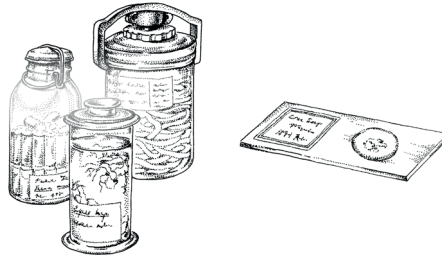


PART 1

HISTORY OF FISH PARASITOLOGY IN AFRICA



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Introduction

Freshwater systems in Africa cover a surface area of almost 30,000 km² and include 12 major freshwater habitat types ranging from closed basins, small lakes, floodplains and swamps to large tropical rivers (Van As *et al.* 2012). More than 3,200 species of fish species belonging to 76 of the world's 170 freshwater fish families are known from Africa, with representatives of the families Cichlidae and Cyprinidae dominating African ichthyofauna (Lévêque *et al.* 2008). However, they are irregularly distributed over the continent and include highly diverse systems such as Lake Malawi (800 species) and the Congo River (700 species), as well as low diversity areas further north and south of the tropics.

Diversity of fish parasites in Africa and a brief history of their exploration

In contrast to the known high diversity of the freshwater fish hosts, the relatively low number of identified fish parasites of Africa, with the exception of the species-rich monogenean genus *Cichlidogyrus* Paperna, 1960 (see Pariselle & Euzet 2009), shows a clear paucity of research on this group of parasites. It is even more obvious when the numbers of the parasites reported from African fishes are compared with those in other continents, especially Europe (see, e.g., Scholz *et al.* 2016 for data on fish trematodes). Our knowledge of the diversity of freshwater fish parasites (and the same is valid for parasites of marine bony fishes – Smit & Hadfield 2015) was kick-started in the second half of the 19th century (see Khalil 1971).

In the following paragraphs, the history of studies on the parasites of teleost fishes in Africa is briefly surveyed. However, this account does not represent an exhaustive search of the history of fish parasite exploration in the African continent, partly due to the fact that many papers of African fish parasitologists were published in hardly accessible, regional or local journals, and that nowadays, research from the Global South is unfortunately all too often published in so-called predatory journals. Exhaustive data (updated until 2003) on the parasites of freshwater fishes in Africa can be found in the Host-Parasite Database generated at the Natural History Museum in London (Gibson *et al.* 2005).

Leydig (1853) described the bothriocephalidean cestode *Tetrabothrium polypteri* (now *Polyonchobothrium polypteri*) from bichir, and Wedl (1861) described another bothriocephalidean *Tetracampos ciliotheca* from *Clarias* catfish. Fritsch (1886) described two proteocephalidean cestodes, *Corallobothrium fimbriatum* and *Taenia malapteruri*, from electric catfish *Malapterurus electricus* (Gmelin). At the turn of the 20th century, A. Looss published a series of papers from 1896 to 1907 on the parasitic fauna of Egypt (see Khalil 1971), including the first two species of trematodes recorded from Africa, namely *Acanthostomum spiniceps* (Looss, 1896) and *Haplorchoides cahirinus* (Looss, 1896) found in the bagrid catfishes *Bagrus bajad* (Forsskål) and *Bagrus docmak* (Forsskål). Looss' work on the Nile River in Egypt was continued by T. Odhner (1902-1911), who also dealt mainly with trematodes and described eight new species from the Sudan, based

on material collected as part of the Swedish zoological expedition to the Nile River (see Canaris & Gardner 2003).

Khalil (1971) published the first checklist of the helminth parasites of freshwater fishes in Africa. He reported 223 species of adult helminth parasites from African freshwater fishes (86 species of monogeneans, 44 trematodes, 41 cestodes, 41 nematodes and 11 acanthocephalans). Twenty-six years later, an updated checklist (Khalil & Polling 1997) recorded 568 adult helminth parasites, *i.e.*, an increase of 155%, including 342 species of monogeneans (4 times more than in 1971!), 62 trematodes (increase of 41%), 61 cestodes (49%), 80 nematodes (95%) and 21 acanthocephalans (91%). In addition, numerous larval forms have been reported (Khalil & Polling 1997).

However, the species discovery rate over the following years dropped drastically. For example, only five species of trematodes, including one new genus *Malawitrema* Bray et Hendrix, 2007, have since been added to the known fauna of adult trematodes (Scholz *et al.* 2016). In total, 67 species of adult trematodes of 34 genera from 20 families and 35 species of metacercariae of 20 genera from eight families from African freshwater fish are now known (Scholz *et al.* 2016).

Another group of parasites of African freshwater fishes that has received relatively high attention is the parasitic crustaceans, especially the Copepoda. The first record of African freshwater parasitic copepods is that by Cunnington (1914) describing *Lernaea dicerocephala* Cunnington, 1914 and *L. haplocephala* Cunnington, 1914 collected during an extensive expedition to Lake Tanganyika during 1904 to 1905. Since that first description, approximately 45 more species of the family Lernaeidae have been described from freshwater fishes in various localities in Africa, making it the species-richest of all the fish parasitic Crustacea reported from Africa (Oldewage & Avenant-Oldewage 1993).

The largest contribution to our knowledge of freshwater fish parasitic Crustacea was by the British zoologist, Geoffrey Fryer, who described more than 20 branchiuran and copepod species over a twenty-two year period (1955 to 1977). This includes seven species of the African endemic branchiuran genus *Chonopeltis* Thiele, 1900. Fryer (1968) also summarised the known distribution of the parasitic crustaceans of African freshwater fishes, which included just over 80 species at that time, and provided information on the taxonomy, biology and evolution of certain species. Although Fryer's (1968) work is almost 50 years old and in need of an update, it is still considered as one of the most valuable contributions to our understanding of parasitic crustaceans of African freshwater fishes.

Data on protists and myxozoans of African fishes have not been summarised in a form similar to that of the trematodes and crustaceans and thus it is difficult to provide total numbers for these parasites. Several ectoparasitic protists appear to have a cosmopolitan distribution and have also been reported from various places in Africa. Van As and Basson (1984) and Paperna (1996) reported the flagellate *Ichthyobodo necator* (Henneguy, 1883), the pathogenic ciliophorans *Chilodonella hexasticha* (Kiernik, 1909) and *C. piscicola* (Zacharias, 1894), as well

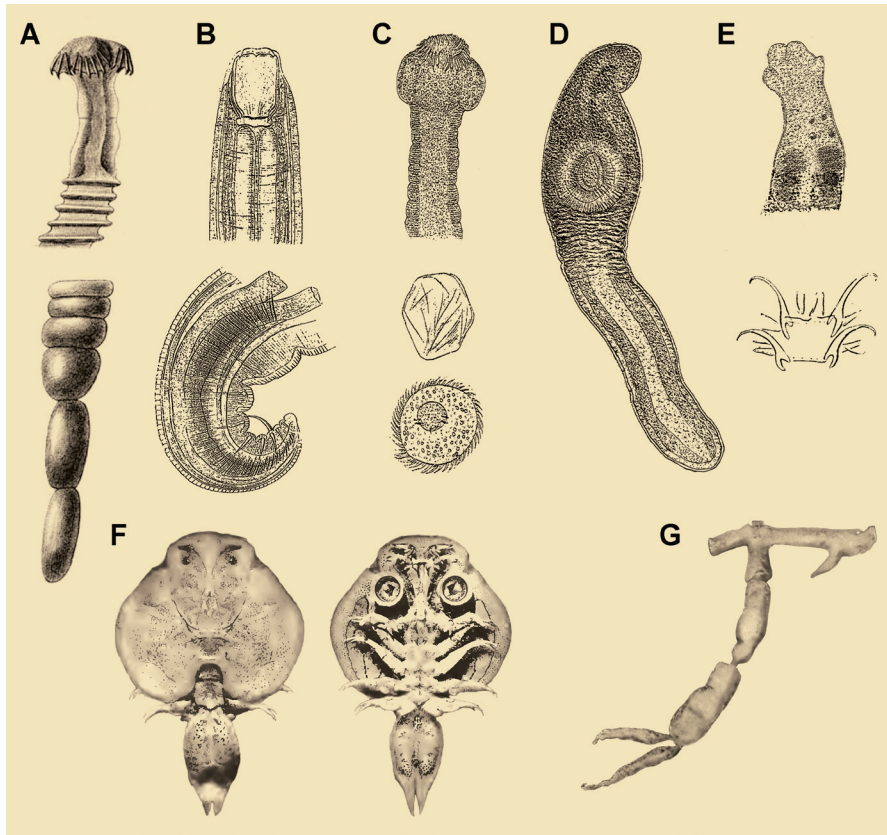


Fig. 1. First documentations of freshwater fish parasites in Africa. **A.** Cestoda – *Tetrabothrium polypteri* Leydig, 1853 (now *Polyonchobothrium polypteri*) from *Polypterus bichir*; **B.** Nematoda – *Cucullanus laeiviconchus* Wedl, 1861 (now *Procamallanus laeiviconchus*) from *Synodontis schall*; **C.** Cestoda – *Tetracampos ciliotheca* Wedl, 1861 from *Clarias anguillaris*; **D.** Trematoda – *Distoma bagri incapsulatum* Wedl, 1861 (now *Nephrocephalus bagriincapsulatus*) from *Bagrus* sp.; **E.** Monogenea – *Dactylogyrus gracilis* Wedl, 1861 (now *Annulotrema gracilis*) from *Hydrocynus forskahlii*; **F.** Branchiura – *Argulus incisus* Cunningham, 1913 from *Auchenoglanis occidentalis*; **G.** Copepoda – *Lernaeocera diceracephala* Cunningham, 1914 (now *Lernaea diceracephala*) from *Clarias gariepinus*. (Modified from Leydig 1853; Wedl 1861; Cunningham 1913, 1914.)

as the equally notorious pathogenic ciliophoran *Ichthyophthirius multifiliis* Fouquet, 1876 from southern Africa. Paperna (1972) also reported *I. multifiliis* from Uganda. The fish blood trypanosomes also seem to have a wide African distribution, but only three species are reported from a wide range of African freshwater fishes from Egypt, West Africa, the Congo, Sudan, Uganda, Botswana, Mozambique and South Africa (see Smit *et al.* 2004).

Protist groups that have been studied in more detail are the two ciliophoran orders of the subclass Peritrichia, *i.e.*, the Sessilida and Mobilida. In the case of the former, there were vague reports of sessilines from fishes in Africa, but more in

depth work was done in South Africa in the 1980s by Viljoen and Van As (1983, 1985). These authors collectively described a total of 14 sessiline species (of which 12 were described as new species) representing four genera, *i.e.*, *Epistylis* Ehrenberg, 1830, *Apiosoma* Blanchard, 1885, *Scopulata* Viljoen and Van As, 1985 and *Ambiphrya* Raabe, 1952.

The Mobilida have received far more attention, specifically representatives of the family Trichodinidae. The first mention of a fish trichodinid species in Africa was made by Fantham (1918) from a marine host, while the first valid species description was published by Basson *et al.* (1983). Since then, 50 trichodinid species, representing five genera have been described, the vast majority from freshwater fishes and most of these in southern Africa. The southern African trichodinid (from South Africa, Namibia and Botswana) fauna stands at 35 freshwater species due to the contributions of authors such as Basson *et al.* (1983), Basson and Van As (1987, 1989, 1991, 1993, 2002), Basson (1989), and Van As and Basson (1989, 1992), whereas six marine fish trichodinids have been described from South Africa (Basson *et al.* 1990; Van As and Basson 1996) and Namibia (Aljoshkina & Stein 1984). In the rest of Africa, a total of 16 trichodinid species have been found (of which nine were not encountered in southern Africa): three species from marine fish in Senegal (Loubser *et al.* 1995), five species from freshwater fishes in Egypt (El-Tantawy & Kazubski 1986; Kazubski & El-Tantawy 1986; Abdel-Meguid 1995), five species from brackish water in Benin (Maslin-Leny 1988), two species from Kenya (Kazubski 1986; Kazubski & El-Tantawy 1986) and a single species from a freshwater fish in Nigeria (Obiekezie & Ekanem 1995). Probably the least studied fish parasitic protists from Africa are blood protozoans. Currently only a single species, the dactylosomatid, *Babesiosoma mariae* (Hoare, 1930), has been described from African freshwater fishes (Smit *et al.* 2003).

One of the highest numbers of helminths has been reported from the sharp tooth catfish, *Clarias gariepinus* (Burchell), an economically important species occurring in almost all the major river systems. This fish harbours as many as 12 species of adult trematodes, five species of metacercariae, 20 species of monogeneans and at least four species of adult cestodes (Mashego & Saayman 1989; Gibson *et al.* 2005 and references therein; Barson & Avenant-Oldewage 2006; Přikrylová *et al.* 2012; Beletew *et al.* 2016; Scholz *et al.* 2016). Even more impressive, the Nile tilapia *Oreochromis niloticus* (Linnaeus) is infected by 23 trematodes and 20 monogeneans, two cestodes, two acanthocephalans, seven nematodes and it is the African cichlid with the highest number of formally reported helminth species (data from Vanhove *et al.* 2016 and references therein).

The relatively low number of parasites of freshwater fishes in Africa almost certainly does not reflect a naturally low diversity, but rather is due to the lack of dedicated biodiversity studies (Smit & Hatfield 2015; Van As 2015; Scholz *et al.* 2016). The distribution of the currently known fish parasites over the continent is another indication of uneven research. In the case of trematodes, there are no records from almost 40% of African countries. The highest numbers of fish trematode species were reported from the countries where foreign fish parasitologists were

active, such as Egypt and the Sudan (Barson & Avenant-Oldewage 2006; Smit & Hadfield 2015).

In 2003, the Sixth International Symposium on Fish Parasites was organised for the first time on the African continent, in Bloemfontein, South Africa (the principal organiser was Jo Van As). This conference was an important stimulus for the development of ichthyoparasitology in the African continent. In addition to stimulation of a new generation of African fish parasitologists, this meeting accelerated intensive international cooperation, including research and teaching visits by foreign experts to Africa and collecting trips with participation of local fish parasitologists. As a result, the number and quality of scientific outcomes dealing with fish parasites in Africa have increased considerably. This latter is clearly demonstrated in the recent review by Jo Van As on the history of freshwater fish parasitology in southern Africa (Van As 2015). In that review, the contribution by South African fish parasitologists from seven different academic institutions was summarised and it was concluded that despite the fact that the country has arguably the largest community of aquatic parasitologists in Africa, the investigation and mapping of fish parasite biodiversity is still in its infancy, because all rivers and their fish parasite fauna of southern Africa have not been explored. Southern African fish parasitology is also visible on the international scene through other ways, e.g., Maxwell Barson from Zimbabwe is a member of the Aquatic Animals Health Standards Commission of the World Organisation for Animal Health (OIE).

Shortly afterwards, in 2009, the Sixth International Symposium on Monogenea was also held in South Africa, namely in Cape Town (principal organisers were Louis Du Preez and Kevin Christison). Monogeneans take up a special place in African fish parasitology, in view of their species richness (see above), but also in view of the large contribution of African researchers to our knowledge of these parasitic flatworms. The first African freshwater monogenean reported from fishes, *Annulotrema gracilis*, however, was described by the Austrian pathologist Wedl (1861) (as *Dactylogyrus gracilis*) from *Hydrocynus forskahlii* (Cuvier) in Egypt. Afterwards, things went rather silent regarding African monogeneans, with the notable exception of some new species from non-fish hosts. *Oculotrema hippopotami* was proposed by the American Stunkard (1924), based on museum specimens probably retrieved from hippopotamus in an Egyptian zoo, and Vercammen-Grandjean (1960) described *Gyrdicotylus gallieni* from the frog *Xenopus victorinus* in the Congolese South Kivu province. Change came in the second half of the 20th century, following the discovery of some typical African monogenean genera infecting fishes. For example, *Macrogyrodactylus polypteri* was described by Malmberg (1957) from *Polypterus senegalus* Cuvier in Gambia (paper dated 1956 but published in 1957) and *M. congolensis* (Prudhoe, 1957) (described as *Neogyrodactylus congolensis* as the author was unaware of Malmberg's aforementioned paper) reported by Prudhoe (1957) from *Clarias lazera* Valenciennes (now *C. gariepinus*) from the Democratic Republic of the Congo, also in 1957. Afterwards, Ilan Paperna became well-known for his substantial contribution to our understanding of African monogeneans (Paperna 1960). He

described numerous genera and species, among which the genus *Cichlidogyrus* Paperna, 1960, currently has the most nominal species known in Africa.

In subsequent decades, research efforts on, and knowledge of, monogeneans and other fish parasites proliferated, mainly throughout French-speaking Africa, largely originating from the 'school' of Louis Euzet and his first PhD student Claude Combes. Subsequent generations of French parasitologists active in Africa (not only dealing with monogeneans) include(d) Emile Birgi, Georges Bouix, Laurence Douëllou, Jacques Dupouy, Claude Gabrion, Alain Lambert, Claude Maillard, Guy Oliver, André Raibaut, Jean-Paul Trilles and, more recently, Jean-Lou Justine and Antoine Pariselle. Especially the latter spent much of the last decades based in Africa training a next generation of monogenean workers. Some African (senior) researchers that can be mentioned, at the risk of forgetting people, are Ouafae Berrada-Rkhami, Fouzia El Hafidi and Salwa El Gharbi (Morocco), Faiza Amine and Fadila Tazerouti (Algeria), Christian Dossou (Benin), Charles Félix Bilong Bilong and Jacques Nack (Cameroon), Mohammed El-Naggar (Egypt), Valentin N'Douba and K.G. Blahoua (Ivory Coast), Sylvère Rakotofiringa and Jeanne Rasamy (Madagascar), Austin Ikechukwu Obiekezie and M. Taege (Nigeria), Arfang Diamanka (Senegal), Lotfi F. Khalil (Sudan), Mohamed Hedi Ktari, Lassad Neifar and Lobna Boudaya (Tunisia), Annie Chishawa (Zimbabwe) (many of whom have benefited from the training and advice of L. Euzet), and, of course, the South African teams referred to above. Also, an even younger generation of young African parasitologists has started to publish on monogeneans over the last five years, e.g., Chahrazed Rahmouni and Zouhour El Mouna Ayadi (Algeria), Dieu ne dort Bahanak and Etienne Didier Bassock Bayiha (Cameroon), Fidel Muterezi Bukinga and Gyrhaiss Kapepula Kasembele (Democratic Republic of the Congo), Imane Rahmouni (Morocco), Amira Chaabane (Tunisia), and others.

A brief history of marine fish parasitology in Africa

The history of studies on the parasites of marine fishes in Africa is even longer than that on freshwater fish. The first marine parasite recorded from an African fish was the isopod *Anilocra capensis* Leach, 1818, found in the water around the Cape of Good Hope almost 200 years ago (see Smit & Hatfield 2015). However, the number of parasites reported from marine fishes of Africa is considerably lower than that found in freshwater hosts (see Gibson *et al.* 2005 for an exhaustive database).

The most comprehensive data are available on the parasites of marine fishes of South Africa (Smit & Hatfield 2015). Among the parasites reported from this country, the most famous is the myxozoan *Kudoa thyrsites* (described as *Chloromyxum thyrsites* by Gilchrist in 1924), which causes myoliquefaction of the flesh of commercially important fish and it is responsible for significant economic losses worldwide (Henning *et al.* 2013). Regarding myxozoans of South African fishes, the contribution of Czech parasitologists, especially Jiří Lom and Iva Dyková, should be mentioned (Smit & Hatfield 2015).

Parasites of marine fishes of the other countries/regions of the African continent have not been studied so intensively as in South Africa. In the Maghreb, which belongs to the Palaearctic zoogeographical region, studies on fish parasites are mainly focused on commercially important fish, especially perciforms. Numerous studies, mostly faunal surveys, but also ultrastructural studies, have been published in Morocco, Algeria and Tunisia (see, e.g., papers by Lassad Neifar), often in collaboration with fish parasitologists from Spain, France, Italy and other European countries (e.g., Gargouri ben Abdallah & Maamouri 2002, 2005; Marzoug *et al.* 2012a, b, 2014; Bellal *et al.* 2016). The most recent work on marine fish parasites in Africa focused on those infecting commercially important fishes (reviewed by Reed 2015 and Smit & Hadfield 2015).

Reed (2015) reviewed studies on the parasites of marine fishes in sub-Saharan Africa and also found that information is only available from a few countries where concerted efforts have been made by local parasitologists (e.g., Nigeria, Senegal, South Africa). Reed (2015) concluded her review with the statement that: "Aquatic parasitologists (marine and freshwater) in Africa have a tremendous opportunity to rapidly advance this field of research by documenting new species and also recording species assemblages associated with certain hosts in different regions."

Prospects

Africa, with its extraordinarily rich fish fauna, especially in freshwater, has a big potential to serve as an important model continent for ecological and evolutionary studies on fish parasites and their interactions. However, fish parasites are still poorly known, which makes it impossible to assess reliably their diversity, interrelations, distribution and potential effects on their fish hosts. Future studies on the evolutionary history of individual parasite groups will certainly yield interesting results as indicated by the very few molecular phylogenetic studies that included African fish parasites (e.g., Barson *et al.* 2010; Chibwana *et al.* 2013; Příkladová *et al.* 2013; Bartošová-Sojková *et al.* 2015; Brabec *et al.* 2015; Vanhove *et al.* 2015). There is also an urgent need to get much more data on host-parasite interactions with focus on potential pathogens of commercially important fish.

The number of African fishes that have not been examined for parasites is extremely high and thus the present knowledge of the parasite fauna of African fishes is fragmentary and incomplete. Similarly, data from a majority of African countries are scarce or even lacking completely. Therefore, future research efforts should be focused on poorly studied fish hosts as well as the regions from where limited or no information is available. Capacity development through training of, and collaboration with, African scholars is crucial in this regard. The application of adequate methods of collecting fish parasites, their processing and evaluation is critical, because much valuable material of African fish parasites has been lost or is not usable due to the application of inappropriate methods.

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