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Behaviour: an important diagnostic tool for Lake Malawi cichlids

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Abstract

Historically, the cichlid fishes of Lake Malawi, which probably represent one of the best examples of rapid radiation of vertebrates, have been diagnosed with morphological and genetic data. Many of the populations once thought to be conspecific have been hypothesized to be separate species based on behavioural data. The use of behavioural data, as expressed in mate choice based on colour patterns or bower shapes, has been successfully used to diagnose both rock-dwelling and sand-dwelling cichlid species. Additionally, a combination of bower shapes and courtship patterns have been used as synapomorphies to diagnose genera within the Lake Malawi cichlid flock. It is concluded that taxonomists need to include behavioural data with morphological and genetic databases to diagnose species and to determine the phylogenetic relationships within this diverse assemblage of fishes.

Keywords allopatry, behaviour, Cichlidae, mate choice, sexual selection, species concepts, species recognition, sympatry

Introduction

In the lakes of East Africa, fishes of the family Cichlidae have undergone an extraordinarily rapid and extensive radiation. Within Lake Malawi, over 450 species have been formally described, and many undescribed species are being discovered and described from newly explored areas (Keenleyside 1991; Stauffer and McKaye 2001). It is estimated that in Lake Malawi, there may be as many as 1500 cichlid species (Stauffer *et al.* 1997; Turner *et al.* 2001). Cichlid fishes have been the focus of considerable ecological, evolutionary, and behavioural research (Fryer and Iles 1972; Keenleyside 1991; Seehausen 1996; Kawanabe *et al.* 1997; Konings 1998, 2001; Barlow 2001; Coleman 2001). Unfortunately, many of these research efforts have been slowed and often confused as a result of the uncertain systematic status of some of the cichlids being examined. Certainly, the discrimination among species of Lake Malawi cichlids can be difficult because differences among species may be very small (Konings 2001) and because morphological characters may be prone to convergence (Kocher *et al.* 1993). The existence of distinct species (e.g. *Tropheops* 'Gome Yellow'; *Tropheops* 'yellow gular' (Konings 2001) that possess minimal morphological differences (Lewis 1982) and display the results of parallel evolution (Kocher *et al.* 1993) probably constitutes the greatest problem to the taxonomist attempting to distinguish cichlid species (Stauffer and McKaye 2001).

Historically, most attempts to diagnose cichlid species have used morphological characters (Stiassny 1991). Many species were described based on meristic characters such as number of gill rakers (Iles 1960), dentition of the lower pharyngeal bone (Günther 1893; Trewavas 1931), the presence or absence of enlarged suborbital canals (Trewavas 1988), and the presence of an enlarged cleithrum (Stauffer and McKaye 1985). Morphometric relationships such as the size of the mouth expressed as percentage standard length (Boulenger 1901) were also used to diagnose species (e.g. *Protomelas pleurotaenia* (Boulenger)). To further compound the problem of species diagnoses of Lake Malawi cichlids, many of the original descriptions were based on one or two specimens (e.g. *Copadichromis eucinostomus* (Regan), *Metriaclima zebra* (Boulenger)) with no specific locality information within Lake Malawi. Thus, the range in morphological characters could not be estimated and additional topotypes could not be collected to effectively compare the variance of selected characters among populations.

Fortunately, within the last two decades, the analyses of morphometric data have evolved from the use of ratios and univariate morphometric analysis, to attempts to quantify the shapes of organisms (Atchley 1971; Humphries *et al.* 1981; Reyment *et al.* 1984; Bookstein *et al.* 1985). In effect, distances are measured between identified landmarks of the individual fish (Stauffer 1991). These data are analysed using a sheared principal component analysis (SPCA) in which the covariance matrix is factored (Humphries *et al.* 1981; Bookstein *et al.* 1985). These analyses ordinate the morphometric factors independently of a main linear ordination (Reyment *et al.* 1984). The first sheared principal component examines size differences, while subsequent components are independent of size (Humphries *et al.* 1981; Bookstein *et al.* 1985); thus, ratios are not needed to standardize the size of small and large specimens. Simultaneously, meristic data are analysed using principal component analysis (PCA), in which the correlation matrix is factored. Differences among species or populations can be illustrated by plotting one of the sheared components against the first principal components of the meristic data (Stauffer and Hert 1992). If the minimum polygon clusters of different populations are significantly different along one axis, independent of the other axis, a range test can be used to determine which clusters differ. If, in fact, the clusters are not significantly different along one axis independent of the other, then a MANOVA, in conjunction with a Hotelling–Lawley trace, can be used to determine whether the mean multivariate scores of the clusters formed by the minimum polygons are significantly different (Stauffer *et al.* 1997).

Although such techniques have greatly improved our resolution of slight morphometric differences (Stauffer *et al.* 1997), taxonomists are still stymied because in many cases, distinct species within the Lake Malawi cichlid species flock are morphologically similar (e.g. number of lateral line scales, number of cheek scales, horizontal eye diameter, head length). To attempt to diagnose these similarly shaped populations, colour patterns have also been used as morphological characters. The great diversity of colour patterns within the haplochromine cichlids is phenomenal (see Konings 2001) and the existence of unique colour patterns has been recognized to be a reliable character for distinguishing species (Barlow 1974; Barel *et al.* 1977; Greenwood 1981, 1991; Hoogerhoud and Witte 1981; McKaye *et al.* 1982, 1984; Bowers and Stauffer 1993; Stauffer *et al.* 1995, 1997).

Genetic approaches are also problematic because the Lake Malawi cichlids are speciating faster than alleles are fixed within a species (Kornfield *et al.* 1985; Kornfield and Parker 1997). Attempts to use mtDNA haplotype frequencies have met with limited success (Stauffer *et al.* 1995); however, the coalescence of mtDNA haplotypes found within populations predates the origin of many species (Parker and Kornfield 1997). A new method of using amplified fragment length polymorphisms (AFLP) may be promising for identifying distinct species (Albertson *et al.* 1999).

Trewavas (1983) pioneered the use of behavioural data to characterize cichlids when she diagnosed three genera of tilapiine fishes depending on whether they were substrate spawners, maternal mouth brooders, or paternal/bi-parental mouth brooders. In the past several decades, authors (e.g. Holzberg 1978; Schröder 1980; Stauffer 1988; Stauffer *et al.* 1997) have used behavioural characteristics (i.e. bower shape, colour patterns) (McKaye *et al.* 1993; Stauffer *et al.* 1993) to distinguish among sympatric populations and species. The lack of morphological differentiation and the inability of allozyme data to distinguish species prompted Stauffer and McKaye (2001) to conclude that a combination of genetic, morphological, and behavioural data should be utilized to describe new species of Lake Malawi cichlids. The purpose of this paper is to discuss how various behavioural studies have proved invaluable in recognising species, diagnosing species, and estimating phylogenetic relationships.

Definition of Lake Malawi fish species

Delineation of species of Lake Malawi cichlids is challenging, in part because of the plethora of species concepts that could be applied to the fauna. There is a tremendous controversy surrounding species definitions/concepts, and more than 21 different species concepts appear in the literature (Mayden 1997). The species definition that we propose for Lake Malawi cichlids is based primarily on the evolutionary species concept, but we also include criteria put forth as part of the biological and morphological species concepts (Stauffer and McKaye 2001).

Simpson (1951) originally proposed an evolutionary species concept that Wiley (1978) later defined as '. . . a single lineage of ancestor-descendant populations, which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.' The evolutionary species concept is therefore a species definition that uses as a unifying framework the idea that all species form a lineage, which is separate from all other species lineages. The species is therefore a natural entity on an independent evolutionary trajectory. Since, regardless of the type of reproduction (i.e. sexual vs. asexual), genetic material is passed from parent(s) to offspring; thus, this lineage concept applies to all reproductive modes. In doing so, this concept encompasses a wide array of possible species, both extant as well as extinct. Mayden (1997) concluded that the evolutionary species concept was the only concept that was apropos to all organisms.

The shortcomings of the evolutionary species concept are that it relies heavily on a well-resolved phylogeny, and it is nonoperational (Mayden 1997; Stauffer and McKaye 2001). The reality is that in many systems, including Lake Malawi cichlids, a comprehensive and well-supported phylogeny is not available. Hence, we are proposing several criteria to aid in the definition of Lake Malawi species. The first is reproductive isolation. This criterion has been traditionally associated with the biological species concept, which Mayr and Ashlock (1991) defined as 'A reproductively isolated aggregate of populations, which can interbreed with one another because they share the same isolating mechanisms.' Reproductive isolation is assessed through observations of mating activities or analysis of gene flow. We want to stress that we are using reproductive isolation as an indicator of the independence of evolutionary lineages and not as a species concept in and of itself. Second, we employ the morphological/behavioural similarity criteria that are typically associated with the morphological/phenetic species concepts to aid in species delineation. Again, we are not promoting the morphological/phenetic species concepts as such, but rather that sufficient morphological differences are evidence for separate evolutionary lineages.

The two criteria, reproductive isolation and morphological differentiation, can be used for species delineation; while behavioural similarities and morphological synapomorphies are used for phylogenetic reconstruction. For Lake Malawi cichlids, only a few phylogenetic hypotheses have been suggested (e.g. Parker and Kornfield 1997).

Role of behaviour in the evolution of Lake Malawi cichlids

Behavioural traits are important diagnostic tools for the delimitation of the Lake Malawi cichlid species, primarily because behavioural traits were responsible for and facilitated the rapid radiation of these fishes. The cichlid species inhabiting the lakes of East Africa are recognized to have arisen through processes of intralacustrine speciation (Greenwood 1991; Stiassny 1991; Takahashi *et al.* 1998, 2001). Also, biologists generally agree that female mate choice can be a driving force in evolution (Barlow 1991, 1998; Clutton-Brock 1991; McKaye 1991; Andersson

1994; Johnsgard 1994; Hogland and Alatalo 1995). Although allopatric speciation events certainly played a major role in this diverse assemblage of fishes, the existence of geographical barriers between populations may not in all cases be a prerequisite for speciation; thus, behaviour may have played a role in sympatric speciation events in cichlids (Dominey 1984; McKaye 1984; Smith and Todd 1984; McKaye 1991; Turner and Burrows 1995).

Sexual selection may have facilitated either allopatric or sympatric speciation events. In essence, theoretical studies have stressed that the complete absence of gene flow (Endler 1977; Rosenzweig 1978; Lande 1981; Slatkin 1982) or small population sizes (Barton and Charlesworth 1984) are not always needed for speciation events to occur. As early as 1871, Darwin suggested that sexual selection could play a major role in character divergence and the production of new species; however, sexual selection and behaviour have not been incorporated into many of the neo-Darwinism theories of speciation (Mayr 1963; Lewontin 1974). Sexual selection has been re-examined as a possible driving force for speciation in rapidly evolving groups (Lande 1981; Dominey 1984; Johnsgard 1994; Hogland and Alatalo 1995; Turner and Burrows 1995), but its importance may be limited (Barlow 1998).

Lekking (arena) behaviour among animals has attracted considerable recent attention among behavioural and evolutionary biologists (see Johnsgard 1994; Hogland and Alatalo 1995 for major reviews). These breeding aggregations of males offer excellent opportunities for examining: (i) the processes of mate choice when a large number of partners are available (Bradbury *et al.* 1985); (ii) the evolution of sexual preference and a 'runaway' nonadaptive feedback leading to the rapid formation of new species (Fisher 1930; Lande 1981; Dominey 1984; McKaye 1991); (iii) the importance of 'good-genes' and how these traits are selected by females (Hamilton and Zuk 1982); and (iv) the role of receiver bias in female choice (Basolo 1998).

Speculation and research upon these fundamental questions have a long history. Darwin's (1871) *The Descent of Man and Selection in Relation to Sex* first addressed the role of intersexual selection (female choice) as an evolutionary force for producing seemingly maladaptive traits. Where males provide no resources or parental care and females have numerous males among which to choose, 'extravagant' male secondary characteristics could result solely from sexual selection.

Theoretically, positive 'runaway' feedback provides a mechanism that could accelerate the joint evolution of female mate choice and male secondary sexual attributes. Fisher (1930) hypothesized that 'an evolution of sexual preference due to this cause would establish an effective isolation between two differentiated parts of a species, even when geographical and other factors were least favourable to such separation.' Furthermore, Fisher (1930) postulated that the following conditions would result under his model of runaway sexual selection: (i) the development of a male character and female choice for such a character would advance together until checked by severe counter-selection; and (ii) that the characters would change at an exponential rate so that even small initial effects would rapidly become exaggerated.

Lande (1980, 1981) expanded upon Fisher's original thesis and hypothesized that divergence in male traits, such as behavioural patterns, colour, and size, could originate rapidly throughout the range of a species due to local population differences in female choice. In particular, Arnold (1983) argued that lek-breeding species should exhibit 'extraordinary geographical variation in male attributes. Since the classic works of Fisher and Lande, additional models stressing the indirect selection of mating preferences have been developed. Perhaps the most prominent of these models includes various good genes hypotheses (Kirkpatrick 1987; Pomiankowski 1988; and many others). Models of host–parasite coevolutionary cycles also fall under the good genes heading (Hamilton and Zuk 1982). In addition to models incorporating indirect selection of preferences, direct selection models have also surfaced. Pleiotropic effects of preference genes, disease transmission, and the costs associated with searching for mates have all been the focus of such models (Kirkpatrick and Ryan 1991).

Many of the Lake Malawi cichlids exhibit lekking behaviour during the spawning season. Over the past 25 years, we have studied the reproductive ecology of approximately 50 cichlid fish species in southern Lake Malawi. We have observed a wide variety of bower forms among the cichlid species (McKaye 1983, 1984, 1991; McKaye and Stauffer 1988; McKaye *et al.* 1990; Stauffer *et al.* 1993; McKaye *et al.* 2001). These bower forms can be broadly divided into 10 types (McKaye 1991; McKaye *et al.* 2001). They range in size from giant craters 3 m in diameter (McKaye and Stauffer 1988) to small depressions in the sand, and to 'sand castles' with base diameters of 1 m

(McKaye 1984). Given the wide variability in bower shape (e.g. craters, mounds, and 'bumps' in the sand), it appears that no single bower form or size is best for the laying of eggs. We have studied variables associated with female choice in *Copadichromis conophoros* (Stauffer, LoVullo, and McKaye) and *Otopharynx* cf. *argyrosoma* (Regan) and several species of *Tramitichromis*/*Lethrinops*. Males of these species establish themselves on the lek prior to bower building and mating. The females move over the arena and lay eggs with several of the males on the arena (McKaye 1991). The entire egg-laying process takes anywhere from 25 to 65 min from the time a female lays the first egg (Kellogg *et al.* 2000) until she leaves with the eggs in her mouth. Our genetic studies of paternity clearly indicate extensive multiple matings by females (with as many as six males!), for both these sand-dwellers and the rock-dwelling cichlids (Kellogg *et al.* 1995). The process of female mate choice is complex. For example, *O.* cf. *argyrosoma* females selectively chose males that occurred in the centre of the lek (McKaye 1991), while *C. conophoros* and *Lethrinops* cf. *parvidens* Trewavas females chose males that built the largest bowers (McKaye *et al.* 1990; Kellogg *et al.* 2000). Recent analyses have shown that mating success in *L.* cf. *parvidens* is dependent on a bower's position in the lek as well as bower height. The rapid radiation of the Lake Malawi cichlid flock was probably accelerated by sexual selection acting in either allopatric or sympatric populations within this group. Therefore, the differences in behaviour between species might be the best way to distinguish between sibling species that differ little morphologically.

Application of behavioural parameters to analysing the taxonomy of Lake Malawi cichlids

Observations of mate choice and assortative mating among the rock-dwelling cichlids (Hert 1991; Oppen *et al.* 1998) indicate that female choice has influenced male colour. Forms previously thought to be colour morphs were in fact separate species (Holzberg 1978; Schröder 1980). Once differences in colour patterns suggested specific status of either sympatric or allopatric populations, investigators were able to support their hypotheses by discovering morphological (e.g. Burgess and Axelrod 1976; McKaye and Stauffer 1986; Stauffer 1988; Stauffer and Boltz 1989; Stauffer and Hert 1992) and genetic (McKaye *et al.* 1982, 1984, 1993; McElroy *et al.* 1991) divergences. In some cases, colour differences of females (Holzberg 1978; Schröder 1980; Stauffer and Hert 1992) supported hypotheses that certain populations were heterospecific.

Mate selection under laboratory conditions can also be used to test whether populations are heterospecific. If two populations breed and produce fertile offspring under laboratory conditions that does not necessarily indicate that they are conspecific. Certainly, the artificial conditions of the laboratory may have disrupted premating isolating mechanisms, which occur *in situ*. Furthermore, it is now recognized, particularly in rapidly radiating groups, that species can hybridize and produce fertile offspring because of the retention of the ancestral ability to do so (Zink 1997; Stauffer and McKaye 2001). On the other hand, if the offspring produced in the laboratory between two populations are inviable or sterile, that is good evidence that the populations are heterospecific. Many Lake Malawi cichlid species will hybridize in the laboratory and produce fertile offspring for successive generations when males of one species are held with females of another. Therefore, we cannot depend on offspring sterility to test the specific status of many of these cichlids. Recently, investigators have given fishes choices between conspecific and heterospecific individuals in the laboratory. To date, these experiments have resulted in females choosing conspecific males 100% of the time (Oppen *et al.* 1998; Kellogg 1997; Turner, personal communication), thus suggesting that the two populations are representing different lineages.

In general, the shallow-water sand-dwelling haplochromines in Lake Malawi are not as brilliantly coloured as the rock-dwelling cichlids. These sand-dwelling forms spend considerable energy in building bowers, however. By taking a series of measurements of these bowers (Fig. 1) and analysing these

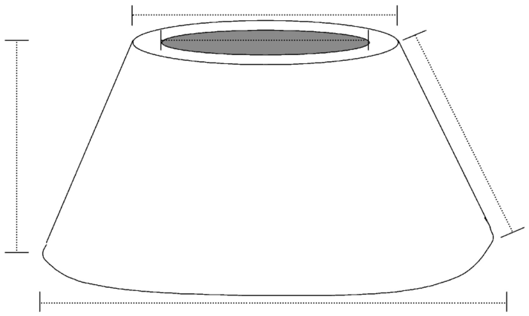

Figure 1 Schematic of a bower indicating the measurements taken to quantify shape.

data using a sheared principle component analysis, we have quantified bower shape. For example, extensive research on the ecology and behaviour of sand-dwelling fishes that fit the original description of *C. eucinostomus* indicated that three allopatric populations constructed bowers with three different population-specific shapes. Multivariate shape analysis confirmed that bower shapes for the three populations were significantly different ($P < 0.05$) (Stauffer *et al.* 1993). An analysis of the morphology of these fishes found that the minimum polygon clusters formed by plotting the principal component analysis scores of the morphometric and meristic data were distinct (see Humphries *et al.* 1981 and Bookstein *et al.* 1985 for a discussion of shape analysis). On this basis, three species (*C. conophoros* Stauffer, LoVullo and McKaye, *C. cyclicos* Stauffer, LoVullo and McKaye, *C. thinos* Stauffer, LoVullo and McKaye) were described (Stauffer *et al.* 1993). Subsequent to the description of these taxa, mtDNA haplotype frequencies of *C. conophoros, C. cyclicos, C. thinos*, and an undescribed species from Thumbi West Island were examined (Stauffer *et al.* 1995). Haplotype frequencies were significantly different ($P < 0.05$) among populations. These data confirmed the genetic uniqueness of *C. conophoros, C. cyclicos,* and *C. thinos*, which had been inferred from morphological and behavioural evidence.

Furthermore, if we compare these three *Copadichromis* species and two undescribed *Tramitichromis* species, we see that species within a genus build similarly shaped bowers (Fig. 2). Although we can qualitatively describe these differences between the two genera, they are also quantitatively different. Despite some overlap between the minimum polygon clusters formed by the two genera, the two groups are significantly different ($P < 0.05$; MANOVA). Thus, bower shape may in effect be a synapomorphy for diagnosing genera of these shallow-water sand-dwelling fishes.

In addition to bower shape, courtship behaviour may play a role in mate selection. McElroy and Kornfield (1990) suggested that Lake Malawi cichlids do not show any significant species-specific variation in spawning behaviour, at least among comparisons of rock-dwellers. Our video observations, however, demonstrate that variation does occur among the sand-dwellers. These differences in male courtship dances are often associated with differences in bower shapes (Fig. 3). The figure-8 courtship dance of *Tramitichromis* species and the S-shape dance of *Taeniolethrinops* species are both associated with distinctive bower forms (Stauffer *et al.* 1995; McKaye *et al.* 2001). The usefulness of these behavioural characters is further reinforced by the occurrence of a synapomorphic morphological character in *Tramitichromis* species. All of the *Tramitichromis* species were examined and found to possess an enlarged keel (Fig. 4) on the lower pharyngeal bone (Eccles and Trewavas 1989). Additionally, all the *Tramitichromis* spawning leks, for which specific locality information was known, including leks of many undescribed forms, were observed and the existence of a figure-8 courtship pattern and a bower with a distinct crown was recorded. Thus, the following three synapomorphies diagnose the genus *Tramitichromis*: enlarged keel on the lower pharyngeal bone, distinct crown on the cone-shaped bower, and figure-8 courtship pattern of the male. Two of the three synapomorphies that are used to diagnose the genus *Tramitichromis* are based on behaviour.

To illustrate the importance of such behavioural data to diagnose the haplochromine flock of Lake Malawi, we want to briefly illustrate the complexity of one species group, *Aulonocara stuartgranti* (Meyer and Riehl). This taxon varies throughout the lake and is presently considered to be single species with great geographical variation (Konings 2001). This species/species complex is a model group to utilize

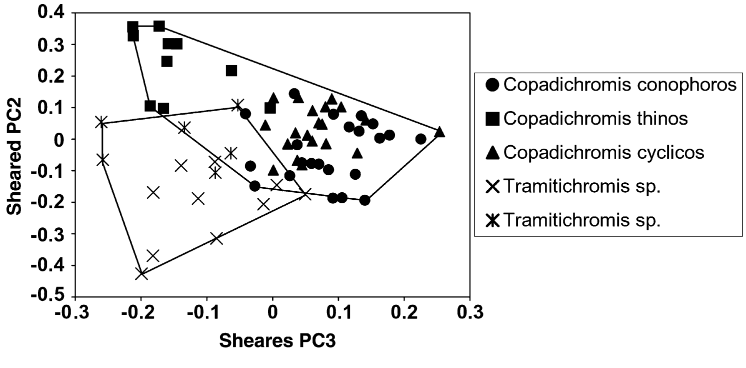

Figure 2 Plot of individual sheared PC2 scores and sheared PC3 scores of bowers constructed by five shallow-water sand-dwelling species.

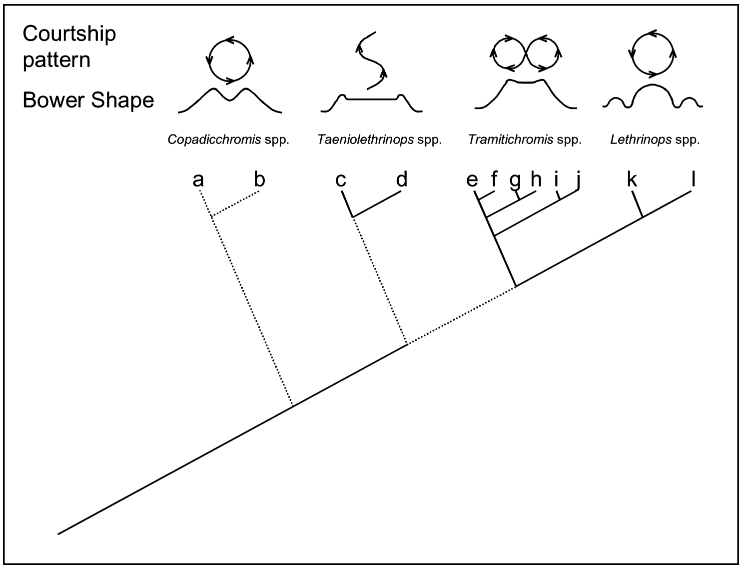

Figure 3 Association of bower types and courtship dances for a series of shallow-water sand-dwelling cichlids from Lake Malawi.

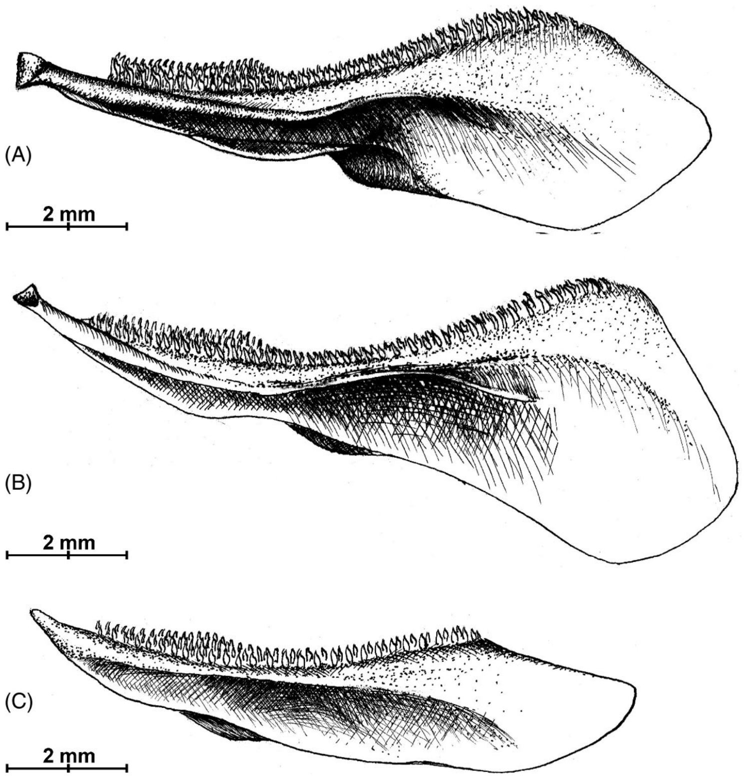

Figure 4 Lateral view of the pharyngeal bones of two *Tramitichromis* spp. (A; B) and *Lethrinops furcifer* (C).

the behavioural-based techniques proposed by Barlow (2002).

Aulonocara stuartgranti occurs along the entire north-western coasts, and on the eastern shores shore of the Ruhuhu River (Fig. 5). On the north-western coast, *A. stuartgranti* occurs at every locality between Kande Island and Ngara. Between Charo and Mara Rocks, the male breeding coloration of the different populations of *A. stuartgranti* varies from all blue to blue-yellow to completely yellow, and then

Figure 5 Distribution and colour morphs of *Aulonocara stuartgranti*.

back again to all-blue. The stretch of coast along which these various populations are found is no longer than 40 km.

There are two populations of *A. stuartgranti* in Chitimuba Bay (Fig. 5). One form inhabits the shallow intermediate area at a depth of about 5 m while the other is found at a deeper locality in the same bay, about 2.5 km offshore, where the biotope consists of sheets of sandstone. The *A. stuartgranti* is, with a maximum length of 9–10 cm, much smaller than the deeper water variant, which is estimated to have a maximum size of about 13 cm (Fig. 5).

Furthermore, Konings (2001) regards *Aulonocara steveni* (Meyer, Riehl, and Zetzsche) (Fig. 5, Kande Island), also known as 'Usisya *Aulonocara*', as a junior synonym of *A. stuartgranti*. In this form/species, the male breeding coloration is quite different to that of the blue-coloured holotype of *A. stuartgranti*. Konings (2001) found that on several occasions there were no clearly defined borders between the all-blue and the all-yellow populations. There is a gradual change from one extreme (all-blue) to the other (all-yellow), although males of any given population show a more or less constant coloration; the coloration changes with the population, not within a population. It may be that these *A. stuartgranti* forms represent a case where the fish look different, but are possibly a single species. We postulate that without detailed behavioural experiments the specific status of many of these populations will continue to be unresolved.

Conclusions

The cichlid fishes of Lake Malawi probably represent one of the best examples of rapid radiation of vertebrates. Historically, these species have been diagnosed with morphological and genetic data. The species status and phylogenetic relationships of many of these fishes continue to remain unresolved. The taxonomic uncertainty of these fishes prompted us to promote the use of a combination of morphological, genetic, and behavioural data (Stauffer *et al.* 1995; Stauffer and McKaye 2001) to diagnose the taxonomic status of these fishes.

Behavioural differences were first used to suggest that various populations were, in fact, heterospecific. For example, when McKaye, in the early 1980s, presented cichlids from different populations to the authorities on Malawi fishes, these experts identified all of them as *T. lituris*. McKaye knew these were different species because they built differently shaped bowers and the males' courtship dances were distinguishable. When these populations were delimited based on behavioural characters, we were able to identify morphological characters that were also distinct among these taxa.

In addition, McKaye (1983) and McKaye *et al.* (1990) collected extensive behavioural data on a species, which was morphologically identified as *C. eucinostomus*. Only after Stauffer *et al.* (1993) collected detailed data on bower shape, were we able to describe three species of *Copadichromis* in the south-east arm of Lake Malawi. Again, it was bower shape, which first suggested that the different populations were heterospecific. The use of behavioural data, as expressed in mate choice based on colour patterns, has also been successfully used to delimit many rock-dwelling cichlids (Stauffer *et al.* 1997). The populations of *A. stuartgranti* may be at the other end of the spectrum (i.e. fish in different populations are coloured different, but may represent a single species). Without the behavioural information, many of the species taxa can not be resolved.

The importance of behavioural information has been undervalued in the assignment of autapomorphic and synapomorphic characters to the varying levels in the Linnean hierarchy of these fishes. We have shown (Fig. 3) that bower shape and the males' courtship dance are synapomorphies that define certain genera of Lake Malawi cichlids. In Eccles and Trewavas' (1989) revision of many of the genera of the sand-dwelling cichlids of Lake Malawi, they diagnosed the genus *Tramitichromis* by the presence of a keel on the lower pharyngeal bone; however, they kept *L. parvidens* in the genus *Lethrinops*. Underwater observations revealed that the species that we morphologically identified as *L. parvidens* in the south-east arm of Lake Malawi, builds a cone-shaped bower and the males display a figure-8 courtship dance. Thus, we hypothesized that this species belonged to the genus *Tramitichromis* (Fig. 3). Examination of the lower pharyngeal bone shows a distinct keel. Finally, given the diversity of these Lake Malawi fishes, we conclude that only through detailed *in situ* and laboratory studies on the behaviour of these organisms, evolutionary processes and patterns of speciation among Lake Malawi haplochromine cichlids will be revealed (see Barlow 2002).

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