


Transmission of parasites from introduced tilapias: a new threat to endemic Malagasy ichthyofauna

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Abstract Invasive species are a major threat to biodiversity. In Madagascar, one quarter of freshwater fish fauna consist of introduced species. The introduction of non-native species affects native biota by means of direct interactions but also through indirect interactions including those mediated by parasites, as parasites are usually co-introduced with their hosts. Almost nothing is known about the parasites co-introduced with their fish hosts into Madagascar and

their potential impact on native endemic fish fauna. We studied the metazoan parasites of native and introduced cichlid fishes (and some non-cichlids) in the northern part of Madagascar. Using parasite data we evaluated the effect of fish introduced from mainland Africa on native Malagasy cichlid fauna. We documented the co-introduction into Madagascar of parasite species from mainland Africa and also probably from Eurasia. Malagasy cichlids and some other species living in sympatry with non-native cichlids acted as competent hosts for generalist parasites and also for host-specific parasites of African mainland cichlids. However, African mainland

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cichlids were not susceptible to infection by parasites specific to Malagasy cichlids. The different compositions of parasite communities and infection parameters in endemic and non-native cichlids in the regions investigated may be potentially explained by the different sources and timings of fish introductions. In addition, native endemic parasite fauna even seem to be outcompeted by introduced parasites, which cross the barriers of host specificity. The transmission of non-native parasites associated with the introduction of non-native freshwater fishes may represent a serious risk to endemic freshwater fish and parasite fauna in Madagascar.

Keywords Endemic cichlids · Invasive fish species · Madagascar · Parasites · Co-introduction

Introduction

Madagascar is among the top hotspots for biodiversity conservation worldwide (Myers et al. 2000; Vieites et al. 2009). The biogeographical history of Madagascar has resulted in unique and highly endemic fauna. The high level of endemism primarily results from the radiation of African founder individuals arriving during the Cenozoic (65.5 Mya to present) and from relict species radiating after the separation of the island from the African mainland (183–158 Mya), Antarctica (~ 130 Mya), and India (96–65 Mya) (Vences et al. 2009).

The native biodiversity of Madagascar is threatened primarily by two factors—human destruction of the natural habitats of endemic species and the introduction of non-native species. At least 24 fish species were deliberately introduced into Madagascar's freshwaters during the 1950s to increase food production, to develop aquaculture, and to control malaria-transmitting mosquitoes (Kiener 1963; Moreau 1979; Reinthal and Stiasny 1991). Most of them found very favourable conditions and spread and reproduced quickly to the point of becoming dominant in fish communities in most of the lakes and rivers of the island. Current knowledge suggests that Malagasy fish fauna is composed of 173 species, of which 71 are endemic and 26 are introduced (Froese and Pauly 2017).

Several species such as African bony-tongue, black bass, carp, goldfish, snakehead, and livebearers are frequently found all over the island, but African 'tilapias' (*Oreochromis* and *Coptodon*) are the most common group (De Rham and Nourissat 2004). They are extremely prolific and therefore represent one of the main causes of the decline of native cichlids. This is because native cichlids are less fertile, have a shorter, well-defined breeding season leading to a single reproductive event per year, and exhibit slower growth when compared to the introduced tilapias, which can breed multiple times each year (De Rham and Nourissat 2004). In addition, native cichlid species require specific physical and chemical water conditions (De Rham and Nourissat 2004).

The native representatives of Malagasy cichlid fauna belong to six genera i.e. *Katria*, *Oxylapia*, *Paratilapia*, *Paretroplus*, *Ptychochromis* and *Ptychochromoides*. Molecular phylogenetic studies suggest that Malagasy cichlids do not represent a monophyletic group. *Paretroplus* is closely related to *Etroplus* (both representatives of Etroplinae) from Sri Lanka and India, whilst the clade including *Ptychochromoides*, *Ptychochromis*, *Oxylapia* (Ptychochrominae) and *Paratilapia* (Paratilapiinae) is sister to the clade of all African and Neotropical cichlids, according to studies based on nuclear or mitochondrial markers or mitogenomes (Sparks and Smiths 2004; Azuma et al. 2008; Friedman et al. 2013).

There are numerous impacts of biological invasions on native biota (Simberloff et al. 2013). Invasive species affect native fauna through direct interactions, i.e. resource and space competition (reviewed for tilapias by Deines et al. 2016), or through indirect interactions mediated by parasites (Prenter et al. 2004; Dunn 2009; Kelly et al. 2009; Britton 2012). Parasites introduced with their non-native hosts into new areas modify natural host-parasite interactions, which may result in the emergence of disease in native species. Several mechanisms lead to parasite-mediated effects on native biota (Prenter et al. 2004; Goedknecht et al. 2016, 2017; Morand 2015). The co-introduction of parasites with their invasive host species may result in so-called parasite spillover to native host species, which can lead to the emergence of disease and, in many cases, also to increased mortality among native host species (Goedknecht et al. 2016). Native hosts may have also evolved strong immune defenses, which

confer resistance against the spillover of introduced parasites (Morand 2015). Alternatively, introduced species may lose their natural parasites, which enhances their ability to establish and invade a newly-colonized area, as predicted by the enemy release hypothesis (Mitchell and Power 2003; Colautti et al. 2004). In contrast, the invasive host species may also be infected by native parasites. When an invasive species acts as a competent alternative host for native parasites, parasite populations increase in size and thus increase their negative effect on the native host (parasite spillback, Kelly et al. 2009). When invasive species are incompetent hosts for native parasites, they act as a sink by diluting the native parasite population and thereby reduce the risk of high infection levels and the resulting consequences for native host species (parasite dilution, Kelly et al. 2009). Finally, if the parasites are not present in the invaded localities, introduced species may allocate energetic resources from costly immune defense into growth and reproduction, which increases their competitive ability and facilitates their establishment and spreading in new areas (Blossey and Notzol 1995).

Recent information about the parasite fauna of freshwater fish in Madagascar is scarce. With respect to metazoan parasites, monogeneans have been the most closely studied fish parasites in Madagascar (Rakotofiringa 1986). They are a group of mainly gill and fin ectoparasites generally exhibiting a high degree of host specificity (i.e. they infect either a single host species or a limited range of phylogenetically closely related host species). Cichlids of the African mainland and Madagascar harbour monogeneans of different genera. African mainland cichlids are infected with species of five genera of dactylogyridean monogeneans including host-specific ectoparasites (species of *Cichlidogyrus*, *Scutogyrus* and *Onchobdella*) and endoparasitic species of *Enterogyrus* and *Urogyrus*, and one representative of gyroactylidean monogeneans, i.e. *Gyroactylus* (Přikrylová et al. 2009). In contrast, Malagasy cichlids harbour host-specific species of *Insulacleidus* (see Pariselle and Euzet 2009). Common evolutionary histories of host-parasite systems (i.e. coevolution) result in tight associations between hosts and their specific parasites, which should prevent the infection of incorrect hosts by host-specific parasites. As a result, spillover may be expected for generalist parasites infecting a wide range of phylogenetically

unrelated species, whereas the colonization of native species by non-native specific parasites is unlikely (Wünnemann et al. 2016; Clark et al. 2018). Indeed, Rakotofiringa (1986) did not identify parasite transmission between native and non-native cichlids in Madagascar.

The aim of the present study was (1) to investigate the metazoan parasite fauna of native endemic and introduced cichlid species (and some non-cichlid species) living in the northern part of Madagascar, and (2), using these data, to estimate whether fish introduction could affect native Malagasy fish fauna through parasite transmission.

Materials and methods

From 8th to 26th April 2016, we performed a field study to investigate the metazoan parasites primarily of cichlid fishes, although some non-cichlid fishes living in sympatry with cichlids were also examined for the presence of metazoan parasites. More specifically, cichlids and some non-cichlid species were sampled in Lake Ravelobe (Ankarafantsika National Park) 16°18'23.14"S–46°48'43.32"E, the Anjingo River (near Antsohihy) 14°50'40.89"S–48°14'43.36"E, the crater lakes of Mont Passot (on Nosy Be Island) 13°19'1.84"S–48°14'3.60"E, and the Canal des Pangalanes (at Andevoranto) 18°57'17.50"S–49° 6'29.90"E (Fig. 1). These areas belong to the eastern basins and freshwater systems of north-western Madagascar, all recognized as hotspots of Malagasy fish diversity (Benstead et al. 2003). The fish sampling was carried out following permission N° 06/AR.ED./15 issued on April 1, 2016 by the General Directorate for Fishery Resources and Fisheries, Ministry of Fisheries Resources and Fisheries, Madagascar. All applicable institutional, national, and international guidelines for the care and use of animals were followed.

The fish were measured and identified, and a fin clip from each specimen was preserved for molecular analysis. All fish specimens were transported live to the field laboratory, sacrificed by severing the spinal cord, and dissected within 48 h following classical parasitological dissection procedures (Ergens and Lom 1970). Fish were inspected for parasites (first for gyroactylids) immediately after sacrificing. Fish body, fins, skin, gills, eyes, nasal cavity and all

Fig. 1 Map of Madagascar indicating the sampling localities (the source of map is Department of Botany and Zoology, Faculty of Science, Masaryk University, see also Table 1)



internal organs were examined for metazoan parasites. All metazoan parasites were removed and fixed in 70% ethanol, 4% formaldehyde, or a glycerin ammonium picrate mixture for further identification to genus or species levels. Taxonomical evaluation was performed using an Olympus BX50 microscope equipped with phase contrast and DIC optics, and digital image analysis software (Olympus Stream Motion 1.9.2).

A segment of DNA from the mitochondrial large ribosomal subunit (16S) of the RNA gene was analyzed in all sampled fish species using the same primers and protocols as applied for cichlids by Sparks and Smiths (2004). A segment of the mitochondrial cytochrome *b* gene was analyzed using the primers and protocols applied for cichlid fish by Mendlová et al. (2012). The sequences were deposited in GenBank under Accession numbers MH767413–

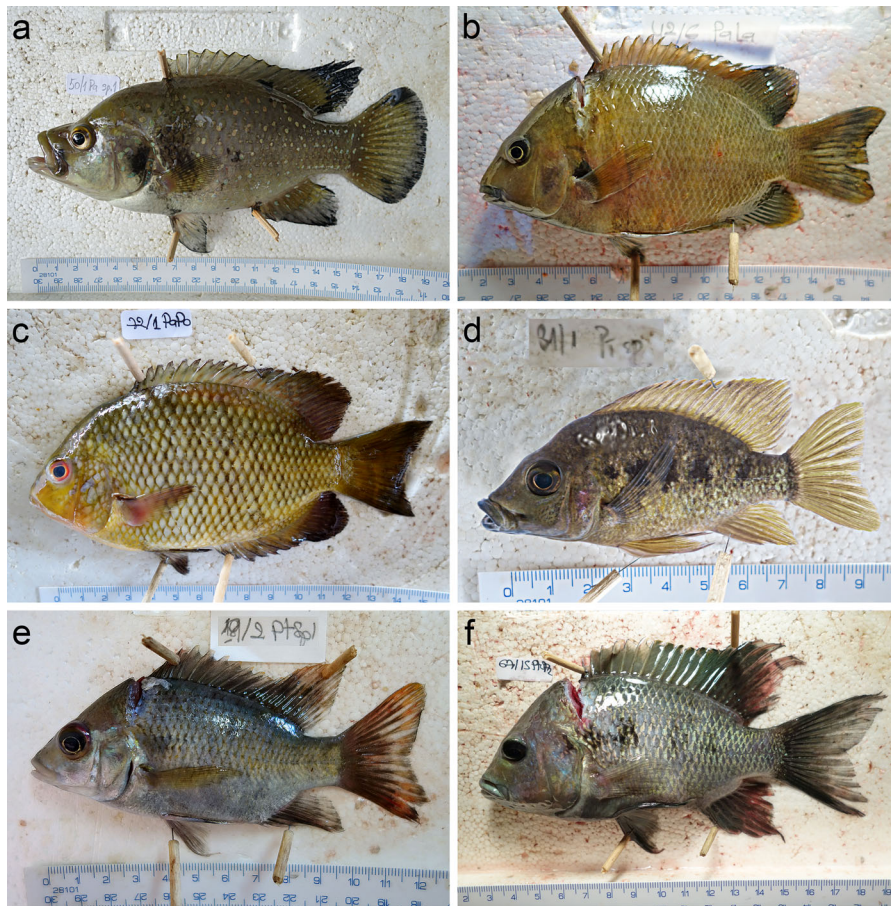


Fig. 2 Endemic cichlid hosts examined for the present study: **a** *Paratilapia polleni*, Lake Ambalavato (Lakes Mont Passot); **b** *Paretroplus lamnabe*, Anjingo River; **c** *Paretroplus polyacris*, Andevoranto; **d** *Ptychochromis grandidieri*, Andevoranto;

e *Ptychochromis inornatus*, Anjingo River; **f** *Ptychochromis oligacanthus*, Lakes Mont Passot. Photos by E. Řehulková and J. R. Rasoloariniaina

MH767448. Representative samples of the host populations were fixed in formaldehyde and deposited in the ichthyological collection of the Royal Museum for Central Africa (Belgium) under collection number 2016-15-P, stored in denatured ethanol (70%). Representative samples of parasites were deposited as vouchers in the invertebrate collection of the Royal Museum for Central Africa, Tervuren, Belgium (MRAC MT 38343–38431, 38581–38583 and 38268) and in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS C-773/2-3, C-283/3-5, C-15/35). Partial 18S rDNA with entire ITS1 regions, and partial 28S rDNA were analyzed for the specimens of non-native monogenean parasites from cichlid fish in

Madagascar in order to check their molecular similarity with specimens originated in mainland Africa. The primers and protocols followed Šimková et al. (2003, 2006). The sequences were deposited in GenBank under Accession numbers MH767390–MH767412.

Results

In the field, six endemic cichlid species (Fig. 2), three non-native cichlid species, and five other non-cichlid species (four native and one introduced) were examined for metazoan parasites (Table 1).

Five fish species were found in Lake Ravelobe of Ankarafantsika National Park (Table 1). Three of

Table 1 List of fish species sampled in Madagascar during the 3-week field study

Locality	Fish species	Fish family	Fish status	N	Body length	Date of collection
PN Ankarafantsika	<i>Oreochromis mossambicus</i>	Cichlidae	Introduced	3	15.0 ± 2.2	April 10–12, 2016
	<i>Oreochromis niloticus</i>	Cichlidae	Introduced	3	16.8 ± 5.4	April 10–12, 2016
	<i>Coptodon rendalli</i>	Cichlidae	Introduced	6	10.8 ± 1.8	April 10–12, 2016
	<i>Heterotis niloticus</i>	Arapaimidae	Introduced	2	12.5 ± 5.5	April 10–12, 2016
	<i>Megalops cyprinoides</i>	Megalopidae	Native	1	12.0	April 10–12, 2016
Anjingo River	<i>Oreochromis niloticus</i>	Cichlidae	Introduced	3	11.0 ± 0.9	April 13–15, 2016
	<i>Paretroplus lamnabe</i>	Cichlidae	Native endemic	9	13.2 ± 3.2	April 13–15, 2016
	<i>Ptychochromis inornatus</i>	Cichlidae	Native endemic	15	8.7 ± 2.2	April 13–15, 2016
	<i>Osteomugil robustus</i>	Mugilidae	Native	1	21	April 13–15, 2016
	<i>Pachypanchax omalonotus</i>	Aplocheilidae	Native endemic	2	6.4 ± 0.3	April 13–15, 2016
	<i>Glossogobius giuris</i>	Gobiidae	Native	3	11.5 ± 1.5	April 13–15, 2016
Lakes Mont Passot	<i>Paratilapia polleni</i>	Cichlidae	Native endemic	1	19.3	April 17–19, 2016
	<i>Oreochromis mossambicus</i>	Cichlidae	Introduced	2	13.8 ± 0.4	April 17–19, 2016
	<i>Ptychochromis oligacanthus</i>	Cichlidae	Native endemic	15	11.3 ± 6.0	April 17–19, 2016
	<i>Coptodon rendalli</i>	Cichlidae	Introduced	2	12.2 ± 1.6	April 17–19, 2016
Andevoranto	<i>Oreochromis niloticus</i>	Cichlidae	Introduced	5	14.7 ± 1.8	April 22–24, 2016
	<i>Paretroplus polyactis</i>	Cichlidae	Native endemic	20	11.1 ± 2.0	April 22–24, 2016
	<i>Ptychochromis grandidieri</i>	Cichlidae	Native endemic	5	10.1 ± 2.5	April 22–24, 2016

N, number of specimens studied

them are introduced (*Oreochromis mossambicus*, *O. niloticus*, and *Coptodon rendalli*) and two are native Malagasy non-cichlid species. We reported the co-introduction of seven African monogeneans specific to cichlids (five species of *Cichlidogyrus*, *Scutogyrus longicornis*, and *Gyrodactylus cichlidarum*) (Table 2). More specifically, four monogenean species on both *O. mossambicus* and *C. rendalli* and five on *O. niloticus* were found. Two monogenean species, *Cichlidogyrus thurstonae* and *C. tilapiae*, were present on all three non-native cichlid species. The intensities of infection were low for all monogenean species except for *C. tilapiae*, which parasitized 9 out of 12 specimens of the non-native cichlids investigated and achieved the highest levels of intensity of infection. All non-native cichlid species were heavily parasitized by larval stages of gryporhynchid cestodes (7 of 12 specimens of non-native cichlids were parasitized with an intensity of infection reaching up to 369 larval cestodes in a single host specimen). Two species of these cestode larvae, which could not be reliably distinguished without their flattening and fixing in GAP, namely *Neogryporhynchus lasiopeiuis* and *Parvitaenia macropeos*, occurred in the intestinal wall

of *Coptodon rendalli*, *O. mossambicus*, and *O. niloticus*.

Concerning the parasites of non-cichlid fish, host specific monogeneans were found in *Heterotis niloticus* and *Megalops cyprinoides* (*Heterotesia voltae* and *Diplectanocotyla megalopis* respectively—see Table 2). In addition, representatives of two endoparasite groups in *H. niloticus* (larval stages of gryporhynchid cestodes and undetermined nematode species) and a digenean gill metacercaria in *M. cyprinoides* were also found.

Six fish species were collected in the Anjingo River (near the city of Antsohihy), including five native fish species and one introduced cichlid species (Table 1). Concerning native species, two endemic species of cichlids (*Paretroplus lamnabe* and *Ptychochromis inornatus*) and one aplocheilid species (*Pachypanchax omalonotus*) were found. Five monogenean species were co-introduced with non-native *O. niloticus* (Table 3). Among them, *Cichlidogyrus thurstonae* infected the highest number of host specimens and achieved the highest intensity of infection on its introduced host. This species was also found on a few specimens of endemic cichlid species at a low

Table 2 Metazoan parasite infection in cichlids and non-cichlid fish species sampled in Ankarafantsika National Park

Parasite group	Parasite species	<i>Oreochromis mossambicus</i>		<i>Oreochromis niloticus</i>		<i>Coptodon rendalli</i>		<i>Heterotis niloticus</i>		<i>Megalops cyprinoides</i>	
		Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf
Monogenea	<i>Cichlidogyrus halli</i>	3/1	1	3/1	1	–	–	–	–	–	–
	<i>Cichlidogyrus sclerosus</i>	–	–	3/1	1	–	–	–	–	–	–
	<i>Cichlidogyrus thurstonae</i>	3/2	2	3/2	2–3	6/1	2	–	–	–	–
	<i>Cichlidogyrus tiberianus</i>	–	–	–	–	6/2	2	–	–	–	–
	<i>Cichlidogyrus tilapiae</i>	3/3	2–5	3/1	3	6/5	1–19	–	–	–	–
	<i>Scutogyrus longicornis</i>	–	–	3/1	1	6/1	1	–	–	–	–
	<i>Gyrodactylus cichlidarum</i>	3/1	2	–	–	–	–	–	–	–	–
	<i>Heterotesia voltae</i>	–	–	–	–	–	–	2/2	3–5	–	–
	<i>Diplectanocotyla megalopis</i>	–	–	–	–	–	–	–	–	1/1	7
Digenea	Digenea sp. metacercariae	–	–	–	–	–	–	–	–	1/1	1
Cestoda	Gyrorhynchidae spp. larvae	3/2	15–369	3/2	29–50	6/3	18–60	2/2	9–50	–	–
Nematoda	Nematoda sp.	–	–	–	–	–	–	2/1	1	–	–

Ex/Inf, number of sampled/number of infected specimens; IInf, minimum–maximum intensity of infection

intensity of infection. Surprisingly, *Cichlidogyrus tilapiae* was found to exhibit a very high intensity of infection on the endemic aplocheilid *P. omalonotus*. Molecular variability was reported between *C. tilapiae* parasitizing *P. omalonotus* and cichlid species (including non-native and endemic species collected in different localities) i.e. p -distance = 0.004 was reported for 28S rDNA and also for ITS1. No endemic monogeneans were found on endemic cichlids. The host-specific monogenean parasite *Ligophorus* sp. was found on a native mugilid species, *Osteomugil robustus*. Concerning endoparasites, the presence of cestodes and nematodes was documented only in endemic cichlid species, with the highest intensities of infection for *Schyzocotyle acheilognathi* (Cestoda) and *Rhabdochona* sp. (Nematoda) in *P. inornatus* and *Rhabdochona paski* in *P. lamnabe*. Larval stages of digeneans were found in native non-cichlid species (i.e. *Posthodiplostomum* sp. with a high intensity of infection and Diplostomidae gen. sp. with a low intensity of infection in *Pachypanchax omalonotus*, and *Cardiocephaloides* sp. 1 with a moderate intensity of infection in *Glossogobius giuris*).

Four fish species were collected in crater lakes of Mont Passot (Nosy Be Island). Two of them were endemic and two were non-native cichlid species (Table 1). Overall, endemic cichlids were more parasitized than non-native cichlid species (Table 4). The

non-native monogenean *C. tilapiae* was found in all endemic and non-native cichlid species. This species achieved higher levels of infection in endemic cichlid species compared to its level of infection in introduced cichlids. Another non-native monogenean species, *Cichlidogyrus tiberianus*, was found solely in a single specimen of non-native *C. rendalli*. In addition, endemic cichlids were more parasitized by endoparasites when compared to non-native cichlids. Larval stages of *Cardiocephaloides* sp. 2 (Digenea) represented the dominant endoparasite in endemic *Ptychochromis oligacanthus*. Approximately one-third of the collected specimens of this endemic cichlid species were also infected by larval stages of *Contracaecum* (Nematoda) and by *Acanthogyrus tilapiae* (Acanthocephala), each of these parasites reaching a low or moderate intensity of infection. Unidentified cestode larvae were found in endemic *Paratilapia polleni* and *Ptychochromis oligacanthus* and non-native *C. rendalli*.

Finally, three cichlid species were examined in the last region, Andevoranto—Canal des Pangalanes, including two endemic and one non-native species (Table 1). In this region, *O. niloticus* harboured four species of *Cichlidogyrus*, three of them parasitizing a high number of *O. niloticus* specimens and reaching a higher intensity of infection compared to that on cichlids from the other three regions studied (Table 5). Endemic *Paretroplus polyactis* was also infected by

Table 3 Metazoan parasite infection in cichlids and non-cichlid fish species sampled in Anjingo River (Antsohihy)

Parasite group	Parasite species	<i>Paretroplus lamenabe</i>		<i>Ptychochromis inornatus</i>		<i>Oreochromis niloticus</i>		<i>Pachypanchax omalonotus</i>		<i>Osteomugil robustus</i>		<i>Glossogobius giuris</i>	
		Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf
Monogenea	<i>Cichlidogyrus halli</i>	–	–	–	–	8/1	2	–	–	–	–	–	–
	<i>Cichlidogyrus sclerosus</i>	–	–	–	–	8/1	2	–	–	–	–	–	–
	<i>Cichlidogyrus thurstonae</i>	9/2	1	15/1	5	8/6	1–10	–	–	–	–	–	–
	<i>Cichlidogyrus tilapiae</i>	–	–	–	–	8/3	1–3	2/2	7–55	–	–	–	–
	<i>Scutogyrus longicornis</i>	–	–	–	–	8/4	1–4	–	–	–	–	–	–
	<i>Ligophorus</i> sp.	–	–	–	–	–	–	–	–	1/1	11	–	–
Digenea	<i>Cardiocephaloides</i> sp. 1.	–	–	–	–	–	–	–	–	–	–	3/2	3–13
	<i>Posthodiplostomum</i> sp.	–	–	–	–	–	–	2/1	90	–	–	–	–
	Diplostomidae gen. sp.	–	–	–	–	–	–	2/1	3	–	–	–	–
	Lissorchiidae gen. sp.	9/1	1	–	–	–	–	–	–	–	–	–	–
Cestoda	<i>Schyzocotyle acheilognathi</i>	–	–	15/6	2–18	–	–	–	–	–	–	–	–
Nematoda	<i>Rhabdochona paski</i>	9/5	2–12	–	–	–	–	–	–	–	–	–	–
	<i>Rhabdochona</i> sp.	–	–	15/1	1	–	–	2/1	4	–	–	–	–
	<i>Spinitectus</i> sp.	–	–	15/3	1–5	–	–	–	–	–	–	–	–
	<i>Spiroxys</i> sp. larvae	–	–	15/1	2	–	–	–	–	–	–	–	–

Ex/Inf, number of sampled/number of infected specimens; IInf, minimum–maximum intensity of infection

Table 4 Metazoan parasite infection in cichlids and non-cichlid fish species sampled in the crater lakes of Mont Passot (Nosy Be Island)

Parasite group	Parasite species	<i>Ptychochromis oligacanthus</i>		<i>Paratilapia polleni</i>		<i>Oreochromis mossambicus</i>		<i>Coptodon rendalli</i>	
		Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf	Ex/Inf	IInf
Monogenea	<i>Cichlidogyrus tiberianus</i>	–	–	–	–	–	–	6/1	2
	<i>Cichlidogyrus tilapiae</i>	15/5	2–7	1/1	22	8/1	1	6/1	3
Digenea	<i>Cardiocephaloides</i> sp. 2	15/7	2–21	–	–	–	–	–	–
Cestoda	Cestoda sp.	15/1	3	1/1	1	–	–	6/1	7
Nematoda	<i>Contracaecum</i> sp. larvae	15/5	1–2	–	–	–	–	–	–
Acanthocephala	<i>Acanthogyrus tilapiae</i>	15/4	2–6	1/1	7	–	–	–	–

Ex/Inf, number of sampled/number of infected specimens; IInf, minimum–maximum intensity of infection

four species of *Cichlidogyrus* (*C. tilapiae* is shown in Fig. 3). However, in this case, both endemic cichlid

species were also parasitized by endemic and host-specific monogeneans such as *Insulacleidus paretropli*

Table 5 Metazoan parasite infection in cichlids and non-cichlid fish species sampled in Andevoranto (Canal des Pangalanes)

Parasite group	Parasite species	<i>Paretroplus polyactis</i>		<i>Ptychochromis grandidieri</i>		<i>Oreochromis niloticus</i>	
		Ex/Inf	IInf	Ex/Inf	Iinf	Ex/Inf	IInf
Monogenea	<i>Cichlidogyrus halli</i>	20/5	1	–	–	5/5	3–24
	<i>Cichlidogyrus sclerosus</i>	–	–	–	–	5/1	1
	<i>Cichlidogyrus thurstonae</i>	20/5	1	–	–	5/4	2–13
	<i>Cichlidogyrus tilapiae</i>	20/5	1	–	–	5/5	1–28
	<i>Insulacleidus paretropi</i>	20/7	1–24	–	–	–	–
	<i>Insulacleidus ptychochromidis</i>	–	–	5/3	1–5	–	–
	<i>Gyrodactylus thlapi</i>	20/5	1	–	–	–	–
Copepoda	<i>Ergasilus</i> sp.	20/18	5–330	5/1	4	–	–
Digenea	<i>Holorchis</i> sp.	20/3	2–5	–	–	–	–
Cestoda	Gyrorhynchidae spp. larvae	20/3	1–4	5/1	1	5/4	6–311
Acanthocephala	<i>Acanthogyrus tilapiae</i>	–	–	–	–	5/1	1

Ex/Inf, number of sampled/number of infected specimens; IInf, minimum–maximum intensity of infection

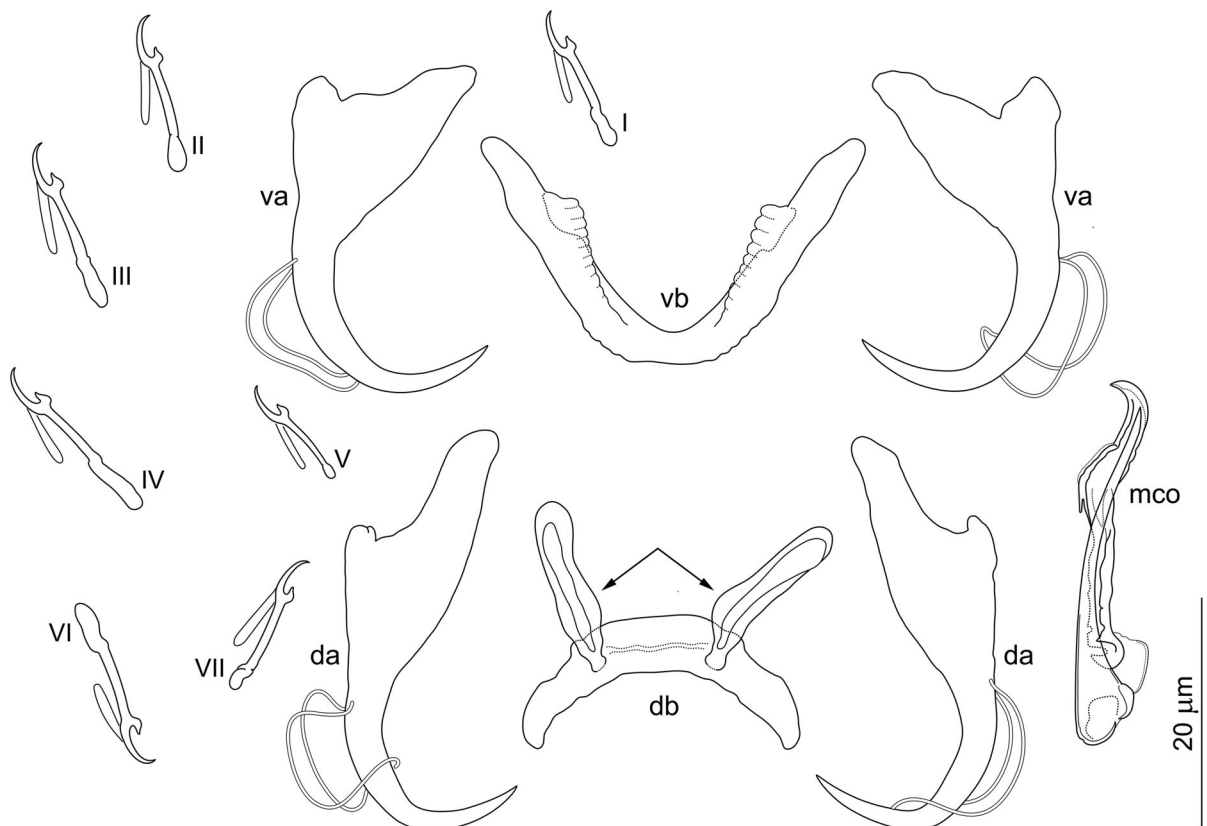


Fig. 3 Sclerotized structures of *Cichlidogyrus tilapiae* Paperna, 1960 from the gills of *Oreochromis niloticus*, Andevoranto. The arrows indicate the presence of auricle-like projections on dorsal bar, the main feature that distinguishes

species of *Cichlidogyrus* from those of *Insulacleidus*. va, ventral anchor; vb, ventral bar; da, dorsal anchor; db, dorsal bar; I–VII, hooks; mco, male copulatory organ

(Fig. 4) in 35% of specimens of *P. polyactis* and *I. ptychochromidis* in 60% of specimens of *Ptychochromis grandidieri*. Both endemic cichlids were parasitized by unidentified representatives of *Ergasilus* (Copepoda), which exhibited very high intensities of infection in some specimens of *P. polyactis*. Concerning endoparasites, only gryporhynchid cestodes were found in endemic and non-native cichlid species (Table 5). These cestodes (including *Neogryporhynchus lasiopeius* and *Parvitaenia macropeos*) exhibited significantly higher intensities of infection in the intestinal walls of non-native *O. niloticus* when compared to their infection levels in the two endemic cichlid species. The larva of another gryporhynchid cestode, *Valipora minuta*, was also found in the gall bladder of *P. grandidieri*. Rare occurrences of *Holorchis* sp. (Digenea) in endemic *P. polyactis* and *A. tilapiae* in non-native *O. niloticus* were also documented.

Total abundance of non-native (*Cichlidogyrus* and *Scutogyrus*) and endemic (*Inculacleidus*) monogeneans in non-native cichlids and endemic fish species is shown in Fig. 5 and Supplementary table. The highest abundance of non-native dactylogyrid monogeneans is shown for endemic fish species in Anjingo River and lakes of Mont Passot. However, non-native *O. niloticus* exhibited the highest abundance of non-native dactylogyrid monogeneans in Andevoranto. In this locality, abundance of native *Inculacleidus* exceeded the abundance of non-native *Cichlidogyrus* in endemic cichlids.

Discussion

In the present study, we focused on metazoan parasite infection in native endemic Malagasy cichlids and non-native cichlids originating from the African mainland. At our sampling sites in northwestern Madagascar, endemic cichlids were scarce at those locations where they lived in sympatry with introduced cichlids. Indeed, in the protected area included in our study, i.e. Lake Ravelobe in Ankarafantsika National Park, no native cichlids at all were found during 3 days of intensive sampling, which seems to indicate that native endemic Malagasy cichlids have become rare. The most plausible explanation is that native cichlids are outcompeted by non-native cichlids, as native cichlids exhibit disadvantageous

reproductive strategies and a low tolerance of environmental factors (De Rham and Nourissat 2004) in comparison to non-native cichlids such as Nile tilapia (Zengeya et al. 2013, 2017).

Torchin et al. (2003) analyzed the parasite diversity in native and introduced populations of different invertebrate and vertebrate species and showed that the number of parasite species found in native populations is generally twice that found in non-native populations, and that introduced populations are less heavily parasitized when compared to native populations. This is in accordance with the observation that the intensity of infection and parasite species richness is higher in the native range of African mainland cichlids when compared to their populations introduced into Madagascar. The species richness of *Cichlidogyrus* on *O. mossambicus*, *O. niloticus* and *C. rendalli* in their natural range, and where they were introduced, is high (Douëllou 1993; Pariselle and Euzet 2009; Vanhove et al. 2013; Jorissen et al. 2018; Řehulková et al. 2018). However, only a subset of the dactylogyridean monogenean species that infect the gills of e.g. Nile tilapia (see Pariselle and Euzet 2009) was found in our study, as indicated by the absence of *Cichlidogyrus cirratus* and *Cichlidogyrus rognoni*. This supports the enemy releases hypothesis (Prenter et al. 2004). Firmat et al. (2016) documented a complete loss of gill parasites in the invasive cichlid *O. mossambicus* in New Caledonia. The authors explained this finding by an initial population bottleneck and the lack of multiple host introductions. In contrast, our short-term study showed the widespread co-introduction of African mainland parasites with their cichlid hosts and subsequent spillover to endemic Malagasy cichlids, this evidenced for generalist parasite taxa, but also for host-specific parasites of African mainland cichlids. In addition, it seems that some parasite introductions are of non-African origin.

Gill monogeneans exhibit a high level of host specificity and their life cycle is direct (Poulin 2002). In the present paper, we confirm the co-introduction of gill monogeneans of *Cichlidogyrus* and *Scutogyrus* with the introduction of their African mainland cichlids into Madagascar, already reported by Rakotofringa (1986). In contrast, we did not record the endoparasitic monogeneans of *Enterogyrus* that occur in cichlids from the African mainland and Southeast Asia (Pariselle et al. 2011). Native Malagasy cichlids serve as competent hosts for species of *Cichlidogyrus*

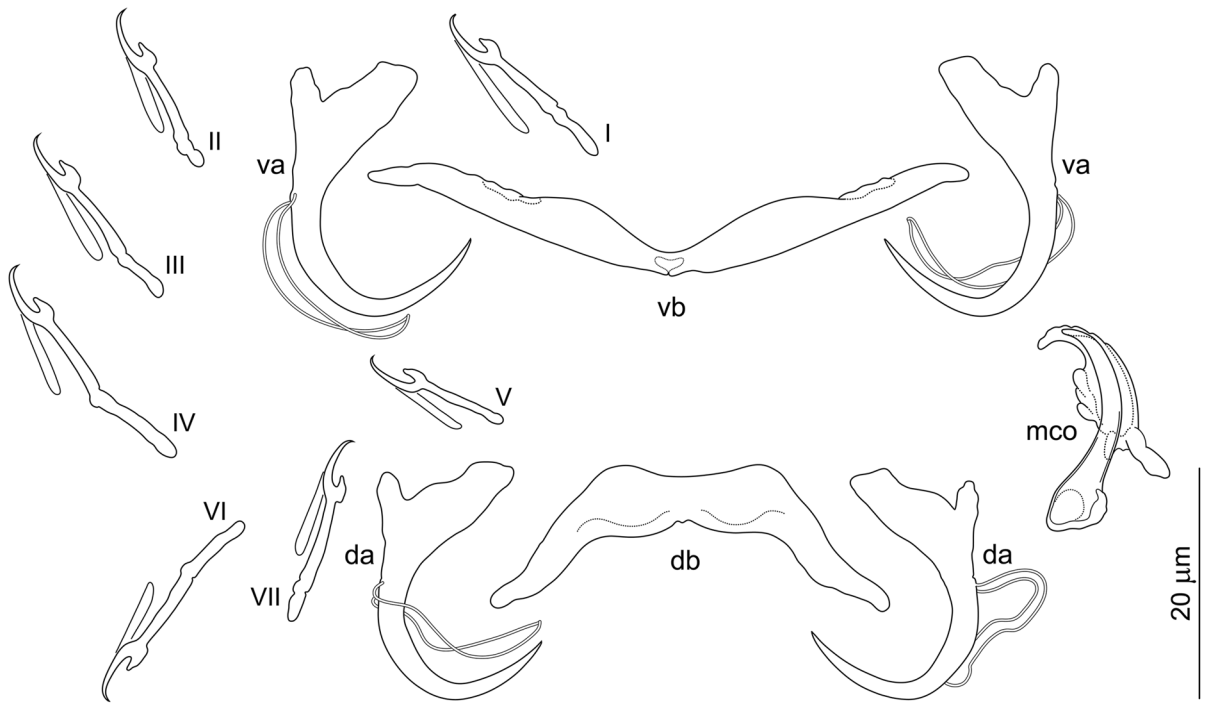


Fig. 4 Sclerotized structures of *Insulacleidus paretropli* Rakotofiringa et Euzet, 1983 from the gills of *Paretroplus polyactis*, Andevoranto. va, ventral anchor; vb, ventral bar; da, dorsal anchor; db dorsal bar; I–VII, hooks; mco, male copulatory organ

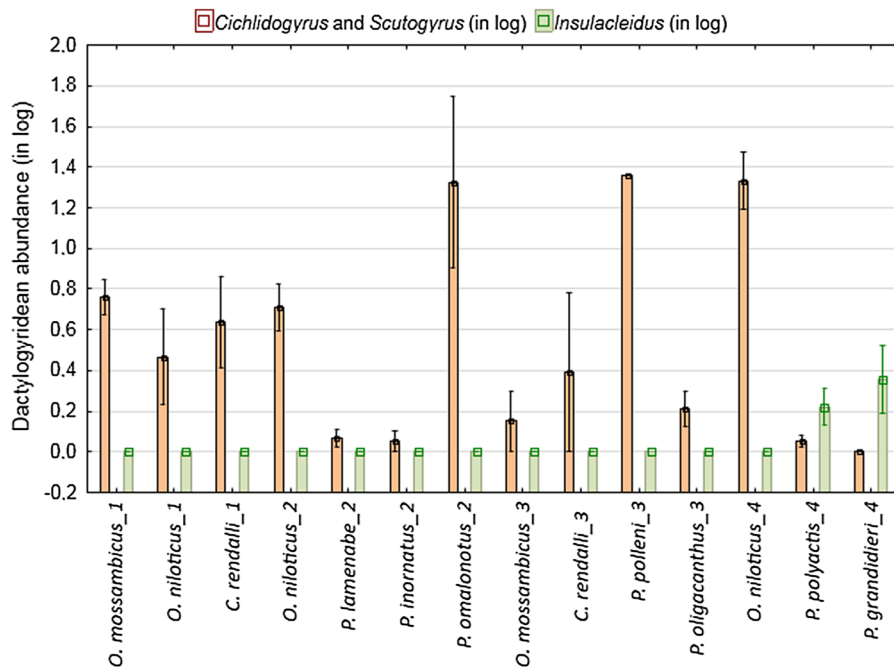


Fig. 5 Total abundance for non-native (*Cichlidogyrus* and *Scutogyrus*) and endemic (*Insulacleidus*) dactylogyridean monogeneans. 1—Lake Ravelobe (PN Ankarafantsika), 2—Anjingo River, 3—lakes of Mont Passot, 4—Canal des Pangalanes (Andevoranto)

that are specific to cichlids from the African mainland, which was not observed in a thorough study of Madagascar's monogenean fish fauna some 30 years ago (Rakotofiringa 1986) despite this study including many native and introduced cichlid hosts. However, monogeneans specific to Malagasy cichlids (i.e. species of *Insulacleidus*) were not found on introduced cichlids co-occurring with native ones. The presence of several species of *Cichlidogyrus* was documented in all four regions studied; a total of five out of six endemic cichlid species harboured these gill parasites.

The co-introduction of species of *Cichlidogyrus*, *Scutogyrus* and/or *Enterogyrus* with their African mainland cichlid hosts was documented in the Americas (i.e. Jiménez-García et al. 2001; Mendoza-Franco et al. 2006; Aguirre-Fey et al. 2015) and Asia (Maneepitaksanti and Nagasawa 2012; Lerssutthichawal et al. 2012; Lim et al. 2016) but these reports only mention co-introduction, not transmission to native hosts. Salgado-Maldonado and Rubio-Godoy (2014) reported 10 monogenean species (including 5 *Cichlidogyrus* species, 3 *Enterogyrus* species, two *Gyrodactylus* species and *Scutogyrus longicornis*) co-introduced with African *Oreochromis* to Mexico and the transmission of three *Cichlidogyrus* species (*C. longicornis*, *C. sclerosus* and *C. tilapiae*) to native cichlids. They also listed the presence of *Cichlidogyrus sclerosus* on cyprinodontiform fish *Goodea atripinnis* (Goodeidae). Unfortunately, no epidemiological data are available from their study to estimate the invasive capacity of *C. sclerosus* for non-cichlid fishes. Also in cyprinodontiform fish, a low level of infection by *Gyrodactylus cichlidarum* co-introduced with African tilapia hosts to Mexican highlands was reported in three species of Poeciliidae within their native distribution range (García-Vásquez et al. 2017). The most interesting (and to our knowledge, only) example of bidirectional host-switching, i.e. from introduced cichlid fish to native ones and vice versa, was documented by Jiménez-García et al. (2001) in Catemaco Lake in the Neotropical part of Mexico. The authors found three species of *Cichlidogyrus* and one species of *Enterogyrus*, parasites of introduced African tilapias, in two Mexican native cichlids, which indicates the ability of these host-specific parasites to infect phylogenetically distant cichlids under non-natural conditions. The low prevalence and abundance of these monogeneans in native hosts may, however, suggest accidental infection or a

recent introduction event. Interestingly, tilapias introduced into Catemaco Lake harboured species of *Sciadicleithrum*, which are gill parasites of Neotropical cichlids (Jiménez-García et al. 2001).

In Madagascar, representatives of *Cichlidogyrus* were the most diverse among co-introduced parasites and *C. tilapiae*, *C. thurstonae* and *C. halli* spilled over to native cichlids. When investigating parasite distribution across native and introduced ranges of fish, epidemiological data represent a useful tool to understand the role of co-introduced parasites. For example, Sarabeev et al. (2017) using Taylor's power law showed that the pattern of parasite aggregation may explain the success of invasive fish species. Later, Sarabeev et al. (2018) showed that invasive parasites are detectable by their abundance-occupancy relationships. However, the calculation of epidemiological parameters (prevalence and abundance) in the case of invasive Malagasy parasites requires more samples and more populations, and epidemiological analyses may represent an interesting topic for future studies on introduced cichlids and their co-introduced parasites. On the basis of ecological performance expressed solely by the total number of host species infected, the number of infected host specimens, and the intensity of parasite infection, *C. tilapiae* and *C. thurstonae* seem to represent the most successful invaders potentially threatening native endemic cichlids. *Cichlidogyrus tilapiae* even infected the cyprinodontiform fish *Pachypanchax omalonotus* (Aplocheilidae) and its intensity of infection exceeded that on non-native *O. niloticus* in Madagascar. Species of *Cichlidogyrus* are considered specific to African and some Middle-Eastern cichlids (Pariselle et al. 2011). There are some exceptions; for example, *Cichlidogyrus amieti* is only known from cyprinodontiforms belonging to *Aphyosemion*, which represents a host-switch followed by parasite speciation on an evolutionary timescale (Birgi and Euzet 1983; Messu Mandeng et al. 2015). However, until now, tilapia-specific species of *Cichlidogyrus* were not documented to perform host switching to non-cichlid Malagasy fish. Another finding from our study is the rarity of host-specific monogeneans (*Insulacleidus* spp.) in native cichlids. Their presence was confirmed only in a single region, which seems to indicate that these host specific parasites may be endangered by the introduction of non-native parasites.

Our study seems to suggest that the source and time of introduction may determine the parasite fauna in

endemic Malagasy cichlids living in distant regions, as was previously shown for freshwater goby species (Gendron et al. 2012; Ondračková et al. 2015). The low species diversity of African mainland monogeneans and their low intensity of infection in non-native cichlids in the lakes of Mont Passot may support the enemy release hypothesis, which predicts parasite loss by introduced species and highlights the risk to native endemic cichlids resulting from increasing infection rates of specific gill monogeneans following spillover. However, the low diversity exhibited by species of *Cichlidogyrus* may also suggest a limited number of introduction events in Mont Passot. In this region, infection by African mainland cichlid-specific species of *Cichlidogyrus* was higher in endemic cichlids compared to that in non-native cichlids. However, the region of Andevoranto seems to have been colonized by non-native cichlids more recently, as their host-specific species of *Cichlidogyrus* reached higher intensities of infection when compared to native endemic cichlids that were weakly susceptible to *Cichlidogyrus* but still harboured their own host-specific endemic monogenean fauna. Unfortunately, no exact data on the introduction of African mainland cichlids into the regions studied are available to support our hypothesis.

Regarding endoparasites, we reported the introduction of a highly invasive cestode parasite species—namely, *Schyzocotyle acheilognathi*, reported in more than 200 fish species worldwide as final hosts (Scholz et al. 2018a). Considering that cichlids are not typical definitive hosts for this parasite species and that cyprinids, especially *Cyprinus carpio*, which represents a fish group frequently imported into Madagascar, are most susceptible to *S. acheilognathi* infection, the latter are the most likely source of infection for native endemic cichlids. In our study, *S. acheilognathi* parasitized a high number of *Ptychochromis inornatus* with a high intensity of infection, but this parasite was not found either in other endemic (*Paretroplus lamenabe*) or introduced (*Oreochromis niloticus*) cichlids, or in three non-cichlid species, all living in sympatry with susceptible endemic cichlid species. We have no data concerning the presence of cyprinids in the Anjingo River, the only region where the presence of *S. acheilognathi* was found. However, our finding strongly highlights the potential risk to endemic Malagasy cichlid fish resulting from the co-introduction of such highly invasive parasites.

Unlike Asian fish tapeworms, other cestodes that occur in the African mainland were not frequently found in native species of cichlids. Larvae of two gryporhynchids, *Neogryporhynchus lasiopeius* and *Parvitaenia macropeos*, were found in the intestinal wall of three introduced species of tilapias, namely *Coptodon rendalli*, *O. mossambicus* and *O. niloticus*, and one introduced arapaimid, *Heterotis niloticus*, from two distant localities—Ankarafantsika National Park and Canal des Pangalanes. The larva of another gryporhynchid, *V. minuta*, was found in the gall bladder of native endemic *Ptychochromis grandidieri*. Unfortunately, the gryporhynchid cestodes found in *Paretroplus polyactis* could not be identified to species level because of the inappropriate fixation of these larvae. However, our results clearly indicate the absence of *N. lasiopeius* and *P. macropeos* in endemic cichlids of Madagascar, even though these larvae are frequent in cichlids in the African mainland (Scholz et al. 2018b). The occurrence of the abovementioned species and their high intensities of infection in non-native Malagasy tilapias indicate that they were likely introduced into Madagascar recently with their cichlid hosts. In contrast, the present record of *V. minuta* in a native cichlid endemic to Madagascar indicates that the Malagasy fauna of cestodes originally included some members of gryporhynchid cestodes.

Representatives of four digenean taxa were found in fishes collected in three out of the four regions studied. The genus *Cardiocephaloides* (Strigeidae) comprises marine species recorded from the Mediterranean and both Afrotropical and Neotropical regions (Dubois 1968; Randall and Bray 1983; Brandão et al. 2013). Two unidentified species were found, *Cardiocephaloides* sp. 1 in the native gobiid *Glossobogius giuris* from the Anjingo River and *Cardiocephaloides* sp. 2 in the native endemic *Ptychochromis oligacanthus* from the crater lakes at Mont Passot (Nosy Be Island). We assume that these species of *Cardiocephaloides* might originate from the southern African coast. In Southern Africa, adults of *Cardiocephaloides physalis* were found in the jackass penguin *Spheniscus demersus*, which most likely became infected by preying upon *Engraulis capensis* (see Randall and Bray 1983). The breeding range of *S. demersus* is confined to the coast of Namibia down to South Africa's Eastern Cape Province (Parsons et al. 2016); however, *C. physalis* is well known from the Brazilian and Uruguayan coasts (Brandão et al. 2013),

indicating the wide geographical range of this species. Moreover, adults of this genus are also reported from larids (Dubois 1968), which might be potential definitive hosts in Madagascar, or may potentially serve as a source of *Cardiocephaloides* introduction from the African mainland to Madagascar. *Cardiocephaloides* was observed to exhibit a significant pathogenic impact on fish and bird hosts leading to mortality (Randall and Bray 1983; Sánchez-García et al. 2015; Parsons et al. 2016).

Digeneans of *Holorchis* (Aepnidiogenidae), with gastropods and bivalves as first and second intermediate hosts, respectively, are parasites of marine fishes in tropical and subtropical oceans (Bray 2005). The representative of *Holorchis* found only in native endemic *Paretroplus polyactis* resembled *H. legendrei* and *H. pycnopus*, both reported in the Mediterranean from sparids and mullids, though the former species was also found in the Eastern Cape Province of South Africa (Bartoli and Bray 1996; Bray and Cribb 1997). The infection of *P. polyactis* with a marine trematode is perhaps unsurprising, as the Canal des Pangalanes is a brackish water system (de Rham and Nourissat 2004). Digeneans of Lissorchiidae using freshwater fishes, mainly Cypriniformes, as definitive hosts are so far known from North America, the Palearctic, India and South East Asia, but not from Africa (Bray 2008). Therefore, this finding in Madagascar is interesting, especially considering that freshwater fishes are less motile compared to marine teleosts or birds. Representatives of Diplostomidae were found as metacercariae in the native endemic cichlid *Ptychochromis oligacanthus* from the lakes at Mont Passot and in the native aplocheilid *Pachypanchax omalonotus* from the Anjingo River. The definitive hosts of diplostomids are fish-eating birds (Niewiadomska 2000), which likely introduced these digeneans from the African mainland into Madagascar.

Acanthogyrus tilapiae is the single acanthocephalan found in freshwater fish in Madagascar. This species was found in *Ptychochromis oligacanthus* and *Paratilapia polleni* from lakes at Mont Passot, where it did not occur in the non-native cichlids examined. A single specimen of *A. tilapiae* was also found in non-native *O. niloticus* in Andevoranto, suggesting its potential co-introduction with non-native cichlids in this region. As *Acanthogyrus tilapiae* is a species with a very wide host range (43 species, with the majority

of them belonging to Cichlidae including *O. niloticus* and *C. rendalli*—Amin et al. 2008; Sures et al. 2018) we cannot clearly determine whether its presence in native cichlids in one region of Madagascar reflects the natural range of its distribution or results from the introduction of non-native cichlids.

Concerning nematodes, their records in Madagascar are also scarce. Until now, the presence of three nematode species in fishes had been documented: *Rhabdochona srivastavai* in *Sicyopterus fasciatus* (Gobiidae), *Procamallanus armatus* in *Anguilla australis*, and *Falcaustra therezieni* from the critically endangered (possibly extinct) *Ptychochromoides bet-sileanus* (Cichlidae) and the widespread marine catfish *Arius madagascariensis* (Ariidae) (Campana-Rouget and Therezien 1965; Chabaud 1970; Petter 1979). In the present study, six nematode species were found, but some of them (larvae) could only be morphologically identified to a generic level. Larvae of *Contraecium* sp. (Anisakidae) in *Ptychochromis oligacanthus* from the crater lakes of Nosy Be Island and larvae of *Spiroxys* sp. (Gnathostomatidae) in *Ptychochromis inornatus* from the Anjingo River use cichlids as intermediate or paratenic hosts. Birds play the role of definitive hosts for species of *Contraecium*, whereas adult nematodes of the genus *Spiroxys* are localized in the stomach walls of turtles and snakes, and the intestines of amphibians. Their third-stage larvae are encapsulated in various paratenic hosts including fish (Hedrick 1935). The only known species from Madagascar, *Spiroxys ankarafantsika*, was described from the turtles *Pelomedusa subrufa* and *Pelusios castanoides* (Pelomedusidae) in the Ankarafantsika National Park (Roca et al. 2007; Roca and García 2008).

Adults of unidentified species of *Spinitectus* (Cystidicolidae) were found in endemic *Ptychochromis inornatus*. Currently, 10 species of *Spinitectus* are known from various fish species living on the African mainland (Boomker and Puylaert 1994; Moravec and Scholz 2017), but none of these species occurs in cichlids, which indicates that this nematode may be native to Madagascar. Two species of *Rhabdochona* (Rhabdochonidae) were found in three endemic native species, including two cichlids. *Rhabdochona paski* (Rhabdochonidae) was found in *Paretroplus lamnabe*. This nematode was previously reported from various fish species in the African mainland, including cichlids. Another species of *Rhabdochona*

unidentified to species level (only juvenile worms were found) was found in the other two endemic cichlids, *P. inornatus* and *Pachypanchax omalonotus*. The only species of *Rhabdochona* previously reported from Madagascar is *R. srivastavai*, found in the gobiid *Sicyopterus fasciatus* (Gobiidae) by Chabaud (1970).

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