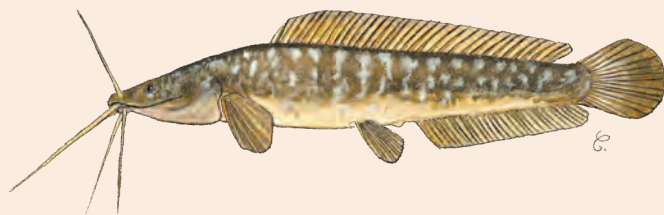# Diversity
# of African fish:
heritage of evolution

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The present African ichthyological fauna took shape over time. It is a biological heritage, the product of a long history of evolution, marked by periods during which life diversified, but also punctuated by dramatic events and major "disasters" that led to the extinction of many species.

Knowledge on the speciation processes for African fishes have seen much progress in recent years, thanks mainly to advances in molecular biology as well as international attention focussing on the East African Great Lakes, where hundreds of endemic Cichlidae species are threatened by extinction even as they represent a unique model for the study of speciation.

Review of theories of evolution

From creationism to transformism

In the early 17th century, scientists viewed organisms as fixed. In accordance with the sacred Judeo-Christian texts, it was believed that the earth had been populated some 6,000 years earlier, and that the living creatures of that time were faithful copies of the ones created by God. This led to the emergence of so-called creationist theories.

Subsequent advances in knowledge rapidly showed that the age of the planet had been vastly underestimated and that flora and fauna had changed considerably over time. Briefly speaking, in the early 19th century, Lamarck questioned the "fixed species" dogma and proposed a new concept, transformism, which upended the prevailing ideas. Lamarck hypothesized that all of an individual's characters could be transmitted to its offspring, including those it had acquired over its lifetime. This hypothesis, based on the postulate that acquired characters could be passed on, was widely discussed and – rightly – called into question. Half a century later, Darwin proposed another transformist theory that recognized the existence of intraspecific variability, as opposed to the 'typological' concept of the species, that made natural selection the driver of evolution. In other words, in a population living in a given set of environmental conditions, only the fittest individuals for that environment would participate effectively in reproduction.

The existence of mutations was discovered in the early 20th century, and a new theory (mutationism) developed, according to which mutations were the sole

driver of evolution. Although it was abandoned quickly, the inclusion of mutations nonetheless remained a major event in the history of evolutionary theories.

The synthetic theory of evolution

The synthetic theory of evolution takes into account the two notions that mutations led to variability, and that natural selection, with every generation, selected the genotypes that were most suited to living and reproducing in a given set of conditions. In a way, the theory is a summary of the Darwinian and mutationist approaches. In an environment that perpetually changes, organisms are forced to adapt by finding physiological or morphological solutions to the problems posed by changes in the physical system they inhabit or risk extinction. Changes in certain factors of the environment such as temperature or salinity may be behind such adaptations. But these innovations may also come about from the appearance of new habitats or new ecological niches that organisms can colonize, and in which they will evolve and diversify to maximize the use of available food resources.

Mechanisms of speciation

Contrary to the beliefs of some creationists, species do not appear spontaneously. Speciation is the phenomenon by which a species gives rise to two or more distinct species, called sister species. This process is also known as cladogenesis. Not only does speciation lead to new species; it also gives rise to new groups, and the history of evolution and the appearance of different phyla is the result of this speciation.

The mechanism behind speciation implies two essential and distinct steps:
• on one hand, the appearance and spread of a mutation within a population;
• on the other hand, genetic isolation of that population from the other populations as a result of this mutation.

The genetic mutations or chromosomal recombinations that frequently occur lead to a genetic diversity that could allow species to adapt to changes in the environment. Many of these mutations are lethal or unfavourable for the individual, and are eliminated by natural selection. Others are neutral and will be maintained or eliminated at random. Only a small fraction will be advantageous. Among these, a few will lead to the emergence of a new species.

Mutations as the driver of evolution

Life begins at the molecular level, and the origins of the diversity of organisms and the adaptive potential of species should be sought at this level of infra-specific variability. Each individual belonging to a species or sub-species is slightly different genetically from all other individuals, and this genetic diversity is the necessary condition for the biological diversity that allows species to carry out alternative strategies that are their adaptive response to changes in the environment. Intraspecific variability is not restricted to the genetic component, but is expressed as a range of different phenotypes.

Mutations at the molecular level

A mutation occurs at the genetic level. It is a change in the structure of the DNA molecules forming the genes which are the main building blocks of heredity. In most organisms, genetic information is found in chromosomes which are a long chain of deoxyribonucleic acid (DNA) carrying hereditary characteristics and biological information needed for cell, organ, and tissue function. The different variants of genes are known as alleles. An individual's full set of genes is its genotype, which serves, in a way, as the initial capital that can be used by the individual in different ways depending on the conditions in the physical system it inhabits.

Cell division or mitosis allows the creation of two daughter cells that are similar to the mother cell. In principle, the copies of chromosomes and genes are identical, but "errors" may occur in the order of the nucleic acid sequence during DNA duplication. These spontaneous genetic mutations create new gene variants or alleles. Genetic diversity within a species is a function of these alleles.

If a gene controls the production of a certain molecule, it may produce a different one after a mutation. These genetic mutations can be lethal, in which case there are no consequences. On the other hand, if the individual is viable and fertile, the mutations are transmitted to the descendants of that individual, and can manifest as evolutionary transformations, such as a change in morphology. They may also be undetectable at this level, and/or affect physiological, biochemical, or behavioural processes.
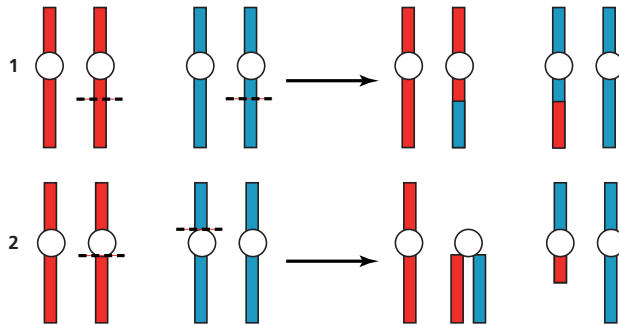
Given the high number of genes, mutations are not rare, but many of these mutants are not viable, nor are they visible in the phenotype (in which case the mutations are called neutral). Only after a veritable obstacle course that eliminates many of the mutants will the survivors have a chance to create a population that is large enough to become established and sustainable. For species that reproduce sexually, that is, 95% of organisms, a mixing of the population's genes occurs during reproduction, and new genotypes appear while others go away.

Up to about ten years ago, electrophoresis was the technique most commonly used to reveal the polymorphism of proteins and thus a gene's allelic differences in order to assess genetic diversity. Nowadays it is possible to analyse a gene's structure, and DNA polymorphism can be revealed using increasingly powerful molecular biology techniques. Like the human genome, several fish genomes have been or are currently being sequenced (fugu, *Danio*, carp).

Chromosomal recombinations

Mutations can also occur during mitosis via changes in chromosome structure. Each species has a fixed number of chromosomes, but all or part of a chromosome may break or, on the contrary, fuse, thus changing the chromosome set (or karyotype). This can range from simple inversions of some arms to a reduction in the number of chromosomes (figure 7.1).

In fishes, this evolution in the number and shape of chromosomes is particularly spectacular in the Cyprinodontiformes, for which it has been shown that

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there are numerous species that are morphologically similar but have different karyotypes, preventing them from creating hybrids (see the work of Scheel, 1968). In the *Aphyosemion*, the haploid number varies from n = 24 (the basic number, according to Scheel) in *A. rectoogoense* to n = 9 in *A. christyi*. There is an especially interesting example of speciation with a reduction in chromosome number from 15 to 13, 11, 10 and 9 pairs respectively, in the series *Aphyosemion melanopteron-cognatum-schoutedeni-elegans-christyi*. The phenotypes of these species are very similar and they cannot be identified using metric or meristic characters alone. They are only distinguishable based on the colouring of adult males. These differences were initially attributed to intraspecific polymorphism until the investigation of their karyotypes and hybridation experiments showed that they were distinct species in terms of reproduction.

Polyploidy that manifests as a significant increase in the number of chromosomes is not rare in fishes compared with other vertebrates. This phenomenon appears to have played a major role in particular in the evolution of the karyotypes of the Cyprinidae family. It was also shown recently that some of the large African *Barbus* species were hexaploid and possessed 148-150 chromosomes (see chapter *Taxonomy and systematics*, table 8.l). Polyploidization can also be induced experimentally in certain fish species (Don & Avatlion, 1988a and 1988b).

Speciation and environmental variability: natural selection

A population is a collection of individuals that can interbreed and have shared genetic properties. A species can be composed of a single population, or of several populations that are more or less geographically isolated (in which case the term "metapopulation" is used).

The principle of natural selection involves two complementary processes: the existence of hereditary genetic variability, and a phenomenon that selects for the most successful individuals in terms of reproduction in a given type of environment. In theory, each species is adapted to a type of environment, but all the individuals in a population are not strictly identical on a genetic and phenotypic level. Owing to genetic polymorphism, the individuals of a population can respond in different ways to the constraints imposed by the environment.

When conditions change, the genotypes that produce the phenotypes most suited to the new constraints have an adaptive advantage and are selected in subsequent generations. Generally speaking, natural selection rewards the characters that provide an advantage to the organisms in question.

While genetic mutations favour the appearance of new phenotypes on an individual level, natural selection is what allows the mutant genes controlling these innovations to spread in the population provided that these mutants are fitter for survival and reproduction. Should this not be the case, the mutation has little chance of spreading and may even totally disappear if the environmental conditions do not change.

Thus, natural selection is a process that concerns each individual of a population. It implies:

• the presence of variability between the individuals in this population, in terms of performance or phenotypic characteristics (colour, growth rate, resistance to anoxia, swimming speed);

• that these characters can be transmitted hereditarily;

• that they have a significant influence on the reproduction or survival rate.

Selection essentially affects gene frequency. Any gene controlling adaptations that reinforce the chances of reproductive success will be favoured, and its frequency can then increase over generations.

Current ecosystems have undergone numerous changes in the past, under the influence of climate change and geological history (see chapter *Variability of climate and hydrological systems*). Thanks to genetic diversity, species were able to use new strategies as their adaptive response to changes in the environment. In some cases, particularly when the populations of the same species were isolated geographically, the desire to adjust to the environment's characteristics led to the appearance of new species. Speciation can thus be considered a fortunate result of a population's adaptation to its environment.

Mechanisms of speciation: how do species appear?

As all species evolved from a common ancestor, ancient species gave rise numerous times to two or more daughter species. What circumstances surround the process of subdivision that we call speciation? Two theories have been the subject of fierce debate: the allopatric theory (speciation in "another place"), which states that geographic isolation is needed for speciation to occur; and the sympatric theory (speciation in "the same place") which states that isolation is not necessary (figure 7.2).

Allopatric speciation

In this traditional model, populations of the same ancestral species with a continuous distribution become geographically isolated from the rest of the species. In the absence of genetic exchanges between these populations,

they evolve independently and give rise to new species that cannot interbreed. It follows geological or climatic events that favoured the fragmentation and isolation of populations of the same species. It's obviously the most common situation. The majority of hydrographic basins are currently isolated from each other, and act as virtual islands wherein populations of the same species can evolve independently of each other. If the isolation lasts long enough, populations can diverge until they become different species.

A limited case of allopatric speciation is that of peripatric speciation. In simple terms, this is speciation that occurs in small populations that are isolated on the edge of a species' area of distribution. One example of peripatric speciation is that of species closely related to *Brycinus imberi*. Three endemic species are known in limited zones on the edge of the distribution zone for *B. imberi*: *B. abeli* (Ubangi), *B. carolinae* (upper Niger), *B. nigricauda* (Cess, Côte d'Ivoire) (see chapter *Taxonomy and systematics*). These three species are very similar to *B. imberi* in terms of morphology, and are differentiated mainly by colour (Paugy, 1986).

Parapatric speciation refers to speciation that takes place in an environment where genetic exchange can occur but is highly limited as a result of, for instance, the presence of a geographic cline or environmental segregation. A well-known example is that of *Sarotherodon melanotheron* which is distributed all along the West African coast, and for which there are three sub-species that are relatively well-demarcated geographically but which can be in contact on the edges of their distribution areas (see box "Genetic differentiation of *Sarotherodon melanotheron* populations").
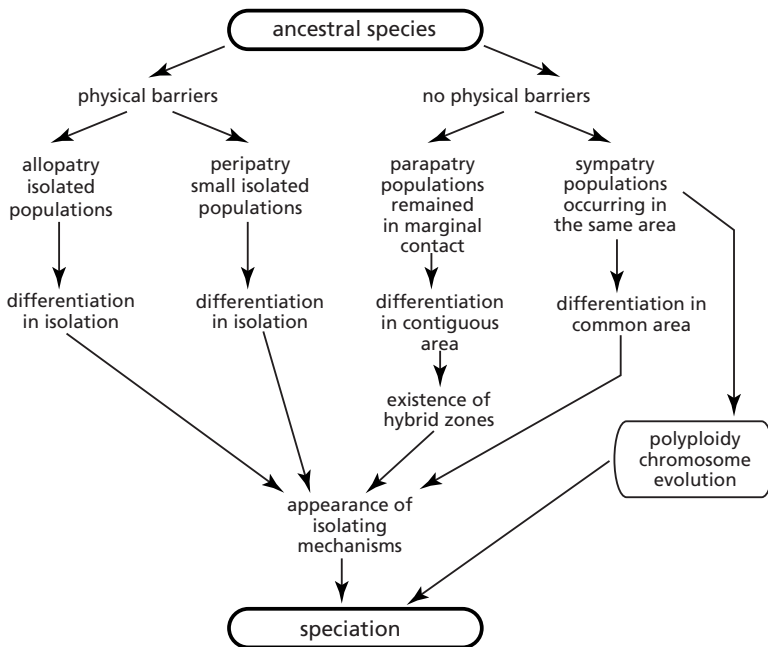

FIGURE 7.2.
Main pathways of speciation for African fishes (modified from Endler, 1977).

GENETIC DIFFERENTIATION OF
SAROTHERODON MELANOTHERON POPULATIONS

Sarotherodon melanotheron is a tilapia that lives in the brackish waters of lagoons and estuaries on the coastal zone stretching from Senegal to the Congo.

While this species is always classified in the genus *Sarotherodon,* its genetic characters place it closer to the genus *Oreochromis.*

It may even form a distinct genus, as it displays rather marked differences compared with other *Tilapia s. l.* species (Pouyaud & Agnèse, 1995).

Moreover, it should be noted that it is the only known paternal incubator in the group.

The study of the enzymatic polymorphism of different *S. melanotheron* populations of the West African coast (Pouyaud & Agnèse, 1995), has also confirmed the existence of genetic differences between three sub-species described by Trewavas (1983) based on morphological characters:

- *S. m. heudeloti* from Senegal to Guinea;
- *S. m. melanotheron* from Côte d'Ivoire to Cameroon;
- *S. m. nigripinis* from Rio Muni to DRC.

These observations have been confirmed by mitochondrial DNA studies (Falk *et al.*, 2003).

The presence from Sierra Leone to Liberia of another sub-species, *S. m. leonensis*, is also mentioned by Trewavas.
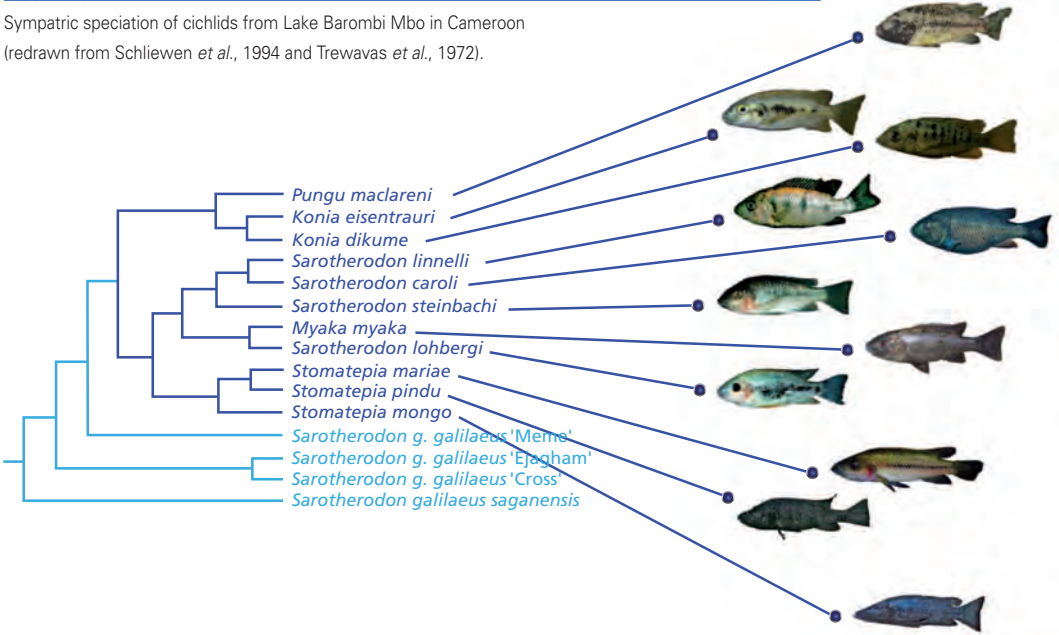
Sympatric speciation

Sympatric speciation occurs in a population that occupies the same geographic area and in which genetic exchange is theoretically possible. This type of speciation was very controversial and even rejected by some scientists. Based on the principle that the concept of biological species implies that each species is composed of populations that can interbreed, it was deemed that the flow and constant circulation of genes within a population was an obstacle to the emergence of new species. According to Mayr (1989), the sympatric theory leads to the following paradox: the coexistence of two forms is impossible without reproductive isolation. However, this isolation cannot occur unless the two forms coexist in a stable fashion. Nonetheless, a number of facts tend to show that isolation mechanisms can occur in sympatric conditions as an effect of natural selection, and the principle of sympatric speciation progressively gained ground (Gibbons, 1996). The processes involved can be described as follows: first, within a species' continuous area of distribution, natural selection promotes the appearance of two forms that may have different ethological behaviours (dietary preferences, habitat preferences, non-simultaneous reproductive seasons, etc.). If selection pressure is high enough, and if the process continues long enough, the two forms may end up diverging into two distinct species.

An example of sympatric speciation was proposed by Schliewen *et al.* (1994) for the Cichlidae of the crater lakes (Lakes Barombi Mbo and Bermin) in Cameroon (figure 7.3). Using mitochondrial DNA analysis, they showed that the nine species of Lake Bermin and the eleven found in Lake Barombi Mbo are monophyletic sets that each evolved in the lake itself from a single colonizing species. Given the size and shape of each lake, it is unlikely that geographic micro-barriers encouraged micro-allopatric speciation. The authors suggest, rather, that the

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FIGURE 7.3.

Sympatric speciation of cichlids from Lake Barombi Mbo in Cameroon
(redrawn from Schliewen *et al.*, 1994 and Trewavas *et al.*, 1972).

Pungu maclareni
Konia eisentraui
Konia dikume
Sarotherodon linnelli
Sarotherodon caroli
Sarotherodon steinbachi
Myaka myaka
Sarotherodon lohbergi
Stomatepia mariae
Stomatepia pindu
Stomatepia mongo
Sarotherodon g. galilaeus 'Meme'
Sarotherodon g. galilaeus 'Ejagham'
Sarotherodon g. galilaeus 'Cross'
Sarotherodon galilaeus saganensis

diversification of trophic behaviour (and the ecological behaviour resulting from it) was the main factor in the sympatric speciation for each of these lakes.

The *Labeobarbus* of Lake Tana (Ethiopia) also show remarkable morphologic diversity. They were initially described as species, then as morphotypes of the same species (Banister, 1973). Following a detailed investigation, Nagelkerk & Sibbing (2000) distinguished 16 morphotypes, of which 15 are endemic, and pointed out differences in the dietary habits of the morphotypes. It appears that the species differentiated because of their dietary niche and their preferences in terms of habitat (Nagelkerke *et al.*, 1994). They added that it was probably a sympatric speciation event and that the ancestral *Labeobarbus intermedius* species could have been at the origin of the flock present in Lake Tana. However, Mina *et al.* (1996) showed that morphologic diversification only took place at a late growth stage. Hence, while they support the hypothesis of sympatric speciation, they believe that it is an ongoing process rather than a completed one.

Given the aforementioned observations, it is quite possible that the process known as adaptive radiation, that is, the colonization of several niches of the same ecological system by populations or species descended from a common ancestor, is an illustration of sympatric speciation. This phenomenon does indeed encourage speciation, as colonizers develop morphological and behavioural adaptations that are specific to their new way of life.

A well-known example of adaptive radiation in fish can be seen in the Cichlidae of the East African Great Lakes. It appears that the Cichlidae of Lake Victoria are descended from a single species of fluvial origin that colonized the lake and spawned some 300 living species that occupy all the major ecological niches

SPECIES FLOCKS

"**S**pecies flock" (loosely translated in French as "essaim d'espèces" or "foule d'espèce") is the term used to designate groups of very closely-related species sharing a common ancestor (monophyletic) and endemic to the same physical system (Greenwood, 1984).
These species flocks contain an unusually high number of neighbouring species which are the product of especially rapid speciation (sometimes referred to as explosive speciation). This could correspond to the evolutionary response of a fauna that, after colonizing a new physical system, differentiates by specializing in the use of the various resources offered by this system.

While numerous Cichlidae genera of the East African Great Lakes meet the definition for a species flock, this phenomenon is also observed in other groups, such as the catfish of the genus *Bathyclarias* (10 species) of Lake Malawi, the *Chrysichthys* (6 species), *Mastacembelus* (8 species), *Lates* (4 species) of Lake Tanganyika, the *Labeobarbus* of Lake Tana (16 species), and the *Brienomyrus* of Gabon (only 6 species described among 38 Operational Taxonomic Units that constitute the *Brienomyrus* clade). This clade is the first freshwater fish species flock wholly within a riverine, as opposed to a lacustrine, environment.

available for freshwater fishes. For some adaptive functions related to diet, we can observe different stages of specialization, from the early stages of morphological change to very extreme body forms. For example, in molluscivorous fishes, some species only have a few enlarged pharyngeal teeth used to crush shells, while other species have a large number, and some even have pharyngeal bones mixed with the teeth (see chapter *Diets and food webs*).

Behavioural specialization is probably an important element in the success of adaptive radiation. In addition to trophic specialization, there is also specialization in reproductive behaviour, including mating rituals, sexual and specific colour, and territorial and parental behaviour. This brings together all the conditions that favour sympatric speciation.

Speciation of cichlids in the Great Lakes of East Africa: what processes are involved?

With their several hundred coexisting cichlid species, the African Great Lakes have been compared to natural laboratories for the study of speciation. Many scientists have puzzled over the origins of this high species diversity and the mode of speciation (allopatric or sympatric?) that allowed it. Strongly influenced by the idea that allopatric speciation was the dominant model, they wondered about the conditions that could have led to it, as fishes could in principle move freely throughout the lake and thus maintain gene flows across populations. (see boxes "Mechanisms involved in cichlid speciation" and "Cichlid palaeo-flock record").

To explain how such allopatric speciation could have taken place in these lakes, different but complementary mechanisms have been suggested (Martens *et al.*, 1994).

MECHANISMS INVOLVED IN CICHLID SPECIATION

When observing the cichlid species flocks in the Great Lakes of East Africa, what grabs one's attention is not just the extraordinary richness of shapes and colours that the fish come in, but also the great resemblance of forms from one lake to another.

This resemblance had led to the belief that these species flocks had a common origin. But Meyer *et al.* (1990) clearly showed that this was not the case and that each lake had developed its own species flock.

This raises the question of how, in such different lakes, evolution could have led to such similar forms. What does the very deep (1,470 m) and very old (20 million years) Lake Tanganyika have in common with Lake Victoria, which is only some forty metres deep and had probably dried out, at least partially, around 15,000 years ago? Why do identical phenomena occur repeatedly and independently in these lakes?

To understand this, one must first understand that in each lake, the species flock originated from a fluviatile species that colonized the lacustrine environment.

It then appears that evolution operated simultaneously on two main aspects: skull shape, particularly the jaw; and colour.

Once the fluviatile Cichlidae arrived in a lacustrine environment, it got the opportunity to colonize a large number of different biotopes, each with its own set of food resources: seaweeds to graze, molluscs and pelagic preys to capture, and so on. Groups rapidly specialized in a type of diet, as shown by Alberston *et al.* (1999) in Lake Malawi, where species split into two groups early on: those that preferred rocky habitats, and those that preferred the sandy bottom.

This type of adaptation was possible owing to the extraordinary plasticity of the skull and jaw of these species. Albertson *et al.* (2003a and b) also showed that only about a dozen genes would

have been involved in the emergence of the different phenotypes observed (between grazers, filter feeders, predators, etc.).

These genes are for the most part grouped (or "linked") within the genome and often have multiple effects. For example, some genes can affect both the height and the length of a jaw. Albertson *et al.* (2003 b) also showed that selection phenomena were involved in leading to the shapes that we see today.

If we consider that the fluviatile species that led to these different species flocks had the same genetic potential for jaw evolution, it is no longer surprising that identical selective pressures in different lakes could have led to identical phenotypes.

In other words, in two different lakes, the selection pressures that would compel a species to specialize in, for instance, grazing seaweed, would lead to the same solution regardless of the lake.

Finally, colour variations are another form of diversification that involves sexual selection, which is particularly well studied in the Cichlidae of Lake Victoria. Males are often brilliantly coloured while females are colourless. Reproduction often depends on visual signals related to these colours. Generally, the female selects the male based on colour criteria. Seehausen *et al.* (1997) have shown that water turbidity (for instance, due to eutrophication) can change colour perception in fishes and thus break the ethological barriers between species (thus leading to hybridizations.)

If we also add that the genes controlling skull morphology may be linked to those controlling partner choice (sexual selection), we can then predict a directional selection linking morphology and colour, and understand why the species flocks of the East African Great Lakes are so similar.

CICHLID PALAEO-FLOCK RECORD
ALISON MURRAY & OLGA OTERO

When did their ability to rapidly speciate and form species flocks evolve in cichlids? It may be that this ability arose early in the history of the family.

A major impediment to our understanding of the history of the family Cichlidae is not just a lack of fossils, but a lack of osteological characters that can be used to assign the fossil remains to a living group. Cichlids are conservative in their anatomy, with a diversity of external morphologies mainly associated with small changes in relative growth without major structural modification (Greenwood, 1974, 1984; Strauss, 1984; Stiassny, 1991). The large amount of convergent evolution and the extensive radiation of species make interpreting their interrelationships based on anatomical data very difficult. But anatomical or osteological characters are needed to determine cichlid interrelationships if fossil species are to be studied. Fortunately, there are a few skeletal characters that have been identified and found useful for interpreting cichlid relationships. Also, scales and squamation patterns have been studied and found useful for indicating cichlid relationships (Lippitsch, 1993, 1995, 1998).

Fossils cichlids are known from Africa, Saudi Arabia, the Levant, Europe, South America and Haiti. Their African fossil record starts in the Eocene (56Ma - 34Ma), with *Mahengechromis* in Tanzania (Murray, 2000) (figure 7.4) and a fish reported as being closely related to the modern genus *Tylochromis* found in the Fayum, Egypt (Murray, 2002). By the Oligocene (34Ma - 23Ma), there are a few records of fossil cichlids in Africa and Saudi Arabia. Conversely, during the Neogene (23Ma - Present), cichlids are known from a greater number of deposits throughout Africa. So far, the African cichlid fossil record provides only one example of a potential flock. These are among the oldest known fossils of the family, about 45Myrs ago (Murray, 2001). These fossils, from the Mahenge site in northwestern Tanzania, were identified as belonging to a single genus, based on their scales and squamation pattern (Murray, 2000), and five different species within the genus are identified by differences in osteological features. Can we be sure they represent a species flock? In fact, we cannot. In order to qualify for species flock status, the members of the flock must all be each others' closest relatives, and be confined to a limited geographical area. Neither of these criteria can be determined for fossils. It may well be that some of these fish also lived outside the area in which they were found, or other species may have been more closely related to one or the other species. However, we have no fossil record for similar species outside of the small area of the lake deposit. So, although this group of Eocene species may well have been a flock, we have no method of determining this.

Instead of trying to find fossils to document the age of the flocking ability of cichlids, one group of scientists instead examined the diversity of living riverine cichlids in southern Africa to determine the time when they flock (Joyce *et al.* 2005). Molecular relationships and molecular clock dating of the extant cichlid flocks indicate that the flocking ability arose in these lineages millions of years ago. But conflicting results on divergence dates of different lineages prevent any agreement on how old these flocks may have been. This intriguing characteristic of cichlids may well have evolved millions of years ago, but we have yet to determine if this is the case.
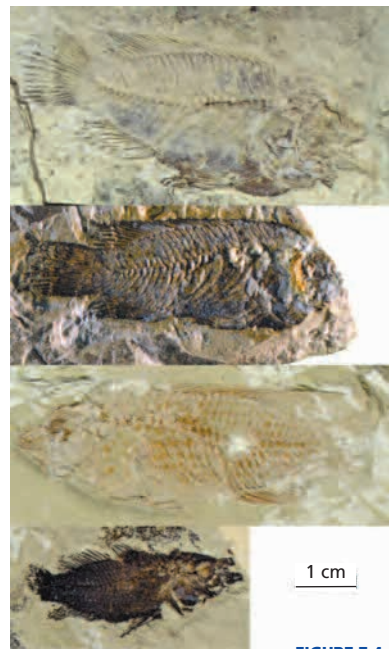

1 cm

FIGURE 7.4.

Members of four species of *Mahengechromis* from the Eocene of Mahenge (Tanzania) (photos by Alison Murray).

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Fragmentation of the lacustrine system in several smaller lakes

Proof now exists that the level of the African Great Lakes was not stable but fluctuated significantly even in the recent past. For instance, 15,000 years ago, the level of Lake Victoria was lower than its current one. The fluctuations of Lake Malawi's level reached 250 to 300 metres over the last 25,000 years (Owen *et al.*, 1990).

As for Lake Tanganyika, research has shown that its level 25,000 years ago was 600 metres lower than the current one (Tiercelin *et al.*, 1989). During the Pleistocene, Lake Tanganyika was fragmented into two or three separate basins as well as numerous small lakes occupying the graben.[1] This created conditions that favoured allopatric speciation (Martens *et al.*, 1994). The faunas could have mixed once again when the water level rose, but sexually isolated species continued to survive. If such a mechanism occurred repeatedly over a geological scale, this could explain the great wealth of species in the East African Great Lakes.

A great variety of diets

While the fluvial ancestors that populated the great lakes were apparently generalists, the Cichlidae, like Darwin's finches, developed a wide range of diets in the lacustrine physical system. This resulted in a number of morphological adaptations to the type of food and its capture, as well as ecological and behavioural adaptations such as a more systematic presence in certain habitats where food is present (see the aforementioned adaptive radiation).

Allopatric/sympatric speciation in the lake itself

Allopatric speciation can take place even without a fragmentation of the lacustrine physical system. Investigations on the population of the Great Lakes by fishes showed that many of the benthic Cichlidae species are only present at certain depths and certain bottom types from which they hardly move throughout their lifetime. This sedentary behaviour (also called stenotopy) is associated with reproductive behaviour that implies staying in a territory, as well as parental care, which does not promote dispersion either.

Numerous 'Mbuna' species, which are cichlids endemic to Lake Malawi, thus have very specific habitats and are likely to pass their entire lifetime, from fecundation to death, in the only habitat they are dependent on. It is therefore possible that in lakes covering a large area, the existence of heterogeneous islands and/or bottoms scattered in patches encourages the maintenance of isolated populations that, owing to their stenotopy, have little contact with each other. Such a situation favours the speciation of sympatric species following a model that can be compared, in a way, to allopatric speciation, as behavioural and ecological barriers within the same lacustrine system limit or prevent gene flows between sub-populations. Ribbink (1994) believes that the particularly marked stenotopy of the haplochromines would largely explain the extraordinary diversification observed in this group (nearly 1,000 species). It is accepted that the ancestors of the Cichlidae species flocks of the Great Lakes were eurytopic fluviatile species, and that their evolution went in the direction of

NOTE 1

In geology, a graben (graben is German for ditch or trench) is a depressed block of land bordered by parallel faults.

greater specialization. The evolutionary potential of these eurytopic colonizers was probably poor, but could have become increasingly important as certain lineages specialized and became stenotopic (Ribbink, 1994).

Another hypothesis states that the variability of the riverine environment selects for eurytopic species to the detriment of stenotopic ones, which are unable to survive. This would explain why there are more Cichlidae species in African lakes compared with rivers. Moreover, tilapias, which are eurytopic – that is, less selective in terms of habitat – are only represented by about a dozen species in the Great Lakes. However, stenotopy is only possible in the lakes, where conditions remain relatively stable over the long term. The smaller number of Cichlidae in Lake Tanganyika could be related to the fact that demersal habitats are too unstable (upwelling of anoxic deep waters, in particular) to allow the evolution of specializations that would lead to stenotopy and the development of a large species flock (Eccles, 1986).

Similarly, the low number of Cichlidae (sixteen haplochromine species) observed in Lake Kivu could be due to geological instability since the Pleistocene which could have caused widespread species extinctions and inhibited the diversification of surviving species. The latter survived the unstable periods by seeking refuge in neighbouring rivers, whence they recolonized the lake during more favourable periods. Unlike most of the other haplochromines species in the Great Lakes, these species are generalists and eurytopic, which supports previous conclusions regarding the role of stenotopy.

The role of predation

African fish speciation, particularly that of the Great Lakes Cichlidae, has been much discussed. According to some hypotheses, because they patrol in areas that have shelter, predators play a role in fragmenting populations and keeping them in isolated patches, which encourages speciation (Lowe-Mc Connell, 1987). In pelagic populations, meanwhile, predation pressure appears to lead to uniformity and a reduction in diversity. This hypothesis is confirmed by Coulter (1991 a) for Lake Tanganyika species, where *Lates spp.* and the Cichlidae *Boulengerochromis microlepis* exert strong influence over juveniles and small fishes that are forced to either hide or adopt schooling behaviour. These predators also have a strong influence on the reproductive strategies, behaviour, and mortality rate of prey. Meanwhile, it appears that the role of predators is less significant in Lakes Victoria and Malawi, where the many predators are themselves limited to certain types of habitat. The consequences of the introduction of *Lates* in Lake Victoria show in retrospect that the many Cichlidae species that disappeared did not, in fact, possess the behavioural mechanisms or adequate shelter needed to evade predation.

How fast is speciation?

There is little data on the speciation rate of African fishes, but it obviously varies enormously depending on phylogenetic group and the environmental conditions (Coulter, 1994).

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The speed at which speciation occurs is still under debate, and improbable figures have been put forward. There are five endemic species in Lake Nabugabo, a satellite of Lake Victoria, that has been isolated from the latter for a little over 5,000 years. Some scientists thus believe that in this lake, speciation could have occurred in this time frame. If we note today that these species are not present in the larger lake, this does not mean that they were not there at another period.

Geologists have shown that Lake Victoria probably dried up entirely between 15,600 and 14,700 years ago. For some scientists, the current fauna probably diversified after this period. Many ichthyologists thus raised the following question: how can we explain the appearance of so many species in so short a time? While some biologists accept this scenario, for the majority of specialists this time length is in contradiction to biological reality, and they believe it impossible for so many species (around 500) to have differentiated in such a short time period (around 15,000 years) from one or a few ancestor species. Specialists now consider that this is not possible indeed, and that the lineage must have diversified around 100,000 years ago. What explanation can therefore be proposed? Several hypotheses were made, including one that suggested that the lake did not dry out completely and that some small residual lakes subsisted. In these lakes, two strains more adapted to lacustrine conditions could have differentiated here, and are thus behind the two major lineages now found in Lake Victoria. While geophysicists acknowledge this possibility, they nonetheless believe that the physico-chemical conditions of the time were incompatible with the coexistence of numerous species (Stager *et al.*, 2004).

This debate between the adherents of the two scenarios is still ongoing. However, more recent investigations (Elmer *et al.*, 2009) suggest a new one: that Lake Victoria could have been recolonized by haplochromines from Lake Kivu after Lake Victoria was once again filled with water some 15,000 years ago (Verheyen *et al.*, 2003). Indeed, in the past, water flowed from Lake Kivu to the Victoria basin (2.6 Ma-12,000 BP) before the Virunga massif's volcanic activity blocked the Kivu outlet and isolated the two entities around 14,000 to 11,000 years (Pouclet, 1978) or 25,000 to 12,000 years (Beadle, 1981) ago.

According to the most accepted scenario, the complex evolutionary history of haplochromines in Lake Victoria began well before the dry period that affected the Victoria basin. Molecular studies all confirm that the genetic lineages, and thus the species, are at least 100,000 years old (Verheyen *et al.*, 2003 and 2004). At least part of this history could have taken place outside the basin of Lake Victoria, perhaps in Lake Kivu (figure 7.5).

Despite being the most popular scenario today, it still remains a hypothesis that simply reflects the current state of knowledge.

As for the haplochromines of Lake Malawi, Owen *et al*. (1990) believe that speciation was very rapid and proposed a period of 200 years, which seems to be extremely farfetched!

Evolution-wise, Vrba (1980) advanced the hypothesis that the differences observed for speciation rates within a "clade" were the result of a
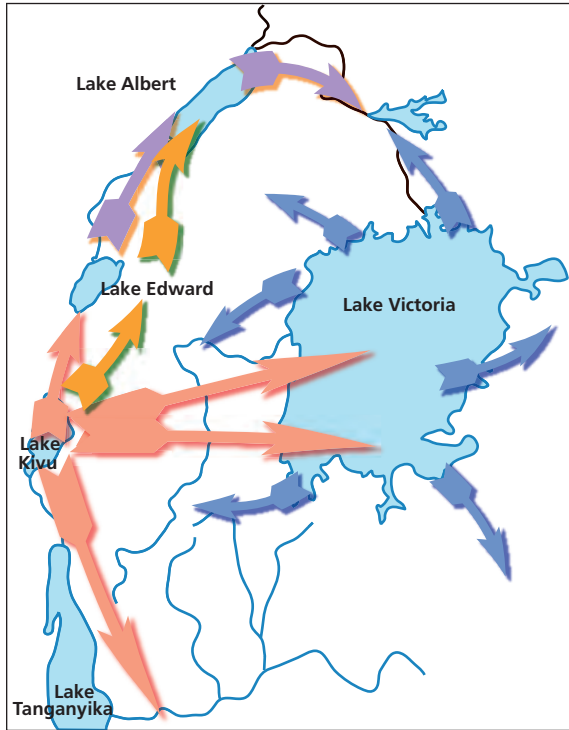
eurytype/stenotype differentiation, that is, high speciation and extinction rates were associated with strong stenotopy. In other words, when stenotopy increases as a result of greater specialization, the speciation rate increases. This hypothesis appears to be verified in the Cichlidae of the African Great Lakes. Haplochromines, which are much more stenotopic than tilapias, also have many more species. Moreover, among the haplochromines, the species flocks with the most stenotopic members also have the greatest number of species (Ribbink, 1994).

Convergent evolution: chance or necessity?

Convergence occurs during evolution when similar characteristics appear in different species that may come from very distant lineages. Such convergences are often tied to the fact that the species are subjected to similar constraints when occupying comparable ecological niches found in different ecological systems.

Species from different taxonomic groups may display remarkable convergence in form. This is the case, for instance, of the African species *Hepsetus odoe* (Hepsetidae), which strongly resembles the northern pike *Esox lucius* and the South American genus *Boulengerella* (Ctenoluciidae) (figure 7.6).

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Esox lucius — Europe

Boulengerella maculata — South America

Hepsetus odoe — Africa

Abramis brama — Europe

Jupiaba keithi — South America

Citharinus citharus — Africa

Alburnus alburnus — Europe

Alestes baremoze — Africa

Rutilus rutilus — Europe

Brycinus nurse — Africa

Perca fluviatilis — Europe

Lepomis gibbosus — North America

Saratherodon melanotheron — Africa
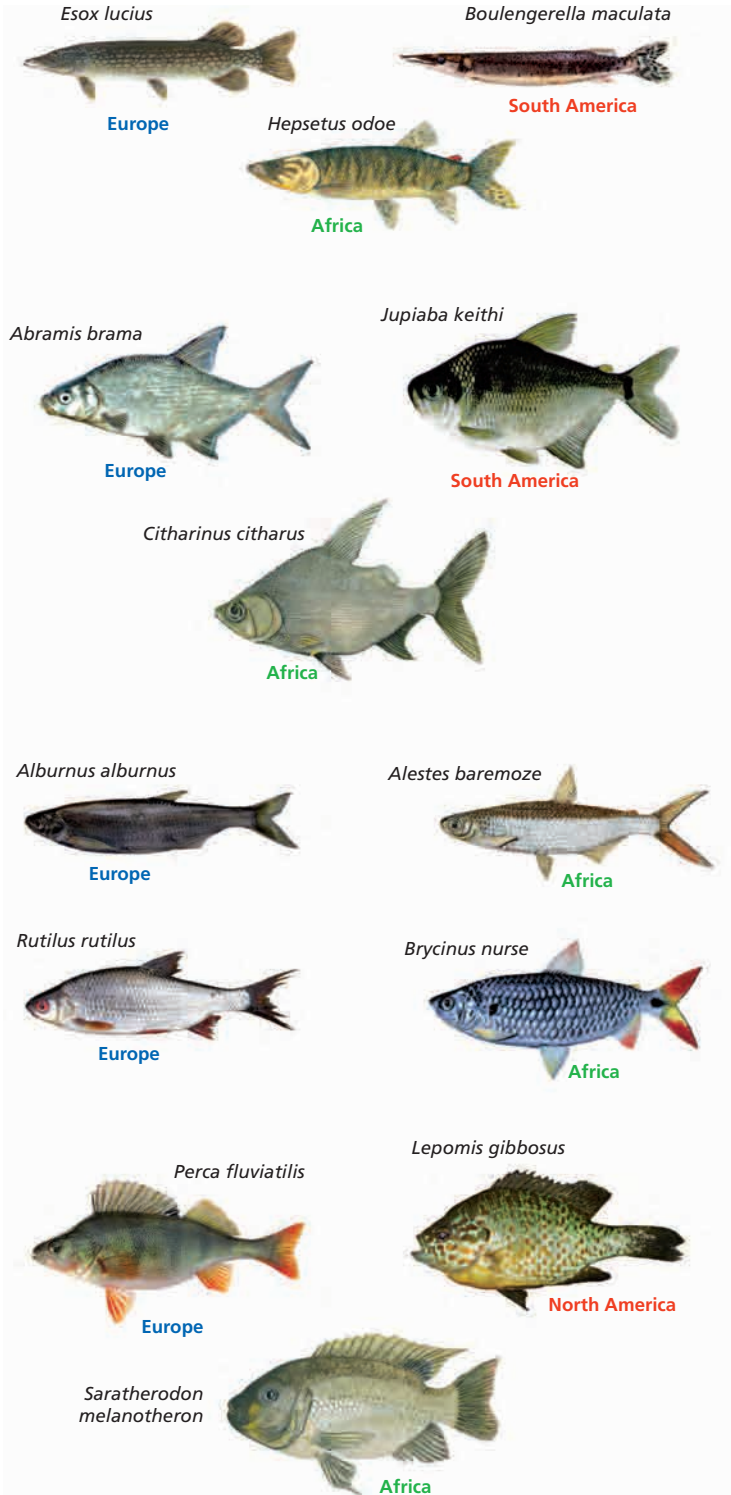
FIGURE 7.6.

Some examples of form convergence between species belonging to different families from Europe, America and Africa (sources: *Esox lucius* (Timothy Knepp); *Boulengerella maculata* (Clinton & Charles Robertson); *Jupiaba keithi* (Boujard *et al.*, 1997); *Abramis brama* (Iduns Kokbok); *Rutilus rutilus* (Algirdas); *Alburnus alburnus* (Kagor); *Perca fluviatilis* (Geshafish); *Lepomis gibbosus* (H. Krisp); *Hepsetus odoe*, *Citharinus citharus*, *Alestes baremoze*, *Sarotherodon melanotheron* (Cécile Paugy); *Brycinus nurse* (Pierre Opic).

Species of the African genera *Alestes* and *Brycinus* (Characidae) resemble, respectively, the Bleak *Alburnus,* the Roach *Rutilus*, or the Rudd *Scardinius* (Cyprinidae) in body shape, mouth, anal fins, and colouration (figure 7.6).

Citharinus (Citharinidae) of the Nilo-Sudanian basins or *Distichodus* (Distichodontidae) are also close to the Bream (*Abramis brama*) in terms of body and fin shape (figure 7.6).

Finally, the shape and some characteristics of Cichlidae recall those of some European Percidae and North American Centrarchidae (figure 7.6).

In the case of the East African Great Lakes, we also see examples of the convergent evolution of some anatomical or behavioural characters in Cichlidae. Specialization for the use of the same resources occurred simultaneously in several lakes, and often gave rise to comparable morphological changes in species that do not share an evolutionary lineage. These species have been referred to as "ecologically equivalent" (Fryer & Iles, 1972).

The study of small cichlids raises fundamental questions about the nature of evolution. Does it happen simply by "chance" or does it meet a deterministic pattern? In other words, is evolution contingent (something that may or may not happen) or does it address a "need"? The notion of "chance", as discussed by S.J. Gould,[2] does not mean the absence of a cause, but the impossibility of acquiring a precise knowledge of such a cause.

Chance or contingency probably play a central role in the phenomenon of species dispersion. Species may or may not seize opportunities to disperse that are offered by a series of geological or climatic phenomena. The colonization of new physical systems is thus a matter of chance, to a large extent. That said, adaptive radiations appear to be a form of determinism, as they involve diversifying diets or behaviours to maximize the use of available resources. As for ecological convergence, evolution appears to wear the mantle of "necessity", as it selected comparable shapes in the face of the same environmental constraints. This convergence thus reflects a type of adaptation.

This is how the genera *Bathybates* and *Rhamphochromis* that are endemic to Lakes Tanganyika and Malawi, respectively, are piscivorous open water fishes that share similar characters: elongated heads and bodies, and pointed teeth (Stiassny, 1981). These two genera are not phylogenetically close and evolved independently in each of the lakes (figure 7.7).

NOTE 2

Stephen Jay Gould was a champion of contingency, and thus of unforeseeable events ("chance"):
"Wind back the tape of life to the origin of modern multicellular animals in the Cambrian explosion,
let the tape play again from this identical starting point, and the replay will populate the earth
(and generate a right tail of life) with a radically different set of creatures. The chance that this alternative set
will contain anything remotely like a human being must be effectively nil, while the probability of any kind
of creature endowed with self-consciousness must also be extremely small […].
At any of a hundred thousand steps in the particular sequence that actually led to modern humans,
a tiny and perfectly plausible variation would have produced a different outcome, making history cascade
down another pathway that could never have led to *Homo sapiens*, or to any self-conscious creature."
(Gould S.J., 2011 – *Full House. The spread of Excellence from Plato to Darwin.* Belknap Press, 256 p.).

Bathybates ferox (Lake Tanganyika)   Rhamphochromis macrophthalmus (Lake Malawi)

In molluscivorous cichlids, the development of thick pharyngeal bones to crush shells in the *Gaurochromis* of Lake Victoria as well as in Lake Malawi species such as *Mylochromis sphaerodon* or *Lethrinops mylodon* can be observed.

Other examples of morphological convergences (some authors prefer the term "parallelism") related to feeding behaviour have also been noted in paedophagous or lepidophagous fishes of the Great Lakes.

FIGURE 7.7.
Example of endemic species that are "ecologically equivalent" and "phylogenetically distant". *Bathybates ferox* from Boulenger, 1898 and *Rhamphochromis macrophthalmus* from Regan, 1922.

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The Inland Water Fishes of Africa

Diversity, Ecology and Human Use

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