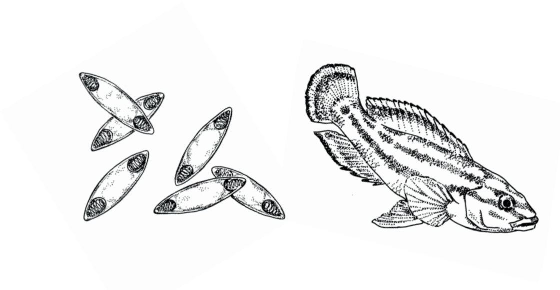
PART 6

EVOLUTIONARY PARASITOLOGY OF AFRICAN FRESHWATER FISHES

AND ITS IMPLICATIONS FOR THE SUSTAINABLE MANAGEMENT OF AQUATIC RESOURCES



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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.

References

Akoll, P., Konecny, R., Mwanja, W.W., Nattabi, J.K., Agoe, C. & Schiemer, F. 2012a. Parasite fauna of farmed Nile tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*) in Uganda. *Parasitology Research* 110: 315-323.

Akoll, P., Konecny, R., Mwanja, W.W. & Schiemer, F. 2012b. Risk assessment of parasitic helminths on cultured Nile tilapia (*Oreochromis niloticus*, L.). *Aquaculture* 356: 123-127.

Amin, O.M., Van Oosterhout, C., Blais, J., Robinson, R.L. & Cable, J. 2008. On the ecology and host relationships of *Acanthogyrus* (*Acanthosentis*) *tilapiae* (Acanthocephala: Quadrigyridae) from cichlids in Lake Malawi. *Comparative Parasitology* 75: 278-282.

Amin, O.M., Evans, R.P., Boungou, M. & Heckmann, R. 2016. Morphological and molecular description of *Tenuisentis niloticus* (Meyer, 1932) (Acanthocephala: Tenuisentidae) from *Heterotis niloticus* (Cuvier) (Actinopterygii: Arapaimidae), in Burkina Faso, with emendation of the family diagnosis and notes on new features, cryptic genetic diversity and histopathology. *Systematic Parasitology* 93: 173-191.

Barson, M., Přikrylová, I., Vanhove, M.P.M. & Huyse, T. 2010. Parasite hybridization in African *Macrogyrodactylus* spp. (Monogenea, Platyhelminthes) signals historical host distribution. *Parasitology* 137: 1585-1595.

Blais, J., Rico, C., Van Oosterhout, C., Cable, J., Turner, G.F. & Bernatchez, L. 2007. MHC adaptive divergence between closely related and sympatric African cichlids. *PLoS ONE* 2: e734.

Bondad-Reantaso, M.G., Subasinghe, R.P., Arthur, J.R., Ogawa, K., Chinabut, S., Adlard, R., Tan, Z. & Shariff, M. 2005. Disease and health management in Asian aquaculture. *Veterinary Parasitology* 132: 249-272.

Caffara, M., Locke, S.A., Echi, P.C., Halajian, A., Benini, D., Luus-Powell, W.J., Tavakol, S. & Fioravanti, M.L. 2017. A morphological and molecular study of clinostomid metacercariae from African fish with a redescription of *Clinostomum tilapiae*. *Parasitology* 144: 1519-1529.

Chibwana, F.D., Blasco-Costa, I., Georgieva, S., Hosea, K.M., Nkwengulila, G., Scholz, T. & Kostadinova, A. 2013. A first insight into the barcodes for African diplostomids (Digenea: Diplostomidae): brain parasites in *Clarias gariepinus* (Siluriformes: Clariidae). *Infection, Genetics and Evolution* 17: 62-70.

Chibwana, F.D., Nkwengulila, G., Locke, S.A., McLaughlin, J.D. & Marcogliese, D.J. 2015. Completion of the life cycle of *Tylodelphys mashonense* (Sudarikov, 1971) (Digenea: Diplostomidae) with DNA barcodes and rDNA sequences. *Parasitology Research* 114: 3675-3682.

De Baets, K., Dentzien-Dias, P., Upeniece, I., Verneau, O. & Donoghue, P.C. 2015. Constraining the deep origin of parasitic flatworms and host-interactions with fossil evidence. *Advances in Parasitology* 90: 93-135.

El Hafidi, F., Berrada Rkhami, O., de Buron, I., Durand, J.D. & Pariselle, A. 2013. *Ligophorus* species (Monogenea: Ancyrocephalidae) from *Mugil cephalus* (Teleostei: Mugilidae) off Morocco with the description of a new species and remarks about the use of *Ligophorus* spp. as biological markers of host populations. *Folia Parasitologica* 60: 433-440.

Florio, D., Gustinelli, A., Caffara, M., Turci, F., Quaglio, F., Konecny, R., Nikowitz, T., Wathuta, E.M., Magana, A., Otachi, E.O., Matolla, G.K., Warugu, H.W., Liti, D., Mbaluka, R., Thiga, B., Munguti, J., Akoll, P., Mwanja, W., Asaminew, K., Tadesse, Z. & Fioravanti, M.L. 2009. Veterinary and public health aspects in tilapia

(*Oreochromis niloticus niloticus*) aquaculture in Kenya, Uganda and Ethiopia. *Ittiopatologia* 6: 51-93.

Francová, K., Seifertová, M., Blažek, R., Gelnar, M., Mahmoud, Z.N. & Řehulková, E. 2017. *Quadriacanthus* species (Monogenea: Dactylogyridae) from catfishes (Teleostei: Siluriformes) in eastern Africa: new species, new records and first insights into interspecific genetic relationships. *Parasites & Vectors* 10: 361.

Grégoir, A.F., Hablützel, P.I., Vanhove, M.P.M., Pariselle, A., Bamps, J., Volckaert, F.A.M. & Raeymaekers, J.A.M. 2015. A link between host dispersal and parasite diversity in two sympatric cichlid fishes of Lake Tanganyika. *Freshwater Biology* 60: 323-335.

Hablützel, P.I., Vanhove, M.P.M., Deschepper, P., Grégoir, A.F., Roose, A.K., Volckaert, F.A.M. & Raeymaekers, J.A.M. 2017. Parasite escape through trophic specialization in a species flock. *Journal of Evolutionary Biology* 30: 1437-1445.

Hablützel, P.I., Vanhove, M.P.M., Grégoir, A.F., Volckaert, F.A.M. & Raeymaekers, J.A.M. 2014. Intermediate number of major histocompatibility complex class II*B* length variants relates to enlarged perivisceral fat deposits in the blunt-head cichlid *Tropheus moorii*. *Journal of Evolutionary Biology* 27: 2177-2190.

Hablützel, P.I., Grégoir, A.F., Vanhove, M.P.M., Volckaert, F.A.M. & Raeymaekers, J.A.M. 2016. Weak link between dispersal and parasite community differentiation or immunogenetic divergence in two sympatric cichlid fishes. *Molecular Ecology* 25: 5451-5466.

Hecht, T. & Endemann, F. 1998. The impact of parasites, infections and diseases on the development of aquaculture in sub-Saharan Africa. *Journal of Applied Ichthyology* 14: 213-221.

Ho, J.S. 1998. Cladistics of the Lernaeidae (Cyclopoida), a major family of freshwater fish parasites. *Journal of Marine Systems* 15: 177-183.

Kabunda, M.Y. & Sommerville, C. 1984. Parasitic worms causing the rejection of tilapia (*Oreochromis species*) in Zaire. *British Veterinary Journal* 140: 263-268.

Keune, H., Flandroy, L., Thys, S., De Regge, N., Mori, M., Antoine-Moussiaux, N., Vanhove, M.P.M., Rebolledo, J., Van Gucht, S., Deblauwe, I., Hiemstra, W., Häsler, B., Binot, A., Savic, S., Ruegg, S., De Vries, S., Garnier, J. & van den Berg, T. 2017. The need for European OneHealth/EcoHealth networks. *Archives of Public Health* 75: 64.

Kmentová, N., Gelnar, M., Mendlová, M., Van Steenberge, M., Koblmüller, S. & Vanhove, M.P.M. 2016. Reduced host specificity in a parasite infecting non-littoral Lake Tanganyika cichlids evidenced by intraspecific morphological and genetic diversity. *Scientific Reports* 6: 39605.

Kuchta, R., Burianová, A., Jirků, M., de Chambrier, A., Oros, M., Brabec, J. & Scholz, T. 2012. Bothriocephalidean tapeworms (Cestoda) of freshwater fish in

Africa, including erection of *Kirstenella* n. gen. and description of *Tetracampos martinae* n. sp. *Zootaxa* 3309: 1-35.

Leung, T.L. 2017. Fossils of parasites: what can the fossil record tell us about the evolution of parasitism? *Biological Reviews* 92: 410-430.

Locke, S.A., Al-Nasiri, F.S., Caffara, M., Drago, F., Kalbe, M., Lapierre, A.R., McLaughlin, J.D., Nie, P., Overstreet, R.M., Souza, G.T.R., Takemoto, R.M. & Marcogliese, D.J. 2015. Diversity, specificity and speciation in larval Diplostomidae (Platyhelminthes: Digenea) in the eyes of freshwater fish, as revealed by DNA barcodes. *International Journal for Parasitology* 45: 841-855.

Maan, M.E., Van Der Spoel, M., Jimenez, P.Q., Van Alphen, J.J. & Seehausen, O. 2006. Fitness correlates of male coloration in a Lake Victoria cichlid fish. *Behavioral Ecology* 17: 691-699.

Maan, M.E., Van Rooijen, A.M., Van Alphen, J.J. & Seehausen, O. 2008. Parasite-mediated sexual selection and species divergence in Lake Victoria cichlid fish. *Biological Journal of the Linnean Society* 94: 53-60.

Madanire-Moyo, G.N., Luus-Powell, W.J. & Olivier, P.A. 2012. Diversity of metazoan parasites of the Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), as indicators of pollution in the Limpopo and Olifants River systems. *Onderstepoort Journal of Veterinary Research* 79: 1-9.

Marshall, J. & Cowx, I.G. 2003. Will the explosion of *Ligula intestinalis* in *Rastrineobola argentea* lead to another shift in the fisheries of Lake Victoria? *In*: Cowx, I.G. (Ed). *Interactions Between Fish and Birds: Implications for Management*. Blackwell Science Ltd., Oxford, pp. 244-258.

Mendlová, M., Desdevises, Y., Civáňová, K., Pariselle, A. & Šimková, A. 2012. Monogeneans of West African cichlid fish: evolution and cophylogenetic interactions. *PLoS ONE* 7: e37268.

Mendlová, M. & Šimková, A. 2014. Evolution of host specificity in monogeneans parasitizing African cichlid fish. *Parasites & Vectors* 7: 69.

Messu Mandeng, F.D., Bilong Bilong, C.F., Pariselle, A., Vanhove, M.P.M., Bitja Nyom, A.R. & Agnèse, J.-F. 2015. A phylogeny of *Cichlidogyrus* species (Monogenea, Dactylogyridea) clarifies a host switch between fish families and reveals an adaptive component to attachment organ morphology of this parasite genus. *Parasites & Vectors* 8: 582.

Nack, J., Nyom, A.B., Pariselle, A. & Bilong Bilong, C.F. 2016. New evidence of a lateral transfer of monogenean parasite between distant fish hosts in Lake Ossa, South Cameroon: the case of *Quadriacanthus euzeti* n. sp. *Journal of Helminthology* 90: 455-459.

Ndeda, V., Owiti, D., Ndong'a, M. & Miruka, D.O. 2013. Occurrence and effect of *Diplostomum* parasites in cultured *Oreochromis niloticus* (L.) and distribution in vector snails within Kisumu City, western Kenya. *Ecohydrology & Hydrobiology* 13: 253-260.

Otachi, E.O., Locke, S.A., Jirsa, F., Fellner-Frank, C. & Marcogliese, D.J. 2015. Morphometric and molecular analyses of *Tylodelphys* sp. metacercariae (Digenea: Diplostomidae) from the vitreous humour of four fish species from Lake Naivasha, Kenya. *Journal of Helminthology* 89: 404-414.

Paperna, I. 1996. *Parasites, Infections and Diseases of Fishes in Africa. An Update*. CIFA Technical Paper, no. 31, FAO, Rome: 220 pp.

Pariselle, A., Boeger, W.A., Snoeks, J., Bilong Bilong, C.F., Morand, S. & Vanhove, M.P.M. 2011. The monogenean parasite fauna of cichlids: a potential tool for host biogeography. *International Journal of Evolutionary Biology* 2011: 471480.

Pariselle, A., Morand, S., Deveney, M. & Pouyaud, L. 2003. Parasite species richness of closely related hosts: historical scenario and "genetic" hypothesis. *In*: Combes, C. & Jourdane, J. (Eds). *Hommage à Louis Euzet – taxonomie, écologie et évolution des métazoaires parasites. Taxonomy, Ecology and Evolution of Metazoan Parasites.* Presses universitaires de Perpignan, Perpignan, pp. 147-166.

Paugy, D., Guégan, J.F. & Agnèse, J.F. 1990. Three simultaneous and independent approaches to the characterization of a new species of *Labeo* (Teleostei, Cyprinidae) from West Africa. *Canadian Journal of Zoology* 68: 1124-1131.

Pouyaud, L., Desmarais, E., Deveney, M. & Pariselle, A. 2006. Phylogenetic relationships among monogenean gill parasites (Dactylogyridea, Ancyrocephalidae) infesting tilapiine hosts (Cichlidae): systematic and evolutionary implications. *Molecular Phylogenetics and Evolution* 38: 241-249.

Přikrylová, I., Vanhove, M.P.M., Janssens, S.B., Billeter, P.A. & Huyse, T. 2013. Tiny worms from a mighty continent: high diversity and new phylogenetic lineages of African monogeneans. *Molecular Phylogenetics and Evolution* 67: 43-52.

Přikrylová, I., Shinn, A.P. & Paladini, G. 2017. Description of *Citharodactylus gagei* n. gen. et n. sp. (Monogenea: Gyrodactylidae) from the moon fish, *Citharinus citharus* (Geoffroy Saint-Hilaire), from Lake Turkana. *Parasitology Research* 116: 281-292.

Raeymaekers, J.A.M., Hablützel, P.I., Grégoir, A.F., Bamps, J., Roose, A.K., Vanhove, M.P.M., Van Steenberge, M., Pariselle, A., Huyse, T., Snoeks, J. & Volckaert, F.A.M. 2013. Contrasting parasite communities among allopatric colour morphs of the Lake Tanganyika cichlid *Tropheus*. *BMC Evolutionary Biology* 13: 41.

Schaeffner, B.C., Jirků, M., Mahmoud, Z.N. & Scholz, T. 2011. Revision of *Wenyonia* Woodland, 1923 (Cestoda: Caryophyllidea) from catfishes (Siluriformes) in Africa. *Systematic Parasitology* 79: 83-107.

Scholz, T., Besprozvannykh, V.V., Boutorina, T.E., Choudhury, A., Cribb, T.H., Ermolenko, A.V., Faltýnková, A., Shedko, M.B., Shimazu, T. & Smit, N.J. 2016. Trematode diversity in freshwater fishes of the Globe I: 'Old World'. *Systematic Parasitology* 93: 257-269.

Šimková, A., Benovics, M., Rahmouni, I. & Vukić, J. 2017. Host-specific *Dactylogyrus* parasites revealing new insights on the historical biogeography of Northwest African and Iberian cyprinid fish. *Parasites & Vectors* 10: 589.

Smit, N.J., Bruce, N.L. & Hadfield, K.A. 2014. Global diversity of fish parasitic isopod crustaceans of the family Cymothoidae. *International Journal for Parasitology: Parasites and Wildlife* 3: 188-197.

Smit, N.J., Malherbe, W. & Hadfield, K.A. 2017. Alien freshwater fish parasites from South Africa: diversity, distribution, status and the way forward. *International Journal for Parasitology: Parasites and Wildlife* 6: 386-401.

Sures, B., Selbach, C., Marcogliese, D.J., & Nachev, M. 2017. Parasite responses to pollution: what we know and where we go in 'Environmental Parasitology'. *Parasites & Vectors* 10: 65.

Vanhove, M.P.M., Pariselle, A., Van Steenberge, M., Raeymaekers, J.A.M., Hablützel, P.I., Gillardin, C., Hellemans, B., Breman, F.C., Koblmüller, S., Sturmbauer, C., Snoeks, J., Volckaert, F.A.M. & Huyse, T. 2015. Hidden biodiversity in an ancient lake: phylogenetic congruence between Lake Tanganyika tropheine cichlids and their monogenean flatworm parasites. *Scientific Reports* 5: 13669.

Vanhove, M.P.M., Hablützel, P.I., Pariselle, A., Šimková, A., Huyse, T. & Raeymaekers, J.A.M. 2016. Cichlids: a host of opportunities for evolutionary parasitology. *Trends in Parasitology* 32: 820-832.

Vignon, M., Pariselle, A. & Vanhove, M.P.M. 2011. Modularity in attachment organs of African *Cichlidogyrus* (Platyhelminthes, Monogenea, Ancyrocephalidae) reflects phylogeny rather than host specificity or geographic distribution. *Biological Journal of the Linnean Society* 102: 694-706.

Zahradníčková, P., Barson, M., Luus-Powell, W.J. & Přikrylová, I. 2016. Species of *Gyrodactylus* von Nordmann, 1832 (Platyhelminthes: Monogenea) from cichlids from Zambezi and Limpopo river basins in Zimbabwe and South Africa: evidence for unexplored species richness. *Systematic Parasitology* 93: 679-700.