current island endemics arose through colonization of the newly flooded islands by species followed by their subsequent extinction in their former ranges. Alternately, when the southern portion of the lake was flooded, the newly formed islands were initially colonized at random by individuals of various mbuna species that are still extant elsewhere in the lake; these founding individuals subsequently diverged to produce new taxa. Repeated lake-level fluctuation events could be viewed as facilitating taxon-cycles (63) and, depending upon biogeography and lake basin topography, could act as “species pumps” (148) to increase endemic diversity.

An appreciation of the details of this process offers opportunities to understand the roles that natural selection and genetic interchanges may play in the overall process (Figure 2). In the most general model, discrete basins and their surrounding habitats would act as refugia during lake regressions. Extinction would be elevated during these periods; taxa that are resident in such areas would not be tested by intense competition to the same extent as species that were forced to move into them. Previously allopatric taxa that were trophically distinct, or those that exploited some novel aspect of reproduction, would be candidates for persistence.

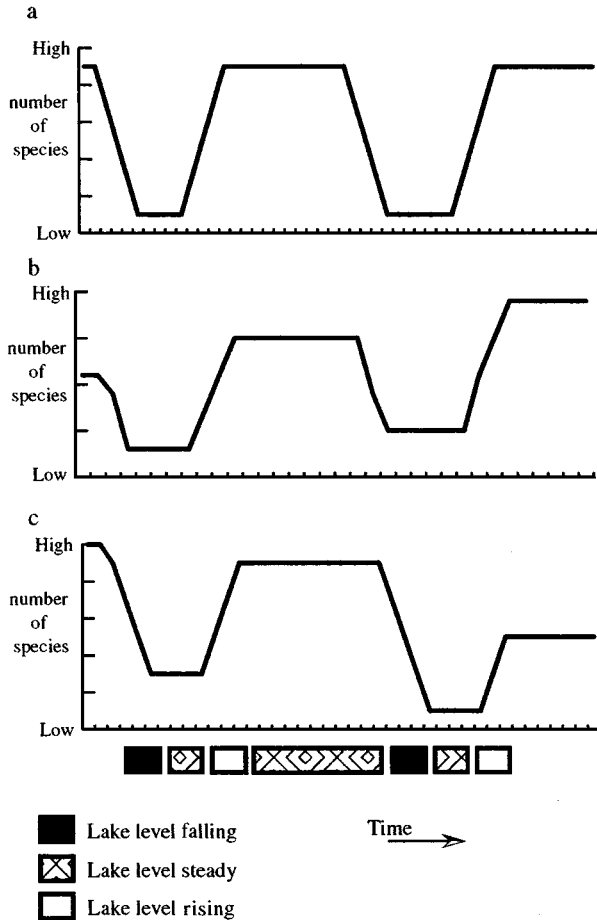


Figure 2 The effects of repeated lake fluctuations in cichlid species diversity. Extinction rates are high during periods of lake level drops (*black*), while speciation rates are high during lake level rises (*white*); when lake level is constant (*hatched*), speciation and extinction are in equilibrium. (a) Net number of species remains constant; (b) number of species increases with fluctuation cycles, the species pump (63, 148); (c) number of species decreases. See Sturmbauer (173) for alternative figure and discussion. See text for details.

During such ecological crunches, significant trophic differentiation might occur in some lineages, though overall species diversity should decrease. Reproductively isolated ecological cognates would be particularly susceptible to extinction. Narrow endemics that were uncommon or rare (145) would be expected to have high rates of extinction relative to taxa with large population sizes. In aggregate, diversity in refugia would increase as new taxa were added, but absolute space limitations for trophic and reproductive activities would suggest episodes of

increased competition in such shrinking environments. Depending upon the extent of crowding, opportunities for hybridization may be extensive (see Mechanisms Driving Differentiation below). With lake level increases, new habitats would become available; during this phase, opportunities for speciation might increase due to rapid population growth and reduced competition. During periods of relatively stable lake levels, speciation and extinction might be at equilibrium or, depending upon the mechanisms driving speciation (below), there might be an increase in species diversity. Overall, species diversity might remain constant at extended high water stands if extinction during regressions balanced speciation during expansion (Figure 2a). However, net species diversity might expand with increases in lake level cycles if new trophically differentiated lineages regularly arose (Figure 2b). With a large number of cycles, if selection during low stands were sufficiently intense, net species diversity might decrease and eventually fluctuate around some equilibrium (Figure 2c). Lake level cycles over long periods of evolutionary time contributed to the differentiation of major lineages in Lake Tanganyika (173), but it is not clear whether such cycles continue to contribute to species diversity.

Sympatry

The origin of tilapias in the Cameroon lakes (155) has been extensively acknowledged as demonstrating sympatric speciation (e.g. 136), and has been a model for this mode of divergence in cichlids. Analysis of mtDNA sequences of eleven taxa endemic to the Barombi-Mbo crater lake suggested that these species formed a monophyletic group to the exclusion of geographically proximate riverine taxa, presumably the ancestors of this small species flock. Given the characteristics of the species involved, the study suggested that speciation in this endemic fauna was based on trophic differentiation and not sexual selection (155). In a wide diversity of fishes, radiation via trophic differentiation is a common pattern in recently founded populations (89). Extremely rapid specialization into planktonic and benthic feeding modes within multiple independent groups suggests the generality of this pattern (156).

Given its centrality, further consideration of the Barombi-Mbo radiation is warranted. Analyses of portions of the molecular data were ambiguous: species trees and gene trees may have been conflated, and sample size limitations may have influenced resolution of these data (158). Potential ancestors from the Niger River, an area that is periodically connected with Cameroon drainages (147), were not examined. As in most phylogenetic investigations, assessment of monophyly depends entirely on the taxa included in the analysis. mtDNA restriction assays of Barombi-Mbo cichlids supported the idea that at least two lineages of tilapias were present in this fauna (S Seyoum & I Kornfield, unpublished information). Regardless, despite the possibility that the species flock of Barombi-Mbo may have had more than one progenitor, sympatric speciation appears to have been the mode of origination of much of the current diversity.

A second example of rapid speciation of tilapias has emerged from careful study of the *Alcolapia (Oreochromis)* flock of Lakes Natron and Magadi in East Africa (158, 159). These two small soda lakes support four endemic taxa, three of them syntopic. Like the endemics of Barombi-Mbo, these cichlids are distinguished by morphological features associated with ecological specialization. While speciation in this system may have been sympatric, the complex hydrological history of the area suggests the possibility of repeated lake fragmentation and reunion; analysis of mtDNA sequences is equivocal (158).

Application of Sympatric Speciation Scenarios to the East African Great Lakes

The extreme youth of the species flocks of the African Great Lakes suggests that some mode of divergence different from the traditionally accepted models of allopatry has operated. It has been suggested that sympatric speciation may happen more rapidly than allopatric speciation (107). The inferences of sympatric speciation in the faunas of the Cameroons and in the soda lakes of Natron and Magadi have encouraged workers to consider sympatry as the dominant geographical mode of speciation in the Great Lakes of East Africa (35). Rapid sympatric divergence due to ecological adaptations could apply to initial diversification of lineages in the African great lakes (148). Under such scenarios, the deepest levels of divergence in any radiation would be based on marked trophic differences. Indeed, conventional (24) and molecular (173) phylogenies of cichlids from both Lakes Malawi and Tanganyika are consistent with this idea: major lineages are trophically divergent.

However, models of contemporary sympatric speciation in the African Great Lakes differ from other hypotheses of sympatric speciation. Because there is little evidence that ecological differences are associated with the most closely related species of African haplochromines, sympatric differentiation is presumed to occur by mechanisms not involving rapid ecological divergence, differences in habitat preference or performance mediated by disruptive natural selection. Hypotheses of sympatric speciation in African cichlids facilitated by runaway sexual selection are discussed below.

MECHANISMS DRIVING DIFFERENTIATION

Our review of geographical models of speciation in cichlid fishes (above) suggests the validity of various mechanisms by which reductions in gene flow may be realized and wherein evolutionary trajectories may diverge and give rise to new species. We now focus on the forces responsible for the divergence of hundreds of ecologically similar species in Lakes Malawi, Victoria, and Tanganyika. Many of the factors responsible for the great diversity of cichlid species in the African lakes remain unknown. While genetic drift and natural selection are thought to be the primary factors responsible for evolutionary divergence in general, the extent

and rapidity of the African radiations have evaded conventional logic in many cases. The most important elements of any divergence scenario are those that lead to testable hypotheses. Table 1 summarizes several theoretical frameworks within which cichlid speciation has been studied and emphasizes testable predictions of each model. In this section, we review theoretical and empirical research on speciation by sexual selection following treatment of more conventional evolutionary forces.

How Important Is Local Adaptation to Species Diversity?

Some New World cichlids exhibit trophic polymorphisms (87, 152) or are phenotypically plastic (84, 117). In the Old World, however, aside from the mollusc crusher *Astatotilapia alluadi* (43), there are few examples of ecologically significant plasticity. Indeed, there is little evidence to date that these factors contribute to apparent species diversity in the African faunas.

Although cichlids are known for a vast diversity of trophic morphologies, it is generally considered unlikely that differentiation in feeding specializations leads to speciation (185). Even in the absence of the necessary phylogenetic information, it is clear that many sibling species differ only in coloration (145, 185), while significant trophic morphologies differ at the level of genera (34, 81). Unlike the Trinidadian guppy system studied by Endler, which demonstrated natural selection in the form of local adaptation to predators, many East African cichlids have few natural predators once they are mature. In Lake Tanganyika, predation influences reproductive behaviors in some sand-dwelling fishes (61). Geographical variation in predation pressures has not been documented in Lakes Victoria and Malawi. In general, local natural selection pressures on coloration and behavior will likely be subtle. Two studies that have attempted to correlate coloration with ecological and biological variables found no (21) or weak (110) associations. Interspecific competition (48) and changes in the biotic community may exert strong pressures in an episodic manner, but their presence and significance have yet to be documented. Knowledge of local variation in selective regimes would benefit from additional consideration.

Is Genetic Drift Critical to Diversification?

Large size is thought to buffer a population against genetic and phenotypic changes, making small population size requisite for rapid divergence by drift (105). The postulated effects of random genetic drift following colonization events have been central to several models of cichlid speciation (22, 173). Tests of this concept are beginning to appear with the recent advances in molecular genetics; objective protocols for evaluating the magnitude of genetic bottlenecks are available (101). Studies of mbuna population structure in presumably recently submerged habitat in southern portions of Lake Malawi have been informative. The very low level of mtDNA haplotype variation exhibited by *Melanochromis auratus* (12) is consistent with a historical bottleneck, although current population size is quite large.

TABLE 1 Models of cichlid speciation

Dominant geographical model	Mechanisms driving speciation	Model system	Testable assumptions	Author (citations)
Allopatry	None specified ^a	Malawi <i>mbuna</i>	Limited gene flow between populations	Fryer (32)
Allopatry	None specified ^a	Victorian haplochromines	Biogeography and phylogenetic relationships of extant taxa	Greenwood (46)
Allopatry	Sexual selection Founder events	Malawi <i>mbuna</i>	Bottlenecks Mate choice on male coloration ^b	Dominey (22)
Allopatry	None specified ^a	Tanganyikan haplochromines	Limited gene flow between populations	Rossiter (148)
Allopatry	Runaway sexual selection on bower size	Malawi sand dwellers	Mate choice on bower size/shape ^b	McKaye (113)
Sympatry	Runaway sexual selection on male coloration	Victorian haplochromines	Mate choice on male coloration ^b Genetics of color/preference	Seehausen & van Alphen (162, 164)
Sympatry	Runaway sexual selection	Malawi <i>mbuna</i>	Mate choice on male coloration Genetics of color/preference	Turner & Borrows (186)

^aNone specified. Mechanisms driving speciation are not emphasized. Classical allopatric divergence sensu Mayr (105) is implied.

^bProving mate choice is the minimal first step to inferring speciation by sexual selection. See text for additional consideration.

In contrast, an mtDNA study of Malawi zebras showed very little reduction in diversity when narrow endemics were compared with cosmopolitan species (124, see also 19a). In such cases, decreases in allelic diversity could also be artifacts of the non-uniform sampling of haplotypes due to small samples sizes and highly variable markers (151). Initial surveys of nine Malawi taxa using microsatellite loci showed high levels of allelic diversity (190).

In two other microsatellite-based studies in Lake Malawi, significant population structure was revealed over very small spatial scales, suggesting reduction of gene flow under a specific colonization scenarios (3, 103). These studies correlated loss of observed genetic diversity [either effective number of alleles (3) or heterozygosity (103)] with proxies for isolation [distance from nearest conspecific population (3) or depth of sand-rock interface (103)]. Although genetic diversity was consistently high and no evidence for severe bottlenecks was observed, the data suggested a slight loss of genetic diversity after the presumed colonization events. In each case, however, the significance of a bottleneck effect to speciation is speculative. In Lake Victoria, preliminary characterizations of several species using microsatellite markers detected substantial of genetic variation (192). Extensive mtDNA-based population studies on the fauna of Lake Tanganyika have revealed considerable variation within a number of narrow endemics (119, 173). In summary, there is no general evidence that founder events have contributed to cichlid radiation in the Africa Great Lakes.

What Role Might Hybridization Play in Faunal Evolution?

Hybridization of heterospecific cichlids in nature has been observed to occur as a result of anthropogenic insults or accidental translocations in Lake Malawi (168, 169), and by eutrophication of Lake Victoria (165, 191). These observations and the relative ease of making crosses of divergent lineages in the laboratory (109) indicate that diversity of sympatric forms in nature is maintained by pre-zygotic, rather than post-zygotic, factors. Although distinctiveness is maintained under normal conditions, rapid environmental changes in the past may have contributed to hybridization and the diversity of cichlids observed today. Sudden drops in lake level, for instance, would bring adjacent populations into secondary contact. Color-differentiated ecological cognates might be among the first wave of taxa to hybridize, because of their ecological identity. The results of such hybridizations are unknown and may differ depending on the genetic architecture of underlying reproductive traits. Interspecific hybridizations might be facilitated under conditions of extreme population density, perhaps exacerbated by rapid changes in community composition. Whether hybridization can generally cause speciation in animals (4, 23, 41) is a subject of speculation, as it is in cichlids (19, 173). Certain predictions of the effects of hybridization can be made. In general, levels of genetic variation in hybrids should increase, but distinctive characters such as unique reproductive coloration might be altered if they are polygenic in nature. Alternatively, if each reproductive character is encoded by a separate locus, mosaic

phenotypes qualitatively different from parental strains might emerge (5). For example, hybrids between divergent mbuna geneva display novel morphology (109). Hybrids that do not suffer a decrease in fitness should thrive, making speciation by hybridization potentially a major contributor to overall species diversity. However, if hybrids suffer a decrease in fitness, the evolution of mate discrimination behaviors that facilitate pre-zygotic isolation in areas of secondary contact could be a result of reinforcement. Distinctive male colorations might evolve at the time of secondary contact, rather than during isolation. Reinforcement of female preferences has been modeled in *Drosophila* (69) and experimentally demonstrated in the three-spine stickleback (150). The role of reinforcement in cichlid speciation has not been appropriately addressed (21, 144, 185) and in part may have been lost in the semantic arguments of species concepts and adaptations (see 47 for a discussion). However, detection of reinforcement in cichlids might be extremely difficult. Variations in numbers of offspring normally observed in species with extremely low fecundities may make detection of post-zygotic fitness effects impossible.

Is Sexual Selection Driving Cichlid Speciation?

That sexual selection operates in cichlid fishes was suggested very early in the study of the group (88). Although critical empirical support is rare, many investigators have assumed that female mate choice on male coloration is a common phenomenon in cichlids (113, 118, 144, 173, 185). While interspecific discrimination has been extensively demonstrated (see above for molecular research and 72, 73, 164–166), strong evidence for intraspecific mate choice per se is limited.

Proposed Mechanisms of Divergence by Sexual Selection Models of cichlid speciation by sexual selection fall into two major categories: rapid divergence of sexual characters in allopatry (22, 113) and disruptive or divergent sexual selection in sympatry (cichlid references: 162, 164, 166, 186, 189; general references: 51, 80, 92, 93). Both scenarios employ the process of Fisherian runaway sexual selection. The distinction of the Fisherian process from other mate choice scenarios, such as “good genes” or “handicap” processes, is that the female preference for a sexually selected trait increases in frequency as a result of co-inheritance of trait and preference, rather than via direct selection owing to increased fitness of females that choose quality males (2). Assumptions of the runaway process include (a) heritable genetic variation in male trait(s), (b) heritable genetic variation in female preference, (c) increased mating success of males with exaggerated trait, and (d) genetic covariance of trait and preference (2). Allopatric models posit that geographical variation in sexual characteristics (e.g. coloration and bower form) is generated by founder effects and maintained by limited dispersal. Sympatric models have had to overcome the theoretical restriction imposed by the effects of recombination on reproductive traits and preferences, and the elimination of intermediate genotypes (57). This has been done by assuming genetic dominance

in female preference traits (186), variation in habitat fidelity (189), and extreme mating preferences (51).

Appeal of Speciation by Sexual Selection The association of species diversity with exaggerated sexual characteristics is appealing. A recent body of literature has addressed this phenomenon among birds by identifying sexual dimorphism or ornamentation as a correlate of species richness (7, 122, 135, 140). However, this result begs the question of the causal relationship between these two factors. Despite the need for rigorous hypothesis testing and the data that are required for empirical support of sexual selection, the ability to infer mechanisms causing species diversity is limited by the time scales during which divergence events occur. Barraclough and his coworkers (8) suggested several methods for inferring past divergence events using species level phylogenies. The need for such reconstructions among closely related African cichlid species is clear.

Testing Divergence Hypotheses Female cichlids are able to discriminate males of their own species and closely related species by body color (54, 72, 73, 162, 164, 166). This ability is important in the maintenance of diversity, especially where closely related species are sympatric, and not ecologically differentiated (165). Documentation of interspecific mate choice, though, does not facilitate assessment of competing hypotheses of divergence by sexual selection. Indeed, current data do not allow rejection of completely allopatric divergence in which sexual selection plays no role. For example, in evaluating evidence of assortative mating of closely related sympatric species (165), a hypothesis of secondary contact is equally parsimonious with that of divergence *in situ*.

Intraspecific mate choice has been recorded in field observations (62, 113) and field experimentation (49). Although these studies suffer from small sample size and limited replication, they present compelling evidence for the existence of mate choice within species. The male traits under selection in these studies were bower size (113), pelvic fin length and symmetry (62), and number of egg spots on the anal fin (49). In general, studies have not demonstrated heritability of male traits, female preferences, or the covariation of those traits through breeding experiments.

Alternative hypotheses for the evolution of exaggerated sexual dimorphism deserve attention. For instance, intrasexual selection via male contest competition is very likely to operate in cichlids and remains largely unstudied (61). Divergence of male coloration in allopatry may be as likely under intrasexual as it is under intersexual selection, and intrasexual selection does not require a change in female preference traits. For example, observations previously considered supportive of female choice (114) could be explained by the effects of male competition. McKaye's documentation of female mate choice on bower size and position in Lake Malawi cichlids depends on the use of bower morphology as an "extended phenotype" of males. Two later studies of mate choice in Lake Tanganyika (61) and Lake Malawi (86) bower-building cichlids failed to find evidence for choice in relation to bower morphology, and further found that males are often ousted

from their bowers by males that defend territories in the absence of a bower (61). These additional data suggest that male competition is important in the acquisition and defense of breeding territory. Size affects competition between males (I Kornfield, unpublished data) but the use of conspicuous male coloration as an intermale signal is also an alternative.

In light of the available models (22, 113, 162, 164, 166, 186, 189) and limited data (49, 62, 113), several scientists have interpreted their experimental findings as de facto consistent with speciation by sexual selection (21, 159a). Such associative orientations are of limited value in evaluating alternative ideas, since no hypothesis-testing framework is formulated. Future studies will need to address alternative hypotheses more directly so that mechanisms of divergence or components of those mechanisms can be systematically supported or rejected. Phylogenetic hypotheses based on biogeographic patterns and competing methods of divergence are one example of such hypothesis testing (141; PF Smith & I Kornfield, in preparation).

EVOLUTIONARY GENERALIZATIONS AND FUTURE STUDIES

In this paper we have reviewed basic information as well as current research in the study of African cichlid evolution. Discussion of information on cichlids and their natural environments provides the basic data necessary to formulate testable hypotheses regarding the divergence of the many hundreds of cichlid species endemic to the lakes of Africa. For the last several decades, cichlid species flocks (25) have served as model systems in which to study the evolutionary process. As more empirical studies become available to critically evaluate the theories of cichlid evolution, resolution of some issues may be achieved. However, comprehensive understanding of the evolutionary history of these faunas and the processes currently at work remains elusive, and there is growing consensus that a single mechanism may be insufficient to explain the origins of these fishes (113, 173). We caution against premature adoption of particular divergence scenarios in the absence of sufficiently strong evidence.

Understanding the Genetic Basis of Relevant Traits

Cichlid diversification should be intensively studied at the genomic level. *What is the genetic basis of male phenotypes and of female choice? How is trophic differentiation controlled?* For example, preliminary breeding studies for some Malawi taxa do not support simplistic models for inheritance of coloration (20, 84; D McElroy, personal communication). The lack of post-zygotic isolation between divergent species lends itself to QTL (quantitative trait loci) analysis of color and behavioral characteristics. The genomic mapping studies pioneered by Kocher and colleagues (1a, 77) will provide a basis for such work.

Understanding Coloration in Cichlids

The role of color in cichlids is considered central to diversification, so knowledge about the physiological basis of color production and of color perception is required. *Are cichlids different than other fishes in their use of colors? What is the significance of UV coloration?* For example, in some cichlid systems, limitations to female color perception may be expected to differ because of habitat characteristics, yet sensory ranges may be great. Comparative differences between physiological abilities and abiotic constraints among taxa within and between lakes may reveal processes molding these attributes.

Studying Behavior

Male coloration varies extensively, but little is known about variation in female preference. *For what male traits is female preference displayed? Are some types of preferences common to diverse lineages within or between lakes?* Quantification of the magnitude and variation in female preference for coloration (as well as other attributes of male phenotypes) is necessary to understand the process of diversification. Information on search strategies is necessary to model and understand the evolution of male traits and female preferences (56b, CRB Boake, in preparation). Importantly, the implications of extensive polyandry and polygyny need be considered within this framework. Such research is demanding; in situ observations are opportunistic, although territoriality facilitates study of male characteristics subsequent to mating. Experimentation in aquaria must be undertaken with caution since mating is infrequent and artifacts may occur; common proxies for female behavior in choice experiments, such as differential time allocation or proximity to particular males, merit verification. Experimentation under seminatural conditions may be necessary, for example, in large ponds with adequate space for territories. In some aquatic systems, female choice could be determined by the use of molecular markers with subsequent assessment of male attributes.

Insights from Population Genetics

Preliminary population studies suggest very limited gene flow among taxa over short distances, but this is contradicted by early studies of migration (112). *How extensive is gene flow among discontinuously distributed populations? Is isolation by distance a universally demonstrable attribute in these systems?* A test for genetic differentiation at several scales (100 m–100 km) in putatively stable populations (e.g. those associated with deep basins) might provide information on the extent of isolation/gene flow. Observations of population differentiation over distance would suggest that the behavioral characteristics of the species studied are insufficient to produce population subdivision in stable populations in the absence of physical barriers to migration.

Criteria for Evaluating Models of Divergence

Construction of accurate phylogenies is central to evaluate the influence of geography on speciation. *Are molecular phylogenies consistent with hypotheses that can exclude allopatric differentiation?* For example, discrimination between recolonization scenarios, allopatric differentiation, and sympatric divergence can be achieved by examining relationships among clusters of closely related species over large distances (e.g. 141). Similarly, with comprehensive geographic coverage, secondary contact can be examined using sensitive molecular frameworks. Species-level phylogenies will also provide a basis on which to infer the evolution of important characteristics among sibling species. Such inferences may point to particular characters that are involved in early divergence.

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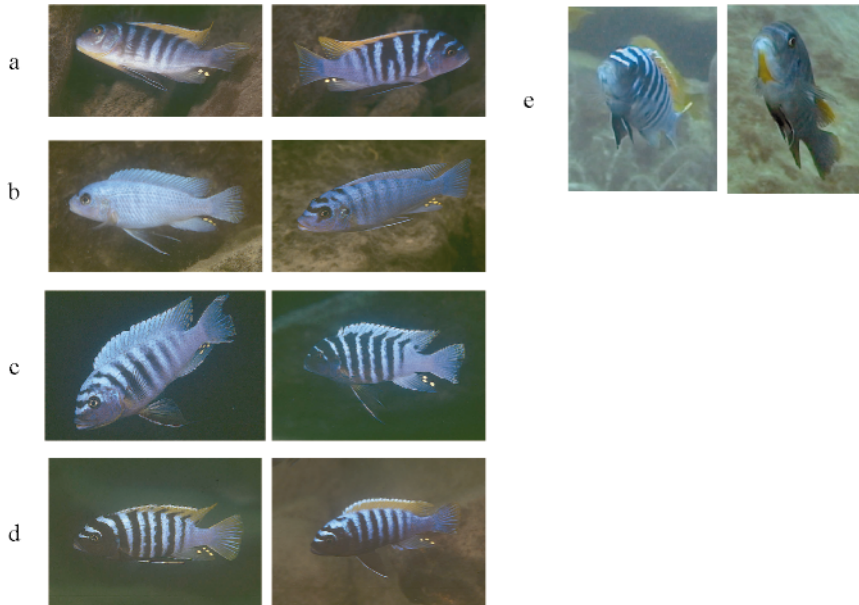


Figure 1 Intrapopulation color diversity within the Lake Malawi *Metriaclima zebra* species complex. Variation in the illustrated phenotypic traits is continuous; presented are examples of extreme phenotypes. (a) Pattern asymmetry (flanks of a single “red dorsal” individual—Chimwalani); (b) bar density [Mazinzi Reef—*Metriaclima benetos* (167)]; (c) dorsal fin bar penetration (“Blue-Black” Meponda Rocks); (d) dorsal fin bar penetration [“red dorsal” Nakantenga Island—*Metriaclima pyronotos* (167)]; (e) throat patch coloration (Eccles Reef—*Metriaclima thapsinogen* (167)). (Photographs a–d by A Konings.)