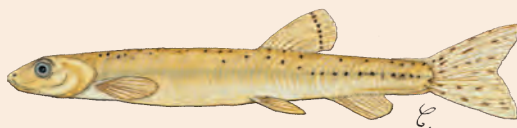


# Taxonomy and systematics



DIDIER  
PAUGY

CHRISTIAN  
LÉVÊQUE

**T**axonomy is the science of naming and describing organisms. It is a highly formalized science whose rules are established and revised regularly by an International Commission of Zoological Nomenclature created in 1895. The International Code of Zoological Nomenclature contains all the rules for designating animal species which are the same for all zoological groups.

One of its basic principles is that the first name given to a species has priority over the others. It is not uncommon for taxonomic revisions of a group to reveal that some species had been described under different names, because the authors did not have access to all available information or had made an error. In these conditions, the so-called priority rule must be applied. This sometimes leads to a change in the name used for the species up to that time. The situation may prove even more complex, as illustrated by the case of *Schilbe mystus* (see box “Who is *Schilbe mystus?*”).

Another well-known case of ambiguity is that of the mounted holotype of *Synodontis xiphias* described in 1864 by Günther, which has a long and pointed snout similar to a swordfish. The species had never been recorded since then, for a perfectly good reason: an x-ray showed that the long snout was a fake nose, resulting from a metal frame used in mounting the animal (Poll, 1971) (figure 8.1). The holotype of *Synodontis labeo* Günther, 1865, described later, belongs to the same species, but the name *S. xiphias* remains valid in application of the principle of priority, and despite the deformity of the specimen retained as the type.

Systematics is the study of the diversity of organisms and the relationships between these organisms. Its goal is to classify species and detect phylogenies – a purpose that differs from the objectives of taxonomy. Classification consists of recognizing and defining groups or taxa (that is, a set of organisms that share a specific character) that taxonomists will then have to name. According to the hierarchical classification proposed by Linnaeus (1758), each level of the hierarchy corresponds to a taxon name. While ideas governing classification in particular have evolved significantly since the 18th century, the basic rules stated by Linnaeus remain solid. The discipline currently known as biosystematics is a modern approach to taxonomy and phylogeny that makes use of information from different sources: morphology, genetics, biology, parasite specificity, behaviour, and ecology. This type of approach is undoubtedly set to develop further.

WHO IS *SCHILBE MYSTUS*?

**A**fter examining the presumed holotype of *Schilbe mystus*, De Vos & Skelton (1990) showed that the specimen, described in 1758 by Linnaeus, actually belonged to the same species as the one named *S. (Eutropius) niloticus* described later in 1829 by Rüppell.

If the two species are synonyms, application of the International Code of Zoological Nomenclature means that the older name *S. mystus* takes priority over *S. niloticus*. In keeping with this, all fishes that had been identified as *S. niloticus* up to that time need to be renamed *S. mystus*.

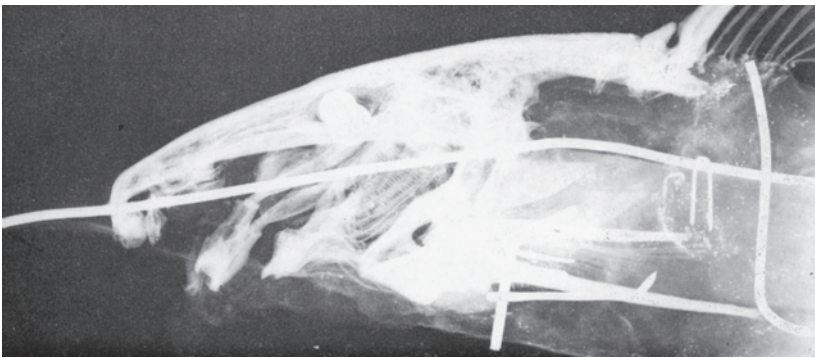
While the holotype of *S. mystus* is a synonym of *S. niloticus*, this is not the case for all the other fishes identified up to then as *S. mystus* but different from *S. niloticus* and the *S. mystus* type. What species do they belong to? Among the species erroneously considered a synonym of the *S. mystus* type, the oldest is *S. intermedius* described

by Rüppell in 1832, and whose description matches that of the *ex-mystus*.

As a result, fishes described before 1990 under the name *S. mystus* must be renamed *S. intermedius*.

The application of perfectly reasonable taxonomic rules can therefore lead to a particularly confusing situation for non-specialists. The name *S. mystus* is now used for a species that was widely cited in literature under the name *S. niloticus*, and the former *S. mystus* take the name *S. intermedius*.

However, this change in nomenclature is not always rigorously applied by everyone everywhere, to the point that one often wonders if the name being used is the former or the post-revision name. In this specific case, the legendary formal discipline of the taxonomist did not take into account the confusion that would result for ichthyologists, biologists and ecologists alike.



**FIGURE 8.1.**  
Head radiography  
of the holotype  
of *Synodontis xiphias*  
(from Poll, 1971).

## What is a species?

The binomial system originally proposed by Linnaeus (1758) is used by naturalists the world over to designate and identify species. But the concept itself of “species” has long been debated. To date, no definition is entirely satisfactory.

## The typological species concept

Until the mid-19th century, systematists viewed species as fixed. They were as God had created them, immutable and limited in number. The purpose of taxonomy then was to draw up an inventory of all existing life forms and describe their specific characters. In the words of Linnaeus, "(...) there are as many species as the infinite being created diverse forms (...)", and he formalized this view by establishing the species through a type individual, the holotype (see box "International Code of Zoological Nomenclature"), to which a Latin binomial was assigned in order to identify and classify them.

### EXTRACT OF THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE FOURTH EDITION

adopted by the  
XXth General Assembly of the International Union of the Biological Sciences  
December 1999

**type**, n. A term used alone, or forming part of a compound term, to denote a particular kind of specimen or taxon.

**allotype**, n. A term, not regulated by the Code, for a designated specimen of opposite sex to the holotype [Recommendation 72A].

**cotype**, n. A term not recognized by the Code, formerly used for either syntype or paratype, but that should not now be used in zoological nomenclature [Recommendation 73E].

**genotype**, n. A term not recognized by the Code, formerly used for type species, but that should not now be used in zoological nomenclature [Recommendation 67A].

**hapantotype**, n. One or more preparations consisting of directly related individuals representing distinct stages in the life cycle, which together form the name-bearing type in an extant species of protistan [Arts 72.5.4, 73.3]. A hapantotype, while a series of individuals, is a holotype that must not be restricted by lectotype selection; however, if a hapantotype is found to contain individuals of more than one species, components may be excluded until it contains individuals of only one species [Art. 73.3.2].

**holotype**, n. The single specimen (except in the case of a hapantotype, q.v.) designated or otherwise fixed as the name-bearing type of a nominal species or subspecies when the nominal taxon is established.

**lectotype**, n. A syntype designated as the single name-bearing type specimen subsequent to the establishment of a nominal species or subspecies [Art. 74].

**neotype**, n. The single specimen designated as the name-bearing type of a nominal species or subspecies when there is a need to define the nominal taxon objectively and no name-bearing type is believed to be extant. If stability and universality are threatened, because an existing name-bearing type is either taxonomically inadequate or not in accord with the prevailing usage of a name, the Commission may use its plenary power to set aside that type and designate a neotype.

**paralectotype**, n. Each specimen of a former syntype series remaining after the designation of a lectotype [Art. 72.1.3, Recommendation 74F].

**paratype**, n. Each specimen of a type series other than the holotype [Recommendation 73D].

**syntype**, n. Each specimen of a type series (q.v.) from which neither a holotype nor a lectotype has been designated [Arts. 72.1.2, 73.2, 74]. The syntypes collectively constitute the name-bearing type.

**topotype**, n. (**topotypic**, a.). A term, not regulated by the Code, for a specimen originating from the type locality of the species or subspecies to which it is thought to belong, whether or not the specimen is part of the type series.

For practical reasons, the typological species concept is still used to this day: a species is a set of individuals that are identical to each other and to the “type” specimen, *i.e.*, the specimen used to describe and characterize the species in morphological terms. This type is deposited in a museum where it serves as a reference or a sort of standard for comparisons or future revisions.

## The biological species concept

The typological species concept gradually gave way in the early 20th century to the concept of a biological species. In 1798, Cuvier had already used a biological criterion in defining a species as “the collection of all organized bodies, borne of each other or common parents, and of all those that resemble them as much as they resemble each other.” The definition given by Mayr (1942) a century and a half later is not fundamentally different but emphasizes the biological aspect: species are groups of populations whose members can interbreed, and who are reproductively isolated from other groups. One of the major criteria for differentiating neighbouring species was the fact that any eventual hybrids were not viable or were sterile. “The origin of species is therefore simply the evolution of some difference – any difference at all – that prevents the production of fertile hybrids between populations under natural conditions” (Wilson, 1992).

On the genetic level, the concept of a biological species implies the existence of a gene pool that could recombine within the population during sexual reproduction, but that this gene pool is somehow “protected” from mixing with other pools by biological, physiological, or behavioural mechanisms.

While the concept of biological species is not debatable, it is nonetheless difficult to apply in fishes, in the sense that systematic cross-breeding trials in various natural populations are particularly difficult to carry out.

## Concept of specific-mate recognition system

In reaction to the concept of reproductive isolation that undergirds that of the biological species, Paterson (1985) considers that there is no obvious reason for species evolving independently in isolated geographic areas to find it advantageous to develop mechanisms that lead to reproductive isolation.

The concept of a specific-mate recognition system, meanwhile, is based on the premise that conspecific sexual partners must share specific characters, such as a co-adapted set of signals and responses between males and females of the same species during their mating rituals, in order to meet and ensure fertilization of gametes (Ribbink, 1988). A species is thus made up of individuals possessing the same system of fertilization, that is, the set of adaptations that encourage and facilitate the encounter between sexual partners to ensure reproduction: visual, chemical, or sonic recognition signals; colouring; mating dances; synchronous reproductive periods; preference for the same types of habitat and laying sites; territoriality, etc.

This concept is an interesting alternative. The existence of selective recognition systems for conspecific partners, rather than barriers to hybridization, serves as an important criterion for speciation. In other words, we are in the realm of ethology.

### Sister species

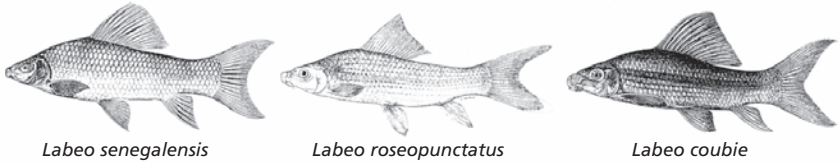
Sister species are biological species that have achieved reproductive isolation but are still difficult to discern based on morphology alone. These species probably result most frequently from recent speciation.

Here are two examples that provide a good illustration of how some recent techniques can help separate species with similar phenotypes and that probably thus result from fairly recent speciation.

- **Labeo** from Senegal and Niger. In the upper course of these two basins, we found numerous specimens that were intermediate between *L. senegalensis* and *L. coubie*, and initially thought they could be hybrids. While the shape is closer to *L. senegalensis* in terms of general morphology, the buccal anatomy was closer to *L. coubie*. Similarly, the number of gill rakers on the first gill arch was not conclusive and also suggested a hybrid form. Comparative analysis of gill parasite fauna (Monogeneans) of the three forms of *Labeo* made it possible to determine that the specimens were not hybrids but a separate valid species that had specific parasite fauna. Genetic analysis of the three forms using protein electrophoresis also lifted all doubt about the true specificity of the presumed hybrid. It was named *L. roseopunctatus* (Paugy *et al.*, 1990) (figure 8.2) for its distinctive colour.

**FIGURE 8.2.**

General morphology of three sympatric species of *Labeo* from Western Africa (from Paugy *et al.*, 1994).



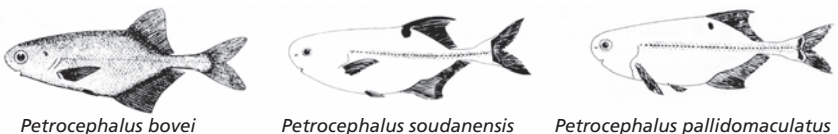
- **Petrocephalus** from the Niger. Three *Petrocephalus* forms found in the upper Niger basin have identical metric and meristic characteristics and only differ in their colour pattern:

- Form A: uniformly silver colouring.
- Form B: first dorsal fin rays strongly black; black spot under and touching the base of the dorsal fin.
- Form C: grey spot under and not touching the dorsal fin.

Form A, long known to science, corresponds to *P. bovei*, a widely-distributed species but whose morphology – aside from colouring – does not differ from the other two forms. To draw a conclusion on the possible specificity of the three forms, the characteristics of the electrical discharges of these Mormyridae were studied. While forms A and C could not be distinguished, individuals of group B showed different characteristics. Also, while the type of discharge could

**FIGURE 8.3.**

General morphology of three sympatric species of *Petrocephalus* from Western Africa (from Paugy *et al.*, 1994).

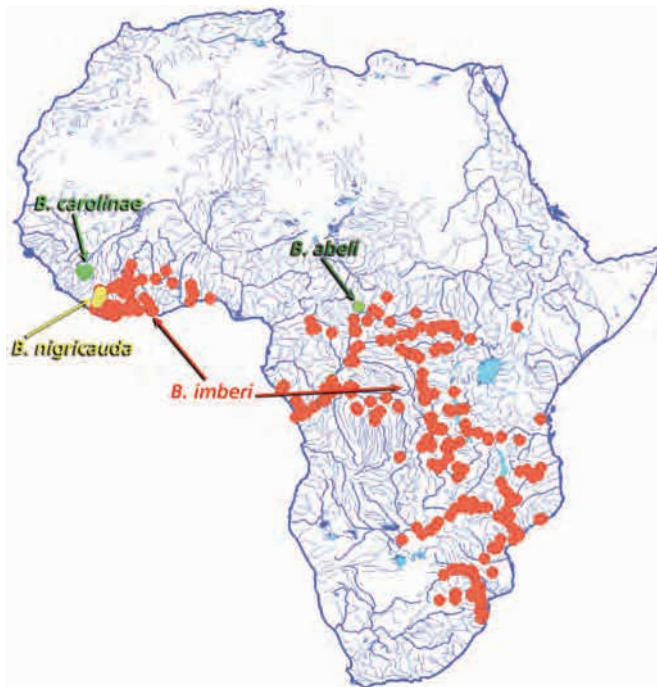


not distinguish A and C, genetic separations confirmed the specific level of these three forms (Agnèse & Bigorne, 1992). In addition to the already identified *P. bovei*, two new species, *P. soudanensis* and *P. pallidomaculatus* were described with the help of new techniques that allowed recognition of the specific validity of these two other forms (Bigorne & Paugy, 1991) (figure 8.3).

### Polytypic species

In a species' area of distribution, environmental factors are generally not uniform. Populations can react locally to changes in these factors through morphological changes. The concept of a polytypic species refers to a species that can present several forms and/or which is composed of several subspecies that may show differences on the morphological, physiological, ecological or behavioural level.

Recognizing variability within a population can lead to two positions between which ichthyologists have long hesitated. Either "varieties" are local adaptations of the same species, or they are truly different species. Thus, for the species *Brycinus nurse* common in the Sahelian zone, there are two known lacustrine dwarf populations, each sympatric with riverine populations: *B. nurse dageti* in Lake Chad and *B. nurse nana* in Lake Turkana. The first subspecies was initially described as a different species, *B. dageti* (see Paugy, 1986). There are also numerous examples of polytypic species among the Cyprinidae (Lévêque, 1989a and b) and Mormyridae (Bigorne, 1987 and 1989; Bigorne & Paugy, 1991). In reality, given that hydrographic basins currently act as geographic islands, a species is most often split in several isolated populations with little or no contact among them (figure 8.4). In such conditions, it is unsurprising



**FIGURE 8.4.**

Distribution of *B. imberi*, *B. abeli*, *B. carolinae* and *B. nigricauda*.

for isolated populations to begin developing certain adaptations in response to their environmental conditions, which would explain the variability observed.

In tropical zones, several studies have shown the influence of food habits on the morphological variations of fishes (see chapter *Diets and food webs*).

### Geographical clines

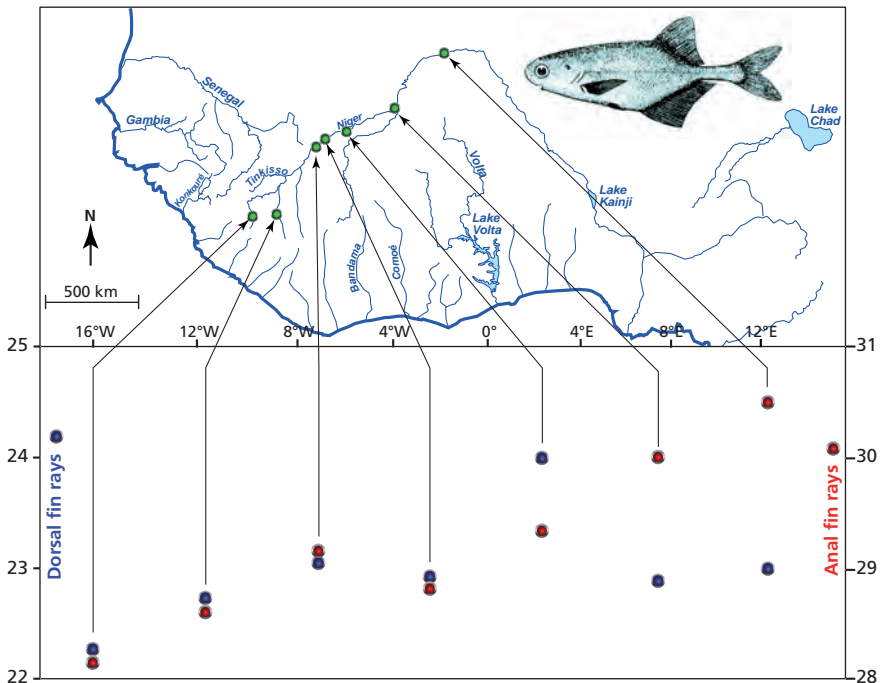
In a terrestrial physical system, we have observed that when environmental factors vary gradually, there may also be gradual changes in certain morphological or morphometric characteristics in the populations of a species. These geographic variations result from the response of organisms to environmental conditions and/or the limitation of gene exchanges between isolated populations.

Endler (1977) defined cline as follows: "a geographic gradient in a measurable character, or gradient in gene, genotype, or phenotype frequency." Thus, phenotype variability or variability in morphological or meristic characters observed in a species can be considered a cline.

### Regional scale

In the upper Niger basin, the number of soft rays in the anal and dorsal fins of *Petrocephalus bovei* (Bigorne *et al.*, unpublished) changes along an upstream-downstream gradient (figure 8.5). There is an average difference of two rays between extreme populations. No solid explanation has been given for this phenomenon.

**FIGURE 8.5.**  
*Petrocephalus bovei*:  
clinal changes  
in two meristic  
characters (average)  
along an upstream-  
downstream  
gradient  
(Upper Niger).

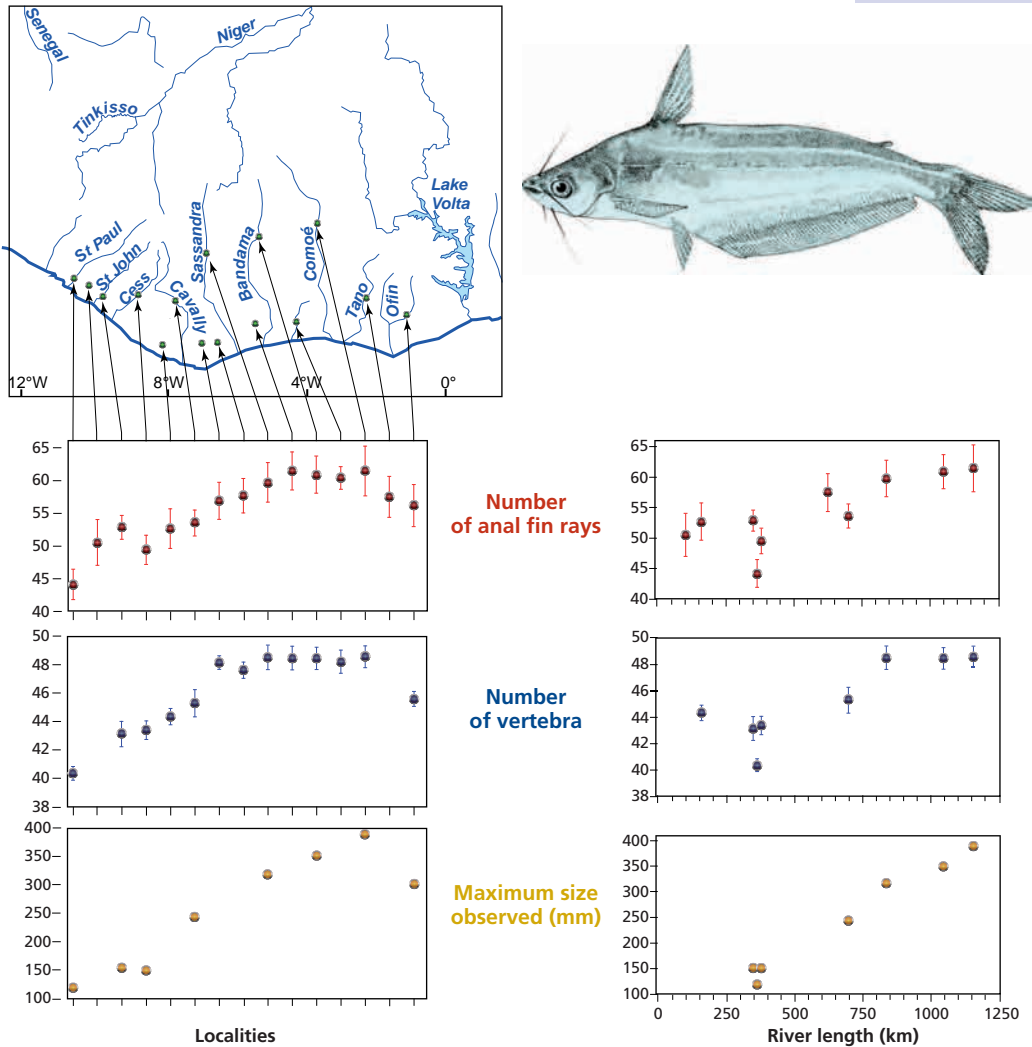




**West African scale:**  
***Schilbe mandibularis***

*Schilbe mandibularis* (Schilbeidae) is found in the Atlantic basins of Upper Guinea, from eastern Liberia to western Ghana (Lévêque & Paugy, 1999). The number of anal fin rays and vertebrae in this species increases from west to east, as is also the case for body size, size at first maturity, and maximum size (figure 8.6) (Lévêque & Herbinet, 1982). From an ecological viewpoint, the west-east gradient corresponds to the transition from forest rivers (Cess, Cavally) to savannah rivers (Comoé) with intermediate situations (Sassandra and Bandama). In this example, there is also a correlation between the maximum size of individuals and the number of vertebrae.

**FIGURE 8.6.** *Schilbe mandibularis*: clinal changes in two meristic characters (average) and maximum size observed along an east-west gradient in river catchments of Côte d'Ivoire.



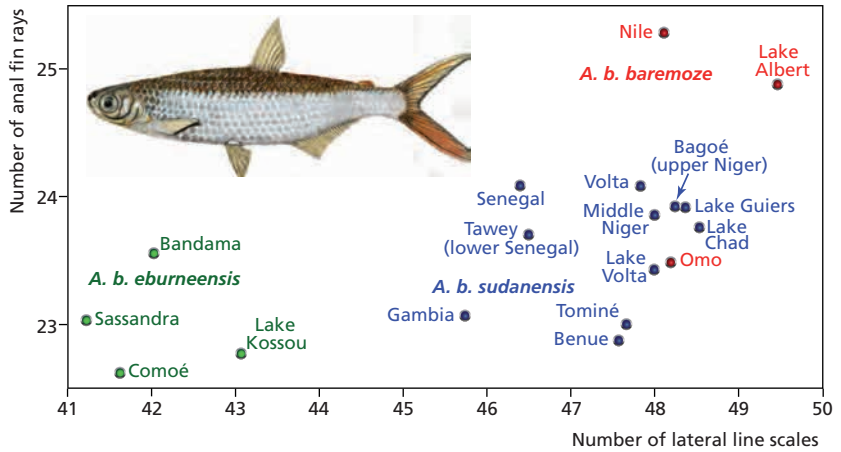
**Subcontinental scale:**

***Alestes baremoze*, *Brycinus macrolepidotus* and *Barbus bynni***

*Alestes baremoze* (Alestidae) is found in all the basins of the Nilo-Sudanian zone (Paugy *et al.*, 1994; Lévêque & Paugy, 1999). Populations are not identical and, depending on the sub-regions, there are geographic variations in some meristic characters such as the number of scales along the lateral line, the number of vertebrae, and the number of soft rays of the anal fin (figure 8.7). The values of these three characters decrease along the cline from the Nile to the Côte d'Ivoire with intermediate values for the Sudanian basins. Three subspecies were described on the basis of the variations of these meristic characters. No detailed explanation has been given to explain this trend.

**FIGURE 8.7.**

*Alestes baremoze*:  
clinal changes in two  
meristic characters  
(average).



Prior to the morphometric analysis of *B. macrolepidotus*, two species had been identified throughout its area of distribution in tropical north Africa: *Brycinus rutilus* in the forest sector and *B. macrolepidotus* in the savannah zone. On the basis of two main morphometric characteristics (body height and position of the dorsal fin in relation to the pelvic fin), we were able to highlight the existence of a geographic cline (figure 8.8), and only *B. macrolepidotus* is now considered a valid species (Paugy, 1982a). There are in fact two extreme morphs and several intermediate forms. A look at the forest-savanna gradient shows that the bodies of individuals lengthen and become more slender, and that the position of the anal fin retreats in relation to the insertion of the pelvic fins.

Within the *Barbus bynni* complex, three allopatric species have been identified: *B. bynni* (Nile basin), *B. occidentalis* (Sahelian zone: Chad, Niger, Ouémé, Volta, and Senegal basins) and *B. waldroni* (coastal basins of Côte d'Ivoire and Ghana). In fact, a parasitology study (fauna of gill parasites, Monogenean) (Lévêque & Guégan, 1990) show that the two West African species *B. waldroni* and *B. occidentalis* had the same Monogenean fauna as *B. bynni*. The strict specificity of this type of parasite thus proves that these three forms belong to the same species and must each be considered a subspecies of that group. The

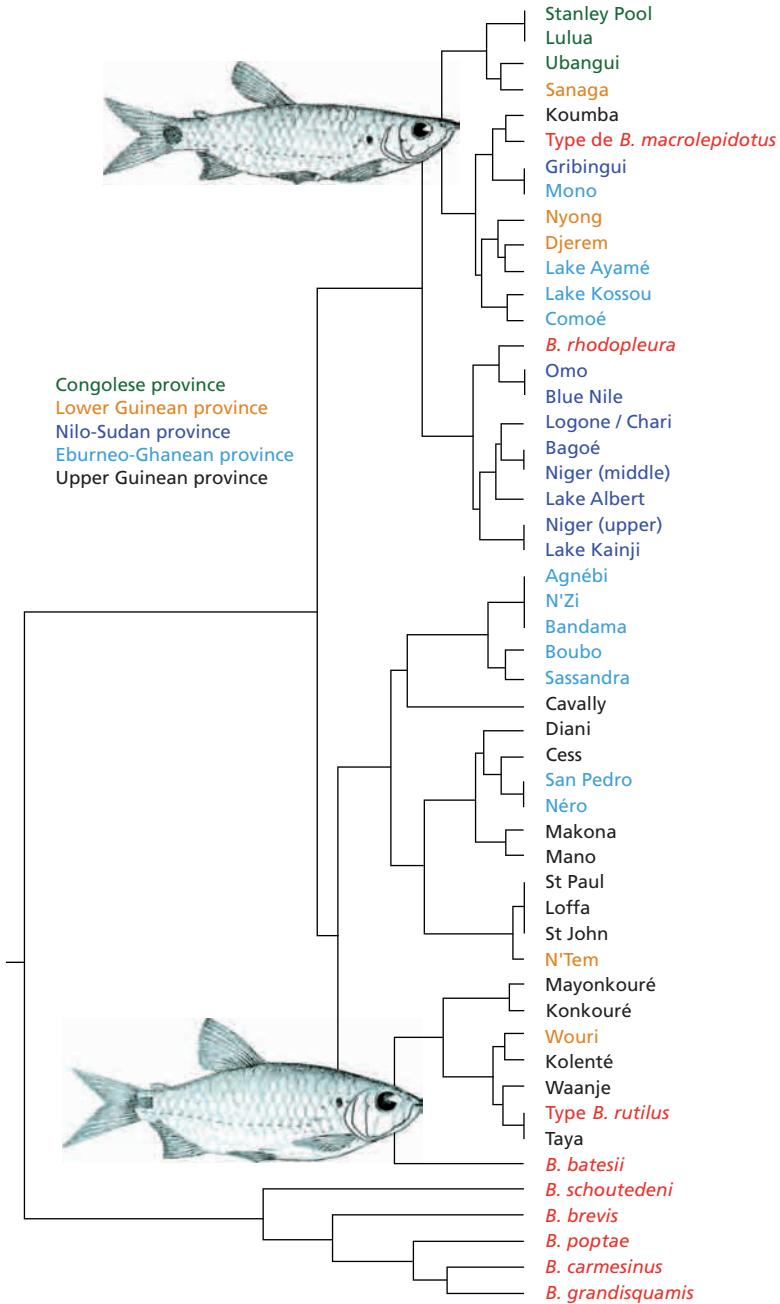


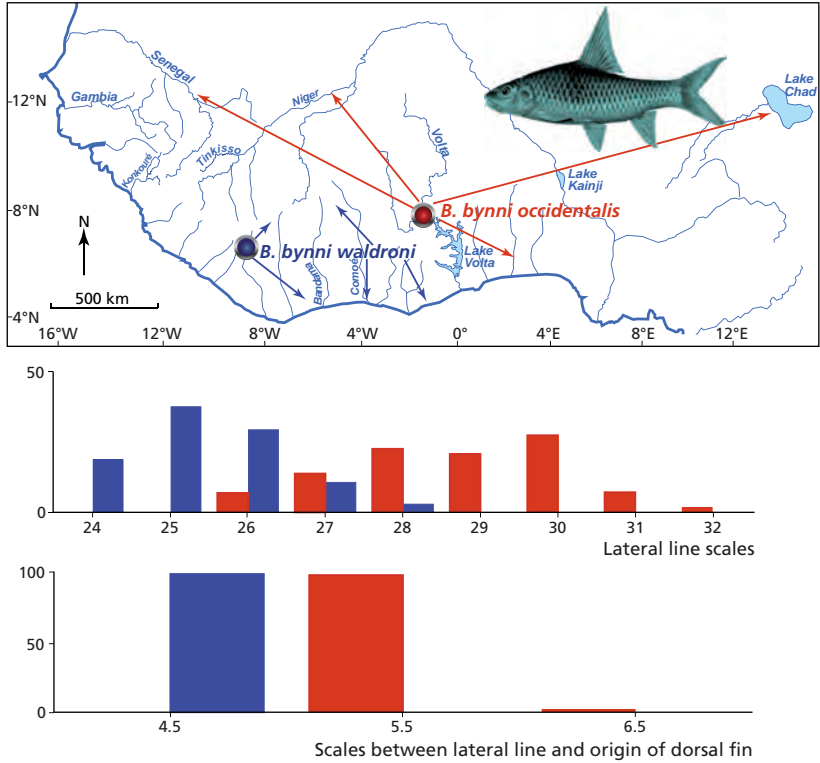
FIGURE 8.8.

*Brycinus macrolepidotus*: clinal changes in two morphological characters (average) across the whole distribution area of the species.

parasitology study showed that there was but one species whose meristic characters change according to a geographic cline. In West Africa, the two subspecies (respectively *B. b. occidentalis* and *B. b. waldroni*) are distinguishable through the number of scales (figure 8.9).

FIGURE 8.9.

*Barbus bynni*: clinal changes in two meristic characters (average).



### Question of hybrids

Natural or artificial hybridization is a way of testing the concept of biological species. Hybridization in the natural world has been observed, but it remains a rare phenomenon to the extent that there has been little systematic research in the matter and that hybrids are not always identifiable to an untrained eye. Daget (1963) was able to identify young specimens from the Benue as hybrids of *Citharidium ansorgii* and *Citharinus distichodoides*. In Lake Itasy in Madagascar, *Oreochromis macrochir* and *O. niloticus* that were introduced in the 1960s hybridized to produce a form called tilapia 3/4 which co-existed for many years with the parental species (Daget & Moreau, 1981). A similar phenomenon was observed in Lake Naivasha in Kenya between the introduced species *Oreochromis spilurus niger* and *O. leucostictus* (Elder *et al.*, 1971).

More recently, natural hybridization between *Coptodon zillii* and *Tilapia guineensis* was observed in the lake of the Ayamé dam (Côte d'Ivoire). These two species are usually parapatric, with *C. zillii* found exclusively in fresh water and *T. guineensis* in brackish water. It is probable that with the building of the dam in 1958, populations of the two species were trapped, forcing them to cohabit (Pouyaud, 1994). Another example of hybridization that involved three Cichlidae species (*Coptodon zillii*, *T. guineensis* and *T. dageti*) was also found in the Comoé River in Côte d'Ivoire and confirmed by protein analysis, as was the previous case (Pouyaud, 1994).

The last two cases are probably an illustration of what is called a hybrid zone, that is, a contact zone where parapatric populations may hybridize. It is likely that the phenomenon was underestimated up to now owing to limited technical means and a lack of interest.

Generally speaking, hybridizations in the natural environment among Cichlidae occur when environmental changes remove the barriers that ensure reproductive isolation between species, or when a species colonizes or is introduced to a physical system where similar species already exist.

Another example is the case of an Alestidae hybrid between *Alestes baremoze* and a *Brycinus* which was observed in Côte d'Ivoire with the closure of the Kossou storage lake. Finally, there is the case of a *Hydrocynus somonorum* species described in the Niger River by Daget (1954) which was then found to be a hybrid of *H. forskalii* and *H. brevis*. In all these cases, we see the rather elusive nature of the appearance of a hybrid form.

Artificial hybridization was much used by aquariologists studying Cyprinodontiformes in an attempt to identify the biological species among the numerous, sometimes highly similar forms, some of which possess different karyotypes (Scheel, 1968).

## Genetics and species concept

Given the difficulty of recognizing the existence of species using morphology alone, ichthyologists sought to use other data, notably from genetics (see box "Genetic differentiation of *Sarotherodon melanotheron* populations" in chapter *Diversity of African fish: heritage of evolution*).

### Number and shape of chromosomes

Each living cell contains several chromosome pairs. Each pair contains one chromosome from the mother's egg cell and another from the father's sperm. The number of chromosomes is constant in a given species, and  $2n$  ( $n$  being a set of chromosomes, either paternal or maternal) is used to define the number of chromosomes in somatic cells, which are diploid. Gametes or sex cells (eggs, sperm) contain only one set of chromosomes ( $n$ ) and are called haploid. After fertilization, the gametes fuse and yield diploid cells. In some cases when the number of chromosomes in a cell is higher than  $2n$ , such cells are called polyploid.

The number, shape, and size of chromosomes vary from one species to another. These characters can be useful for taxonomic or phylogenetic research, and are increasingly used given the advances in karyotype preparation techniques (Ozouf-Costaz & Foresti, 1992). In particular, we can expect significant progress to be made in chromosome marking techniques which would make them easier to identify.

The number of chromosomes for several African fish species has been determined (table 8.1). For many of them, this number ranges between  $2n = 48$  and  $2n = 52$ , but in some cases the number is different owing to diverse reasons:

- In some Cyprinidae species,  $2n$  can be as high as 148-150. In this case it is a hexaploid number resulting from a polyploid phenomenon that consists of a mutation that leads to an increase in the number of chromosomes within a population. This number may be double (tetraploid individuals), triple (hexaploid individuals), or any other multiple of the number of chromosomes usually observed. The recent discovery of large hexaploid *Barbus* in South, East, and West Africa suggests that the origin of Cyprinidae should be reconsidered.
- In the Siluriformes,  $2n$  is between 70 and 72 in species of the genera *Clarotes* and *Chrysichthys*. This higher number, compared for instance with the genera *Bagrus* and *Auchenoglanis*, could trace its origin to centromere fissions in some chromosomes (Agnèse, 1989).
- The highly variable karyotype of Cyprinodontiformes ( $2n$  between 9 and 24) appears to be unique among fish, if not in the animal world altogether. The mechanism behind the reduction in the number of chromosomes apparently results from the fusion of centromeres in some ancestral chromosomes (referred to as Robertsonian fusion).

### Genetic distances and morphological differences: two separate phenomena

Speciation and morphological evolution are two independent phenomena. In particular, there is not necessarily a correlation between the genetic distance between species and the morphological divergence observed. Thus, Cichlidae in the Great Lakes that evolved rapidly through adaptive radiation are close from a genetic perspective, even though many of the species are well-differentiated morphologically (figure 8.10). For ten *Haplochromis* species in Lake Victoria, for instance, there is little divergence in terms of protein analysis but the same species show significant anatomical divergence (Sage *et al.*, 1984).

**FIGURE 8.10.**  
Genetics as marker  
of phylogeny:  
example of Cichlidae  
(from Meyer, 1993).

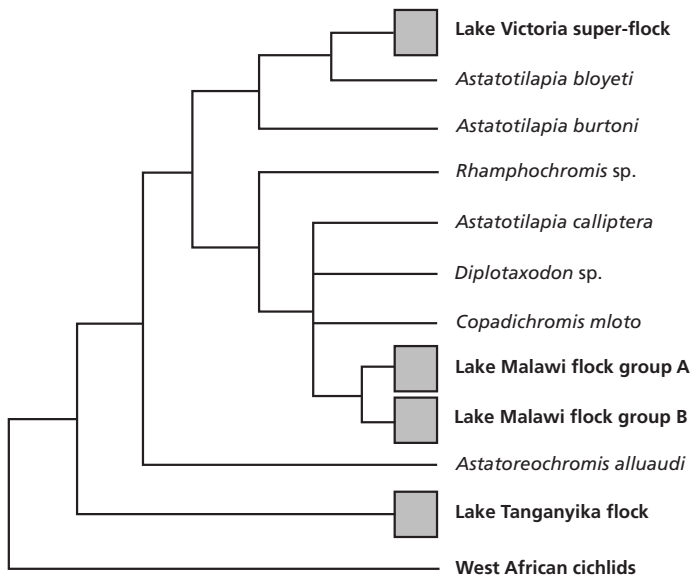


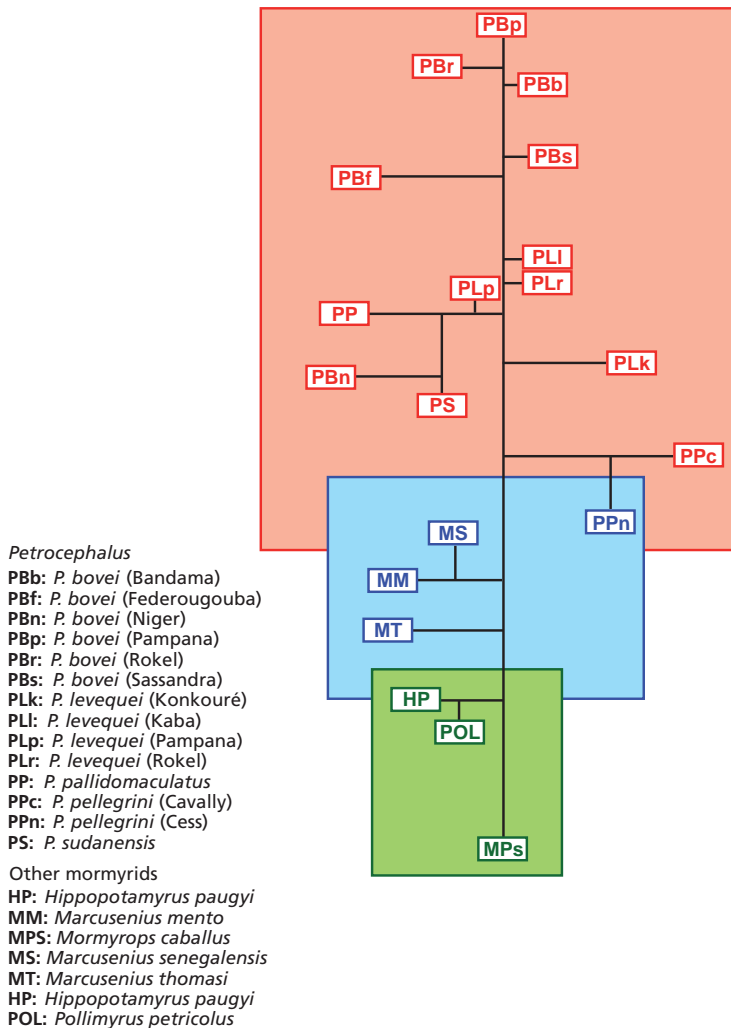
TABLE 8.1

Number of chromosomes for different African species (2n: diploid number of chromosomes).

Families / species	2n	Authors	Families / species	2n	Authors
<b>Protopteridae</b>			<b>Cyprinodontiformes (cont.)</b>		
<i>Protopterus annectens</i>	34	Wickbom, 1945	<i>Aphyosemion christyi</i>	18	Scheel, 1968
<b>Polypteridae</b>			<i>Aphyosemion exiguum</i>	36	Scheel, 1968
<i>Eripetoichthys calabaricus</i>	36	Denton & Howell, 1973	<i>Aphyosemion filamentosum</i>	36	Scheel, 1968
<i>Polypterus palmas</i>	36	Denton & Howell, 1973	<i>Aphyosemion franzwerneri</i>	22	Scheel, 1972
<i>Polypterus senegalensis</i>	36	Urishido <i>et al.</i> , 1977	<i>Aphyosemion gardneri</i>	40	Scheel, 1968
<b>Phractolaemidae</b>			<i>Aphyosemion guineense</i>	38	Scheel, 1968
<i>Phractolaemus ansorgii</i>	28	Vervoort, 1979	<i>Aphyosemion gularae</i>	32	Scheel, 1968
<b>Pantodontidae</b>			<i>Aphyosemion labarrei</i>	28	Scheel, 1972
<i>Pantodon buchholzi</i>	48	Uyeno, 1973	<i>Aphyosemion louessense</i>	20	Scheel, 1972
<b>Notopteridae</b>			<i>Aphyosemion luzajae</i>	40	Scheel, 1968
<i>Notpterus afer</i>	34	Uyeno, 1973	<i>Aphyosemion mirabile</i>	32	Scheel, 1972
<b>Cyprinidae</b>			<i>Aphyosemion obscurum</i>	34	Scheel, 1968
<i>Barbus bynni</i>	150	Golub. & Krys., 1993	<i>Aphyosemion rolffi</i>	42	Scheel, 1968
<i>Barbus bynni occidentalis</i>	148	Guégan <i>et al.</i> , 1995	<i>Aphyosemion scheeli</i>	40	Scheel, 1972
<i>Barbus capensis</i>	150	Oellerm. & Skelt., 1990	<i>Aphyosemion sjoestedti</i>	40	Scheel, 1968
<i>Barbus ethiopicus</i>	150	Golub. & Krys., 1993	<i>Aphyosemion walkeri</i>	36	Scheel, 1968
<i>Barbus intermedius</i>	150	Golub. & Krys., 1993	<i>Poropanchax luxophthalmus</i>	48	Scheel, 1972
<i>Barbus natalensis</i>	150	Oellerm. & Skelt., 1990	<i>Poropanchax normani</i>	48	Scheel, 1972
<i>Barbus petitjeani</i>	150	Guégan <i>et al.</i> , 1995	<i>Epiplatys annulatus</i>	50	Scheel, 1972
<i>Barbus wurtzi</i>	148	Guégan <i>et al.</i> , 1995	<i>Epiplatys barmoiensis</i>	34	Scheel, 1972
<i>Barbus ablakes</i>	48	Rab <i>et al.</i> , 1996	<i>Epiplatys bifasciatus</i>	40	Scheel, 1968
<i>Barbus anema</i>	50	Golub. & Krys., 1993	<i>Epiplatys chaperi</i>	50	Scheel, 1972
<i>Barbus bigornei</i>	50	Rab <i>et al.</i> , 1996	<i>Epiplatys dageti</i>	50	Scheel, 1968
<i>Barbus holotaenia</i>	50	Rab, 1981	<i>Epiplatys duboisi</i>	48	Scheel, 1968
<i>Barbus macrops</i>	50	Rab <i>et al.</i> , 1996	<i>Epiplatys fasciolatus</i>	38	Scheel, 1968
<i>Garra dembeensis</i>	50	Krys. & Golub., 1993	<i>Epiplatys sexfasciatus</i>	48	Scheel, 1968
<i>Garra quadrimaculata</i>	50	Krys. & Golub., 1993	<i>Epiplatys spilargyreus</i>	34	Scheel, 1968
<i>Labeo senegalensis</i>	50	Paugy <i>et al.</i> , 1990	<i>Nothobranchius guentheri</i>	35	Scheel, 1981;
<i>Labeo coubie</i>	50	Paugy <i>et al.</i> , 1990	<i>Nothobranchius guentheri</i>	36	Ewulonu <i>et al.</i> , 1985
<i>Labeo roseopunctatus</i>	50	Paugy <i>et al.</i> , 1990	<i>Nothobranchius kirki</i>	36	Scheel, 1972
<i>Raiamas steindachneri</i>	58	Rab <i>et al.</i> , 2000	<i>Nothobranchius melanospilus</i>	36	Ewulonu <i>et al.</i> , 1985
<b>Bagridae/Claroteidae</b>			<i>Nothobranchius palmquisti</i>	34	Scheel, 1968
<i>Auchenoglanis occidentalis</i>	56	Agnèse, 1989	<i>Nothobranchius palmquisti</i>	36	Ewulonu <i>et al.</i> , 1985
<i>Bagrus docmak</i>	54	Agnèse, 1989	<i>Nothobranchius patrizii</i>	36	Ewulonu <i>et al.</i> , 1985
<i>Chrysiichthys auratus</i>	72	Agnèse, 1989	<i>Nothobranchius rachovii</i>	18	Scheel, 1981
<i>Chrysiichthys maurus</i>	70	Agnèse, 1989	<i>Nothobranchius rachovii</i>	16	Ewulonu <i>et al.</i> , 1985
<i>Claroetes laticeps</i>	70	Agnèse, 1989	<b>Cichlidae</b>		
<b>Clariidae</b>			<i>Astatotilapia burtoni</i>	40	Thompson, 1981
<i>Clarias anguillariss</i>	56	Agnèse, 1989	<i>Aulonocara kornelia</i>	44	Foerster & Scharlt, 1987
<i>Clarias gariepinus</i>	56	Teugels <i>et al.</i> , 1992	<i>Aulonocara huesheri</i>	44	Foerster & Scharlt, 1987
<i>Heterobranchius longifilis</i>	52	Teugels <i>et al.</i> , 1992	<i>Aulonocara stuartgranti</i>	44	Foerster & Scharlt, 1987
hybrid <i>C. gariepinus</i> x <i>H. longifilis</i>	54	Teugels <i>et al.</i> , 1992	<i>Hemichromis bimaculatus</i>	44	Zahner, 1977
<b>Mochokidae</b>			<i>Heterotilapia multispinosa</i>	48	Zahner, 1977
<i>Synodontis bastiani</i>	54	Agnèse <i>et al.</i> , 1990	<i>Melanochromis auratus</i>	46	Thompson, 1981
<i>Synodontis budgetti</i>	54	Agnèse <i>et al.</i> , 1990	<i>Alcolapia alcalica</i>	48	Park, 1974
<i>Synodontis courteti</i>	54	Agnèse <i>et al.</i> , 1990	<i>Oreochromis aureus</i>	44	Kornfield <i>et al.</i> , 1979
<i>Synodontis filamentosus</i>	56	Agnèse <i>et al.</i> , 1990	<i>Oreochromis karongae</i>	38	Harvey <i>et al.</i> , 2002
<i>Synodontis membranaceus</i>	54	Agnèse <i>et al.</i> , 1990	<i>Oreochromis macrochir</i>	44	Jalabert <i>et al.</i> , 1971
<i>Synodontis ocellifer</i>	54	Agnèse <i>et al.</i> , 1990	<i>Oreochromis mossambicus</i>	44	Fukoka & Muram., 1975
<i>Synodontis schall</i>	54	Agnèse <i>et al.</i> , 1990	<i>Oreochromis niloticus</i>	44	Jalabert <i>et al.</i> , 1971
<i>Synodontis sores</i>	54	Agnèse <i>et al.</i> , 1990	<i>Sarotherodon galilaeus</i>	44	Kornfield <i>et al.</i> , 1979
<i>Synodontis violaceus</i>	54	Agnèse <i>et al.</i> , 1990	<i>Tilapia guineensis</i>	44	Vervoort, 1980
<b>Cyprinodontiformes</b>			<i>Oreochromis macrochir</i>	44	Vervoort, 1980
<i>Aphyosemion ahli</i>	36	Scheel, 1968	<i>Tilapia mariae</i>	40	Vervoort, 1980
<i>Aphyosemion arnoldi</i>	38	Scheel, 1968	<i>Coptodon rendalli</i>	44	Michele & Takah., 1977
<i>Aphyosemion bivittatum</i>	40	Scheel, 1968	<i>Tilapia sparnanni</i>	42	Vervoort, 1980
<i>Aphyosemion, bualanum</i>	40	Scheel, 1968	<i>Coptodon zillii</i>	44	Kornfield <i>et al.</i> , 1979
<i>Aphyosemion calliurum</i>	26	Scheel, 1972	<b>Channidae</b>		
<i>Aphyosemion cameronsense</i>	34	Scheel, 1972	<i>Parachanna obscura</i>	34	Nayyar, 1966

Meanwhile, significant genetic differences have been observed for populations of the genus *Tropheus*, a group of Cichlidae in Lake Tanganyika that dates back around 1.25 million years, whereas these populations are only distinguishable through minor morphological variations and some marked differences in colouring. In Mormyridae, genetic distances measured using enzymatic polymorphism are greater between *Petrocephalus* populations from different West African basins than between the genera *Mormyrops*, *Pollimyrus* and *Marcusenius* which are very well-differentiated morphologically (Agnès & Bigorne, 1992) (figure 8.11). This result shows that there is no correlation between genetic distance and morphological similarity in fish.

**FIGURE 8.11.**  
Phylogenetic network of some West African mormyrids (from Agnès & Bigorne, 1992).



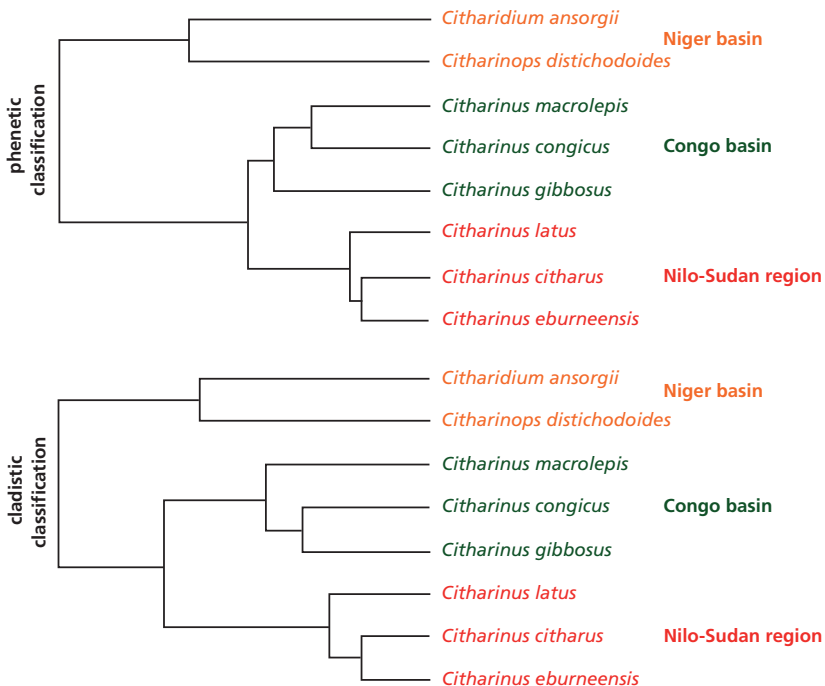
Some Cyprinodontiformes species are also similar in appearance while having very different karyotypes.



## The rules of classification

Classification of the living world is hierarchical, with groups included in larger sets that do not overlap. But this hierarchy can be based on different principles. Phenetic hierarchy is based on the similarity of appearance of the classified groups: number and position of fins, presence or absence of barbels, number of fin rays, etc. Phylogenetic hierarchy, meanwhile, is based on evolutionary relationship: groups are defined according to the closeness of their relationships and the age of their common ancestors. These two classification systems, which gave rise to different schools of thought, can provide concordant results but may also differ in their conclusions. The numerical taxonomy school fosters phenetic classification, whereas phylogenetic classification is supported by the so-called cladistic school.

Supporters of numerical taxonomy believe that organisms sharing common characteristics have a similar evolutionary history, but do not make hypotheses on genealogy. By using a large number of characters in a large number of individuals, and assigning them equal weights, statistical methods are expected to identify homogeneous sets. However, morphological convergences during evolution occasionally led to artificial groupings, and the biases that could be generated by statistical methods were also criticized (Ridley, 1989). This school peaked in the 1960s but lost much of its relevance since. An example of its application in African fishes was proposed by Daget (1966); he was able to establish a phenogram of Citharinidae (figure 8.12) that confirmed the empirical classification used up to that time.



**FIGURE 8.12.**

Phenetic and cladistic classifications of the citharinids (from Daget, 1966 and 1980).

Cladistic classification (sometimes called Hennigian classification) is based on the principle that during evolution, an ancestral species gave rise to two daughter species. For each species, it is therefore necessary to determine with which other species it shares the most recent common ancestor, because this will form the basis for the first group. A monophyletic group is derived from a single common ancestor, whereas a polyphyletic group includes species that have similarities but are not direct descendants of a common ancestor.

Unlike phenetic relationships, phylogenetic relationships cannot be observed directly. How, then, can they be identified? The method proposed by Hennig (1950) consists of looking for characters that can be qualified as evolutionary innovations. We can thus distinguish evolved or apomorph characters in opposition to ancestral characters, referred to as primitive or plesiomorph. This method, which often used comparisons with distant groups to determine if characters were evolved or primitive, also shows a bias – it considers that evolution always proceeds from a plesiomorph state to an apomorph state, and never the reverse (Daget, 1980).

This method was also applied to the Citharinidae (Daget, 1980). We see (figure 8.12) that it would be possible to include the species *C. distichodoides* and *C. ansorgii* in the genus *Citharidium*, a sister group of the genus *Citharinus* comprising six species. A conservation measure would be to consider that the species *C. distichodoides* is perhaps not the sister species of *C. ansorgii*, and create a genus *Citharinops*. We would then have two monotypic genera which are also sister groups, and this set would be a sister group of the genus *Citharinus*. The phylogenetic proximity between *Citharidium* and *Citharinops* does not contradict the possibility of hybridization of these two species in a natural physical system as signalled by Daget (1963). Among the *Citharinus*, the group of three Nilotic species is a sister group of three other Congolese species. Phenetic and cladistic classifications lead to similar conclusions on the systematic level, which means that in the present case, the morphological similarity reflects the phylogenetic relationship. The only difference with regard to the phenetic analysis is that *C. congicus* is closer to *C. gibbosus* than to *C. macrolepis*.

Using 15 anatomical and morphological characters, Daget & Desoutter (1983) also proposed a phylogenetic classification of Polypteridae from a common ancestor. The group *Polypterus bichir-endlicheri* probably diverged very early on, whereas the monospecific genus *Calamoichthys*, with a distinct morphology compared to the others, is curiously classified with the other *Polypterus*, which could indicate that it is of recent origin (figure 8.13).

Using her own work as well as results obtained by other ichthyologists, Stiassny (1991) proposed a cladogram summarizing the current state of knowledge on phylogenetic relationships within the Cichlidae family. In Africa and South America, this family forms two sister groups. There are nonetheless indications that the genus *Tylochromis* could be the sister group of other African Cichlidae, whereas the Congolese genus *Heterochromis*, phylogenetically different from the other African species, could be a sister group of Asian Cichlidae (Etroplines). Malagasy Cichlidae (Ptychochromines) form the sister group of all other Cichlidae (figure 8.14).

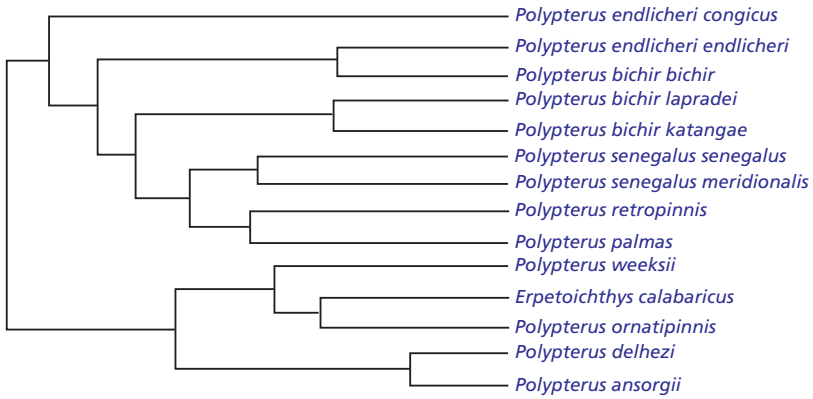


FIGURE 8.13.

Cladogram illustrating the phylogenetic relationships between the African Polypteridae (from Daget & Desoutter, 1983).

For many scientists, phylogenetic classification is currently preferred to phenetic classification, even if methods are not quite perfected. While anatomical studies have revealed both their relevance and their limitations, molecular tools currently in development are hoped to yield spectacular technical progress in coming years, thereby allowing a better understanding of the relationships between species.

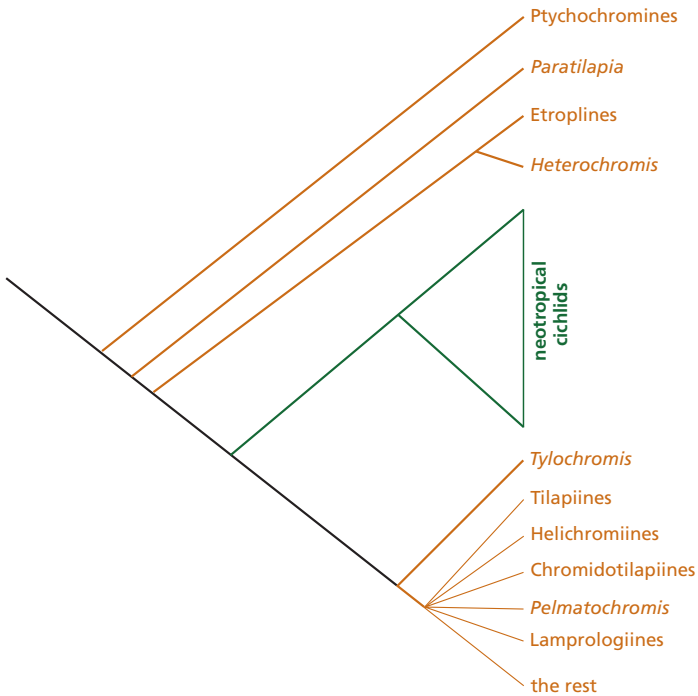


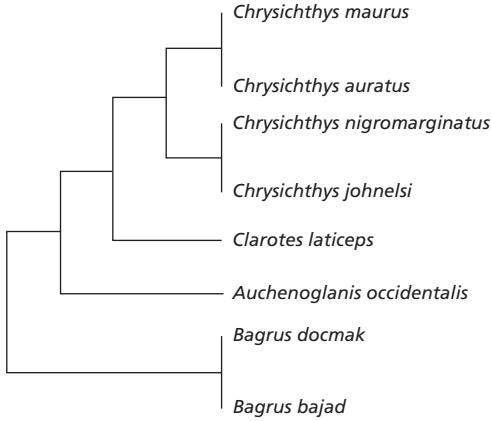
FIGURE 8.14.

Summary cladogram of cichlid intrafamily relationships (from Stiassny, 1991).

Thus, based on enzymatic polymorphism and chromosome studies, a phylogeny of West African Bagridae was proposed by Agnèse (1989) (figure 8.15). For the eight species investigated, two sister groups can be distinguished: on one hand *Bagrus* and perhaps *Auchenoglanis* which possess 54 and 56 chromosomes, and *Chrysichthys-Clarotes* on the other hand with 70-72 chromosomes. Within

**FIGURE 8.15.**

Phylogenetic relationships among West African Bagridae and Claroteidae (from Agnèse, 1989).



*Chrysichthys* we can also observe two sister groups, the sub-genera *Chrysichthys* (*C. maurus*, *C. auratus*) and *Melanodactylus* (*C. nigrodigitatus* and *C. johnelsi*) as Risch (1986) proposed on the basis of anatomical and morphological studies. *Clarotes* is a sister group of the *Chrysichthys* and they were both separated, along with *Auchenoglanis*, in the Claroteidae family by Mo (1991).

The use of genetic markers such as mitochondrial DNA, which are more precise than protein markers, is also becoming more widespread. Kornfield (1991) managed to propose a phylogenetic classification of *Oreochromis niloticus* subspecies in East Africa, and the phylogeny of Tanganyika Cichlidae of the genus *Tropheus* was established by Sturmbauer & Meyer (1992). For other groups, phylogeny was determined thanks to molecular biology techniques. This is the case for the Mormyridae whose familial phylogeny was defined (Lavoué, 2001), and for the Alestidae, for which group monophyly was underscored, confirming the clearly individualized status of this strictly African family (Calcagnotto *et al.*, 2005; Hubert *et al.*, 2005a and 2005b). In the same way, some families with an indeterminate status could be grouped together afterwards. For instance, within the Gonorynchiformes, the monophyly of the Cromeriidae, Grasseichthyidae, and Kneriidae has been proven (Lavoué *et al.*, 2005).

A fairly recent study on the phylogeny of the Protopteriformes highlights the monophyly of the African forms of the genus *Protopterus* (Tokita *et al.*, 2005). Within this genus, three clades are identified: *P. amphibius* (Eastern province), *P. dolloi* (Congolese and Lower Guinea provinces) and *P. aethiopicus/P. annectens* (*P. aethiopicus*: lakes Victoria, Edouard, Tanganyika and Albert; *P. annectens*: Nilo-Sudanian province). However, the differentiation of each of these three units does not enjoy strong support.

It has long been thought that the divergence of the three Protopteriforme genera followed the fragmentation of Gondwana (see chapter *General characteristics of ichthyological fauna*). *Protopterus* and *Lepidosiren* (Amazon) have always been considered sister groups, and analysis of all the species in this study confirms it. The authors' hypothesis on the closeness of relationships among the species is based on the more or less sustained presence of a neotenic character, the external gills. According to them, this character is not generated during the ontogeny of *Neoceratodus* (Australia), disappears rapidly in the juveniles of *P. dolloi* and *P. aethiopicus*, but can persist longer in *P. annectens* and even remain in the adult *P. amphibius*.

### THE CLARIIDAE: AN EXAMPLE WHERE MORPHOLOGICAL DIFFERENTIATION DOES NOT NECESSARILY REFLECT EVOLUTIONARY HISTORY

JEAN-FRANÇOIS AGNÈSE

The genus *Clarias* Scopoli 1777 is an interesting example of a fairly well-defined group in terms of appearance based on a set of morphological criteria, whereas they actually represent a discontinuous evolutionary unit. Günther (1864) defined the genus *Clarias* based on about ten characters including the shape of the gill accessory organ, the presence of a spine in the pectoral fin, and the absence of an adipose fin.

Although Teugels (1986) had recognized six sub-genera within *Clarias*, this genus appeared to be composed of a set of closely-related species from an evolutionary viewpoint.

Recently, a number of phylogenetic reconstitutions carried out using mitochondrial markers clearly showed that the genus *Clarias* was in fact extremely paraphyletic (Agnèse & Teugels, 2000, 2001, 2005) (figure 8.16). Some species that are currently classified in other genera of the Clariidae family (because they are highly differentiated morphologically), are in fact very closely related

genetically to species of the genus *Clarias*. Among the Clariidae, it thus seems that there is no link between morphological differentiation and genetic differentiation.

As a result, morphological criteria are inadequate for classifying species in one genus or another, and a revision of the family that takes genetic affinities into account is now needed.

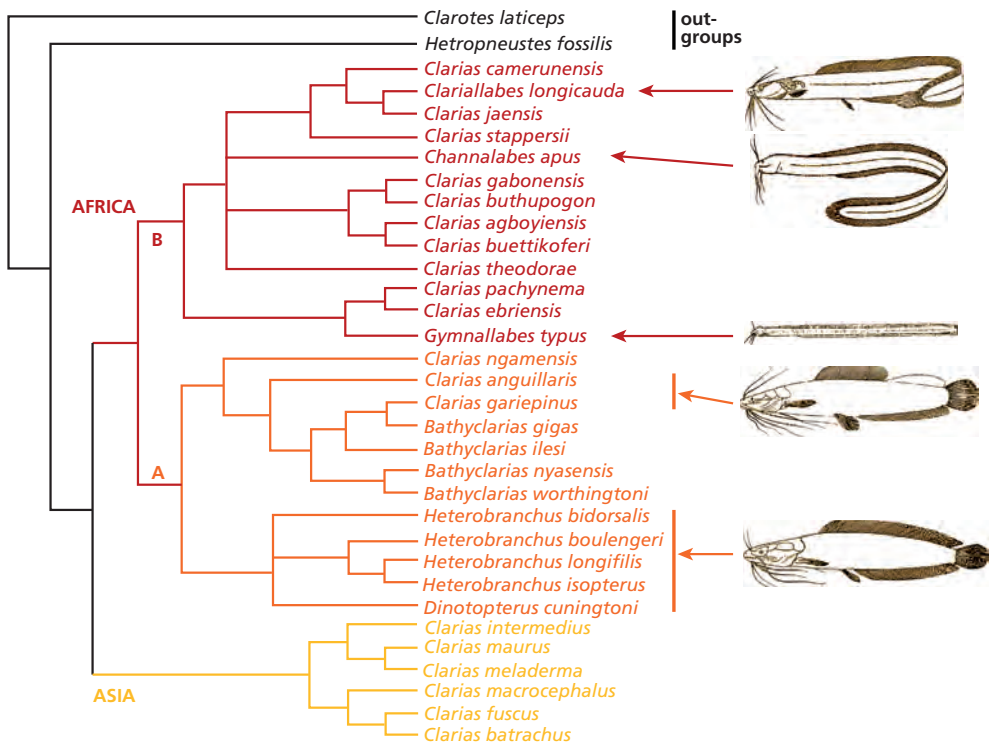
**FIGURE 8.16.**

Phylogenetic relationships among Clariidae species.

Morphological and osteological evolution (in this example “anguilliform body”) in Clariidae did not follow an orthogenetic series (from Agnèse & Teugels, 2005).

Group A represent the “big head and numerous fins” species, eel-like species are only found in group B.

Sketches with particular body shapes are represented on the right side, arrows indicated their position in the tree.



Moreover, genetic differentiation is not necessarily linked to morphological differentiation, as seen in the Clariidae (Agnèse & Teugels, 2005). In this case, it was shown that the 'anguilliform' criterion of some species was a character independent of the phyletic groups to which they belong. It clearly seems to be an adaptive response that appeared independently in several groups (see box "The Clariidae: an example where morphological differentiation does not necessarily reflect evolutionary history").

## The genus concept

While the notion of the species concept is relatively clear, despite some difficulties related to the concept's implementation, how about higher taxonomic levels? Are they conventional sets, or can they be defined on a similar basis as that used to distinguish species?

According to the principles of taxonomy, each species must belong to a genus, which is a category comprising at least one species or according to the principles of phylogenetic classification, a monophyletic group of species. Obviously, the principle of interbreeding cannot be used to define higher taxonomic levels.

On the other hand, we can distinguish morphologic sets, with the attendant uncertainties (bias resulting from convergences, for instance) regarding their affiliation to the same evolutionary line.

The improvement of ideas about classification and the lack of standardization in defining taxa higher than species gave rise to a certain anarchy, and led to many nomenclature changes as a result of advances in knowledge of phylogenetic relationships. It was suggested (Dubois, 1988) that the genus should constitute a discontinuous evolutionary unit that could be defined through a set of genetic, phylogenetic, and ecological characters.

An interesting example is that of the genus *Tilapia sensu lato* that Trewavas (1983) split into three genera based on their reproductive behaviour:

- *Tilapia sensu stricto* which lays eggs on substrate;
- *Sarotherodon*, which includes paternal and biparental mouth breeders;
- *Oreochromis* which includes only maternal mouth breeders.

This classification, based on behavioural aspects, sets itself apart from the conventional approach based on morphology and anatomy. It aroused many reactions, and Thys van den Audenaerde (see Teugels & Thys van den Audenaerde, 1992) long argued that it was preferable to not split the genus *Tilapia* according to these criteria. This debate attracted the interest of molecular biologists, and results of genetic studies showed on the whole that Trewavas' division was quite right from the phylogenetic viewpoint, with a few exceptions for species such as *Sarotherodon galilaeus* that is close to *Oreochromis* (Sodsuk & McAndrew, 1991; Pouyaud & Agnèse, 1995) and *S. melanotheron*, the sole paternal incubator among the *Tilapia* (Seyoum, 1990; Pouyaud, 1994) and whose position is indeterminate.

## Higher classification of African fishes

In this chapter, the classification schema above genus level is limited to the ranks of class, order and family. This has the advantage of simplicity, but ignores some important groups in fish phylogeny such as Chondrichthyes, Teleostei, Acanthomorpha, and Percomorpha.

In general, it follows Nelson's "Fishes of the World" (2006) with the notable exception of Elasmobranchii and Holocephali being elevated to class rank. But at family level, we may follow Eschmeyer's "Catalog of Fishes", as it is updated more frequently to integrate new stable groupings.

Wiley & Johnson published a new classification for Teleostei (2010). They proposed the stabilization of several recent or (much) older published hypotheses by listing known evidence (synapomorphies). We will follow this new arrangement as soon as the ichthyological community endorses it, e.g., through publication in a subsequent edition of Fishes of the World. In the meantime, to avoid confusion for non-specialists, we shall continue to use the current one.

We adopted the rules followed by FishBase, as it is currently the better updated database.

Note that the numbers of species given below do not take subspecies into account.

For the world as a whole, total count of genera is 5,056 and total count of species is 33,148

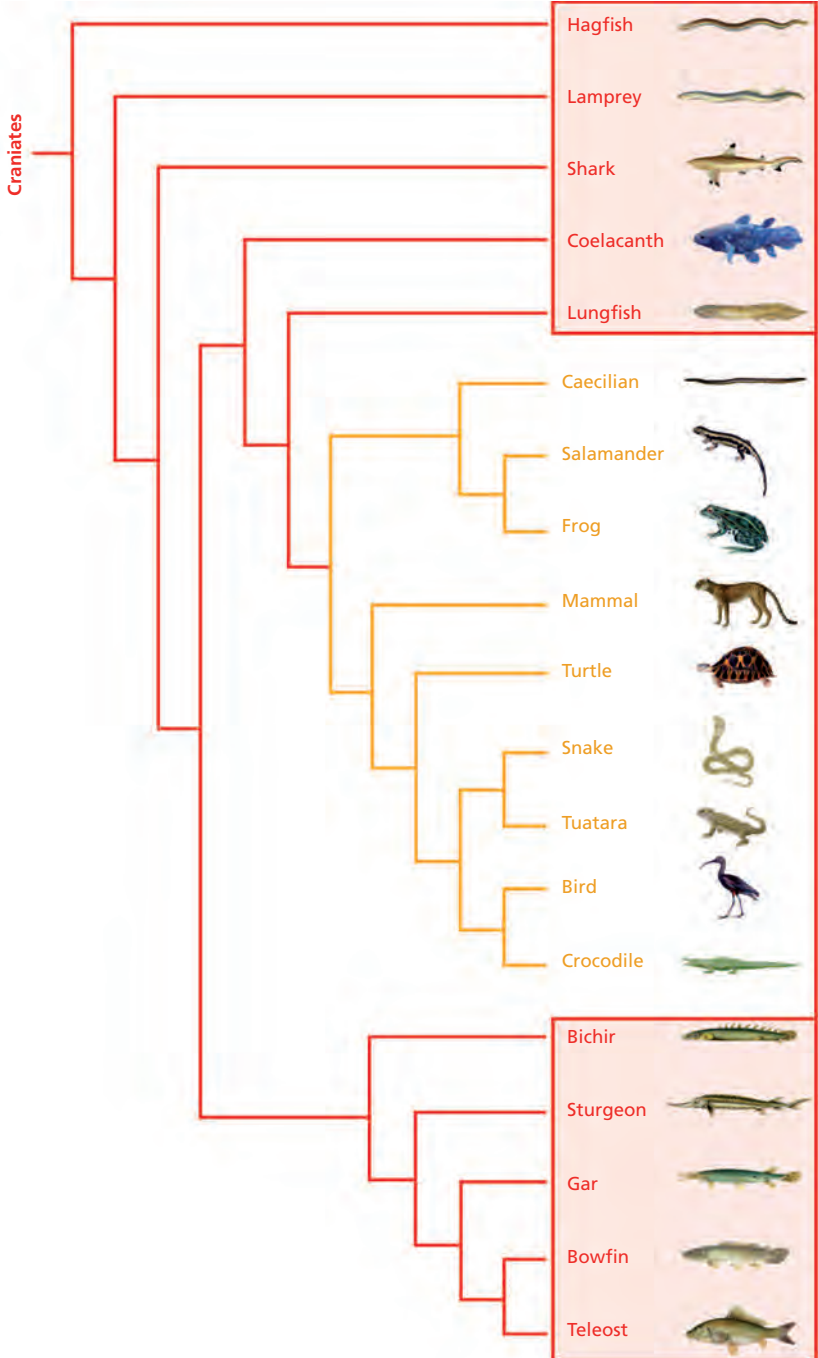
The origin and evolution of species could be reconstituted through the study of fossils. Like all palaeontological investigations, conclusions from such studies can be called into question upon the discovery of new deposits and new fossils. Current hypotheses must thus be viewed as conclusions based on the current state of knowledge rather than statements of fact.

We have also seen that for existing fishes, systematics has far from resolved all issues, and the introduction of new molecular techniques in phylogenetic classifications will probably lead to changes in these classifications, most of which were established using anatomical and morphological criteria. Moreover, ichthyologists are not always in agreement regarding the proposed novel phylogenies, which complicate the situation. There is nevertheless a sort of consensus for the broad lines of the fish classification that we present here.

The oldest known fish remains date to the Cambrian (over 500 million years ago). A form of lamprey, *Hardistiella montanensis*, from the Upper Carboniferous was found in Montana, USA (-325 M.A.), but a fossil that may have been related to lampreys, *Haikouichthys ercaicunensis*, was found in Lower Cambrian layers in Yunan, China (-530 M.A.) (Lecointre & Leguyader, 2001). Jawless fishes (Agnatha, still represented today by lampreys) and Placodermi initially dominated but gave way to bony and cartilaginous fishes in the late Devonian and Carboniferous (-400 to -350 million years) eras, during which they diversified greatly in seas and freshwaters. New groups, the holostei, then radiated during the Triassic (-250 to -210 million years) and Jurassic (-210 to -150 million

years), followed by teleosts during the Jurassic and Cretaceous. The radiation of teleosts is behind most of the marine and freshwater species that we know today.

**FIGURE 8.17.**  
Cladogram representing the phylogeny of the major living group of current craniata (from Lecointre & Le Guyader, 2001).





We shall only mention the Myxini (hagfish: 1 family, 6 genera, 78 species) and the Cephalaspidomorphi (lampreys: 3 families, 10 genera, 47 species), two jawless Craniata that do not exist in the inter-tropical zone. Forms likely to be encountered in Africa belong to the Gnathostomata, that is, jawed vertebrates.

The **Elasmobranchii** contain the craniata with cartilaginous skeletons, commonly known as rays or sharks. From a phylogenetic viewpoint, these “fishes” are very distant from the bony fishes (see box “Systematic ichthyology”; figure 8.17).

The **Osteichthyes** include other vertebrates including bony fishes that are unevenly distributed in two groups: the Sarcopterygii (lungfish and coelacanth, but also mammals, birds, squamata, etc.) and the Actinopterygii (or ray-finned fishes).

### LIVING FOSSILS

**G**roups of archaic fish can still be found on the African continent. The best-known of these is certainly the **coelacanth** which, in the sixties, was the star of a media frenzy. We shall not devote much space to this species, which remains oceanic and therefore distant from our continental concerns. It is worth noting that this very ancient group, which appeared in the Devonian (400-350 10<sup>6</sup> BP) and disappeared at the same time as the dinosaurs (around 70 10<sup>6</sup> BP), was once found throughout the planet and thought to have lived in fresh waters.

**Polypterus or bichir:** this group is endemic in Africa. The only known fossils were also found in Africa (135-65 10<sup>6</sup> BP) in the same area of distribution as modern species. These fishes have a swim bladder whose highly vascularized wall serves as a “lung” that allows the animal to survive in oxygen-poor waters.

Note as well that juveniles have external gills (see box “Polypterids”, chapter *Geographical distribution and affinities of African freshwater fishes*).

**Lungfishes** currently exist in the Amazon (*Lepidosiren*), Australia (*Neoceratodus*), and Africa (*Protopterus*).

African *Protopterus* can survive during dry periods by entering a state of aestivation.

To do so, *P. annectens* burrows a tunnel into the mud when the water level begins to go down but before the water dries out completely.

Once the water goes below the level of the tunnel opening, the animal blocks the entrance with mud then goes to the end of the tunnel, where it covers itself with a layer of integumentary mucus that hardens and forms a cocoon to keep itself moist. Thus protected, the lungfishes can live for up to four years in the cocoon, using their own muscle fibres as food.

Like their South American cousins, African lungfish larvae have external gills whose level of development depends on the water's oxygen content.

As the juveniles age, the external gills are generally resorbed and the fish breathe using their lungs and internal gills.

Among the **Sarcopterygii**, the **lungfishes** or **Dipnoi** are the oldest freshwater bony fishes, and their origins can be traced to the Devonian (Rosen *et al.*, 1981) (see box “Living fossils”). The swim bladder is connected to the oesophagus and can serve as a lung. They were represented by many forms in the primitive era, but only a few species survive, including those belonging to the genus *Protopterus* in Africa.

Recent studies have shown that the mitochondrial DNA of Protopteridae is closer to an amphibian's DNA than to a coelacanth's, which tends to support the hypothesis that terrestrial vertebrates could come from a split in a line that gave rise to lungfishes (Meyer & Wilson, 1990). Dipnoi would thus be the sister group of tetrapods (figure 8.17).

The Polypteridae are currently considered to be the earliest line of **Actinopterygii**. Their bodies are covered with bony scales. The swim bladder can serve as an accessory respiratory organ. Juveniles possess arborescent external gills that disappear in adults, and which are perhaps morphological characteristics of primitive Actinopterygii. In the past, this primitive character misled zoologists into classifying them away from Actinopterygii, and even placing them among Sarcopterygii.

In continental Africa, the Actinopterygii comprise the majority of other families and species grouped among the teleosts, whose most ancient known fossil, *Pholidophorus*, dates to the lower Triassic (-195 Myrs). This extremely diverse

### SYSTEMATIC ICHTHYOLOGY

The term "fishes" is not scientific and in any case refers to a grade, that is, a group without its own history. In fact, the relationship is not stronger between a teleost and a shark (figure 8.17) than between birds and bats, or even some flying or gliding reptiles or fishes. We could even note that they are in truth more distant. In concrete terms, "fishes" comprise a vast heterogeneous set traditionally defined as legless craniata.

This definition is fitting, if, like Nelson (1994) or more recently Lecointre & Le Guyader (2001), we agree that this current fauna includes:

- Myxini or hagfish (without vertebrae or jaws)
- Cephalaspidomorphi = lampreys (jawless)
- Elasmobranchii = cartilaginous fishes (sharks, rays)
- Actinopterygii = ray-finned fishes
- Sarcopterygii = vertebrates with fleshy members (coelacanth and lungfishes, closer to tetrapods than to the other "fishes")

Until around the 1960s, this "fishes superclass" was considered a valid taxon, owing to lack of recognition or use of phylogenetic criteria.

The shift from a purely utilitarian classification to a phylogenetic one only took place later, even though the Darwinian theory of evolution (Darwin, 1859) had already been long accepted. It appears that the situation only moved forward after the translation of Hennig's method (1966). Cladistics – which is what we are discussing now – has the advantage "(...)" of highlighting the feasibility – or refutability – of a theory of phylogenetic relationships" (Janvier, 1986).

Following the palaeontologists, palaeoichthyologists and ichthyologists rapidly began using cladistics and, in doing so, gained an advantage over other disciplines involving vertebrates.

The classification of "fishes", by becoming phylogenetic, was obviously going to be overthrown. As such, compared with previous classifications (Bertin & Arambourg, 1958) that still served as the reference until recently, things changed considerably, particularly under the initial impetus of Greenwood *et al.* (1966) which was a sort of pre-cladistics classification that was not informed by the works of Hennig. Even if the classifications can be debated, it is mentally easier to arrange taxa in categories that include groups or species that have the most similarities.

As such, the notions of species, genus, family, or even order are still generally accepted or tolerated by the cladistic school.

We have summarized data on current forms following the structure orders/families/genera/species in table 8.II which is necessarily incomplete, as not everything is known, and reflects only the specific interest focused on the different taxa.

Thus, we have cause to believe that the number of mammal and bird species is close to being accurate, which is certainly not the case for amphibians and fishes, for which the number of species is by all indications underestimated.

TABLE 8.II.

Number  
of Craniata known  
at the present time.

Craniata	Common name	Order	Families	Genus	Species
Hyperotreti	hagfishes	1	1	6	78
Claspidomorphi	lampreys	1	3	10	47
Elasmobranchii	sharks, rays	12	51	190	1164
Holocephali	chimera	1	3	6	50
Aves	birds	28	163	1 975	9 672
Crocodylomorpha	crocodiles	1	3	8	23
Squamata	lizards, snakes	1	31	821	6 850
Sphenodontida	tuatara	1	1	1	1
Testudines	turtles	1	13	75	290
Synapsida	mammals	20	133	1 041	4 496
Amphibia	frogs, newts	3	34	398	4 975
Dipnoi	lungfishes	2	3	3	6
Actinistia	coelacanth	1	1	1	1
Polypteriformes	bichirs	1	1	2	14
Acipenseriformes	sturgeons	1	2	6	27
Lepisosteiformes	gars	1	1	2	7
Amiiformes	bowfin	1	1	1	1
Teleostei	teleosts	42	482	4 829	31 752
<b>total</b>		<b>119</b>	<b>927</b>	<b>9 375</b>	<b>59 454</b>

group in fact represents the overwhelming majority of modern fishes. There are several major subdivisions, some of which are represented in continental Africa (Wiley & Johnson, 2010):

- **Osteoglossomorpha** (bony-tongued fishes) including the most primitive of modern teleosts. They have been known since the late Jurassic and are currently represented by five families in Africa (figure 8.18);
- **Elopomorpha** comprises different families and species that are almost exclusively marine, but which can occasionally penetrate into freshwater. Eels belong to this group;
- **Otomorpha** is composed of 4 large monophyletic groups:
  - **Clupeiformes**, which appeared in the lower Cretaceous. They include primarily marine species, but some have adapted to freshwater;
  - the order **Gonorynchiformes** which has 3 families in Africa, including the Kneriidae (which now covers the former Cromeriidae and Grasseichthyidae families) and two other families represented by a single species (Phractolemidae and Chanidae);
  - the order **Cypriniformes** whose origin is under debate;
  - the order **Characiformes** represented by numerous species. The origin of the Characiformes and the Cypriniformes could date back to the end of the Cretaceous or the Palaeocene (Cavender, 1991);
  - the order **Siluriformes** (catfishes) forms a highly characteristic group of fishes with scale-free bodies and bony spines in their dorsal and pectoral fins.

- the **Euteleosteomorpha** including the majority of species, in particular:
  - the **Osmeriformes** represented by a single family (Galaxiidae) in Africa;
  - the **Cyprinodontiformes** including numerous fresh and brackish water species.
  - the **Synbranchiformes** represented by two families: the Synbranchidae of marine origin, and the Mastacembelidae (spiny eels) that were formerly classified among the Perciformes (Travers, 1984).
  - the **Perciformes** which is poorly defined and whose classification is unclear and problematic, as it is probably not a monophyletic grouping. In total it includes 150 mostly marine families, some of which have adapted to continental waters. This is the case in particular for the Cichlidae, Latidae, Nandidae, and Anabantidae. The Cichlidae probably appeared very early in the Cretaceous and their evolution was already well on its way prior to the separation of Gondwana (Stiassny, 1987; 1991).
  - the **Pleuronectiformes** and the **Tetraodontiformes** including families of marine origin of which certain species have adapted to freshwater. The Tetraodontiformes and Pleuronectiformes appeared in the lower Eocene and mostly include marine forms.

## Advances in African freshwater ichthyology

Currently 3,360 species of fresh and brackish water fish have been described from Africa, belonging to 95 families (Lévêque *et al.*, 2008). Numerous other species collected in the East African lakes are awaiting description.

The knowledge of the ichthyological brackish and freshwater fauna in Africa is a very long story (Paugy, 2010a). From the time of the Ancient Egyptians to the present, more than 3,300 species (95 families and 542 genera) have been discovered, drawn and described. Michel Adanson (mid-18th century) initiated the first material collections during the eighteenth century. During the 19th century, the work of travelling scientists (Étienne Geoffroy Saint-Hilaire, Andrew Smith) and explorers (including Mungo Park, Pierre Savorgnan de Brazza and Henry Morton Stanley) added substantially to developing zoological collections from their field trips. At that time, many species descriptions were based on fish preserved in these collections. Towards the end of the 19th and into the early part of the 20th century, knowledge of African fishes was greatly enhanced, especially through the work of Georges A. Boulenger, Albert C.L.G. Günther and Franz Steindachner who, respectively, described 640, 119 and 53 species. Boulenger did visit Africa once during his life, in 1905 when he went to Cape Town for a conference. With this one exception, none of these scientists ever travelled to Africa themselves. In contrast to those of the previous century, the majority of naturalists of the 20th century who were interested in African fishes took part in collecting expeditions. The majority of the naturalists working in Africa during the middle and later parts of the 20th century tended to specialize in particular groups.

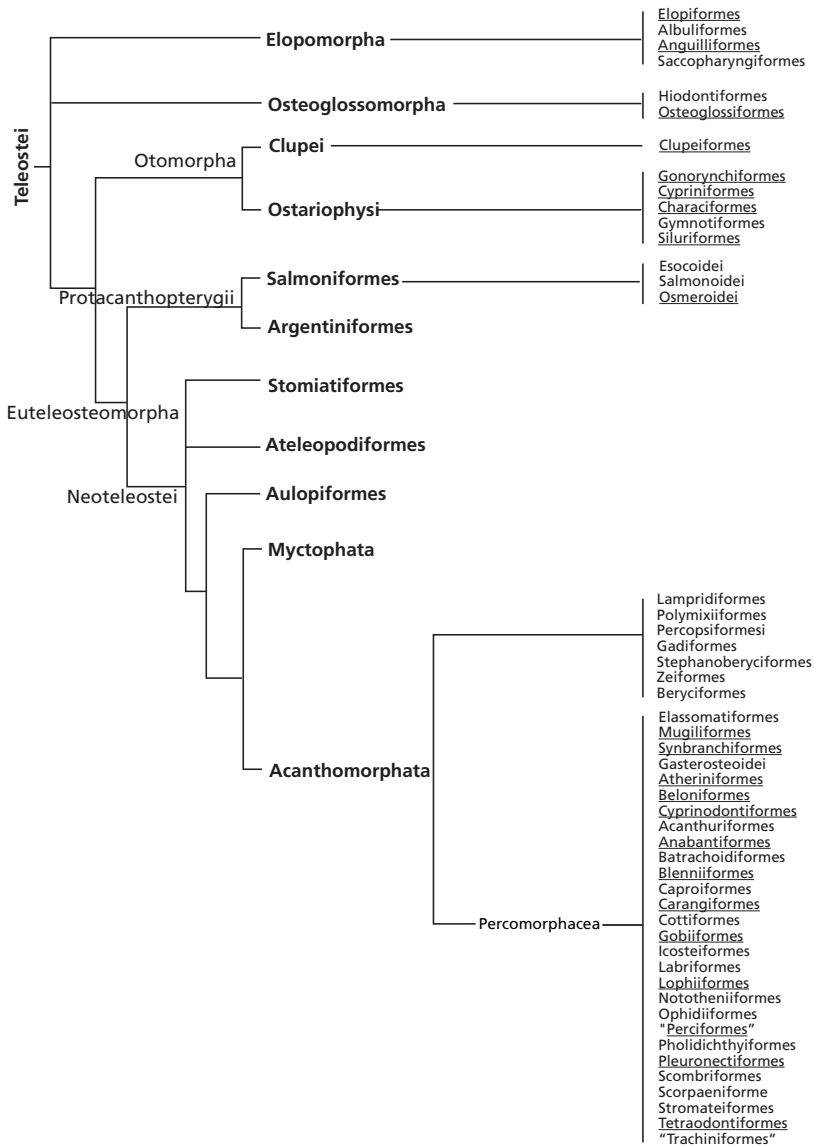
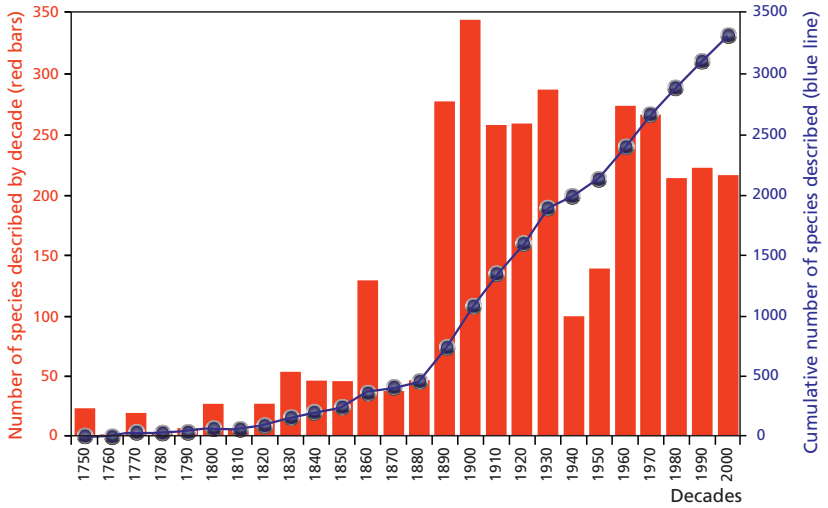


FIGURE 8.18.

Cladogram representing the phylogeny of the major living group of teleosts (adapted from Wiley & Johnson, 2010). In the right column, taxa existing in inland Africa (fresh and brackish waters) are underlined.

Thanks to these naturalists the number of known African freshwater fish species reached 1,900 before the Second World War, 2,150 at the end of the 1950s and finally more than 3,300 at present (figure 8.19). In addition to conventional systematic studies, there was a steady rise in the number of contributions dealing with genetics, specific parasites, and electrophysiology, amplifying fish identification using criteria other than morphology. These methods have proved helpful in finding explanations for the radiation of cichlids in the Rift Valley Lakes of East Africa. Blending all these methods, descriptions of hitherto unknown species continue to be published (see also chapter *General characteristics of ichthyological fauna*).

**FIGURE 8.19.**  
Number of African freshwater fish species currently described (updated from Paugy, 2010a).



Most of the African continent has remained above sea level since more than 600 Myrs ago (Precambrian). Such a long period of land emergence may explain the diversity of the freshwater fish fauna and its unparalleled assemblage of so-called archaic families of which most are endemic.

Scientific editors

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# The Inland Water Fishes of Africa

*Diversity, Ecology and Human Use*



**Africa**  
TERVÜREN

KONINKLIJK MUSEUM  
VOOR MIDDEN-AFRIKA  
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**SCIENTIFIC EDITORS:  
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