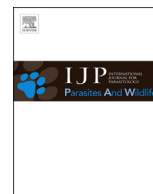




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Alien freshwater fish parasites from South Africa: Diversity, distribution, status and the way forward

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ABSTRACT

The global translocation and introduction of freshwater fish into non-native regions has created the perfect opportunity for the co-introduction of their parasites. In a recent review on non-native freshwater fish introductions in South Africa, 55 fishes were reported as introduced into novel environments in South Africa, with 27 alien and 28 extralimital. However, the parasites potentially co-introduced by these non-native fishes have received much less attention from researchers than the hosts themselves. Thus far, the only attempts at summarising our knowledge on the diversity of introduced freshwater fish parasites in this region dates back to the 1980s when only four parasite species were considered to be alien, with a further eight species as doubtful. Over the last thirty years, more records have been added and this paper aims to provide an up-to-date review of our knowledge on the diversity, distribution, status (co-invasive or co-introduced) and the direction for future studies on introduced freshwater fish parasites in South Africa. Here we consider seven species (four ciliates, and one cestode, copepod and branchiuran respectively) as confirmed co-invaders, and 16 species (one flagellate, four ciliates, one cestode and ten monogeneans) as co-introduced. In addition, six species (three ciliates, two monogeneans and one copepod) previously recorded as invasive are deemed to be of uncertain status, and one ciliate is removed from the list of known invasive parasites from this region. It is further proposed that future research should focus on extralimital co-introductions, especially in the Eastern and Western Cape regions of South Africa where more than half of the fishes present are introduced species. It is also recommended that all new records of introduced parasites and new distribution records of known invasive parasites should include the deposition of voucher specimens in museums and, as far as possible, include molecular confirmation of its identification.

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1. Introduction

Worldwide, the translocation and subsequent introduction of freshwater fish into non-native regions is known to cause an effect on the native biota. However, a secondary ecological and economical risk is also created but often disregarded. This risk is the co-introduction of the alien invasive fish parasites. Potential impacts of parasites due to host switching from introduced to a native host have been well documented (Adlard et al., 2015). Probably the best studied example is the introduction of the swim bladder nematode, *Anguillicoloides crassus* (Kuwahara, Niimi and Itagaki, 1974), into Europe and subsequent impact on wild European eels, *Anguilla anguilla* (Linnaeus, 1758). In a recent review on non-native freshwater fish introductions in South Africa, Ellender and Weyl (2014) listed a total of 55 fishes that have been introduced into novel environments in South Africa, with 27 alien and 28 extralimital (native to South Africa that have been translocated into areas where they did not naturally occur) introductions. These authors also emphasised that the introduction of associated parasites is a serious threat to native fish communities in South Africa.

To date, the only available checklist for freshwater fish parasites from southern Africa is the work done in the 1980s by Van As and Basson (1984). Ninety-five species of parasites were listed from 52 hosts and included 13 presumed alien parasites, although the authors did not specifically identify them as alien. Most of these (10) were protozoans with the remaining three being a cestode, a copepod, and a branchiuran respectively (see Table 1). Of the 52 hosts listed, only four were invasive fishes infected with nine of the alien parasites recorded from southern African fishes at that stage. The common carp, *Cyprinus carpio* Linnaeus, 1758, was clearly responsible for most of the co-introductions and co-invasions into South Africa with seven of the thirteen parasites recorded from this host (Table 2). The first attempt to summarise the extent of aquatic

introductions into southern Africa was by Bruton and Merron (1985), who compiled a checklist of alien and translocated aquatic animals from this region. In their report, Bruton and Merron (1985) listed 12 fish parasites, including 11 reported by Van As and Basson (1984) with the addition of the copepod *Achtheres pimelodi* Kroyer, 1863 (syn. *Achtheres micropteri* Wright, 1882). However, they only regarded four as alien with the status of the remaining eight species considered doubtful; suggesting that further taxonomic research might reveal that they are indigenous. In a book chapter on biological invasions in southern Africa, Bruton and Van As (1986) confirmed the assessment made by Bruton and Merron (1985) without adding additional information. Two years later, De Moor and Bruton (1988) published the first atlas of alien and translocated aquatic animals from southern Africa and only included the four fish parasites considered by Bruton and Merron (1985) as alien. These were the European trichodinid, *Trichodina acuta* Lom 1961 (ciliate); whitespot, *Ichthyophthirius multifiliis* Fouquet, 1876 (ciliate); Asian fish tape worm, *Schyzocotyle (Bothriocephalus) acheilognathi* Yamaguti, 1934 (cestode); and the Japanese fish louse, *Argulus japonicus* Thiele, 1900 (branchiuran). The most recent checklist of alien animals of southern Africa is a photo guide book by Picker and Griffiths (2011) that included all freshwater, marine and terrestrial species. These authors included two of the four species reported by De Moor and Bruton (1988) (*A. japonicus* and *S. acheilognathi*) and added the gill flukes *Gyrodactylus kherulensis* Ergens, 1974 and *Pseudodactylogyrus anguillae* (Yin and Sproston, 1948).

In addition to the checklist, atlas, and guides mentioned above, many independent studies on specific aspects of alien freshwater parasites were undertaken during the past four decades, however, not a single publication attempted to provide a concise summary of our knowledge on this important subject. The aim of this review is thus to provide an up-to-date review of our knowledge on alien

Class: Phyllopharyngea
 Order: Chlamydodontida
 Family: Chilodonellidae

<i>Chilodonella hexasticha</i>	Co-invasive	<i>Coptodon rendalli</i>	Lebowa Fisheries Station	Basson (1982); Van As and Basson (1984)		
		<i>Enteromius (Barbus) paludinosus</i>	Turloop Dam	Basson (1982); Van As and Basson (1984)		
		<i>Pseudocrenilabrus philander</i>	Nwanedzi River; Pietersburg Dam	Van As and Basson (1984)		
		<i>Oreochromis mossambicus</i>	Olifants River; Pietersburg Dam; Kouga River; Nyl River; Lebowa Fisheries Station; Nwanedzi River	Paperna and Van As (1983); Basson (1982); Van As and Basson (1984)		
		<i>Tilapia sparrmanii</i>	Olifants River; Lebowa Fisheries Station	Paperna and Van As (1983)		
		<i>Chilodonella piscicola</i> (syn. <i>C. cyprini</i>)	Co-invasive	<i>Coptodon rendalli</i>	University of Johannesburg aquarium; Olifants River	Basson (1982); Van As and Basson (1984)
				<i>Oreochromis mossambicus</i>	Lowveld Fisheries Research Station	Van As and Basson (1984)
				<i>Pseudocrenilabrus philander</i>	Vaal River (Christiana); Orlando Dam (Klip River in Vaal River)	Basson (1982); Van As and Basson (1984)
				<i>Tilapia sparrmanii</i>	Lowveld Fisheries Research Station	Van As and Basson (1984)

Phylum: Platyhelminthes

Class: Cestoda
 Order: Bothriocephalidea
 Family: Bothriocephalidae

<i>Schyzocotyle acheilognathi</i> (syn. <i>B. acheilognathi</i>)	Co-invasive	<i>Cyprinus carpio</i>	Komatipoort - commercial ponds; Olifants River; Vaal River; Mtata River	Boomker et al. (1980); Brandt et al. (1980, 1981); Van As et al. (1981); Schramm (1992)
		<i>Enteromius annectens</i>	Phongolo River	Current study
		<i>Enteromius argenteus</i>	Olifants River	Mashego (1982)
		<i>Enteromius bifrenatus</i>	Phongolo River	Current study
		<i>Enteromius brevipinnis</i>	Marite River (Sabie River)	Schult and Schoonbee (1999)
		<i>Enteromius mattozi</i>	Olifants River	Mashego (1982)
		<i>Enteromius paludinosus</i>	Olifants River	Mashego (1982)
		<i>Enteromius trimaculatus</i>	Mooi River; Olifants River	Van As et al. (1981); Mashego (1982)
		<i>Labeobarbus maraquensis</i>	Olifants River	Mashego (1982)
		<i>Labeobarbus aeneus</i>	Vaal River; Great Fish River	Bertasso and Avenant-Oldewage (2005); Stadlander et al. (2011)
		<i>Labeobarbus kimberleyensis</i>	Vaal River	Brandt et al. (1981); Bertasso and Avenant-Oldewage (2005)

Order: Caryophyllidea
 Family: Lytocestidae

<i>Atractolytocestus huronensis</i>	Co-introduced	<i>Cyprinus carpio</i>	Olifants River; Letaba River; Vaal River; Riet River	Schol et al. (2015); Current study
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Class: Monogenea
 Order: Dactylogyridea

(continued on next page)

Table 1 (continued)

Classification	Genus Species	Status	Host fish	Location - River system	Reference
Family: Ancyrocephalidae	<i>Clavunculus bursatus</i>	Co-introduced	<i>Micropterus salmoides</i>	Friedrichskrön Dam; Thomas Baine Nature Reserve	Truter et al. (2017)
	<i>Onchocleidus dispar</i>	Co-introduced	<i>Micropterus salmoides</i>	Thomas Baines Nature Reserve	Truter et al. (2017)
	<i>Onchocleidus furcatus</i>	Co-introduced	<i>Micropterus salmoides</i>	Mooi River and Potchefstroom Dam; Friedrichskrön Dam	Truter et al. (2017)
	<i>Onchocleidus principalis</i>	Co-introduced	<i>Micropterus salmoides</i>	Thomas Baines Nature Reserve	Truter et al. (2017)
	<i>Syncleithrium fusiformis</i>	Co-introduced	<i>Micropterus salmoides</i>	Friedrichskrön Dam	Truter et al. (2017)
	Family: Dactylogyridae	<i>Acolpenteron ureteroecetes</i>	Co-introduced	<i>Micropterus salmoides</i>	Jonkershoek inland fish hatchery; Groot-Letaba River (Tzaneen Dam)
			<i>Micropterus punctulatus</i>	Jonkershoek inland fish hatchery	Du Plessis (1948)
			<i>Micropterus dolomieu</i>	Jonkershoek inland fish hatchery	Du Plessis (1948)
<i>Dactylogyrus extensus</i>		Co-introduced	<i>Cyprinus carpio</i>	Vaal River (Vaal Dam)	Crafford et al. (2014a, b)
<i>Dactylogyrus lamellatus</i>		Co-introduced	<i>Cyprinus carpio</i>	Vaal River (Vaal Dam)	Crafford et al. (2014a, b)
<i>Dactylogyrus minutus</i>		Co-introduced	<i>Cyprinus carpio</i>	Vaal River (Vaal Dam)	Crafford et al. (2014a, b)
Family: Pseudodactylogyridae	<i>Pseudodactylogyrus anguillae</i>	Uncertain	<i>Anguilla mossambica</i>	Between Fish and Buffalo Rivers (Eastern Cape); Great Fish River; Koonap River; Kei River; Keiskamma River	Christison and Baker (2007); Parker et al. (2011); McHugh et al. (2017)
Order: Gyrodactyliidea					
Family: Gyrodactylidae	<i>Gyrodactylus kherulensis</i>	Co-introduced	<i>Cyprinus carpio koi</i>	Kuilsrivier; Durban	Maseng (2010)
	<i>Gyrodactylus kobayashii</i>	Uncertain	<i>Cyprinus carpio</i> <i>Carassius auratus</i>	Vaal River (Vaal Dam) Kuilsrivier	Crafford et al. (2014a) Maseng (2010)
Phylum: Arthropoda					
Subphylum: Crustacea					
Class: Maxillopoda					
Subclass: Copepoda					
Order: Cyclopoida					
Family: Lernaeidae	<i>Lernaea cyprinacea</i>	Co-invader	<i>Coptodon rendalli</i>	Phongolo River	Smit et al. (2016)
			<i>Labeo capensis</i>	Orange River	Robinson and Avenant-Oldewage (1996)
			<i>Labeo congoro</i> (syn <i>L. rubropunctatus</i>)	Mogalakwena River; Olifants River;	Van As and Viljoen (1984); Robinson and Avenant-Oldewage (1996)
			<i>Labeo cylindricus</i>	Limpopo River	Van As and Basson (1984)
			<i>Labeo rosae</i>	Olifants River; Selati River;	Robinson and Avenant-Oldewage (1996)
			<i>Labeo ruddi</i>	Olifants River	Robinson and Avenant-Oldewage (1996)
			<i>Labeo umbratus</i>	Olifants River	Robinson and Avenant-Oldewage (1996)
			<i>Labeobarbus marequensis</i>	Crocodile (West) River; Olifants River; Lowveld Fisheries Station	Van As and Basson (1984); Robinson and Avenant-Oldewage (1996)
			<i>Labeobarbus kimberleyensis</i>	Vaal River	Robinson and Avenant-Oldewage (1996)
			<i>Oreochromis mossambicus</i>	Olifants River; Selati River; Crocodile River (West); Lowveld Fisheries Station; Phongolo River (Nyamiti pan)	Robinson and Avenant-Oldewage (1996); Van As and Viljoen (1984); Van As and Basson (1984); Viljoen (1986); Smit et al. (2016); Welicky et al. (2017)
			<i>Pseudocrenilabrus philander</i>	Harts River (Barberspan)	Truter et al. (2016)
Order: Cyclopoida					
Family: Siphonostomatoida	<i>Achtheres pimelodi</i>	Uncertain	<i>Micropterus dolomieu</i>	Not specified	Barnard (1955); Fryer (1968)

Class: Ichthyofracostraca Subclass: Branchiura Order: Arguloida Family: Argulidae	Co-invasive Argulus japonicus	Clarias gariepinus	Vaal River; Olifants River; Pienaars River	Kruger et al. (1983); Van As and Basson (1984); Avenant-Oldewage (1994); Avenant-Oldewage (2001)
		Cyprinus carpio	Vaal River; Harts River; Pienaars River; Komati River; Olifants River; Pienaars River	Kruger et al. (1983); Van As and Basson (1984); Avenant-Oldewage (1994); Avenant-Oldewage (2001)
		Enteromius mattozi	Pienaars River	Van As and Basson (1984)
		Laboe capensis	Vaal River; Harts River; Mooi River; Pienaars River	Kruger et al. (1983); Van As and Basson (1984); Avenant-Oldewage (1994)
		Laboe rosae	Olifants River	Avenant-Oldewage (1994)
		Laboe umbratus	Vaal River; Harts River; Mooi River; Olifants River	Kruger et al. (1983); Van As and Basson (1984); Avenant-Oldewage (1994); Avenant-Oldewage (2001)
		Laboebarbus aeneus	Vaal River; Harts River; Mooi River	Kruger et al. (1983); Van As and Basson (1984); Avenant-Oldewage (1994)
		Laboebarbus kimberleyensis	Vaal River; Harts River	Kruger et al. (1983); Van As and Basson (1984)
		Laboebarbus marequensis	Crocodile River (West) (Hartebeespoort Dam); Pienaars River; Bronkhorstspuit River	Van As and Basson (1984); Avenant-Oldewage (2001)
		Oncorhynchus mykiss	Lydenburg Fish Hatchery	Van As and Basson (1984)
		Oreochromis mossambicus	Crocodile River (West); Pienaars River; Olifants River	Avenant-Oldewage (1994); Van As and Basson (1984); Avenant-Oldewage (2001)

invasive freshwater fish parasites from South Africa with the specific focus on their status (co-introduced or co-invasive), known distribution, and hosts. Based on our current knowledge and international trends, this paper also aims to provide direction for future studies.

2. Confirmed co-invasive freshwater fish parasites

2.1. Phylum Ciliophora

2.1.1. Ichthyophthirius multifiliis

The ciliate *I. multifiliis*, the causative agent of the disease ichthyophthiriosis, is an important pathogen of freshwater teleosts globally, and accounts for significant economic losses to the aquaculture industry (Matthews, 2005). Similar to many other invasive parasites, *I. multifiliis* was most likely co-introduced into freshwater ecosystems throughout the world with the introduction of its native cyprinid hosts from Asia (Nigrelli et al., 1976). It was first reported from Africa (Uganda) by Paperna (1972), followed by Jackson (1978) reporting *I. multifiliis* from the longfin eel, *Anguilla mossambica* Peters, 1852, collected in the Keiskamma, South Africa (Table 1, Fig. 1A). Other records of *I. multifiliis* from South Africa include infestations on the introduced *C. carpio*, *Salmo trutta* Linnaeus, 1758 and *Oncorhynchus mykiss* (Walbaum, 1792), with spillover to the native *Oreochromis mossambicus* (Peters, 1852) and straightfin barb, *Enteromius (Barbus) paludinosus* (Peters, 1852) also recorded (Basson, 1982; Van As et al., 1984; Bragg, 1991). During a pilot study on the health status of ornamental freshwater fishes imported to South Africa, Mouton et al. (2001) recorded *I. multifiliis* from guppies, *Poecilia reticulata* Peters, 1859 and goldfish, *Carassius auratus* (Linnaeus, 1758). This study clearly demonstrated the potential for continual introductions of this pathogenic parasite through the ornamental fish trade and further emphasised the need for proper health screening of all imported fishes into South Africa.

2.1.2. Apiosoma piscicola

Apiosoma piscicola, first described more than 120 years ago from *C. carpio* collected in France, is a sessile peritrich from the Epistylididae that lives on the gills and body surface of its host (Li et al., 2008). With its native host being *C. carpio*, it is no surprise that this species has a similar global distribution and status as an invasive species, and has been reported as such from, amongst others, Canada (Cone and Odense, 1987), Egypt (El-Tantawy et al., 2013), and Mexico (Aguilar-Aguilar and Islas-Ortega, 2015). The first report of *A. piscicola* from South Africa was by Viljoen and Van As (1983) from the skin of the southern mouthbrooder, *Pseudocrenilabrus philander* (Weber, 1897), collected from the Westdene Dam in the Jukskei River (Table 1). In a follow-up study on sessile peritrichs from freshwater fishes in South Africa, Viljoen and Van As (1985) reported *A. piscicola* from an additional seven hosts collected in more than ten rivers as well as three fisheries stations (Table 1, Fig. 1B). This wide distribution and host range clearly indicated that this species has been a well-established co-invader long before its first report in the 1980s. As the focus of the Viljoen and Van As (1985) study was the northern regions of South Africa (Gauteng, Limpopo, North West and Mpumalanga provinces), it would be important to determine the presence, distribution and hosts of this alien in the rest of South Africa's rivers.

2.1.3. Chilodonella hexasticha

Members of the chilodonelid genus *Chilodonella* Strand, 1928 that parasitise fishes are known to cause the disease chilodonellosis, which can lead to extreme high host mortalities, especially under aquaculture conditions (Mittra and Haldar, 2004; Pádua et al.,

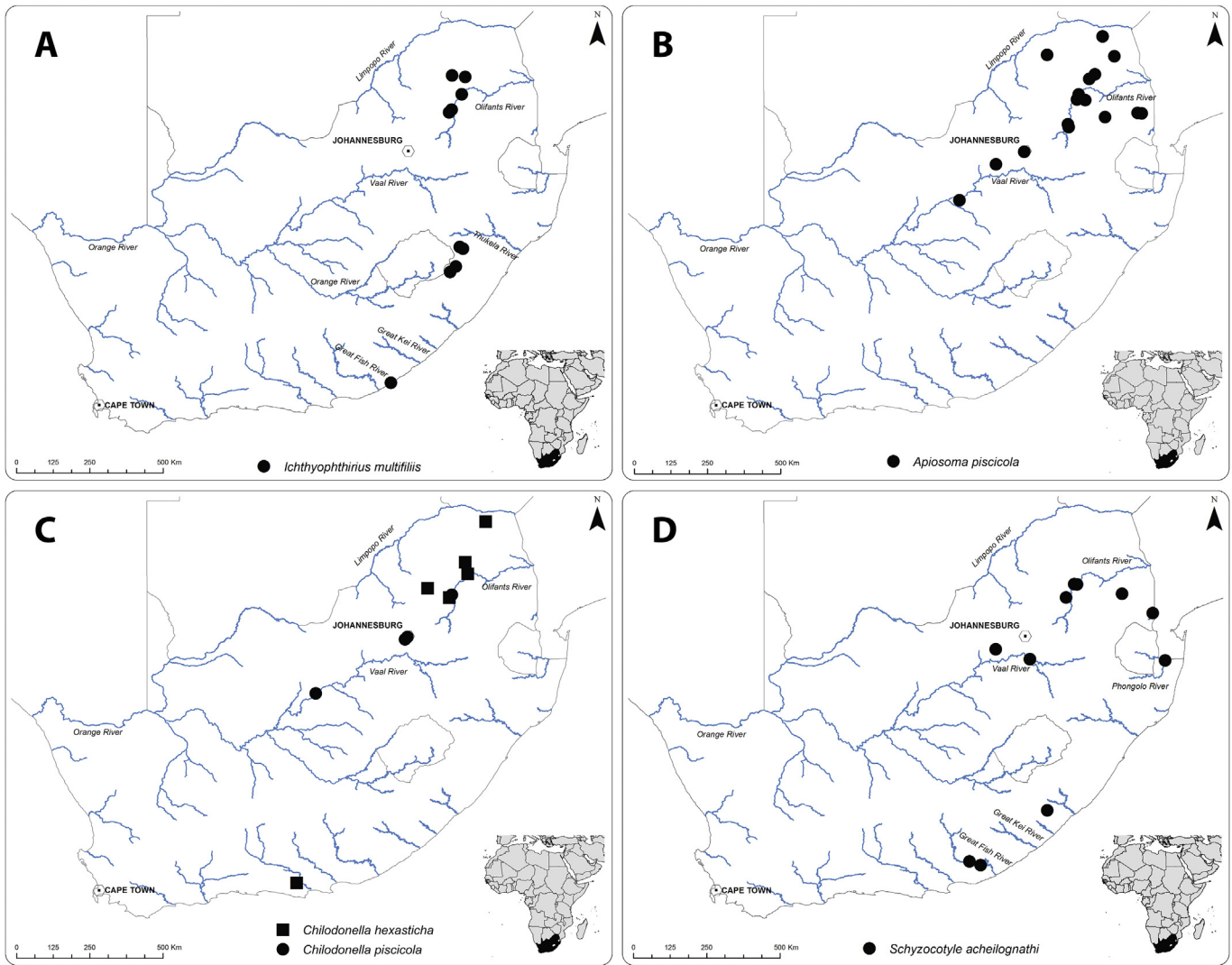


Fig. 1. Maps indicating the South African distribution records for (A) *Ichthyophthirius multifiliis* Fouquet, 1876; (B) *Apiosoma piscicola* (Blanchard, 1885); (C) *Chilodonella hexasticha* (Kiernik, 1909) and *Chilodonella piscicola* (Zacharias, 1894); (D) *Schyzocotyle (Bothriocephalus) acheilognathi* (Yamaguti, 1934).

2013; Bastos Gomes et al., 2017). Two species, *C. hexasticha* and *C. piscicola* (Zacharias, 1894) are considered to be the main agents of chilodonellosis and occur globally on the body surface, gills, and fins of freshwater fish hosts. Although the majority of records of pathology caused by *Chilodonella* spp. are from aquaculture facilities, such as those in Finland (Rintamäki et al., 1994), these parasites have also been reported as the main cause of deaths of native fish in natural habitats, such as the Finke River near Alice Springs, Australia (Langdon et al., 1985). In the latter case, Langdon et al. (1985) reported that *C. hexasticha* induced severe generalised epithelial hyperplasia in the gills, which possibly compromised respiratory exchange and killed the fish through hypoxaemia.

The first record of *C. hexasticha* in South Africa, according to Paperna and Van As (1983), was most probably a conference contribution by Du Plessis (1952). This publication reported mass mortalities of the native Mozambique tilapia, *Oreochromis mossambicus*, due to heavy infections of a *Chilodonella* sp., from various fish ponds in South Africa. Its presence in South Africa, and the pathology it caused on native wild caught and farmed fishes, was confirmed by Paperna and Van As (1983) and Van As et al. (1984). Thus far, *C. hexasticha* has been reported from four cichlids and one

cyprinid collected in more than five river systems and two aquaculture facilities (Table 1, Fig. 1C). No research in South Africa has been conducted on this important pathogen since the 1980s and specifically not regarding the control thereof. Therefore, in the light of the current global and South African drive towards increasing fresh water aquaculture, it is imperative that research into this and other disease causing invasive parasites are prioritised (Bastos Gomes et al., 2017).

2.1.4. *Chilodonella piscicola* (syn. *C. cyprini*)

The taxonomic status of this *Chilodonella* species was only resolved in the 1970s when *C. cyprini* was synonymised with *C. piscicola* and clear evidence was provided that *C. hexasticha* and *C. piscicola* are distinct species (Mittra and Haldar, 2004; Bastos Gomes et al., 2017). It is therefore no surprise that the first records of *C. piscicola* in South Africa, noted by Basson (1982) and Van As and Basson (1984), initially referred to this species as *C. cyprini*. These records from South Africa were not included in the recent review of the *Chilodonella* by Bastos Gomes et al. (2017), most probably due to the original identification as *C. cyprini*; however, it can now be included with the other seven countries listed as

confirmed records of *C. piscicola*. In addition, its presence on two wild caught cichlids, *Coptodon rendalli* (Boulenger, 1896) and *Pseudocrenilabrus philander*, is together with the record from Tibet (see Bastos Gomes et al., 2017), the only records of this parasite on native wild caught fishes (Table 1, Fig. 1C). Similar to *C. hexasticha*, *C. piscicola* has also been found to cause mortalities in fish aquaculture, however, the former is associated with warmer climates (between 26 and 31 °C), while the latter exhibits a wide thermal tolerance in the lower range (between 4 and 20 °C) (reviewed by Bastos Gomes et al., 2017). With the majority of South Africa's river and impoundment temperatures dropping down to below 20 °C in winter, the potential for *C. piscicola* to proliferate under these conditions in the wild needs to be investigated.

2.2. Phylum Platyhelminthes

2.2.1. *Schyzocotyle (Bothriocephalus) acheilognathi*

It has been well documented that the Asian tapeworm, *S. acheilognathi*, was most likely first introduced during 1975 into South Africa with its native host, the grass carp *Ctenopharyngodon idella* Valenciennes, 1844 (Boomker et al., 1980; Bertasso and Avenant-Oldewage, 2005; Stadtlander et al., 2011). Following its introduction, it successfully established itself in the common carp, *Cyprinus carpio* (introduced for commercial carp farming). The first published report of this invasive parasite was thus in *C. carpio* by Boomker et al. (1980), from a commercial fish farm in the Komati-poort area, Mpumalanga Province of South Africa (Table 1, Fig. 1D). As *S. acheilognathi* appears to not be host specific both on an intermediate or definitive host level, this parasite quickly spilled over to native hosts across South Africa when *C. carpio* was introduced for aquaculture and recreational angling purposes and *C. idella* for controlling aquatic weeds (Stadtlander et al., 2011; Ellender and Weyl, 2014). The first record of this species as a co-invader following spillover was that of Brandt et al. (1981) reporting it parasitising the Vaal-Orange largemouth yellowfish, *Labeobarbus kimberleyensis* Gilchrist and Thompson, 1913, collected from the Vaal Dam in the Vaal River (Fig. 1D). In the same year, Van As et al. (1981) reported another spillover event, this time in Boskop Dam, Mooi River, with the three-spot barb, *Enteromius (Barbus) trimaculatus*, as the infected host (Fig. 1D). Since these first reports, *S. acheilognathi* has been reported from at least 10 native hosts (Table 1) from six rivers (Fig. 1D) in South Africa (Mashego, 1982; Barkhuizen, 1991; Schramm, 1992; Retief et al., 2007; Stadtlander et al., 2011; Kuchta et al., 2012; Swanepoel, 2015), making it one of the most widespread co-invasive parasites reported in South Africa.

The pathological effects of *S. acheilognathi* on native hosts in aquaculture conditions, as well as its threat to wild populations, have been well documented globally (Dove et al., 1997; Salgado-Maldonado and Pineda-López, 2003; Pullen et al., 2009). However, research in South Africa has mainly focussed on its distribution, ecology, and potential use as bioindicators of metal pollution (Bertasso and Avenant-Oldewage, 2005; Retief et al., 2007; Degger and Avenant-Oldewage, 2009), with a paucity of data on its population and community level impact on threatened native species. Future studies should specifically focus on these impacts and on regions of high endemism, such as the Cape Floristic Region of the southern and southwestern Cape Province where the largest percentage of South Africa's threatened freshwater fishes occur.

2.3. Phylum Arthropoda

2.3.1. *Lernaea cyprinacea*

The global distribution of the copepod *Lernaea cyprinacea* as an invasive ectoparasite, and the severe effects of it on native

freshwater fish hosts, has been well documented (see Welicky et al., 2017). Despite the first record of the introduction of this ectoparasite into Africa dating back to the 1960s (Robinson and Avenant-Oldewage, 1996), it was only recorded for the first time from South Africa twenty years later. Van As and Basson (1984) recognise the unpublished Masters dissertation of Viljoen (1982) as the first document to report *L. cyprinacea* from South Africa. In addition to Viljoen (1982) records of *O. mossambicus* and *Labeobarbus mar- equensis* (Smith, 1841) from Hartbeespoort Dam in the Crocodile River (West) and *Labeo cylindricus* Peters, 1852 from the Limpopo River as hosts, Van As and Basson (1984) recorded an infestation of *L. cyprinacea* on *O. mossambicus* from the Lowveld Fisheries Station (Table 1, Fig. 2A). Further confirmation of the presence of *L. cyprinacea* on South African native fishes was by Van As and Viljoen (1984) and Viljoen (1986) who also reported the presence of *L. cyprinacea* on *O. mossambicus* in Hartbeespoort Dam as well as from *Labeo congoro* Peters, 1852 (syn. *Labeo rubropunctatus*) in the Glen Alpine Dam, Mogalakwena River (Table 1, Fig. 2A).

Interestingly, Bruton and Merron (1985) included *L. cyprinacea* in their list of what they considered to be doubtful alien species and therefore De Moor and Bruton (1988) did not include this species in their atlas to alien aquatic animals in southern Africa. More than ten years later Robinson and Avenant-Oldewage (1996) increased our knowledge on the distribution and hosts of *L. cyprinacea* and added another six cyprinid hosts collected from three different rivers (Table 1, Fig. 2A). These authors also provided a detailed morphological study of *L. cyprinacea* as well as an updated geographical distribution in Africa. Recently the identity of *L. cyprinacea* in South Africa was genetically confirmed and two more hosts and three localities were added (Smit et al., 2016; Truter et al., 2016; Welicky et al., 2017). The most surprising fact regarding the host records of *L. cyprinacea* in South Africa is that it does not include any of the invasive cyprinids which were potentially responsible for the co-introduction and subsequent co-invasion of this parasite. Globally, the severe effects on native freshwater fish hosts by *L. cyprinacea* have been well documented; however, the first study on the impact of this co-invader on native fish health in South Africa is the recent work by Welicky et al. (2017). In their paper, the authors reported on the change in host health following a natural drought induced treatment for *L. cyprinacea*, leaving hosts without this parasite in a much better overall health state than those infected. Future work should include host immune response to infection as well as laboratory based studies on the effect of *L. cyprinacea* on host fitness.

2.3.2. *Argulus japonicus*

With a very low host specificity, and one of its hosts from its native range (*C. carpio*) being considered among 100 of the world's worst invasive alien species (Lowe et al., 2000), it is no surprise that the Japanese fish louse, *A. japonicus*, is one of the most prevalent and widespread co-invaders in South African freshwater systems. Although reports exist that *C. carpio*, and its other native host, the goldfish *Carassius auratus*, were already introduced into South Africa in 1859 and 1726 respectively (De Moor and Bruton, 1988), the first official record of the co-invading *A. japonicus* was only in 1983. Kruger et al. (1983) reported it from 11 hosts, including *C. carpio*, from two sites (Lake Baberspan and Bloemhof Dam) in the Orange-Vaal River system (Table 1, Fig. 2B). However, it was clear that the introduction of *A. japonicus* happened much earlier, with Van As and Basson (1984) adding another five hosts and four more localities, including sites from the Crocodile River (West) (Hartbeespoort Dam and Roodeplaat Dam), showing a wide spread occurrence not typically associated with a recent introduction. Van As (1987) supported this and went further by proposing that the records of *Argulus* spp. by Du Plessis (1952) and Lombard (1968)

from the South African Mpumalanga Province were in fact *A. japonicus*, indicating a much earlier introduction. Following the above reports, additional records of its co-invasion have been published, clearly indicating its wide distribution throughout South Africa (Fig. 2B) and successful spillover onto at least nine native hosts (Avenant-Oldewage, 1994, 2001). Although more recent work on *A. japonicus* in South Africa focussed on its anatomy, ultra-structure, and reproduction (Tam and Avenant-Oldewage, 2006; Avenant-Oldewage and Everts, 2010), there are still gaps in our knowledge on the full extent of its distribution throughout South Africa and its impact on native fishes at population and community levels.

3. Confirmed co-introduced freshwater fish parasites

3.1. Phylum Euglenozoa

3.1.1. *Ichthyobodo necator*

The ectoparasitic flagellate *I. necator* has been implicated in disease and mortality of cultured fish globally and is, amongst other things, probably the major cause of death of cultured salmonid fry

in Scottish fish farms (Robertson, 1985). In South Africa, specimens identified as *I. necator* have been reported in the early 1980s from three native cyprinids and the alien *C. carpio*. These specimens were collected from impoundments in two rivers in the Limpopo Province (Paperna and Van As, 1983; Van As and Basson, 1984), and an aquaculture facility and a river (Kougou River) in the Eastern Cape Province of South Africa (Van As and Basson, 1984) (Fig. 2C). More recently, *Ichthyobodo* Pinto, 1928 isolates collected from pond-reared koi-carp *C. carpio* fry from South Africa (specific locality not known) were included in a molecular study by Todal et al. (2004) that aimed to test previous suggestions that *I. necator* comprises a complex of species. Todal et al. (2004) concluded that there were at least eight strains or species from the 14 isolates tested. The South African isolate showed the highest sequence similarity with the isolate from *C. auratus* collected in Singapore and grouped together with isolates from an *Apistogramma* sp. (Brazil) and a *Morone* Mitchell, 1814 hybrid (USA) (Todal et al., 2004). This molecular evidence suggests that the *Ichthyobodo* isolate from *C. carpio* in South Africa can be considered as co-introduced. However, the *I. necator* identified from native fishes needs to be molecular characterised in order to determine whether

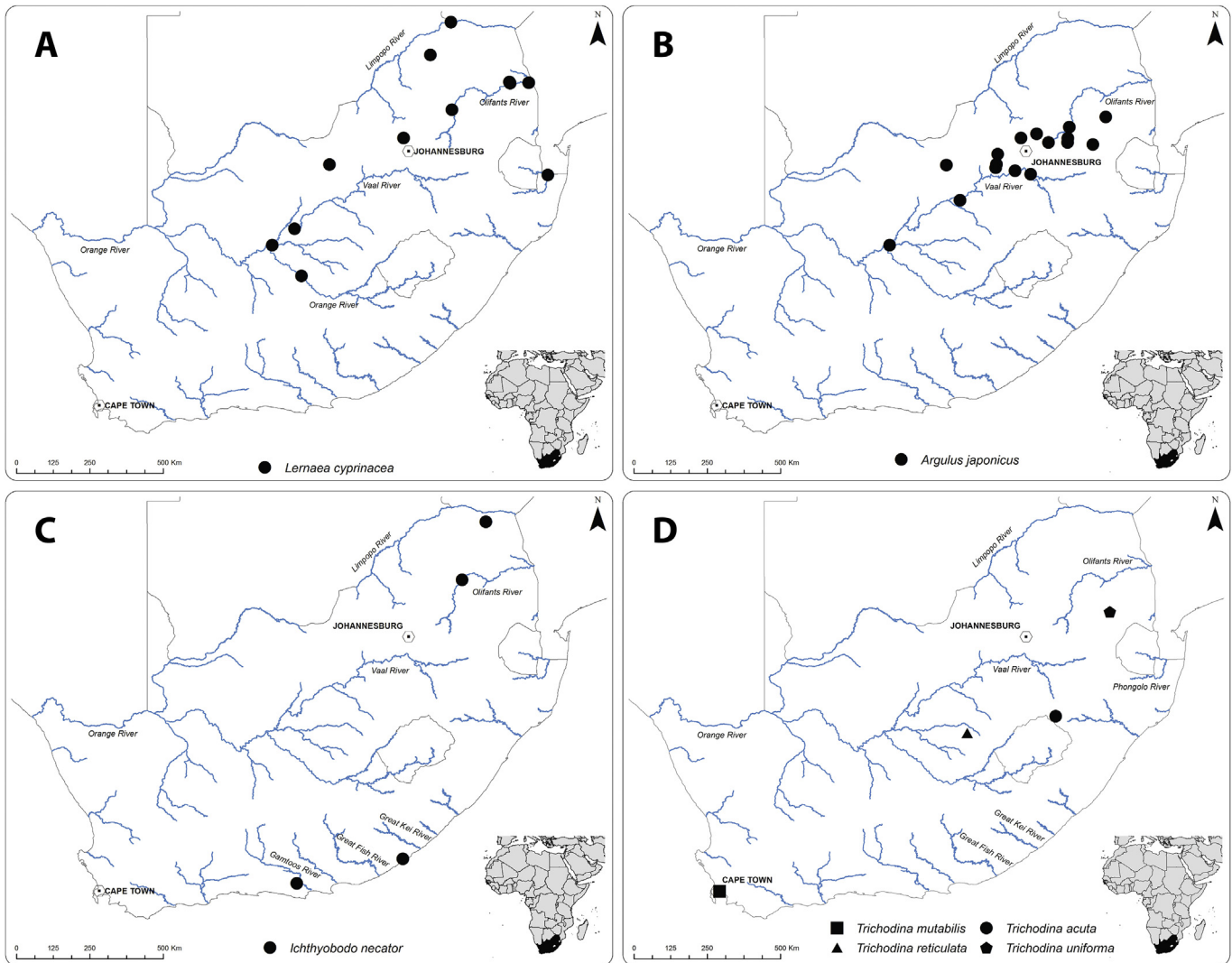


Fig. 2. Maps indicating the South African distribution records for (A) *Lemnaea cyprinacea* Linnaeus, 1758; (B) *Argulus japonicus* Thiele, 1900; (C) *Ichthyobodo necator* Henneguy, 1883 (needs molecular confirmation); (D) *Trichodina acuta* Lom, 1961, *Trichodina mutabilis* Kazubski and Migala, 1968, *Trichodina reticulata* Hirschmann and Partsch, 1955, and *Trichodina uniforma* Van As and Basson, 1989.

they are co-invaders spilled over from *C. carpio* or are a native South African sibling species.

3.2. Phylum Ciliophora

3.2.1. *Trichodina acuta*

The mobilid peritrich, *T. acuta*, is a known invasive parasite and has, since its original description, been reported from at least seven different non-native regions (Basson and Van As, 1993). In South Africa, Basson et al. (1983) reported *T. acuta* from four cichlids and two cyprinid species collected at more than six different localities in the northern provinces of South Africa. These hosts included *T. acuta*'s type host, *C. carpio*, and thus further strengthened their conclusion that this parasite is a co-introduced species that spilled over to South African native fishes. However, in their remarks on the species, Basson et al. (1983) commented on the distinct variability in size and denticle dimensions between the South African population and those reported from Israel and the Philippines. Van As et al. (1984) also reported what they identified as *T. acuta* from a Fisheries Research Station where it was implicated in the mortalities of two different fish species. Bruton and Merron (1985) and De Moor and Bruton (1988) further included this species in their respective lists of confirmed invasive aquatic invertebrates. In their review on the taxonomic status of fish ectoparasitic trichodinids, Van As and Basson (1989), with new information available to them, re-evaluated their original records of *T. acuta* from South Africa. By using additional characteristics which enabled them to provide a better understanding of differences in denticle shape, Van As and Basson (1989) described what was previously identified as a South African population of *T. acuta*, as all belonging to a new species, *Trichodina compacta* Van As and Basson, 1989, thereby removing *T. acuta* from the list of invasive parasites from South Africa. However, a few years later, Basson and Van As (1993) accurately identified *T. acuta* in South Africa and this time on rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792). This species was collected from a cage culture on a trout farm in the Free State province of South Africa (Table 1, Fig. 2D) confirming its status as a co-introduced parasite in South Africa. Basson and Van As (1993) also provided a detailed discussion on possible routes of introduction into South Africa, especially since its native hosts are European and Asian cyprinids and not salmonids, and concluded that it must have been a recent introduction and future research should focus on the potential spillover to South African native hosts.

3.2.2. *Trichodina mutabilis*

The history of discovery of *T. mutabilis* from South Africa is similar to that of *T. acuta* (see above) and thus not repeated here in detail. In short, Basson et al. (1983) reported this species from various invasive and native hosts in South Africa and then later Van As and Basson (1989) redescribed those specimens thought to be *T. mutabilis* as two species new to science, *Trichodina kazubskii* Van As and Basson, 1989 parasitising native fishes and *Trichodina uniforma* Van As and Basson, 1989 from the introduced *C. auratus* (see section 3.2.4). More than ten years later, Mouton et al. (2001) reported *T. mutabilis* again from South Africa, describing this parasite from *C. carassius* during a health survey of ornamental fishes imported to South Africa (Table 1, Fig. 2D). The fact that spillover of *T. mutabilis* to native non-cyprinid hosts in India (Mitra and Bandyopadhyay, 2005), and its heavy infection on moribund *C. carpio* in an aquaculture facility in the USA (Kritsky and Heckmann, 2002) has been reported, shows the potential threat of this co-introduced parasite to both native species and aquaculture in South Africa.

3.2.3. *Trichodina reticulata*

As one of the most prevalent ectoparasites of the goldfish, *C. auratus*, it is not surprising that *T. reticulata* has a similar global distribution to that of its popular ornamental fish host. Basson and Van As (1993) found this to be true when they recorded *T. reticulata* from *C. auratus* obtained from a local ornamental fish distributor in Bloemfontein, South Africa (Table 1, Fig. 2D). Notwithstanding being reported from more than 12 countries (Martins et al., 2012), it has never been implicated in spillover to native hosts. This is confirmed by the study of Dove and O'Donoghue (2005) who examined 2003 fishes belonging to 33 species from 58 sites in Queensland, Australia, and only found *T. reticulata* on wild caught *C. auratus* and another introduced species, the Eastern mosquitofish *Gambusia holbrooki* Girard, 1859. Based on current available information, it is most likely that if *T. reticulata* does get into South Africa's natural waterways it will remain a co-introduced parasite with a low possibility of spillover, however this needs to be further investigated.

3.2.4. *Trichodina uniforma*

As mentioned above (section 3.2.2), *T. uniforma* described by Van As and Basson (1989) from *C. auratus* was originally identified as the invasive *T. mutabilis*. The same authors further concluded that despite extensive surveys throughout southern Africa, they did not find this species in any other locality other than the original fish farm in the Komatipoort River, which they described it from, nor on any other hosts other than the introduced *C. auratus* (Table 1, Fig. 2D). This raised the question as to whether *T. uniforma* was co-introduced with *C. auratus* or if it was spillback from its native hosts. Since its description in 1989, various authors have reported this species from (amongst other hosts) *C. auratus* and *C. carpio* from their native range in China (see Tang et al., 2007; Qi et al., 2011; Li et al., 2014), thus confirming its status as a co-introduced parasite in South Africa. Recently, Tang and Zhao (2016), using 18S rDNA, supported Van As and Basson (1989) morphological identification of *T. uniforma* as a separate species to *T. mutabilis*.

3.3. Phylum Platyhelminthes

3.3.1. *Atractolytocestus huronensis*

One of the most recent reports of a co-introduced parasite from South Africa is that of the cestode *A. huronensi*. Scholz et al. (2015) reported this tapeworm from the intestine of *C. carpio* from four localities in the Limpopo Province of South Africa (Table 1, Fig. 3B). Their paper was also the first to include morphological and molecular confirmation of the identity of the introduced parasite. Although Scholz et al.'s (2015) report on this co-introduction is recent, the co-introduction of *A. huronensi* into South Africa might not be. During parasitological surveys conducted between 2013 and 2016 by the authors of this review in the Vaal River (North West Province), as well as in the Riet River (Northern Cape Province), *A. huronensi* specimens were collected from *C. carpio* at both sites (Smit unpublished records). These records are now included here (Table 1, Fig. 3A) and demonstrate a much wider distribution in different river systems than originally thought, and thus an unlikely pattern usually seen in a recent introduction. We concur with Scholz et al. (2015) that future work on this tapeworm should include phylogeographic studies employing molecular markers to reveal the source of introduction of this co-introduced parasite.

3.3.2. *Acolpenteron ureteroecetes*

The first record of a co-introduced parasite into South Africa is, according to our records, that of Du Plessis (1948), who reported the presence of the monogenean *A. ureteroecetes* in the urethras of three bass species, *Micropterus dolomieu* (Lacepède, 1802),

Micropterus punctulatus (Rafinesque, 1819), and *Micropterus salmoides* (Lacepède, 1802), bred in the Jonkershoek Fish Hatchery, Western Cape Province. Although all three species were infected, only *M. salmoides* had high parasite loads that directly lead to the mortality of large numbers of fingerlings (Du Plessis, 1948). Mortality of cultured *M. salmoides* due to *A. ureteroecetes* infections were more recently reported by Petrie-Hanson (2001) from pond reared fish in Mississippi, USA, confirming Du Plessis' (1948) original observation of *A. ureteroecetes*' pathogenicity. The only record of *A. ureteroecetes* in wild *M. salmoides* from South Africa is a non-peer reviewed published conference abstract by Matla et al. (2010) reporting a very low infection of this species from the ureter-urinary bladder of *M. salmoides* collected in the Tzaneen Dam, Limpopo Province (Table 1, Fig. 3B). As the stocking of most of the *M. salmoides* populations in South Africa was via the Jonkershoek Fish Hatchery (De Moor and Bruton, 1988), the co-introduction of *A. ureteroecetes* into the Limpopo Province was most likely from the original Jonkershoek Fish Hatchery stock. Research into the parasites of other populations of *M. salmoides* will most probably reveal a much wider distribution of *A. ureteroecetes* in South Africa and warrants further research.

3.3.3. *Dactylogyrus extensus*, *Dactylogyrus minutus* and *Dactylogyrus lamellatus*

The three dactylogyrids, *D. extensus*, *D. minutus*, and *D. lamellatus* are well documented known co-invaders, with their widely introduced host, *C. carpio*, for the former two and the grass carp, *Ctenopharyngodon idella* for the latter (Dove and Ernst, 1998; Yang et al., 2016). Crafford et al. (2014a) recorded all three of these species from their respective wild caught introduced hosts from the Vaal Dam in the Vaal River, South Africa (Table 1, Fig. 3C), with *Dactylogyrus extensus* and *D. minutus* collected from *C. carpio*, and *D. lamellatus* from *C. idella*. With representatives of *Dactylogyrus* Diesing, 1850 considered to be very host specific, the chances of host switching to native fish by these co-invaders are limited (Dove and Ernst, 1998; Simková et al., 2001). This is further supported by the work of Crafford et al. (2012; 2014a,b) on the monogeneans of fishes from the Vaal Dam, who did not report any spillover of these introduced *Dactylogyrus* species onto any of the native hosts studied.

3.3.4. *Gyrodactylus kherulensis*

The gyrodactylid *G. kherulensis* is a parasite of the common as well as the koi carp, *C. carpio koi*. Similar to the dactylogyrids

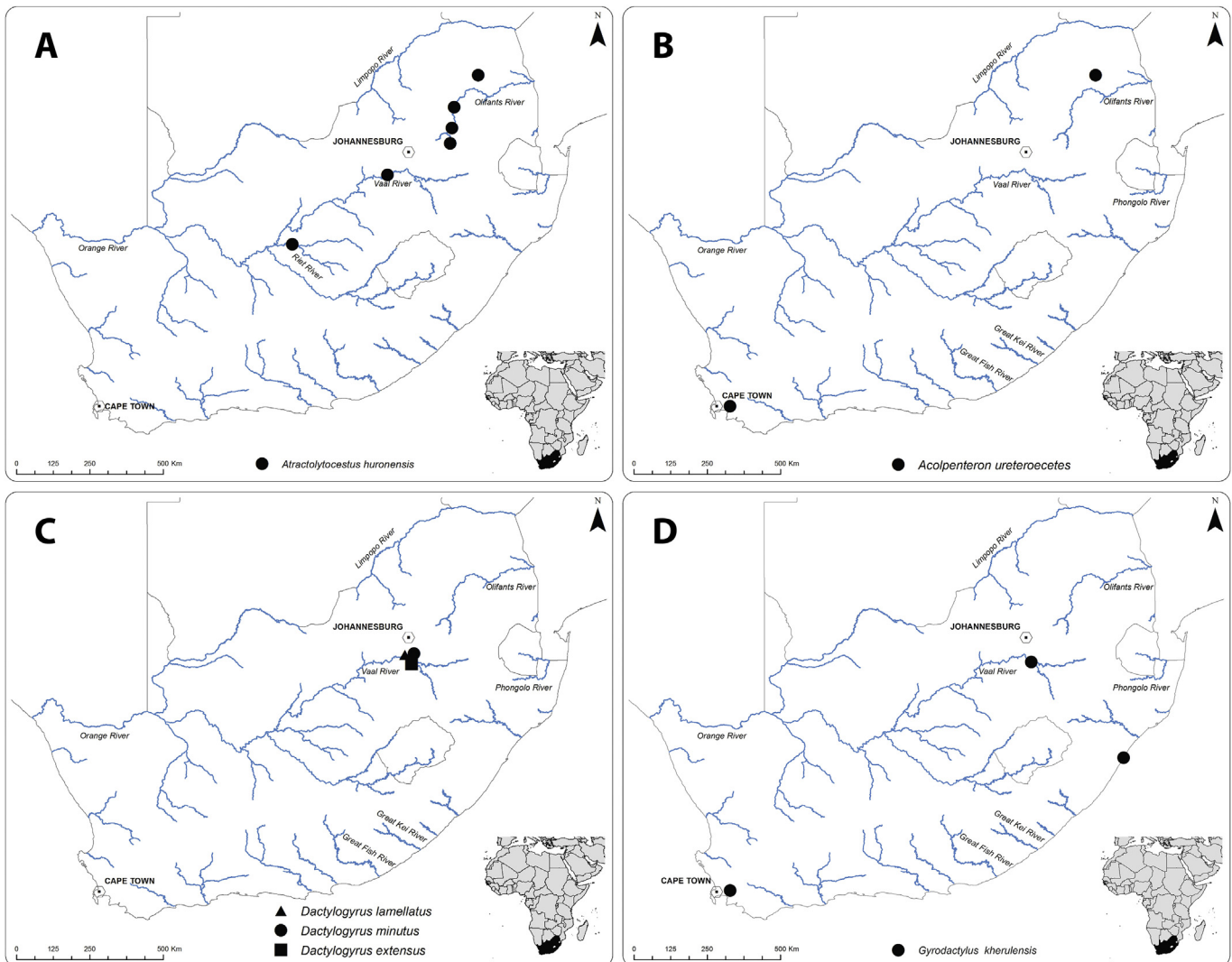


Fig. 3. Maps indicating the South African distribution records for (A) *Atractolytocestus huronensis* Anthony, 1958; (B) *Acolpenteron ureteroecetes* Fischthal and Allison, 1940; (C) *Dactylogyrus extensus* Mueller and Van Cleave, 1932, *Dactylogyrus minutus* Kulwiec, 1927 and *Dactylogyrus lamellatus* Achmerow, 1952; (D) *Gyrodactylus kherulensis* Ergens, 1974.

reported above, *G. kherulensis* has also been co-introduced world-wide due to the popularity of its natural host as an aquaculture and ornamental species. The first report of *G. kherulensis* in South Africa was in a non-peer reviewed published conference abstract by Maseng et al. (2010). These authors collected *G. kherulensis* from commercially bought, as well as wild caught, *C. carpio* in the Western Cape Province of South Africa (Table 1, Fig. 3D). Recently Crafford et al. (2014a) found a total of three *G. kherulensis* specimens on the body surface of a single *C. carpio*, collected from the Vaal Dam in the Vaal River (Table 1, Fig. 3D), confirming its status as a co-introduced parasite in South Africa.

3.3.5. *Ancyrocephalid monogeneans of largemouth bass, *Micropterus salmoides**

As part of this special issue on invasive parasites, Truter et al. (2017) provided the first peer reviewed published record of five ancyrocephalid monogeneans from largemouth bass, *Micropterus salmoides*, collected at three localities in South Africa. In that paper the authors provide full descriptions as well as distribution records and maps (see Truter et al., 2017), for these species. For completeness of the current review these species, *Clavunculus bursatus* (Mueller, 1963), *Onchocleidus dispar* (Mueller, 1936), *O. furcatus* (Mueller, 1937), *O. principalis* (Mizelle, 1936) and *Synclithrium fusiformis* (Mueller, 1934) are only listed here and not further discussed.

4. Parasites of uncertain invasive status

4.1. Phylum Ciliophora

4.1.1. *Apiosoma nasalis*

This sessile peritrich was originally described from the nasal cavities of cyprinids from the Amur River Basin, Russia; however, in his taxonomic revision of this genus, Lom (1966) suggested that re-examination of live specimens of this species is needed to confirm its identity. Its possible presence in South Africa was first recorded by Viljoen and Van As (1983) from *Pseudocrenilabrus philander* collected in the Westdene Dam, Johannesburg (Table 1). The authors acknowledged the uncertainty regarding its identity, especially as they collected it from the skin and gills and not the nasal cavities, and therefore proposed that their identification be provisional until more material from other localities and fish species are collected. However, in Viljoen and Van As (1985) the same authors recorded *A. nasalis* from *P. philander*, again from the Westdene Dam, but this time without stating any uncertainties. It is thus not clear if the 1985 record was from new material or just a repeat of the 1983 record. As the 1985 record did not include more fish hosts from different localities as proposed by Viljoen and Van As (1983), the invasive status of this species is considered as uncertain.

4.1.2. *Trichodinella epizootica* and *Trichodina nigra*

Both *T. epizootica* and *T. nigra* were included in the report by Basson et al. (1983) on trichodinids from selected fishes of South Africa (also see section 3.2.1.). Basson and Van As (1993), however, suspected that their original identification was incorrect and that re-evaluation of these species will most likely show that they are not representatives of either *T. epizootica* or *T. nigra*. Until proper re-evaluation, we place both these species here in the uncertain invasion status category.

4.2. Phylum Platyhelminthes

4.2.1. *Gyrodactylus kobayashii*

The gyrodactylid, *G. kobayashii*, is a parasite of the goldfish, *C. auratus*, and has a world-wide distribution due to it being co-

introduced with its ornamental fish hosts. In a non-peer reviewed published conference abstract by Maseng et al. (2010), the authors reported *G. kobayashii* present on both commercially bought, as well as wild caught, *C. auratus* in the Western Cape Province of South Africa (Table 1). Maseng et al. (2010) did not list the specific locality of the wild caught fish in the conference abstract but indicated the locality as the Kuils River in her unpublished Masters dissertation (Maseng, 2010). As this record of the co-introduction of *G. kobayashii* into South Africa is in non-peer reviewed publications, these records are classified as uncertain until formal publication thereof.

4.2.2. *Pseudodactylogyus anguillae*

The monogenean, *P. anguillae*, is an ectoparasite originally described from the gills of the Japanese eel, *Anguilla japonica* Temminck and Schlegel, 1846. Following its original description, it was discovered to have invaded Europe where it was first found in 1977 on the gills of the European eel, *Anguilla anguilla* from an eel farm in the western Soviet Union (Buchmann et al., 1987). *Pseudodactylogyus anguillae* has subsequently been recorded from wild populations of the American eel, *Anguilla rostrata* (Lesueur, 1817) in Canada (Cone and Marcogliese, 1995) and the USA (Hayward et al., 2001). The first report from South Africa was by Christison and Baker (2007) who reported *P. anguillae* from the gills of the long-fin eel, *Anguilla mossambica* collected from four rivers in the Eastern Cape (Table 1). Parker et al. (2011) and McHugh et al. (2017) subsequently extended the distribution range by including additional sites from the Eastern Cape (Table 1). However, Ogawa et al. (2015) and McHugh et al. (2017) raised concerns about the identity of what was thought to be *P. anguillae* from South Africa as its origin in this region is uncertain since no record of the introduction of *A. japonica*, or any other non-native eels into South Africa, can be found (Ellender and Weyl, 2014). Until further molecular analysis on the South African population of *P. anguillae*, using a combination of different genetic markers, has been completed and its identity confirmed, we provisionally assign this species to the uncertain invasive status category.

4.3. Phylum Arthropoda

4.3.1. *Achtheres pimelodi* (syn. *Achtheres micropteri*)

The lernaepodid copepod, *A. pimelodi*, is an ectoparasite found on the gills of various fish host in the USA, including the smallmouth bass, *M. dolomieu* (Muzzall and Whelan, 2011). Barnard (1955) presumed that *A. pimelodi* (using the synonym *A. micropteri*) might have been introduced into South Africa with the smallmouth bass, *M. dolomieu*, but it is not clear whether he actually collected any from South Africa. Later, Fryer (1968) listed this species (also using the synonym *A. micropteri*) in his paper on the distribution of parasitic Crustacea from African freshwater fish, but once again there was no indication on whether he collected any himself or if he was just referencing Barnard (1955). No other record of this parasite from South Africa exists and thus its current status as alien in South African waters is doubtful and needs further study.

5. Species previously reported as invasive but hereby removed from the list

5.1. Phylum Ciliophora

5.1.1. *Trichodina pediculus*

Basson et al. (1983) originally reported *Trichodina pediculus* Ehrenberg, 1838 from two cichlids in South Africa, but later Van As and Basson (1989) corrected the original identification and

Table 2

Fish hosts with known alien parasites from South Africa.

Classification	Genus species	Parasite species	
Family: Mormyridae	<i>Marcusenius macrolepidotus</i>	<i>Apiosoma piscicola</i>	
Family: Anguillidae	<i>Anguilla mossambica</i>	<i>Ichthyophthirius multifiliis</i>	
Family: Cyprinidae	<i>Carassius auratus</i>	<i>Ichthyophthirius multifiliis</i> <i>Trichodina mutabilis</i> <i>Trichodina reticulata</i> <i>Trichodina uniforma</i>	
	<i>Cyprinus carpio</i>	<i>Argulus japonicus</i> <i>Atractolytocestus huronensis</i> <i>Dactylogyrus minutus</i> <i>Dactylogyrus lamellatus</i> <i>Gyrodactylus kherulensis</i> <i>Ichthyophthirius multifiliis</i> <i>Ichthyobodo necator</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius annectens</i>	<i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius brevipinnis</i>	<i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius bifrenatus</i>	<i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius trimaculatus</i>	<i>Apiosoma piscicola</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius argenteus</i>	<i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius paludinosus</i>	<i>Apiosoma piscicola</i> <i>Chilodonella hexasticha</i> <i>Ichthyophthirius multifiliis</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Enteromius mattozi</i>	<i>Argulus japonicus</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Labeobarbus kimberleyensis</i>	<i>Argulus japonicus</i> <i>Lernaea cyprinacea</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Labeobarbus aeneus</i>	<i>Argulus japonicus</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Labeobarbus marequensis</i>	<i>Argulus japonicus</i> <i>Lernaea cyprinacea</i> <i>Lernaea cyprinacea</i> <i>Schyzocotyle acheilognathi</i>	
	<i>Labeo umbratus</i>	<i>Argulus japonicus</i> <i>Lernaea cyprinacea</i>	
	<i>Labeo capensis</i>	<i>Argulus japonicus</i> <i>Lernaea cyprinacea</i>	
	<i>Labeo rosae</i>	<i>Argulus japonicus</i> <i>Lernaea cyprinacea</i>	
	<i>Labeo ruddi</i>	<i>Lernaea cyprinacea</i>	
	<i>Labeo congoro</i>	<i>Lernaea cyprinacea</i>	
	<i>Labeo cylindricus</i>	<i>Lernaea cyprinacea</i>	
	Family: Clariidae	<i>Clarias gariepinus</i>	<i>Argulus japonicus</i> <i>Dactylogyrus extensus</i>
	Family: Salmonidae	<i>Salmo trutta</i>	<i>Ichthyophthirius multifiliis</i>
		<i>Oncorhynchus mykiss</i>	<i>Argulus japonicus</i> <i>Ichthyophthirius multifiliis</i> <i>Trichodina acuta</i>
	Family: Centrarchidae	<i>Micropterus salmoides</i>	<i>Acolpenteron ureteroecetes</i> <i>Clavunculus bursatus</i> <i>Onchocleidus dispar</i> <i>Onchocleidus furcatus</i> <i>Onchocleidus principalis</i> <i>Synclathrium fusiformis</i>
		<i>Micropterus dolomieu</i>	<i>Apiosoma piscicola</i> <i>Acolpenteron ureteroecetes</i>
		<i>Micropterus punctulatus</i>	<i>Acolpenteron ureteroecetes</i>
	Family: Cichlidae	<i>Pseudocrenilabrus philander</i>	<i>Apiosoma piscicola</i> <i>Chilodonella piscicola</i> (syn <i>C. cyprini</i>) <i>Chilodonella hexasticha</i> <i>Ichthyobodo necator</i> <i>Lernaea cyprinacea</i>
		<i>Tilapia sparrmanii</i>	<i>Ichthyobodo necator</i> <i>Chilodonella piscicola</i> (syn <i>C. cyprini</i>) <i>Chilodonella hexasticha</i>
<i>Coptodon rendallii</i>		<i>Apiosoma piscicola</i> <i>Chilodonella piscicola</i> (syn <i>C. cyprini</i>) <i>Chilodonella hexasticha</i> <i>Lernaea cyprinacea</i>	
		<i>Apiosoma piscicola</i>	
<i>Oreochromis mossambicus</i>			

Table 2 (continued)

Classification	Genus species	Parasite species
		<i>Argulus japonicus</i>
		<i>Chilodonella piscicola</i> (syn <i>C. cyprini</i>)
		<i>Chilodonella hexasticha</i>
		<i>Ichthyobodo necator</i>
		<i>Ichthyophthirius multifiliis</i>
		<i>Lernaea cyprinacea</i>
Family: Poeciliidae	<i>Poecilia reticulata</i>	<i>Ichthyophthirius multifiliis</i>

described the original specimens as *Trichodina magna* Van As and Basson, 1989. This correction was confirmed by Basson and Van As (1993), and as no further reports of *T. pediculus* from South Africa exists, it is hereby removed from the list of invasive freshwater fish parasites of South Africa.

6. Conclusions and future direction

All previously reported alien freshwater fish parasites were reviewed and categorised according to their invasive status. Based on available information, seven species were classified as co-invasive, 16 as co-introduced, six as uncertain invasive status, and a single species previously reported as invasive was removed from the list. The total confirmed number of alien parasites (23) in South Africa is low when considering that at least 17 species of alien freshwater fishes are established in South African waters, with the majority of the first introductions dating back to the mid twentieth century (Ellender and Weyl, 2014). Possible reasons for the low numbers of alien parasites might include that the original introductions were from stock already low in parasite diversity, for example, largemouth bass were introduced into South Africa from breeding facilities in Europe (De Moor and Bruton, 1988); or that the South African environment, although suitable to the host, is not suitable for its parasites. However, the most likely reason is probably the lack of extensive parasitological surveys in all the different regions of South Africa, as the current distribution records of alien parasites in South Africa is more related to the distribution of fish parasitologists than that of the parasites themselves [see Van As (2015) and Smit and Hadfield (2015) for reviews on the history of fish parasitology in South Africa]. A more targeted approach focussing specifically on South Africa's coastal provinces should provide more accurate information on the current distribution and diversity of invasive freshwater fish parasites.

The role of invasive parasites in mass fish-kill events in natural systems has already been established, for example, in Australia Langdon et al. (1985) identified invasive *Chilodonella* spp. as the main cause of death of native fish in the Finke River near Alice Springs (also see section 2.1.3.). In South Africa, mass fish-kill events are often reported and usually attributed to sudden change in water temperature, oxygen levels, and stressors such as pollution, and potentially even invasive fishes (Wepener et al., 2011), however, thus far invasive parasites have not been considered as a contributing factor or even the cause of these incidents. Future research on invasive parasites in South Africa should therefore include their potential role in mass fish-kill events.

To date, no research in South Africa (and very limited internationally) has focussed on the co-introduction of parasites by translocated species, especially those that were introduced through inter-basin water transfer schemes. Ellender and Weyl (2014) listed 21 extralimbed fish species that were already established in their new environments. Future research should therefore also focus on the parasites of these species in both their native and introduced

range, as well as the possible spillover to native fishes.

One of the biggest challenges when working with invasive parasites is the confirmation of the identity of the species, especially if representatives of the same family or even genus occur naturally in that region. We therefore propose that all future work on invasive parasites should include both morphological and molecular approaches when determining the species. It is also of utmost importance to deposit voucher specimens into recognised collection facilities for future verification, comparison, and research in general.

Although this review specifically deals with freshwater fish parasites introduced into South Africa, the information presented on the majority of the different parasites is also applicable to the rest of Africa and other countries worldwide. Similarly, the need for future research on the role of invasive parasites in fish-kills, parasites introduced by extralimbed fishes, as well as the molecular identification and deposition of voucher specimens, should be prioritised globally.

Conflict of interest

The authors declare there is no conflict of interest.

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