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PROBLEMS OF SPECIES DEFINITION IN LAKE MALAWI
CICHLID FISHES (PISCES: CICHLIDAE)

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ABSTRACT

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The evolution of the cichlid species flock in Lake Malawi has taken place very rapidly and resulted in the proliferation of a large number of species many of which are similar to one another. This has given rise to a situation in which traditional methods of distinguishing species based on preserved specimens are often of limited value. There are many instances of different species having almost identical morphologies, of single populations of one species showing considerable morphological variation and of marked geographical intraspecific variation. Polymorphism is considered not to be as widespread as previously thought, and pronounced random intraspecific colour variation within a population is discounted. Sympatric sibling species may be distinguished by observing behavioural and habitat differences in the field, but no means has been devised for ascertaining whether morphologically and behaviourally similar allopatric forms are specifically distinct. Lack of access to fresh specimens and lack of information on distribution and habitat have resulted in numerous errors appearing in taxonomic works on Lake Malawi cichlids.

Great care is needed when attempting scientific descriptions of cichlid species from the African Great Lakes, and it is suggested that such work be left to specialists with knowledge of living and fresh fish in these lakes.

PROBLEMS OF SPECIES DEFINITION IN LAKE MALAWI
CICHLID FISHES (PISCES: CICHLIDAE)

by
Digby S.C. LEWIS¹

INTRODUCTION

The endemic cichlid species flocks of the African Great Lakes pose taxonomic problems at a number of levels. Particularly perplexing is the primary task of defining and delimiting species.

The concept of a species as a group of interbreeding natural populations which are reproductively isolated from other such groups, as proposed by Mayr (1963), is almost universally accepted. Nevertheless, the majority of taxonomists concerned with descriptions of new species of fish are restricted to the study of preserved material and thus denied access to much of the information required for conclusive establishment of specific distinctness. As the majority of recognised species are morphologically distinct to a greater or lesser extent, most species diagnoses based solely upon morphology correspond to biological species. But where speciation has taken place unusually rapidly and resulted in the proliferation of groups of reproductively isolated but morphologically similar species, the separation of species on morphological grounds alone becomes difficult or impossible. Such "explosive speciation" has taken place amongst the cichlid fishes of Lake Victoria, Tanganyika and Malawi (Greenwood, 1981). Recent investigations of the cichlids of Lake Malawi have highlighted some of the practical problems associated with taxonomic studies of such young and speciose faunas.

SIBLING SPECIES AND POLYMORPHISM

The acquisition of reproductive isolation with minimal morphological change probably constitutes the greatest problem to the taxonomist attempting to distinguish species. This phenomenon, which results in the evolution of sibling species (as defined by Mayr, 1963) occurs widely in Lake Malawi. The specific distinctness of morphologically similar Lake Malawi cichlids was first recorded by Trewavas (1941) amongst the endemic members of the genus *Oreochromis* (then referred to as *Tilapia*). The four described species of *Oreochromis* endemic to Lake Malawi *Oreochromis saka*, *O. squamipinnis*, *O. lidole* and *O. karongae* show marginal morphological differences yet the males have distinctive breeding coloration, they breed at different times of year and in different depths of water and, have colonized different habitats (Lowe, 1953). Another male colour form, which probably represents a fifth species, has recently been discovered in the north of the lake (personal observation).

Sibling species are also to be found amongst the haplochromine species flock, and a number of examples of differentiation in male colour pattern, with very slight accompanying differences in morphology, have recently been found in sympatric populations of *Lethrinops* and *Aulonocara* (Lewis, unpublished data). As most of the descriptive work on Lake Malawi cichlids has been based on preserved specimens, live coloration has played little part in species diagnoses. Yet it should not be surprising that amongst fishes that display complex courtship behaviour, coloration, particularly of the males who initiate the mating ritual, plays an important role in species recognition. Differences in coloration, even when quite subtle, can therefore often be of considerable taxonomic value.

Colour polymorphism or polyphasy is a well known feature of a number of members of the 'mbuna' group of rock-dwelling cichlids (Fryer, 1959; Fryer and Iles, 1972), though recent work has shown that some of these so-called morphs are distinct species. Holtzberg (1978) studied blue-black (BB), blue (B), white (W) and orange-blotch (OB) colour morphs of *Pseudotropheus zebra* in the field. He observed that the BB and OB morphs differed from the B and W morphs in territory size, aggressiveness and habitat preference and

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that mating did not occur between the BB/OB and B/W morphs. Schroder (1980) made comparative studies of the agonistic behaviour of the *P. zebra* colour morphs in aquaria and also compared the anatomy of 164 specimens of the four morphs. His results confirmed the suggestion of Holtzberg (1978) that the BB/OB and B/W gene pools represent sibling species and not morphs of a single species.

Recent field and laboratory studies by biologists at the Monkey Bay Fisheries Research Unit have shown that a number of other supposedly polymorphic species of 'mbuna' are groups of sibling species which differ from one another in behaviour, habitat preference and depth range. *Pseudotropheus tropheops* was previously thought to be a variable species with a large number of colour forms. Fryer (1959) went as far as synonymising three previously described species and two subspecies into the species *P. tropheops*. In the Nkhata Bay region, which was the area most studied by Fryer, seven species which conform to the description of *P. tropheops* have been distinguished (Lewis, unpublished data and B. Marsh pers. comm.) They have distinctive coloration, in some cases occupy different habitats, have consistent small differences in anatomy (particularly of the jaws and neurocranium) and show no evidence of interbreeding. Marsh *et al.* (1981) have shown that *Petrotilapia*, which was considered to be a monotypic genus, is also a complex of numerous species. These differ in coloration, depth range and territory size yet are indistinguishable from one another anatomically.

INTRASPECIFIC VARIATION

Intraspecific variation poses another problem for the taxonomist. It may be divided into two forms:- variation amongst members of a population from a single locality and geographical variation. Whenever a large sample of a single species has been collected from one locality considerable variation has been found. If more than one morphologically similar but variable species occur sympatrically, such variation can cause difficulties in identification. Eccles and Lewis (1977) found individual variation was such that no single character could be used to distinguish with certainty all specimens of *Lethrinops stridei* from *L. microdon* and *L. micrentodon* and only by examining a number of features in conjunction could a reliable identification be made. Lewis (1982) found that the degree of morphometric overlap between species of *Labidochromis* made it impossible to construct a key based on morphological characters other than colour.

Geographical variation within a species is usually greater than variation between individuals from one population. Eccles and Lewis (1979) used differences in the shape of the pharyngeal bone of populations of *Lethrinops mylodon* from central and southern Lake Malawi to distinguish two subspecies. However they noted that in the absence of material from between the two collection sites it was not possible to state whether the two subspecies represented populations unlinked by morphological intermediates or merely points on a morphocline. The situation has recently been confused by the discovery that specimens of *L. mylodon* from the far north of Lake Malawi are morphologically more similar to the southern specimens than to those from the centre of the lake (personal observation).

Many rock-dwelling cichlids of the mbuna complex show considerable geographical variation in colour with no discernible differences in morphology. The colour difference between populations may be very slight or prominent. Without knowing the specific mate recognition signals for a species it is not possible to tell whether a particular difference in coloration would be sufficient to inhibit mating between forms. The procedure that I have adopted (Lewis, 1982) is to attribute geographical colour differences to intraspecific variation if the colour forms are behaviourally identical and occupy the same niche in different localities and if the differences apply only to intensity of coloration or to minor colour disparities. However, it is appreciated that an apparently minor colour difference can play an important role in mate recognition; thus this approach could result in the inclusion of a number of sibling species in a singly nominal species. The alternative is to consider all populations that show colour discontinuity, however slight, as separate species;

this would undoubtedly result in a number of biological species being subdivided into nominal species. Splitting species solely on the basis of small colour differences would be further confounded because the coloration of an individual can show considerable variation dependent upon breeding condition, degree of stress, food supply (in aquaria at least) and health.

Coloration differences between allopatric populations may represent early stages in the process of speciation, and only recombination of such populations under natural conditions can demonstrate whether or not speciation has occurred.

Labeotropheus fuelleborni Ahl, 1926 is currently considered to be a single widespread species displaying a considerable degree of geographical colour variation (Ribbink *et al.*, in press). It is a polymorphic species, the more common morph having blue males and brown females and the less common being orange with black blotches (OB) in both sexes (though OB males are very uncommon). Along most of the rocky coast in southern Lake Malawi the male of the common morph is royal blue with prominent dark bars and orange-red soft dorsal, anal and pelvic fins. On the small island of Chinyankwazi in the southeast arm of the lake, the males have a black dorsal fin. On Kantenga Island also in southern Lake Malawi, males are pale blue with a bright orange flush on the flanks. Yet on Maleri Island which is separated from Kantenga by a mere 800 meters of water, the males of *L. fuelleborni* are pale blue with no trace of orange on the flanks but with a pinkish tint to the dorsal fin. The narrow tract of water between Maleri and Kantenga Island is more than 50m in depth, which greatly exceeds the recorded depth range of *L. fuelleborni* (Ribbink *et al.* in press) and apparently constitutes a physical barrier to this species. In other parts of the lake, males are uniform pale blue, pale blue with dark bars, pale blue with an orange dorsal fin or pale blue with a yellow chin and belly. The OB morph also displays geographical variation and may have small spots, large blotches or may be pure orange. Geographical variation in *Labeotropheus* is discussed at greater length by Ribbink *et al.* (in press) who also consider the differences to be intraspecific. Similar geographical colour variation occurs in *Pseudotropheus zebra* and in members of the *Petrotilapia* complex (personal observation).

DISCUSSION

It should be clear from the above account that there are many potential pitfalls facing the taxonomist proposing to differentiate and describe cichlids from Lake Malawi, or from Lake Tanganyika and Victoria which have similar speciose faunas. Different species can look alike and a single species can exist in different forms. How then can taxonomists working on preserved collections without information on colour, behaviour, distribution or habitat be sure of assigning specimens to their correct species? In many cases they cannot, and consequently there are many errors of species distinction in the published taxonomic works on Lake Malawi cichlids.

Having examined large numbers of fresh specimens from various localities, observed many species in the field and gained some knowledge of distribution patterns and the slight morphological differences that separate certain species, I have been able to study the collection of Malawi fishes at the British Museum (Natural History) with background information not available to the original describers. Not surprisingly I have found that number of type-series comprise more than one species, and that other described species are not valid. For example, the type-series of *Labidochromis vellicans* Trewavas 1935 includes three species (Lewis 1982); also *Rhamphochromis esox* (Boulenger, 1908) and *R. leptosoma* Regan 1921 are almost certainly synonymous.

Taxonomic errors are not restricted to the early works on Lake Malawi cichlids, and there have been a number of recent examples of confusion between morphologically similar species. Johnson (1974) described *Labidochromis joanjohnsonae* from two specimens that were subsequently found to belong to different

species. The confusion that this error engendered has been discussed by Lewis (1980). Oliver (1975) described *Labidochromis textilis* from 13 specimens obtained from various aquarist dealers and from colour photographs of other specimens published in the aquarist literature. What Oliver assumed to be a single variable species was in fact a number of species with very similar colour patterns and fairly similar anatomy. His lack of field knowledge of the species concerned resulted in his describing the colour pattern of one species and the anatomy of four others (Lewis, 1982).

It would be satisfying to be able to lay down a set of rules for delimiting cichlid species of the African Great Lakes, but this is no easy task. When considering similar sympatric species, the problems are usually surmountable, as field observations combined with intensive collecting can often establish specific distinctness even if there is little corresponding morphological differentiation. But where samples from different areas display morphological or colour differences the problem is far more complex. Extensive collection may show that distribution is widespread and continuous, and that variation is clinal; though by the very nature of the topography of Lake Malawi, the distribution of many species, especially the rock dwellers, is markedly disjunct. In such instances there is no absolute means of determining whether genetic differentiation has proceeded to the stage where, if two populations were brought together, they would maintain their identity.

In describing allopatric species of *Lethrinops*, Eccles and Lewis (1978) considered populations as specifically distinct if the differences between them were consistent and of a similar magnitude to differences separating related sympatric species. If there appeared to be clinal variation, or if differences were very minor, then the populations were regarded as conspecific. Such a means of deciding whether or not populations are specifically distinct is obviously artificial, but no practical alternative has yet been devised. In a recent, and as yet unpublished study, K. Mckaye and T. Kocher (pers. comm.) used starch-gel electrophoresis to compare allele frequencies in morphs of both the *Pseudotropheus* and *Petrotilapia* species groups. In neither taxon did they find alternative fixed alleles at any of the 25 loci examined though they discovered heterogeneous gene frequencies at a number of polymorphic loci in both groups. These results suggest the presence either of sibling species or incipient species with minimal gene flow between them. Such electrophoretic examination may provide a valuable tool for species distinction in the absence of morphological difference.

In the case of shallow water species, and particularly the rock dwelling mbuna, observation in the field is usually possible and ethological traits can be used as taxonomic characters. Thus separate populations displaying different traits are likely to represent different species though the converse is not necessarily true and reproductive isolation could be effected by differences in coloration and might arise before any change in behaviour.

In view of the complexity of the situation, a great deal of care is required when attempting descriptions of new species of cichlids from the African Great Lakes. Unfortunately, as a result of the recent interest in African cichlids as aquarium fishes, descriptions of new species have been appearing in aquarist publications. With barely an exception these have been inadequate by present day standards and have obviously been written with little if any understanding of the problems just discussed. Because of the confusion that can arise from erroneous descriptions of new species, it is hoped that future descriptions of new species will appear only in scientific journals specialising in taxonomy, that wherever possible studies will cover whole taxonomic groups rather than single species, that the problems of intraspecific variation and sibling speciation will be considered, that outgroup comparisons will be made with related taxa, and that when possible, descriptions will include the often neglected biological characters of live coloration, habitat choice and behaviour.

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