(*P.*) laeviconchus, *P*. (Spirocamallanus) dalenae, Procamallanus (Spirocamallanus) sp., Synodontisia thelastomoides

Synodontis pleurops Boulenger: Ne - Synodontisia thelastomoides

Synodontis rebeli Holly: Mo – Synodontella apertipenis, S. melanoptera, S. sanagaensis

- Synodontis schall (Bloch et Schneider): Pr Apiosoma sp., Balantidium sp., Chilodonella sp., Cryptobia sp., Eimeria sp., Entamoeba synodontis, Hexamita africanus, Hexamita sp., Ichthyobodo sp., Ichthyophthirius sp., Trichodina sp., Haemogregarine gen. sp., Microsporidia gen. sp., Mx Myxidium schalli, Myxobolus negmgoda, M. stenosus, Unicauda strongylura, Tr Basidiodiscus ectorchis, Clinostomum sp. [L], Cholepotes ovofarctus, Emoleptalea rifaati, Sandonia sudanensis, Sanguinicola chalmersi, Ce Monobothrioides sp., Proteocephalus beauchampi, P. synodontis, Wenyonia longicauda, W. minuta, W. synodontis, W. virilis, W. youdeoweii, Ne Amplicaecum sp. (type1)[L], Camallanus polypteri, Cithariniella citharini, C. khalili, C. petterae, Cucullanus baylisi, C. clarotis, Falcaustra similis, Labeonema synodontisi, Procamallanus (P.) laeviconchus, P. (Spirocamallanus) dalenae, P. (S.) pseudospiralis, Procamallanus sp., Procamallanus (Spirocamallanus) sp., Rhabdochona (Globochona) paski, Spinitectus allaeri, S. polli, Synodontisia thelastomoides, Cr Argulus cunningtoni, A. rhipidiophorus
- **Synodontis serratus** Rüppell: Tr *Emoleptalea rifaati*, Ce *Proteocephalus synodontis*, Wenyonia minuta, W. virilis, W. youdeoweii, Ne – Cithariniella citharini, C. khalili, Falcaustra similis
- **Synodontis sorex** Günther: Mo Synodontella arcopenis, Tr Sandonia sudanensis, Ce – Wenyonia synodontis, W. virilis, Ne – Cithariniella khalili, Procamallanus (P.) laeviconchus, Synodontisia thelastomoides
- **Synodontis tessmanni** Pappenheim: Ne *Procamallanus* (*Spirocamallanus*) *dalenae*, *P*. (S.) *spiralis*
- Synodontis thamalakanensis Fowler: Ne Procamallanus (P.) laeviconchus, Cr Chonopeltis lisikili
- **Synodontis vanderwaali** Skelton et White: Pr *Trypanosoma mukasai*, Ne *Falcaustra similis*, Labeonema africanum, Procamallanus (P.) laeviconchus, P. (Spirocamallanus) dalenae, Synodontisia okavangoensis, Cr Chonopeltis lisikili
- Synodontis vermiculatus Daget: Tr Sandonia sudanensis, Ce Wenyonia synodontis
- **Synodontis victoriae** Boulenger: Mo Synodontella synodontii, Tr Masenia synodontis, Ne Procamallanus (Spirocamallanus) dalenae
- Synodontis zambezensis Peters: Pr Trichodina heterodentata, Mo Synodontella synodontii, S. zambezensis, Ne Capillaria sp., Labeonema synodontisi, Paracamallanus cyathopharynx, Procamallanus (Spirocamallanus) dalenae, Rhabdochona sp., Spinitectus polli, Synodontisia thelastomoides, Philometridae gen. sp., Cr Dolops ranarum, Ergasilus mirabilis
- **Synodontis sp.**: Tr Allocreadium ghanensis, Cholepotes ovofarctus, Sandonia sudanensis, Ne Cucullanus baylisi, C. clarotis

FAMILY PLOTOSIDAE

Plotosus lineatus (Thunberg): Cr – Lepeophtheirus plotosi

FAMILY SCHILBEIDAE

Parailia pellucida (Boulenger): Mo - Schilbetrema bicornis, Cr - Ergasilus lamellifer

Schilbe banguelensis (Boulenger): Cr – Argulus africanus

Schilbe grenfelli (Boulenger): Ne - Gendria longispiculata

Schilbe intermedius Rüppell: Pr – Trypanosoma mukasai, Mo – Schilbetrema acornis, S. aegyptica, S. calamocleithrum, S. quadricornis, S. undinula, S. vacillans, Schilbetrematoides pseudodactylogyrus, Tr – Clinostomum sp. [L], Emoleptalea nwanedi, Ce – Dendrouterina herodiae [L], Ne – Cithariniella longicaudata, Contracaecum sp. [L], Falcaustra similis, Paracamallanus cyathopharynx, Procamallanus (P.) laeviconchus, Rhabdochona sp., Spinitectus spp., Synodontisia annulata, Atractidae gen. sp., Philometridae gen. sp., Cr – Dolops ranarum, Ergasilus mirabilis

Schilbe laticeps (Boulenger): Cr – Ergasilus cunningtoni

- Schilbe mandibularis (Günther): Mo Schilbetrema biclavula, S. dissimilis, Schilbetrematoides manizani, Ne – Labeonema bainae
- Schilbe marmoratus Boulenger: Ne Gendria sanghaensis

Schilbe multitaeniatus (Pellegrin): Mx – Henneguya camerounensis

Schilbe mystus (Linnaeus): Pr – Trichodina magna, T. sangwala, Mx – Chloromyxum alii, Henneguya ntondei, Myxidium schilba, Thelohanellus njinei, Mo – Schilbetrema eutropii, S. hexacornis, S. spirocirra, S. torula, Tr – Clinostomum vandehorsti [L], Prohemistomum vivax [L], Ce – Kirstenella gordoni (?), Ac – Paragorgorhynchus albertianus, Pararaosentis golvani, Ne – Amplicaecum sp. (type I) [L], Contracaecum sp. [L], Procamallanus (P.) laeviconchus, Rhabdochona (Globochona) paski, Spinitectus allaeri, Cr – Dolops ranarum, Ergasilus latus, E. mirabilis

Schilbe uranoscopus Rüppell: Ne – Amplicaecum sp. (type I) [L]

Schilbe sp.: Mo – Schilbetrema tricera, Cr – Argulus africanus, Dolops ranarum

ORDER SYNBRANCHIFORMES

FAMILY MASTACEMBELIDAE

Mastacembelus flavidus Matthes: Ne – Spinitectus maleficus

Mastacembelus frenatus Boulenger: Pr - Trichodina frenata

Mastacembelus micropectus Matthes: Ne – Spinitectus micropectus

Mastacembelus nigromarginatus Boulenger: Tr – Phyllodistomum ghanense

Mastacembelus sp.: Cr – *Leiperia cincinnalis* [L]

ORDER TETRAODONTIFORMES

FAMILY MONACANTHIDAE

Aluterus monoceros (Linnaeus): Cr – Argulus kosus

FAMILY TETRAODONTIDAE

Tetraodon lineatus Linnaeus: Pr – Trichodina fahaka, Mo – Heterobothrium fluviatilis, Tr – Astiotrema impletum, Ac – Acanthogyrus tilapiae, Paragorgorhynchus aswanensis, Pararaosentis golvani, Ne – Procamallanus (P.) laeviconchus, Cr – Argulus dageti, Dolops ranarum

ORDER ZEIFORMES

FAMILY ZEIDAE

Zeus faber Linnaeus: Cr – Argulus arcassonensis

Zeus sp.: Cr – Argulus alexandrensis

OTHER HOSTS

FISHES

Unidentified fish: Cr – Argulus angusticeps, A. confusus, A. rijckmansii, Caligus pharaonis, Lamproglena wilsoni

Unidentified shark: Cr - Argulus melita

FROGS

ORDER ANURA

UNIDENTIFIED FROG

Unidentified frog: Cr – Dolops ranarum

PART 6

EVOLUTIONARY PARASITOLOGY OF AFRICAN FRESHWATER FISHES

AND ITS IMPLICATIONS

FOR THE SUSTAINABLE MANAGEMENT

OF AQUATIC RESOURCES



Maarten P.M. Vanhove

Faculty of Science, Masaryk University, Brno, Czech Republic; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; KU Leuven, Leuven, Belgium; Hasselt University, Diepenbeek, Belgium; Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland E-mail: maarten.vanhove@uhasselt.be

This book is intended as an aid in investigating the diversity and ecology of parasites of African freshwater fishes. However, given the species richness and degree of endemicity of African freshwater fishes, and the existence of several textbook cases in evolutionary biology, the evolution of their parasite fauna is also a promising subject for research.

When attempting to establish the historical relationships and diversification mechanisms of parasites through a phylogenetic approach, a recurrent question is to what extent the distribution of character states for typical parasitological traits such as host choice, host-specificity or infection site corresponds to the animals' classification. In this respect, the analysis of morphological or other phenotypic traits in combination with molecular data is critical to understanding parasite evolution. However, any morphology- or genetics-based phylogenetic approach requires coverage of as many representatives of the taxa under study as possible. Despite the progress in molecular techniques, achieving adequate taxon coverage (not to mention phenotypic characterisation) remains a challenge that hampers the development of comprehensive hypotheses about their evolutionary relationships.

Data on African fish parasites are relatively scarce and the rate of species discovery has not kept up with recent advances in phylogenetics and molecular biology. For example, regarding the evolution of cymothoid isopods, whose historical relationships have traditionally been regarded as correlated with their infection site, Smit *et al.* (2014) assert that the small numbers of representatives covered is a point of attention for recent molecular phylogenetic work. Phylogenetic studies on African lineages of fish parasites, or on fish parasite taxa that are well-represented in African freshwater bodies, are quite rare, with some notable exceptions, *e.g.* the morphology-based phylogeny of lernaeid copepods by Ho (1998). Therefore, there is no comprehensive view at present of the evolution of many of the taxa covered in this book. Another constraint is that the fossil record of parasites worldwide is often patchy or non-existent and rarely taken into consideration, despite its obvious potential, *e.g.* in developing a timeframe for parasite evolution (De Baets *et al.* 2015; Leung 2017).

A number of systematic studies on the tapeworms of African freshwater fishes have used molecular data to assess phylogenetic relationships and potential intraspecific variation (*e.g.*, Schaeffner *et al.* 2011; Kuchta *et al.* 2012). A pattern of low species richness, relatively narrow host-specificity and a wide geographical range, seems to emerge. Conversely, there has been little research into the molecular phylogeny and intraspecific genetic diversity of African fish acanthocephalans (Amin *et al.* 2016) and examination of these aspects could be worthwhile. For example, *Acanthogyrus tilapiae* has a broad host range among cichlids (Amin *et al.* 2008).

Indeed, for the study of host-specificity, in-depth understanding of parasite (molecular) taxonomy is a necessity, as several seemingly generalist species have proven to be incorrectly identified or to consist of complexes of closely related but more host-specific species (Pouyaud *et al.* 2006; Smit *et al.* 2014). Likewise, the current knowledge of digeneans infecting African freshwater fishes appears too fragmented to identify conclusive evolutionary patterns (see Scholz *et al.* 2016).

The scarce molecular work has mainly focused on diplostomids and clinostomids, with some recent advances in barcoding and classification (*e.g.*, Chibwana *et al.* 2013; Caffara *et al.* 2017). In the absence of reliable morphological characters for species-level identification in non-adult stages, such genetic work has also facilitated species delineation (Otachi *et al.* 2015) and life cycle reconstruction (Chibwana *et al.* 2015). When sequence data from a wider host and geographic range are included, patterns do emerge, *e.g.* on the link of infection site (eye lens or other tissues) with diplostomid evolution and host-specificity (Locke *et al.* 2015).

For monogeneans, with several relatively well-studied genera that are endemic or mostly constrained to Africa, some patterns in host use, host-specificity and speciation mechanisms can be discerned on an African scale. For example, congruence between the phylogeny of representatives of *Cichlidogyrus* and their cichlid hosts has been shown several times, although the speciation mechanisms underlying this pattern seem to differ between cichlid-monogenean systems (Mendlová *et al.* 2012; Vanhove *et al.* 2015). Relatively extensive sampling, especially of certain groups of cichlids, also indicated correlations between host genetic diversity and parasite species richness (Pariselle *et al.* 2003; Grégoir *et al.* 2015), and between host-specificity and host behaviour, phylogeny or ecology (Mendlová & Šimková 2014; Kmentová *et al.* 2016).

As with other parasite taxa, we are reminded that taxon sampling remains of the utmost importance. Whereas earlier work suggested that the morphology of the attachment organ in representatives of *Cichlidogyrus* was poorly influenced by host choice (Vignon *et al.* 2011), the addition in a phylogenetic reconstruction of a species that resulted from a distant host-switching event indicated an adaptative component to haptor morphology (Messu Mandeng *et al.* 2015). Unexpectedly distant host-switches are known from other African dactylogyridean monogeneans, such as *Quadriacanthus* (see Nack *et al.* 2016).

The monogeneans of other African freshwater fish families have recently also become the subject of molecular phylogenetic research, including those infecting catfishes (Francová *et al.* 2017) and cyprinids (Šimková *et al.* 2017). The above-mentioned work on the evolution of African monogeneans deals mainly with representatives of the Dactylogyridea. A different picture emerges for the gyrodactylids. The many endemic African lineages and genera are attractive subjects for evolutionary parasitology (*e.g.*, Přikrylová *et al.* 2017) and mechanisms deemed important in gyrodactylid speciation, such as hybridisation and host-switching, have been demonstrated for their African representatives (Barson *et al.* 2010; Přikrylová *et al.* 2013; Zahradníčková *et al.* 2016).

In addition to studying the patterns and processes underlying parasite biodiversity, evolutionary parasitology also considers the hypotheses that parasites may act as tags for the taxonomy and biogeography of African fishes (*e.g.*, Paugy *et al.* 1990; Barson *et al.* 2010; Pariselle *et al.* 2011; El Hafidi *et al.* 2013), or as drivers of the diversification of their hosts. The latter aspect has been explored for the African Great Lakes, comparing the parasite communities of different cichlid species or populations, and linking these to immunogenetics, trophic specialisation and

sexual selection (Maan *et al.* 2006, 2008; Blais *et al.* 2007; Raeymaekers *et al.* 2013; Hablützel *et al.* 2014, 2016, 2017).

There are several practical applications of evolutionary and ecological fish parasitology. For instance, fish parasites may be used as indicators for anthropogenic stressors such as pollution (Sures *et al.* 2017). This approach has also been taken for African fishes (*e.g.*, Madanire-Moyo *et al.* 2012).

Greater knowledge of the diversity and speciation of African fish parasites will increase understanding of their host range and host-specificity. This is important in view of the co-introduction of parasites that potentially accompanies the translocation of fishes for aquaculture or fisheries (Vanhove *et al.* 2016). Alien parasites in Africa have already caused mass fish mortalities in hatcheries (Hecht & Endemann 1998). An overview for South Africa by Smit *et al.* (2017) lists 23 alien fish parasites, of which seven are considered invasive. The authors suggest that a lack of monitoring is the most likely explanation of this relatively modest number.

There have not been many reports of fish diseases in Africa and they have been given little attention. However, fish parasites are expected to gain importance with the further development of aquaculture (Hecht & Endemann 1998). This requires increased efforts to protect fish health but, as pointed out by Akoll et al. (2012a), African countries may lack the capacity to control fish health and implement biosecurity systems and hence, more awareness of fish parasites and their ecology is important to Africa. Although parasite infections do not always demonstrably harm their fish hosts (e.g., Ndeda et al. 2013), Paperna (1996) lists numerous cases where fish parasites have detrimental effects, especially in aquaculture. It is therefore not surprising that Akoll et al. (2012b) emphasise the risks of fish parasites for the productivity and sustainability of African aquaculture. In addition, though seldom reported, there are potential dangers to fish populations in nature (e.g., Marshall & Cowx 2003 discuss a tapeworm infecting an economically important cyprinid in Lake Victoria), to fisheries economics (consumer rejection of infected fish: Kabunda & Sommerville 1984) and to human health (fish-borne zoonoses: Florio et al. 2009). Building capacity for pathogen monitoring, identification and risk analysis in developing countries is vital for aquatic health management (Bondad-Reantaso et al. 2005) and for any integrated approach to health (Keune et al. 2017). It is hoped that this book can contribute to this endeavour.

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PART 7

PROSPECTS AND RECOMMENDATIONS



Tomáš Scholz Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic E-mail: tscholz@paru.cas.cz

Nico Smit

Water Research Group (Parasitology), Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa E-mail: nico.smit@nwu.ac.za

Maarten P.M. Vanhove

Faculty of Science, Masaryk University, Brno, Czech Republic; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; KU Leuven, Leuven, Belgium; Hasselt University, Diepenbeek, Belgium; Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland E-mail: maarten.vanhove@uhasselt.be

The present book aims to summarise the current state of knowledge of the diversity of the parasites of freshwater fishes in Africa. It does not attempt to be an exhaustive monograph covering in detail every fish parasite group reported from freshwater ray-finned fishes (Actinopterygii) in Africa. The systematic chapter documents the progress achieved and reveals the existing gaps in our attempts to better define the parasite fauna of a continent that encompasses the whole Ethiopian (Afrotropical) zoogeographical region and the far southwestern part of the Palaearctic region. A simple comparison of the number of species and genera of helminth parasites listed in the current publication with those in two earlier checklists (Khalil 1971; Khalil & Polling 1997) shows a considerable increase over the last two decades. However, there is still much to discover.

The information summarised in the systematic chapter clearly demonstrates, as did the checklists of Khalil (1971) and Khalil and Polling (1997), how unbalanced the present knowledge of African fish parasites is in several aspects. First, attention paid to individual groups has been uneven, with the data available on protists and helminth larvae the most limited. Second, there are conspicuous differences in the number of studies on different fish hosts, with cichlids and catfishes the most intensively studied groups. Third, and probably most importantly, there are marked differences in the amount of data accumulated in the different regions and countries of Africa. The information for some regions such as the Nile Basin (Egypt and Sudan), African Great Lakes (especially Lake Victoria and Lake Tanganyika) and South Africa is reasonably representative but there are vast areas of Africa for which there is limited or no data.

Another important message that the editors would like to emphasise is in the methodological chapters. Though they may appear at first sight too succinct, the authors of individual chapters have used their long experience in parasite studies to present the most relevant information for processing fish parasites correctly and for the application of the best methods to ensure that valuable parasite material is available for subsequent morphological, taxonomic, histopathological, ecological, genetic and other studies. The book will serve as a guide to all principal steps including catching fish, their examination for different groups of unicellular and metazoan parasites and the appropriate processing of the parasites found.

The remaining chapters complement these two core parts of the book to provide a compendium of useful information for both advanced fish parasitologists and inexperienced beginners. However, the editors are aware that the present book represents only an initial attempt to support the advancement of fish parasitology in Africa. Therefore, any critical comments and suggestions for additional information are welcome and should be sent to the Editors.

The future progress of African fish parasitology is difficult to predict as it depends on many factors, such as the economic situation in individual countries, sufficient funding for basic and applied research, the availability of human resources including the development of a new generation of fish parasitologists trained in the best methods of modern biological and veterinary research, and also in assessing ecosystem health and richness of aquatic habitats. Several recommendations important for the further development of studies on the fish parasites in Africa are suggested below:

1. Any study of fish parasites should be preceded by a comprehensive literature search to avoid repetition of work already done.

2. The exact purpose of a new study should be established before the start. The availability of facilities, expertise and funding should be assessed realistically. A study that is too ambitious may result in methodological mistakes.

3. Only fresh or recently dead fish should be examined, including those in outbreaks of mass mortality in aquaculture.

4. Suitable methods and proper equipment should always be used, especially good quality optics and chemicals (as fixatives, etc.).

5. There should be a focus on quality rather than quantity. It is better to examine fewer fish correctly than many fish incorrectly. Inadequate examination will result in unreliable data.

6. Faunal surveys should be the first step in exploring fish parasites in a given region and vouchers of parasites found should always be preserved, preferably in an internationally accessible collection.

7. International cooperation with experts on individual parasite groups and research areas is strongly recommended (and often inevitable) but only properly processed parasite material should be used. Avoid making requests for the identification of parasites from poor quality pictures of improperly processed material.

The present book is the outcome of a long term international cooperation of more than two generations of fish parasitologists and other specialists from South Africa and several European countries. We hope that our efforts will facilitate the further advancement of fish parasitology in the African continent.

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Profile of the editors



Tomáš Scholz

Tomáš has been studying helminth parasites for the past 30 years (defended his PhD on fish tapeworms in 1989). He deals with the systematics, phylogenetics and life cycles of parasitic flatworms, especially tapeworms (Cestoda) and trematodes (Digenea) including causative agents of fish-borne diseases. He is the Co-Principal Investigator of the European Centre of IchthyoParasitology (ECIP) project and was the leading Editor of the book.



Maarten P.M. Vanhove

Maarten is an ECIP researcher studying molecular and morphological diversity of (monogenean) parasites in an evolutionary and policy-relevant context, focusing on Africa and the Mediterranean. He teaches at Hasselt University. While preparing this book, he worked on capacity building in Africa as a biodiversity policy scientist at the Royal Belgian Institute of Natural Sciences, and as curator of worms at the Finnish Museum of Natural History.



Nico Smit

Nico's research focuses on the biodiversity, taxonomy and ecology of parasitic Crustacea and blood protozoa of African marine and freshwater fishes. Recently he has been the first South African aquatic parasitologist to be rated by the South African National Research Foundation as an internationally acclaimed scientist. He is currently the Director of Research and Professor of Ecology at North-West University, South Africa.



Zuzana Jayasundera

Zuzana is PR manager of Faculty of Science, Masaryk University in Brno, including the ECIP project. She was responsible for images as Graphics Editor. She is studying her Ph.D. in Philosophy of Science at Faculty of Arts, Masaryk University, concerning on popularisation of science and scientific communication.



Milan Gelnar

Milan works on organismal and structural diversity, morphology, biology and ecology of monogeneans. He has also dealt with parasite population and community ecology, parasite specificity, specialisation and microhabitat distribution, host-parasite co-evolution, evolutionary ecology and epidemiology of fish parasites. Milan is the Principal Investigator of the ECIP project, responsible for scientific, economic and personnel management.

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