

# An historical review of African freshwater ichthyology

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## Abstract

The history of ichthyology in Africa is reviewed. From the time of the Ancient Egyptians to the present, more than 3200 species have been discovered, drawn and described. Michel Adanson initiated the first material collections during the 18th 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. The majority of the naturalists working in Africa during the middle and later parts of the 20th century tended to specialise in particular groups. In addition to conventional systematic studies, there was a steady rise in the numbers of contributions invoking 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, one of the most rapid and extensive involving vertebrates. Blending all these methods, descriptions of hitherto unknown species continue to be published. Whereas, until the mid-20th century, descriptions of new species and inventories of existing ones were the principal objectives of ichthyology, interests during the last 50 years have moved much more to the ecology of fish and to its application in aquaculture and aquariology: it is only during this period that most of the publications dealing with the biology and ecology of freshwater fishes and the science of fish culture have appeared. Brief biographies of the modern ichthyologists are presented, together with outlines of their main contributions.

Keywords: Africa; African fishes; biography; expeditions; freshwater; history; ichthyology.

## Introduction

The oldest African freshwater fish known is a mawsoniid coelacanth, discovered in southern Morocco, from the Cretaceous (certainly Cenomanian, i.e. 100 million years ago) Kem Kem beds (Cavin & Forey, 2004), but only a few bones of this fish still exist. Similarly, some bones from a late Cretaceous (Maastrichtian, i.e. 70 million years ago) galaxiid fish were discovered in a crater lake in the Karoo, South Africa (Anderson, 1998). While few freshwater fish remains are known from the Mesozoic, many from the Cenozoic have been described (see reviews by Murray (2000) and Stewart (2001)). Nevertheless, while some specimens are more or less complete, and very close to modern forms (Otero et al., 2006), none has been preserved by 'the hand of man' to build a possible inventory. Moreover, the first 'modern men' (more or less 10 000 BP) neither kept fish nor represented them in rock drawings. While fish-fences, fish-traps or fish-headed anthropomorphs were sometimes stylised (Huyge, 1994), fish themselves were never illustrated in the way that crocodiles or hippopotami were (F. Soleilhavoup, personal communication).

Ancient Egyptians were almost certainly the first to become interested in the fish of the Nile and, from the

earliest times, they were keen observers of nature. This is reflected in their precise descriptions of the many characteristics needed to identify Nile fish. It is also reflected in their observations of many biological features, such as reproduction, behaviour and diet. For example, they knew the peculiar habits of *Synodontis batensoda*, which swims upside-down, a characteristic depicted on several frescos (Brewer & Friedman, 1989). In the Late Period (26th dynasty of Egypt, ca. 685–525 BC), the association of some fish with certain gods or goddesses became general, as were those other animals that they venerated. For example, *Lates niloticus* symbolised the goddess Neith, queen of the sky's gods. Numerous specimens of *Lates* were mummified in her honour and offered as a token of worship, particularly at Esna (Fig. 1). Other species (*Barbus bynni* and *Mormyrus kannume* or *M. cashive*) were also mummified; this kind of preservation is the oldest token (and first examples) of preserved African freshwater fish that we have (Fig. 2A).

Near Saqqara (Fig. 1), there are three fishing scenes illustrated on the tombs of Ti, Méra and Akhethétep (dynasties V and VI, i.e. Old Kingdom) in which we can recognise nearly 35 different fish species. In all these scenes the fishing tackle (harpoon, hooks, traps and nets) and fish are accurately drawn and naturalists can compare most of these fish images, which are 4000 to 5000 years old, with the best of modern drawings of Nile fish (Fig. 2B).

In Ancient Egypt, fish were obviously used as food but they were also the object of many taboos. Fish appear early in Egyptian mythology. In some temples, the texts give lists of the nomes (provinces) and prohibitions, often in connection with local worship. Thus, for example, fish were forbidden in the nomes related to the worship of Osiris. In the same way, we know that for reasons of ritual purity, the priests were not allowed to consume fish. Lastly, some species were used in writings and from the Thinite time, six fish were represented in hieroglyphic writing (Fig. 2C).

Later, some Greek and Roman writers gave details concerning fishing and fish, which generally concerned marine fish and



Fig. 1. Map of Egypt: largest cities (yellow) and major sites (red) cited in the text.

fisheries. Among the best known, which synthesised such information, were Ovid (BC 43 to AD 17) and Pliny the Elder (AD 23 to 79). However, older details concerning African species are provided by Herodotus (BC 484 or 482 to 425), Strabo (BC 58 to AD 25), Claudius Aelianus (AD 175 to ca. 235) and, especially, Athenaeus (ca. AD 160 to ca. 230), the author of 'Deipnosophistae' (The Deipnosophists, or Banquet of the Learned, or Philosophers at Dinner), a kind of universal repertory of antiquity (Daget, 1994). Nevertheless, except for the Egyptian mummies, we

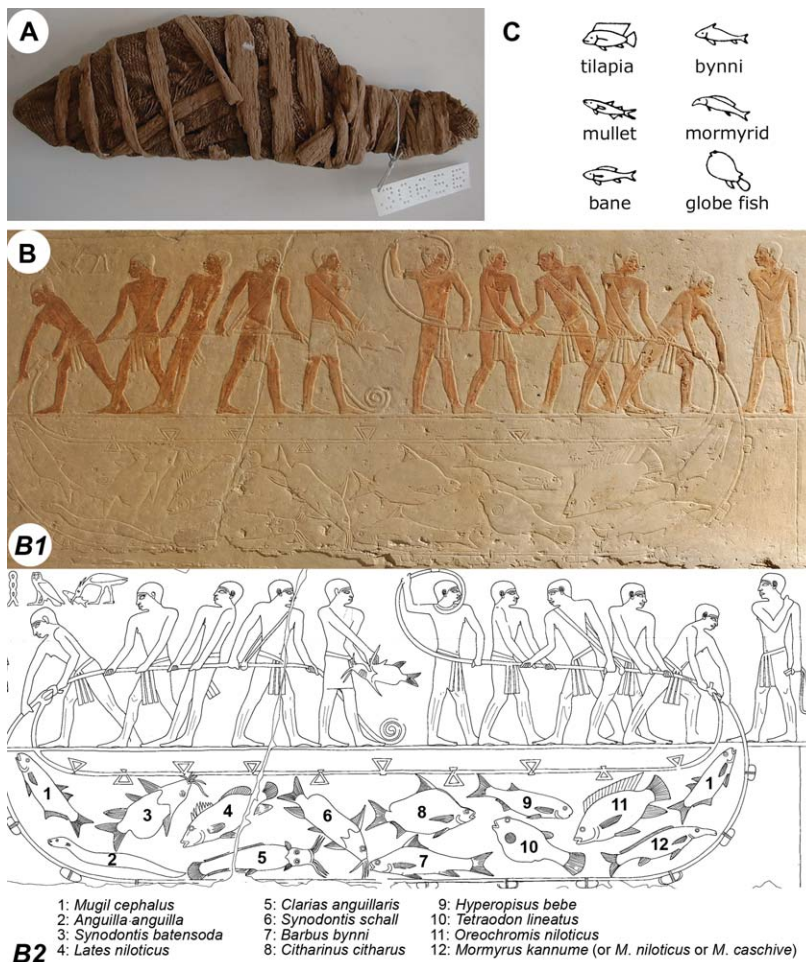
do not have any preserved collection from antiquity and French naturalist Michel Adanson is rightly regarded as the true founder of African ichthyology.

## The first real collection builders (the 18th century)

After the obscurantism of the Middle Ages, the first studies of 'modern ichthyology' appear to have been in the Renaissance period. The best-known naturalists of that era

are Guillaume Rondelet (1507–1566), Ippolito Salviani (1514–1572) and Pierre Belon (1517–1564). Mostly, they based their observations and descriptions on the marine species inhabiting European coasts. Developments in navigation and shipbuilding throughout the Renaissance also facilitated the initiation of a new epoch in ichthyology. The Renaissance culminated in the era of exploration and colonisation and, following the cosmopolitan interest in navigation, specialists in natural history emerged.

At the end of 1748, Michel Adanson (1727–1806) left France on an exploratory expedition to Senegal. He remained there for five years (until 1753), collecting and describing numerous animals and plants. He also collected specimens of objects of commerce, delineated maps of the country, made systematic meteorological and astronomical observations, and prepared grammars and dictionaries of the languages spoken on the banks of the Senegal River. Strictly speaking, he never published on fish but he gathered an important annotated collection



**Fig. 2.** A: Mummified *Lates niloticus* from the Nile (Egypt): the first example of preserved freshwater fish in the collection of the MNHN (Muséum National d'Histoire Naturelle de Paris) (N<sup>o</sup> B 3065).

B: Tomb at Akhethétep Mastaba, Saqqara, Egypt. (B1) Hauling in a seine net in swamps. (B2) Drawing of (B1) and identification of the fish outlined on the stone (© Musée du Louvre/Nathalie Couton-Perche). Each species is easily identifiable.

C: Hieroglyphic writing: some fishes most frequently represented in texts (from an unpublished document of the Musée de Lyon, France).



Fig. 3. *Polypterus bichir lapradei*: prepared as a herbarium specimen, Muséum national d'Histoire naturelle de Paris (No B.562).

of specimens prepared in his herbarium. His method (for details see Yarrell, 1836) was similar to that used for plant specimens: he would preserve dried half fishes, cleared of internal organs and mount them on paper (Fig. 3).

It seems that the Dutch naturalist Gronovius (real name: Jean Frederic Gronow, 1690–1760) was the originator of this means of curation (Gronovius, 1742). Many ichthyologists adopted this method, including Linnaeus, some of whose descriptions of African fish seem to have been based on such specimens. However, as Adanson did not publish on fish, it seems likely that these two scientists were never in contact. Nevertheless, Adanson left many well-documented manuscripts. Altogether, he collected 5211 specimens of all organisms, among which close to 60 species of fish were represented, 49 of which were preserved in the herbarium (Bertin, 1950). In addition to his African collections, Adanson also added other herbarium preparations of fish from various origins (Europe, Asia and America). Eventually, the entire collection of fish rose to 149 species, distributed in 86 genera and 12 families. The 86 genera are numbered from 1 to 150, which indicates that 64 of them could be missing, compared to the initial collection offered to the King (Louis XVI of France). In fact, it seems that Adanson had given only duplicates to the King and kept single specimens for himself. In keeping with this interpretation, Cuvier and Valenciennes cited 130 to 149 African fresh- and brackish-water species reported by Adanson in the 22 volumes of *Histoire naturelle des Poissons* (Cuvier & Valenciennes, 1828–1849).

Nevertheless, by the end of the 18th century, only 50 African freshwater fish species had been described,

even if more were known. Most of these were described by Karl von Linnaeus (1707–1778). Pehr Forsskål (1732–1763) and Marcus Elieser Bloch (1723–1799) either alone or in collaboration with Johann Gottlob Schneider (1750–1822), also published descriptions.

After the fish of Senegal, those of the Nile were studied before the end of the 18th century. In 1789, Johann Friedrich Gmelin (1748–1804) cited 17 species sampled or observed by Fredric Hasselquist (1722–1752) or P. Forsskål. But the outstanding contributor, both in terms of collection and examination, was without any doubt Étienne Geoffroy Saint-Hilaire.

## The rise of freshwater ichthyology in Africa: the 19th century

### Travelling scientists

In 1798, Étienne Geoffroy Saint-Hilaire (1772–1844) was chosen as a member of Bonaparte's great scientific expedition to Egypt, in which 150 scientists and artists participated. On the capitulation of Alexandria in August 1801, he took part in resisting the British General's claim to the collections of the expedition, declaring that if he persisted in his demand, history would have to record that he also had burnt a library in Alexandria. Early in January 1802, Saint-Hilaire returned to Paris with all his collections and writings.

During the expedition to Egypt, Saint-Hilaire collected both marine and freshwater fishes. Most were in alcohol

but a few were later stuffed (Table 1). He also brought back some mummies of *Lates niloticus*. This important collection is kept in the Muséum national d'Histoire naturelle de Paris (MNHN), in an excellent state of preservation.

Most of the fish collected by Geoffroy Saint-Hilaire, had already been described (mainly by Linnaeus, Forsskål and Rüppell). He described only six new species and the remaining material was later described by other authors (mainly Valenciennes). In the end, Saint-Hilaire's principal contribution was the considerable enrichment of the MNHN's collections, mostly with species from the Nile, and the description of more than 10 new freshwater species.

Some years later, Andrew Smith (1797–1872), a British military doctor, became the first to provide a substantial set of descriptions of freshwater fishes from southern Africa. The expedition to the interior (Transvaal) in 1834–1836 was a high point (Skelton, 1996; Gon & Skelton, 1997), during which time several fishes were collected and, later, illustrated and described (Smith, 1838–1849). Smith is regarded as the first museum scientist in South Africa and his collection was the first research collection to be lodged in a South African museum. According to V. Fitzsimons, a former director of the Transvaal Museum (and noted by Gon & Skelton, 1997), Smith is 'the father of South African Zoology'. His most famous work is the drawings of South African wildlife, including 35 species of marine and freshwater fishes (Smith, 1838–1849).

Geoffroy Saint-Hilaire and Smith were each exceptional because they were scientists who undertook collecting missions and themselves described the greater part of the species they brought back. Thereafter, it is probably necessary to distinguish explorers, the travellers, who actually collected the materials, and ichthyologists,

**Table 1.** Number of samples collected by E. Geoffroy Saint-Hilaire during Bonaparte's expedition to Egypt (some of the samples may have several specimens, but generally each sample is only one fish).

	Freshwater	Marine
Alcohol	71	71
Dry	9	4
Mummy	7	
Total	87	75

who examined and described the new species, without necessarily ever collecting samples in the field.

## Travellers and explorers

Some great explorers and colonial governors created numerous collections of wildlife fauna and we shall deal only with the most well known in the different areas explored. Their journeys can be divided into three principal groups:

- the first group explored Western Africa, charting the course of the River Niger and mapping the Lake Chad basin;
- the second group explored the Nile basin and Eastern Africa, discovering the Great Lakes area and the upper Nile basin;
- the third group, centred on Southern Africa, traced the course of the Zambezi and discovered the Congo basin.

In West Africa, the first significant traveller was Mungo Park (1771–1806) who, between 1796 and 1806, explored the Gambia and the Upper Niger (up to Ségou and possibly to Timbuktu) basins. James Richardson (1809–1851), an English pastor, crossed Morocco (1845 and 1850), then the Sahara and arrived in Mali, but never reached Chad. At the end of the 19th century, Jean-Guillaume Jubelin (1787–1860) and Maurice Armand Chaper (1834–1896) were explorers who made fish collections from this area (Table 2). In fact, we will see that the main collections from Western Africa were assembled at the beginning of the 20th century (Table 3).

Abel Gruvel (1870–1941) took part in an important scientific expedition in Mauritania (1905–1907). He was particularly in charge of the study of marine fauna but he undertook other expeditions along the coast (from Morocco to Democratic Republic of Congo), from which he brought a lot of freshwater specimens (Table 3). Dr William John Ansorge (1850–1913) was an English explorer who collected numerous fishes and birds, mainly in Cameroon. Later, Cuthbert Christy (1863–1932) travelled to northern Nigeria (1898–1900), after which he became a member of the First Uganda Sleeping Sickness Commission in 1902, and of a medical expedition to Congo in 1903. He also

**Table 2.** MNHN's collections: the principal fish collectors during the 19th century. Number of samples (brackets: number of species). MNHN: Muséum national d'Histoire naturelle de Paris.

Names of collectors	J.P. d'Arnaud (1812-1884) 1840-1845	N.E. Ballay (1847-1902) 1882-1885	P.S. de Brazza (1852-1905) 1883-1886	M.A. Chaper (1834-1896) 1882	J. Dybowski (1856-1928) 1891-1892	E. Foa (1862-1901) 1895-1899	L. Guiral (???-1885) 1885	D.-L. de Joannis (1803-1868) 1834-1836	J.-G. Jubelin (1787-1860) 1822-1828	A. Marche (1844-1898) 1876	Thollon 1890
Algeria				15 (2)							
Central African Rep.			2 (1)	47 (32)							
Congo		11 (11)	120 (69)	20 (13)							
Côte d'Ivoire				17 (10)							
Egypt	14 (9)							34 (26)			
Equatorial Guinea							12 (6)				
Gabon		1 (1)	60 (37)							20 (17)	32 (23)
Lake Tanganyika						12 (7)					
Lake Victoria						1 (1)					
Malawi						6 (6)					
Senegal										31 (25)	
Somalia					1 (1)						
Sudan	21 (15)										

travelled extensively in East Africa, Uganda, Southern Nigeria, the Gold Coast and the Cameroons. After official appointments in the Congo and the Sudan, he served during the First World War in Africa and Mesopotamia. After the War, he explored the Sudan, Nyasaland and Tanganyika, and was a member of the League of Nations Commission enquiring into slavery and forced labour in Liberia. During the second half of the 19th century, Ansorge and Christy brought back the largest collections originating from Western Africa.

In West Central Africa, Robert Bruce Napoleon Walker (approx. 1840–1880), an English trader and a British government agent (who lived in Gabon from 1859 to 1875), seems to have made a large collection of freshwater fishes from the Ogoewe River. The other well-known traveller was Mary Henrietta Kingsley (1862–1900). From December 1894 to November 1895, she travelled alone to the port of Calabar (now in Nigeria), to Gabon and Cameroon. She collected fish and reptiles for the British Museum (Natural History) in London. In Gabon, she took a steamer up the Ogoewe River to Lambaréné and to an American mission at Talagouga, and then paddled a canoe to the rapids at Ndjolé. Finally, she made an overland trip from the Ogoewe to the Rembowe River. Mary Kingsley brought valuable freshwater fish specimens back to England, including some 65 species,

of which 18 were new to Gabon and 7 were new to science. They were later described by Albert Günther (see below). Other well-known travellers explored this area but their contribution to our knowledge of the African ichthyofauna is arguably less important. They included: Paul Belloni du Chaillu (1837–1903); Alfred Marche (1844–1898); Louis Eugène Henri Dupont, Marquis de Compiègne (1846–1877); and Pierre Savorgnan de Brazza (1852–1905) (Table 2).

Numerous explorers went to the Congo basin. Savorgnan de Brazza has already been mentioned but the most famous was undoubtedly Henry Morton Stanley (1844–1904), one of whose achievements was to solve the last great mystery of African exploration by tracing the course of the River Congo to the sea. However, his contribution to fish collections was negligible. Historically, Belgian collectors were the most numerous in that region. Among them, we can highlight Lieut. Eugène Wilwerth (1866–1916), Anton Greshoff (director of the N.A.H.V. – the Nieuwe Afrikaansche Handelsvennootschap = ‘New African Commercial Society’) and P. Delhez, who brought back many of the fish collections that are kept in the Africa Museum of Tervuren (Belgium). Other important collectors who sent numerous specimens back from this area at the end of the 19th and beginning of the 20th century include: Herbert Lang (1879–1957) and James Paul Chapin (1889–1964) who took part in the American Museum’s 1909–1915 expedition to the Congo, Scott C. Christy (see above) and the Frenchman

Jean Dybowski (1856–1928) who stayed in Central Africa around 1891, particularly in the Ubangi River region.

In eastern Africa and the Rift lakes the most important fish collector was certainly John Edmund Sharrock Moore (1870–1947), who brought back

numerous specimens, mainly from Lake Tanganyika. The French explorer Édouard Foa (1862–1901) also made zoological collections from the Zambezi and Congo rivers and from Lakes Nyassa (now Malawi) and Tanganyika.

## Scientists

In the middle of the 19th century, under the influence of the French scientist Achille Valenciennes (1794–1865), the German naturalists and explorers Eduard Rüppell (1794–1884) and Wilhelm Carl Hartwig Peters (1815–1883), and the Dutch medical doctor and ichthyologist Pieter Bleeker (1819–1878), the number of described species grew rapidly. Collectively, they described many new freshwater or brackish-water species from Africa, respectively each contributing 45, 22, 37 and 34 new descriptions (Table 4). Thus, by 1850, more than 300 African freshwater fish species had been described. Subsequently, with increased travels and explorations, a lot more species were described during the second half of the 19th century. Important scientists from this period include Albert C.L.G. Günther (1830–1914), Franz Steindachner (1834–1919) and, especially, Georges A. Boulenger (1858–1937) (Fig. 4). Boulenger did visit Africa once during his life, in 1905 when he went to Cape Town for a conference, where, apparently, he met Gilchrist (Gon & Skelton, 1997). With this one exception, none of these scientists ever travelled to Africa. Their important work

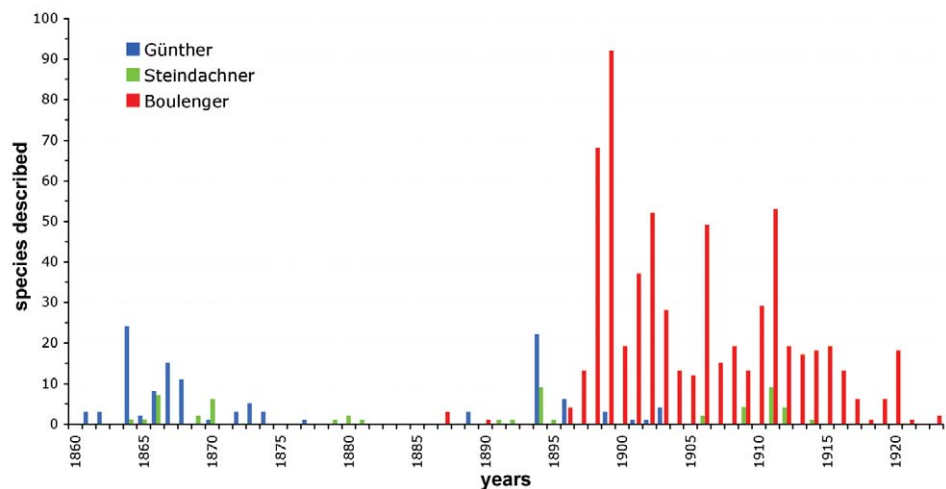


Fig. 4. Number of African freshwater fish species described by the three main naturalists working at the end of the 19th / beginning of the 20th century.

**Table 3.** MNHN's collections: the principal fish collectors at the beginning of the 20th century (1900–1950). Number of samples (brackets: number of species). N.B. Table continues over.

Names of collectors	C. Alluaud	W.J. Ansorge	A. Baudon	A. Chevalier	E. Degen	R. Du Bourg de Bozas	A. Gruvel
Life span	(1861- 1949)	(1850-1913)		(1873-1956)		(1871-1902)	(1870- 1941)
Years of collection	1904-1932	1910-1911	1919-1931	1904-1932	1905-1906	1902	1905-1933
Algeria	5 (1)			1 (1)			
Angola		95 (23)					
Benin				2 (2)			2 (2)
Burkina Faso	19 (10)			3 (1)			
Central African Rep.			577 (147)				
Chad			4 (1)				
Congo			309 (92)	2 (1)		2 (2)	4 (4)
Côte d'Ivoire	33 (15)		3 (1)	5 (3)			2 (2)
Democratic Rep. Congo	5 (2)					21 (15)	4 (2)
Egypt	1 (1)						3 (3)
Ethiopia						5 (3)	
Gabon			106 (50)				
Guinea				5 (3)		6 (4)	14 (7)
Guinea-Bissau							
Kenya	22 (7)						
Lake Victoria	179 (42)				50 (26)		
Madagascar	1 (1)						4 (3)
Mali	4 (2)			7 (6)			
Maroc	70 (9)						15 (6)
Mauritania							
Niger	4 (1)						
Nigeria							
Senegal				4 (2)			17 (15)
Somalia						10 (4)	
Sudan	46 (20)						
Tanzania	2 (1)						
Tunisia							
Uganda	9 (4)						



E. Haug	A. Monard	T. Monod	J. Pellegrin	C.-H. O Pobeguïn	H. Schouteden	J. Thomas	J. Tilho	E.G. Waterlot	Wurtz
(1871-1915)	(1896-1952)	(1902-2000)	(1873-1944)	(1856-1951)	(1881-1972)		(1875-1956)		
1901-1913	1936	1925-1957	1925-1927	1892-1904	1920-1956	1923-1938	1908	1929-1935	1908
		4 (2)							
	77 (44)								
								10 (9)	
						7 (7)			
						3 (3)			
						32 (24)			
				35 (19)					
					486 (162)	1 (1)			
139 (70)				3 (3)					
	2 (2)			25 (14)		20 (15)		62 (32)	39 (13)
	6 (5)								
		14 (8)				41 (30)		2 (2)	
			41 (8)						
		31 (6)							
		3 (2)				8 (5)	53 (22)		
		3 (2)							
						1 (1)			

**Table 4.** Principal descriptors (more than 20 species of fish described) prior to the 20th century.

Surname	First and middle name	Life span	No. of African fish species described
Linnaeus	Carl	1707–1778	23
Valenciennes	Achille	1794–1865	45
Rüppell	Wilhelm Peter Eduard Simon	1794–1884	22
Peters	Wilhelm Carl Hartwig	1815–1883	37
Bleeker	Pieter	1819–1878	34
Günther	Albert Charles Lewis Gotthilf	1830–1914	119
Steindachner	Franz	1834–1919	53
Sauvage	Henri Émile	1842–1917	24
Boulenger	Georges Albert	1858–1937	640

was done on fish preserved in the collections of the various museums. The French naturalist, Henri Émile Sauvage (1842–1917) also contributed to an extent (Table 4).

Albert Günther was born in Esslingen (Württemberg, Germany). He studied theology in Bonn and Berlin and later studied medicine at Tübingen. He went to the British Museum in 1856, where he worked on ichthyology. John Edward Gray, director of the Zoology Department of what is now the Natural History Museum, made it possible for Günther to launch out on an enormous task, the inventory of the fish collections of the British Museum (Natural History), which occupied all his life. The *Catalogue of the Fishes of the British Museum* appeared in eight volumes from 1859 to 1870. He described 6843 species, of which 119 were new from inland waters of Africa. The Catalogue was to play an important part in future ichthyology by stimulating the development of studies on fishes. Following Gray's death in 1875, Günther was made Keeper of the Zoology Department at the Natural History Museum, remaining so until 1895. Apart from fishes, he also worked on the reptiles and amphibians in the Museum's collection.

Franz Steindachner, an Austrian zoologist, was interested in natural history, and took up the study of fossil fishes. In 1860, he was appointed to the position of director of the Fish Collection at the Naturhistorisches Museum of Vienna. Steindachner's reputation as an ichthyologist grew and, in 1868, he was invited by Louis Agassiz to accept a post at Harvard University in Cambridge, Massachusetts, USA. In 1874, he returned to Vienna and, in 1887, was appointed Director of the Zoological Department of the

Naturhistorisches Museum. In 1898, he was promoted to Director of the Museum. Steindachner made the collections of the Naturhistorisches Museum of Vienna one of the most important in the world, containing specimens provided by officers of the Austrian army and purchased collections, which he often financed himself. He also organised and led his own expeditions, a rare thing at a time when the curators of large museums did not go away on fieldwork themselves. Apparently he never went to Africa but, nevertheless, described 53 new freshwater species from that continent.

Georges Albert Boulenger is certainly the zoologist who could claim to have discovered the most new species in his career. Indeed, he is credited with first descriptions of 2522 species, including 1095 fishes (640 from Africa), 556 amphibians and 871 reptiles. By comparison, Linnaeus himself described only 1318 species, including birds and mammals.

Boulenger was of Belgian origin. He graduated in 1876 from the Free University in Brussels and then worked for a while at the Museum of Natural History in Brussels as an assistant naturalist, studying amphibians, reptiles, and fishes. He also made frequent visits during this time to the Muséum National d'Histoire Naturelle de Paris and to the British Museum (Natural History), in London. In 1880, he was invited by Günther to work at the BM(NH), London, and was assigned the task of cataloguing the amphibians in the collection. His position in the British Museum meant that he had to be a civil servant of the British Empire, so he became a naturalised British subject. In 1882, he became

a first-class assistant in the Department of Zoology and remained in that position until his retirement in 1920.

According to biographical accounts (Poll, 1967a, b), Boulenger was extremely methodical and had an amazing memory that, reputedly, enabled him to remember every specimen and scientific name he ever saw. He also had extraordinary powers of writing and seldom made a second draft of anything he wrote, his manuscripts showing but few corrections before going to the publisher. He was famous for his monographs on amphibians, lizards and other reptiles, and fishes, as well as for his monographs on the fishes of Africa, namely: *Matériaux pour la faune du Congo. Poissons nouveaux* (1898–1900); *Les poissons du Bassin du Congo* (1901); *Fishes of the Nile* (with 97 lithographic plates: 1907) and *Catalogue of Fresh-Water Fishes of Africa in the British Museum* (four volumes: 1909–1916).

Boulenger was an expert on African freshwater fishes, despite never having carried out fieldwork in Africa himself. His contribution is essential and we owe to him 640 new, valid species of African freshwater fish. Today, however, we know that Boulenger described barely 20% of the total species actually known.

Thanks to these three monumental naturalists, after the First World War the number of species known increased from 300 to 1360. Since then, such a rate of increase has never been equalled for Africa.

## The 20th century up to the second world war

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. Ethelwynn Trewavas and Max Poll began their careers before the Second World War but a large part of their work was done later. Jacques Pellegrin and Charles Tate Regan were the main contributors to knowledge of the African freshwater fish fauna in the first half of the 20th century.

Pellegrin (1873–1944) was a French zoologist who, in 1894, became assistant at the laboratory of Zoology at the Muséum National d'Histoire Naturelle, replacing Léon Vaillant (1834–1914). He obtained his doctorates in

medicine (1899) and in science (1904) and, in 1908, was named assistant chair. After many missions abroad (in Morocco for example), he became sub-director of the museum in 1937, replacing Louis Roule as the chair of herpetology and ichthyology. He published over 600 scientific books and articles and discovered around 350 new species. These included 145 species of freshwater fish. His major contribution concerned fish from the French Congo, Central Africa (the Ubangi and Chad basin), Chad and Ogowe, but he also worked on the faunas of other areas.

Regan (1878–1943) was a British ichthyologist, working mainly at the beginning of the 20th century, who did extensive work on fish classification schemes. Born in Sherborne, Dorset, he graduated from Cambridge University and, in 1901, joined the British Museum (Natural History), where he followed Boulenger in charge of the zoology programme. Later, he became Director of the entire museum, in which role he served from 1927 to 1938. Regan tackled the African cichlid species, making extensive use of dissections and skeletal preparations, in an attempt to arrive at a natural classification. Among the 83 new species Regan described (79 himself and 4 with E. Trewavas), his contribution centres on the cichlids (77 new cichlid species were described).

Three other authors from this period deserve mention. John Treadwell Nichols (1883–1958) was curator of recent fishes at the American Museum of Natural History. In 1913, he founded *Copeia* which, in 1923, became the official journal of the American Society of Ichthyologists and Herpetologists. From 1920 to 1941, he was associate curator in charge of the Department of Ichthyology at the Museum. Nichols wrote approximately one thousand articles and books (not only about fish but also about birds) and he made many expeditions around the world. Concerning freshwater fishes of Africa, he personally described five new species (1923–1928), 18 with Ludlow Griscom (1917), two with Rudyerd Boulton (1927) and eight with Francesca Raimonde La Monte (1931–1953).

Ernst Ahl (1898–1943/1944), a German zoologist, was the director of the Department of Ichthyology and Herpetology in the Museum of Berlin. He was also the editor-in-chief, from 1927 until 1934, of the review

**Table 5.** The 20th century: principal descriptors (more than 20 species of fish described) before the Second World War.

Surname	First and middle name	Life span	No. of African fish species described
Pellegrin	Jacques	1873–1944	145
Regan	Charles Tate	1878–1943	83
Fowler	Henry Weed	1878–1965	44
Nichols	John Treadwell	1883–1958	33
Ahl	Ernst	1898–1943/44	40
Trewavas	Ethelwynn	1900–1993	159
Poll	Max	1908–1991	209

*Das Aquarium*. He described many new species, the majority of which have now fallen into synonymy. Ahl is believed to have been an active militant of the Nazi party who took part in the programme intended to make Germany the country that had described the greatest number of species. Ahl himself described 40 valid freshwater African species, mainly cyprinodonts (27) and cichlids (8). He was mobilised in August 1939 and was wounded in Poland. After he recovered, he was sent to North Africa, then to Yugoslavia where he disappeared.

Henry Weed Fowler (1878–1965) was born in Pennsylvania, USA. His post-high school academic career was limited to two years (ca. 1900) spent at Stanford University as a special student under David Starr Jordan. His entire professional life was spent in association with the Academy of Natural Sciences in Philadelphia where he was employed from 1903 until 1965. While Fowler published papers on crustaceans, birds, reptiles and amphibians during his lifetime, ichthyology was his main interest and the area in which he did most of his work. He was a founder of the American Society of Ichthyologists and Herpetologists and its President in 1927. Fowler's main interest and activity was directed at Africa and its fresh waters and, among all the species he described from all parts of the World, 44 remain valid for the freshwater African fauna.

Thanks to these naturalists and some others (for whom an historical sketch by Worthington (1996), of the principal early 20th century research (1927–1931) on East African Lakes, provides additional information), the number of known African freshwater fish species reached 1900 before the Second World War.

## The 20th century: the post-war years

As mentioned previously, Ethelwynn Trewavas and Max Poll (Table 5) began their careers before the Second World War but the greater part of their work was achieved thereafter.

Trewavas<sup>1</sup> (1900–1993, known as 'ET', see Balon et al., 1994) was recognised as the senior scientist in the Fish Section of the British Museum (Natural History) for almost half a century, and she was known internationally as an authority on several widely different groups of fishes, principally cichlids (freshwater fishes) and sciaenids (marine fishes). She is most widely known for her major taxonomic revisions of the African cichlids but she also published extensive revisions and descriptions of other groups. She combined meticulous laboratory studies with extended field trips where she relied on her insights and interviews with local people in order to understand the biology of the fishes she was studying. Her monograph on *Tilapiine Cichlids* (Trewavas, 1983) is regularly cited in the extensive literature on this group.

Poll (1908–1991) became a collaborator of the Museum of Tervuren in 1928, and began the study of fish after 1932. In 1967, he was named Chief of the Department of African Zoology, a position that he held until his retirement in 1973. After the war he took part in several field expeditions to Africa, including the scientific expedition to Lake Tanganyika (1945–1947), the mission for examination of

<sup>1</sup> For a well documented biography see Noakes 1994a, b and c; Greenwood, 1994.

the fishing potential of African Coastal Water (Mbizi, 1948–1949), and exploration of the Stanley Pool (1957–1958).

Until 1940, Poll's publications were primarily descriptions of collections recently received in Belgium, including new species that they contained. Thus, he added several tens (38 alone and 15 as co-author) of new species to the scientific inventory of African fresh water. After 1945, he devoted his time particularly to the study of the large collections from the scientific explorations in which he, himself, was involved. Thus were born his substantial publications on African coastal waters (1954), Lake Tanganyika (1953, 1956) and Stanley Pool (1959a, b). These studies included descriptions of new species (171 alone and 45 as co-author, just for the freshwater species), but he also carried out some generic revisions and detailed fish fauna inventories. After 1960, he started, among other things, generic revisions of the protopterids (1961), dwarf African characids (1967c), *Symodontis* (1971a) and marine sparids (1971b).

After the Second World War, many more authors began to publish with co-authors, a practice which was infrequent thitherto but became more common thereafter (Table 6).

Jacques Daget (1919–2009) must be considered as the founder and stimulator of the rich French research endeavours throughout Western Africa. In 1946–1947, Daget carried out his first field expedition to the Inner Central Delta of the Niger (French Sudan, currently Mali). In 1949, he defended his thesis, in Paris, in which he concluded that polypterids represent an evolutionary branch, isolated very early on from all the actinopterygians and maintained in Africa since the Cretaceous, without appreciable evolution ('living fossils'). From 1949 to 1963, he resided in the flood zone of the Middle Niger. There,

at Diafarabé, he built the first West African Laboratory of Hydrobiology from where he carried out several expeditions and brought back many fish from numerous countries of Western Africa: Senegal, Guinea, Ivory Coast, Dahomey (today Bénin), Upper Volta (today Burkina Faso) and Niger (approximately 1400 batches of fishes were actually preserved in the MNHN collections; see below). Then he created, and led, a multi-disciplinary team in Fort Lamy (today Djaména) that carried out a comprehensive hydrobiological study of Lake Chad. After 1965, when he returned to France, he devoted himself to the study of African freshwater fishes in association with the Muséum national d'Histoire naturelle de Paris. He also taught on the 'Dynamics of Exploited Stocks' and contributed to spreading the use of factorial analysis, as well as taxonomy and ecology (École Normale Supérieure, Paris). Promoted to Professor in 1975, to replace Théodore Monod, he created the Laboratory of General and Applied Ichthyology (previously: Laboratory of Overseas Fisheries). In 1976, he was named, with Jean-Pierre Gosse and Dirk Thys van den Audenaerde, as a member of the editorial board of CLOFFA (*Check-List of the Freshwater Fishes of Africa*), a valuable reference work for all African ichthyologists. He is the author of many publications on fishes of Western Africa, describing four new genera and 60 new species presently considered valid (Table 5).

Peter Humphry Greenwood (1927–1995) was born in Redruth, Cornwall (south-western England). Humphry (he hated his first name) was a respected ichthyologist who spent most of his working life on the staff of the British Museum (Natural History). He was particularly known for his work on the haplochromine cichlids of Lake Victoria, although he worked on most other African

**Table 6.** The 20th century: principal descriptors (with more than 20 species of fish described as the only author) after the Second World War.

Surname	First and middle name	Life span	No. of African fish species described	
			(alone)	(co-author)
Daget	Jacques	1919–2009	52	8
Greenwood	Peter Humphry	1927–1995	47	27
Thys v. d. Audenaerde	Dirk F.E.	1934	24	28
Roberts	Tyson Robert	1940	23	25
Seegers	Lothar	1947	24	11

cichlids as well. In addition, his work covered the anatomy and phylogenetic relationships of diverse groups of fishes, encompassing elopomorphs, osteoglossomorphs, clupeomorphs, alepocephalids, ostariophysans, various percormorphs, coelacanth and lungfish. He was as much at home working on fossil as on Recent taxa, and he had particular interests in the evolution and classification of fishes (in the broadest sense) and in their biogeography. In all, he produced over 150 publications.

Most of Greenwood's childhood and early adulthood was spent in South Africa. In 1950, he entered London University and first made contact with Trewavas at the BM(NH). The following year he secured a Colonial Fisheries Research Studentship with the East African Fisheries Research Organisation (EAFRO) based in Jinja, Uganda, on the northeast shore of Lake Victoria. Originally, he had wanted to work on a doctoral thesis supervised by Trewavas but, in 1959, he was appointed to the BM(NH) as a Senior Research Officer; from 1959–1967, he was Principal Scientific Officer and, thereafter, Senior Principal Scientific Officer (a special merit promotion). Greenwood's interest in the classification of bony fishes developed during the 1960s. His discussions with C. Patterson in the BM(NH), and increasing contact with D. Rosen (with whom he developed a deep and lasting friendship) led, in 1966, to a landmark paper on teleostean classification co-authored with D. Rosen, S. Weitzman, and G. Myers. Greenwood's name appears first by dint of alphabetical ordering, Myers having requested that his name be put last. From 1967–1974, Greenwood was Chairman of the International Biological Programme subcommittee on Lake George, Uganda. From 1970, he formed a lasting collaboration with a group of workers from Leiden University, The Netherlands, headed by C. Barel. On his initiative, the Dutch set up a research team, at Mwanza on Lake Victoria, to study the ecology and functional anatomy of haplochromines (HEST: *Haplochromis* Ecology Survey Team). On his retirement from the BM(NH) in 1989, Greenwood chose to settle in Grahamstown, South Africa, where he continued his taxonomic and anatomical research at the J.L.B. Smith Institute of Ichthyology (now South African Institute for Aquatic Biodiversity, SAIAB).

He described 74 new species, mainly cichlids, presently considered valid (Table 5). Rhodes University awarded Greenwood with the honorary degree of DSc in 1991 and he was made an Honorary Research Associate of the J.L.B. Smith Institute of Ichthyology in 1992.

Dirk F.E. Thys van den Audenaerde (born 1934) was born in Malines (Belgium). Initially an agricultural engineer (1956), he then took a masters degree in Zoology (1959), after which he began his career in Tervuren (Royal Museum of Central Africa: RMCA). He became Doctor in Agronomic Sciences in 1970 and succeeded Poll as the Head of the Vertebrates Section in 1974. In 1980, the interim Directorship of RMCA was entrusted to Thys van den Audenaerde, who was eventually confirmed in this post in 1985. He was also a part-time teacher at the University of Antwerp, from 1973 to 1982, and the University of Louvain (1975–1999). He retired in 1999. He was the author of many publications on fishes of Central and Western Africa. Alone, or with contributors, he described three new genera and 52 new species considered to be valid (Table 5). His favourite group was the cichlids (26 new species described), but he contributed to knowledge of other families, among them cyprinids (10 new species described) and mormyrids (6 new species described). Finally, he knew how to choose his collaborators: these included Guy G. Teugels, Luc De Vos and Jos Snoeks.

Two other ichthyologists who have described some tens of species also deserve mention. The first is Tyson Robert Roberts (b. 1940 in Los Angeles), an independent American ichthyologist who described alone, or mainly with D.J. Stewart, 48 species in different families and from different parts of the continent. In contrast, Lothar Seegers (b. 1947), a German ichthyologist, is especially known for his work on killifishes from Africa, but also from all over the world. In a remarkable monograph about *The Fishes of the Lake Rukwa Drainage* (1996), L. Seegers also described some species from other groups, mainly *Chiloglanis* (Mochokidae). He is also well known for his very numerous photographs of living fish that have been published. His last contribution is an impressive monograph about *The Catfishes of Africa* (2008).

In addition to these five major descriptors, many other modern ichthyologists must also be cited. In contrast to

former times, these scientists generally specialised in a particular group of fish. Thus, among the best known, we can note: amphiliids (Paul H. Skelton), anabantids and malapterurids (Steven Norris), bagrids and claroteids (Luc M. Risch), alestids (Didier Paugy), cichlids (Yves Fermon, Anton Lamboj, Anthony Ribbink, Melanie Stiasny Jos Snoeks and Guy Teugels), clariids (Guy Teugels, 1954–2003), cyprinids (Christian Lévêque and Paul H. Skelton), Gobiesocoidei (Ian J. Harrison, Peter J. Miller and Frank Pezold), killies (Jean-François Agnèse, Jean Huber, Rudolf H. Wildekamp and Jouke R. Van de Zee), mastacembelids (Emmanuel Vreven), mormyrids (Rémy Bigorne, Carl Hopkins, Sébastien Lavoué and Louis Taverne) and schilbeids (Luc (Tuur) de Vos, 1957–2003).

Until about 80 years ago, most species were described primarily on the basis of their morphological and meristic differences or coloration (e.g. killies). Since then, other tools have become available and are increasingly used, among which the best known are genetic markers, parasites and electrophysiology.

### Modern trends (genetics, parasites, electrophysiology...)

Alongside conventional systematic studies, there has been a steady rise in the number of genetic and cytogenetic studies that have phylogenetic or taxonomic applications for fish species. In Africa, among the first work using different, modern methods is the description of *Labeo roseopunctatus* from the Niger and Senegal basins (Paugy et al., 1990). In this study, three separate techniques were used to test the two competing hypotheses: morphological/morphometric analysis, chromosomal/enzymological analysis and comparative parasitology.

Some species, such as mormyrids, produce weak electric organic discharges (EOD) which are generally species-specific (Kramer, 1990). Even if some precautions must be taken (e.g. water conductivity, intraspecific variability), it is interesting to use EOD in species diagnosis because there is excellent agreement between electric data and diagnostic characteristics (Crawford & Hopkins, 1989; Bigorne & Paugy, 1991). Nevertheless, this

method occasionally has 'defects', because it is sometimes possible to encounter cases of sympatric, morphologically indistinguishable forms, within which different EOD waveforms may be observed (Sullivan et al., 2002).

Cytogenetic and molecular studies of African freshwater fishes have been emphasised within the last few years. They have been conducted to describe the attributes of a group of taxa, to solve systematic or phylogenetic questions and to assess the genetic variability of a species that could potentially be used in aquaculture. These methods are increasingly used for systematics and sometimes this tool is useful to help the descriptor to distinguish between very close species, and pushes him to find morphological characters, when possible, for the diagnosis of these different species. There are many examples of this concerning the cichlids of the Great Lakes of the Rift Valley. Thus, since the use of molecular methods in systematics began, the estimate of the number of cichlid species in the Great Lakes of Eastern Africa has increased markedly during the last few years (Malawi: 800 instead of 500; Tanganyika: 300 instead of 200; Victoria: 500 instead of 250). Conversely, these methods sometimes confirm that species, previously considered distinct, are in fact synonymous. Thus, *Chrysichthys filamentosus* was synonymised with *C. auratus* (Risch, 1992). However, it is necessary to be careful because there are examples where the genetic distance between two genera of the same family is weaker than the distances that exist between species of the same genus of this family (Agnèse & Bigorne, 1992). In fact, the systematic status of a taxon is often a question of interpretation.

Thanks to these new methods that open the way for discoveries of unknown species that could not be detected by the old methods, the ratio of species described seems on the increase. Today, we can estimate that the total number of valid fresh- and brackish-water species described from within African borders is 3200 (Fig. 5).

Phylogeny and phylogeography of particular groups, such as cichlids or Siluriformes, can also provide an excellent tool for trying to explain the history and the evolution of the fauna in a particular region. Studied together, these groups can also provide excellent models for comparative evolutionary and phylogeographic analyses.

Finally, progress in these methods will certainly provide a part of the key to explaining the radiation of the cichlids in the Rift Valley Lakes, which constitutes one of the most rapid and extensive radiations of vertebrates known. In fact, there is a growing debate over the roles of natural or sexual selection in creating this remarkable assemblage of species. For example, the first results seem to reveal that, in Eastern Africa, there was a faunal split, the timing of which coincided with East African rifting events (Day & Wilkinson, 2006). So these new methods will allow major contributions to this debate.

## Ecologists, systematists, ethologists, aquaculturists

### The ecologists and systematists

At the beginning of the 20th century, most ichthyologists devoted all their efforts to describing new species and to drawing up faunal inventories. Few of them were concerned with ecology or such applied sciences as aquaculture or fishkeeping. In fact, it was only at the beginning of the 1950s that the first publications appeared

concerning the biology or the ecology of freshwater fishes, as well as the first treatises on pisciculture.

M. Poll, J. Daget and T. Roberts, who have already been discussed, were certainly among the pioneer descriptors of information about the biological preferences of the main species in Central and Western Africa.

Reginald (Rex) Arthur Jubb (1905–1987) was born in Britstown, South Africa and obtained a BSc degree in Physics and Chemistry at Rhodes University. Jubb made one of the first collections of fishes from Rhodesia in 1933. He started writing about the fishes in local magazines and, in the absence of other experts, soon became the local authority on the freshwater fishes of the Federation. In the early 1950s, he was made the Honorary Keeper of Fishes for the Queen Victoria Museum in Salisbury (now Harare) and established the national collection of fish (Jubb, 1954), which is today a well-curated collection housed in the National Museum of Natural History in Bulawayo. In 1957, Jubb joined the Department of Ichthyology at Rhodes University as the freshwater ichthyologist. In 1961, as a consequence of contraction at the Department of Ichthyology, Jubb moved to the Albany Museum, taking with him the freshwater fish collection. Jubb was not a paid member of staff and worked in the Albany

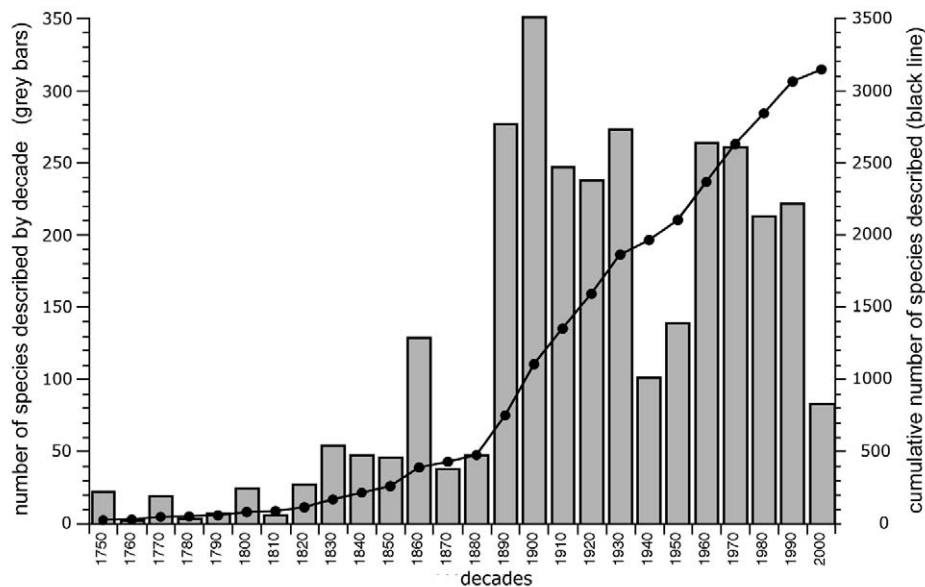


Fig. 5. Number of African freshwater fish species described to date.



Museum in the capacity of Honorary Curator of Fishes. The Museum established a new post of ichthyologist in order to ensure continuity of this work. This was the first established post for freshwater ichthyology in the history of South African systematic ichthyology. Jubb was offered the post but declined in favour of appointing a younger ichthyologist researcher, Frank Farquharson. His taxonomic contribution was weak, but he had a very interesting biogeographic approach. His theory of a series of waves of invasion to explain the distribution of cyprinids in southern Africa (Farquharson, 1962) was expanded to form a more comprehensive view on fish distribution in Southern Africa (Jubb & Farquharson, 1965). Farquharson, who was appointed in 1962, was succeeded by Skelton in 1972. Jubb, together with his wife Hilda, continued to conduct research and to build the collection until the mid-1970s. Through a prolific series of publications, including the book *Freshwater Fishes of Southern Africa* (Jubb, 1967), the Jubbs firmly established the Albany Museum as the leading centre for freshwater ichthyology in southern Africa. Jubb died in East London in 1987.

Edgar Barton Worthington (1905–2001) lived a full and varied life, first as a pioneer explorer of African lakes and their fisheries. Following his graduation from Cambridge University, he joined the first African Lake Fishery Survey (1928–1929), exploring the huge equatorial Lake Victoria. He became so ‘hooked’ that he then organised Cambridge Expeditions to other East African lakes. These laid the foundations for the present immense investment in research on these lakes, both for fish as food and for their unique scientific opportunities. He headed the East African Freshwater Fisheries Research Organization (EAFFRO) in 1947 and the Joint Fisheries Research Organization (JFRO) of Northern Rhodesia (now Zambia) and Nyasaland (now Malawi) in 1951. In 1951 the need for cooperation between 14 African countries led to his involvement in the creation of the Scientific Council for Africa (CSA) of which he became Secretary-General (1951–1955). For his African exploration, Worthington received the Gill Memorial Medal of the Royal Geographical Society and the Mungo Park Medal of the Royal Scottish Geographical Society (1938).

Rosemary Helen (known as Ro to all her friends and ichthyologists) Lowe-McConnell<sup>2</sup> (born Lowe in Liverpool, England, on 24 June 1921; married Richard McConnell in 1953) is also one of the pioneers of tropical fish ecology. During a colourful and eventful career spanning more than 45 years, she did field work in the tropical waters of Africa and South America and contributed significantly to our understanding of the ecology, zoogeography, evolution and taxonomy of tropical fishes. Later, at the Natural History Museum, Ro wrote her first book synthesising studies on the ecology of freshwater fishes from the tropics of Africa, South America and Asia, *Fish Communities in Tropical Freshwaters. Their Distribution, Ecology and Evolution* (Lowe-McConnell, 1975). This was followed by another synthesis volume, *Ecology of Fishes in Tropical Waters* (Lowe-McConnell, 1977), which also covered marine fishes. Ro later expanded both books into *Ecological Studies in Tropical Fish Communities* (Lowe-McConnell, 1987), the definitive title on this subject. Throughout her career Ro has been driven by the need to understand the ecology of fishes in order to ensure their sustainable utilisation.

Kate Bertram (1912–1998), born Cecily Kate Ricardo, was one of the 1930s’ ‘Cambridge School’ of biologists whose expeditionary research added greatly to knowledge of freshwater fish in Central and East Africa. Her supervisor was the doyen of African freshwater fish research, Dr E.B. Worthington. He invited her to help him to assess the results of his 1930–1931 Cambridge University Expedition and to study the fish and fisheries of the East African lakes. In 1936, Kate Ricardo undertook her own Cambridge University Expedition. Its aim was to make a study of the fish and fisheries of Lakes Rukwa and Bangweulu. After six months in the field, of which four weeks were spent in the swamps, a year was spent assessing the results at Cambridge. The Colonial Office then asked her to take part in the Platt nutrition survey around Lake Malawi. The fish and fisheries report, known as the ‘1939 Survey’ (Bertram et al., 1942), was equally valuable to JFRO. She joined the Joint Fisheries Research Organization of Zambia and Malawi (JFRO) in late

<sup>2</sup> For a well documented biography see Bruton, 1994a, b and c. See also her ‘autobiography’ (Lowe-McConnell, 2006)

1951. She published papers alone and with her husband Colin Bertram. She retired from Cambridge in 1979.

Jacques Blache (1922–1994) was born in Ronchamp (Vosges, France). He joined Orstom (Office de la Recherche Scientifique et Technique d'Outre-Mer) in 1948 and was first posted to Kampuchea. Then he moved to Chad, where he stayed from 1953 to 1959. During this period, with some collaborators, he collected all the elements of an important systematic and biological study on *Les Poissons du Tchad et du bassin adjacent du Mayo Kebbi* (Blache et al., 1964). Later he stayed in other African countries (Congo and Senegal) to work on marine fishes and, particularly, Apode fishes (thesis in 1974). He moved to the Paris Museum in 1973 where he stayed until his retirement in 1979.

Over about 20 years, David H. Eccles carried out a lot of work concerning the biology, the evolution and the taxonomy of cichlids from Lake Malawi. His most important contributions were the revision of the *Docimodus* (Eccles & Lewis, 1976) and *Lethrinops* genera (Eccles & Lewis, 1977–1979). With Trewavas, he published a book-length revision (Eccles & Trewavas, 1989) of Lake Malawi's non-mbuna haplochromine flock that introduced new generic names for numerous morphologically isolated species and for many phenetic groups often based on colour pattern. Later, as FAO consultant, he published a complete guide to the freshwater fishes of Tanzania (1992)

Peter B.N. Jackson (1924–2007) was an experienced researcher on African freshwater fisheries and administrator of research institutions. He was educated at Rhodes University (BSc, 1949) and the University of Cape Town (MSc, 1950). In 1951, he joined the Joint Fisheries Research Organization (JFRO) in Zambia and Malawi and was soon promoted to the post of Chief Fisheries Research Officer. In 1963, he became the Director of the East African Fisheries Research Organization (EAFRO) and moved to its headquarters in Jinja, Uganda. Both the JFRO and the EAFRO were involved with fisheries development in the British Central African colonies and much survey and taxonomic work was necessary. The collections that resulted from these studies were usually sent to the British Museum (Natural History) in London although lesser components were sent to other institutions. On joining the J.L.B. Smith

Institute in 1972, and on the recommendation of Rex Jubb of the Albany Museum, Jackson revived the development of a freshwater fish component to the fish collection that had been practically nonexistent since Jubb moved to the Albany Museum in 1961. Jackson's studies included research programmes on Lake Cahora Bassa in Mozambique, Lake Le Roux on the Orange River, and Lake Malawi. He was Chief Professional Officer at the J.L.B. Smith Institute of Ichthyology from 1972 to 1984, after which he became an Honorary Fellow of the Institute. He retired in March 1984 and was replaced by Paul H. Skelton, a freshwater fish systematist. Jackson wrote a personal account on his work experiences in Africa that stands as a historical document on its own (Jackson, 2000). He passed away in Port Elizabeth on 24 February 2007, after a month in intensive care.

Robin L. Welcomme (b. 1938) was employed in the late 1950s and into the 1960s as Assistant Scientific Officer at the Water Pollution Research Laboratory, and later at the Salmon and Freshwater Fisheries Research Laboratory, in the UK. He then became Scientific Officer at the East African Freshwater Fisheries Research Organisation, Jinja (Uganda). While he was working in Jinja, he completed his PhD at Makerere College (University of East Africa, today Makerere University) on the effects of climatic change on the biology and ecology of certain fishes of the Lake Victoria basin. With FAO he was first a Fisheries Biologist in Benin, West Africa, then at FAO headquarters in Rome from 1971, successively a Fishery Resources Officer, Senior Fishery Resources Officer and, in 1989, Chief of the Service. As Chief, he was responsible for the overall supervision of inland fisheries and aquaculture programmes. Additionally, he was Secretary of the European Inland Fisheries Commission (EIFAC) and Technical Secretary to the Committee on Inland Fisheries for Africa (CIFA) and the Comisión para la Pesca Continental de Latino America (COPESCAL). He assisted with the FAO-wide programme on biological diversity and participated in the drafting of the Convention on Biological Diversity. So far he has authored approximately 130 publications including four books, of which *Fisheries Ecology of Floodplain Rivers* (1979) is probably the best known. He retired from FAO in January 1998 but has continued to work as a Senior

Research Advisor to Imperial College, London and continues to participate in national and international initiatives concerning the fisheries and ecology of rivers.

Anthony J. Ribbink (b. 1942), a lecturer at the Department of Zoology, Rhodes University, was employed in 1975 by the J.L.B. Smith Institute as the project leader in charge of studying the impact of the aquarium trade on the cichlid fishes of Lake Malawi. He assembled a team that spent the next eight years in Malawi. Ribbink, a skilled fish ethologist and ecologist, spent a great deal of time SCUBA diving and observing the fishes in their natural habitats. Collections of large numbers of Lake Malawi cichlids, including many undescribed species, were made and incorporated into the Institute's collection. Ribbink returned to Grahamstown in 1983 and became Deputy Director of the Institute in 1989. At the end of 1994 M.N. Bruton resigned and Ribbink became Acting Director of the J.L.B. Smith Institute until the appointment of Skelton to the post of Director in April 2005. Ribbink then returned to Malawi to take charge of the SADC/GEF<sup>3</sup> Lake Malawi/Nyasa/Niassa Biodiversity Conservation Project (1995–1999). This was a programme that had components such as research, conservation, science education and public awareness of science, and employed about 200 people.

James Alfred Cambray (b. 1945) was born in Canada in 1945. He received his BSc in Zoology from Carlton University, Ottawa (1969), and MSc (1982) and PhD (1993) from Rhodes University, Grahamstown. Cambray took over from Skelton as Curator of fish collection of the Albany Museum in 1984. His research interests include the early life history, ecology, conservation, and management of African freshwater fishes. His various projects have brought in specimens from a number of river systems, mostly in the Cape area, on a regular basis. Two projects Cambray had in Lesotho (1986, 1991) also contributed specimens to the collection.

Michael N. Bruton (b. 1946) was born in East London (South Africa) and completed his undergraduate studies in zoology at Rhodes University in 1968. In 1970, after completing an Honours degree, he moved to Lake Sibaya

in Zululand, where the University had established a field station in 1967. In 1972, he became Officer-in-Charge of the station, and stayed until the station was closed in 1977. During that time, he actively pursued a wide range of ecological studies at Lake Sibaya and elsewhere in Maputaland (an ecologically distinct part of Zululand), and made collections of fish and other vertebrates. For his studies on the fishes of Lake Sibaya, Bruton obtained his MSc degree in 1972 and his PhD in 1977 from Rhodes University. Bruton was appointed lecturer at the Institute in 1978, while he was still on his post-doctoral fellowship at the then British Museum. This was when he had forged a good relationship with Greenwood who later retired in Grahamstown. In 1980, the Institute was declared a Cultural Institution (= national museum) funded by the South African Department of National Education. This was followed by Rhodes University re-establishing, in 1981, J.L.B. Smith's old Department of Ichthyology under the name Department of Ichthyology and Fisheries Science (DIFS) to continue with the teaching of ichthyology. The university then appointed Bruton senior lecturer and Acting Head of Department. In 1981 the university also decided to confer the status of professor on the Director of the J.L.B. Smith Institute of Ichthyology, and Margaret Smith (wife of coelacanth-famed J.L.B. Smith) was the first to receive this title. She retired in 1982 and Bruton was appointed Director (by the Department of Education) and Professor (by Rhodes University). In the same year, the university appointed Tom Hecht as head of the new DIFS, but until he came down to Grahamstown later in the year Bruton wore the two hats of Institute Director and Head of Department at the university (Pote, 1996). Bruton's interest in wetland ecology attracted him to study the ecology of fishes in the Okavango Delta, Botswana.

Paul Harvey Skelton (b. 1948) joined the Albany Museum as Curator of Fishes and Vertebrates in 1971 after completing his BSc in Zoology at Rhodes University. He was fortunate to have Rex Jubb introduce him to, and guide him in, the systematics of the southern African freshwater fish fauna. He was also the first student to register, in 1973, and complete a postgraduate course with the J.L.B. Smith Institute. In 1980, he obtained a PhD from Rhodes University

<sup>3</sup>SADC: Southern African Development Community. GEF: Global Environmental Facility (of United Nations).

for research on the systematics and biogeography of redfin minnows, genus *Pseudobarbus* (Cyprinidae). In 1980, Skelton gained considerable curatorial experience through developing the fish collection at the Albany Museum and began to develop the Institute's freshwater fish collection through his own collecting trips. Skelton became involved in Bruton's Okavango programme (see above) before joining the J.L.B. Smith Institute. After his appointment he increased his involvement by joining expeditions and leading the surveys on the Okavango River in Namibia. He has contributed significant collections from Namibia, Zimbabwe, Malawi, Lesotho, and various parts of South Africa, including Natal, Transvaal, and the north-eastern Cape. The collection included about 1700 samples at the time of his appointment and grew nearly six-fold, to almost 10 000 in the 12 years before he left to join the J.L.B. Smith Institute, in January 1984. Although some attention was paid to fishes beyond the Cape Province, most of Skelton's research concentrated on the fishes of the Cape Fold Mountains. Skelton has also been concerned with the conservation of freshwater fishes and produced the first *South African Red Data Book – Fishes* (Skelton, 1977, 1987) as well as the data sheets for threatened southern African species for the IUCN (International Union for Conservation of Nature) Red Data book. Recently he published a *Complete Guide to the Freshwater Fishes of Southern Africa* (1993).

Denis Tweedle (b. 1949) was born in Corbridge, Northumberland (England). He received his BSc in Marine Biology/Zoology from University College of North Wales, Bangor (1970). Captivated by Africa, he left the United Kingdom and joined the Project for Promotion of Integrated Fisheries Development, Monkey Bay, Malawi in 1973, where he stayed until 1995. Then, as Research Associate, he joined the J.L.B. Smith Institute of Ichthyology to study the taxonomy and distribution of Malawi and southern African river fishes. After a three-year stay at Jinja, Uganda (1997–2000), he again joined SAIAB. As research associate, he contributes actively to the programme on taxonomy, distribution and conservation of southern African river fishes.

Glenn S. Merron (b. 1955) was born in New York. He received his BSc (1978) in Zoology from the New York State

University at Genesco, and MSc (1981) in Fishery Science from the University of Michigan, Ann Arbor. Following preliminary expeditions led by Bruton in Botswana, the J.L.B. Smith Institute of Ichthyology was invited to study the commercial fishery potential of the Okavango Delta. G.S. Merron, then a student of Bruton, was given the project. He established a research station in Maun, Botswana in 1985, from which he made extensive ecological collections in the Delta. Until 1987, he, together with scientists and students from Grahamstown, thoroughly sampled the river and the Delta, in all habitats, from Rundu, Namibia, down to Maun. Following the successful completion of this project, Merron continued working in the Okavango Delta with a three-year study of the effect on fishes of insecticides used to control the tsetse fly. Merron also worked in Zululand on the Phongolo River where he supervised a study of the effect of the timing of flood release from the Phongolopoort Dam on the fish populations of the Phongolo floodplain (1983–1987). For his work on the fishes of the Okavango Delta he was awarded a PhD from Rhodes University, Grahamstown, in 1991.

Previously, Roger Bills had worked in Zambia and on Lake Tanganyika for 10 years. In 1995, he was appointed to the J.L.B. Smith Institute of Ichthyology to succeed Paul Skelton as Curator of the Freshwater Fishes collections. At present, he is a senior aquatic biologist at the South African Institute for Aquatic Biology in Grahamstown (ex J.L.B. Smith Institute of Ichthyology). He has two main research interests, first on the biogeography and systematics of southern African freshwater fishes, and second on the conservation genetics and management of threatened freshwater fishes.

Melanie L.J. Stiassny, an American zoologist, received her BSc (1976) and her PhD (1980) from the University of London. Melanie, a student of Greenwood, became captivated by African cichlids during the research for her PhD. Now she is the Axelrod Research Curator in the Department of Ichthyology at the American Museum of Natural History (New York) and Adjunct Professor at Columbia University where she has active graduate and undergraduate teaching programmes. She has conducted extensive research throughout the world's

tropical waters, studying the evolution, behaviour, and conservation of fishes. Melanie's research aims at a synthesis of systematics, biogeography, and fish biology with strategies that integrate these into conservation planning. In Africa her projects were, and are, mainly focused on the freshwater fishes of Madagascar, Gabon and Congo. Recent fieldwork has focused on the fishes of west-central Africa, as part of Melanie's work on the soon to be published volume on this region (co-edited with the late Guy Teugels and Carl Hopkins *The Fresh and Brackish Water Fishes of Lower Guinea, West-Central Africa*).

Professor Lauren Jeanette Chapman is based at the Makerere University Biological Field Station and Fisheries Resources Research Institute in Uganda (for field studies) and at McGill University, Montreal in Canada (for laboratory studies). At the present time, her research focuses on aquatic ecology and aquatic conservation, with an emphasis on the physiological ecology, population ecology, and community ecology of freshwater fishes. In the field of aquatic conservation, she is currently focusing on patterns of species loss and resurgence in waters of the Lake Victoria basin of East Africa. Her recent work is focused on divergent selection across oxygen gradients in fishes, the interaction of hypoxia with other environmental stressors (e.g. introduced species), and the value of tropical wetlands in the maintenance of fish faunal structure and diversity.

In the early 1970s, with the assistance of the Dutch, the Tanzanian authorities planned to set up a large project of extensive fishing in the Mwanza area of Lake Victoria. Dutch funds allowed the construction of trawlers and a fishmeal factory. This factory was intended 'to treat' sixty tonnes of Cichlidae per day. In view of this threat, Kes D.N. Barel, of University of Leiden, sent to Tanzania some young collaborators who were very keen on fieldwork. Thus was born the HEST (*Haplochromis* Ecology Survey TEAM) in 1977. This multidisciplinary team undertook to study the Lake Victoria environment<sup>4</sup>. Of the various topics investigated, most of the research focused on the systematics, ecology and fisheries. The names of researchers who have mainly established the reputation of HEST are listed below.

HEST always worked in close cooperation with the local institution TAFIRI (Tanzanian Fisheries Research Institute).

Frans Witte (PhD 1987, Leiden) has built up an impressive track record as an ichthyologist and expert on Lake Victoria's fish communities. He worked as a member and leader of the HEST team. Now, as an expert on Lake Victoria cichlids based at Leiden University, he focuses on the adaptive responses of these species. In his lectures, F. Witte describes how Lake Victoria reacted to the decline of its biodiversity after the introduction of Nile perch. The dramatic decline of the haplochromines in Lake Victoria, due to ecological changes in the 1980s, and the subsequent recovery of some species, provided an excellent opportunity to study such responses. Particularly, he notes that heavy exploitation of Nile perch enabled a resurgence of some cichlid species, which show remarkable ecological and morphological responses.

Martien J.P. van Oijen, now also at Leiden, mainly deals with the piscivorous haplochromine cichlids of Lake Victoria. Nowadays, piscivorous cichlids have virtually disappeared from the catches in Lake Victoria, along with many other species, but prior to the Nile perch upsurge the piscivores were the most speciose trophic group among the haplochromines.

Kees Pleun Cornelis Goudswaard (b. 2 August 1950 in Dordrecht) considered the different factors which affected the life of Lake Victoria. His work was summarised in a thesis (2006) in which he elaborates on the different processes that took place concomitantly and explores their possible role in the changes that were observed in the lake.

Tijs Goldschmidt (b. 30 January 1953 in Amsterdam) is an internationally acclaimed expert on the evolutionary biology and ecology of the cichlids of Lake Victoria, the background scenery of his bestselling book, *Darwin's Dreampond* (1996). This book was shortlisted for the major AKO Literature Prize and was awarded the prestigious Science Prize from the Dutch Organization for Scientific Research.

Jan H. Wanink (b. 26 April 1953 in Laren) is a guest researcher at the Institute of Biology, University of Leiden, and an ecology project leader at Koeman en Bijkerk BV, Ecological Research and Consultancy. He mainly studied

<sup>4</sup> For a large bibliography of Lake Victoria, see Crul et al., 1995.

the pelagic cyprinid *Rastrineobola argentea* (vernacular name: dagaa) whose biomass considerably increased after the introduction of Nile perch. His work was summarised in a thesis (1998) whose central theme is the question *What caused the success of dagaa in the perturbed ecosystem of Lake Victoria?*

In conclusion, the HEST team has recorded the decline and loss of many endemic haplochromine species but they have also discovered a whole suite of previously unrecognised zooplanktivorous haplochromines. In the 1990s, they found another hundred species of cichlids living on rocky shores with life styles comparable to those in Lake Malawi. Finally, HEST also found a resurgence of some haplochromine species after the Nile perch started to decrease in the lake, following the huge export of fillets by fish factories.

The cichlid fishes are an extremely important group and they are widely used in scientific research and are popular with aquarists. So, in the last five decades, interest in this family has shown a spectacular rise. The behaviour, the ecology and the evolution of the numerous species of cichlids are spectacular, posing manifold scientific questions. Among some landmark publications, that by G. Fryer & T.D. Iles (1972), *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution*, constituted for a long time a kind of 'Bible' to all ichthyologists involved in cichlid studies. In the book, the authors synthesised all available information on the biology and evolution of the cichlids found in Lakes Victoria, Tanganyika, Malawi and some smaller lakes of East Africa. Since 1972, there has been a rapid increase in the number of publications on cichlid fishes especially at the beginning of the 1990s when the molecular techniques appeared. As the least known among those scientists particularly involved in cichlid studies, it is correct to accord homage to Professor Geoffrey Fryer, now an Honorary Professor of Biological Sciences at Lancaster University, England. Through this book and many original papers, Geoffrey Fryer has made a major contribution to the study of African ichthyology and evolution, and its remarkable demonstration of adaptive radiation.

In recent years, many investigators have undertaken new studies on the evolution and speciation of cichlids in the East African Great lakes. Perhaps most of these

might be considered mainly molecular biologists but they are also naturalists with wide interests and deep knowledge of the fishes in their favoured regions.

Professor Axel Meyer (b. 1960) is a German evolutionist who heads the Department of Biology, University of Konstanz (Germany). He and his team are among the major specialists concerning the evolution, particularly speciation, genetic differentiation and phylogeny of cichlid fishes in the East African cichlid radiations where, amongst other things, they have documented explosive rates of speciation, widespread parallel evolution in morphological, ecological and behavioural traits, and the importance of paleoclimatological influences on intralacustrine speciation patterns. They have also demonstrated that the lungfish – rather than the textbook favourite, the coelacanth – is the closest living relative among fishes to the land vertebrates (Brinkmann et al., 2004)<sup>5</sup>. Meyer has published more than 250 original articles, among which about 40 are especially dedicated to African cichlids.

Professor Ole Seehausen is a Swiss evolutionary ecologist who heads the Department of Fish Ecology and Evolution at Eawag (Swiss Federal Institute of Aquatic Science and Technology) in Dübendorf, Switzerland, which is among the world's leading aquatic research institutes. He is interested in the evolutionary processes and ecological mechanisms of origins and maintenance of biological diversity. This includes the ecology and genetics of ecological and behavioural polymorphisms and speciation, evolutionary community ecology, macro-ecology and conservation biology. In recent years, he has concentrated mostly on studying the large adaptive radiations of cichlid fish in African lakes, and, in particular, the radiation of haplochromines in Lake Victoria and smaller lakes in Tanzania and Uganda, as well as in the Zambezi region of southern Africa. He has published more than 80 original papers, almost all of which are concerned with cichlids in Lake Victoria.

Professor Christian Sturmbauer (b. 1960) is an Austrian ecologist who heads the Department of Zoology at the Karl Franzens University of Graz (Austria). He has

<sup>5</sup> For a complete bibliography about this subject see Meyer Lab Publications (<http://www.evolutionbiologie.uni-konstanz.de/index.php?section=51>)

collaborated on many works concerning the evolutionary history of Lake Tanganyika cichlids but, as an ecologist, he is mainly concerned with biological traits and behaviour of species. He has published about 30 original papers related to the Lake Tanganyika cichlids, and most of them are co-authored with W. Salzburger (see above).

Professor George Francis Turner is a British biologist who heads the School of Biological Sciences, Bangor University (Wales). Turner's research group works mainly on the behaviour, ecology, evolution and genetics of Lake Malawi cichlids, and is particularly aimed towards an understanding of the reasons for their explosive evolution. This work involves field work in Africa (including underwater research), molecular genetic studies, and mate choice and breeding experiments in the aquarium. He has co-authored about 60 original papers among which almost all of them are related to the Lake Malawi cichlids.

Professor Thomas D. Kocher is an American geneticist who works at the Department of Biology, University of Maryland (USA). His research is focused on the evolutionary genetics of cichlid fishes, mainly from Lake Malawi. Kocher's research team is interested in knowing how new species evolve and to elucidate the forces that contribute to speciation. His approach is to map and identify genes responsible for phenotypic differences among species; the ultimate goal is to identify the genes underpinning cichlid speciation and to account for the geographic distribution of allelic variants among populations and species in the wild. He has co-authored more than 60 original papers related to African cichlids, the most part of them dedicated to Lake Malawi.

Jay R. Stauffer is a distinguished Professor of Ichthyology of the Pennsylvania State University, School of Forest Resources (USA). His academic interests are dedicated to the behaviour, systematics and zoogeography of freshwater fishes. He and his colleagues are searching for congruence among morphological, genetic and behavioural data to delimit and describe effectively the cichlid species of Lake Malawi. As one of his major interests is also the biological control of the human disease bilharzia by Lake Malawi molluscivores, he has co-authored more than 70 publications concerning the biodiversity of the Lake Malawi cichlids.

Professor Kenneth Robert McKaye is an American biologist who is now a permanent resident of Malawi. Like many evolutionary biologists, he is attracted by the challenge of understanding the forces driving the explosive speciation among African Great Lakes cichlids. He has co-authored over 50 original papers referring to African fishes, many of them with J.R. Stauffer and most being dedicated to Lake Malawi cichlids.

Professor Norihiro Okada (b. 1947) is a Japanese geneticist who heads the Molecular Evolution Laboratory at the Tokyo Institute of Technology. His laboratory studies evolution using molecular biological techniques. Okada is not only concerned with fish studies but also works on the phylogeny of mammals. In fact, his laboratory comprises four primary research groups that approach the evolution of life from various viewpoints. Among them there is a 'cichlid group' that works on elucidating the molecular mechanisms of speciation. Using the diverse species of cichlid fishes in the Great Lakes of East Africa as a model, this group aims to identify genes that participated in the speciation of these fishes and apply this knowledge to the molecular mechanism of speciation. These studies started at the beginning of the year 2000 and Okada has co-published about 20 original papers. In 2008, a book entitled *Live Cichlids in the Southern Lake Victoria – On-going Speciation* was completed (Mizoiri et al., 2008). This book is in Japanese and not yet translated.

Building on the contribution made by these ichthyologists, a younger generation of researchers have now worked their way through the laboratories and established themselves in permanent posts. Craig R. Albertson is an American molecular biologist working as assistant professor at the Department of Biology, Syracuse University (USA). His research interests lie at the intersection of genes, development and evolution. His experimental model is the craniofacial skeleton in bony fishes. Specifically, he uses a cichlid model of Lake Malawi as a natural mutant screen for craniofacial shape. He views cichlid radiations as a collection of craniofacial mutants because cichlid radiations are characterised by extensive trophic diversity. Closely related species exhibit dramatic variation in head shape, providing a unique opportunity to

study patterns of natural variation in jaw morphogenesis. He has co-authored about 20 original papers about this subject of which half are with T.D. Kocher (see above).

Martin J. Genner is a biologist working at the University of Bristol and the Marine Biological Association of the UK. He mainly studies the molecular, population and community ecology of aquatic organisms, and currently focuses his work on European marine fishes and cichlid fishes of the African Great lakes. Males of many species of lekking cichlid fish build elaborate spawning craters from sand known as 'bowers'. He is investigating the evolution of these 'bowers' from a functional perspective, specifically testing whether they are traits developed by females to evaluate male fitness, or if they are mainly used by males to display species identity and social status in spatially explicit male hierarchies. He has co-published about 20 original papers about cichlid fishes of which the most part concern the Lake Malawi species.

Hans A. Hoffmann is a German biologist, Principal Investigator at the Section of Integrative Biology, University of Texas (Austin, USA). The research in the Hofmann laboratory seeks to understand the molecular and hormonal mechanisms that underlie social behaviour and its evolution. African cichlid fishes are an ideal model system to address these questions because of their recent, repeated and rapid radiations that have resulted in hundreds of phenotypically diverse species. In this context, this research has made considerable impact with its more physiological approach, about 10 papers being published in the past ten years.

At present, Mairi E. Knight is British lecturer in molecular ecology at the University of Plymouth (England). Before taking up this post, her research was centred on two study systems of which one is the African Great Lake cichlids. Her PhD was entitled *Sexual selection and speciation in Lake Malawi fishes*. She has co-published about 10 original papers about Lake Malawi cichlids.

Walter Salzburger (b. 1976) is an Austrian molecular biologist who works at the present in the Zoological Institute of the University of Basel (Switzerland). He has published many works about the speciation, adaptive radiation and phylogeny of East African cichlids, mainly in Lake Tanganyika. This young, but very promising

researcher is a student of Axel Meyer, with whom he always collaborates. He also participates in important work on the phylogeny and the phylogeography of East African squeaker catfishes (*Symodontis*).

Todd J. Streebman is an American postdoctoral fellow at the Department of Zoology and Program in Genetics, University of New Hampshire (USA). He works on cichlid fishes and their relatives and is primarily interested in the evolution of cichlid jaws, teeth and colour patterns. In collaboration with C. Albertson and T. Kocher (see above), he has mapped differences in the shape of cichlid jaws and teeth to common chromosomal regions. They have also shown that these phenotypes experienced a history of strong directional selection. This work suggests that the rapid and replicative nature of cichlid trophic evolution is the result of divergent selection on chromosomal packages encoding functionally linked elements of the craniofacial skeleton. He has co-published about 20 articles on this subject.

Sigal Balshine is a Canadian ethologist, associate professor at the Department of Psychology, McMaster University (Canada). Among her research interests, two topics concern Lake Tanganyika cichlid fishes. In many species of animals, it has been noticed that, sometimes, some individuals will forgo opportunities to reproduce in order to help others. Using the cooperative breeding fish, *Neolamprologus pulcher*, her team are investigating 'why helpers help'? To test models of parental care evolution, they use *Eretmodus cyanostictus* and have investigated the factors that maintain its monogamy. Although males can easily desert their mates, it has been discovered that they are both socially and genetically monogamous. She and her team have published about 20 papers on these topics.

Outside East Africa, some scientists have also carried out very interesting studies on species flocks. We may note two main examples: the work of Uli Schliewen on the Cameroonian crater lakes cichlids and that of the Dutch team at the Wageningen University on the Lake Tana barbs.

Ulrich Schliewen is a German ichthyologist heading the Ichthyology Section, Zoologische Staatssammlung München (ZSM, Germany). Scientific research at this section of the ZSM focuses on the assessment, systematics and biogeographic research of Bavarian fishes, and on



the assessment, description and evolutionary biology of African and Indonesian freshwater fishes. This laboratory works both with classical methods (description and analysis of morphological characters) as well as with molecular methods (DNA-analysis). Schliewen's studies are particularly focused on systematics, phylogeny, biogeography, diversity and speciation of freshwater fishes of West- and Central Africa. With his colleagues, his work on Cameroonian crater lakes (Schliewen et al., 1994) is evidently a strong contribution to speciation and to understanding sympatric speciation in animals generally. His laboratory is associated with a faunistic project on the described and undescribed ichthyofaunal diversity and distribution of the Cameroonian part of the Congo basin.

Ferdinand A. Sibbing (known as Nand Sibbing) is a Dutch ecologist, associate professor at the Experimental Zoology Group, Wageningen University (The Netherlands). Leopold A.J. Nagelkerke (known as Leo Nagelkerke) is a Dutch ecologist, senior lecturer at the Aquaculture and Fisheries Group, Wageningen University (The Netherlands). These two biologists have a long experience of working on the barbs of Lake Tana (Ethiopia). The source of the Blue Nile River, this lake harbours a unique species flock of 'labeobarb' fish, which certainly developed from a riverine ancestor that moved into open niches provided by the incipient lake. Nand Sibbing and his team pursued studies on these Tana barbs analogous to those conducted on cichlids. Some 15 original papers have emanated from their work.

As mentioned earlier, J. Daget set up a hydrobiology project in Chad in the 1960s. The team included several researchers working on the topic 'Study of a tropical lake under a semi-arid climate: Lake Chad' as part of the International Biological Programme. Following this, in the mid-1970s, two of them were also involved in a new programme in Côte d'Ivoire, the main topic of which was 'An aquatic monitoring of the rivers treated with larvicides in the OCP area<sup>6</sup>'. Initially carried out in the core area

of the OCP programme, this monitoring was extended first eastwards, then also to the western part of the OCP area. A team loaned by Orstom (now IRD: Institut de Recherche pour le Développement) was in charge of carrying out this monitoring, first in Côte d'Ivoire then in Mali. A lot of field research led to better knowledge of the systematics and ecology of fish in Western Africa.

Although many researchers took part in this programme for varying lengths of time, three in particular contributed to the ichthyological knowledge of the area. Christian Lévêque (b. 1940) was the first director in charge of the Laboratory of Hydrobiology in Bouaké (Côte d'Ivoire) from 1974. At the beginning of the 1980s, he also set up a multidisciplinary programme on freshwater fish in West Africa (PEDALO: Poissons d'Eau Douce d'Afrique de L'Ouest) that allowed him, with assistance from other institutes, to add significantly to our knowledge. The present author became head of the laboratory of Hydrobiology in Bamako (Mali) in 1984 from where he coordinated the various parts of the PEDALO programme in the field. These two researchers focused their work on inland waters *sensu stricto*, while Jean-Jacques Albaret (b. 1948) carried out work on the ecology of brackish-water fishes in Côte d'Ivoire and in Senegal. A synthesis of all the results obtained in Africa, and most particularly in Western Africa, was recently published by Lévêque & Paugy (2006).

In Lake Chad (Nigerian banks) and in Lake Turkana (Kenyan banks), A.J. Hopson and his wife Jane Hopson carried out a lot of ecological work published in a famous report which was edited into six volumes (Hopson, 1982). In addition, they also published some papers about *Barbus* species, particularly from Ghana.

Tomi Petr was a FAO Fishery Resources Officer. His main focus was dedicated to fisheries. He published or edited numerous syntheses about natural lakes and reservoirs (Ita & Petr, 1983; Kapetsky & Petr, 1984), mainly in western Africa, where he tried to evaluate their contribution to yield and potentials for exploitation. In the middle of the 1980s, his research was directed more towards other locations, mainly in Asia.

To the authors already mentioned, we may add the names of other recent contributors to our knowledge of

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<sup>6</sup>OCP = Onchocerciasis Control Programme. It includes the following countries: Western Senegal and Guinea Bissau, Guinea, Sierra Leone, Northern Liberia, Côte d'Ivoire, Southern Mali, Burkina Faso, Central and Northern Ghana, Northern Togo and Benin.

the African freshwater-fish fauna: Carl Hopkins (working in Lower Guinea), André Kandem Toham (Cameroon), Philippe Laléyé (Bénin) and Beniño Roman (Upper Volta basin and Rio Muni, today Equatorial Guinea).

### The ethologists

The East African Great Lakes are well known as 'biodiversity hotspots', with spectacular endemic fish faunas, of which the cichlid flocks offer unique opportunities for the investigation of the mechanics of species evolution and coexistence. To assess the behaviour of each species, underwater observations (by SCUBA divers) have been made, especially in the clear waters of lakes Tanganyika and Malawi. In the former, Japanese and African scientists, led by Hiroya Kawanabe, used SCUBA to observe cohabitation in the highly diverse rocky-shore communities (Kawanabe et al., 1977). Kawanabe (born in Kyoto on 10 May 1932) was employed in the Department of Zoology, Faculty of Science, Kyoto University, as instructor (1960–1961), lecturer (1961–1967), associate professor (1967–1977) and then professor (1977–1993). He devoted his final working years to being Director of the Centre for Ecological Research (1991–1996). After his retirement, he was employed as Director General of the Lake Biwa Museum (for a complete biography see Yuma & Harada, 1998). These underwater studies (1977–2004) had highlighted the intense inter- and intraspecific competition for breeding and feeding sites, also examples of cooperative behaviour and many unusual breeding strategies (Lowe-McConnell, 2006). In Lake Malawi, Tony Ribbink (see above) and his team also used underwater observation to determine 'Mbuna' relationships (Ribbink et al., 1983). Aquarists (see below) have also published much valuable information on cichlid ecology and behaviour in these lakes based on underwater observations using SCUBA (Koning & Diekhoff, 1992; Konings, 2001).

The behaviour of African river fishes was also studied by Bernd Kramer, a prominent ethologist who described the (intra- and inter-specific) electro-communication (Kramer, 1990) and the acoustic signalling behaviour among mormyrid fishes (Kramer,

1996). Kramer also published numerous papers about the systematics and taxonomy of African mormyrids.

### The aquaculturists and aquarists

The findings of the ecologists mentioned above constitute a biological framework for application in fisheries and, particularly, in aquaculture. Although aquaculture is of considerable antiquity, especially in the Far East, and even though the first record of fish in ponds is from an Egyptian bas-relief, fish farming in Africa is an activity of very recent origin. However, although fish were not held in captivity, practices such as trapping them behind fences (e.g. 'acadjas') are an old tradition in places like Benin. If we consider only indigenous species, the first keeping of tilapia is recorded in Kenya in 1924 (Copley, 1954). However, such fish culture was sporadic until an upsurge of activity in Africa, after World War II.

Among the best known specialists in aquaculture, we can list pioneers such as J. Lemasson, A.F. De Bont, Jean-Claude Micha (b. 1941), Marcel Huet, J. Bard, Paul Planquette (1940–1996) and Paul De Kimpe (b. 1927). During the first phase, aquaculture was more or less empirical and carried out following European techniques. Later, pisciculture evolved by adapting the techniques to the local species based on developing knowledge of their biology and through the work of aquaculturalists such as Thomas Hecht (b. 1948), Jérôme Lazard and Marc Legendre (b. 1955).

As a result of the late and restricted development of aquaculture in Africa, fish culture production in tropical Africa still amounts to only 10 000 tonnes per annum. Among the species used for fish culture, many cichlids have excellent attributes and they are easily bred in captivity, with tilapias – 'the aquatic chicken' – undoubtedly most popular in Africa. The Belgians in Congo were certainly the first to describe the advantages of using tilapias for warm-water fish culture. The use of tilapias as culture fish was later stimulated by Roger Pullin from ICLARM (International Center for Living Aquatic Resources Management; today the WorldFish Center) (Lowe-McConnell, 2006). ICLARM organised an International Conference on the Biology and Culture of Tilapias in 1980. This first major conference

about 'the aquatic chicken' brought together many aquaculturists including Jean-Claude Philippart (Belgium), Eugene K. Balon and David L.G. Noakes (Canada) and, obviously, Ethelwynn Trewavas and Ro Lowe-McConnell (UK). Later, ICLARM and other institutes organised a regular International Symposium on Tilapia Aquaculture (ISTA) which shows the interest in these species' culture. The first (ISTA I) was held in Nazareth (Israel) in 1982 and the most recent (ISTA VII) in Veracruz (Mexico) in 2006. Tilapias have now been distributed to fish culture centres outside Africa – *Oreochromis niloticus*, for example, has been introduced to some 90 countries – and the 'aquatic chicken' has now entered economic globalisation with the 'success story' of the GIFT (Genetic Improvement of Farmed Tilapia) programme (Gupta & Acosta, 2004). It is not certain, however, that the GIFT project was a gift for Africa as the GIFT patent was subsequently sold to a private company (GenoMar), operating in Asia rather than Africa.

Reference should also be made to the problems associated with the introduction of exotic species, and in particular, the exotic tilapiine introductions into Lake Victoria. *Oreochromis esculentus* (local name 'ngege') and *O. variabilis* (local name 'mbiru') were two tilapia species endemic to Lakes Victoria and Kyoga, until they were artificially spread around East Africa and introduced into small lakes, dams and ponds. In 1954, in an attempt to boost tilapia catches, *Tilapia zillii*, a macrophyte-feeder present in Lake Albert, was introduced into Lake Victoria. With it came *O. leucostictus*, and more importantly for future events, the Nile tilapia *O. niloticus*. *T. zillii* first appeared in gillnet catches in 1956. It spread rapidly at the north end of the lake and became the dominant species in former *O. variabilis* areas. The ousting of *O. variabilis* by *T. zillii* appeared to be attributable to interspecific competition for breeding and nursery grounds. *O. niloticus* and *O. leucostictus* became much more abundant after 1964. *O. leucostictus* became the dominant species in lagoons around the lake, and near papyrus beds, while *O. niloticus* became dominant on the former *O. esculentus* grounds. Very quickly, introduced species replaced *O. esculentus* (it now seems with also some hybridisation with *O. niloticus*; Lowe-McConnell, 2006). At the present, *O. esculentus* is thought to

be 'extinct' from the main Lake Victoria but it is still found in certain small satellite lakes that are free of *O. niloticus*.

If fish farming constitutes an important economic challenge for developing countries, the ornamental fish trade may also emphasise the economic value of biodiversity. However, it is estimated that African species represent only approximately 3 % of the global wholesale trade value of ornamental fishes (Bassler, 1994). Nevertheless, small though this trade may be on a world scale, use of natural and wild resources of ornamental fish is associated with many risks, including over-exploitation of natural stocks. According to trade sources, the majority of freshwater fish in the aquarium trade are derived from captive breeding or aquaculture. In fact, we do not know the true percentage of fish that are collected directly from the wild (Rosser, 2003). Even if no African species seem to be listed in the IUCN Red List, the aquarium industry has a key role to play and a greater emphasis on pond culture would take the pressure of exploitation from sensitive wild stocks.

In Africa, cichlids make up the main group reared for trade; these fishes are reared quite easily, and are traded significantly through exchanges between hobbyists. Killies (cyprinodontiforms) constitute another valuable group to hobbyists but not for traders. Among the best specialists in these groups, there are both scientists and hobbyists. Among the latter, the following have acknowledged, strong reputations.

In the case of cichlids, each ichthyologist is generally concerned with one group, or one area. I quote below the more famous: Pierre Brichard (Lake Tanganyika), Stuart Grant and Ad Koning (Lake Malawi), Anton Lamboj (Western Africa), Paul V. Loiselle (Madagascar, West Africa, lakes Victoria and Tanganyika), Lothar Seegers (Lake Rukwa) and Jos Snoeks (lakes Kivu and Tanganyika).

For killies: Jean-François Agnès (*Aphyosemion*, Cameroon), Jean-Louis Amiet (*Aphyosemion*, Cameroon), John Paul Arnold (Western Africa), André Brosset (ecology of killies from Gabon), Jean Huber (*Aphyosemion*, Gabon, Congo, 'killidata'), Alfred C. Radda (Aplocheilidae, Western Africa, Cameroon), Erhard Roloff (Liberia, Sierra Leone, Mozambique; 1903–1980), Raymond Romand (Guinean province), Jørgen Jacob

**Table 7.** The 10 main collectors for the freshwater fish collection of the Paris Museum. Numbers indicate the number of samples brought (a registration number for each sample). \*Collections were made before the name change from Orstom (Office de la Recherche Scientifique et Technique d'Outre-Mer) to IRD (Institut de Recherche pour le Développement). AMNH: American Museum of Natural History (New York, USA); ENSA: École Nationale Supérieure Agronomique (Yaoundé, Cameroon); MRAC: Musée Royal de l'Afrique Centrale (Tervuren, Belgium).

Collectors Organisation	Daget		Lévêque		Paugy		Stauch		Depierre		Bigorne		Teugels		Lavoué		Blache		Fermon	
	MNHN	Orstom*	Orstom*	Orstom*	Orstom*	Orstom*	Orstom*	Orstom*	ENSA	Yaoundé	Orstom*	Orstom*	MRAC	AMNH	Orstom*	Orstom*	Orstom*	MNHN		
Benin	16	44	96	13																
Burkina Faso	174	21	3	2																
Burundi												21								
Cameroon							140	572												2
Central African Rep.	1						8													
Chad	24	21					21													288
Congo	1	546																		
Côte d'Ivoire	255	323	157	67	1	180	1													
Democratic rep. Congo					1	15														9
Ethiopia							4													
Gabon																385				
Ghana		87	9	5		57														72
Guinea	369	510	195	390		176														
Lake Tanganyika																				
Lake Victoria																				
Mali	445	15	107	65																
Niger	1	1		1																
Nigeria	2				3															
Senegal	91	45	44	17																
Sierra Leone		33	331																	
South Africa	1	8	1																	
Togo		111	154	3																
Total	1380	1198	1097	563	724	572	449	385	288	173										

Scheel (cyprinodontiforms, Africa; 1916–1989) and Rudolf H. Wildekamp (cyprinodontiforms, Africa).

In conclusion, it must be stressed that there are still numerous gaps in our knowledge of African freshwater fish, particularly in their ecology, but also in phylogeny and phylogeography. To answer these questions, advances depend mainly on new collections coming from little explored areas, such as the Congo basin, or from conflict areas such as Angola, for example, which are dangerous places to work. Nevertheless, new collecting trips continue to depend largely on development programmes. In Western Africa, for example, during recent decades the researchers of Orstom (now IRD: Research Institute for Development) were among the main providers of collections for the Paris Museum (Table 7).

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