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Walking the tightrope: trends in African freshwater systematic ichthyology

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Africa is blessed with an abundance and rich diversity of freshwater fishes, reflecting its Gondwanan history and geographical position astride the equator. Africa is, however, relatively poorly serviced scientifically, in this respect presenting a challenge to the tension between conserving biodiversity and sustainable development. Biosystematics has experienced several paradigm shifts in the past half century, including the rise of cladistics and more recently the adoption of molecular DNA applications to taxonomy and phylogeny and the assembly and manipulation of large data sets in an era of major development of bioinformatics. The richness of African biodiversity is a magnet to the global systematic community that, to a degree, offsets the disadvantage of an impoverished indigenous scientific capacity. Conservation biology, however, is rooted more closely to the local situation and therefore requires indigenous taxonomic services that are inevitably scarce. Balancing this network of tensions between scientific knowledge generation and application is like walking a tightrope for existing African scientific resources, and to cope it is essential to embrace modern innovative approaches such as barcoding to identify organisms. This paper considers the historical development of African freshwater ichthyology, presents a suite of recent examples illustrating trends in systematic ichthyology in Africa and draws conclusions to suggest that both traditional and new-age approaches to taxonomy are necessary for a complete understanding and appreciation of African freshwater fish diversity and its conservation. The chosen examples also suggest that the tensions between the approaches can be effectively managed provided exponents work collaboratively. The emerging evidence indicates that the combined skills and insight of complex scientific teams including systematists, ecologists, molecular biologists and earth scientists are needed to resolve the deep complexity of evolution in terms of space, time and form.

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Key words: Barcode of Life; freshwater fishes; historical ichthyology; molecular systematics; taxonomy.

INTRODUCTION

Africa is the first continent to receive a comprehensive assessment of the conservation status of major elements of its freshwater biodiversity, including freshwater fishes (Darwall *et al*., 2011). This assessment revealed the character of freshwater biodiversity across the continent thereby explicitly documenting in clearer detail than ever before the diversity and distribution of freshwater fishes, molluscs, odonates, crabs and freshwater plants. Not only is there a rich diversity of these organisms but they are largely endemic and incompletely described.

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In conducting the IUCN conservation assessment of freshwater fishes for the southern African region of the study, it was evident that current taxonomy is trailing the discovery of species (Tweddle *et al*., 2009). The situation is similar elsewhere in Africa (Lowenstein *et al*., 2011; Snoeks *et al*., 2011) and this resurrects the spectre of a taxonomic impediment to the conservation of biodiversity in a rapidly developing continent (Stiassny, 2002).

So, what is the situation regarding the taxonomy and systematics of freshwater fishes in Africa? What are the current trends and prospects? Daget (1994) and Lévêque (1997) record much of the taxonomic history of Africa but an up-to-date comprehensive history of the continent's ichthyology has yet to be written. The tools for such an analysis are becoming increasingly available with the development of modern digital databases (Peterson *et al*., 2010). Understanding the history can reveal key factors driving the science in Africa and while this will not resolve the situation going forward, it could assist by indicating areas where strategic interventions may be made.

This paper reflects a personal perspective and presents an account that attempts to capture the dynamics of the present taxonomic situation in African freshwater fishes through exposing the trends and illustrating these with contemporary examples.

METHODS

Historical and taxonomic data were extracted from the *California Academy of Sciences Catalog of Fishes* database up to the end of 2010 (Eschmeyer & Fricke, 2011). Descriptions of species are attributed equally to all authors in a multi-authored paper.

FRESHWATER FISHES OF AFRICA

Africa is blessed with an abundance and rich diversity of freshwater fishes, reflecting its Gondwanan history and geographical position astride the equator. The most recent assessments of African freshwater fish diversity indicate that there are *c*. 3000 species described with sound indications that the discovery curve is rising (Lévêque, 1997; Lévêque *et al*., 2008; Snoeks *et al*., 2011). The tropics are especially rich in diversity and the Great Lakes of the African Rift and the Congo River are biodiversity hotspots (Thieme *et al*., 2005; Snoeks *et al*., 2011). Recent comprehensive reviews of the well-watered rivers of the coasts of Central West and West Africa (Low Africa) further expose this rich and incompletely discovered diversity of tropical fishes (Paugy *et al*., 2003*a*, *b*; Stiassny *et al*., 2007*a*, *b*). By contrast the diversity in the rivers of High Africa, essentially eastern and southern Africa from the Ethiopian highlands to the Cape, is low, with increasing paucity in species numbers to the far south (Skelton, 1994). The great African drylands and deserts, in particular the Sahara and Kalahari–Namib, as well as the Sahel and the Horn of Africa are naturally ichthyologically impoverished regions with isolated relict fish populations in oases and underground caverns and lakes (Lévêque, 1990; Thieme *et al*., 2005). African lakes, both large and small, frequently have distinctive fish faunas. The Great Rift Lakes are well known for their extensive species flocks of cichlids (Fryer & Iles, 1972; Coulter, 1991; Snoeks, 2000, 2004; Thieme *et al*., 2005). Less extensive

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species flocks of other fishes are also characteristic of African lakes (Stiassny *et al*., 2002; Brown *et al*., 2010; Getahun, 2011).

The African freshwater fish fauna is dominated by a few distinct lineages, species of the diverse ostariophysan orders Cypriniformes, Characiformes and Siluriformes, the family Cichlidae, due to its particular proliferation in especially the Great Rift Lakes and large tropical rivers, and the cyprinodontiform family Nothobranchiidae (Snoeks *et al*., 2011; Table I). A distinctive character is imparted to the continental fauna by the presence of relict ancient lineages, Polypteridae and Protopteridae, or otherwise relatively primitive lineages like the Osteoglossiformes and Mormyridae. The African ostariophysan families also are largely endemic, exceptions being the Cyprinidae and siluriform families Clariidae and Bagridae. In addition to primary and secondary division freshwater fishes, the lower reaches of African freshwater systems harbour a large number of characteristically marine families, with some imparting significant character to the ichthyofaunal communities, *e.g.* the Clupeidae, Gobiidae, Eleotridae, Mugilidae, Tetraodontidae and Anguillidae.

SYSTEMATIC ICHTHYOLOGY IN AFRICA: A HISTORICAL PERSPECTIVE

In contrast to this natural wealth of fish biodiversity, Africa has a dire poverty of functional systematic scientific institutions and resources. This is, in part, an important element in the taxonomic impediment and absence of local drivers for conservation (Stiassny, 2002; Skelton, 2007). Understanding this situation is relevant if changes are to be made or the dependency properly managed for biodiversity conservation.

The scientific discovery of African freshwater fishes spans the full period since Linnaeus (1758) introduced the binomial nomenclature [Fig. 1 (a), (b)]. Linnaeus (1758) is credited with describing six species of African fishes. The initial pace of discovery remained low until around the 1860s when there was a sudden spike in contributions from a number of mostly German ichthyologists including Günther based at the British Museum of Natural History (BMNH) (Table II). The tempo increased from the 1890s through to the 1930s, with an all-time peak after the turn of the century in tune with the expansion of exploration accompanying the colonial scramble for Africa. It was in this phase that Boulenger (768 descriptions) at the BMNH and Pellegrin (269 descriptions) at the Museum National d'Histoire Naturelle (MNHN) in Paris, the top two most prolific contributors, were active (Table II). The pace of discovery remained high over the first half of the 20th century but declined significantly around the 1940s due to the Second World War, and escalated again in the 1960s and 1970s before declining to current moderate levels of discovery. Poll, working for 58 active years beginning in the 1930s at the Royal Museum for Central Africa in Tervuren, Belgium (MRAC), is the third most prolific author of African species descriptions (252). He effectively established a tradition of major contributions from the MRAC that persists through four generations to the present.

Current levels of new species descriptions are lower than they were in the 1960s and 1970s or in the first four decades of the 20th century, 254 new species descriptions were made in the past decade (2001–2010) [Fig. 1 (a), (b)], a total of 6% of all descriptions since 1758. The 50 years since 1960 has delivered 1296 descriptions,

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Table I. Number of species per family of fishes in African fresh waters, arranged in descending species richness. Percentage rounded to nearest whole number where 1% or >1%, or 0·5 where <1% but >0·5% or to nearest 0·1% where <0·5%. Data derived from Eschmeyer & Fricke (2011)

Family	Species	Per cent of total
Cichlidae	937	33·0
Cyprinidae	503	18·0
Nothobranchiidae	238	8·0
Mochokidae	193	7·0
Mormyridae	189	7·0
Alestidae	111	4·0
Distichodontidae	94	3·0
Claroteidae	83	3·0
Amphiliidae	82	3·0
Clariidae	78	3·0
Poeciliidae	67	2·0
Mastacembelidae	41	1·0
Schilbeidae	31	1·0
Kneriidae	31	1·0
Anabantidae	28	1·0
Clupeidae	25	1·0
Gobiidae	21	1·0
Malapteruridae	17	1·0
Eleotridae	12	0·5
Polypteridae	12	0·5
Bagridae	9	0·5
Citharinidae	6	0·2
Mugilidae	6	0·2
Tetraodontidae	6	0·2
Syngnathidae	5	0·2
Anguillidae	5	0·0
Ariidae	4	0·1
Protopteridae	4	0·1
Channidae	3	0·1
Cyprinodontidae	3	0·1
Dasyatidae	3	0·1
Notopteridae	3	0·1
Sciaenidae	3	0·1
Carangidae	2	0·1
Lutjanidae	2	0·1
Soleidae	2	0·1
Synbranchidae	2	0·1
Ambassidae	1	0·0
Atherinidae	1	0·0
Blenniidae	1	0·0
Cobitidae	1	0·0
Denticipitidae	1	0·0
Elopidae	1	0·0
Hepsetidae	1	0·0
Pantodontidae	1	0·0

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TABLE I. Continued

Family	Species	Per cent of total
Phractolaemidae	1	0·0
Plotosidae	1	0·0
Polynemidae	1	0·0
Pristidae	1	0·0
Sparidae	1	0·0
Total	2874	

30% of all descriptions since 1758. This is reflected in the period of activity by the top 50 authors (Table II), 62% were primarily active between 1950 and 2010, 22% between 1900 and 1950, 12% between 1850 and 1900 and two (4%) between 1801 and 1850.

Of the top 50 authors of African freshwater fish species 37 (74%) are from Europe, 10 (20%) are from the U.S.A. and only three (6%) are African based. Of the African based, all three are from South Africa. Extending the analysis to the top 100 contributors, the percentages are essentially similar (Europe 76%, North America 16% and Africa 6%). The European scientists in the top 50 authors are mainly drawn from four nations, Germany (11), France (9), Belgium (7) and the U.K. (6) with the total descriptions by nationality reflected in Fig. 2. Descriptions from the U.K. (1407; 33%) far exceed other nations when those of the Belgian scientist Boulenger and the German Günther are included. Both these leading taxonomists were tenured at the BMNH at a time (1860–1920) when collections emanating from colonial Africa were escalating to a peak. The number of German (689; 16%) and French (650; 15%) are similar, and the Belgian (426; 10%) and North American (411; 10%) contributions are similar, with the differences between the nations found in temporal factors (*i.e.* when scientists were active) and the institutional bases of the taxonomists. In the case of France and Belgium the taxonomists are primarily from a single active institution (MNHN and MRAC respectively), in contrast to Germany and North America, where researchers were based from a spread of institutions.

The global sociopolitical history of each nation has, to a greater or lesser extent, affected the temporal fortunes of each of its contributions to African freshwater fish systematics. The colonial history of European nations is an important factor. The major African colonial powers were Britain and France. The African freshwater fish collections of the national natural history museums of these nations are large, scientifically rich resources derived from exploration of their extensive colonial territories. In both cases, multiple generations of researchers beginning in the 19th century and throughout most of the 20th century actively described new species from these collections. In the case of both the BMNH and the MNHN, taxonomic activity on African freshwater fishes essentially ceased at the end of the 20th century with the passing of the generation of researchers that assumed research around the end of the colonial period. Germany was also an active colonial power in Africa and therefore had notable African freshwater fish taxonomic inputs in the 19th century based on pre-colonial [*e.g.* in the case of Rüppell (1829) and Peters (1868)] and colonial collections to its various museums up until the First World War in 1914. Significant taxonomic inputs from German researchers resumed late in the 20th century. Belgium has

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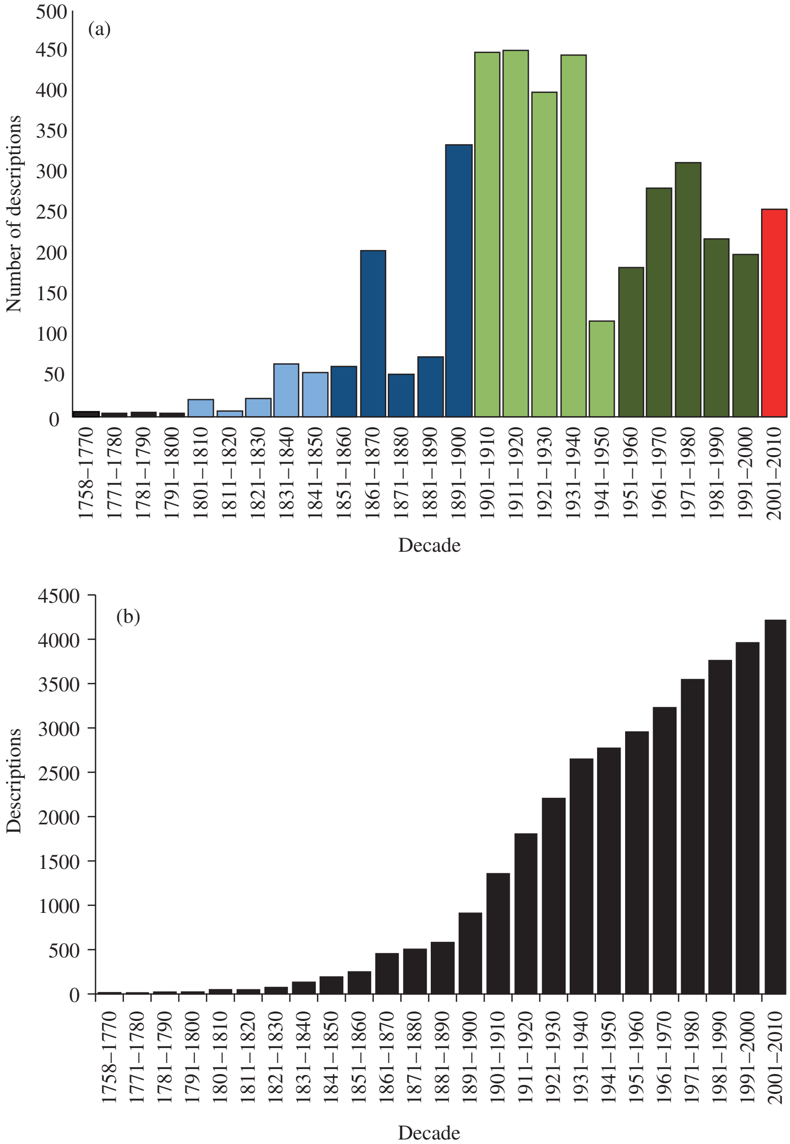

FIG. 1. (a) The number of taxonomic descriptions of fish species in African freshwaters described per decade from 1758 to 2010. The span of decades within a century where a lighter shade represents the first five decades and a darker shade the last five decades are 18th (■), 19th (■) 20th (■) and 21st (■). (b) The accumulative number of valid taxonomic descriptions of fish species in African freshwaters, by decades since 1758. Data derived from Eschmeyer & Fricke (2011).

achieved a disproportionate influence (in relation to its colonial presence in Africa) through the extensive collections in the MRAC that was established specifically for the purpose of housing collections from the Belgian Congo in 1898. The freshwater fish collections in the MRAC derived over the first half of the 20th century until the 1960s were therefore mostly from the ichthyologically hyperdiverse colony of the

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TABLE II. Top 50 authors of fish species in African freshwaters by number of described species as at December 2010. Data derived from Eschmeyer & Fricke (2011). Nationality ascribed by P. H. S. Active years measured from the year of publication of a first description to the year of publication of the last description

Author	Nationality	Described	Valid (n)	Valid (%)	First	Last	Active years
Boulenger	U.K. (Be)	768	543	71	1887	1923	37
Pellegrin	Fr	269	150	56	1899	1941	43
Poll	Be	252	209	83	1932	1987	56
Trewavas	U.K.	163	146	90	1928	1984	57
Günther	U.K. (De)	151	104	69	1860	1903	44
Fowler	U.S.A.	107	41	38	1903	1958	56
Steindachner	Au	92	42	46	1864	1915	52
Regan	U.K.	89	70	79	1906	1929	24
Ahl	De	86	33	38	1922	1939	18
Greenwood	U.K.	74	72	97	1956	1994	39
Daget	Fr	60	49	82	1948	1984	37
Peters	De	60	36	60	1844	1882	39
Nichols	U.S.A.	60	32	53	1917	1954	38
Thys van den Audenaerde	Be	59	48	81	1960	1996	37
Valenciennes	Fr	58	18	31	1835	1850	16
Radda	De	57	43	75	1970	1987	18
Stauffer	U.S.A.	55	53	96	1985	2009	25
Gilchrist	SA	50	8	16	1908	1917	10
Thompson	SA	49	7	14	1908	1917	10
Roberts	U.S.A.	46	45	98	1966	2010	45
Stiassny	U.S.A.	40	40	100	1989	2010	22
Seegers	De	38	36	95	1981	2008	28
Hanssens	Be	36	36	100	2003	2004	2
Stewart	U.S.A.	34	33	97	1975	1984	10
Wildekamp	Ned	33	33	100	1977	2010	34
Lönnberg	Swedish	33	13	39	1895	1924	30
Huber	Fr	32	29	91	1976	2007	32
Konings	De	29	28	97	1990	2009	20
Holly	De	29	18	62	1926	1930	5
P. Skelton	SA	28	28	100	1974	2010	36
H. Sauvage	Fr	27	20	74	1874	1884	11
Griscom	U.S.A.	27	17	63	1917	1917	1
David	Be	27	14	52	1935	1937	3
Vinciguerra	Fr	26	18	69	1883	1931	49
Rüppell	De	26	17	65	1829	1852	24
Castelnau	Fr	26	8	31	1855	1861	7
Teugels	Be	25	25	100	1987	2005	19
Berkenkamp	De	25	18	72	1973	2003	31
Pfeffer	De	25	16	64	1889	1896	8
De Vos	Be	24	23	96	1981	2001	21
Worthington	U.K.	23	13	57	1929	1937	9
Blache	Fr	22	5	23	1960	1964	5
Lambert	Be	21	21	100	1958	1968	11

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TABLE II. Continued

Author	Nationality	Described	Valid (n)	Valid (%)	First	Last	Active years
Lewis	U.K.	21	19	90	1974	1982	9
Pappenheim	De	21	19	90	1903	1914	12
Hilgendorf	De	20	18	90	1888	1905	18
McKaye	U.S.A.	20	18	90	1982	1997	16
Géry	Fr	19	18	95	1964	2003	40
Bowers	U.S.A.	19	17	89	1993	1997	5
La Monte	U.S.A.	19	8	42	1931	1953	23

Au, Austria; Be, Belgium; De, Germany; Fr, France; Ned, Netherlands; SA, South Africa; valid, the currently accepted senior synonym for a described species.

Belgian Congo. In the period since the independence of the Democratic Republic of the Congo (post 1960), the MRAC has adopted progressive collection policies focused primarily on Central and West Africa. More importantly, the institution has employed and trained a succession of proactive freshwater fish systematists who have sustained the Belgian influence in African freshwater fish taxonomy to the present time.

By contrast with these institutionally driven contributions, the North American influence on African freshwater ichthyology is an outcome of efforts by individuals at various museums and universities to engage in specific expeditions and projects designed to explore the biodiversity of Africa. Substantial descriptions of species have been made from the collections returned by these expeditions (Nichols & Griscom, 1917; Fowler, 1930). There are several institutions involved but the main

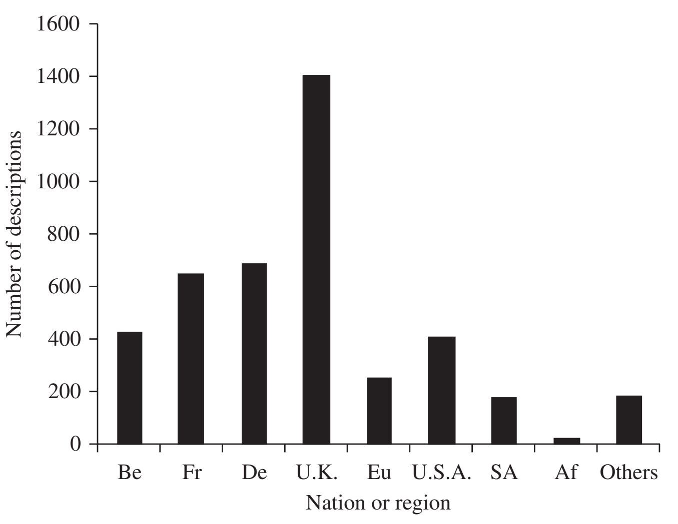

FIG. 2. The number of taxonomic descriptions of African freshwater fish species by nationality of authors from selected nations or regions. Data derived from Eschmeyer & Fricke (2011). Af, Africa; Be, Belgium; De, Germany; Fr, France; SA, South Africa.

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ones are The Academy of Natural Sciences in Philadelphia, The American Museum of Natural History in New York City, Cornell University in Ithaca and the National Museum of Natural History (Smithsonian Institution) in Washington, DC.

African contributions to the description of African freshwater fishes are few by comparison with scientists from non-African nations (Table II). The majority of African-based descriptions are in publications from South African scientists based at South African institutions, although sporadic descriptions have come from other countries, *e.g.* Bell-Cross (1975) from Zimbabwe (then Rhodesia). There is a growing recent trend for African students and researchers to publish freshwater fish systematic research jointly with external ichthyologists (Katongo *et al.*, 2005, 2007; Kramer *et al.*, 2007; Stiassny & Getahun, 2007; Kramer & Swartz, 2010; Lowenstein *et al.*, 2011).

The first major freshwater fish faunal account from South Africa was by Gilchrist & Thompson (1913, 1917) based on collections in the South African Museum (SAM) in Cape Town. Barnard's (1938, 1943) studies were also derived from the SAM collection. Freshwater ichthyology ceased at the SAM after Barnard, and the focus in South Africa shifted to the Albany Museum, Grahamstown, where Jubb was active in the late 1950s and the 1960s (Skelton & Stuart, 1987). Jubb (1967) described new species from southern Africa and synthesized an overview of the fauna. The first author succeeded Jubb at the Albany Museum and in 1984 moved to the JLB Smith Institute of Ichthyology [renamed the South African Institute for Aquatic Biodiversity (SAIAB)]. SAIAB is currently the main centre for African freshwater fish systematics in South Africa, and several researchers based there are engaged in the discipline.

Elsewhere in Africa, there are practically no well-established institutions with functional freshwater fish collections or practising ichthyologists. The National Museum in Kenya is a possible exception as it has a fish collection with dedicated staff, but there is no record of freshwater fish taxonomic publications. The national museums of Zimbabwe and Namibia have small freshwater fish collections at their national museums of natural history, but currently no attached researchers are working on them. The MRAC in Belgium has been engaged in training several African scientists in freshwater fish taxonomy to MSc or PhD level. Outputs from these research dissertations have been published in recognized journals (Gourene & Teugels, 1991), but once the individuals return to Africa their taxonomic research effort appears to fade. A similar comment can be made for individuals trained in taxonomy through projects such as the Global Environment Facility (GEF) funded project on Lake Malawi–Nyassa in the late 1990s and by the University of Wageningen on the fisheries of Lake Tana beginning in 1986. Of course, there are various reasons for this, but one main reason is the absence of suitable research platforms (collections, equipped laboratories, institutions and research funds) in home nations for trained individuals to be employed by on their return.

There is therefore a serious lack of resident freshwater fish taxonomists in Africa, a situation that contrasts with the great need for exploration and description of species in many areas (Snoeks *et al.*, 2011). The absence of local taxonomists also decreases the chance of exposure that might be given to faunal aspects such as narrowly endemic or naturally rare species in the face of environmental development projects such as dams and deforestation (Dudgeon *et al.,* 2011). In South Africa, at least the conservation of freshwater systems and species has undoubtedly benefited

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from such input from freshwater fish taxonomists. For example, beginning with words of caution by Barnard (1943) about the effects of introduced bass *Micropterus salmoides* (Lacépède 1802) and *Micropterus dolomieu* Lacéepède 1802 on indigenous freshwater fishes in the south-west Cape, to the ringing of alarm bells by Jubb (1966) and the synthesis of threatened species in South Africa by Skelton (1987), the roots of a strong freshwater fish conservation movement grew (Skelton, 2000, 2002). In particular, this movement has contributed to the development of various national programmes on freshwater ecosystem conservation (O'Keeffe *et al.,*1989; Roux *et al*., 2006) and even a strong public action group, the Yellowfish Working Group of the Federation of Southern African Flyfishers (Mincher, 2007). Without champions well versed in local knowledge and networked within local and national systems, the actions and long-term changes required for conservation measures to be effective are difficult to achieve.

There are other downsides to not having resident taxonomists in Africa such as the sustained dependency on relatively expensive external agents and agencies for scientific advice and services on biodiversity. Another area is in the establishment and care for natural-history collections where Africa is poorly serviced (Skelton, 2007). Taxonomists need, and therefore build collections. Without established institutions and healthy reference collections, the science of taxonomy cannot be practised effectively. Whilst on the one hand it is extremely positive having African freshwater fish collections in the museums of Europe and the U.S.A., on which the continent's ichthyofaunal taxonomy is founded, at the same time those vital collections are physically remote and difficult and expensive to access by African ichthyologists. The net result is that there is little fertile ground for the establishment and development of taxonomic careers in most of Africa. Without study collections and other essential resources on hand, the continent's dependency on external expertise will most likely endure. Comprehensive research platforms, including the administrative and financial resources required for operation, must be established by African nations if science in Africa is ever to shake off the shackles of history and become the socioeconomic driving force it needs to be (Adams *et al*., 2010; Pouris, 2010).

GLOBAL TRENDS IN SYSTEMATICS

O'Hara (1997) described the 1960s paradigm shift in biosystematics as one from 'population thinking' to 'tree thinking'. Population thinking prevailed from the early 1900s through to the 1960s and was broadly characterized by the understanding of species within a framework of a 'biological species concept' (Mayr, 1975). Tree thinking embraces the paradigm of phylogenetic systematics or 'cladistics' as a process of dichotomous branching during phylogeny (Hennig, 1966). Ichthyologists were among the most enthusiastic early advocates for cladistics and the higher classification of fishes has been a dynamic field of scientific investigation since the 1960s (Greenwood *et al*., 1966, 1973; Stiassny *et al*., 1996; Nelson *et al*., 2010).

Scientific and technological innovations have also had major influence on biosystematics in recent decades. Two developments are especially relevant, the first is the introduction of molecular DNA analysis (Chen & Mayden, 2010) and the second is the computing power and global communications of digital electronics (Wheeler, 2008). Digital electronic technologies have revolutionized database systems, enabling

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the assembly and the analysis of large data sets and facilitated communication between parties (Chen & Mayden, 2010; Peterson *et al*., 2010). This allows vast amounts of new knowledge to be released from existing data for modern applications of management and development. The potential is created for projects such as the recent IUCN analysis of the diversity of life in African fresh waters (Darwall *et al*., 2011). Such projects characteristically comprise large teams of collaborators of a multidisciplinary nature drawn from international sources.

The pervasiveness and capacity of both molecular and digital technologies has tended to mask the line between science and methodology. Methods have become ends in themselves and science is lost in the process (Mooi & Gill, 2010). Several strong and divisive debates focused around integrating traditional and new-age technologies in taxonomy have rocked biosystematics in the last decade or so (Wheeler, 2004, 2008; de Carvalho *et al*., 2008; Williams & Ebach, 2010). Two fundamental issues emerge, the first is the swamping of taxonomy (description and naming of species) by phylogenetic studies based solely or mainly on molecular data (Wheeler, 2004). The second is the use of optimized algorithms in place of evaluated characters to generate trees reflecting relationships between organisms (Mooi & Gill, 2010; Williams & Ebach, 2010).

With the development of molecular technologies, DNA barcoding has emerged as a modern technique designed to facilitate the identification of organisms (Hebert *et al*., 2003; Vernooy *et al*., 2010). There has been some debate around the role of DNA barcodes in taxonomy and systematics (de Carvalho *et al*., 2008; Wheeler, 2008). In spite of these reservations, a growing number of studies is proving the efficacy of barcoding as an aid to identifying organisms and a guidepost to taxonomy (Lowenstein *et al*., 2011). The size and taxonomic scope of the Barcode of Life (BOLD) data system (http://www.boldsystems.org/) is reaching the point where, as a large specific gene DNA database, it can also serve scientific uses other than taxonomy (*e.g.* in ecological analysis), or as a complement to multigene phylogenetic analyses (Vernooy *et al*., 2010).

EFFECT OF GLOBAL TRENDS ON AFRICAN FRESHWATER ICHTHYOLOGY

High level global revisions naturally add value to the African circumstance. Extensive morphological phylogenetic studies such as Zanata & Vari (2005) and Poyato-Ariza *et al*. (2009) as well as the series of comprehensive contributions to the recent volume on the origin and phylogenetic interrelationships of teleosts (Nelson *et al*., 2010) advance understanding of the relationships of the African components. Whilst the tempo of alpha taxonomy is evidently robust given the rising number of descriptions in recent times, so also is the tempo of phylogenetic studies. Attention is being given to a broad spectrum of higher lineages (Stiassny *et al*., 2004; Nelson *et al*., 2010). Progress has been significant at all levels, *e.g.* the various studies on catfishes by Diogo (2003, 2005), Kapoor *et al*. (2003), Roberts (2003), Diogo & Bills (2006) and Vigliotta (2008). Morphological studies remain important for both taxonomy and phylogeny (Stiassny, 1997; Stiassny & Mamonekene, 2007; Vreven, 2005), but there is undoubtedly a strong shift to integrated studies with molecular analyses or to fully molecular contributions (Markert *et al*., 2010).

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The increasing number of high level molecular studies is affecting a broad spectrum of lineages of fishes in Africa (Rüber *et al*., 2006; Sullivan *et al*., 2006; Chenhong & Orti, 2007; Lundberg *et al*., 2007; Wilson *et al*., 2008; Tang *et al*., 2010). The emerging phylogenomic approach to systematics is expected to rapidly refine the higher phylogeny of fishes even further (Chen & Mayden, 2010). More specific African-focused contributions also have been made at generic levels within certain families such as the cichlids (Klett & Meyer, 2002; Katongo *et al*., 2005, 2007; Koblmüller *et al*., 2010). Earlier attention to the cichlid species flocks of the Great Lakes is now exclusively being tackled through molecular analyses on extensive data sets with new insights and rapid advances in understanding the situation (Sturmbauer *et al*., 2001; Kocher, 2004; Joyce *et al*., 2005; 2011). Attention is being given also to other species flocks of fishes from African lakes including synodontid catfishes (Day *et al*., 2009), mastacembelid eels (Brown *et al*., 2010) and large barbs (genus *Labeobarbus*) (de Graaf *et al*., 2010). Molecular phylogeny of the large African hexaploid barbs reported by Tsigonopoulos *et al*. (2010) provides context for the insight on the Lake Tana species flock studied by de Graaf *et al*. (2010). Several studies on cypriniforms with Asian and African components begin to expand understanding of this large but poorly understood element of the fauna (Durand *et al*., 2002; Saitoh *et al*., 2006; Tang *et al*., 2009, 2010; Yang & Mayden, 2010). Multigene approaches such as by Lowenstein *et al*. (2011) are likely to rapidly clarify phylogenetic relationships with such complex lineages. The study by Lowenstein *et al*. (2011) also indicates the value of including African species in large reference databases such as BOLD.

CONTEMPORARY STUDIES IN SOUTHERN AFRICA

Taxonomic studies in southern Africa traditionally have been conventional morphological analyses. A broader suite of approaches has emerged more recently, including genetic and behavioural components with the latter especially pertinent to mormyrids that generate electric discharges for communication purposes. Genetic approaches started with several allozyme studies that were done from the 1990s and these suggested more diversity than previously thought in *Barbus* (Engelbrecht & van der Bank, 1994, 1996*a*, *b*), *Pseudobarbus* (Swartz *et al*., 2004) and *Petrocephalus* (van der Bank & Kramer, 1996; Kramer & van der Bank, 2000). Allozyme markers, however, may be under selection pressure and may therefore not necessarily reflect historical isolation but could reflect selection pressure after recent cessation of gene flow. Allozymes therefore suffer from similar constraints to morphology. The sequencing of essentially neutral mitochondrial DNA genes has increased the understanding of the population history of South African fishes.

The DNA sequencing study on *Galaxias zebratus* Castelnau 1861 by Waters & Cambray (1997) was the first on a South African species and revealed that this Cape Floristic Region (CFR) endemic is a species complex with at least four divergent lineages. Four additional lineages in the complex were identified by Wishart *et al*. (2006) and van Niekerk (2004), but further study (E. R. Swartz, unpubl.data) is suggesting that there may be as many as 14 historically isolated lineages possibly representing different species (Table III). The taxonomic diversity in other CFR fishes also appears to be underestimated (Linder *et al*., 2010). Skelton (1988) recognized six

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Pseudobarbus species in the CFR, but subsequently allozyme and molecular DNA analyses have revealed at least 14 historically isolated lineages (Table III) (Bloomer & Impson, 2000; Swartz *et al*., 2004, 2007, 2009; Swartz, 2005). The widespread anabantid species *Sandelia capensis* (Cuvier 1829) also seems likely to be a species complex with possibly three lineages (Roos, 2004). Current investigations by SAIAB researchers also indicate more complex differentiation in *Austroglanis gilli* (Barnard 1943), *Labeo umbratus* (Smith 1841), *Barbus pallidus* (Smith 1841) and *Sandelia bainsii* (Castelnau 1861).

The geomorphological and climatic complexity of the CFR and Eastern Cape Province, South Africa, may have contributed to the historical isolation and differentiation of fish lineages (Skelton, 1994). The CFR is intimately associated with the Cape Fold Mountain belt in which there are numerous currently isolated river systems that favour speciation. Several previously unrecognized lineages of fishes, however, have also been discovered in larger systems to the north and east. Studies of electric organ discharges in combination with genetic and morphological investigations have revealed hidden diversity in South Africa's mormyrids. These studies led to the revalidation of *Marcusenius pongolensis* (Fowler 1934) and the identification and description of *Petrocephalus wesselsi* Kramer & van der Bank 2000 (Kramer & van der Bank, 2000; Kramer *et al*., 2007).

Some lineages are being discovered through research as part of environmental impact assessments for developments in southern Africa. This has led to targeted conservation actions where the newly exposed lineages are considered threatened. One of the better known cases is in the Maloti Mountains of Lesotho where *Pseudobarbus quathlambae* (Barnard 1938) is threatened by the development of large reservoirs and inter-basin water transfer schemes of the Lesotho Highlands Development Project (Skelton, 2000). Genetic analysis of individuals from the known populations revealed two unique evolutionary lineages within this critically endangered species (Table III) (Skelton *et al*., 2001; Swartz, 2005; Swartz *et al*., 2009). The population threatened by the construction of the Mohale Dam comprises one of these lineages, and specific

TABLE III. Indigenous primary freshwater fish species in South Africa with multiple species-level lineages currently known

Species	*N*
Austroglanis gilli	2
Barbus anoplus	7
Barbus pallidus	2
Galaxias zebratus	14
Marcusenius pongolensis	2
Pseudobarbus afer	4
Pseudobarbus burchelli	4
Pseudobarbus burgi	2
Pseudobarbus quathlambae	2
Pseudobarbus tenuis	2
Sandelia bainsii	2
Sandelia capensis	3

N, number of identified lineages.

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conservation steps to protect this population from adverse effects of the construction of the dam were taken as a result (Rall *et al.*, 2002; Tweddle *et al.*, 2009; Swartz & Tweddle, 2011). Similar genetic investigations have revealed unique lineages within other *Pseudobarbus* species within the CFR, and conservation interventions are being implemented for the most restricted and threatened taxa, including a brace of undescribed taxa currently encompassed within *Pseudobarbus burchelli* Smith 1841.

The identification of some species complexes inevitably challenges the current taxonomy. For example, another widespread minnow, *Barbus anoplus* Weber 1897, is now recognized as a species complex with a conservative morphology (Barnard, 1943; Engelbrecht & van der Bank, 1994, 1996*a*, *b*). Recent genetic (nuclear and mitochondrial DNA) and morphological analyses suggest that there are more than seven historically isolated lineages in the *B. anoplus* complex. As in the case of the large *Labeobarbus* species flock from Lake Tana (de Graaf *et al.,* 2010; Getahun, 2011), there are also indications from current studies that reveal that the *Labeobarbus* from southern Africa are more genetically complex than previously considered (Bloomer & Oosthuizen, 2011). In total, at least 46 or more genetically distinct evolutionary lineages have been identified within the 93 primary indigenous freshwater fish species currently known in South Africa and Lesotho (Table III). If these genetic lineages represent different evolutionary species, it indicates that the primary freshwater fish fauna of South Africa is only around 75% described, in contrast with the estimation of 90% by Skelton (1996). The identification of distinct lineages within species is a prelude to taxonomy, clearly much more research is needed to verify and describe new taxa.

CONCLUSIONS: SOLUTIONS TO A PROBLEM?

The freshwater fish fauna of Africa is a rich assemblage, with an interesting and complex taxonomic history in tune with the sociopolitical history of the continent. Present circumstances provide a different context and setting for scientific endeavour than in the past. Major taxonomic pulses over time reflect the ebb and flow of nations and institutions and their vested interests in Africa. The 19th century, when exploration and exploitation of natural resources was central to the colonial imperative, collection building and systematic research was fundamental to providing a platform of knowledge, and determined the pattern of taxonomy and species discovery. Now, six or seven decades after the major pulse of African independence in 1950s and 1960s a new pattern of scientific discovery has emerged, from one where the taxonomy was dominated by research on the collections of a few large institutions to one where individuals engaged in research projects on target groups or ecosystems are most productive. When the research is a prerogative of individual choice and not long-term institutional policy, the researcher's contribution period is more likely to be relatively short-term. Because its collections are African in content, the continued involvement of the MRAC in Belgium in African biodiversity science including ichthyology provides an exception to this situation and researchers based there are likely to have extended involvement.

An overwhelming dominance by out of Africa taxonomy remains characteristic of African freshwater ichthyology at the present time. This account is written from

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an inside perspective, and, given the minor role played historically by resident taxonomists, it reflects a desire for a greater contribution from an African scientific base that actually does not exist. Excluding Antarctica, Africa is probably the only continent where its ichthyology is dominated so extensively by non-resident scientists. The situation seems to be a persistence of a dependency originally generated in the deprivation of its colonial history. From that perspective, and for Africans to have a greater sense of pride and ownership of the discipline, it is desirable that the situation changes. It might be reasonably expected that five or six decades after the end of colonialism an indigenous capacity for a fundamental science like taxonomy would be in place. Another reason is that there is a growing concern from developing nations around the question of access and benefit sharing of natural biodiversity resources for commercial purposes (Schindel, 2010). Tighter bureaucracy around collecting and exporting specimens is a tendency in many countries as a clear line of distinction is not always drawn between commercial and scientific bioprospecting. Most African nations are poorly equipped to service their interests in this regard. Furthermore, the few established and functional natural history museums with suitable collections in Africa remain too weak for anything other than a local, or at best, a regional scope for ichthyological research. It will take time before African nations create or regenerate the sort of institutional platforms necessary for the ichthyology to function effectively.

The continued involvement of the international scientific community is essential if Africa is to deal with the biodiversity crisis and manage sustainable development effectively. It is also the source of a solution to the problem of capacity development. The situation is similar to that faced by South America over the latter half of the 20th century. Initially, South American ichthyofaunal expertize resided to a large extent in taxonomists in North America and there were relatively few resident taxonomists dealing with the extremely rich ichthyofaunal diversity of the Amazon and other tropical and temperate South America systems. Many ichthyologists from the U.S.A willingly mentored and trained taxonomists and students from South America. The outcome is that, at present, South America has a wealth of resident taxonomists and competent museums and research institutions as clearly reflected in comprehensive volumes such as by Malabarba *et al*. (1998) and the existence of the *Sociedade Brasileira de Ictiologia* (http://www.sbi.bio.br/) and its journal *Neotropical Ichthyology* (http://www.ufrgs.br/ni/; http://www.scielo.br/ni/).

The collections in developed nations are large, generally well curated and have the type material essential for the research. The onus for the cost of the care and responsibility for those collections falls on the institutions themselves. Research infrastructure, facilities and finances are generally excellent in the major institutions and the scientists and students are well trained and skilled, often working across multiple generations. All this allows for studies that are broad and comprehensive, embracing more than local or regional scope, and thus providing effective advances in scientific knowledge. This advantage is well demonstrated by the many examples cited in this account, such that it can be fairly concluded that, mainly as a result of international interest and investment, African freshwater fish systematics and taxonomy is advancing at a pace in tune with global trends.

There is little doubt that good basic taxonomy is still being applied to African freshwater fishes as the accumulation curve for descriptions has yet to level off [Fig. 1(b)]. Research projects such as the Congo Project of the American Museum

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of Natural History (http://research.amnh.org/vz/ichthyology/congo/index.html/) are driving discovery and the description of new species from Africa and providing African students and researchers opportunities to develop international skills. The MRAC is a model institution with regard to its vested African interests, and stands out in terms of training and education for African ichthyologists. The MRAC runs large projects over several years in different regions and countries of Africa through which it attracts students for training at post-graduate up to doctoral levels. It also offers specific training in bioinformatics skills to professionals, technicians and students from Africa through the FishBase programme (www.fishbase.org). The challenge for African researchers and students is to not only to engage in constructive collaborations with such projects and opportunities, but to return and use the skills gained in Africa where they are needed most. A receptive environment is equally essential if this is to happen successfully. The ultimate ideal will be to establish institutions and build national collections and scientific capacity that will allow Africa to handle its own scientific needs. Most African nations have very weak scientific infrastructure and economy, so a development strategy probably should be directed at regional centres of competence and excellence.

The richness of African biodiversity attracts the international systematic community and this in many respects offsets the disadvantage of an impoverished indigenous scientific capacity. Conservation biology that inevitably requires local taxonomic services, however, is always rooted more closely to local individuals (who drive conservation effort or initiatives) and communities. When these services are unavailable or scarce, the knowledge base is remote and disconnected (as it inevitably will be). Africa is undergoing rapid development and exploitation of its natural resources and environments. The identification of organisms is a premium requirement in the environmental impact assessment process and this is one reason why knowledge of local taxonomy is essential in Africa. The development and application of modern technology and tools like DNA barcoding for identifying organisms has relevance in these circumstances (Swartz *et al*., 2008). Barcoding on its own, however, will not solve the taxonomic challenge, but it is a useful analytical tool and a component in the process. There simply is no easy or short-term solution to the problem. The reality is that developed nations have the expertise, the institutions and the finances to do the necessary science. Africa, by and large, does not have these essentials and remains to a large extent a dependency, as it has been since the beginning of the age of discovery. It will be up to Africans themselves to change the equation. The establishment of the Pan African Fish and Fisheries Association (PAFFA) and the holding of an international conference in different regional centres in Africa under its auspices every 5 years since 1993 is a healthy sign that the challenge is being taken up and the situation is changing positively.

Balancing this network of tensions between science, scientific knowledge generation and application is like walking a tightrope for existing limited African scientific resources. To cope with increasing pressure on biodiversity resources and environmental stresses, it is essential for Africa to increase its scientific capacity, develop national and regional institutions and to embrace modern innovative approaches to taxonomy and systematics.

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