

14 Cichlid Fish Diversity and Speciation

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ABSTRACT

Cichlids are one of the most species rich families of vertebrates, with conservative estimates citing more than 2,000 extant species. Although native to tropical areas of the world, with the exception of Australia, some 70–80% of cichlids are found in Africa, with the greatest diversity found in the Great Lakes (lakes Victoria, Tanzania and Malawi). Their highly integrated pharyngeal jaw apparatus permits cichlids to transport and process food, thus enabling the oral jaws to develop specialisations for acquiring a variety of food items. This distinct feature has allowed cichlids to achieve great trophic diversity, which in turn has led to great species diversity. The high species diversity of this vertebrate family is not accompanied by an appropriately high genetic diversity. The combination

of rapid radiation of the group and relatively low genetic diversity has confounded attempts to diagnose species and discern phylogenetic relationships. Behavioural traits appear to be important characters for diagnosing many cichlid species.

14.1 INTRODUCTION

Cichlids (Cichlidae) are a species rich group of fish from the lowland tropics¹ and are indigenous primarily to the fresh waters of Africa, South America and Central America, with one species extending its range to the Rio Grande River in southern North America. In addition, cichlids are found in Madagascar, the Levant and India and have also been introduced into nearly all tropical and subtropical regions of the world, either through escapes from aquaculture or ornamental fish operations or intentionally to provide sport fishing opportunities or to control exotic plants². They have established breeding populations in warm waters of industrial effluents in temperate areas³ and have been introduced into some marine environments⁴. Numerous investigators⁵⁻¹⁴ have focused on cichlid fishes for their ecological, evolutionary and behavioural research.

Without doubt, the cichlids' explosive speciation, unique feeding specialisations, diverse mating systems and great importance as a protein source in tropical countries have been factors stimulating research interest in this group¹⁵⁻¹⁸. In fact, Greenwood¹⁹ referred to the cichlid species flocks as "evolutionary microcosms repeating on a small and appreciable scale the patterns and mechanisms of vertebrate evolution". Many of these research efforts, however, have been slowed and results often confused because of the uncertain systematic status of some of the cichlids being studied^{20,21}. The conservative bauplan of cichlids¹ and relatively low genetic divergence is coupled with a great morphological diversity that makes it difficult to diagnose species using morphological criteria alone (Figure 14.1). Systematic confusion exists within Cichlidae and also within and between its higher taxonomic ranks such as suborders. Such relationships are currently being debated. The reasons why cichlids have managed to speciate so successfully, often within a restricted geographic range such as the Great Lakes of Africa, have also been under investigation^{14,15,22}.

14.2 CICHLID PHYLOGENY

14.2.1 HIGHER LEVEL TAXONOMIC RELATIONSHIPS OF CICHLIDS

Morphological studies have provided insight into the phylogenetic position of Cichlidae. The resultant relationships, however, differ considerably from that of molecular investigations. Kaufman and Liem²³ (see also Stiassny and Jensen²⁴) grouped cichlid fishes (Acanthopterygii: Perciformes) with Embiotocidae, Labridae and Pomacentridae in the suborder Labroidei on the basis of the following three pharyngeal characters: fusion of the fifth ceratobranchial bones into one unit; contact of the upper pharyngeal jaws and the basicranium; and lack of a dorsal subdivision of the sphincter oesophagi muscle. As it is now recognised, this suborder includes some 1,800 species and represents some 5–10% of all extant fishes²⁴. Müller²⁵ was the first to group the above families together, and morphological data support the view that Labroidei has phyletic integrity²⁴ based on the following synapomorphies: bladelike keel on the lower pharyngeal bone and the change in insertion of at least part of the transversus ventralis onto the keel; division of the transversus dorsalis anterior muscle²⁶; bony facets of the third pharyngobranchials of the upper pharyngeal jaws are exposed; ventrally projecting rounded form of the neurocranial apophysis; and no subdivision of the sphincter oesophagi muscle. The cichlids appear to be the sister group of all the other labroids¹.

The monophyly of Labroidei is, however, confused, because many homoplasies exist in the morphological data sets^{24,27}. Moreover, studies of nuclear DNA suggest that Labroidei are not monophyletic, and that embiotocids and pomacentrids are more closely related to more basal perciforms²⁸. This view is corroborated by Sparks and Smith²⁹ who believe that the sister group to the cichlids "might comprise a large assemblage of diverse perciform lineages, including but

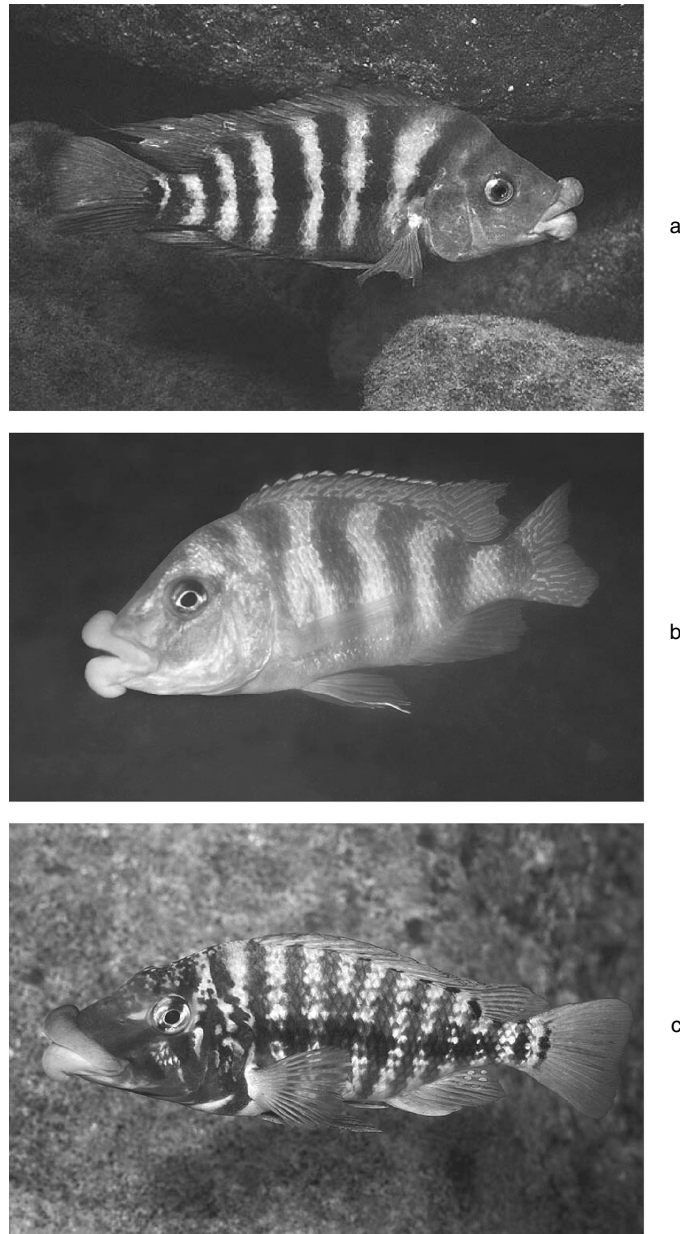


FIGURE 14.1 (A colour version of this figure follows page 240) Cichlid fishes. Cichlids have a conservative bauplan, and specialised attributes, such as hypertrophied lips are the result of parallel evolution, thus making species and higher level diagnoses difficult. (a) *Amphilophus* sp. 'fatlip' in Lake Xiloa, Nicaragua; (b) *Placidochromis milomo* at Nkhomo Reef, Lake Malawi, Malawi; (c) *Loboichilotes labiatus* at Nkondwe Island, Lake Tanganyika, Tanzania. (Photos reproduced with permission from A.F. Konings.)

presumably not limited to the other 'labroid' lineages, sparids, anabantids-nandids, haemulids, percids, moronids, and kyphosids". Westneat and Alfaro²⁷ reported maximum *RAG2* DNA sequence divergence between wrasses and outgroups ranging as high as 23% between parrotfishes and some of the cichlids they examined. Nevertheless, they supported the inclusion of the parrotfish as a subgroup of Labridae; thus, it is doubtful if these families belong to the same suborder.

Boulenger³⁰ first speculated that the cichlids form a natural group within the perciform Acanthopterygians. Stiassny¹ recognised Cichlidae as a monophyletic group based on five apomorphic characters:

- Loss of a structural association between parts A₂ and A₁₀ of the adductor mandibulae muscle and the attachment of a large ventral section of A₂ onto the posterior border of the ascending process of the anguloarticular
- An extensive cartilaginous cap on the front margin of the second epibranchial bones
- An expanded head of the fourth epibranchial bones
- Presence of characteristically shaped and distributed microbranchiospines on the gill arches
- The subdivision of the traversus dorsalis anterior muscle into three distinct parts as described by Liem and Greenwood²⁶

The monophyly of Cichlidae is further supported by the morphology of otoliths and configuration of the digestive tracts. Gaemers³¹, based on the structural configuration of the sagitta, also hypothesised that the cichlids are monophyletic. The sagitta is usually the largest otolith in most teleosts, including cichlids. The sagitta of cichlids is strong, thick, with a more or less oval, short, elliptical to rounded pentagonal shape³¹. If the pseudocolliculum in the sagitta of cichlids is a synapomorphic character, it supports other evidence of monophyly of the family^{26,32}. Finally, three structural attributes of a cichlid's digestive tract support cichlid monophyly: the stomach's extendible blind pouch; the left hand exit to the anterior intestine; and the position of the first intestinal loop on the left side³³.

14.2.2 INTRAFAMILIAL RELATIONSHIPS OF CICHLIDS

Many subfamilial names have been used to indicate groupings within Cichlidae, but do not necessarily represent hierarchical patterns³⁴. Etroplinae (that is *Etroplus* and *Paretroplus*) has been proposed to be the sister group of all other cichlids²⁹. Following this separation, Ptychochrominae were considered to be the sister group to the remaining cichlids. What then is left has been divided further into two purportedly monophyletic groups, the African Pseudocrenilabrinae and the New World Cichlinae. It should be noted that Schlieven and Stiassny³⁵ used the term Haplotilapiines to refer to non-*Heterochromis* cichlids from Africa and the Levant.

Within the family, a Congolese genus, *Heterochromis*, was proposed to be the most primitive of the African cichlids³⁶. Stiassny³⁷ diagnosed *Heterochromis* to be the sister group of all the other cichlids, based on the presence of a single ligament attaching the lower pharyngeal bone to the cartilaginous fourth basibranchial. The monophyly of Neotropical cichlids was questioned by Cichocki³⁸, who postulated that *Cichla*, a Neotropical genus, was grouped with the cichlids of Africa. This was debated by Stiassny¹, who favoured a *Cichla*-crenicichline clade within the Neotropics. Stiassny¹ postulated a close etropline relationship with *Heterochromis*, while Kullander³⁴ regarded *Heterochromis* as the sister group of the majority of Neotropical cichlids. Despite this relationship, Kullander³⁴ emphasised that the dichotomy of Old and New World cichlids was well supported by the following character states:

- Short anterior arm of epibranchial, which is a reduction that occurs in several lineages, including the Etroplinae and *Astatotilapia*, and which is reversed in groups such as Cichlasomatinae
- Interdigitating suture connecting the vomerine shaft and the parasphenoid bar (requires independent development in *Ptychochromis* and reversal in *Biotocetus*, *Dicrossus* and *Nannacara*)
- Presence of an anterior palatoethmoid ligament, which occurs in all Neotropical cichlids and *Heterochromis*, but in no other Old World cichlids

Retroculus is regarded as the earliest diverging lineage of Neotropical cichlids and the sister group of *Cichla-Crenicichla*, which is placed in a new subfamily, Cichlinae³⁴. Kullander³⁴ recognises the following Neotropical subfamilies: Astronotinae (*Astronotus*, *Chaetobranchus*), Geophaginae (for example, *Geophagus*, *Apistogramma*) and Cichlasomatinae (Cichlasomines, Heroines *Acaronia*).

Mitochondrial DNA supports the monophyly of Cichlidae, but differs in its interpretation of intrafamilial relationships³⁹. In particular, *Heterochromis* is sister to the remaining African cichlids, and *Retroculus* is the most basal taxon of the Neotropical cichlids. Farias et al.⁴⁰ believed that *Astronotus*, *Cichla* and *Retroculus* formed three independent basal lineages, even though one of their trees favoured *Astronotus* as the sister group to *Cichla*. Therefore, Astronotinae, sensu Kullander, is not accepted by molecular biologists, whereas *Chaetobranchus* and *Chaetobranchopsis* are grouped together as Chaetobranchines. Farias et al.⁴⁰ remove *Crenicichla* and *Teleocichla* from Cichlinae (sensu Kullander) and transfer that group to Geophaginae. In the molecular phylogeny, *Acaronia* is no longer regarded as the sister group of the *Heroini*/Cichlasomatini group⁴⁰.

14.3 CICHLID DISTRIBUTION

Apart from Australia and Antarctica, cichlids occur on all the major fragments of the former supercontinent Gondwana. The extant distribution of cichlids and phylogenetic relationships suggest that the family was well established before the separation of Gondwanaland. Thus, the family should be at least 160 million years old^{41,42}. This view, however, is not supported by studies based on the fossil record, and the time of origin of this taxon is still hotly debated. For example, many authors believe that the cichlids are not old enough to have been present on that supercontinent⁴³. India and Madagascar drifted away during the Late Jurassic (160 million years before present, mybp) and not during the Middle Cretaceous, as Van Couvering⁴⁴ apparently believed. Molecular evidence presented by Vences et al.⁴⁵ suggests that the extant distribution pattern of the cichlids came into being well after Gondwana fell apart. In that respect, it should be mentioned that Murray⁴⁶ believed that a Gondwanan origin is not needed to explain the present distribution of cichlids.

The oldest known fossil cichlids, the species of the genus *Mahengochromis*, have an age of 46.3 mybp, which means that they date from the Middle Eocene⁴⁶. Fossil cichlids from the Oligocene of Africa have been described by Van Couvering⁴⁴, and because of the highly specialised dental features of these fishes, Stiassny¹ concluded that the origin of the family predates the earliest fossils considerably and that the cichlids probably arose in the Early Cretaceous, some 135 mybp.

This view is incompatible with the fossil record. In a recent paper, Arratia et al.⁴⁷ have emphasised, once more, that thus far no perciform fishes have been found that are older than the latest Cretaceous (85–65 mybp). That age differs dramatically from that postulated by molecular studies (Salmoniformes and Gadiformes versus Perciformes divergence of some 285 mybp). In this respect, it should be remembered that the cichlids are regarded as advanced perciforms, which means that they should be much younger than the primitive forms that have been found in the Late Cretaceous sediments. Cichocki³⁸ postulated that the cichlids with the most plesiomorphic characters are found in Madagascar and India, which was endorsed by Kullander³⁴, discussed by Stiassny¹, and supported by mtDNA analysis by Farias et al.³⁹.

14.4 CICHLID DIVERSITY AND SPECIATION

Between 70 and 80% of all cichlid fishes are native to African freshwaters, of which the majority are part of the major lacustrine radiations; for example, Lake Victoria (c. 500 species), Lake Tanganyika (c. 200 species) Lake Malawi (c. 850 species)^{15,48}. The remainder occur in the freshwaters of the New World, with the exception of a single genus, *Etoplus*, which is found in the coastal waters of Southern India and Sri Lanka; five genera, which are found on Madagascar; the genus *Tristramella*, which is endemic to the Levant; and one genus, *Iranocichla*, which is endemic to Southern Iran.

By far the greatest radiation of cichlids is found in the Great Lakes of Africa, with Lake Malawi alone having as many as 850 species⁴⁹. The phylogenetic diversity ranges from the single invasion of Lake Malawi, which resulted in the endemism of all but a few species, to multiple invasions in Lake Tanganyika, which resulted in the presence of 12 different tribes⁵⁰. The rich fauna of these lakes is primarily attributable to the explosive adaptive radiation and speciation^{51–53} of the haplochromines *sensu lato* (see Schlieven and Stiassny³⁵). The driving mechanism for these speciation events is unknown. The two most widely proposed methods are allopatric speciation^{5,15,54–57} and intrinsic isolating mechanisms^{14,22,58–64}. Furthermore, biologists generally agree that female mate choice can act as a strong driving force in runaway speciation where the average female preference for a specific male trait differs between two allopatric populations^{65–69}. Thus, behavioural traits are important tools for the diagnosis of these African cichlids, primarily because behavioural traits played a very important role in and facilitated the rapid radiation of these fishes, which may not always be accompanied by discernable morphological changes⁷⁰.

Certainly, there are fewer species of cichlids in South and Central America than in the Old World. Greenwood¹⁹ noted that the focus on African cichlids has distracted attention from the South American Cichlidae, a fact which he regarded as 'sad but understandable'. Nevertheless, the neotropical cichlid fauna is varied and diverse¹, comprising some 50 genera and 450 species³⁴, with new species still being discovered⁷¹. In the last decade, on average more than 20 species of cichlids have been formally described each year. The existence of literally hundreds of species awaiting description is likely to continue this trend.

14.5 CICHLID ADAPTIVE RADIATION

The cichlids of the Great Lakes of Africa have undergone one of the most rapid radiations of any known vertebrate group^{47,72–74}. This rapid speciation rate, however, is not correlated with a high genetic diversity⁷⁴, as discussed earlier. Conversely, the neotropical cichlids, especially the geophagines, have a significantly higher rate of genetic divergence than their African counterparts^{39,75}, but this does not seem to be expressed in the more diversified group. This makes the taxonomy and systematics of the group challenging. The high genetic diversity of the Neotropical cichlids, when compared to the ones from Africa, is somewhat surprising considering the greater species diversity of Old World cichlids. A number of the following adaptations may be associated with cichlid speciation.

14.5.1 FEEDING ADAPTATIONS

High trophic diversity of the Old World cichlids results in the consumption of virtually every food type available in the environment^{76,77}. The successful radiation of cichlids in the rift valley (for example, in Lake Malawi and Lake Tanganyika) is purported to be a result of cichlids' differential ability to acquire food⁷⁸. In cichlids, mouth structure, dentition, gill raker number⁷⁹ and jaw structure vary tremendously, and this variation in structure seems to be tied to a variety of feeding techniques^{15,80}. Documented feeding strategies of Lake Malawi fishes, for example, illustrate numerous feeding specialisations including death feigning⁸¹, paedophagy^{82,83}, lepidophagy⁸⁴, cleaning⁸⁵ and scraping and raking of an algal, diatomaceous and detrital biolayer (*aufwuchs*) from the rock surfaces⁵. Phenotypes, such as reverse counter shading, are associated with such bizarre strategies as hunting upside down⁸⁶.

Primarily through the work of Liem and his coworkers^{26,76,77,87} it became evident that the trophic diversification of cichlids does not require major structural adaptations. Liem⁷² attributes the great colonising success of cichlids to their possession of a highly integrated pharyngeal jaw apparatus. Thus, the pharynx has been a particular focus of modification in Labroidei, including the cichlids¹. Liem⁷² further states that this specialised innovation allows cichlids to transport and prepare food, enabling the premaxillary and mandibular jaws to develop specialisations for collecting diverse

food items. It is this distinct feature of cichlids that has permitted them to dominate colonisation of many habitats and adopt feeding opportunities available in lacustrine environments^{72,76}.

Phenotypic plasticity is defined as the possible environmental modification of the phenotype⁸⁸. The degree of phenotypic plasticity that cichlids exhibit is congruent with the ability of cichlids to take advantage of many habitats and feeding opportunities. Despite the morphological plasticity observed in other fishes^{89–91}, the morphology of African cichlids initially was thought to be rigid⁹²; however, much morphological variability has been observed^{93–98}. In particular, the observed phenotypic plasticity in some instances has involved the pharyngeal jaw apparatus. For example, the phenotypic diversity of the pharyngeal jaws of the New World *Herichthys minckleyi*^{99,100} has been documented extensively. Furthermore, differences in bone structure of the lower pharyngeal jaw of *Astatoreochromis alluaudi* resulted from different diets^{101–103}. In addition to these observations, Meyer⁹⁴ and Wimberger^{97,98} have experimentally demonstrated the effects of diet on plasticity of head morphology in New World cichlids, but Meyer⁹⁴ hypothesised that the plasticity of mouth brooding Old World cichlids may not be as pronounced due to constraints on jaw morphology for mouth brooding. Stauffer and Van Snik Gray¹⁰⁴ effected significant differences in head morphology of Lake Malawi rock-dwelling cichlids by experimentally manipulating diets. The magnitude of plasticity in these mouth brooding Lake Malawi cichlids, however, was not as pronounced as that observed for the New World substrate brooder *Herichthys cyanoguttatum*. They did postulate, however, that phenotypic plasticity might have contributed to the extensive trophic radiation and subsequent explosive speciation observed in Old World haplochromine cichlids. Lewontin¹⁰⁵ postulated that colonising species, possessing a high degree of phenotypic plasticity, may have a selective advantage because of their ability to exploit additional resources in differing environments.

14.5.2 BREEDING ADAPTATIONS

Cichlids have also a number of reproductive strategies associated with their speciation. Barlow^{65,66} and Keenleyside^{16,17} give an excellent review of reproductive strategies and parental care in cichlid fishes. The breeding tactics of cichlids can be separated into two major groups: substrate brooders and mouth brooders^{65,106–109}. Substrate brooding cichlids are generally monogamous and exhibit biparental care of the eggs and brood, although some species are polygynous¹¹⁰. Substrate brooding appears to be the plesiomorphic character state. The primitive cichlids of Asia and Madagascar (that is Etroplinae and Ptychochrominae), most of the New World species, Old World *Tilapia* spp., and selected Old World pseudocrenilabrinines are substrate brooders^{109,111–113}.

Most mouth brooders are polygamous, although monogamy is found in a few species^{107,114}. Some New World cichlid mouth brooders begin as substrate brooders, but then gather either the eggs (ovophilous mouth brooders) or the hatched fry (larvophilous mouth brooders) into their mouths, including some *Aequidens*, *Geophagus*, *Gymnogeophagus* and *Satanoperca*^{115,116}. Some *Chromidotilapia* from Africa employ a similar delayed mouth brooding strategy^{117,118}, while male *Chromidotilapia guentheri* brood the eggs and larvae. *Saratherodon galilaeus* exhibits an intermediate form of biparental care, where both the male and female gather the eggs into their mouths after fertilisation and then separate⁶⁵.

The vast majority of African mouth brooders are polygamous. The rock dwelling cichlids of lakes Malawi and Tanganyika defend territories and attract females to spawn in either rock crevices, small caves, on the rock surface, or in the water column above rocks. Males of these fishes presumably rely on their brilliant and diverse colour patterns to attract females⁷⁰. In addition, many of the Lake Malawi sand dwelling cichlids construct a wide variety of bower forms in leks with a hundred to many thousand individuals^{119–123}. These bowers can be broadly divided into 10 types¹²¹ and range in size from giant craters three metres in diameter¹²⁴ to small depressions in the sand. The females move over the arena and lay eggs with several males. The entire egg laying process takes 25–60 minutes from the time a female lays her first egg¹²⁵ until she leaves the arena with

eggs in her mouth. Genetic studies of paternity for several Lake Malawi species show that females mate with as many as six males per brood¹²⁶.

The process of female choice is complex. Female *Otopharynx* c.f. *argyrosoma* selectively chose males that occupy bowers in the centre of the arena¹²¹, while female *Mehenga conophoros* and *Lethrinops* c.f. *parvidens* chose males that build the largest bowers^{122,125,127}. If the rapid radiation of the Lake Malawi cichlid flock was accelerated by sexual selection, the observed differences in behaviour might be the best way to distinguish between sibling species that differ little in morphology⁷¹.

14.6 FUTURE DIRECTIONS

Barlow⁶⁶ dedicated an entire chapter in his excellent book, *The Cichlid Fishes: Nature's Grand Experiment in Evolution*, to the problems associated with the Earth's growing population. Whilst he discussed the risks of burgeoning human populations and the associated pattern of diminishing resources on the Earth's biota, he focused on cichlids in particular. Certainly, one of the detrimental aspects of human populations is the decrease in genetic diversity connected to the increase in the rate of extinction of natural populations. Probably the most drastic incident of mass extinction in our lifetimes occurred with the destruction of the cichlid species flock in Lake Victoria that was associated with the introduction of the Nile Perch^{128,129}. The relatively small and colourful cichlids endemic to the lake were suddenly confronted with a huge predator, which, a few decades after its introduction, had severely decimated the cichlids and established itself as the new food source for the local populace. In addition to the loss of cichlids due to introductions, the introduction of cichlids has had detrimental impacts on native fish faunas throughout the world^{2,3,130}.

The high morphological diversity of the cichlids coupled with their conservative bauplan and the relative low genetic divergence of the Old World cichlids makes it difficult to diagnose species using morphological criteria alone. The extremely recent diversification of several cichlid lineages presents serious challenges for the use of genetic techniques for alpha and beta taxonomy. Initially, the attempts to use allozymes to resolve phylogenetic relationships were limited¹³¹. Kocher et al.¹³² have discovered a large number of polymorphisms in the tilapia genome, and Arnegard et al.¹³³ and Markert et al.¹³⁴ have used microsatellites to study population structure of several Lake Malawi rock dwelling cichlids. The use of amplified fragment length polymorphisms by Albertson et al.¹³⁵ was promising for the determination of supraspecific relationships and species diagnoses. As stated previously, behavioural traits are important characters for diagnosing many of these cichlids and determining phylogenetic relationships⁷⁰. Thus, Stauffer and McKaye⁷¹ recommended that a combination of morphological, genetic and behavioural data be used to diagnose these species and determine phylogenetic relationships.

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