

## Chapitre 2

## EVOLUTION AND SPECIATION OF AFRICAN CICHLIDS

## ÉVOLUTION ET SPÉCIATION DES CICHLIDÉS D'AFRIQUE

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So spectacular are the extent and rate of evolution and speciation of the fishes of the Great Lakes of East Africa that the terms «evolutionary avalanche» (Liem, 1973), «explosive evolution» and «explosive speciation» (Greenwood, 1964, 1974, 1981; Fryer & Iles 1972; Mayr, 1976) have been used to describe the phenomena. Furthermore, Fryer (1972) and Greenwood (1973) suggest that the cichlid fishes provide better and more illuminating examples of evolution and speciation than the traditionally cited Darwin's finches. There are, for example, more than 800 species of cichlid in the East African Great Lakes (Table 1), but no more than 14 species of finch in the Galapagos Islands (Lack, 1947).

**Table 1 :** The number of cichlid and non-cichlid species found in three of the Great Lakes of Africa. Data from Fryer & Iles (1972), Greenwood (1974), Lowe-McConnell (1975) and authors cited in the table.

	No. of cichlid species	No. of non-cichlid species	No. of endemic species	
			cichlids	non-cichlids
Lake Victoria	250 + Van Oijen <i>et al.</i> (1981)	39	all but 3	17
Lake Tanganyika	140 + Brichard (1978)	67	all	47
Lake Malawi	400-500 Ribbink <i>et al.</i> (1983a)	44	all but 4	24

Although adaptive radiation and speciation has occurred in the non-cichlid families, it is clear from Table 1 that these families are overshadowed by the Cichlidae. Indeed, the differences between the cichlids and non-cichlids with regard to these evolutionary phenomena are so great that some workers questioned whether the evolutionary processes involved were unusual and whether the cichlid fishes possess characteristics not shared by the other families with which they co-exist (see Greenwood, 1981 for comment). The cichlids dominate the ichthyofauna of these lakes in a taxonomic sense as well as ecologically (Greenwood, 1974), and in all habitats

except the pelagic zones they have a numerical dominance. The Cichlidae are of great commercial importance as food and aquarium fishes. For these reasons, and also because of the interest stimulated by their evolutionary success, most work on the fishes of the Great Lakes of Africa has focussed upon cichlids. This focus does not exaggerate the commercial value of, and interest in, cichlids, but it leads to a general tendency to associate these Great Lakes with cichlids and to virtually ignore the contributions of many of the non-cichlids. A great deal of excellent work has been done on these non-cichlids (Poll, 1953; Jackson, 1959; Whitehead, 1959; Corbet, 1961; Coulter, 1976, 1981), but a clear synthesis is lacking. I am not qualified to provide such a synthesis, so in this chapter I follow the established trend and concentrate almost exclusively on the evolution and speciation of cichlids.

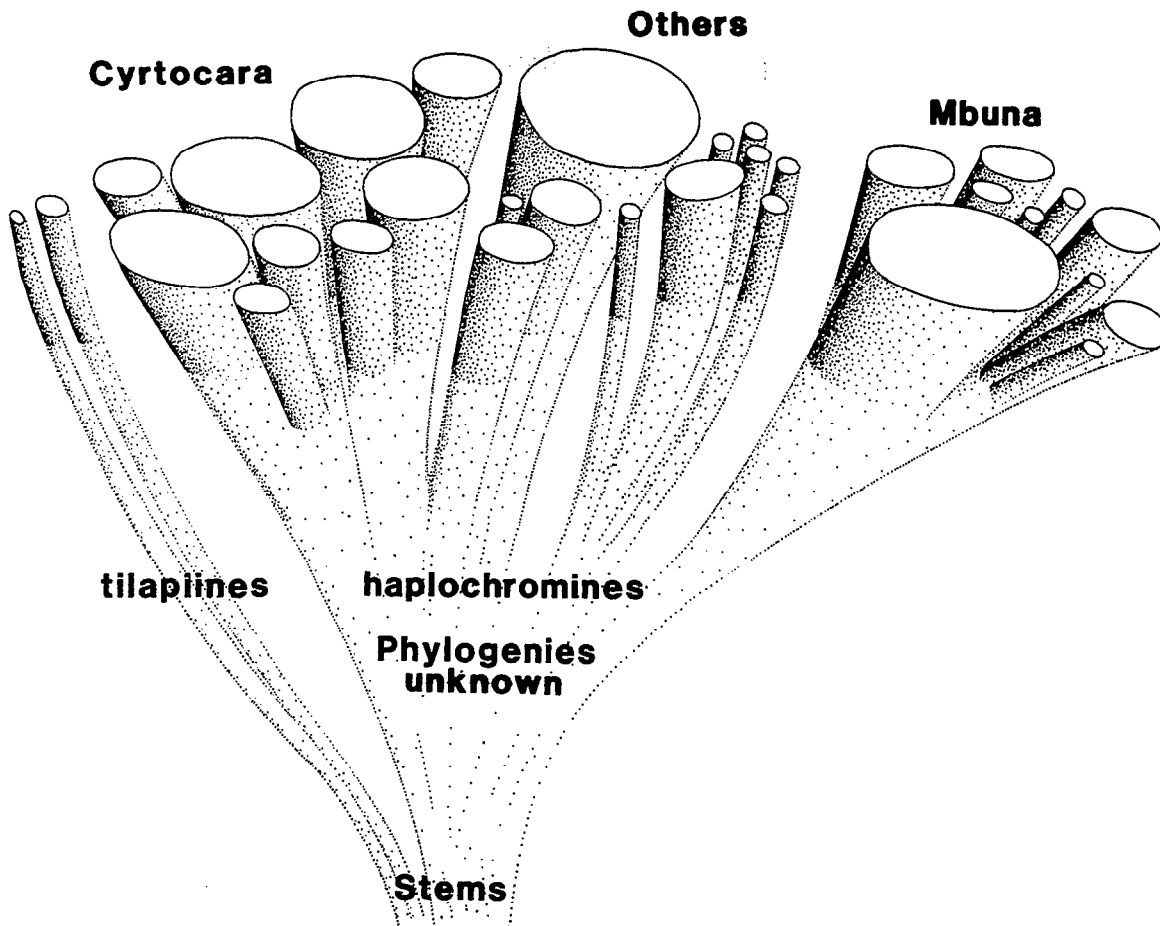
In this essay attention is focussed on adaptive evolution and its effect (speciation) as portrayed by the Recognition Concept of Paterson (1978). In so doing a repetition of the content of several important publications on evolution and speciation is avoided. It is necessary, therefore, that readers should consult the publications of Greenwood, Fryer (particularly Fryer & Iles, 1972), Lowe-McConnell and Ribbink *et al.* for details of those subjects omitted or given scant attention here. For example, little or no reference is made to the effects of predators, multiple invasions and breeding seasonality on speciation. Furthermore, I have not considered here the possible contributions sympatric and other non-allopatric modes of speciation (for which there is no convincing evidence) may have made to the species flocks. Nor have I discussed how our knowledge could be advanced by electrophoretic, cytogenetic and genetic studies.

## 1 - EVOLUTION

Evolution is an historical process concerned with the origin, ancestry and differentiation of organisms. In a study of evolution, the adaptations of organisms to the environment are traced. Ideally, to unravel the evolutionary history of any group a long series of fossils as well as recent forms should be available. There are, however, very few known fossils of African fishes, and those which have been found throw virtually no light on the stages through which the contemporary forms have passed (Greenwood, 1959; Fryer & Iles, 1972). To understand the evolution of the extant species, therefore, it is necessary to call upon all the available information on the morphological, ecological, behavioural and zoogeographical aspects of extant species. These should be viewed against the geological history of the lakes. Such historical aspects are summarised by Fryer & Iles (1972), Greenwood (1974) and Beadle (1981). Of importance to our discussion is the age of the lakes (Table 1) as this gives an indication of the overall rate at which diversification occurred. Furthermore, the way in which the Rift Valley Lakes formed is such that most evolutionary changes are likely to have occurred in one, or perhaps, two basins (Fryer & Iles, 1972; Fryer 1977). Lake Victoria, however, is not a Rift Valley Lake and it seems that during its history lake levels changed markedly in response to climatic and tectonic events (Greenwood, 1974). Consequently, a variety of smaller or larger lakes existed, at times partially or wholly interconnected, at other times partially or wholly isolated from one another. It is argued that, during periods when the lake comprised a number of smaller water bodies, the isolated populations might have diverged and that since this differentiation occurred in a number of lakes it is not strictly intralacustrine (Fryer, 1977).

## 2 - ORIGIN OF THE FISHES

The original colonisers of the newly formed lakes were, almost certainly, riverine species. Those which have adapted most successfully to the new conditions in the developing lakes are the cichlids, particularly the haplochromines, which constitute the vast majority of contemporary species (Fig. 1). Although all haplochromine species are believed to have had a single common ancestor (Greenwood, 1979) it seems that different, but closely related, ancestral forms colonised each lake. Regan (1921), Trewavas (1935) and Fryer & Iles (1972) consider the endemic haplochromines of Lake Malawi to have had a common ancestor with many features in com-



**Figure 1** :The cichlid fishes of Lake Malawi are composed of two main lineages : the tilapiines, comprising 6 *Oreochromis* spp. and 2 *Tilapia* spp., and the haplochromines comprising numerous genera and 400-500 species. The phylogenies of the haplochromines are largely unknown, but several contemporary groups may be recognized : (a) the 10 Mbuna genera ; (b) the genus *Cyrtocara* which comprises a number of distinct groups (as illustrated) which will probably be recognized as separate genera when a revision of the genus is completed ; (c) «the others» which comprise the *Lethrinops* spp., *Aulonocara* spp. and *Trematocranus* spp. which are closely related to some *Cyrtocara* spp., as well as the more distantly related *Rhamphochromis* spp. and several mono- and ditypic genera.

mon with *Astatotilapia calliptera* (= *Haplochromis callipterus*), a contemporary widespread species which lives in a variety of waterbodies, including rivers and streams, as well as in Lake Malawi. However, Greenwood (1979) believes that the Malawi species are likely to have had a polyphyletic origin and that lineages related to *Thoracochromis* (= *Haplochromis* : see Greenwood, 1979), *Serranochromis* and *Chetia* (= *Haplochromis* : see Greenwood 1979) may have contributed to the flock in addition to *Astatotilapia calliptera*. No evidence is given to support this suggestion.

The haplochromines of Lake Victoria appear to have had a monophyletic ancestry (*Astatoreochromis alluaudi* excepted) originating from a «*Haplochromis*» *bloyeti*-like ancestor (Greenwood, 1974).

Lake Tanganyika poses a more difficult problem. Its cichlid species are older and more markedly differentiated than those of the other two lakes and it is not now possible to define the ancestral forms. Indeed, there is at present considerable doubt as to whether certain species should be assigned to the haplochromines or tilapiines (Wickler 1963; Fryer & Iles, 1972; Greenwood 1978) and some species may not belong to either (Greenwood, 1978). A great deal of study is required to define accurately the origins and trace the phylogenies of these fishes.

### 3 - ADAPTATIONS

The high degree of endemism of the fishes of the Great Lakes indicates that virtually all contemporary species originated within the lakes or, in the case of Lake Victoria, within the protolakes now encompassed by the present lake basin. The generalized riverine ancestral forms which colonised the developing lakes had opportunities to adapt to a variety of new, unoccupied habitats. These opportunities were most efficiently taken by the cichlids, which now occupy a greater variety of microhabitats in each lake than all the other families of Great Lakes fishes combined (Greenwood, 1974). The adaptations necessary to enable the fishes to adjust to the various microhabitats resulted in the spectacular radiation and species diversification for which these lakes are now well known.

It seems that different populations became adapted to live over sand, among aquatic vegetation, among rocks and in open water. Within the communities which occupied each of these habitats fishes became specialized to occupy particular parts of those habitats (microhabitats). For example, within a relatively uniform habitat, different species occur at different depths (Ribbink & Hill, 1979; Marsh *et al.*, 1981; Ribbink *et al.*, 1983a) or utilize different parts of the rocky or sandy substrata (Eccles & Lewis, 1979; Van Oijen *et al.*, 1981; Ribbink *et al.*, 1983a; Ribbink & Eccles 1986). Most overt structural and behavioural specializations of the Cichlidae in these lakes are associated with different, but specific modes of feeding. The generalized haplochromine ancestors are considered to have been small, omnivorous species with a preference for carnivorous (mainly invertebrate) diets. The teeth of such ancestors were unspecialized, but well suited to their varied diet and the skull was largely unmodified (Fryer & Iles, 1972). From these unspecialized ancestors arose the many trophically specialized species found today, details of which may be found in Poll (1953, 1956) Greenwood (1974, 1979, 1981) Fryer & Iles (1972) and Barel *et al.* (1977).

Numerous close morphological, trophic, ecological and behavioural parallels are exhibited by the cichlids occupying the different Great Lakes. Comparisons of the rock-frequenting fishes of three Great Lakes (Malawi, Tanganyika and Victoria) show that, in general, the communities are similar; virtually all member-species are small, darkly or brightly coloured and sedentary (Fryer & Iles, 1972; Van Oijen *et al.* 1981; Ribbink *et al.* 1983a). Similarly, those communities whose members are adapted to sandy habitats, vegetated habitats or open water show a number of striking parallels (Fryer & Iles, 1972). The incredible similarity between the *Petrotilapia* species of the rocky zones of Lake Malawi and the *Petrochromis* species of rocky habitats in Lake Tanganyika, which resemble each other behaviourally, ecologically and structurally - possessing virtually identical teeth and jaws - is a well known example (Fryer & Iles, 1972; Yamaoka 1982). Other very similar species are the *Labidochromis* of Lake Malawi, *Tanganicodus* of Lake Tanganyika and *Paralabidochromis* of Lake Victoria (Greenwood 1956; Fryer & Iles 1972). Indeed, the genus *Pseudotropheus* of Lake Malawi was so named because of its close resemblance to the genus *Tropheus* of Lake Tanganyika (Regan, 1921). In addition, fishes of paedophagous habits, those showing cleaning behaviour, various scale eaters, a number possessing hypertrophied lips and fishes showing several other trophic adaptations, have evolved inde-

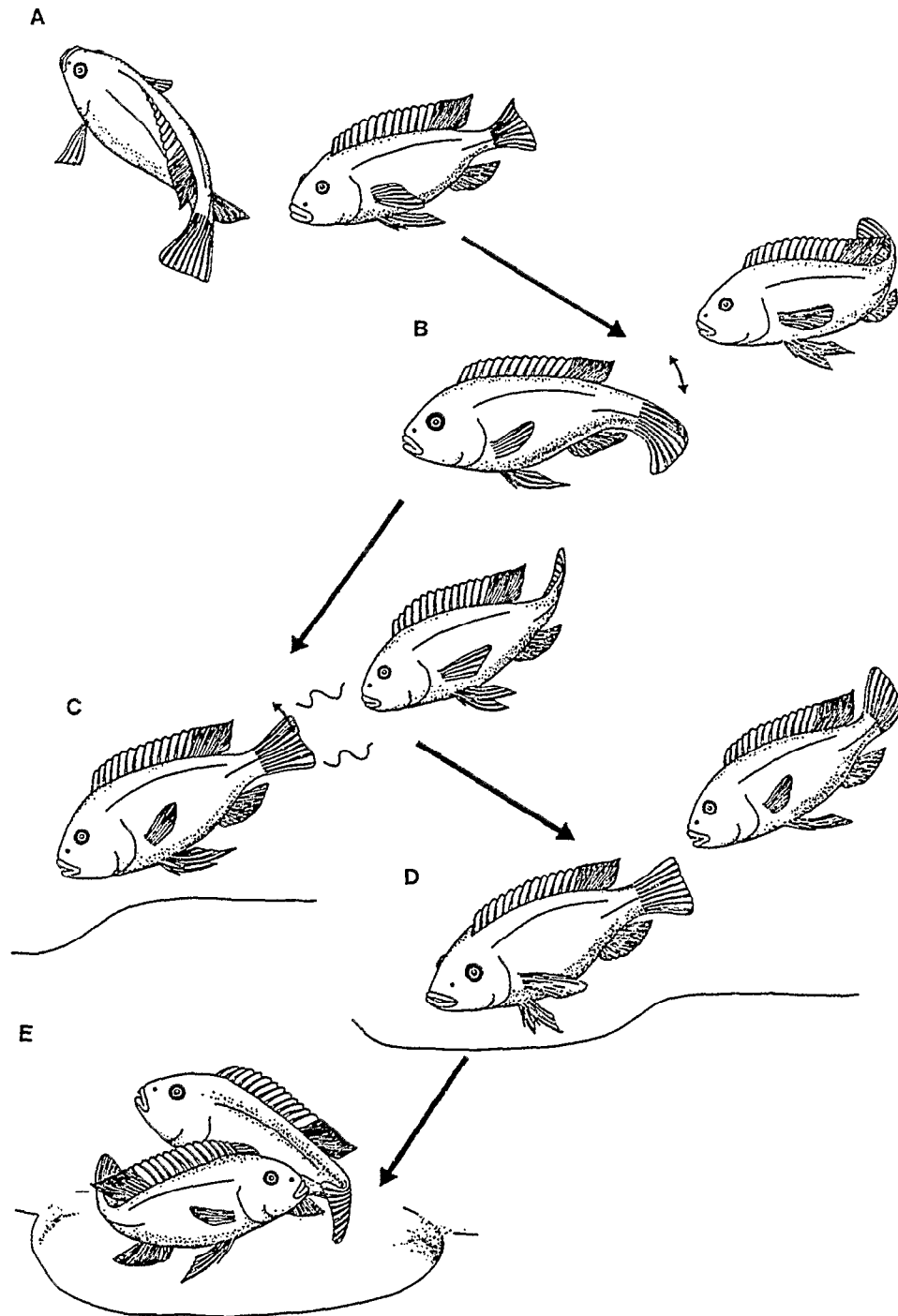
pendently in two or more lakes (Fryer & Iles, 1972, Mayland, 1978; Van Oijen *et al.*, 1981; Witte & Witte-Maas, 1981; Ribbink & Lewis, 1982; Ribbink *et al.* 1983a). The parallel evolution of these cichlids is impressive, but perhaps not entirely unexpected since the responses of fishes of common heritage to similar selection pressures in each lake are likely to be similar.

#### 4 - SPECIATION

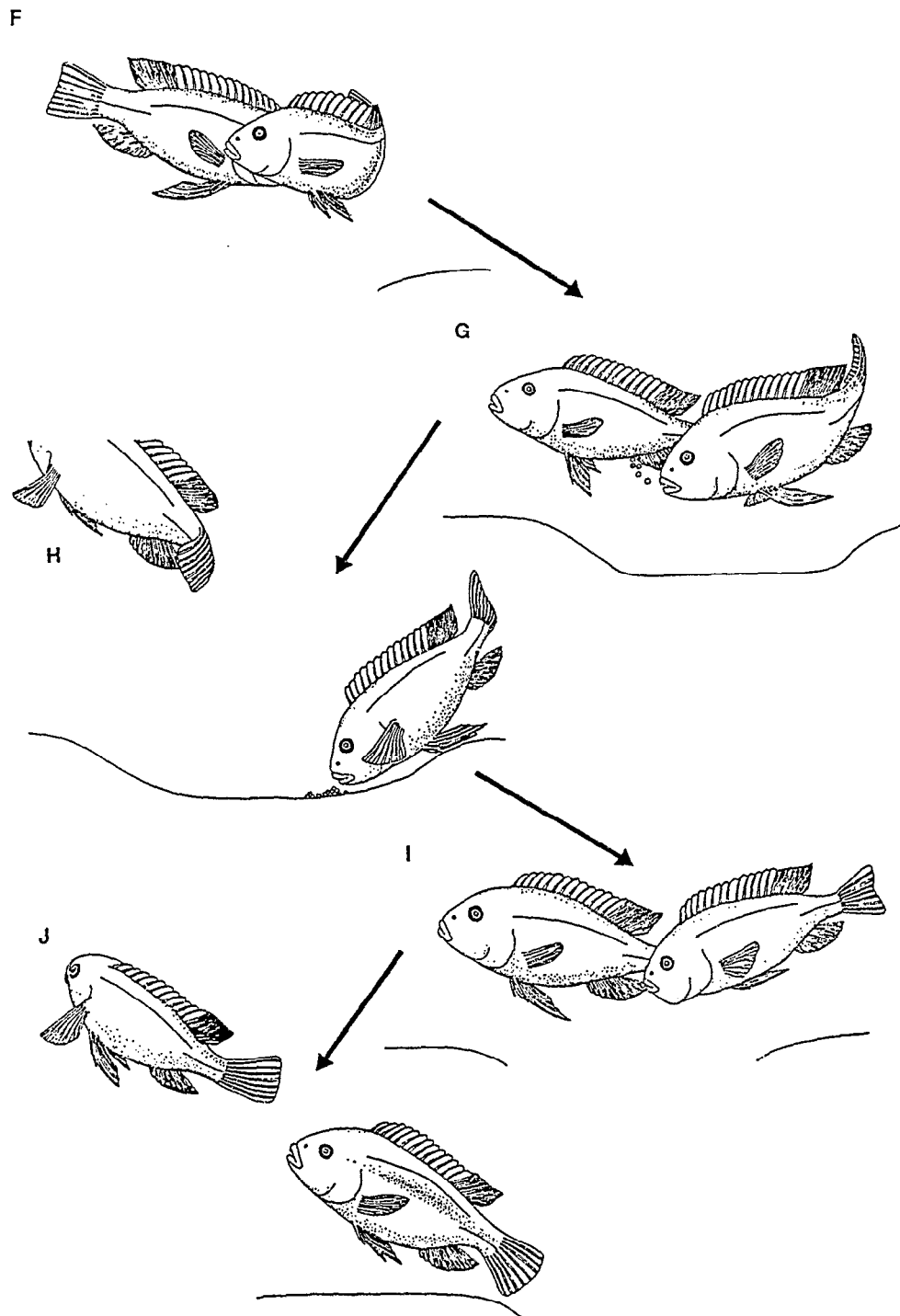
The process by which one species gives rise to two or more species is speciation. It is generally accepted that this process originates with the geographic isolation of populations of a species. In time such populations diverge genetically, principally as a consequence of adaptations to their differing environments and also as a result of their genetic differences (no two populations are genetically identical; Mayr, 1963). Ultimately members of each population become reproductively incompatible with those of the populations from which they are geographically isolated. These reproductively incompatible products of speciation are species. As species are not always readily recognised by practising biologists and because taxonomists often differ in their interpretation of «species concepts» and in the categorisation of taxa, it is necessary to define more precisely the meaning of «species». It is also necessary to focus upon some of the taxonomic problems which make it very difficult to recognise many of the cichlid species in the Great Lakes of Africa.

The Biological Species Concept is currently most widely accepted and probably represents the orthodox viewpoint. It defines species as «groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups» (Mayr, 1963). Similarly, Dobzhansky (1970) states that «species are... systems of populations; the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps a combination of several such mechanisms». A tenet stressed by this concept is that a species possesses a set of *isolating mechanisms* which keeps it distinct from other species. Accordingly, Paterson (1978, 1980, 1982) refers to it as the *Isolation Concept* and criticizes this concept by arguing that premating isolating mechanisms are unlikely to evolve in order to serve the *function* (*sensu* Williams, 1966) of reproductively isolating the members of one species from those of another. He believes that the isolating role is better accounted for if it is viewed as an *effect* (*sensu* Williams, 1966), and that the post «isolating mechanisms» seem to isolate only incidentally. Paterson (1985) points out that the Isolation Concept has led to conceptual difficulties, and, that Mayr (1963) had difficulty in comprehending how isolating mechanisms could evolve as a consequence of natural selection in geographically isolated populations whose members never encounter one another. It is argued further (Paterson, 1985) that it is unsound to define a species in terms of negative properties which, most likely, originated as *effects* (incidental consequences). The Isolation Concept is further criticized since it seems to demand that isolating mechanisms should arise as a consequence of group selection - apparently protecting the «integrity of the species» - while most models of speciation invoke only individual selection. Paterson thus provides evidence to falsify the Isolation Concept and proposes in its place the Recognition Concept (Paterson, 1973, 1978, 1980, 1981, 1982, 1985).

The Recognition Concept has its basis in the well established fact that for effective fertilization it is essential that conspecific sexual partners should share a system of closely co-adapted species-specific characters which ensure their meeting and also the fertilization of their gametes. This system is referred to as a Specific-mate Recognition System or simply SMRS (Paterson, 1978). A major component of the SMRS of cichlid fishes would be the chain of closely co-adapted signals and responses which operate between males and females of the same species during courtship rituals (see Baerends & Baerends-van Roon, 1950; Ribbink, 1971; Fryer & Iles, 1972 and Fig. 2).



**Figure 2 :** The co-adapted courtship displays of a maternal mouthbrooding cichlid fish. Male in A side-shake, B follow-shake, C lead-swim, D inviting female to enter spawning site, E & F circling with female in spawning site, G watching during egg laying, H chasing encroaching fish while female collects eggs, I displaying anal fin to encourage intrabuccal fertilization, J chasing



the female from the territory after spawning (after Ribbink, 1971). Many mouthbrooders lay very few eggs in a batch, sometimes only one, which they retrieve before the male can effect extra-buccal fertilization. For these fishes intrabuccal fertilization is imperative (Fryer & Iles, 1972).

According to the Recognition Concept, a species is composed of those individuals which share a common fertilization system. The fertilization system is the total set of adaptations which have evolved to serve the function of «bringing about fertilization. It includes the subset of «the Specific-mate Recognition System» which is crucial in motile organisms. Thus, the SMRS is made up of those fertilization mechanisms which involve signalling between the mating partners or their cells (e.g. sperm and ova or pollen and stigma). In cichlids the signals between partners are essential to mate recognition. Under the artificial conditions of aquaria, hybridization of cichlid fishes is common (Loiselle, 1971), suggesting that cell recognition is not acute. By contrast, in sessile organisms cell recognition is acute, but specific mate recognition may be virtually or entirely absent.

The characters of an SMRS are adapted to function most efficiently in the preferred or normal habitat of the species (Paterson 1980, 1982) and are considered to be adaptive. Indeed, normal habitat is viewed as a basic aspect of the Recognition Concept, and is characteristic of a species. Hence, a new species is considered to have arisen when all members of a small, isolated subpopulation of a parental species have acquired a new SMRS, which facilitates the achievement of syngamy under the conditions of the new normal habitat, and which, quite fortuitously, makes effective signalling very difficult or impossible between members of the daughter and parental populations (Paterson, 1982).

The Recognition Concept differs fundamentally from the Isolation Concept in that it is postulated that the SMRS and other fertilization mechanisms evolved in isolated populations as adaptational responses of members of each population to their new environment. The function of the fertilization system is to ensure fertilization of the individuals within the population and this involves mate recognition. Thus, it is the fertilization system (including the SMRS) which defines the limits of a species by restricting fertilization to conspecifics under normal circumstances i.e. a species is «a group of organisms which shares a common fertilization system» (Paterson, 1985). It is clear that a fertilization system (including the SMRS) does not evolve in order to dictate the limits of a species gene pool; its function is to provide for effective fertilization. An incidental effect of this is that a fertilization system conscribes a species gene pool (Paterson, 1978, 1980; Passmore, 1981).

The two concepts are confused and conflated in the literature on cichlid fishes of the Great Lakes of Africa. For example, Greenwood (1974 : 112), when discussing the complexity of cichlid courtship behaviour, writes that : «... in this complexity may lie a pointer to the ease with which barriers to interspecific crosses are evolved. In other words, a slight deviation from an established pattern could provide an effective barrier to successful courtship and mating». Here he apparently favours the Isolation Concept since barriers are synonymous with isolating mechanisms. However, on the same page an implicit adherence to the Recognition Concept is demonstrated when «recognition signals» are discussed. Furthermore, in a discussion of the species in Lake Victoria which gave rise to daughter species of different coloration in Lake Nabugabo, Greenwood (1974 : 112) comments : «.... there can be no ground for thinking that the colour difference evolved in response to strong selection favouring characters that would prevent interspecific hybridization. In this respect the colour differences would seem merely to be one product of the genic reorganisation undergone by isolates». Perhaps this is a tacit rejection of the Isolation Concept in favour of the Recognition Concept.

In similar vein, Fryer & Iles (1972 : 540) demonstrate an adherence to the Isolation Concept and also support speciation by reinforcement when discussing preferred habitats of Mbuna : «In such cases selection will obviously favour those aspects of the ecology of the two species which keep them within their own niches and thereby minimise competition between them, and will also favour those features which tend to prevent interbreeding - in other words will favour those attributes which lead to their becoming more and more distinct». They go on to suggest (p. 540) that colour differences between similar species arose to keep such species apart. However, Fryer (1977) also demonstrates a tacit appreciation of the Recognition Concept when discussing colour differences between parent (Lake Victoria) and daughter (Lake Nabugabo) species when he states that «.... the Lake Nabugabo species developed different colours from their parent populations, not as a means of isolating the members of the species pairs - which



never encounter one another, but as a consequence of fortuitous genetic reorganisation in isolation».

The need for a consistent rationale is clear, particularly in view of the considerable difficulty of species identification experienced by those studying African cichlid species flocks. Numerous closely related species are so similar anatomically that they cannot be readily distinguished from one another when dead. Consequently, there is an increasing tendency for taxonomists to lay emphasis on those factors deemed to be used by the fishes themselves for specific-mate recognition, particularly live coloration of breeding individuals since such colours are species specific. Where possible, a knowledge of the preferred habitat of the species is also employed (Holzberg, 1978; Eccles & Lewis, 1979, Marsh *et al.*, 1981; Van Oijen *et al.*, 1981; Lewis, 1982a; Ribbink *et al.*, 1983a).

The Recognition Concept was invoked by Ribbink *et al.* (1983a) during their survey of the cichlid fishes of rocky habitats in Lake Malawi because the use of biological criteria was the only practical way to identify species. They reported on about 250 species of cichlid of which 196 belong to a closely related group collectively referred to as Mbuna. More than 70 % of the Mbuna are undescribed and the group contains numerous sibling species. The greatest problem, therefore, was to decide what constituted a species. The rationale used was that those individuals which shared a common mate recognition system represented a closed gene pool and were biological species i.e. they constituted a «field for gene recombination». By SCUBA diving it was possible to observe the fishes in their natural environment and to distinguish between sympatric sibling species by virtue of their positive assortative mating and interspecific differences in coloration, preferred habitat and aspects of behaviour. While such direct comparative observations adequately distinguished between sympatric species, the relationship and hence categorisation of allopatric populations of morphologically similar fishes had to be determined in another way. To do this, Ribbink *et al.* (1983a) assumed that if those attributes of a population such as general anatomy and form, coloration and markings, preferred habitat and behaviour were the same as, or very similar to, those of another population from which they were geographically isolated, then mate recognition was likely to occur and the populations were potentially interbreeding. These would be conspecific populations. On the other hand, if components of the SMRS differed between populations, it was concluded that mate recognition between the members of the populations would not take place and that the populations were distinct species.

In those instances where it was not possible to make a clear decision as, for example, when populations share some but not other components of the SMRS, then Ribbink *et al.* (1983a) emphasized differences rather than similarities. In such an approach, a degree of arbitrariness is unavoidable, but taxonomy is an art in which an element of subjectivity is inevitable (except, perhaps the strictest form of numerical taxonomy) with interpretations of how populations should be categorised varying between taxonomists. A further problem with emphasizing differences is that the number of allopatric species may be overestimated by splitting. This, however, is preferable to «lumping» different species.

The zoogeographical data gathered by the survey of Ribbink *et al.* (1983a) strongly support the contentions of Fryer (1959), Matthes (1962) and others that intralacustrine allopatric speciation occurred among many cichlids of the Great Lakes of Africa. During the survey, work was conducted at 121 diving stations. A remarkable finding is that at no site was the species assemblage identical to that of another site. Ribbink *et al.* (1983a) concluded that Mbuna species are, in general, so highly sedentary that populations are readily fragmented by habitat discontinuities, depth and distance. It appears, therefore, that populations divided by such barriers diverged as they adapted to environments in different localities. An example which illustrates this phenomenon graphically was reported by Greenwood (1965) : evidence from rolled charcoal fragments suggest that Lake Nabugabo became physically cut off from Lake Victoria by a sand bar about 4000 years ago. Its fauna includes haplochromine species which are so closely similar to species in Lake Victoria that there is little doubt that the Nabugabo forms are derived from them. However, the live coloration of some of the Lake Nabugabo forms is so different from that of their parent forms in Lake Victoria that Greenwood (1965, 1974) considers

them to be distinct species. Clearly, in the context of the Nabugabo species, Greenwood believes that fish populations which differ from one another in colour are unlikely to interbreed and are accordingly different species. Similarly, the component of the SMRS given the greatest weighting by Ribbink *et al.* (1983a) when distinguishing between structurally similar allopatric cichlid populations in Lake Malawi was colour. Fryer (1977) suggests that colour *per se* may be less important at times of mating than might be assumed from its striking nature and specific distinctness. Colour is used frequently in cichlid communication and intensifies during courtship (Noble & Curtis, 1939; Baerends & Baerends-Van Roon, 1950; Wickler, 1963; Ribbink, 1971; Fryer & Iles, 1972) and colours and markings are so species-specific that they are useful aids to field workers and taxonomists for species identification (Lowe, 1952; Barel *et al.*, 1977; Eccles & Lewis, 1979; Van Oijen *et al.*, 1981; Lewis, 1982a, 1982b). This inferential evidence suggests strongly that species-specific colours are important in specific mate recognition, which may also account for the observation that sympatric sibling species all differ from one another in coloration and markings. The Recognition Concept holds that gene pools separated from one another geographically will diverge as the members of each gene pool develop adaptations to the constellation of environmental factors to which they are subject. They are thus subject to directional natural selection. As the properties of light vary with depth and locality both within a single lake and between different lakes, it is possible that the coloration of different fish populations reflects adaptations to the normal habitat of those fishes. The type of adaptations envisaged are those which would make signalling most effective within the circumstances of the population's normal habitat. At present, however, there is no convincing evidence to suggest that the evolution of a new set of colours in isolated populations of Mbuna, for example, is an adaptive response to the environment. However, pleiotropy - the capacity of a gene to affect several aspects of the phenotype - is another possibility to explain their varied coloration.

The importance of co-adaptation of mating partners to the same preferred (= normal) habitat was stressed by Paterson (1978, 1980, 1982) and there can be little doubt that such a SMRS would be subject to strong stabilizing selection. A notable feature of numerous African Great Lake cichlids is that they occupy species-specific micro-habitats for all or part of each year and it is crucial to the fertilization system that conspecific partners are sympatric during the breeding season. Some normal habitats of a species are remarkably restricted, such as preferences for particular rock types in narrow depth belts (Ribbink *et al.*, 1983a). Normal habitat, therefore, is highly pertinent to the SMRS of these fishes.

Courtship and spawning behaviour of cichlids follows a chain of closely coadapted sequences in which signals are exchanged between males and females (Baerends & Baerends-van Roon, 1950; Ribbink, 1971; Fryer & Iles, 1972). It was suggested that the complexity of cichlid behaviour offers opportunities for the evolution of a variety of «*barriers to interspecific crosses*» (Greenwood, 1974 : 112). Furthermore, Fryer (1977) considers that differences in courtship behaviour (movements) are the «*leading candidates for the maintenance of specific separation*» (italics are mine indicating an adherence by these authors to the Isolation Concept in this instance). However, it appears that the basic components of aggressive, courtship and spawning behaviour of riverine and lacustrine cichlids (Fig. 2) are so similar that interspecific differences in closely related species are difficult to detect (Ribbink *et al.*, 1983a). At present, therefore, those behavioural differences associated with closely co-adapted courtship and spawning sequences, which might well be highly important SMRSs to members of a species flock, such as the Mbuna, are not overtly apparent to human observers and are currently of little value for species identification. In more distantly related species, however, behavioural differences are apparent and may be used in taxonomy (Wickler, 1963; Trewavas, 1973); but even in these distantly related species the execution of the behavioural elements (e.g. side-shake, lead-swim, nest-shake etc.) is similar, though the rate and frequency of execution may be markedly different.

In contrast, those behavioural traits associated with specialized feeding adaptations are overt and do assist humans in the identification of fishes. It is not known whether these features are used by the fishes in specific mate recognition though it seems likely that all behavioural attributes characteristic of all adult members of a population would serve as components of the SMRS. It is argued that as human divers familiar with the fishes can accurately identify distant

silhouettes (i.e. without recourse to details of coloration, markings and anatomical features) by the recognition of species-specific angles of feeding and modes of food collection such as nipping, plucking, brushing, nibbling or predatory lunges at prey, then it is likely that fishes would be better attuned to these and other behavioural nuances characteristic of conspecifics. Indeed, underwater observations strongly indicate that conspecific recognition is acute among cichlids of Lake Malawi and that such recognition is accomplished when potential rivals or mates are as much as 8 m apart, which approximates the normal limit of human visibility range in Lake Malawi. At this distance morphological details are extremely difficult to discern even when visibility in Lake Malawi is particularly good. It is believed, therefore, that heavy reliance is placed on species characteristic behavioural traits (many of which are probably not yet recognized by humans) for specific mate recognition as well as the gross anatomical attributes of the species.

There are numerous fish populations in Lake Tanganyika which are currently categorised loosely and, in certain instances, inaccurately as «colour morphs» or «colour forms». Some are considered to be subspecies (Poll, 1956; Fryer & Iles, 1972; Axelrod & Burgess, 1977; Nelissen, 1977; Brichard, 1978). If the same species definition is applied to these fishes as that used for the Mbuna, then there is little doubt that the number of species recognised in Lake Tanganyika will be increased substantially.

## 5 - ORIGIN OF DIFFERENTIATION

As the fossil record of the fishes of the Great Lakes is virtually non-existent extrapolations from the contemporary status are necessary to form hypotheses regarding the origin of diversification. The zoogeography and ecology of the majority of endemic species is largely unexplored. Nevertheless the general picture which has been emerging over the past thirty years is that the extant species are trophically specialized, most are geographically restricted e.g. for some species of Mbuna the entire area occupied by its members is no more than a few thousand square meters (Ribbink *et al.*, 1983a), and most species have clearly defined microhabitat preferences, particularly during periods of breeding (Lowe, 1952, 1953; Poll, 1953; Marlier, 1959; Matthes, 1962; Fryer & Iles, 1972; Eccles & Lewis, 1977, 1978; Holzberg, 1978; Yamaoka, 1982; Lewis, 1982a, 1982b; Marsh *et al.*, 1981; Van Oijen *et al.*, 1981).

The observations that cichlids are sedentary and habitat specific makes it easy to envisage how intralacustrine speciation could occur if a contemporary species were divided into two or more sub-populations by geographic barriers. Gene flow between such populations would cease and divergence would follow as each population adapted to its new environment. The major conceptual problem of cichlid speciation in the Rift Valley Lakes, however, is to appreciate how the specializations and philopatric tendencies (i.e. tendencies to stay in a home area, usually a birth place) arose originally. If, for example, a generalized ancestor colonised the proto-lakes then, by virtue of its generalized attributes, it might be expected to occupy all habitats with equal facility right around the lake(s). Gene flow would be uninterrupted, but perhaps retarded by distance as the lakes enlarged.

Fryer (1959, 1977) suggested that the original colonisers (1) of Lake Malawi had undergone a degree of specialization when they first entered the lake so that those preferring sandy regions would not be in competition with those preferring other habitats such as rocky substrata. With time the specializations for the respective habitats of the groups increased so that habitat discontinuities came to constitute formidable barriers to dispersion. Eventually the fauna was split into innumerable isolated populations and the stage was set for an accelerating allopatric speciation. We shall never know whether these speculations are correct, but it is true that extant riverine species are adapted to different habits (e.g. piscivory, herbivory) and do occupy species characteristic habitats. It is possible, therefore, that different lines colonised the lake as postulated by Fryer (1959, 1977). However, it is not necessary to postulate such an oligophyletic ancestry if one considers the sedentary nature of cichlids.

(1) Fryer & Iles 1972 : 476 & 478 postulate that a single *Haplochromis*-like ancestor colonised Lake Malawi which is not consistent with the postulate that several ancestors invaded the lake.

Although fishes would appear to be highly mobile it is apparent from the zoogeographical data emanating from each of the Great Lakes that the outbreeding one might expect from high mobility is not a feature of lacustrine cichlids. On the contrary, the majority of cichlids are sedentary. One of the most important reasons for their sedentary nature is the fact that cichlids practice parental care (Poll, 1956), which tends to «increase philopatry and reduce dispersal sharply» (Mayr, 1963 : 569). Furthermore, Dobzhansky (1951) believed that evolution and speciation occur most rapidly in those species in which parental care is developed. Since parental care is well developed in extant riverine species, including those which are believed to resemble the ancestral forms, it is almost certain that it was a feature of those cichlids which colonised the lakes originally. Consequently there is justification for assuming that the colonisers were philopatric. It follows that the increasing size of the growing lakes would have isolated populations as a result of the greater distances it placed between them. If, as Fryer (1959, 1977) suggests, the colonisers also exhibited habitat preferences, then fragmentation of populations would have been greater and was probably accompanied by a commensurate increase in the rate and extent of speciation. Parental care, particularly the aeration of eggs and larvae, in cichlids makes it possible for many species to live, breed and rear their offspring while remaining within a particular habitat (or micro-habitat). Thus, without the need to return to rivers for breeding, as do anadromous fishes (Lowe-McConnell, 1969, 1975), a cichlid population may adapt to the conditions of a single habitat only, which is presumably conducive to ecological specialization and to speciation of allopatric populations. There are, of course, exceptions such as species with lake-wide distribution and those which undergo extensive migrations (Lowe-McConnell, 1969, 1975; Fryer & Iles, 1972), but these species are relatively few in number.

## 6 - LAKE LEVEL

The geological history of the Great Lakes indicates that the level of each has fluctuated widely (Fryer & Iles, 1972; Banister & Clark, 1980; Beadle, 1981) and it is likely that such changes had a marked influence on cichlid speciation (Fryer, 1959, 1977; Fryer & Iles, 1972; Greenwood, 1974; Ribbink *et al.*, 1983a).

Fluctuations in the level of Lake Victoria are believed to have taken place on a scale which probably led, on a number of occasions, to the formation of a variety of smaller and larger lakes. At times these lakes were wholly or partially interconnected, at other times wholly isolated from one another. It is believed that the enforced isolation of populations in different lakes was responsible for the initial differentiation of the main phyletic lines and that the development of trophic radiations within these lines must have taken place among the haplochromine species inhabiting the isolated proto-lakes (Greenwood, 1965, 1974; Fryer, 1959; Fryer & Iles, 1972). It appears that populations were divided on occasion so that sub-populations in a number of peripheral water bodies within the lake basin were isolated for sufficient time to speciate (Greenwood, 1974; Fryer & Iles, 1972).

Similarly, changes in lake level undoubtedly affected speciation of the fishes of Lakes Tanganyika and Malawi. Although it is unlikely that a number of different basins were formed in these Rift Valley Lakes, there is no doubt that islands formed, were drowned and were then re-established. The effect would have been similar to that in Lake Victoria in that populations would be geographically restricted and effectively isolated from one another (Ribbink *et al.*, 1983a). To appreciate the effect changing lake levels might have had on the cichlids of the Rift Valley Lakes it is necessary to examine the depth distribution and the ability of cichlids to penetrate depth. Riverine species inhabit relatively shallow water and all those species tested experimentally were unable to penetrate waters deeper than 30 m (Caulton & Hill, 1973; Caulton, 1975;). This suggests that the colonising species inhabited shallow waters. Most extant lacustrine species also inhabit shallow water (see Ribbink & Eccles this volume) and experimental work done on several shallow-dwelling Lake Malawi cichlids indicates that their ability to live in waters deeper than 50 m is severely restricted (Hill & Ribbink, 1978; Ribbink & Hill, 1979; Marsh & Ribbink, 1981; Ribbink *et al.* 1983b). Moreover, all of the species tested habitually live in water which is shallower than the limits imposed by their swimbladders. Although there

are cichlids which live to the limits of the oxygenated zones (Coulter, 1967), the majority of cichlids living in rivers and lakes are physiologically and ecologically adapted to occupy the shallows. One might anticipate, therefore, that when the shallow proto-lakes began to deepen the fish communities would move up the shore-line with the rising water level. Those populations moving up the shores of an island could become isolated from other populations by intervening tracts of deep water. Those on islands which became drowned would have to adapt to living at greater depth, undergo a forced migration or perish. Falling lake levels could reunite populations which might interbreed if they shared a common fertilization system, but would not interbreed if the fertilization systems had diverged. As with rising levels, a falling level could also force fishes into habitats which they would not normally occupy. For example, a species adapted to living in a purely rocky habitat at the apex of an island might find itself confined to a region of sand and rock at its base and forced to adapt to these intermediate conditions. Some of the possible effects of changing lake level are illustrated in Fryer (1977) and Ribbink *et al.*, (1983a). The important points, however, are that most cichlids are restricted in their ability to penetrate depth, are philopatric and are normally restricted to specific microhabitats. Accordingly, fluctuations in lake level could isolate populations and subsequently reunite them.

The combination of changing lake level and the sedentary tendencies of cichlids would have provided a powerful basis for diversification, if the time periods were adequate. There were marked changes in lake level (more than 100 m) during the history of these lakes, followed by protracted periods of relative stability (Fryer & Iles, 1972). The rate of cichlid evolution was probably accelerated by changes in lake level, but during periods of equilibrium (i.e. periods of relative stability in lake level), the rate probably decreased. Such episodic evolution is consistent with the model of Punctuational Evolution proposed by Eldredge & Gould (1972) but recognised earlier by Simpson and by Mayr (see Mayr, 1963). The applicability of this model to the evolution of the cichlids of the Great Lakes of Africa is noted by Greenwood (1979, 1981), Beadle (1981) and Ribbink *et al.* (1983a). Beadle (1981 : 140), for example, argues that the rate at which new species appeared in the past was certainly not uniform, for changes in environment «were followed by an outburst of speciation in adaptation to the new conditions». Furthermore, Paterson (1981) has pointed out that the Recognition Concept of a species provides a detailed theoretical basis for punctuational evolution.

Many of the populations isolated by changing lake level are likely to have been very small since the islands or peripheral lakes they occupied were themselves small. Provided these populations survived the adversities of the «evolutionary bottle-neck» and the tendencies to homozygosity which are responsible for the extinction of the majority of founder and island populations (Mayr, 1963), it is likely that they would have undergone rapid changes in genotype since this is a characteristic of small closed populations (Mayr, 1963; Fryer & Iles, 1972). Thus allopatric speciation probably occurred in these lakes, with the island populations (which include those isolated in small lakes within the Lake Victoria basin) responding rapidly to the selection pressures of the new environment. Allopatric speciation as envisaged for the Recognition Concept differs from the classical model as the latter postulates that changes to signalling systems occur pleiotropically whereas Paterson sees direct adaptation of the fertilization system to local (new) conditions to be the basis. He does not, however, exclude roles for pleiotropy or stochastic effects (Paterson, 1980, 1985).

## ACKNOWLEDGEMENTS

I am most grateful to Professors M.N. Bruton and H.E. Paterson and to Messrs D.H. Eccles and P.B.N. Jackson for their helpful comments on earlier drafts of the manuscript. I thank Mrs. Huibrè Tomlinson for taking the manuscript through its various stages on the word processor.

## RESUME

La spéciation « explosive » des poissons des lacs Victoria, Tanganyika et Malawi n'a pas d'équivalent parmi les vertébrés. Dans chacun de ces lacs, des centaines d'espèces (400-500 dans le lac Malawi, plus de 290 dans le lac Victoria et plus de 200 dans le lac Tanganyika) se sont différenciées sur une période assez courte, témoignant d'un taux élevé de spéciation. Les Cichlidés sont les plus abondants dans ces lacs avec un taux d'endémicité de 99% dans le Malawi, 100% dans le Tanganyika, 98 à 99% dans le lac Victoria.

Chaque lac a été colonisé initialement par des poissons d'origine fluviale qui sont à l'origine des espèces lacustres actuelles qui présentent une gamme remarquable d'adaptations et occupent une grande variété de biotopes. Les nombreuses spécialisations trophiques sont les adaptations les mieux étudiées. Il existe une grande ressemblance entre les poissons des différents lacs qui présentent des adaptations trophiques identiques.

Très peu de restes de fossiles de poissons ont été retrouvés. Pour comprendre l'évolution des espèces, il est donc nécessaire d'examiner les espèces actuelles, les stocks fluviaux qui peuvent être proches des formes ancestrales, et l'histoire des lacs.

Le concept d'« identification » ou de « Reconnaissance de l'Identité spécifique » (Recognition concept) de Paterson est utile pour identifier les espèces et expliquer certains aspects de l'évolution et de la spéciation. Selon ce concept, les partenaires sexuels conspécifiques doivent partager un ensemble de caractères spécifiques appropriés qui leur permettront de se rencontrer et assureront la fertilisation des gamètes. De telles coadaptations comprennent les modes de comportement, la fréquentation des mêmes biotopes préférentiels durant la saison de reproduction, des périodes de reproduction synchrones et des caractéristiques morphologiques propres. Tous ces caractères sont soumis à l'effet régulateur de la sélection. Le concept d'« identification » diffère fondamentalement de celui d'« isolement » dans la mesure où il pose pour principe que les mécanismes de fertilisation, y compris les modes de reconnaissance propres à chaque espèce avant l'accouplement, se développent dans des populations isolées en tant que réponses adaptatives (soumises à la sélection naturelle) des membres de chaque population vis-à-vis de leur nouvel environnement.

Le concept d'« isolement » insiste quant à lui sur le fait qu'une espèce possède un ensemble de mécanismes qui lui est propre pour assurer sa reproduction et qui lui permette de conserver son identité. Selon Paterson, il est cependant peu probable que ces mécanismes se soient développés dans le but précis d'assurer l'isolement reproducteur des membres d'une espèce par rapport à une autre.

Il n'y a aucune raison pour que deux populations d'une même espèce, isolées géographiquement, et qui peuvent donc n'être jamais en contact, développent des mécanismes assurant leur isolement. Autrement dit, l'isolement est une conséquence fortuite de la divergence qui peut se produire entre deux populations isolées géographiquement et s'adaptant chacune à leur environnement.

La distribution géographique de beaucoup de cichlidés dans des grands lacs d'Afrique de l'Est est limitée à des zones restreintes dans chacun des lacs; quelques espèces n'occupent pas plus de quelques hectares. Cette insularité des espèces est une conséquence de la philopatrie, dûe, dans beaucoup de cas, à des préférences strictes dans l'habitat.

En outre, les cichlidés sont sédentaires du fait de la mauvaise dispersion de leur progéniture qui résulte de la pratique de soins parentaux et d'une incapacité à franchir des zones écologiquement défavorables. Ces facteurs ainsi que la fragmentation des populations à la suite de variations du niveau des lacs, sont en grande partie à l'origine de la spéciation allopatrique qui s'est réalisée dans chaque lac. A l'heure actuelle, il n'y a aucune preuve de phénomènes de spéciation qui ne soient pas allopatriques chez les poissons des grands lacs.

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