Received: 11 December 2021 | Revised: 21 September 2022 | Accepted: 23 September 2022

DOI: 10.1111/raq.12742

REVIEW

REVIEWS IN Aquaculture

A global review of problematic and pathogenic parasites of farmed tilapia

Andrew P. Shinn[1,2] | **Annemarie Avenant-Oldewage**[3] | **Melba G. Bondad-Reantaso**[4] | **Armando J. Cruz-Laufer**[5] | **Adriana García-Vásquez**[6] | **Jesús S. Hernández-Orts**[7] | **Roman Kuchta**[7] | **Matt Longshaw**[8] | **Matthijs Metselaar**[9] | **Antoine Pariselle**[10,11] | **Gerardo Pérez-Ponce de León**[12] | **Pravata Kumar Pradhan**[13] | **Miguel Rubio-Godoy**[6] | **Neeraj Sood**[13] | **Maarten P. M. Vanhove**[5] | **Marty R. Deveney**[14]

[1]INVE (Thailand), Nonthaburi, Thailand

[2]Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Townsville, Australia

[3]Department of Zoology, University of Johannesburg, Johannesburg, South Africa

[4]Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme di Caracalla, Rome, Italy

[5]Hasselt University, Centre for Environmental Sciences, Research Group Zoology: Biodiversity and Toxicology, Diepenbeek, Belgium

[6]Instituto de Ecología A.C, Xalapa, Veracruz, Mexico

[7]Institute of Parasitology, Biology Centre, Czech Academy of Sciences, České Budějovice, Czech Republic

[8]Calysta (UK) Ltd., The Wilton Centre, Wilton, Redcar, UK

[9]Aquatic Vets Ltd., Stirling, UK

[10]ISEM, CNRS, Université de Montpellier, IRD, Montpellier, France

[11]Laboratory "Biodiversity, Ecology and Genome", Faculty of Sciences, Mohammed V University in Rabat, Rabat, Morocco

[12]Escuela Nacional de Estudios Superiores Unidad Mérida, and Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

[13]ICAR-National Bureau of Fish Genetic Resources, Lucknow, Uttar Pradesh, India

[14]South Australian Research and Development Institute and Marine Innovation Southern Australia, SARDI Aquatic Sciences, West Beach, South Australia, Australia

Correspondence
Andrew P. Shinn, INVE (Thailand), 471 Bond Street, Bangpood, Pakkred, Nonthaburi 11120, Thailand.
Email: a.shinn@inveaquaculture.com

Marty R. Deveney, South Australian Research and Development Institute and Marine Innovation Southern Australia, SARDI Aquatic Sciences, West Beach, South Australia, Australia.
Email: Marty.Deveney@sa.gov.au

Funding information
Norwegian Agency for Development Cooperation (Norad), Grant/Award Numbers: GCP/GLO/352/NOR, GCP/GLO/979/NOR;

Abstract

Over the past 80 years, tilapia have been translocated globally for aquaculture; active production is recorded in >124 countries. Of 7 million tonnes of tilapia produced in aquaculture, 79% is from 79 countries outside the natural range of tilapia. Capture fisheries account for a further 723,627 tonnes of tilapia, and >47% of this is landed from established invasive populations outside Africa. Tilapias host a rich fauna of parasites, many of which have been translocated with their hosts. This review summarises >2500 host–parasite records from 73+ countries and >820 recorded tilapia translocations (provided in the supplementary materials). This work focuses on the notable pathogens that threaten the health of cultured populations of tilapia, providing a description of their pathology and includes species that also have substantial impacts on wild tilapia

University of Johannesburg; Central Research Committee Funding; INECOL Institutional Funds; Czech Science Foundation, Grant/Award Number: 19-28399X; Consejo Nacional de Ciencia y Tecnología, CONACyT, Mexico, Grant/Award Number: 177603; ENES-Mérida and Instituto de Biología, UNAM; Research Foundation—Flanders (FWO-Vlaanderen), Grant/Award Number: 1513419N; Special Research Fund of Hasselt University, Grant/Award Numbers: BOF21INCENT09, BOF20TT06; Belgian Federal Science Policy Office, Grant/Award Number: BR/132/PI/TILAPIA

populations, where relevant. For each major parasite taxonomic group, we highlight which parasites have been translocated or have been acquired from the new environments into which tilapia have been introduced, together with remarks on standard treatment approaches and research on them and their management and control. Regarding the theme 'Tilapia health: *quo vadis*?', Africa has enormous potential for aquaculture growth, but substantial knowledge gaps about tilapia parasites in many African states remain, which creates associated production and biosecurity risks. For each parasitic group, therefore, the risks of parasite translocation to new regions as tilapia aquaculture industries expand are highlighted.

KEYWORDS

aquaculture, global translocation, host–parasite record, pathogenicity, production

1 | INTRODUCTION

Cichlids belonging to the genera *Coptodon* Gervais, 1848 (31 species), *Oreochromis* Günther, 1889 (33 species) and *Sarotherodon* Rüppell, 1852 (13 species) are endemic to Africa and the Middle East, while those belonging to the genus *Tilapia* Smith, 1840 (four species) have distribution across southern parts of West Africa. Of these, 12 species and one hybrid of 'tilapia' are cultured intensively, namely *Coptodon rendalli* (Boulenger, 1897); *C. zillii* (Gervais, 1848); *Oreochromis andersonii* (Castelnau, 1861); *O. aureus* (Steindachner, 1864); *O. leucostictus* (Trewavas, 1933); *O. macrochir* (Boulenger, 1912); *O. mossambicus* (Peters, 1852); *O. niloticus* (Linnaeus, 1758); *O. aureus* × *O. niloticus* cross; *O. shiranus* Boulenger, 1897; *O. spilurus* (Günther, 1894); *Sarotherodon galilaeus* (Linnaeus, 1758); and *S. melanotheron* (Rüppell, 1852).[1]

The aquaculture production of tilapia approaches 7 million tonnes of which a staggering 4,866,563 tonnes (79.01%) is produced in 79 states outside their native range (Tables 1 and S1).[2] The collective production of tilapia of 6,192,963 tonnes valued at USD 12.342 billion, from 124 countries currently registering production, ranks first in all production categories above that of grass and silver carps, while Nile tilapia alone with a global production of 4,590,292 tonnes, ranks third. Production trends based on FAO,[2] and current to 2019, indicate that *O. niloticus* has the fastest industry growth, increasing at 4.11% year-on-year (2015–2019), when compared to the other top four fish species, that is, grass carp (*Ctenopharyngodon idella* [Valenciennes, 1844]; 2.61%), silver carp (*Hypophthalmichthys molitrix* [Valenciennes, 1844]; 1.09%), common carp (*Cyprinus carpio* Linnaeus, 1758; 2.78%) and bighead carp (*Hypophthalmichthys nobilis* [Richardson, 1845]; 1.26%). The average growth rate of all cultured tilapia across the same period is 3.73% year-on-year.

Tilapias are farmed in 79 territories outside their native range, mainly in China (1,641,662 tonnes), Indonesia (1,257,000 tonnes) and Bangladesh (350,258 tonnes), these producers accounting for 66.76% of all tilapia grown. Production of cultured tilapia surpassed the volumes landed from capture fisheries in 1993 and currently represents 89.54% of total tilapia production. Of the 723,627 tonnes derived from capture fisheries, 358,025 tonnes (47.71%) of the take is from 24 countries outside the native range of tilapia. Of these, Mexico (136,820 tonnes), Indonesia (68,650 tonnes) and Sri Lanka (51,810 tonnes) are the top three producers (Table S1).

The earliest recorded translocations of tilapia out of Africa were to South East Asia in the late 1930s with the purported unintentional introduction of *O. mossambicus* into the Serang River, Java in 1939,[3] and in the early 1940s with shipments of *O. mossambicus* to Hong Kong, Indonesia, Malaysia and Singapore, followed by consignments of *O. niloticus* to Argentina in 1940 and of *C. zillii* to Mexico and Antigua in 1943–1945 (Table S1). Tilapia host a rich fauna of metazoan parasites and eukaryotic microbial pathogens (protists), many of which have been translocated with the global movement of tilapia or have been acquired from resident fish and environments into which they have been introduced (Tables 1 and S1).

This review provides a list of recorded parasites (metazoans and protists) of tilapia (Tables S2 and S3) and focuses on the notable pathogens that threaten the health of cultured populations of tilapia. It provides comments on their pathology and effects on their hosts, including where relevant, references to the pathogens that also have substantial impacts on wild tilapia. For each major parasite taxonomic group, we provide comments on the translocation of parasites with fish and parasites from these new environments that parasitise tilapia, together with remarks on standard treatment approaches, where these exist, and research towards their management and control.

2 | PARASITIC INFECTIONS OF TILAPIA

The ensuing parasite sections follow the phylogenetic classification of eukaryotes proposed by Adl et al. and Burki et al.[4,5]

2.1 | Amoebozoa Lühe, 1913 (Amorphea: Amoebozoa)

2.1.1 | Taxonomic identity

Amoebozoa is a group of amoeboid protists often possessing blunt, fingerlike pseudopods and tubular cristae. At least seven genera of

TABLE 1 A summary of commercially important tilapia species in aquaculture and global capture fisheries

				Number of countries						
Species	**Common name**	**Aquaculture tonnes (2019)**	**Producing countries (2019)**	**Native**	**Introduced**	**Intro. but not established**	**ID questionable**	**Misident.**	**Capture fisheries tonnes in 2019 (from intro stocks)**	**No. of countries (2019)**
C. rendalli	Redbreast tilapia	2999	4	11	28	0	3	0	0	0
C. zillii	Redbelly tilapia	6	2	28	23	3	3	0	0	0
O. andersonii	Three spotted tilapia	4793	3	6	4	0	0	0	0	0
O. aureus	Blue tilapia	3100	4	10	35	4	0	0	1804 (1799)	2 (1)
O. aureus × *O. niloticus*	Blue-Nile tilapia, hybrid	4,10,553	2	0	2	1	0	0	0	0
O. leucostictus	Blue spotted tilapia	0	0	2	4	0	0	0	0	0
O. macrochir	Longfin tilapia	1800	1	5	18	5	2	0	0	0
O. mossambicus	Mozambique tilapia	74,435	10	7	93	8	2	1	21,450 (21,450)	2 (2)
O. niloticus	Nile tilapia	45,90,292	75	22	6	77	0	0	281,644 (73,337)	13 (7)
O. shiranus	Tilapia shiranus	4711	1	3	0	1	0	0	1082 (0)	1
O. spilurus	Sabaki tilapia	300	1	3	10	0	1	0	0	0
O. urolepis	Wami tilapia	0	0	1	2	0	0	0	0	0
Oreochromis spp.	Tilapias nei	10,99,860	51	39	55		0	0	451,159 (224,283)	23 (11)
S. galilaeus	Mango tilapia	19	2	26	3	1	1	0	255 (0)	1
S. melanotheron	Blackchin tilapia	95	1	15	5	2	0	0	2234 (0)	1
T. sparrmanii	Banded tilapia	0	0	11	2	0	0	0	0	0
Total		61,92,963							723,627 (320,869)	

Note: For each species, the total tonnage and the number of countries supplying returns to FAO in 2019 are provided; for capture fisheries, the tonnages resulting from native stocks are presented alongside those from stocks (in parentheses) that have been introduced and established in the wild. Figures are calculated from the FAO FishStatJ (2021) and Fishbase (Froese and Pauly, 2021) databases and the wider literature.

Abbreviations: BR, brackish water; C, *Coptodon*; FW, freshwater; nei, not included elsewhere; O, *Oreochromis*; S, *Sarotherodon*; T, *Tilapia*.

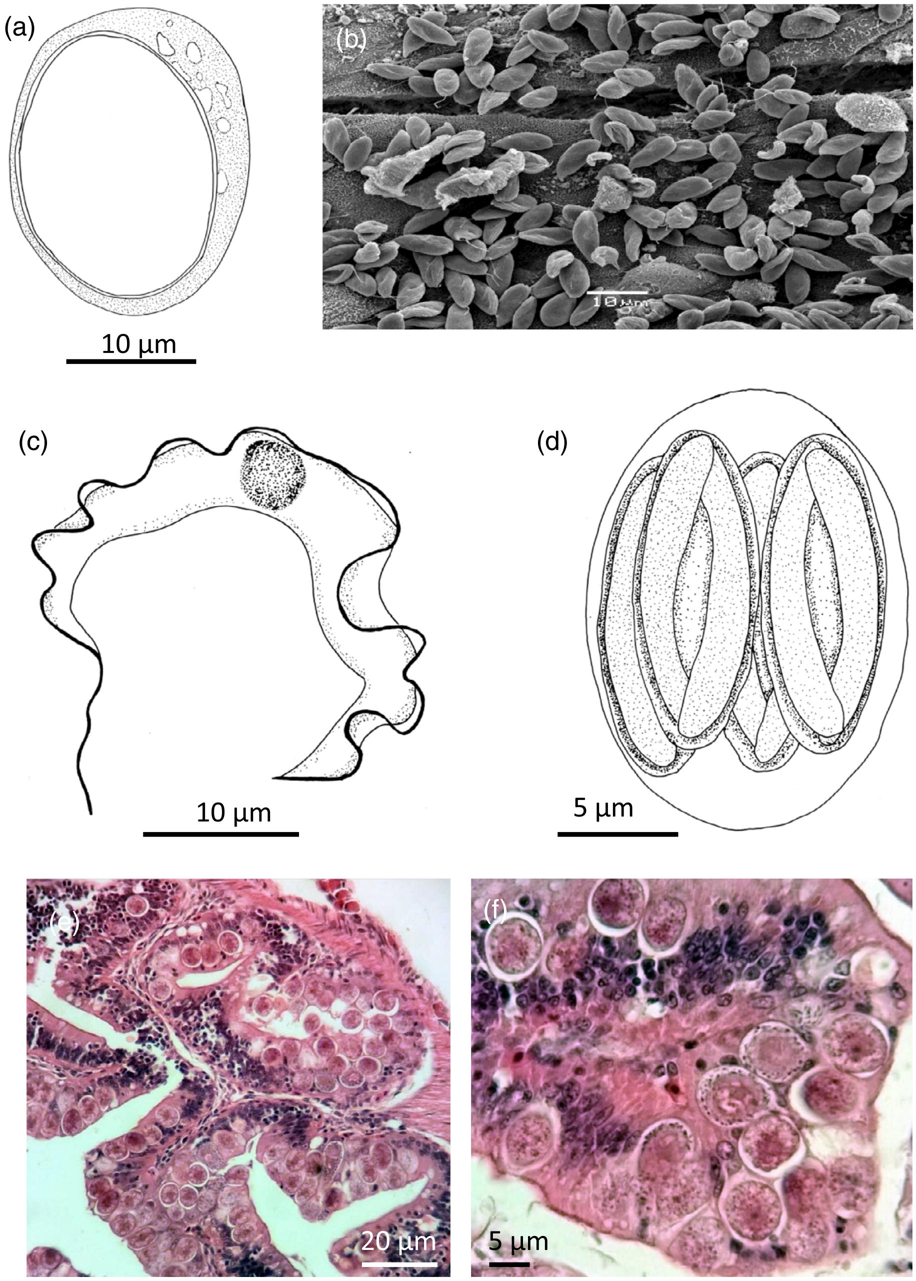

FIGURE 1 Protista. (a) Line drawing of *Dermocystidium aegyptiacus* reported from the intestines of *Oreochromis niloticus* cultured in Egypt. (b) Scanning electron microscope image of *Ichthyobodo necator* on epithelial surfaces. (c) Line drawing of *Trypanosoma mukasai* reported from the blood of a number of farmed and wild tilapia species. (d) Line drawing of *Goussia vanasi*. (e, f) Unidentified coccidian infection within H&E sections through the intestine of juvenile *O. niloticus* reared in lined tanks receiving water from a natural earthen reservoir in Brazil. Image (a) after El-Mansy (2008), image (c) after Baker (1960), image (d) after Molnár et al. (2004), images (e) and (f) courtesy of Leo Galli

free-living amoebae are reported in farmed tilapia, including *Rosculus* Hawes, 1963, *Mayorella* Schaeffer, 1926, *Platyamoeba* Page, 1969 and *Vermamoeba* Cavalier–Smith et Smirnov, 2011, from farmed *O. niloticus* in the Czech Republic,[6] *Acanthamoeba* Volkonsky, 1931, *Naegleria* Alexeieff, 1912 and *Vahlkampfia* Chatton et Lalung–Bonnaire, 1912 from farmed *O. aureus* and *O. niloticus* from the USA[7] and *Vernamoeba* from the intestines of farmed *O. niloticus* from the Philippines[8] and *O. niloticus* from Brazil.[9] Amoebae are single-celled organisms that can alter their overall shape, usually through the extension and contraction of pseudopodia. They are identified using a combination of morphology, transmission electron microscopy, histology of host tissues and culture methods.[6,7] Descriptions should also include molecular data following Milanez et al.[8] to confirm identity. There are no records of amoebae infecting wild tilapia, but this may reflect a lack of studies.

2.1.2 | Pathogenicity

Although Dyková et al.[6] noted granulomas in the pancreas of *O. niloticus* experimentally infected with *Vermamoeba* (syn. *Hartmannella*) *vermiformis* (Page, 1967), no correlation was found between the presence of amoebae and lesions in farmed fish in the Czech Republic. A presumptive *Acanthamoeba* sp. was isolated from the intestine, gills and peritoneal fluid of a kill of invasive *O. aureus* in the USA[7] in which the intestinal mucosa, associated with the amoeba infection, was severely eroded but with limited inflammatory response.

2.1.3 | Global translocations

Infections reported in farmed tilapia appear to be of free-living amoebae normally found in the areas where tilapia were farmed. It is unlikely that they were translocated but it does not preclude the possibility that cryptic infections could be translocated to new areas with infected fish.

2.1.4 | Research

Reports of amoeba infections in tilapia are sporadic and due to either specific studies on amoeba or findings from mortality investigations. Screening fish for infections, confirming species identity, conducting host susceptibility trials and assessing pathogenicity in new hosts could clarify the role of amoebae in disease of farmed tilapia.

2.2 | Euglenozoa Cavalier–Smith 1981 (Excavata: Euglenozoa)

2.2.1 | Taxonomic identity

Euglenozoa are a group of flagellates, mostly with two flagella. Four genera of the group Kinetoplastea: *Cryptobia* Leidy, 1846, *Ichthyobodo* Pinto, 1928, *Trypanoplasma* Laveran et Mesnil, 1901 and *Trypanosoma* Gruby, 1843 and one genus in the class Euglenida: *Phacus* Dujardin, 1841, are reported in farmed and wild tilapia. Euglenozoa was reviewed by Kostygov et al.,[10] including data on phylogeny, life-cycles and identification methods. De Jesus et al.[11] provide further methods for the description of trypanosome infections of tilapia which include morphometric body measurements, DNA sequencing, blood smears and histology to localise and characterise infections. Kinetoplastids are characterised by one or more flagella arising from the body and a kinetoplast within the cytoplasm. A flagellated *Phacus* sp. from the rectum of *O. mossambicus* in India has green pigment in the cytoplasm.[12] *Cryptobia* spp. are recorded from farmed *O. niloticus* from the Philippines, Kenya and Indonesia and *O. niloticus* × *O. aureus* from Israel.[13–21] *Ichthyobodo necator* (Henneguy, 1883; syn. *Costia necatrix*) and *Ichthyobodo* sp. (Figure 1b) are found on a wide range of fish hosts, including farmed *O. niloticus* from Saudi Arabia,[22] Uganda,[17,19,23,24] Kenya,[17,19,20] Costa Rica[25] and Nigeria,[26] *O. niloticus* × *O. aureus* from Israel,[14] *Sarotherodon* sp. from Mexico[27] and *C. zillii* from Iraq.[28] Kinetoplastids are usually found on the gills and occasionally the skin and in the blood. A *Trypanoplasma* sp. is reported from *O. aureus* in Puerto Rico.[29] Three *Trypanosoma* species are recorded from *Oreochromis* spp. *T. mukasai* Hoare, 1932 (syn. *T. choudhuryi*; Figure 1c) occurs in farmed *O. mossambicus* in India[12,30] but has also been reported in a range of wild tilapia in Africa.[31–34] *Oreochromis niloticus* is also infected by *T. tilapiae*[35] and an undescribed *Trypanosoma* sp. in Brazil, Egypt and Sudan.[11,36,37] *Trypanosoma* sp. is also reported from wild tilapia including *Trypanosoma* sp. in *O. andersonii* from Botswana[38] and from Namibia,[39] in *C. rendalii*, *O. macrochir* and *T. sparrmanii* from Namibia,[39] *C. zillii* from Egypt,[40] *O. niloticus* from Kenya,[41] *T. cyanophilum* Mohammed, 1978 and *T. mansouri* Mohammed, 1978 in *C. zillii* from Egypt.[40]

2.2.2 | Pathogenicity

De Jesus et al.[11] noted mortalities in farmed *O. niloticus* infected with trypanosomes in Brazil. Infected fish darkened and had epidermal haemorrhages. Histologically, gills were oedematous with inflammatory infiltration and lamellar fusion while necrosis and infiltration were also noted in the liver, spleen and kidney.

2.2.3 | Global translocations

Ichthyobodo and *Cryptobia* spp. are widespread, but it is difficult to determine if these parasites have been translocated with tilapia or if their range is broad. *Trypanosoma* spp. typically have narrow host specificity and require a leech intermediate host for transmission. Given the relatively wide geographical range of some *Trypanosoma* spp. it is possible, however, that they have been translocated with their fish hosts.

2.2.4 | Research

The identifications of kinetoplastids in tilapia should be confirmed to determine the extent of translocations and the host specificity of those reported. Given the potential pathogenicity of the group, further studies should be directed towards development of suitable mitigation measures such as identifying effective treatments and life cycle intervention strategies.

2.3 | Metamonada Grassé, 1952 (Excavata: Metamonada)

2.3.1 | Taxonomic identity

Metamonads including diplomonads are flagellated protists with anaerobic metabolism. The diplomonads are flagellated protists normally composed of two symmetrical cells with two nuclei and four flagella and include recognised pathogens of fish. An unidentified species of *Spironucleus* Lavier, 1936 infecting farmed red tilapia (*O. mossambicus* × *O. aureus*) in Thailand was described by Supamattaya et al.[42] using a combination of light and electron microscopy. Another pathogenic *Spironucleus* sp. was reported by El-Khatib and El-Hady[43] in the intestine of cultured *O. niloticus* from Egypt and was described using morphology and experimental trials, and cultured using Eagle's Minimum Essential Medium supplemented with 10% bovine serum (MEM 10% BS) culture media. An unidentified species of *Hexamita* Dujardin, 1838 was identified in *O. niloticus*, *O. niloticus* × *O. aureus* and *S. galilaeus* in Israel and Africa by light microscopy.[14,44] Use of transmission electron microscopy and molecular methods is likely to identify these parasites as *Spironucleus*.[45,46] A diplomonad of concern for human health, *Giardia intestinalis* Kulda et Nohýnková, 1995, is a zoonotic parasite found in a range of animals. Ghoneim et al.[47] identified the human strain of *G. intestinalis* in the faeces of farmed *O. niloticus* in Egypt using a strain-specific polymerase chain reaction (PCR) assay. The fish host was considered to contribute to contamination of water and may play a role in the epidemiology of giardiasis.

2.3.2 | Pathogenicity

No pathology was reported for the infections with *Hexamita* sp. and *G. intestinalis*. *Oreochromis mossambicus* × *O. aureus* infected with *Spironucleus* sp. were emaciated and presented with white nodules in the skin. Infected fish were attacked by healthy individuals in the same ponds and died from the resultant wounds.[42] *Spironucleus* sp. infections cause leukocyte infiltration, necrosis of infected tissues and muscle degeneration. *Oreochromis niloticus* infected with *Spironucleus* were dark, with excessive epithelial mucus production, had enteritis, skin lesions along the lateral lines and focal lesions on the surface of the liver.[43]

2.3.3 | Global translocations

Spironucleus spp. are rare in tilapia; it is unclear if these have not been observed due to a lack of appropriate sampling or if they are geographically restricted.

2.3.4 | Research

To understand disease risk, there is a need to confirm the identity of *Spironucleus* and *Hexamita* in tilapia and studies on the role of fish in the epidemiology of giardiasis are likely to inform human health risks.

2.4 | Apicomplexa Levine 1980 (SAR: Alveolata: Apicomplexa)

2.4.1 | Taxonomic identity

Apicomplexans are parasitic alveolates which mostly possess an apicoplast and an apical complex. They are transmitted directly or through an intermediate host and are found in a wide range of terrestrial and aquatic animal hosts, including farmed and wild tilapia. The typical morphology of a coccidian is shown in Figure 1d, which shows two sporozoites within each of the sporocysts which are contained within the oocysts; the number of sporozoites within each sporocyst and the number of sporocysts within each mature oocyst is used to determine the genus within the group. In addition to morphology, molecular methods are used extensively to confirm identity. Most infections in tilapia are of *Goussia cichlidarum* Landsberg et Paperna, 1985 in the swimbladders of *C. zillii* and *O. aureus* from Egypt[48] and Israel,[49] of *O. aureus* × *O. niloticus* and *S. galilaeus* from Israel[49] and of *O. niloticus* from Egypt[48] and Kenya.[17] *Goussia* (syn. *Eimeria*) *vanasi* (Landsberg et Paperna, 1987; Figure 1d) has been reported from the intestine of farmed *O. aureus* × *O. niloticus* and *S. galilaeus* from Israel,[50–53] and of *O. mossambicus* from South Africa,[50] and wild *T. sparrmanii* from South Africa.[50,54] Undescribed coccidian infections are reported in farmed *O. niloticus* from the Philippines,[55] Iraq[56] and Kenya.[19] A coccidian infection in the intestine of farmed *O. niloticus* reared in Brazil is shown in Figure 1e,f. *Cryptosporidium* spp. have been reported from the intestine and stomach of farmed *C. zillii* from Iraq,[56] of *O. niloticus* from Papua New Guinea[57] and Egypt,[58] and of *O. aureus* and *O. aureus* × *O. niloticus* from Israel.[59] Although Paperna and Vilenkin[60] proposed the name *Piscicryptosporidium* for species occurring in fish, this has not been widely accepted.[61,62] The intraerythrocytic *Babesiosoma* (syn. *Dactylosoma*) *mariae* (Hoare, 1930) occurs in numerous tilapias including *Oreochromis* spp. in Uganda,[31,63] Namibia[39] and Botswana.[64] It is not reported in farmed fish, but it may have been overlooked because of its cryptic habitat. The intraerythrocytic, haemogregarine in farmed *O. niloticus* reported by El-Asely et al.[65] may be conspecific with *B. mariae*.

2.4.2 | Pathogenicity

Goussia cichlidarum occurs in the swim-bladder of its hosts where it causes lesions in the thick tissue lining and hypertrophy of the cells surrounding the gas gland. Sloughing, necrosis and degeneration of the swimbladder were associated with developing stages of the parasite.[48] Intestinal infections with *G. vanasi* cause emaciation, growth retardation and occasionally mortality of juvenile *Oreochromis* spp.[50]

2.4.3 | Global translocations

Apicomplexan infections are restricted largely to the African subcontinent and there is limited evidence of translocation. It is unclear if the records of coccidians in the Philippines, Papua New Guinea and Vietnam represent translocations because the organisms associated with these records were not identified to species.[55,57,66,67]

2.4.4 | Research

Wild fish have been surveyed for apicomplexans,[64,68] but research on coccidians of farmed tilapia is limited. Determining the global distribution of these parasites and confirming the taxonomy of the group would inform better surveillance and understanding of their pathogenesis. Understanding life-cycles and identifying methods of control would decrease farm losses and improve management efficiency.

2.5 | Dinoflagellata Bütschli, 1885 (SAR: Alveolata: Dinoflagellata)

2.5.1 | Taxonomic identity

Dinoflagellates are unicellular algae with two dissimilar flagella arising from the ventral side. Three dinoflagellate genera are reported in tilapia: *Amyloodinium* Brown et Hovasse, 1946, *Piscinoodinium* Lom, 1981 and *Pfiesteria* Steidinger et al., 1996. *Amyloodinium ocellatum* Brown et Hovasse, 1946 was noted on the gills, skin and fins of farmed and wild *O. aureus* and *O. mossambicus* in the USA.[69–72] *Amyloodinium ocellatum* is found globally in numerous hosts from saline environments.[73] *Piscinoodinium* sp. and *P. pillulare* (Schaperclaus, 1954) are reported from the skin, fins and gills of farmed *O. niloticus* from Brazil,[74–77] the Philippines[55] and Thailand[78] and *O. mossambicus* from India[79] and Puerto Rico.[29] *Pfiesteria shumwayae* Glasgow et Burkholder, 2001 is reported from *O. mossambicus* in the USA[80] and *P. piscicida* Steidinger et Burkholder, 1996 is reported from *O. aureus*, *O. mossambicus* and *O. niloticus* in laboratory aquaria in the USA.[81,82]

2.5.2 | Pathogenicity

Piscinoodinium spp. are pathogens of their fish hosts and are responsible for mortalities in *O. mossambicus* in India[79] and in *O. niloticus* in Brazil[74,76] and were associated with high mortality in young (<1-year-old and less than 13 cm in length) *O. mossambicus* in the hypersaline Salton Sea, California, USA.[71] Infected fish gasped for air at the water surface, leapt out of the water and lost their equilibrium before dying.

2.5.3 | Global translocations

The dinozoan infections reported in tilapia also occur in native species and it is therefore difficult to determine if tilapia are responsible for any translocations. Wilson et al.[83] considered, however, that *Piscinoodinium* sp. infections in invasive *O. mossambicus* in Australia were co-introduced with its host, and *Piscinoodinium* is also considered invasive in its new habitat.

2.5.4 | Research

Understanding the role of tilapia in the distribution of dinozoans globally would aid determining if they have caused or exacerbated infections in new areas and new hosts. Information on impacts on native hosts, including susceptibility are lacking and should be addressed. Development of improved control methods would improve farm productivity.

2.6 | Ciliophora Doflein, 1901 (SAR: Alveolata: Ciliophora)

2.6.1 | Taxonomic identity

Ciliates are protozoans characterised by small hair-like organelles (cilia). Ciliates from nine orders—Chlamydodontida Deroux, 1970, Endogenida Collin, 1912, Mobilida Kahl, 1933, Ophryoglenida Canella, 1964, Pleurostomatida Schewiakoff, 1896, Prorodontida Corliss, 1974, Sessilida Stein, 1933, Tetrahymenida Fauré-Fremiet in Corliss, 1956 and Vestibuliferida de Puytorac et al., 1974 are reported from farmed and native and invasive tilapia across their geographical range. Most records are from Mobilida and Sessilida, reflecting the pathogenic importance of these two orders. Identifications are based on morphology including the unifying presence of cilia, although molecular techniques allow the elucidation of cryptic species and confirm the identity of species. Although most identifications are correct, caution should be exercised in inferring translocations of ciliates with tilapia due to uncertainty over some of the identifications made in the literature.

Members of the genus *Chilodonella* Strand, 1926 (Chlamydodontida), including *C. hexasticha* (Kiernik, 1909), *C. piscicola* (Zacharias, 1894) (syn. *C. cyprini*) and *Chilodonella* sp. are recorded on the skin and gills of *C. rendalli* from South Africa[84,85] and Turkey,[86] *C. zillii* and *O. aureus* from Israel[85] and from Turkey,[86] *Oreochromis* sp. and *O. mossambicus* from Vietnam,[67] *O. mossambicus* from South Africa,[84] *O. niloticus* from Bangladesh,[87] Brazil,[88] Costa Rica,[25] Egypt,[89] Indonesia,[21] Kenya,[20] Mexico,[90] Saudi Arabia[91] and Turkey,[86] and *S. galilaeus* from Turkey.[86] These parasites have been identified using morphology rather than molecular methods, which are considered necessary for correct identification.[92,93]

Using histology, Afifi et al.[22] identified *Capriniana* (syn. *Trichophrya*) sp. (Endogenida) in *O. niloticus* reared in saline water in Saudi Arabia. This is the only record of this genus and order occurring in tilapia and because the identifications appear to be based on histology only, there is a need to confirm this identification. Similarly, the solitary reports of *Tetrahymena corlissi* Thompson, 1955 (Tetrahymenida) from the gills of *O. niloticus* in Indonesia[21] and of *Tetrahymena* sp. in *O. niloticus* from Nigeria requires confirmation because this ciliate is typically systemic, occurs rarely on the gills[94–96] and is probably a complex of cryptic species.[97] Experimental infections of *O. mossambicus* with *Cryptocaryon irritans* Brown, 1951 (Prorodontida) were used to demonstrate immunity in the host to the parasite.[98,99] Molecular methods were used to confirm the identity of the ciliate infection in *O. mossambicus* although histological methods were used to demonstrate the presence of *Cryptocaryon* sp. in farmed *O. niloticus* from Saudi Arabia.[22] The ubiquitous white spot parasite *Ichthyophthirius multifiliis* Fouquet, 1876 (Ophryoglenida) is recorded from the skin, fins and gills (Figure 2a) of

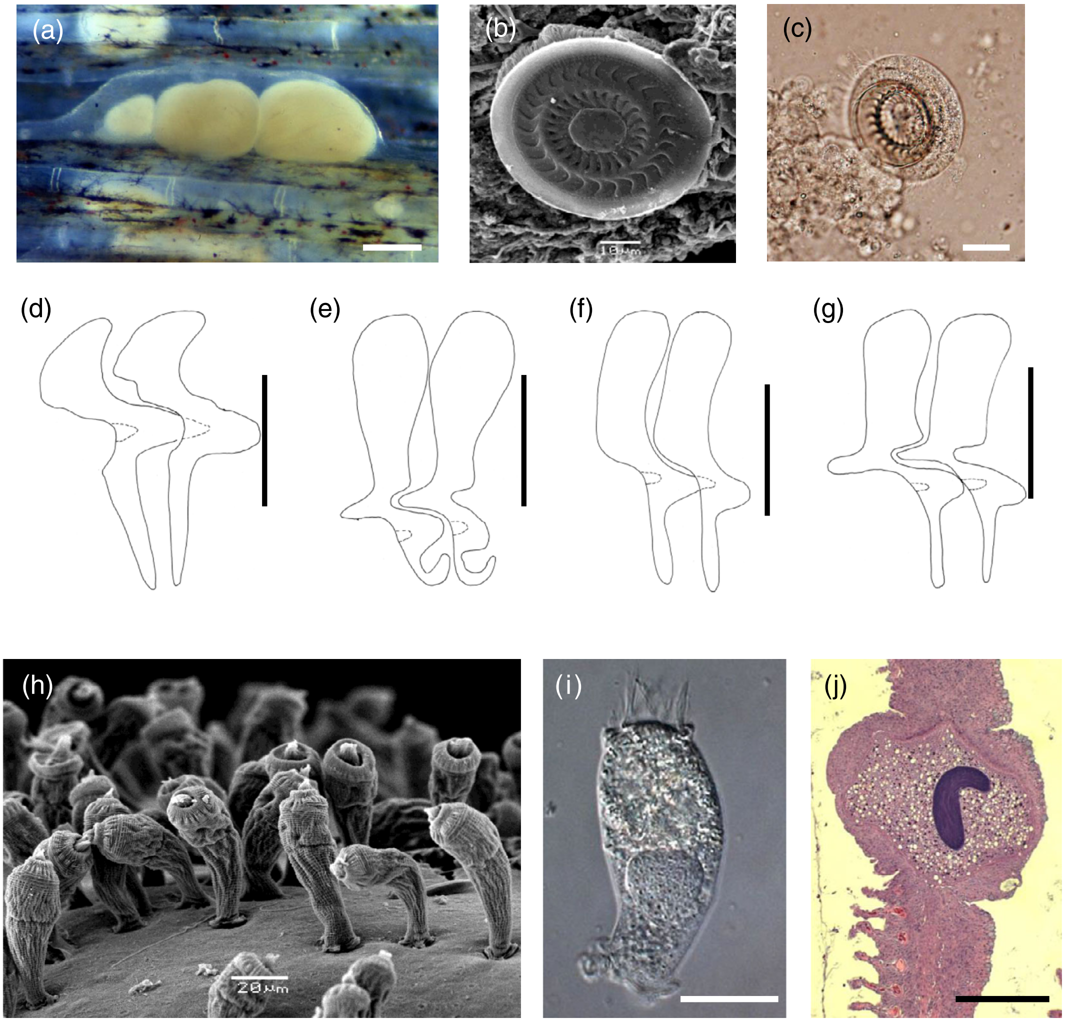

FIGURE 2 Ciliophora. (a) Photomicrograph of *Ichthyophthirius multifiliis* Fouquet, 1876 trophonts in the fin epithelium and (b) scanning electron microscopy image of the aboral surface of an unnamed *Trichodina* sp. collected from farmed *O. niloticus* from Veracruz, Mexico. Note the denticles in a radial pattern. (c) Photomicrograph of an unnamed *Trichodina* sp. from a *O. niloticus* fingerling and (d) line drawing of the denticles of a representative *Trichodina* sp. (e) Line drawing of the denticles of a representative *Trichodinella* sp. (f) Line drawing of the denticles of a representative *Paratrichodina* sp. (g) Line drawing of the denticles of a representative *Tripartiella* sp. (h) Scanning electron microscope image of a group of peritrichous ciliates on the epithelium of its host. (i) Photomicrograph of a solitary *Apiosoma* sp. (j) Histological section of a gill infected with an *Ichthyophthirius multifiliis* trophont. Images (a, i, j) Andrew Shinn, (b) courtesy of Greta Hanako Rosas Saito, (c) courtesy of Dong Ha Thanh, (d–g) after Basson and Van As (1989), (h) courtesy of Giuseppe Paladini. Scale bars: a, j = 300 μm; c, h, i = 20 μm; b, d–g = 10 μm

cultured *C. zillii* from the USA,[100] *Oreochromis* sp. from Vietnam,[67] *O. aureus* from the USA[100,101] and Mexico,[102,103] *O. mossambicus* from Puerto Rico,[29] from South Africa,[84] from the USA,[100] from Vietnam[67] and the Philippines,[16] *O. mossambicus* × *O. urolepis* from the USA,[100] *O. niloticus* from Brazil,[74,77,104–106] Egypt,[107–109] Greece,[110] Indonesia,[21] Nigeria,[26] the Philippines,[16,55] the USA[111] and Vietnam,[66,67] *O. niloticus* × *O. aureus* from Israel,[14] and *O. niloticus* × *O. mossambicus* from Thailand (Table S2).[112] *Ichthyophthirius multifiliis* is considered native in most freshwater systems worldwide and it is possible but unlikely that tilapias are responsible for translocating or exacerbating infections on wild, native fish.

Mobilida (Figure 2b,c) contains the genera *Trichodina* Ehrenberg, 1830 (Figure 2d), *Trichodinella* Srámek-Husek, 1953 (Figure 2e), *Paratrichodina* Lom, 1963 (Figure 2f) and *Tripartiella* (Lom, 1959) (Figure 2g), representatives of which are parasitic and recorded from farmed tilapia. The bulk of these infections occur on the skin, fins, or gills of their hosts. A checklist of trichodinids on tilapia species is provided by Islas-Ortega et al.[113] and Basson and Van As[114]; Van As and Basson[115] provided diagnostic keys to the genera of Mobilida. *Paratrichodina africana* Kazubski et El-Tantawy, 1986, simultaneously described from *O. niloticus* in Egypt and an unidentified tilapia in Africa has been translocated on *O. niloticus* and its hybrids to Brazil,[103,105,116–118] Mexico,[103] China,[119] Egypt[120] and Argentina.[113] It is possible that the record of *P. incissa* (Lom, 1959), described from European minnows from the skin of *O. niloticus* in Vietnam and included in the country summary[67] is a misidentification of *P. africana*. At least 20 *Trichodina* species have been described from tilapia, mostly from *O. niloticus*, with some from *O. mossambicus* (Table S2). *Trichodina* spp. are reported from most areas where tilapias are farmed and on native and invasive wild fish. The taxonomy of the genus is relatively stable although some important species have been synonymised including *T. hypsilepis* (syn. *heterodentata*) Wellborn, 1967, and the record of *T. pediculus* Ehrenberg, 1831 recorded by Basson et al. (1983) was subsequently redescribed as *T. magna* Van As et Basson, 1989.[114,121] *Trichodinella epizootica* (Raabe, 1950) and an undescribed *Trichodinella* are recorded from the gills of farmed *O. niloticus* from Mexico,[113] Egypt,[120] Kenya,[17] Brazil[118] and Uganda,[17] and from *O. mossambicus* and *C. zillii* from the Philippines.[16] At least six species of *Tripartiella* are reported from *O. mossambicus* from Taiwan Province of China,[122] *O. niloticus* and hybrids from Vietnam,[67] the Philippines,[16,123] Brazil,[118,124] Mexico[103] and China[119] and *C. zillii* from the Philippines.[16,125]

At least six genera of Sessilida (Figure 2h) are recorded in tilapia, including *Ambiphrya* Raabe, 1952, *Apiosoma* Blanchard, 1885 (syn. *Scopulata* in part), *Epistylis* Ehrenberg, 1830, *Heteropolaria* Foissner et Schubert, 1977, *Riboscyphidia* Yankovskij, 1980 (syn. *Scyphidia*) and *Vorticella* (Li, 1767). *Ambiphyra ameiuri* Thompson, Kirkegarrd et Jahn, 1974 has been reported from the gills, skin and fins of *O. mossambicus* from Puerto Rico[29] and *O. niloticus* from Saudi Arabia[126]; unidentified *Ambiphrya* spp. have been noted in *O. niloticus* farmed in Indonesia,[21] Mexico,[90] Peru[127] and the Philippines.[55] At least seven *Apiosoma* spp. (Figure 2i) are described from tilapia, along with numerous records of unidentified species. *Scopulata* Viljoen et Van As, 1985 is considered a junior synonym of *Apiosoma*. *Apiosoma constricta* (Viljoen et Van As, 1985), *A. dermatum* (Viljoen et Van As, 1985) and *A. epibranchialis* (Viljoen et Van As, 1985) were described from the skin of farmed *O. mossambicus* and *C. rendalli* from South Africa,[128] *Apiosoma* sp. are reported from *O. mossambicus* from South Africa,[84] from *O. niloticus* from Costa Rica,[25] Indonesia,[21] the Philippines[13,15,16] and Israel,[14] *A. minutum* Chen, 1961 was reported from *O. niloticus* and *Oreochromis* sp. from Vietnam,[67] *A. phiala* Viljoen et Van As, 1985 was reported from *O. mossambicus* from South Africa,[128] *A. piscicola* (Blanchard, 1885) was reported from *O. aureus* and *O. mossambicus* from Puerto Rico,[29] and from *O. mossambicus* from South Africa[128] and Vietnam[67] and *A. viridis* Viljoen et Van As, 1985 was reported from *O. mossambicus* from South Africa.[128] *Epistylis colisarum* (Foissner et Schubert, 1977) was reported on the skin of *C. rendalii*, *O. aureus*, *O. mossambicus*, *O. mossambicus* × *O. urolepis* and *O. niloticus* farmed in Puerto Rico[29] and undescribed *Epistylis* spp. are recorded on *O. niloticus* from the Philippines,[16] Brazil,[74,75,77,88] Egypt[89] and Thailand[78] and on *O. mossambicus* from the Philippines[16] and South Africa.[84] The reports of *Heteropolaria* sp. from farmed *O. niloticus* from Costa Rica[25] and *Riboscyphidia* from *O. mossambicus* in South Africa[84] need confirmation due to their rarity and the potential confusion with other genera. An undescribed *Vorticella* sp. on *O. niloticus* have been recorded from Mexico,[13,129] the Philippines[15] and Saudi Arabia[126] and unidentified peritrichous ciliates have been noted on *O. niloticus* from Kenya[18] and Uganda.[17]

2.6.2 | Pathogenicity

Despite ciliates being known pathogens, there are few reports of mortality or pathology associated with these parasites on farmed tilapia. *Coptodon* spp. and *O. aureus* infected with *Chilodonella hexasticha* displayed emaciation, lethargy and some skin abrasions and the gills had extensive degeneration, necrosis and hyperplastic epithelia[85]; similar responses were noted in *O. niloticus* infected with *I. multifiliis* (Figure 2j).[109] Inflammatory responses, increased lymphocyte counts and reduced neutrophil counts were noted in *O. niloticus* infected with *Epistylis* sp.[130] Heavy infections with trichodinids may lead to lesions and sloughing and erosion of the epidermis.[127,131,132]

2.6.3 | Global translocations

Their direct life-cycles mean that ciliates are readily translocated with their hosts; discrepancies in parasite identifications can, however, complicate understanding translocations. *Ambiphrya* spp. and *Apiosoma* spp. of tilapia are recorded from several countries as noted above but, due to lack of specific identification, translocations cannot be confirmed. Evidence for the translocation of trichodinid infections is clearer. *Paratrichodina africana*, originally described from Israel and Africa, has been translocated to Bangladesh, Argentina, Brazil, Mexico and China.[105,113,116,118–120] *Trichodina acuta* Lom, 1961, *T. centrostrigeata* Basson, Van As et Paperna, 1983, *T. hypsilepis* Wellborn, 1967, *T. siluri* Lom, 1970 and *T. velasquezae* Bondad-Reantaso et Arthur, 1989 and *Tripartiella clavodonta* Basson et Van As, 1987 and *T. tilapiae* (Duncan, 1977) occur in several countries and are considered to have been introduced to the Philippines with fish from Thailand and Israel.[123] Trichodinid ciliates are likely to have been introduced broadly through fish translocations.

2.6.4 | Research

Species identities need to be confirmed using modern methods to understand the role that these hosts have had in translocating pathogens worldwide. Methods to treat infections and to render hosts safe for translocation need to be identified to minimise their impact and further spread.

2.7 | Myxozoa Grassé 1970 (Obazoa: Opisthokonta: Metazoa: Cnidaria: Myxozoa)

2.7.1 | Taxonomic identity

The myxozoans are obligately parasitic cnidarians comprising one or a few cells that have a spore comprising valve cells in the life-cycle. Myxozoans are found in marine and freshwater fish in almost all organs and show variable host and organ specificity. Life-cycles typically involve alternating vertebrate and invertebrate hosts. Often the invertebrate is an annelid or bryozoan but few life-cycles are documented. In rare cases, direct transmission is demonstrated. Myxozoans are multicellular, spore-forming obligate parasites possessing polar capsules containing extrudable polar filaments akin to cnidarian nematocysts. Identification is based on a combination of morphology (including number and arrangement of spore valves and polar capsules), size, and use of molecular tools. Methods for identification include the use of light and electron microscopy, smears and tissue squashes as well as histology for understanding tissue tropism and pathogenicity. Seven genera of myxozoans are reported from farmed tilapia; *Enteromyxum* Palenzuela, Redondo et Alvarez-Pellitero, 2002 has been transmitted experimentally[133] and two genera (*Ortholinea* Shulman, 1962 and *Triangula* Chen et Hsieh, 1984) are reported in wild tilapia. Sporadic reports of myxozoans in farmed *O. niloticus* include an undescribed intestinal *Ceratomyxa* sp. from Indonesia,[134] *Sinuolinea niloticus* Rodrigues, Francisco, Biondi et Araújo Júnior, 2016 (Figure 3a) from Brazil,[135,136] *Sphaerospora melenensis* Fomena, Marques et Boiux, 1993 (Figure 3b) and *S. tilapiae* Fomena, Marques et Boiux, 1993 (Figure 3c) from Cameroon,[137,138] and an undescribed *Sphaerospora* sp. from Kenya and Uganda.[17,19] *Oreochromis mossambicus* from China have intestinal infections of *Thelohanellus talipiae* Chen et Ma, 1998 (Figure 3d) and *Zschokkella tilapiae* Chen et Hsieh, 1984 (Figure 3e).[139] *Zschokkella nilei* Abdel-Ghaffar, El-Tokhy, Al-Quraishy, Al-Rasheid, Abdel-Baki, Hegazy et Bashtar, 2008 (Figure 3f), *Ortholinea africanus* Abdel-Ghaffar, El-Tokhy, Al-Quraishy, Al-Rasheid, Abdel-Baki, Hegazy et Bashtar, 2008 (Figure 3g), *Thelohanellus valeti* Fomena et Bouix, 1987 and *Triangula egyptica* Abdel-Ghaffar, El-Tokhy, Al-Quraishy, Al-Rasheid, Abdel-Baki, Hegazy et Bashtar, 2008 (Figure 3h) are described from wild *O. niloticus* in Egypt.[44,140–142] Undescribed *Henneguya* spp. (Figure 3i) were noted in the gills of farmed *O. niloticus* from Brazil[104] and Saudi Arabia[22]; it is not clear if they are conspecific.

The most speciose myxozoan genus is *Myxobolus* Bütschli, 1882 with over 40 species reported or described from *Coptodon*, *Oreochromis* and *Sarotherodon* spp. Some reports are considered dubious and need re-evaluating including those reported in *O. niloticus*, such as *M. ellipsoides* Thelohan, 1892, which was originally reported from tench, *Tinca tinca* (Linnaeus, 1758), in Europe[143] but was also recorded from Egypt and Cameroon.[89,144,145] The record of *M. exiguus* Thelohan, 1895, which was originally reported from mugilids in Europe[146] but noted from Vietnam,[66,67] *M. dermatobius* Ishii, 1915, originally reported in eels from Japan but noted in Egypt,[147] *Myxobolus cyprini* Doflein, 1898 originally reported on European carp species but reported in *C. zillii* and *O. niloticus* from Nigeria in an undated report by Bello-Olusoji et al., and *M. pseudodispar* Gorbunova, 1936, originally reported in cyprinids in Europe[148] but noted in Cameroon[144,145,149] also require re-evaluation. *Myxobolus* spp. are reported from tilapia cultured in Cameroon,[137,138,150,151] Israel,[152,153] Nigeria,[154–156] Senegal,[138] Benin,[157,158] Egypt,[36,65,120,159–166] Vietnam,[66,67] Ghana,[167] Kenya,[17,18] Uganda[17,23,24] and Burkina Faso[168] (Figure 3j–o). *Myxobolus* spp. occur in a range of organs with some species showing organ specificity, with the bulk of these infections being noted in *O. niloticus*.

2.7.2 | Pathogenicity

Myxozoans are recognised pathogens of fish, and several species are responsible for mortalities in farmed and wild fish. Ovaries of tilapia infected with *M. dahomeyensis* (Siau, 1971) contain a suppurating thick liquid that replaced mature oocytes and infection was considered to sterilise the host.[156,157,169] *Oreochromis niloticus* with ocular infections of *M. sarigi* (Landsberg, 1985) showed exophthalmos.[156] The gills of *O. niloticus* infected with myxozoans typically display hyperplasia or hypertrophy.[65,107,153,161] In *O. niloticus*, inflammation, degeneration and necrosis of the kidney and the spleen have been noted in *Myxobolus* spp. infections,[156,159,160,162,164] in *Sphaerospora* sp. infections of *O. niloticus* from Kenya, Uganda and Ethiopia[17] and in *Sinuolinea niloticus* infections of *O. niloticus* from Brazil.[135]

2.7.3 | Global translocations

The obligate requirement for a specific alternate host limits the likelihood that myxozoans will establish in new geographical areas. *Myxobolus agolus* Landsberg, 1985, *M. brachysporus* (Baker, 1963), *M. camerounensis* Fomena, Marques et Boiux, 1993, *M. equatoralis* (Landsberg, 1985), *M. heterosporus* (Baker, 1963; Figure 3m), *M. homeosporus* (Baker, 1963; Figure 3o), *M. israelensis* Landsberg, 1985, *M. kainjiae* (Obiekezie et Okaeme, 1990), *M. sarigi* (Landsberg, 1985; Figure 3n), *M. tilapiae* Abolarin, 1974 and *M. zillii* Sakiti, Blanc, Marques, Boiux, 1991 are widespread across Africa and Israel, but have not been translocated, probably due to the absence of a suitable intermediate host in new localities. The reports of non-tilapia myxozoans such as *M. exiguus*, *M. pseudodispar*, *M. dermatobius* and *M. ellipsoides* likely represent misidentifications rather than evidence of parasite spillback or infections in other hosts.

2.7.4 | Research

Determining the distribution of myxozoans in tilapia across their range using a combination of molecular and morphological methods and including an assessment of pathogenicity would benefit aquaculture industries by informing responses to detection. Host specificity in the intermediate host has been little studied and would be key to estimating risk of establishment in new geographical areas. Although there are limited apparently pathogenic species in tilapia, efforts should be made to identify mitigation strategies to minimise impacts including development of pharmaceutical treatments, vaccines, environmental manipulation approaches and use of functional feeds.

2.8 | Oomycetes Winter, 1897 (Now Peronosporomycetes Dick, 2001) and Ascomycota Cavalier–Smith, 1998 (SAR: Stramenopiles: Peronosporomycetes and Obazoa: Opisthokonta: Nucletmycea: Ascomycota)

2.8.1 | Taxonomic identity

Oomycetes, commonly known as water moulds, are filamentous heterotrophic microorganisms that reproduce sexually and asexually. Oomycetes are more closely related to chromophyte algae (e.g. brown algae,

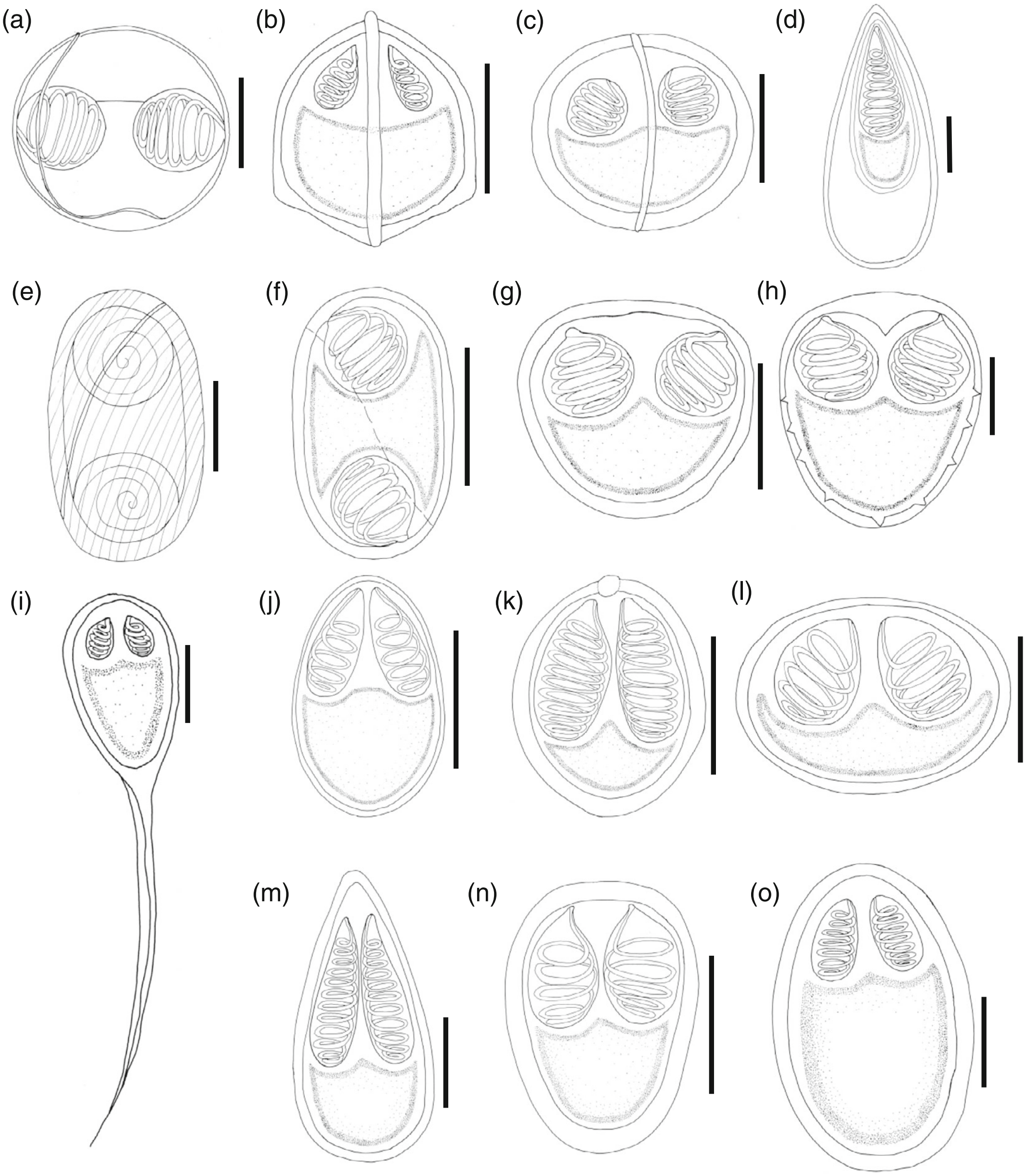

FIGURE 3 Myxozoa. Line drawings of various myxozoan spores reported in tilapia. (a) *Sinuolinea niloticus*, (b) *Sphaerospora melensis*, (c) *Sphaerospora tilapiae*, (d) *Thelohanellus talipiae*, (e) *Zschokkella tilapiae*, (f) *Z. nilei*, (g) *Ortholinea africanus*, (h) *Triangula egyptica*, (i) *Henneguya sarotherodoni*, (j) *Myxobolus bejeranoi*, (k) *M. agolus*, (l) *M. brachysporus*, (m) *M. heterosporus*, (n) *M. sarigi* and (o) *M. homeosporus*. Image (a) after Rodrigues et al. (2016), images (b, c, i, l, m, o) after Fall et al. (2000), images (k, n) after Landsberg (1985), image (d) after Chen and Ma (1998), image (e) after Matsche et al. (2020), images (f-h) after Abdel-Ghaffar et al. (2008), image (j) after Lövy et al. (2018). Scale bar: 5 μm

xanthophytes, diatoms, chrysophytes) than to the kingdom Fungi, as indicated by their heterokont ciliary pattern.[170] Most of the animal-pathogenic oomycetes belong to the subclass Saprolegniomycetidae, consisting of the orders Saprolegniales Fisch, 1892 and Leptomitales Kanouse, 1927.[171] In the Saprolegniales, species of *Saprolegnia* Nees, 1823, *Achlya* Nees von Esenbeck, 1823, *Aphanomyces* de Bary, 1860 and *Branchiomyces* Plehn, 1912 are known to infect finfish.[172–177] This group of pathogens has low host specificity and therefore, can infect a diverse range of fish.[178,179] The oomycetes are ubiquitously distributed, form motile zoospores, and their cell walls are composed of cellulose and glycans rather than chitin.[180,181] Oomycete infections in tilapia are recorded from *C. rendalli*, *C. zillii*, *O. andersonii*, *O. macrochir*, *O. mossambicus*, *O. niloticus*, *O. shiranus*, *Tilapia ruweti* (Poll et Thys van den Audenaerde, 1965) and *T. sparrmanii* (Table S2). Diseases caused by oomycetes and ascomycetes are considered second only to bacterial diseases in economic impacts on aquaculture.[182,183] Among these, diseases caused by oomycetes are more common,[184] although diseases caused by Mesomycetozoea (Ichthyosporea) and true fungi are also important.[185]

2.8.2 | Diseases caused by Oomycetes

Oomycete infections reported from tilapia include *Achlya americana* Humphrey, 1892 from *T. zillii* in Nigeria[186]; *A. bisexualis* Coker, 1927 from *O. niloticus* in Thailand[187,188] and from *O. mossambicus* in India[174]; *A. diffusa* Harvey, 1942 from *T. zillii* in Nigeria[186] and from *O. niloticus* in Thailand[188]; *A. dubia* Coker, 1923 from *O. niloticus* in Thailand[188] and *T. zillii* in Nigeria[186]; *A. hypogyna* Coker et Pemberton, 1908 from *T. zillii* in Nigeria[186]; *A. klebsiana* Pieters, 1915 from *T. zillii* in Nigeria,[186] and from *O. niloticus* in Egypt[173,189] and Thailand[188]; *A. megasperma* Humphrey, 1893 from *T. zillii* in Nigeria[186]; *A. prolifera* Nees von Esenbeck, 1823 from *T. zillii* in Nigeria[186] and *O. niloticus* in Thailand[188]; *A. proliferoides* Coker, 1923 from *O. niloticus* in Egypt[189] and *O. mossambicus* in India[174]; and *A. racemosa* Hildebrand, 1867 from *T. zillii* in Nigeria.[186] It is important to mention that most *Achlya* infections have been reported from the skin and only a few cases regarding infection of the fins. In addition to infection with *Achlya* sp., there are reports of infection with *Allomyces arbuscular* Butler, 1911 from *T. zillii* in Nigeria[186]; *Dictyuchus monosporus* Leitgeb, 1870 from *O. niloticus* in Egypt[189]; *D. sterile* Coker, 1923 from *T. zillii* in Nigeria[186] and *O. niloticus* in Egypt[189]; and a species of *Pythiopsis* de Bary, 1888 from *O. mossambicus* in India.[174] Infections with *Saprolegnia* sp. have been reported from tilapia and these include: *S. aenigmatica* Sandoval-Sierra et Diéguez-Uribeondo, 2015 from an undescribed species of tilapia in Brazil[190]; *S. diclina* Humphrey, 1892 from *O. mossambicus* in India,[174] from *O. niloticus* in Egypt[173,189] and *T. zillii* in Nigeria[186]; *S. ferax* Kützing, 1843 from *O. niloticus* in Egypt[189,191] and from *T. zillii* in Nigeria[186]; *S. litoralis* Coker, 1923 from *T. zillii* in Nigeria[186]; and *S. parasitica* Coker, 1923 from *O. mossambicus* in India,[174] from *O. niloticus* in Egypt,[175,176,191] and from *T. zillii* in Nigeria.[186] In addition to these, there are also reports of infection by an undetermined species of *Saprolegnia* Nees, 1823 from *O. niloticus* in Egypt[189,192] and of *Thraustotheca clavata* Humphrey, 1892 from *T. zillii* in Nigeria.[186]

Infection with *Aphanomyces laevis* de Bary, 1860 has been reported from *O. mossambicus* in India,[174] from *O. niloticus* in Egypt[173,189] and *T. zillii* in Nigeria[186] whereas there is a report of infection with *A. stellatus* de Bary, 1860 from *T. zillii* in Nigeria.[186] As with the *Achlya* species, *A. laevis* infections are reported from the skin. Additionally, *A. invadans* David et Kirk, 1997, the causative agent of epizootic ulcerative syndrome (EUS) has been reported from *C. rendalli* in Namibia, Zimbabwe and Botswana; *O. andersonii* from Namibia, Zambia and Zimbabwe; *O. macrochir* from Namibia; *O. mossambicus* from Zimbabwe; *O. shiranus* from Malawi; and *T. sparmanii* from Namibia and Botswana.[177,193] The *A. invadans* infections are generally observed in the skin and the underlying musculature of the infected fish. Importantly, *O. niloticus* is resistant to infection with *A. invadans*.[194] Other reports include those of *Branchiomyces demigrans* Wundsch, 1929 and *B. sanguinis* Plehn, 1912 from the gills of *O. niloticus* from Egypt,[195,196] whereas infection by an undetermined species of *Branchiomyces* Plehn 1912 has been reported in the gills of *O. niloticus*, *O. mossambicus* and *O. aureus* from Europe, Asia, the Middle East, Australia and North America, and also in *O. niloticus* × *O. mossambicus* hybrids and *O. niloticus* × *O. aureus* hybrids from Israel (Table S2).[172,197]

Oomycetes are transmitted by zoospores released from zoosporangia that develop from the hyphae in fish tissues at the body surface. A lack of nutrients and/or a sudden drop in temperature induces sporulation.[205] Zoospores can encyst on a host, forming primary cysts and subsequently releasing secondary zoospores,[206] which are more motile than primary zoospores and crucial for infection.[207] Zoospores exhibit positive chemotactic responses to amino acids in exudates and metabolites from tissues of susceptible hosts.[208,209] Subsequent contact of the zoospore with the host triggers encystment, which in turn initiates germination and results in infection. During infection, oomycetes secrete effector proteins that modulate its host's immune responses or inhibit the host's cell functions to the advantage of the pathogen.[210–215] Species of the genera *Saprolegnia* and *Achlya* infect the gills, skin, fins and eggs of fish (Figure 4a,c,d).[187,206,216,217] The infection progresses to the development of large wounds on the body surface leading to impaired osmoregulation and haemodilution; extensive lesions in the gills cause respiratory failure; both can lead to mortality. In susceptible fish, *A. invadans* hyphae invade the fish skin and skeletal muscles causing ulceration, often resulting in death.[218–220] In resistant fish, such as *O. niloticus*, *A. invadans* hyphae are unable to proliferate and lesions are restricted to the site of infection (Figure 4b). Conversely, infections with species of *Branchiomyces* which primarily affect the gills (Figure 4e), result in respiratory distress with associated high mortalities,[221] particularly when infections occur in waters exceeding 20°C.[172]

Ascomycetes fungi produce non-motile spores with a chitinous cell wall, which can survive in unfavourable conditions, and the resistance of the spores is an important adaptation strategy to infect susceptible hosts.[242] These spores play a crucial role in dispersal between hosts and dissemination within hosts.[185] Infection with species of *Fusarium* Link, 1809 causes skin ulcers or can become systemic causing kidney and brain necrosis.[180,243] In *O. niloticus*, infection with *F. oxysporum* (Schlecht. emend. Snyder et Hansen, 1940) has been reported to be associated with subcutaneous mycoses.[244] *Candida albicans* Berkhout, 1923 has been reported to colonise the epithelial surface of fish, expanding and invading tissues. During the invasion, morphogenesis of the pathogen from ovoid yeast to a filamentous hypha is important in causing tissue damage and mortality.[245] *Aspergillus* Micheli, 1729 infection in the gills causes damage to gill lamellae with subsequent respiratory distress,[246] but systemic infections from feed contaminated with *Aspergillus* sp. primarily present with high mortality.[247] *Paecilomyces* sp. infections commence with ingestion of the fungal spores in the water by the fish.[248] *Purpureocillium lilacinum* (Thom, 1910) infection has been associated with tilapia wasting disease in wild and farmed tilapia in Puerto Rico.

2.8.3 | Global translocations

Oomycetes and ascomycote fungi are emerging pathogens with increasing geographic distribution.[222,223] These pathogens have a broad host range including nonfish hosts, and this could be responsible for their wide dissemination.[185] A major contributor to the global spread of oomycetes and ascomycotes is international trade in live aquatic animals.[224,225] *Aphanomyces invadans* can be transported and introduced along with resistant exotic hosts such as *O. niloticus*, introducing *A. invadans* to new ecosystems.[171] This pathway likely played a major role in the spread of *A. invadans* in Africa.[226,227] The transport water containing infective spores is further regarded as a pathway for dispersal of this pathogen.[226] Birds have been speculated to play a role in spread of *A. invadans* infection in South Africa.[228] The movement of infected fish and/or encysted oomycetes through interconnected water bodies has increased the geographic range of the pathogen,[226] and boats and contaminated fishing equipment have mechanically spread of the oomycete spores to unaffected regions.[227,228] Once introduced to a new ecosystem, the low host specificity of oomycetes and fungi increases the likelihood that disease outbreaks will occur in native species that have not been recorded as hosts for these pathogens.[185,229]

2.8.4 | Research

Oomycete and ascomycote diseases are difficult to control. The use of malachite green, considered the most effective treatment until the 1980s, was proscribed in most countries because of its carcinogenicity and persistent residues. Formalin immersion treatments are considered effective but may also be proscribed by regulatory processes.[185] There is therefore an urgent need to enhance our understanding of the basic biology of these pathogens to develop alternative methods to control these diseases. It is unclear if oomycetes can infect only wounded or immunocompromised animals or if they can cause infection in healthy fish.[209] In addition, the survival of oomycetes outside the host and during periods between outbreaks is poorly understood. It is also unknown if fish that recover can act as reservoirs of infection, if oomycetes can survive in sun-dried or smoked fish, or if the trade of these fish products can spread infections.[226,230] Genomic studies have mainly focussed on plant–pathogenic oomycetes, and little is understood about oomycete pathogens of aquatic animals. Genomic and proteomic studies of *S. parasitica* and *A. invadans* provide insights into molecular pathogenesis, particularly virulence factors and host gene expression.[212,213,231,232] The identification of complementary genes and proteins involved in the immune response of fish would provide an understanding of how to prevent oomycete diseases through pathogen-informed programmes that breed for resistance. Elucidating the role of virulence genes and identifying pathogen proteins that manipulate host immune systems would aid development of novel control strategies including vaccines.[209,233] It is important to mention that surveillance is key for early detection and disease control. Therefore, surveillance of oomycete and ascomycote pathogens should include natural habitats and reservoirs of infection. Since these diseases are associated with declines in wild fish populations, therefore, it is important to understand their ecological impacts for improving conservation strategies.[179,233] It is, furthermore, important to identify environmental drivers of fungal and oomycete diseases for better understanding of the ecological risks of disease emergence.[234]

2.9 | Mesomycetozoea Mendoza et al., 2002 (Now Ichthyosporea Cavalier–Smith, 1998) (Obazoa: Opisthokonta: Holozoa: Ichthyosporea)

2.9.1 | Taxonomic identity

The Mesomycetozoea (or Ichthyosporea) are an enigmatic group of parasitic organisms that are phylogenetically grouped with the fungi.[4,198] Mesomycetozoans have spherical spores and occur in a range of tissues. Methods for identification, along with a host–parasite list, are included in Rowley et al.[199] The group includes recognised animal pathogens including *Rhinosporidium seeberi* (Wernicke, 1903), species of *Ichthyophonus* Plehn et Mulsow, 1911, *Sphaerothecum destruens* Arkush, Mendoza, Adkison et Hedrick, 2003 and *Dermocystidium* Pérez, 1908. *Dermocystidium* spp. are pathogens of fish and are typically identified based on a combination of culture, tissue tropism, host identity, morphology and molecular techniques.[199] An undescribed *Dermocystidium* sp., which may represent more than one species, is reported from a range of organs in *O. niloticus* and *O. aureus* × *O. niloticus* cultured in Brazil, Egypt and Israel.[200–203] *Dermocystidium aegyptiacus* El-Mansy, 2008 was described from the intestines of *O. niloticus* farmed in Egypt (Figure 1a).[204]

2.9.2 | Diseases caused by Mesomycetozoea (Ichthyosporea)

Mesomycetozoeans are parasitic opisthokonts with large spherical or ovoid spores. Infection with *Ichthyophonus hoferi* Plehn et Mulsow, 1911 is principally transmitted by plasmodia which are formed by the fragmentation of multinucleated schizonts, the most common stage of *Ichthyophonus* in live fish.[235] The pathogen mainly affects internal organs, namely liver, kidneys, spleen and heart (Figure 4f).[236] Infection causes enlargement and the formation of raised nodules in these organs.[221,237] The resulting tissue damage can cause high mortality.[238,239] In case of infection with *Dermocystidium* sp., the zoospores encyst and enlarge to form spherical multinucleate cells with distinct wall inside the host,[198] leading either to gross cutaneous cysts[240,241] or chronic systemic lesions.[204]

2.9.3 | Pathogenicity

Dermocystidium sp. infections of the gills cause hyperplasia and fusion of the gill lamellae, although they do not appear to cause mortality.[202] Mortalities of *O. aureus* × *O. niloticus* cultured in Israel were associated with a *Dermocystidium* sp. infection in the liver which manifested as focal granulomas that occasionally contained a necrotic core.[200] Lesions

FIGURE 4 Oomycete and fungal diseases of tilapias. (a) *Oreochromis niloticus* showing cotton-wool like growths on the body surface following an experimental infection with *Saprolegnia parasitica* Coker, 1923 (image courtesy of Shimaa Ali, WorldFish, Egypt). (b) *Oreochromis niloticus* showing a superficial lesion following infection with *Aphanomyces invadans* (image courtesy of Supranee Chinabut, Thailand). (c) Gross appearance of *O. niloticus* infected with *Achlya* Nees von Esenbeck, 1823, showing ulcers and cotton-like growths on the body surface and caudal peduncle. (d) *Oreochromis niloticus* with prominent hyphal growth on the head, dorsal fin and caudal peduncle following experimental infection with *Achlya klebsiana* Pieters, 1915. Images (c) and (d) courtesy of Panchai, Nakhon Ratchasima Rajabhat University and Hanjavanit, Khon Kaen University, Thailand. (e) Fish gills displaying a marble appearance representing an advanced stage of *Branchiomyces* Plehn, 1912 infection. (f) *Oreochromis niloticus* with an enlargement of the liver with dark grey nodules infected with *Ichthyophonus* Plehn et Mulsow, 1911. Figures (e) and (f) provided courtesy of Heba H. Mahboub and Adel A. Shaheen, Zagazig University, Egypt)

were limited to the liver, unlike other *Dermocystidium* sp. infections. Systemic *Dermocystidium* sp. infection of *O. niloticus* was described by Mahboub and Shaheen,[203] including field sampling and experimental challenges. Infected animals were sluggish, darkened and exhibited scale loss and ulceration, as well as skin and fin damage. Multifocal cysts with minimal inflammatory response were observed in the liver, spleen, stomach and intestines. Ruptured cysts distributed spores into surrounding tissues, with concomitant infiltration of macrophages and lymphocytes.

2.9.4 | Global translocations

The lack of information on species identity makes it impossible to identify likely translocations of *Dermocystidium* spp. with tilapia. Given the variable tissue tropism and limited records, it is unlikely that *Dermocystidium* spp. have been translocated widely with tilapia. These parasites could be translocated to new localities, however, and, particularly for the pathogenic *Dermocystidium* sp. described by Mahboub and Shaheen,[203] there is disease risk associated with its translocation.

2.9.5 | Research

To mitigate risks and improve management, research should aim to improve control, confirm species identities, and assess if transboundary *Dermocystidium* spp. movements have occurred.

2.10 | Microsporidia Balbiani, 1882 (Obazoa: Opisthosporidia: Microsporidia)

2.10.1 | Taxonomic identity

Microsporidia are obligate spore-forming intracellular parasites whose spores contain an extrusion apparatus that has a coiled polar tube ending in an anchoring disc at the apical part of the spore. Molecular data identify microsporidians as basal fungi.[249,250] Their proliferation in cells, undergoing merogonous and sporogonous development leading to the production of thick-walled spores, results in an enlarged cell termed a xenoma. Generic and specific identification is based on morphological characteristics of the coiled polar filament, the number of nuclei and spore dimensions[251,252] and molecular data of 16S rDNA sequences.[253,254] While biorefringent spores can be detected in haemotoxylin and eosin sections, quicker methods that negate the need for tissue embedding and sectioning, including the use of Giemsa or phloxin B can facilitate the rapid detection of spores in fresh material.[255,256] Spores range from 1 to 20 μm in length and their differentiation from cellular debris in some preparations is difficult. Calcofluor white specifically binds to chitin in the spore wall, which, with fluorescence microscopy, facilitates their identification in host tissues.[257] Spores can also be identified using immunohistochemistry[258] and/or in situ hybridization.[259–261]

Microsporidian infections from tilapia in aquaculture include *Loma camerounensis* Fomena, Coste et Bouix, 1992 from the intestinal tract of farmed *O. niloticus* in Cameroon[262]; from farmed *O. niloticus* in Kenya[20] and from the kidneys of *O. aureus* and hybrids in Israel[200]; systemic infection with *Neonosemoides* [syn. *Nosemoides*] *tilapiae* Faye, Toguebaye et Bouix, 1996 in wild *C. zillii* and *S. melanotheron* in Benin[263,264] and *Nucleospora braziliensis* Rodrigues, Francisco, David, da Silva et Araújo Júnior, 2017 infecting wild and farmed *O. niloticus* in São Paulo State, Brazil.[265] Microsporidian infections are recorded from other tilapia including a species of *Glugea* Thélohan, 1891 in invasive *O. niloticus* in Indonesia[266]; a species of *Pleistophora* Gurley, 1893 in the swimbladder of wild *Haplochromis angustifrons* Boulenger, 1914 and *Haplochromis elegans* Trewavas, 1933 from Uganda[19,201,267]; *N. tilapiae* from the stomach of wild *Coptodon guineensis* (Günther, 1862) cited as *T. guineensis* from Senegal,[264] as a systemic infection from the same host from Benin[263]; and in wild *Coptodon nyongana* (van den Audenaerde, 1971) cited as *T. nyongana* from Benin, Cameroon and Senegal.[262] Details of the host–parasites records of tilapia are summarised in Table S2. Taxonomic keys to Microsporidia are provided by Larsson,[268,269] Sprague et al.,[270] Canning et al.[271] and Cali et al.[272] These cases serve as a useful resource for facilitating identification and supporting the management of infections following the discovery of further microsporidian infections of cultured tilapia.

2.10.2 | Pathogenicity

Records of microsporidians in tilapia mostly note only their presence and seasonal prevalence in hosts, but Paperna[200] reported that *Pleistophora* sp. infections in *H. angustifrons* and *H. elegans* caused thickening of the swimbladder walls which contained abundant pansporoblasts. Rodrigues et al.[265] described *N. braziliensis* at 87%–100% prevalence in *O. niloticus* (av. 230–540 g) reared in reservoirs in Brazil. These infections caused xenomas in the gills with hyperplasia and telangiectasis and skin melanisation and inflammation, exophthalmos, stomach congestion with marked inflammatory responses associated with lesions, necrosis and liquefaction of infected muscle and kidney, hepatomegaly, splenomegaly and hepatic haemorrhages.[265] Sakiti and Bouix[263] observed *N. tilapiae* infections in *C. zillii*, *T. guineensis* and *S. melanotheron* and found xenomas in the gills and in the mesenteries, gut wall and liver, but without apparent clinical effect on the fish.

2.10.3 | Global translocations

There are insufficient data to understand transboundary movement of microsporidian infections with tilapia translocations. *Nucleospora braziliensis* is not reported in Africa, and a horizontal transfer from a resident fish in Brazil is the most likely source of infection, but Rodrigues et al.,[265] did not examine resident fish in the reservoirs.

2.10.4 | Research

Research on microsporidian infections of fish centres on the development of diagnostic methods for detection at low abundance that might be overlooked by histology, understanding routes of transmission and factors facilitating infection, development of *in vivo* challenge models to better understand host–parasite interactions, and the efficacy of management and control strategies.[273–275] There are few effective chemotherapeutic agents for treatment of microsporidians. A range of products have been assessed in fish including albendazole,[276] beta-glucans,[277] monensin[278] and quinine hydrochloride[279] against *L. salmonae*, and fumagillin and toltrazuril against *Glugea anomala* (Moniez, 1887).[280] While feed trials with monensin significantly reduced xenoma number, the effective dose of 1000 ppm for up to 3 weeks is above the *Oncorhynchus mykiss* (Walbaum, 1792) 96-h LC_{50} of 1.88 mg.[281] Trials with albendazole, beta-glucans and fumagillin also reduced the abundance of xenomas, while quinine hydrochloride delayed xenoma formation, and toltrazuril destroyed xenomas. Worldwide, there are, however, no veterinary medicines licenced for use against microsporidians in aquaculture. An experimental vaccine using freeze-killed spores of a low-virulence strain of *Loma salmonae* (Putz, Hoffman et Dunbar, 1965) given intraperitoneally, resulted in 85% fewer xenomas in the gills of *O. mykiss*.[282] The study indicates that non-treatment based approaches can be developed for control of microsporidian infections in fish.

2.11 | Monopisthocotylea Odhner, 1912 (Monogenea Carus, 1863) (Obazoa: Opisthokonta: Metazoa: Platyhelminthes)

Monogeneans are flatworms, primarily ectoparasitic on fish, characterised by possessing a haptor (opisthaptor), a specialised structure that uses hooks or clamps to maintain attachment of the parasite to the host.

2.11.1 | Taxonomic identity

Species of the genus *Gyrodactylus* von Nordmann, 1832 are small (100–200 μm long), transparent, ectoparasitic monogeneans that colonise the external surfaces and buccal-opercular cavities of their hosts (Figures 5–7a). The sclerites of the haptor include a pair of anchors (hamuli) linked by a thin dorsal bar which articulate over an

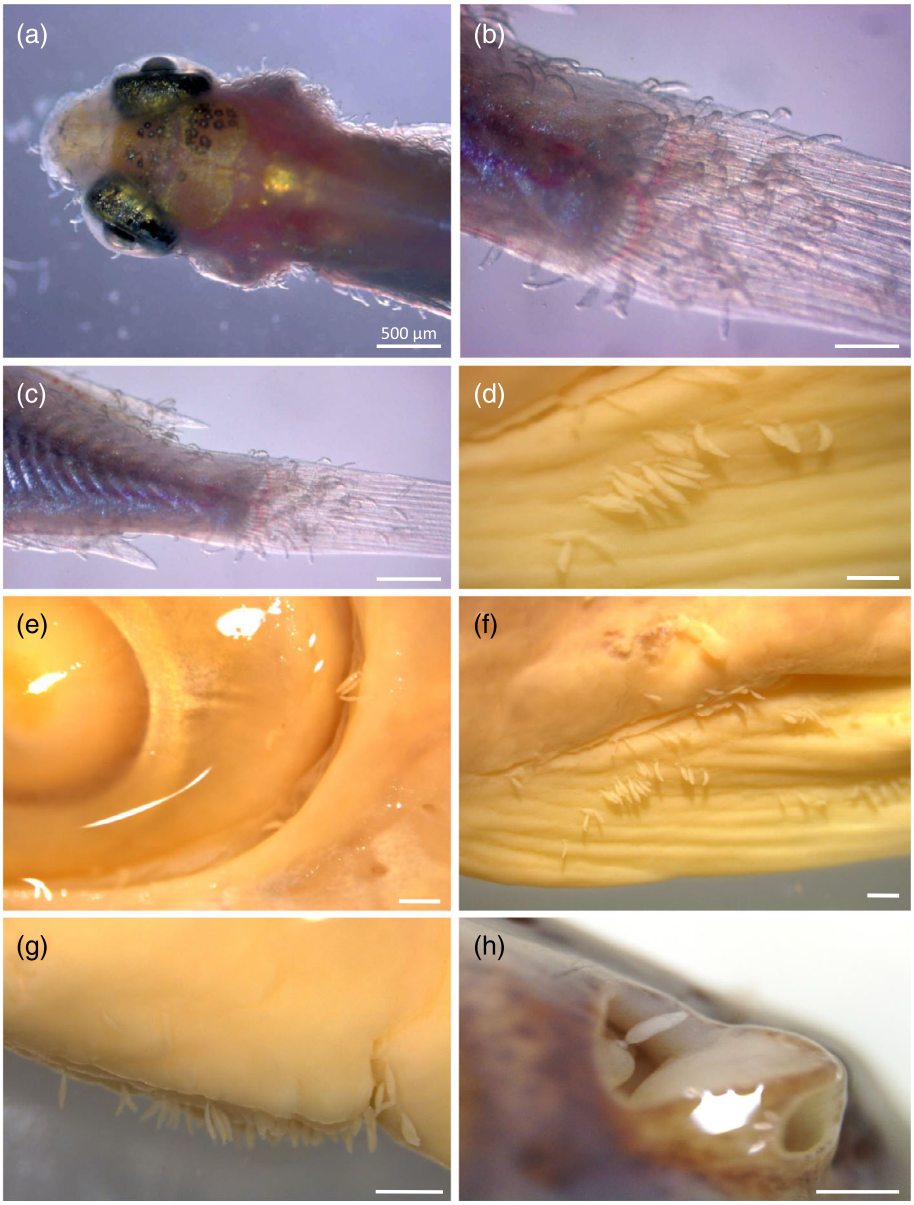

FIGURE 5 Light microphotographs of *Oreochromis niloticus* larvae (~2 cm) with a heavy infection of *Gyrodactylus cichlidarum* Paperna, 1968. (a) Head, (b) Caudal fin, (c) Caudal peduncle, (d, f), Eye, (e), Anal fin, (g) Ventrum and (h) Nares. All scale bars = 500 μm

approximately triangular-shaped ventral bar (Figure 7b–d). Eight pairs of marginals hooks (Figure 7e,f), typically of one morphological type and size, which are distributed around the periphery of the haptor function as the principal means of attachment. *Gyrodactylus* do not have eye spots, have a bi-lobed head with a pair of head organs that aid in anterior attachment to the host and are epidermal grazers. *Gyrodactylus* spp. notably are viviparous polyembryonous and progenetic; the large uterus contains an embryo at birth. Individuals develop a male copulatory organ (a muscular organ armed with small spines) after their first parturition. At least 15 species of *Gyrodactylus* infect tilapia (Table S2; Figure 8)—although this undoubtedly represents an underestimate given that seven new species have been described since 2000,[283–287] that cichlids and gyrodactylids are speciose, and that tilapia–*Gyrodactylus* host–parasite associations have not been extensively studied in Africa. Two *Gyrodactylus* spp. are widely distributed and associated with aquaculture mortalities: *Gyrodactylus cichlidarum* Paperna, 1968 described from *S. galilaeus* in Ghana, but now with a global distribution on numerous hosts,[287,288]; and *G. yacatli* García-Vásquez, Hansen, Christison, Bron et Shinn, 2011 described from *Oreochromis* spp. and *Vieja fenestrata* (Günther, 1860) in Mexico, but originating in Africa, and recorded from Kenya, and possibly Zimbabwe and China.[286,287]

Dactylogyrids possess a haptor with two pairs of anchors or hamuli, seven pairs of marginal hooks and four eyespots (Figure 9a); the configuration of the haptoral elements, the morphological shape of these and the reproductive organs (i.e., vagina and male apparatus) facilitate the identification of genera and species. They infect the gills and intestine of their hosts. There are 72 species of dactylogyrid

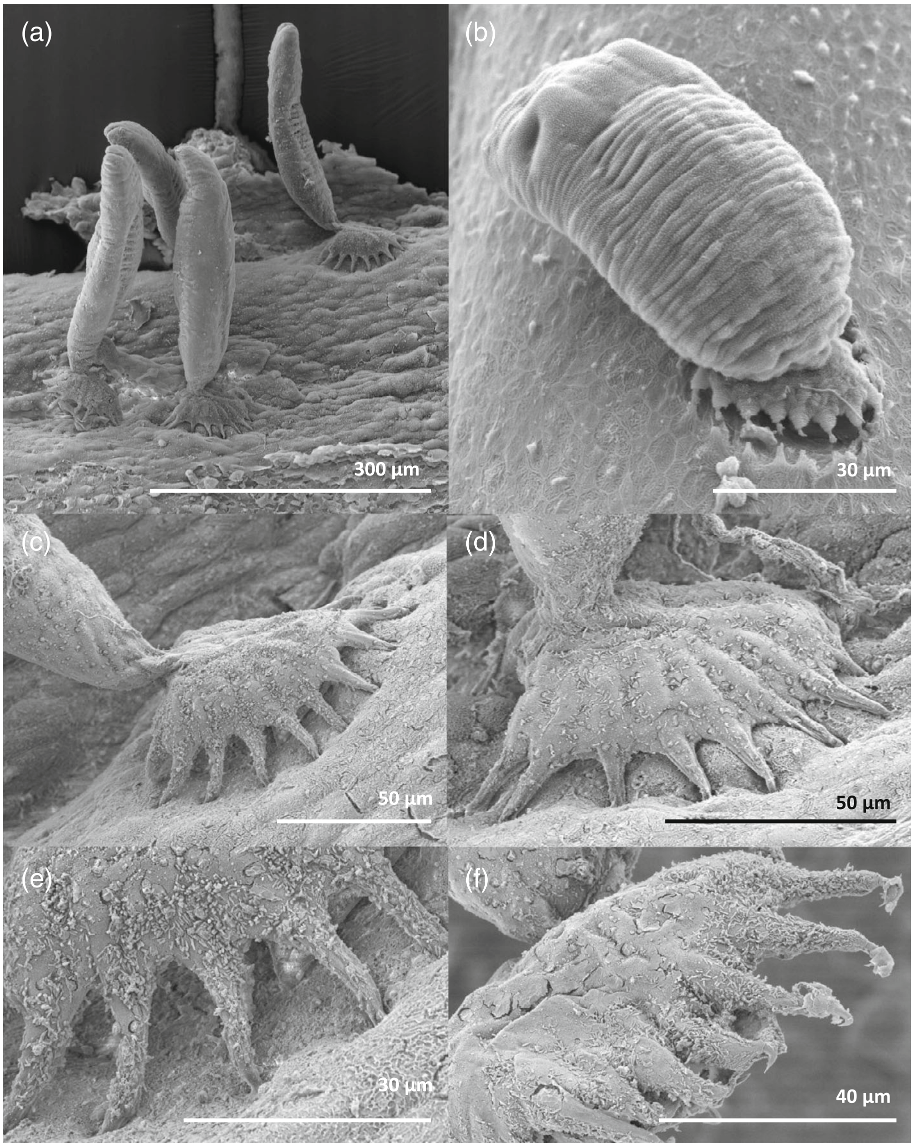

FIGURE 6 Scanning electron micrograph of *Gyrodactylus cichlidarum* Paperna, 1968. (a–e) Attachment on fish skin; (f) Haptoral structure of the worm after detachment from *Oreochromis niloticus*. Images a, c-f courtesy of Mrs Greta Hanako Rosas Saito, Instituto de Ecología A.C., Xalapa, Mexico. Image b courtesy of Giuseppe Paladini, Institute of Aquaculture, University of Stirling, Scotland, UK.

monogeneans described from tilapia (Figure 9a–i) in the genera *Cichlidogyrus* Paperna, 1960 (Figure 9a–d), *Enterogyrus* Paperna, 1963 (Figure 9f) and *Scutogyrus* Pariselle et Euzet, 1995 (Figure 9e). Morphological identification of dactylogyrids is typically based on the hard parts of the haptor (see below) and copulatory organs (Figure 9g–i).

The gill-infecting dactylogyrids of tilapia belong to *Cichlidogyrus* and *Scutogyrus*, and are characterised by a haptor bearing two pairs of anchors (whereas there is only one pair in gyrodactylids), a V-shaped ventral transversal bar (in contrast to the ventral bar of members of *Gyrodactylus*, which possesses a membrane), a dorsal transversal bar with two auricles (in contrast to the simple dorsal bar in *Gyrodactylus*) and seven pairs of marginal hooks (compared to 8 in *Gyrodactylus*; Figure 9c–e, g). Cruz-Laufer et al.[289] identified that numerous gill-infecting species have been co-introduced outside continental Africa and are reported in the peer-reviewed literature from Latin America, Asia, Australia or Madagascar. Five of these have been mentioned as co-introduced in at least 15 publications. Notable species that have been translocated include *C. halli* (Price et Kirk, 1967), *C. sclerosus* Paperna et Thurston, 1969, *C. thurstonae* Ergens, 1981, *C. tilapiae* Paperna, 1960 and *Scutogyrus longicornis* (Paperna et Thurston, 1969). The three species for which only one co-introduction is reported outside Africa have a limited natural distribution: *C. levequei* Pariselle et Euzet, 1996 on *Coptodon coffea* (Thys van den Audenaerde, 1970) in Guinea is reported from *O. niloticus* in China[290]; *C. quaestio* Douëllou, 1993 in Lake Kariba, Zimbabwe[291] and the Congo Basin[292] is reported from *O. niloticus* introduced into Mexico[129]; and *C. rognoni* Pariselle, Bilong Bilong et Euzet, 2003 from Senegal[293] and from cultured tilapia in Côte d'Ivoire[293] is reported from *O. niloticus* introduced into Brazil. Their limited distribution decreases their likelihood of translocation.[294]

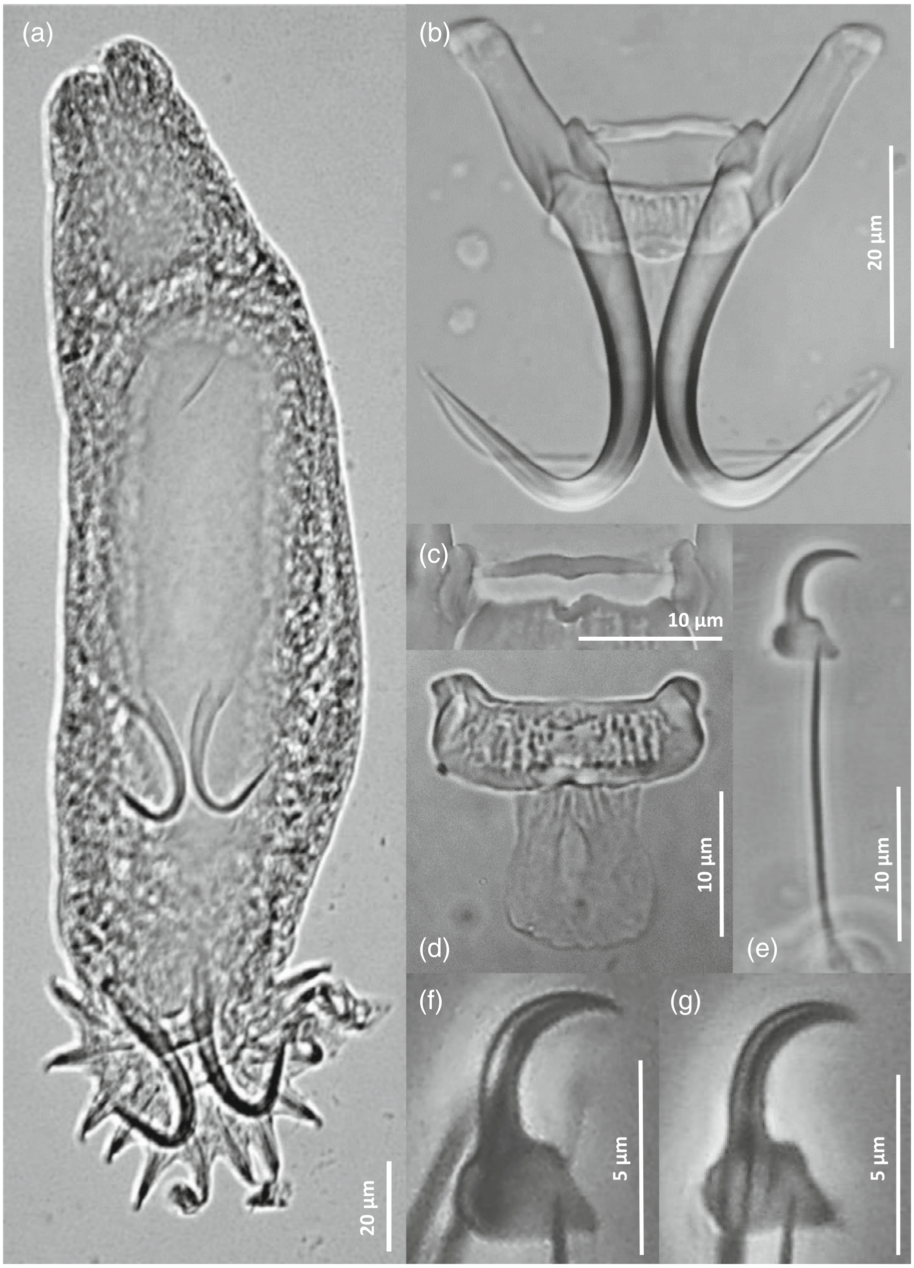

FIGURE 7 Light microphotographs of *Gyrodactylus cichlidarum* from *Oreochromis niloticus*. (a) Whole mount, (b) Hamuli, Ventral and dorsal bars, (c) Dorsal bar, (d) Ventral bar, (e) Marginal hook and (f, g) Marginal hook sickles

Species of *Enterogyrus* infect the stomach of their hosts and can be identified by the shape and configuration of their haptoral elements (Figure 9f).[295,296] They possess seven pairs of marginal hooks, a simple transverse bar, and two pairs of anchors of differing morphologies—the smaller-sized ventral anchors have prominent inner and outer roots, while the significantly larger dorsal anchors have a morphology closely resembling that of the marginal hooks. Of the 12 described species, nine infect tilapia. Some of these species have been co-introduced with tilapia outside Africa, such as *E. cichlidarum* Paperna, 1963,[297] *E. coronatus* Pariselle, Lambert et Euzet, 1991, *E. foratus* Pariselle, Lambert et Euzet, 1991 and *E. malmbergi* Bilong Bilong, 1988[298] in Brazil and Mexico[299]; and *E. coronatus* and *E. malmbergi* in China[300] and Cuba.[301]

Pariselle and Euzet[295] provided the most recent morphological identification key for dactylogyrid monogeneans including those parasitising tilapia, but numerous species have been described subsequently.[302] *Cichlidogyrus mbirizei* Muterezi Bukinga, Vanhove, Van Steenberge et Pariselle, 2012 is the only dactylogyrid described after Pariselle and Euzet[295] that commonly infects commercially important tilapia and has been translocated broadly (Table 1).[300,303–305] New host–parasite records continue to be made from wild populations of commercially important tilapia. *Cichlidogyrus papernastrema* Price, Peebles et Bamford, 1969 was recorded from native *C. rendalli* in the Upper Congo Basin and *C. berradae* Pariselle et Euzet, 2003, *C. cubitus* Dossou, 1982 and *C. flexicolpos* Pariselle et Euzet, 1995 were

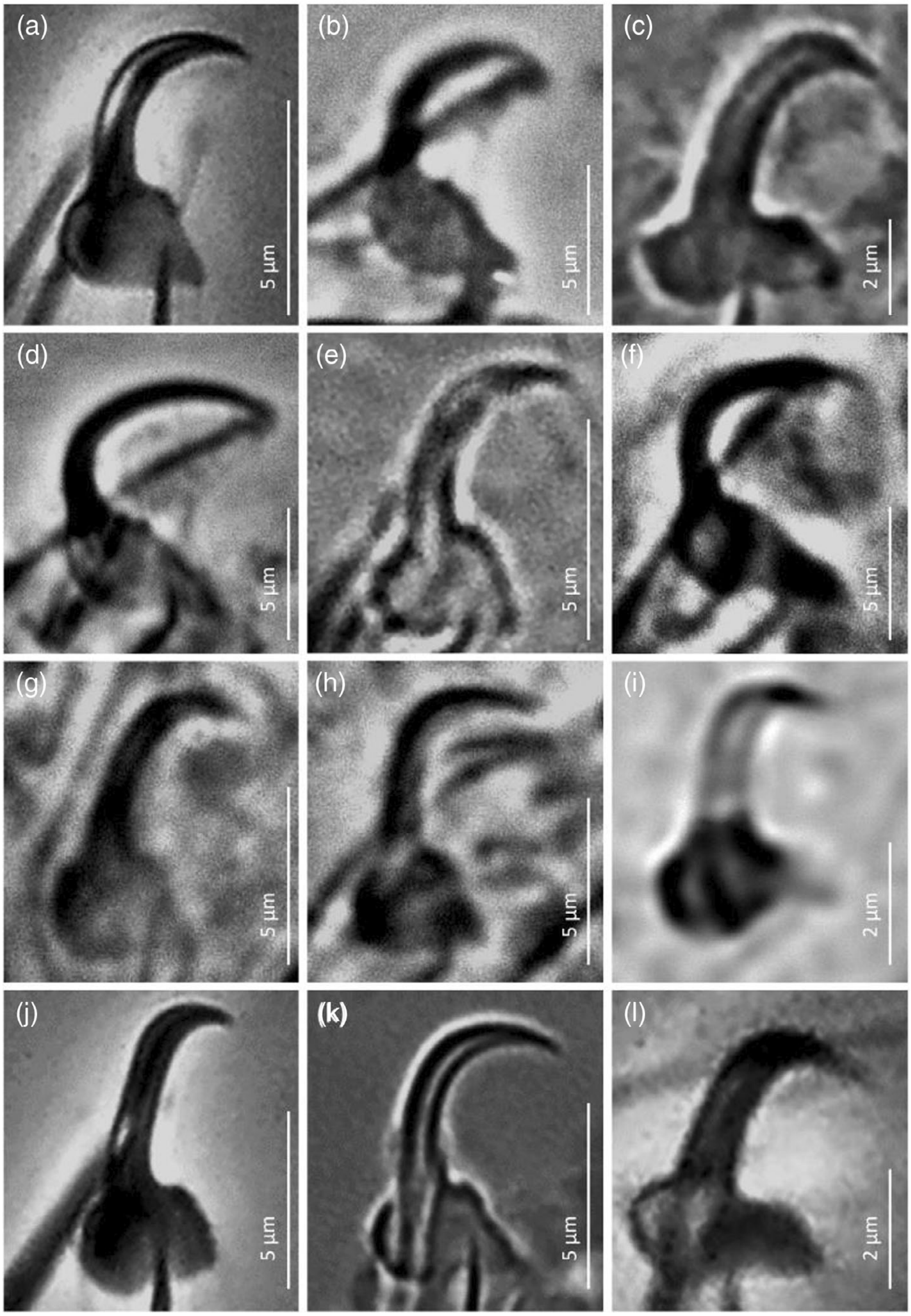

FIGURE 8 Light microphotographs under phase contrast of the marginal hook sickles of *Gyrodactylus* species infecting different species of tilapia. (a) *Gyrodactylus cichlidarum* Paperna, 1968. (b) *Gyrodactylus ergensi* Prikřylová, Matějusová, Musilová et Gelnar, 2009. (c) *Gyrodactylus hildae* García-Vásquez, Hansen, Christison, Bron et Shinn, 2011. (d) *Gyrodactylus malalai* Prikřylová, Blažek et Gelnar, 2012. (e) *Gyrodactylus niloticus* Cone, Arthur et Bondad-Reantaso, 1995 (syn. *G. cichlidarum*). (f) *Gyrodactylus nyanzae* Paperna, 1973. (g) *Gyrodactylus occupatus* Zahradníčková, Barson, Luus-Powell et Prikřylová, 2016. (h) *Gyrodactylus parisellei* Zahradníčková, Barson, Luus-Powell et Prikřylová, 2016. (i) *Gyrodactylus shariffi* Cone, Arthur et Bondad-Reantaso, 1995. (j) *Gyrodactylus shinni* García-Vásquez, Pinacho-Pinacho, Guzmán-Valdivieso, Calixto-Rojas et Rubio-Godoy, 2021. (k) *Gyrodactylus ulinganisus* García-Vásquez, Hansen, Christison, Bron et Shinn, 2011. (l) *Gyrodactylus yacatli* García-Vásquez, Hansen, Christison, Bron et Shinn, 2011

recorded from introduced *C. rendalli* in the Lower Congo Basin.[292] New species also continue to be described from wild populations of economically important tilapia, such as *Enterogyrus mashegoi* Luus-Powell, Madanire-Moyo, Matla et Přikrylová, 2020 and *E. multispiralis* Luus-Powell, Madanire-Moyo, Matla et Přikrylová, 2020 from the stomach of *O. mossambicus* in South Africa,[296] and *C. flagellum* Geraerts et Muterezi Bukinga, 2020, *C. lobus* Geraerts et Muterezi Bukinga, 2020 and *C. maeander* Geraerts et Muterezi Bukinga, 2020 from the gills of *T. sparrmanii* in the Democratic Republic of Congo.[306] Even for well-studied tilapia species, further dactylogyrid diversity is

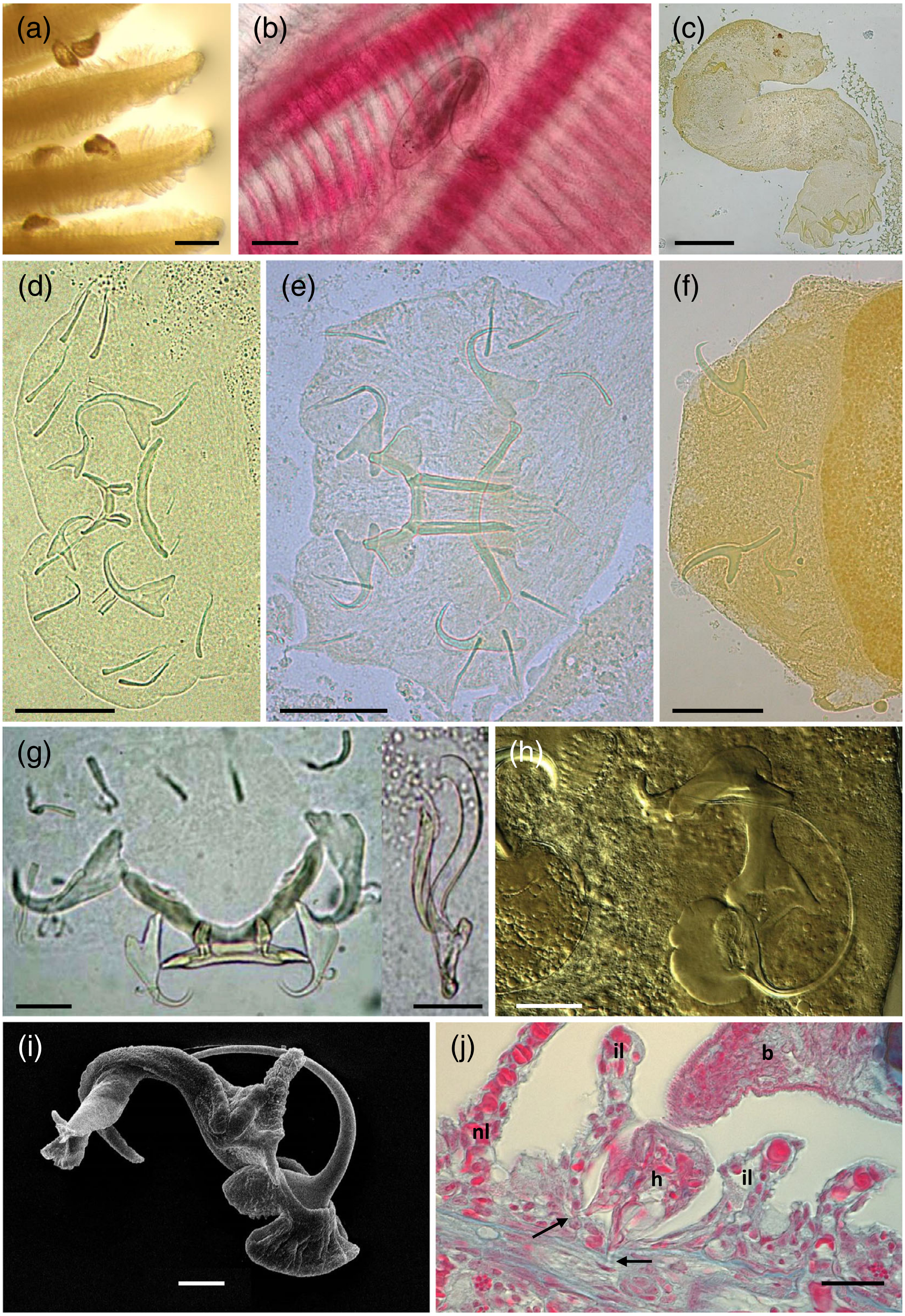

FIGURE 9 (a) *Cichlidogyrus* spp. on the gills of *Sarotherodon melanotheron* (photo A. Pariselle). (b) *Cichlidogyrus* Paperna, 1960 sp. on the gill of *Oreochromis niloticus* from Thailand (photo T. Limakom). (c) *Cichlidogyrus dossoui* Douellou, 1993 (in toto, glycerine ammonium picrate (GAP) medium) (photo A. Pariselle). (d) *Cichlidogyrus tiberianus* Paperna, 1960 (haptor, GAP medium) (photo A. Pariselle). (e) *Scutogyrus gravivaginus* (Paperna et Thurston, 1969) (haptor, GAP medium) (photo A. Pariselle). (f) *Enterogyrus malmbergi* Bilong Bilong, 1988 (haptor, GAP medium) (photo A. Pariselle). (g) *Cichlidogyrus halli* (Price et Kirk, 1967) (haptor, left side; male copulatory organ (MCO), right side, digested material; photo A. García-Vásquez). (h) *Cichlidogyrus agnesi* Pariselle et Euzet 1995 (MCO, phase contrast) (photo V. Sarabeev). (i) *Cichlidogyrus tiberianus* (MCO, scanning electron microscopy) (photo W. Fannes). (j) Histological section of *Cichlidogyrus philander* Douëllou, 1993 on the gills of *Pseudocrenilabrus philander* (Weber, 1897; photo P.C. Igeh/A. Avenant-Oldewage). b, parasite body; h, parasite haptor; il, impacted lamellae; nl, normal lamellae; black arrow: anchor deeply pushed in the gill lamellae. Scale bars: a = 250 μm; b, c = 100 μm; d–f, j = 50 μm; g = 25 μm; h = 20 μm; i = 5 μm

likely to be discovered. Some widespread tilapia monogeneans such as *C. halli* and *C. tilapiae* represent species complexes,[307] complicating identification. Morphological and molecular investigations of *C. halli* in the Upper Congo Basin indicate that introduced and native *O. niloticus*, and local other native tilapia harbour different species.[308,309]

Monogenean specimens are dissected with the hook-bearing haptor and the anterior genital organ-bearing parts used to facilitate morphological studies and vouchering of specimens, while the parts of the monogenean not bearing hard structures are used for molecular studies. Molecular identification of gyrodactylid and dactylogyrid monogeneans is largely based on nuclear ribosomal DNA (rDNA) markers.[310] Ek-Huchim et al.[311,312] designed primer combinations within the nuclear rDNA for non-invasive identification of monogeneans on tilapia.

2.11.2 | Pathogenicity

Attachment of gyrodactylids to fish involves the 16 marginal hooks simultaneously perforating the epithelium and causes damage to the epidermis.[313,314] The two large hamuli contribute to marginal hook attachment by lifting the centre of the haptor (see Figure 7 of the haptor of *G. cichlidarum*) but can also perforate the epithelium. These parasites also use their muscular pharynx to grab mucus and epidermal tissue which creates feeding wounds. *Gyrodactylus* spp. damage and erode the fins of infected fish leading to reduced swimming capacity and increased mortality.[315,316] High parasite burdens cause numerous superficial perforations that cause physiological and histological disturbances that can induce osmoregulatory failure.[317] *Gyrodactylus cichlidarum* is associated with mortality of farmed tilapia worldwide including Scotland,[286] Egypt,[318] Mexico[287] and various Latin American countries.[319] The combined physical damage from attachment and feeding constitutes an important breach to the primary, innate defensive barrier the skin provides, and renders hosts more susceptible to opportunistic pathogens. *Gyrodactylus cichlidarum* feeding and attachment activity damages the epidermis, increasing the susceptibility of fish to bacterial infection, including with *Streptococcus iniae* Pier, 1976[320] and *Aeromonas hydrophila* (Chester, 1901) with subsequent mortality.[318]

In *Cichlidogyrus* or *Scutogyrus*, the sclerites of the haptor penetrate the gill epithelium.[321,322] Attachment of *Cichlidogyrus philander* Douëllou, 1993 in a non-tilapia cichlid caused epithelial rupturing, disturbance and distortion of blood cells, blood cell puncture, distortion and sometimes penetration of the extracellular cartilaginous matrix in the gills, surface deformation of gill lamellae, erosion of epithelial cells, increased mucus production, neutrophilaemia, hyperplasia and fusion of gill lamellae (Figure 9j).[322,323] A humoral immune response[324] and changes in blood biochemistry[325] are observed in *O. niloticus* injected with extracts of *Cichlidogyrus* spp. The role of the marginal hooks of the haptor in attachment to the gills is, however, debated.[323,326,327] In *Enterogyrus*, attachment creates shallow epithelial perforation, damage and compression of the stomach epithelium, nuclear anomalies, metaplasia, hyperplasia, pleomorphism and vacuolation at the attachment site.[321] The apparently moderate pathology explains the lack of observed morbidity or mortality associated with these parasites. Noga and Flowers[328] observed a cultured population of *O. mossambicus* with specimens of *E. cichlidarum* attached to abnormal sites such as the gills, cranial bones, heart, blood vessels, liver, perirenal area, peritoneal cavity and liver with sign of systemic host immune response and severe morbidity and mortality.

Species of *Gyrodactylus* and *Cichlidogyrus* commonly co-occur in fish farms[129]; co-infection induces host immunosuppression and facilitates infection by both parasites.[329] Fish concurrently infected with species of *Gyrodactylus*, *Trichodina* and *I. multifiliis* do not develop immunity after vaccination for *S. iniae* and have higher mortality than uninfected fish.[330] Concurrent infection with *Gyrodactylus* sp. and *Cichlidogyrus* sp. has negative effects on hosts; high parasite burdens correlate with low host condition factor with an estimated 12%–15% decrease in profit margin.[331] Igeh and Avenant-Oldewage[322] outlined that natural infections of *Cichlidogyrus* are not very harmful. Sandoval-Gío et al.[324] noted little direct evidence for dramatic effects on cultured tilapia. Paperna[200] described no ill effects of tilapia dactylogyrids in Africa or Israel. Abundances of up to 800 *Cichlidogyrus* spp. on *C. guineensis* in Ébrié Lagoon (Côte d'Ivoire) had no apparent negative effect on the host (A. Pariselle, pers. obs.). *Cichlidogyrus* spp. are, however, potentially problematic in aquaculture.[332,333] Kabata[334] reported serious gill pathology in tilapia infected with *C. sclerosus* in the Philippines. Concurrent infections with species of *Cichlidogyrus* and *Scutogyrus* induce anaemia and decrease fish condition.[335] These impacts combined with their high prevalence and direct life-cycle caused Akoll et al.[23,24] to assess *Cichlidogyrus* spp. as high-risk parasites for aquaculture.

2.11.3 | Global translocations

Gyrodactylus cichlidarum, *Cichlidogyrus* spp., *Scutogyrus* spp. and other monogeneans have been translocated worldwide with tilapia for aquaculture (Tables S1 and S2)[287,288,300,319,336,337] and infect native fish, mainly cichlids, but also poeciliid fish in Mexico,[287,336,338] in areas where tilapia and their parasites are introduced. *Gyrodactylus cichlidarum* is the most common translocated gyrodactylid of tilapia and has been established in fish farms in Mexico for decades.[287,339] *Gyrodactylus yacatli* is recorded in Mexico and Kenya,[287] and probably in China[300] and Zimbabwe,[285] although more extensive sampling and accurate identification of specimens is needed. Translocation of tilapia parasites has also occurred in Africa, including *G. nyanzae* Paperna, 1973, which was transferred from introduced *O. niloticus* to *C. rendalli* in the Upper Congo Basin,[340] and *G. cichlidarum* and *G. malalai* Přikrylová, Blažek et Gelnar, 2012, which were introduced with *O. niloticus* to Lake Victoria, Kenya where they infect local native fish.[341]

There are many widely cointroduced dactylogyrid tilapia parasites. Of these, some have transferred to cichlid hosts in continental Africa (*C. sclerosus*, *C. tilapiae*),[340] to Malagasy cichlids (*C. halli*, *C. thurstonae*, *C. tilapiae*),[337] to American cichlids (*C. sclerosus*, *C. tilapiae*, *S. longicornis*, *E. malmbergi*),[336,342] and to members of the cyprinodontiform families Aplocheilidae in Madagascar (*C. tilapiae*)[337] and Goodeidae in Mexico (*C. sclerosus*).[336] The transmission of monogenean parasites to new hosts is rarely reported, and reports mostly contain little evidence of translocation or transmission routes; information is too limited to assess frequency or probability of transfer for given monogeneans. It is clear, however, that the dactylogyrids that establish outside their native range can exploit a phylogenetically broad host range. Fannes et al.[343] described that *C. dossoui* Douëllou, 1993 and *C. tiberianus* Paperna, 1960, which normally infect coptodonine tilapia occur on other tilapia and cichlids in their introduced range. These changes in host range can occur wherever tilapias are translocated, because ecological opportunity and host phylogenetic history determine the host range.[289,344] Introduced populations can be free of gill monogeneans, such as *O. mossambicus* in New Caledonia, because of genetic bottlenecks, salinity changes, single introduction events or treatment of translocated stock.[345] Tilapia-infecting monogeneans may become the most widespread tropical freshwater fish parasites, given the ubiquity of tilapia and the prevalence of their monogeneans. Forty helminth species have been introduced to Mexico with introduced fish; 33 of these are monogeneans; of which 14 were introduced with tilapia.[336]

2.11.4 | Research

Most studies focus on epizootiology and ecology of the tilapia-gyrodactylid association. Aquaculture research focuses on the search for natural treatments and products to improve the ability of fish to respond to infections and the immune response elicited by infection. The identification of host immune genes that are activated by *G. cichlidarum* infection[346] and identification of major histocompatibility complex II α alleles associated with parasite resistance make genotype-assisted selection of resistant fish strains possible.[347] Bioinformatic analysis of monogenean parasite excretory/secretory proteins (secretomes) also provides a novel approach to identify potential drug targets.[348] The lack of reports of detrimental effects may be a consequence of a lack of study[349] and greater attention paid to pathogens of more immediate concern. More functional–biological research on monogenean life history and infection dynamics, physiology, including host detection and environmental tolerance, and pathogenicity such as attachment and histopathology, and facilitation of secondary infections would benefit aquaculture.[302] Monogenean phenotyping often focuses on the haptor. In cichlid-infecting dactylogyrids, rapid morphological adaptation of the haptor associated with host-switches is observed,[350] as is haptoral variation within monogenean species infecting populations of the same[351] and different[352] hosts. Morphological variation is observed in *G. cichlidarum* from different hosts and/or geographical regions, although this gyrodactylid displays limited molecular variation.[287] Accurately understanding monogenean translocations and host-switches requires population-level approaches of hosts and parasites. Understanding the influence of phenotypic diversity in the haptor and its role in pathogenicity and host-specificity could aid in predicting and understanding risk and impacts of lateral parasite transfer after tilapia translocations. Better understanding of why some tilapia monogeneans are more tolerant of translocation and more likely to establish could also aid in understanding translocation risks. How anthropogenic translocations alter the geographic and host range of tilapia parasites is a major question in cichlid parasitology, and improved baseline surveys and infection experiments are needed to address it.[353] Absence of parasites should also be more systematically published: reports are rare in the literature, and published accounts often do not explicitly state whether hosts were inspected for a parasite taxon that was not reported, probably because of publication bias against negative results.[302,345] Climate change may help sustain or expand invasive tilapia populations,[354] although its expected impact on directly transmitted aquatic parasites is unclear.[355] A better understanding of any aspect of the physiology and infection dynamics of tilapia monogeneans would aid understanding how global change will influence the poorly understood mechanisms behind monogenean pathology, distribution, host range and host-switching.

Chemotherapeutic agents are expensive, may leave residues in fish tissues and have negative environmental effects. Therefore, assays have been conducted to evaluate the effectivity of various plant extracts, essential oils and other natural compounds to control infections, for example, garlic extract, saponins and other products.[356] Leaf extracts of *Mitracarpus scaber* Zucc. (Rubiaceae), a plant commonly used in West African traditional medicine, improve growth, non-specific immunity and resistance of Nile tilapia to *G. malalai*.[357] *Leucaena leucocephala* (Lam.) (Fabaceae), a plant commonly used as an anthelminthic in cattle, has also shown promising results in controlling gyrodactylid infection of tilapia fingerlings.[358] Dotta et al.[359] found that combined dietary supplementation with bee propolis and *Aloe barbadensis* Miller (Asphodelaceae) extracts reduced abundance of dactylogyrid monogeneans infecting the gills of *O. niloticus*. De Oliveira Hashimoto et al.[360] found that essential oils of a hybrid mint *Mentha piperita* Linnaeus (Lamiaceae) were effective against these parasites.

Taxonomic identification of *Gyrodactylus* spp. and dactylogyrids is time consuming and requires detailed morphometric analysis of microscopic structures of the parasite attachment and/or copulatory organs and specialist knowledge: a practical alternative in aquatic veterinary medicine could be screening fish mucus using PCR to identify parasite molecular markers.[312] The relevance of this approach is limited to situations where precise taxonomic identification is required to meet quarantine regulations for export permits, or where parasite life-cycles are well documented and approaches to strategic control are established. Most reports of farmed tilapia mortality, furthermore, are associated with *G. cichlidarum*. Recent phylogeographic work indicates that genetic structure and host-specificity of *Cichlidogyrus* spp. differ between hosts.[309,352] Molecular markers will be crucial in disentangling the mechanisms that structure monogenean populations, because they are consequential for colonisation dynamics. The wild relatives of tilapia and their parasites are likely to be excellent disease models.[302,361] *Cichlidogyrus berminensis* Pariselle, Bitja Nyom et Bilong Bilong, 2013, for example, infects multiple *Coptodon* spp. in Lake

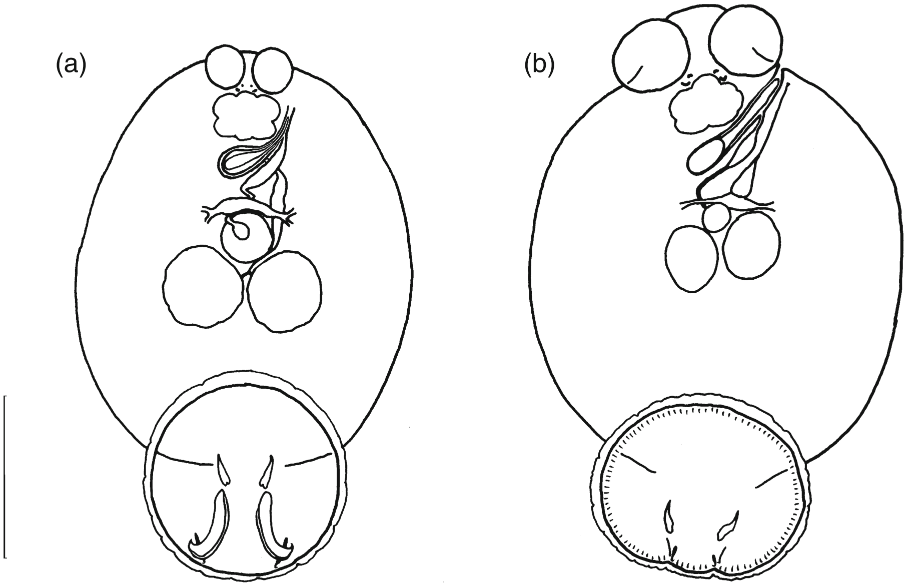

FIGURE 10 Capsalids from tilapia. (a) *Neobenedenia girellae* drawn from Queensland Museum specimen G218281 showing circular haptor, small anterior attachment organs and absence of a vagina. (b) *Benedenia monticellii* drawn from specimens on Hebrew University of Jerusalem slide HUJ-MONO1.0 showing laterally ovoid haptor with posterior notches, large anterior attachment organs and vagina with opening posterior to common genital pore. Scale bar = 750 μm

Bermin, Cameroon,[362] and closer scrutiny could increase our understanding of potential and achieved host-range. More variable markers than the currently widely used nuclear rDNA fragments are needed, for instance, the mitochondrial cytochrome *c* oxidase subunit 1 gene (COX1), which is highly variable in flatworms and therefore currently not widely applicable in monogeneans.[310] Mitogenomics of monogeneans infecting African cichlids[363–365] are likely to facilitate the application of mitochondrial markers to monogenean parasites of tilapia.

2.12 | Capsalidae Baird, 1853 (Obazoa: Opisthokonta: Metazoa: Platyhelminthes)

These monopisthocotylean monogeneans are reported from tilapia grown in brackish and marine systems.

2.12.1 | Taxonomic identity

Capsalids are monogeneans that primarily parasitise the external surfaces of fish; possession of accessory sclerites is a synapomorphy for the family.[366] From tilapia, *Benedenia monticellii* (Parona et Perugia, 1895) was recorded from *O. aureus* in Israel[367] and *Neobenedenia melleni* (MacCallum, 1927) was recorded from *O. aureus* in Cuba,[368] as *Benedenia* sp.,[369,370] *O. mossambicus* in Hawaii,[367,371] *O. niloticus* × *O. aureus* in Martinique,[372] *O. aureus* × *O. mossambicus* in Jamaica[333,373] and *O. aureus* × *O. mossambicus* in the Bahamas.[374–377] A *Neobenedenia* sp. was reported from *O. mossambicus* and *O. niloticus* hybrids in Mexico's Atlantic coast.[378] Invasive *O. mossambicus* and *Tilapia mariae* in brackish water in Australia are parasitised by *N. girellae* (Hargis, 1955; M. Deveney, unpublished data; Figure 10a).

Benedenia monticellii (Figure 10b) possesses a vagina and a transversely ovoid haptor with a muscular periphery and marked indentations in its posterior edge at the approximate positions of the posterior hamuli and large anterior attachment organs.[369] A key to *Benedenia* spp. was provided by Deveney and Whittington,[379] but species have been described subsequently and the key will misidentify some undescribed species. *Neobenedenia* spp. lack a vagina, have an almost circular haptor and small anterior attachment organs.[380] *Neobenedenia* Yamaguti, 1963 has a long and convoluted taxonomic history, but Brazenor et al.,[381] using molecular data, resolved distinct clades within morphologically similar *Neobenedenia* spp. and concluded that aquaculture infections were *N. girellae*. Molecular analyses are needed to identify *Neobenedenia* spp. and some specific tools have been developed for this purpose.[382]

While the life-cycles of benedeniine genera vary, complicating strategic control, all capsalids are susceptible to standard treatments such as freshwater (for marine farmed fish), oxidising agents including hydrogen peroxide, reducing agents such as formalin and anthelmintics including praziquantel, decreasing the importance of precisely identifying these parasites in aquaculture.

2.12.2 | Pathogenicity

Capsalids are important causes of disease in aquaculture: *Neobenedenia* spp. are regarded as notorious[383] and insidious[384] pathogens of cultured fish. Infections damage the epidermis[385] and eyes,[386] decrease epidermal thickness,[387] facilitate secondary infections and can lead to fish death by compromising osmoregulation.[386]

2.12.3 | Global translocations

Capsalids are not recorded as translocated with their hosts; furthermore, capsalids infect tilapia only in brackish and marine systems. Stress associated with osmoregulation in seawater aquaculture systems increases the susceptibility of tilapia to capsalid infections.[367] These parasites are part of the fauna that infect tilapia from the environment when they are translocated, but it is noteworthy that *Neobenedenia* spp. are invasive and have been broadly translocated.[388]

2.12.4 | Research

There are substantial bodies of work on capsalid taxonomy,[381] biology and pathology.[386] Capsalid infections increase cost of production, decrease fish growth and cause mortality with substantial economic impacts on aquaculture.[389] Life-cycle parameters are used as a basis for temperature and salinity dependant strategic control[390,391] that aims to disrupt life-cycles.[386] Although freshwater is an effective, safe treatment,[367,392] substantial efforts have been made to optimise praziquantel[393] and hydrogen peroxide[394] treatments for capsalids and to identify effective natural products.[395] Parasite management is aided by shading[396] and increasing the depth at which fish are held,[397] which both decrease infection. Kishimori et al.[371] noted a specific antibody response to *Neobenedenia* in *O. mossambicus*, although Rubio-Godoy et al.[378] found that injecting purified worm extracts did not decrease *Neobenedenia* infection in tilapia. Ongoing research is likely to focus on management and decreasing the effects of infections on cultured fish and of control on the costs of production.[386]

2.13 | Digenea Carus, 1863 (Obazoa: Opisthokonta: Metazoa: Platyhelminthes)

2.13.1 | Taxonomic identity

Trematodes are parasitic flatworms with a ventral disc or a ventral and an oral sucker. Trematodes infecting 'tilapia' of the genera *Tilapia*, *Coptodon* and *Oreochromis* in their native range in Africa, as well as in at least 10 countries where they have been introduced, are represented by at least 45 taxa. Most of them are metacercariae (larvae) occurring in different tissues and organs of the fish, that is, skin, muscle, gills, operculum, liver, kidney, heart and mesentery. Only two adults were reported from Africa in one study [*Allocreadium ghanensis* Fischthal et Thomas, 1972 and *Alloglossidium corti* (Lamont, 1921) by Simon-Oke][398] and another three species were reported from Latin America [*Crassicutis cichlasomae* Manter, 1936 by Salgado-Maldonado (2006),[399] *Saccocoelioides sogandaresi* Lumsden, 1963 by Salgado-Maldonado et al.,[400] and *S. cichlidorum* (Aguirre-Macedo et Scholz, 2005) by Aguirre-Macedo and Scholz],[401] and the validity of these reports requires confirmation. All these metacercariae require fish to be consumed by a fish-eating bird or mammal including man to complete their life-cycle. Twenty-seven of the 42 metacercariae are identified up to species level. Tilapias are mainly parasitised by metacercariae of the orders Diplostomida (families Diplostomidae Poirier, 1886–13 spp., Clinostomidae Lühe, 1901–1908 spp.) and Plagiorchiida (Heterophyidae Leiper, 1909–15 spp.). The clinostomid *Euclinostomum heterostomum* (Rudolphi, 1809) is widely distributed in African 'tilapia' (Figure 11), although the diplostomids occurring on the skin (*Uvulifer* Yamaguti, 1934 and *Bolbophorus* Dubois, 1935) and in the brain and eyes (*Diplostomum* von Nordmann, 1832 and *Austrodiplostomum* Szidat et Nani, 1951) are of major concern for aquaculture. Among the members of the family Heterophyidae parasitising tilapia, at least six species are considered economically or medically important as fish-borne zoonotic trematodes (FZT). Among them, *Heterophyes heterophyes* (Siebold, 1853), *Haplorchis pumilio* (Looss, 1896) and *Centrocestus formosanus* Nishigori, 1924 are the most important.[403]

2.13.2 | Pathogenicity

Trematode metacercariae may be free in organs such as brain and eyes or encysted in different parts of the fish body. The condition caused by metacercariae of diplostomids in the eye of fish (eye humours, retina and lens) is known as diplostomiasis; fish develop impaired vision associated to clinical signs such as cataract formation, exophthalmia, lens dislocation and eventually blindness. Grobbelaar et al.[404] reported high prevalence of infection by free-moving metacercariae of diplostomids in the aqueous and vitreous humours of *T. sparrmanii* and *C. rendalli* in the Okavango River, Botswana (Figure 12). Histopathological analyses revealed the rupture of the inner eye lining. In another study, in individuals of *O. mossambicus* and *O. aureus* infected with the metacercariae of *Austrodiplostomum compactum* (Lutz, 1928) in Mexico, García-Márquez et al.[406] reported lesions as diffuse corneal edema, severe diffuse eosinophilic optic neuritis, eosinophilic iridiocyclitis, conjunctivitis and severe cortical cataracts. Furthermore, the metacercariae encysted on the skin, gill filaments and heart are also of major concern for fish health. For instance, *C. formosanus*, considered as a parasite originally from Asian cyprinids and co-introduced with their hosts across the globe, causes pathological alterations on the gills leading to respiratory distress and in severe infections causes mortality (Figure 11).[402] The heterophyid *H. pumilio* is of special interest because some studies of experimental infections of tilapia with cercariae of *H. pumilio* evidenced severe pathological effects as haemorrhages in skeletal muscles in heavily infected fish because the cercariae migrate through connective tissue and the final localisation of the metacercariae is in skeletal structures (Sommerville, 1982). Finally, the condition caused by metacercariae of *Uvulifer* spp. encysted on the skin of the fish causing an external melanised host inflammatory response is known as black spot disease; this

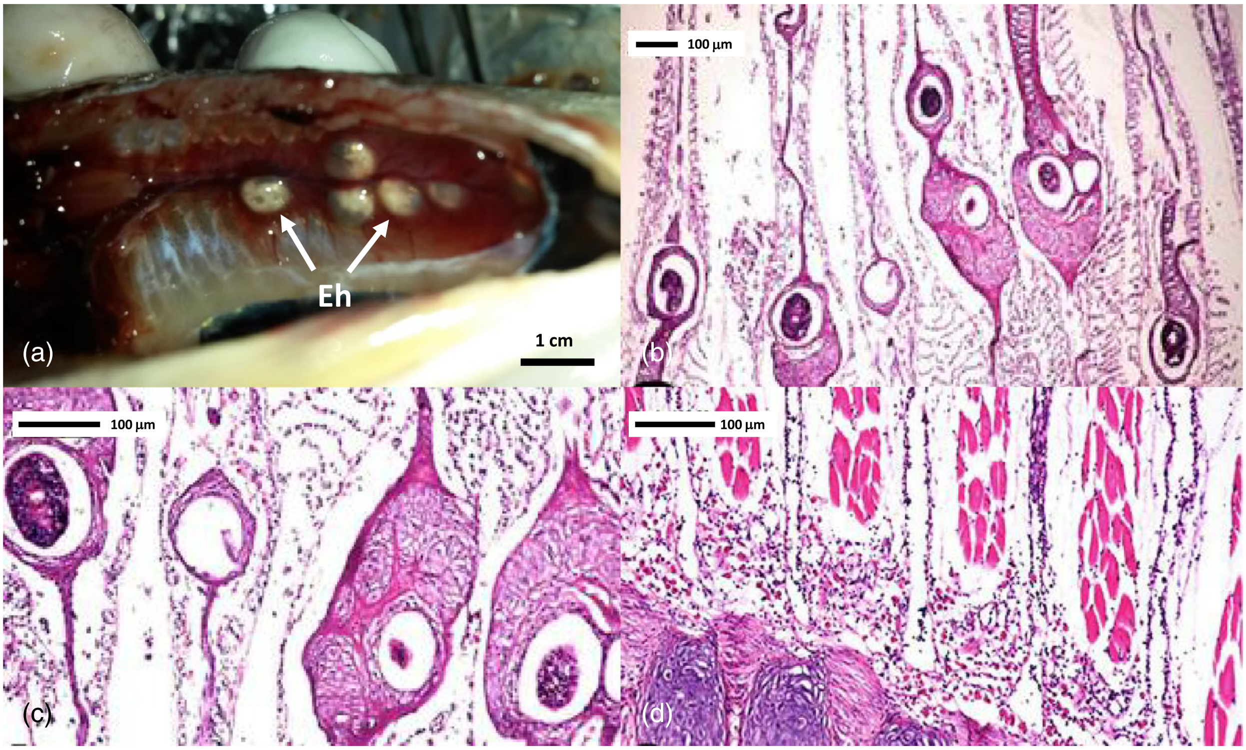

FIGURE 11 (a) Encysted metacercariae of *Euclinostomum heterostomum* (Rudolpi, 1809) (Eh) in the body cavity of *Oreochromis niloticus* (image courtesy of Liesl Van As and Andri Grobelaar from the Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein, Republic of South Africa and the Editorial Office of African Zoology). (b) Photomicrograph of histological gill sections of *O. niloticus* infected with numerous metacercarial cysts of *Centrocestus formosanus* (Nishigori, 1924) within the gill filament. (c) Photomicrograph of gills showing expansive proliferation of cartilage of gill filament which surrounds the metacercariae of *C. formosanus*, with subsequent distortion of the normal gill architecture; (d) Photomicrograph of histological infected *O. niloticus* gill sections showing extensive edema associated with congestion of the blood vessels and intense inflammatory cell infiltration (images courtesy of Mahmoud Abou-Okada from the Faculty of Veterinary Medicine, Cairo University, Egypt reproduced from Abou-Okada et al.[402])

disease causes slow growth, deformities and increases the mortality rate of freshwater fish (Figure 12).[405] These authors analysed the effect of black spot disease in *O. niloticus* in Egypt, and even though they did not report large mortalities or morphological deformities of fish, apparently harvest weight of fish declined as severity of infection increased. They also observed that females were more susceptible to *Uvulifer* infections than males, although their loss of harvest weight on severe infection levels was greater than females.

2.13.3 | Global translocations

In sharp contrast with the pattern shown by monogeneans and the spillover across the globe along with the introduction of tilapia, trematodes associated with this group of cichlids have not been translocated; these parasites are less host-specific in the second intermediate host, but they possess complex life-cycles which involves three hosts and greater specificity may occur in the first and definitive hosts. Even though tilapia act as the second intermediate host harbouring the metacercarial stage, and fish-eating birds or mammals serve as their definitive hosts increasing the potential of dispersal, no species of trematode found thus far in their native range in Africa has been found in places where tilapia have been introduced. The lack of the same species of first intermediate host (a mollusc) in the areas where tilapias are introduced may preclude the completion of their life cycle. For instance, the metacercariae of *E. heterostomum* are widely distributed in Africa; yet, they have never been found in tilapia introduced in Asia or in the Americas. Even other clinostomids such as *Clinostomum phalacrocoracis* Dubois, 1930, *C. cutaneum* Paperna, 1964 and *C. tilapiae* Ukoli, 1966 are also found exclusively in Africa.[407] The fact that species of heterophyids such as *C. formosanus* (originally described from Taiwan Province of China) and *H. pumilio* (first described in Egypt) are found everywhere in the world is not related to the translocation of tilapia; most likely the widespread distribution of these species is due to the translocation of the first intermediate host, the gastropod, *Melanoides tuberculata* (Müller, 1774) or definitive hosts. In addition, the metacercariae of both species are considered as invasive alien species[408–410]; they display extremely wide host specificity and are also found in a wide variety of fish species across the globe. Conversely, tilapia introduced to the Americas show evidence of host-switching events of trematodes from native cichlids (and other freshwater fish) to farmed tilapia. For instance, the metacercariae of *A. compactum*, a diplostomid trematode parasite of cormorants and widely distributed across the Americas and the

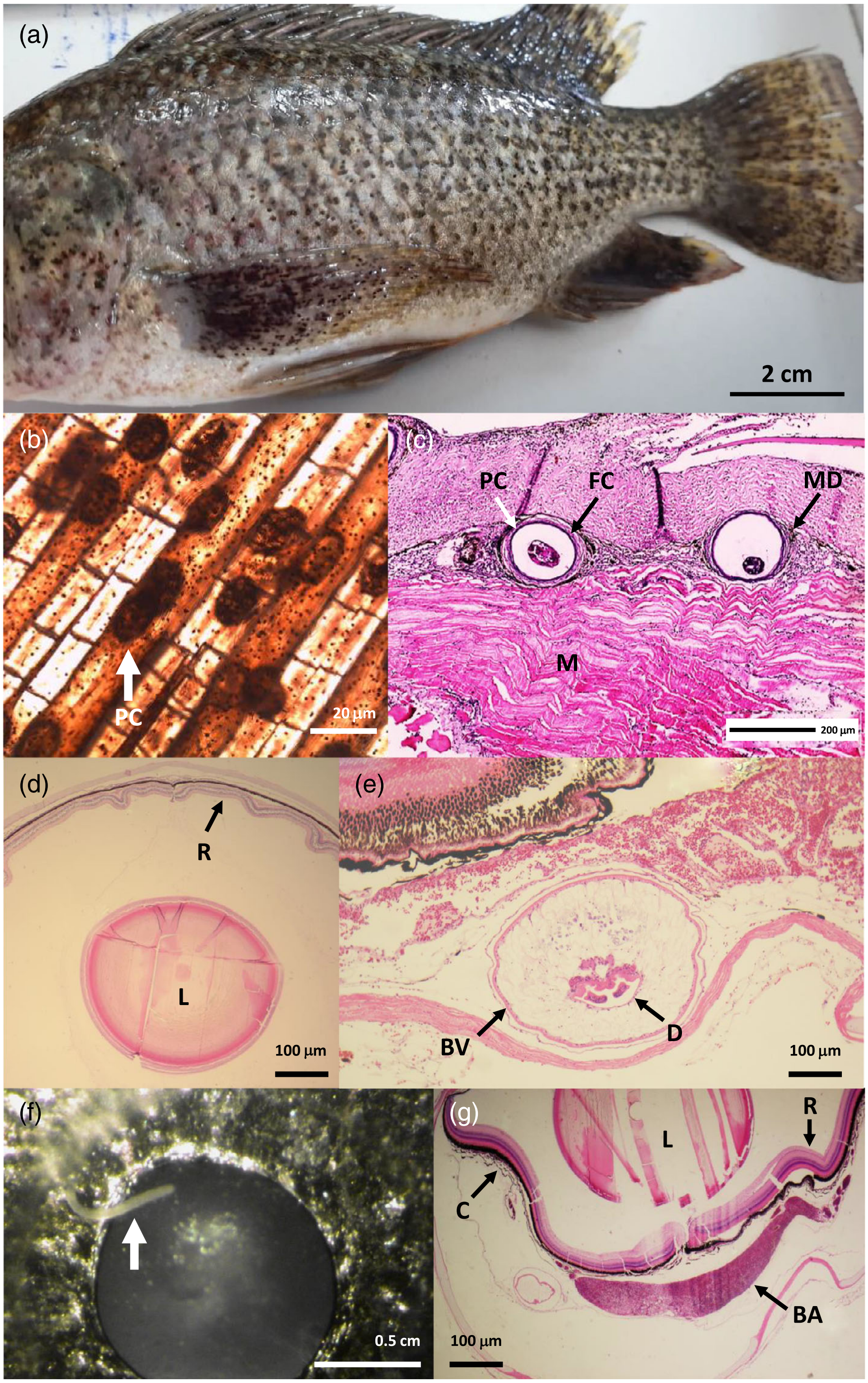

FIGURE 12 (a, b) Gross and microscopic examination of *Oreochromis niloticus* heavily infected with metacercariae of *Uvulifer* sp. (Trematoda: Diplostomidae) (black spot disease). (c) Photomicrograph of a histopathological section of *O. niloticus* skin and muscle infected with *Uvulifer* sp. showing the encysted metacercariae; FC, fibrous capsule; M, muscle; MD melanin deposits; PC, parasite cyst. Images courtesy of Harrison Charo-Karisa, Shimaa E. Ali and John A.H. Benzie from WorldFish, Abbassa, Egypt and Penang, Malaysia. Images reproduced from Charo-Karisa et al.[405] (d) Photomicrograph of a normal, non-infected fish eye with the retinal layers intact; (L) lense. (e) An encapsulated diplostomid (D) within a blood vessel (BV). (f) Gross examination of the eye of *Coptodon rendalli* showing a free-moving diplostomid metacercariae. (g) Photomicrograph of an infected eye of *C. rendalli* showing the accumulation of blood (BA), which has torn the retina (R) and choroid (C) from the sclera. Images courtesy of Liesl Van As and Andri Grobelaar from the Faculty of Natural and, University of the Free State, Bloemfontein, Republic of South Africa. Images reproduced from Grobelaar et al.[404]).

causative agent of diplostomiasis is commonly found in native species of cichlids[411]; however, it has been reported in wild and farmed Nile tilapia of Mexico and Brazil.[412,413]

2.13.4 | Research

Ongoing research on trematodes of tilapias includes the taxonomic report of their presence as a part of their parasite fauna in fish farms, or in aquatic environments where tilapia have been disseminated globally.[407,414,415] Investigations that can be applied practically in aquaculture are designed to assess the epidemiology of FZT using *O. niloticus* as a model because they are highly consumed in several countries. Some studies evaluate the risk of FZT because they are potentially transmissible to humans.[416] FZT are highly prevalent in countries where food traditions include eating raw or improperly cooked fish, such as Thailand, Cambodia, Laos, Vietnam or Korea.[403,417] *Oreochromis niloticus* and their parasites have, furthermore, been used for biomonitoring. Some studies have addressed the relationship between some parasitic infections, including those by trematode metacercariae, and the immunological health condition of *O. niloticus* through gene expression analysis and the assessment of the toxicity of some heavy metals.[166] The use of antiparasitic agents has been assessed to control *O. niloticus* infected with *C. formosanus*, which causes respiratory distress due to pathological alterations to the gills. Abou-Okada et al.[402] assessed the efficacy of acriflavine on *O. niloticus* infected with *C. formosanus* (and with *Trichodina centrostrigeata* Van As et Paperna, 1983) and found that application of 10 mg/L acriflavine for 7-days provided a 91% reduction in metacercariae colonising the gills. There are, however, regulatory limitations on use of acriflavine and it appears to have limited efficacy in the treatment of established infections.

2.14 | Cestoda Carus, 1863 (Obazoa: Opisthokonta: Metazoa: Platyhelminthes)

2.14.1 | Taxonomic identity

Cestodes are flatworms with no digestive system, many of which are elongated with multiplicated genital organs. Adult tapeworms are rare in tilapia except for the Asian fish tapeworm *Schyzocotyle acheilognathi* (Yamaguti, 1934), one of the most successful invasive freshwater fish parasites.[418] This invasive parasite is distributed across all continents except Antarctica, has been reported from >300 freshwater fish species and has been reported to cause mortality in naïve endemic hosts.[418] This parasite has an indirect life-cycle and uses copepods as its intermediate host and freshwater fish as its paratenic or definitive host.[418] In addition, there is another finding of another adult tapeworm, *Proteocephalus bivitellatus* Woodland, 1937 from *Tilapia* sp. (probably *C. zillii*) from Sierra Leone by Woodland.[419] This appears to be a valid species, but no other records of adult proteocephalids in tilapia have been reported to date.

Cestode larvae (metacestodes) are more commonly reported from tilapia, however, as their second intermediate or paratenic host. Most belong to the family Gryporhynchidae (Cyclophyllidea) that use fish-eating birds as their definitive host and copepods as their first intermediate host.[420] The larval stage of gryporhynchids, a merocercoid, is typically encysted or, rarely, free-moving, and is typically small in size at around 1–2 mm (with the exception of the non-encysted *Amirthalingamia macracantha* (Joyeux et Baer, 1935) which can grow up to 17 mm) and can be easily overlooked among internal organs including mesenteries, intestinal and stomach wall, liver, and/or gall-bladder.[421–424] Gryporhynchid merocercoids are easily recognised by the presence of a scolex armed with two rows of rostellar hooks and four suckers.[422,423] The identification of these merocercoids is based almost entirely on morphology and the number of rostellar hooks, but accurate identification depends on the proper flattened preparation of larvae for microscopic evaluation.[422,423]

There are several other cestode larvae (plerocercoids) that have rarely been detected in tilapia. These include the bothriocephalid plerocercoids of *Tetracampos ciliotheca* Wedl, 1861 (syn. *Polyonchobothrium ciliotheca*) or *P. polypteri* (Leydig, 1853) from *O. niloticus* (Figure 12),[425–427] but Eissa et al.[428,429] reported the presence of adult *T. ciliotheca* in 1%–6% of *O. niloticus* specimens and their hybrids from Egypt. This record is unusual and may be incorrect, because *T. ciliotheca* typically matures almost exclusively in catfish of the genus *Clarias* and those of *P. polypteri* occur almost exclusively in bichirs of the genus *Polypterus*.[430] Larvae (plerocercoids) of *Proteocephalus glanduligerus* (Janicki, 1928) (Onchoproteocephalidea) were found in the intestine of *O. mossambicus* from the Ndumo Game Reserve in South Africa (O. Kudlai; personal obs.). Tilapia most likely serve as accidental or paratenic hosts of this tapeworm that matures in clariid catfish.[431] Additional, clearly erroneous records include those of plerocercoids of the human broad tapeworm *Dibothriocephalus latus* (Linnaeus, 1758) (syn. *Diphyllobothrium latum*) from the intestine of *O. niloticus* reported from Côte d'Ivoire,[432] Kenya[433] and Nigeria[434] without supporting evidence. The broad fish tapeworm is not able to infect tilapia and moreover, does not occur in the tropics.[435] In addition, *Cyathocephalus* sp. (Spathebothriidea) has been reported from the internal organs and body cavity of *O. shiranus* in Malawi,[436] a cestode which has a natural distribution only throughout the Palearctic.[437] Likewise, the report of *Caryophyllaeus* sp. (Caryophyllidea) from tilapias in Nigeria (Ukpai 2001) which also is naturally distributed only in the Palearctic[438] or *Wenyonia* sp. (Caryophyllidea) from the intestines of *O. aureus* and other tilapia species in Nigeria[439] maturing exclusively in catfish in Africa[440] also represent clear misidentifications.

2.14.2 | Pathogenicity

The pathological effects *S. acheilognathi* exerts on cultured tilapia have not been documented, but it is likely that this cestode causes mechanical damage and inflammation of the intestinal mucosa, resulting in anorexia, weight loss, abdominal distension, anaemia and, behaviourally, a tendency to swim at the water surface.[319,441–443] This tapeworm is easily identified by its characteristic heart-shaped, unarmed scolex bearing two deep, sucker-like bothria (Figure 13a).[418] *Schyzocotyle acheilognathi* is not a typical parasite of tilapia but may be infective to tilapia because of its low specificity, and the global, cosmopolitan distribution of both.[418]

While the risk posed by gryporhynchid merocercoids to the health of farmed tilapia may be minor, the tissue tropism of some species for the liver can have serious negative effects on host health, if present in sufficient numbers and particularly in juvenile fish.[424] Some unidentified merocercoids are reported from the intestinal wall of cultured and wild *O. niloticus* from Ethiopia, Kenya and Uganda, typically with low prevalence except in a wild population of *O. niloticus* in Kenya (14%).[17] These merocercoids from the intestinal wall of tilapia are represented by several species, including *Cyclustera magna* (Baer, 1959), *Parvitaenia macropeos* (Wedl, 1855) or *Neogryporhynchus lasiopeius* Baer et Bona, 1960 (Figure 13c).[423] Florio et al.[17] examined the histopathology of these larvae and showed encysted merocercoids surrounded by epithelioid cells, sometimes by fibroblasts and lymphocytes. The cyst showed serrated margins with cell detachments and the presence of red blood cells, possibly due to mechanical erosion caused by the larvae. The wall around merocercoids was hypertrophic and chronically inflamed. The cysts were frequently observed to protrude on the outer surface and/or into the lumen.[17]

2.14.3 | Global translocations

Schyzocotyle acheilognathi has been reported from both wild and cultured populations of *O. mossambicus* and *O. niloticus* from South Africa,[200] Cuba,[319] Mexico[399,441] and Nigeria[444] (Table S2).

The first record of a gryporhynchid from a tilapia was *A. macracantha* (Figure 13b) reported by Bray (1974) who isolated specimens from the liver of *O. niloticus* and the intestine of a reed cormorant, *Microcarbo africanus* (Gmelin, 1789), in Sudan. More recently, this species has also been detected in cultured *O. aureus* × *O. niloticus* hybrids in Israel.[424] To date, approximately 10 species have been recorded from domesticated and wild populations of tilapia, mainly from Africa, but also from Israel and Puerto Rico.[319,445]

2.14.4 | Research

There are no detailed studies on tapeworms in tilapia, because almost exclusively only gryporhynchid larvae are reported and tapeworms mostly are not important pathogens of tilapia.

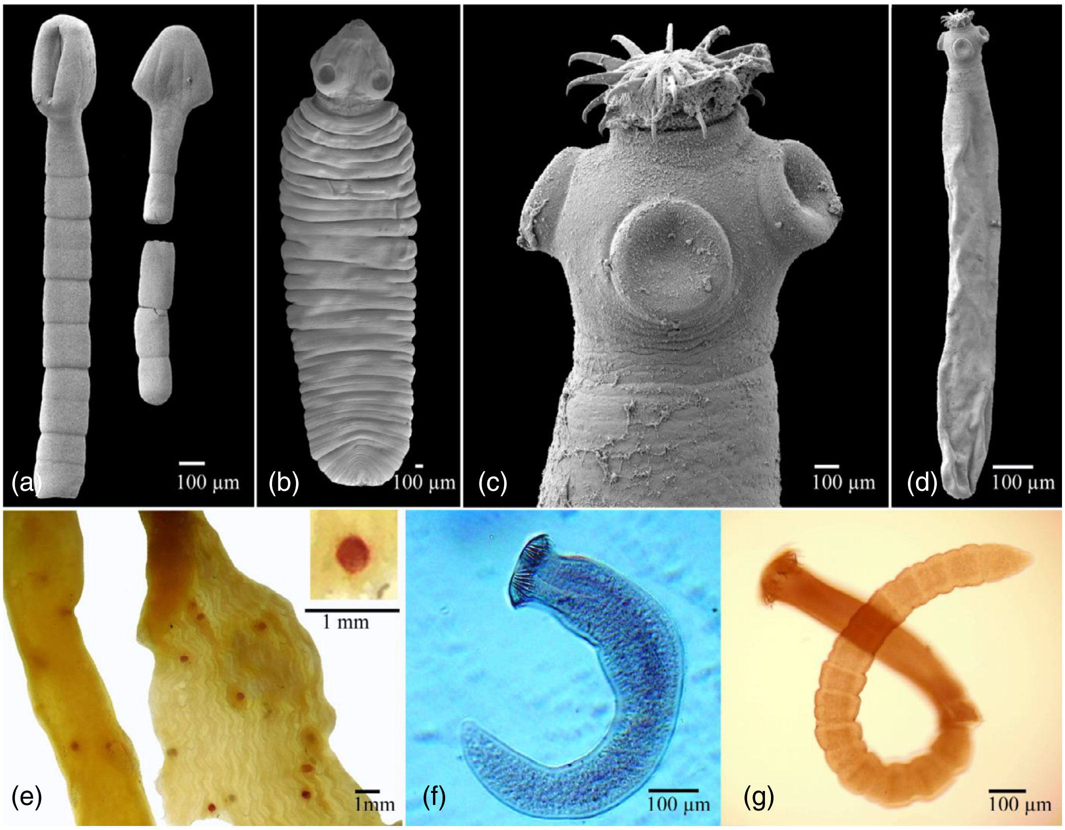

FIGURE 13 Cestodes of tilapias. (a) Immature *Schyzocotyle acheilognathi* (Yamaguti, 1934) from *Symphysodon aequifasciatus* from culture in the Czech Republic. (b) Larval *Amirthalingamia macracantha* (Joyeux et Baer, 1935) from tilapia hybrids in Israel. (c, d) Scolex and whole larva of *Neogryporhynchus lasiopeius* Baer et Bona, 1960. (e) Intestine of *Oreochromis mossambicus* from South Africa infected with gryporhynchid larvae (red). (f) Larva of *Tetracampos ciliotheca* Wedl, 1861 from the intestine of *Clarias gariepinus* from Malawi. (g) Larva of *Polyonchobothrium polypteri* (Leidig, 1853) Lühe, 1900 from the intestine of *Lates niloticus* from Kenya.

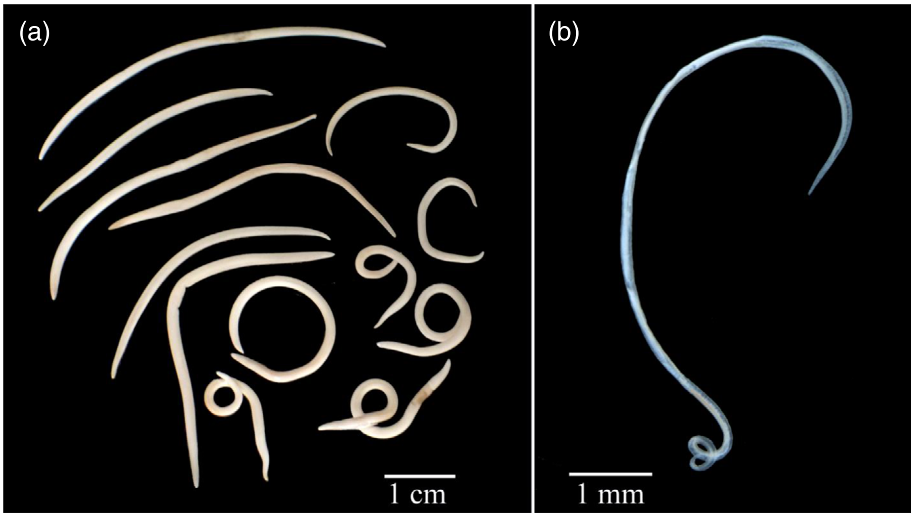

FIGURE 14 Nematodes of tilapias. (a) *Contracaecum* Type 2 larvae from *Oreochromis niloticus* from Egypt. (b) Stage L4 larva of *Rhabdochona* (*Globochona*) *paski* Baylis, 1928 from *O. niloticus* from Lake Victoria, Kenya

2.15 | Nematoda Diesing, 1861 (Obazoa: Opisthokonta: Metazoa: Ecdysozoa)

2.15.1 | Taxonomic identity

Nematodes are slender, cylindrical helminths characterised by a tubular digestive system and are covered by a cuticle. There are several records of nematodes in tilapia, but only a few of adult worms. Most records of adult nematodes are from their non-native range, such as *Goezia nonipapillata* Osorio-Sarabia, 1981 (Anisakidae) reported from *C. zillii*, *O. aureus* and *O. mossambicus* in Mexico (Michoacan),[446,447] *Rhabdochona kidderi texensis* Moravec et Huffman, 1988 (Rhabdochonidae) from *O. mossambicus* in the USA (Texas), and unusual reports of European *Schulmanela petruschewskii* (Shulman, 1948; Capillariidae) from cultured *O. aureus* in Cuba.[447,448] Only *Gendria tilapiae* Baylis, 1930 (Quimperiidae) was described from native *S. galilaeus* from Mali, but this species has not been reported from tilapias since Moravec.[449] There are records of camallanid nematodes such as *Paracamallanus cyathopharynx* (Baylis, 1923), *Paracamallanus laeviconchus* (Wedl, 1861) and *Procamallanus* (*Spirocamallanus*) *spiralis* Baylis, 1923 from *O. niloticus* or *O. mossambicus* in Egypt,[428] Nigeria,[450] the Republic of Benin[451] and South Africa,[452] *Procamallanus* (*S.*) *rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994) from *O. aureus* in Mexico[447] and *Procamallanus* (*Spirocamallanus*) sp. from *O. niloticus* in Pakistan.[453] Identification of these species may be unclear because these nematodes are not specific parasites of tilapia.[449] Other reports of adult nematodes from tilapia represent misidentifications, such as *Hysterothylacium habena* (Linton, 1900) (Raphidascarididae) reported from *O. aureus* in freshwater in Mexico (Michoacan),[446,447] because it is a marine nematode whose distribution does not include Mexico.[454] *Aplectana chamaeleonis* (Baylis, 1929) (Cosmocercidae) was reported by Chen[455] from *O. niloticus* in Lake Langano, Ethiopia, but this species is a specific parasite of reptiles. Moravec[449] mentioned that this finding was probably a misidentification of a *Labeonema* sp. (Atractidae), but no species of this genus has been reported in tilapia and this finding may represent a postcyclic infection in an atypical host.

Larval nematodes are frequently reported from various tissues of tilapia worldwide. Most of these reports refer to third-stage larvae (L3) of *Contracaecum* spp. (Anisakidae; Figure 14), which use fish-eating birds as their definitive hosts. These parasites are important because they have zoonotic potential. These larvae are mostly encapsulated in the internal organs and body cavity of tilapia with prevalence that can reach >50% and infection intensity that can reach up to 117 individuals per fish.[456] These L3 larvae have been frequently found in wild and farmed *O. niloticus* and *O. mossambicus* from Egypt,[457] Ethiopia,[456,458] Kenya,[459] South Africa,[452] Uganda[17] or Zimbabwe,[460] and also farms in Brazil, Mexico, El Salvador[17] and Peru.[461,462] Identification of *Contracaecum* spp. is complicated, but Moravec and Scholz[458] designated specimens from African tilapia as *Contracaecum* Type 2, although this may include several species.

There are reports of *Gnathostoma* spp. (Gnathostomatidae) from the musculature and internal organs of tilapia. Awosolu et al.[463] detected *G. spinigerum* Owen, 1836 in 17% of *O. niloticus* examined from Igbokoda River, Nigeria. Most reports are from tilapia in Mexico (Oaxaca, Puebla, Sinaloa and Veracruz) where three species, including *G. turgidum* Stossich, 1902, were reported from *O. aureus*, *O. mossambicus* and *O. niloticus*[464] and from *O. mossambicus* from Thailand.

Third-stage (L3) larvae of *Anguillicoloides crassus* (Kuwahara, Niimi et Itagaki, 1974) (Anguillicollidae), a typical eel pathogen, were found in the peritoneum and abdominal muscles of cultured *O. niloticus* in Belgium[465] and Egypt.[466] Tilapia can serve as a paratenic host for nematode larvae of this species. The fourth-stage (L4) larva of *Rhabdochona* (*Globochona*) *paski* Baylis, 1928 (Rhabdochonidae) was reported from *O. niloticus* from Lake Victoria, Kenya and DR Congo (Zaire) as *Rhabdochona congolensis* (Campana-Rouget, 1961) by Moravec[449] (Figure 14b). Species of *Amplicaecum* Baylis, 1920 (Ascarididae), *Camallanus* sp., *Capillaria* sp. (Capillariidae), *Cucullanus* sp. (Cucullanidae), *Eustrongylides* sp. (Dioctophymidae), *Procamallanus* sp., *Rhabdochona* sp., *Spiroxys* sp. (Gnathostomatidae) or even *Necator americanus* (Stiles, 1902)

(Ancylostomatidae) and *Porrocaecum* sp. (Toxocaridae) have been reported from *O. niloticus* and *O. mossambicus* in Africa (Table S2)[439,449,463,467] and the Neotropics,[447] but some of these findings could be misidentifications or accidental infections.

2.15.2 | Pathogenicity

Nematode larvae can invade any tissue of the host, including the pericardium, which can have negative effects on the health of the host. Tissue response to infection by *Contracaecum* spp. larvae includes the formation of epithelioids, the fibrous encapsulation of larvae, which can lead to mesenteric infections with extensive fibrosis and visceral adhesions in larger fish.[468,469]

Gnathostoma spp. use a wide range of vertebrates as paratenic hosts, including humans, where they can cause a serious disease, gnathostomiasis, while the adults parasitise in the stomach of mammals.[470] Humans become infected by eating raw or undercooked fish infected with L3 larvae. The disease is characterised by migratory inflammatory edema with larvae encapsulated in the stomach or ocular cavity. Most human cases (about 25,000 reported cases) are caused by *G. binucleatum* Almeyda-Artigas, 1991 in the Neotropical region and *G. spinigerum* Owen, 1836 with a cosmopolitan distribution, including Africa.[470]

2.15.3 | Global translocations

The nematodes of tilapia are not well studied or understood. Most records of adults are not from the native range of tilapia but from the introduced range,[447] except for a few camallanid species, but their identification should be verified.[449] Nematode larvae (mainly those of *Contracaecum* spp.) are also more frequently reported from the introduced range of the fish, but their identification requires the use of specific molecular markers which were not applied in the initial studies.

2.15.4 | Research

The most economically important nematodes in tilapia aquaculture are L3 of *Contracaecum* spp., which are widespread. Their control is difficult because they are associated with fish-eating birds. In addition, the larvae of the genus *Gnathostoma* have zoonotic potential and tilapia infected with them can also infect humans.

2.16 | Acanthocephala Koelreuter, 1771 (Obazoa: Opisthokonta: Metazoa: Gnathifera: Syndermata: Acanthocephala)

Acanthocephalans are a small group of endoparasites closely related to rotifers (Wey-Fabrizius et al. 2014).[471] They are characterised by a spiny eversible proboscis that anchors the parasite to the intestine of their definitive vertebrate hosts. Acanthocephalans have an indirect life-cycle with an intermediate invertebrate host.

2.16.1 | Taxonomic identity

Few species of acanthocephalans are reported from tilapia. These parasites can be identified based on morphological characteristics of the proboscis, the size, shape, number and distribution of proboscis hooks, the shape and dimensions of the trunk and the presence and distribution of trunk spines.[472] Most records of adult acanthocephalans in tilapia involve *Acanthogyrus* (*Acanthosentis*) *tilapiae* (Baylis, 1947; Quadrigyridae), a widely distributed intestinal parasite of >40 freshwater fish species in Africa.[473,474] This species has been reported from domesticated and wild populations of *C. rendalli*, *C. zillii*, *O. andersonii*, *O. aureus*, *O. leucostictus*, *O. macrochir*, *O. niloticus*, *O. spilurus*, *S. galilaeus* and *S. melanotheron* from Burkina Faso, Chad, Egypt, Ethiopia, Kenya, Madagascar, Nigeria, Congo, Senegal, Uganda and Zambia (Table S2).[473] Adult *Acanthogyrus* (*A.*) sp., most probably *A.* (*A.*) *tilapiae*, are reported from farmed and wild *C. zillii*, *O. macrochir*, *O. niloticus*, *O. mossambicus* and *S. galilaeus* from Egypt, Ethiopia, Kenya, Nigeria, Uganda and Zimbabwe (Table S2).[467,475–477] Tilapia become infected with *A.* (*A.*) *tilapiae* after consuming its unidentified invertebrate intermediate host, copepods of the genus *Cyclops* Müller, 1785.[478] *Acanthogyrus* (*A.*) *tilapiae* has a short cylindrical proboscis armed with 24 hooks arranged in three circles of eight hooks each and a trunk armed only anteriorly with circles of spines that are usually dorsally incomplete.[479] This acanthocephalan can occur at high prevalence in cultured (>65%)[480] and wild (>78%)[481] tilapia.

Other adult acanthocephalans are infrequently reported from cultured and wild tilapia in Africa, Asia and Oceania. An unidentified species of *Paragorgorhynchus* Golvan, 1957 (Rhadinorhynchidae) was reported in the intestine of wild *C. zillii* from Kenya[477] and a *Telosentis* sp. (Illiosentidae) was detected in wild populations of invasive *O. mossambicus* in Australia.[83] Adult *Neoechinorhynchus* (*Neoechinorhynchus*) *rutili* (Müller, 1780) (Neoechinorhynchidae) were recorded from wild *C. zillii*, *O. niloticus* and *S. galilaeus* from Nigeria,[482–484] and poorly described specimens ascribed to *N.* (*N.*) *quinghaiensis* Liu, Wang et Yang, 1981 were recorded from wild *O. niloticus* from the Philippines.[485] *Neoechinorhynchus* (*N.*) *quinghaiensis* was reported as *Neoechinorhynchus* sp. or *Acanthogyrus* sp. from cultured and wild *O. niloticus* in the Philippines.[486–489] Records of *N.* (*N.*) *rutili* and *N.* (*N.*) *quinghaiensis* in tilapia seem to be erroneous, because most species of *Neoechinorhynchus* are morphologically difficult to distinguish.[490] *Neoechinorhynchus* (*N.*) *rutili* mature in fresh- and brackish water fish from the northern Holarctic Region,[491] while *N.* (*N.*) *quinghaiensis* infects cyprinids from China,[492] placing doubt on these identifications.

Immature *Pallisentis* (*Pallisentis*) *nandai* Sarkar, 1953 (Quadrigyridae) were reported in the liver of farmed *O. niloticus* from Bangladesh.[493] In this unusual site of infection this acanthocephalan could not produce eggs.[494] *Pallisentis* (*P.*) *nandai* occurred at 23% prevalence in farmed *O. niloticus* from Bangladesh,[493] but this parasite appears unusual in tilapia.

The infective larval cystacanths of acanthocephalans are not typical parasites of farmed or wild tilapia. Infective stages of *Polyacanthorhynchus kenyensis* Schmidt et Canaris, 1967 (Polyacanthorhynchidae) use tilapia as paratenic hosts, but the identities of the intermediate and definitive hosts remain unknown.[495] Cystacanths of *P. kenyensis* are reported encapsulated in the liver of 27% of wild *C. zillii* and 44% of *O. leucostictus* from Kenya.[496] Cystacanths of *Polymorphus spindlatus* Amin et Heckmann, 1991 (Polymorphidae) were observed free in the intestine of wild *O. niloticus* from Peru.[497] This species uses black-crowned night herons (*Nycticorax nycticorax* [Linnaeus, 1758]) as its definitive host,[498] and represents the only acanthocephalan species reported in tilapia from the Americas. Briones et al.[485] ascribed a single specimen of *Bolbosoma* sp. (Polymorphidae) from the mesenteries of *O. niloticus* from the Philippines, but it is obvious from their figure 3 that this worm is a species of *Southwellina* Witenberg, 1932, which mature in fish-eating birds.[499] Cystacanths of *Bolbosoma* spp. are, furthermore, recorded from marine fish and adults infect cetaceans.[500]

2.16.2 | Pathogenicity

The penetration of the proboscis of *A.* (*A.*) *tilapiae* into the intestine destroys the mucosal folds, causes lacerations of the intestinal villi from the proboscis hooks and provokes severe degeneration and necrosis of the mucosal epithelium.[327,481] Other changes observed in infected tilapia include desquamation of the mucosa, interstitial oedema and enteritis.[481,501,502] Aggregated infiltration of eosinophils, fibroblasts, lymphocytes and macrophages occurs at the site of attachment in response to chronic inflammation of the tissue.[481,502] Little is known about the pathological effects of adults of other acanthocephalan species in cultured tilapia, but it is likely that the submucosal lesions, loss of the mucosal layer, decreased haematocrit and red blood cell counts observed in *N.* (*N.*) *quinghaiensis* (syn. *Acanthogyrus* sp.) infections in *O. niloticus* in the Philippines[489] are typical.

The threat that immature *P.* (*P.*) *nandai* poses to the health of cultured tilapia is unknown, but these parasites probably cause mechanical damage, local necrosis, and hepatic inflammation.[503] Pathogenesis of *P. kenyensis* in tilapia is unknown, but its cystacanths may cause local necrosis and inflammation of the liver like that caused by cystacanths of other acanthocephalan species in other fish.[503]

2.16.3 | Global translocations

There is insufficient evidence to indicate that acanthocephalans have been translocated with tilapia, but Golvan[504] suggested that *A.* (*A.*) *tilapiae* was introduced to Madagascar with non-native cichlids from mainland Africa. Translocation of this parasite to native cichlids of Madagascar was not confirmed in the thorough survey there by Šimková et al.[337]

2.16.4 | Research

To better understand the diversity, distribution and life-cycles of acanthocephalans of tilapia, molecular and morphological approaches on larval and adult stages need to be integrated. Sequences of nuclear and mitochondrial genes are necessary to clarify the identity of acanthocephalans[505,506] because of interspecific homogeneity of morphological characters.[507] Future research includes histopathological investigation of alterations caused by larval cystacanths and adult acanthocephalans in tilapia to identify threats to cultured fish and better understand if treatment would be beneficial.

Metabarcoding using high-throughput sequencing technology has advanced our understanding of the endoparasite diversity of fish.[508] Using this technology, Elsaied et al.[509] detected a *Neoechinorhynchus*-like operational taxonomic unit (OTU) in the gut content of wild *O. niloticus* from Lake Nasser, Egypt. The taxonomic assignment of this OTU as *Neoechinorhynchus* by Elsaied et al.,[509] however, appears erroneous; *Acanthogyrus* (*A.*) *tilapiae* is the only acanthocephalan reported from tilapia in Lake Nasser.[502,510] Elsaied et al.[509] extracted DNA from eggs released by gravid females to the lumen of infected *O. niloticus*, and this approach has merit for non-destructive detection and identification of all endoparasites.

2.17 | Pancrustacea Zrzavý et Štys, 1997 (Crustacea) (Obazoa: Opisthokonta: Metazoa: Ecdysozoa: Pancrustacea)

Four groups of parasitic crustaceans (Copepoda, Branchiura, Pentastomida and Isopoda) can infect tilapias. Copepods have short cylindrical, segmented bodies. Branchiurans are obligate parasites with hooked maxillae or sucking discs. Pentastomids are elongate segmented crustaceans with five anterior protruberances; two pairs of hooks for attachment and the mouth. Isopods have rigid, segmented exoskeletons, two pairs of antennae, seven pairs of jointed limbs on the thorax and five pairs of branching appendages on the abdomen that are used in respiration. Crustaceans are mostly ectoparasites with direct life-cycles, and only pentastomids are endoparasites of internal organs with complex life cycles using some fish (including tilapias) as their intermediate host and tetrapods (e.g. crocodiles) as their definitive hosts. Some Copepoda Edwards, 1840 and all Branchiura Thorell, 1864 are ectoparasites of fish including tilapia and inhabit the gills, fins and skin.[511,512] The morphology of adult copepod parasites is adapted for attachment with appendages that are modified into hooks and suckers or cuticular outgrowths of the carapace. They are loosely host specific, most species infecting more than one host species.

The most important crustaceans for tilapias are copepods and branchiurans.

2.18 | Copepoda Edwards, 1840 (Obazoa: Opisthokonta: Metazoa: Ecdysozoa: Pancrustacea)

The parasitic copepods are a diverse group, and some are highly modified as adaptations to parasitism. Common features are a complete or partial loss of segmentation, paired egg sacs that hang from the genital somite of the adult females for the duration of embryonation, some instars are lacking in the larval development and sexual dimorphism occurs (Figure 15b–d, k–m). Larval stages in some families have morphology like their free-living relatives and are free-living for much of their lifecycle. The simplest adaptations to parasitism are observed in Ergasilidae, where adult females have grasping appendages and retain segmentation of the thorax. In the highly modified Lernaeidae, however, in females the second antennae are extensively modified, segmentation is lost, the ovaries have attained enormous proportions and the thorax has consequently enlarged, elaborate attachment structures have developed, and the second maxillae are transformed into powerful attachment structures.

The adult females of *Ergasilus* von Nordmann, 1832, *Lernaea* Linnaeus, 1758, *Opistholernaea* Yin, 1960 and *Lamproglena* von Nordmann, 1832 attach permanently to a host after insemination. A single female produces up to 30 eggs at a time in egg sacs (Figure 15b–d, k–m). No intermediate hosts are required; a single egg-bearing female or two larvae introduced via transportation of infected fish or water can establish an infection.

Adult female *Lamproglena monodi* Capart, 1944 attaches with modified maxillulae on the gills of their hosts (Figure 15a–c). Capart[513] reported it from *Serranochromis thumbergi* (Castelnau, 1861) from Lake Mweru, and later also from *Haplochromis nubilus* (Boulenger, 1906) from the Molindi River, *Haplochromis macrops* (Boulenger, 1911) from the Rutshuru River, *Haplochromis eduardii* Regan, 1921 and *Haplochromis serridens* Regan, 1925 from Lake Edward, *Pseudocrenilabrus philander* (Weber, 1897) from the Kafubu River and *Hemichromis fasciatus* Peters, 1857 from the Legide River, the Congo. In Lake Victoria, Gobbin et al.[514] reported *L. monodi* from 14 sympatric Lake Victoria cichlids [*Mbipia lutea* (Seehausen et Bouton, 1998), *M. mbipi* Lippitsch et Bouton, 1998, *Neochromis gigas* (Seehausen et Lippitsch, 1998), *N. omnicaeruleus* (Seehausen et Bouton, 1998), *Neochromis* sp., *N. rufocaudalis* (Seehausen et Bouton, 1998), *Pundamilia pundamilia* Seehausen et Bouton, 1998, *P. nyererei* (Witte-Maas et Witte, 1985), *Pundamilia* sp., *Lithochromis* sp., *Haplochromis cyaneus* (Trewavas, 1935), *Parachromis chilotes* (Boulenger, 1911), *P. sauvagei* (Pfeffer, 1896) and *Parachromis* sp.].

In Egypt, Ibraheem and Izawa[515] reported this species from *O. niloticus*, *S. galilaeus* and *C. zilli*. In Brazil, Martins et al.[516] reported a *Lamproglena* sp. in the Guandu River, State of Rio de Janeiro and in the State of Santa Catarina. It was later identified and redescribed as (co)introduced *L. monodi* present on the indigenous *Astronotus ocellatus* (Agassiz, 1831) and *Cichla ocellaris* Bloch et Schneider, 1801, and Azevedo et al.[517] reported this species from introduced *O. niloticus* and *T. rendalli* (Boulenger, 1897). In the Philippines, Yambot and Lopez[518] reported *L. monodi* from cultured *O. niloticus*.

Ergasilus species infect tilapia in Africa.[511] They attach to their host's gills or skin with modified antennae and feed on tissue (Figure 15d–g). They are not strictly host specific.

The anchor worms, *Lernaea barnimiana* Hartmann, 1865, *L. hardingi* Fryer, 1956, *L. lophiara* Harding, 1950, *L. palati* Harding, 1950 and *L. tilapiae* Harding, 1950 have been reported on tilapia species in Africa[511] but these species have not been recorded outside Africa, except for a report of *L. lophiara* on a translocated population of *O. mossambicus* in Thailand.[334] Female *Lernaea* spp. can be observed macroscopically, and the head and anterior part of the thorax are embedded in the host muscle, under scales and on fins (Figure 15h). It attaches firmly with cuticular outgrowths forming anchors (Figure 15i), the minute head appendages scrape host tissue into the mouth, while the egg-string bearing thorax and the abdomen protrude from the host.[519]

Opistholernaea laterobranchialis (Fryer, 1959) is reported from *O. niloticus*, *O. andersoni* and *O. macrochir* from the Nile and Zambesi rivers.[520–522] The parasite head embeds in the palate of the fish and grows through the bony tissue to protrude through the eye socket, where it forms a capsule. The egg-bearing thorax and abdomen hangs from the roof of the buccal cavity of the host. Grobler[522] reported that the parasite may reach 18 mm in length and can be removed only after dissection of the bony tissue.

2.18.1 | Pathology

Ibraheen[523] described the pathological changes caused by *L. monodi* on the gill lamellae: attachment of the females is followed by proliferation of gill epithelium with fusion of adjacent filaments in heavy infections (Figure 15c). *Lamproglena monodi* feed on blood and the filament tip may become necrotic when blood supply is interrupted.[523]

Ergasilus spp. feed on gill tissue. Following attachment to the gills, the antennae may fuse in some instances.[524] Encirclement of a gill filament by the antennae causes compression of the gill tissue,[525] which in some instances constricts blood flow in that gill filament leading to its eventual atrophy.[519] Epithelial hyperplasia is seen in the region close to the point of parasite attachment; tissue changes at these points lead to the eventual loss of functionality with subsequent negative impacts on gas exchange (Figure 15d).[525]

Lernaea infections cause irritation that induces agitation in hosts that manifests as rubbing their bodies on objects in their environment. Adult females can be observed macroscopically and the area surrounding the attachment site usually displays an approximate 1 cm diameter field of haemorrhagic skin, impacting fish marketability negatively.[526] Individual *Lernaea* remain attached to the site which they colonise and feed using their appendages to scrape host tissue towards their buccal cavity. Lesions without parasites are commonly observed where parasites have been dislodged or have died; these sites remain inflamed until the wound has healed. Intense infections cause host fish to become sluggish and chronic infection results in the production of proliferative hyperplastic connective tissue that can encapsulate the parasite or may protrude from the skin surface of the host. Infected fish have reduced haematocrit and condition.[334,527] The epidermis surrounding the lesion is spongiotic with eosinophilic granular cells (EGCs) and lymphocytes, and infection sites often

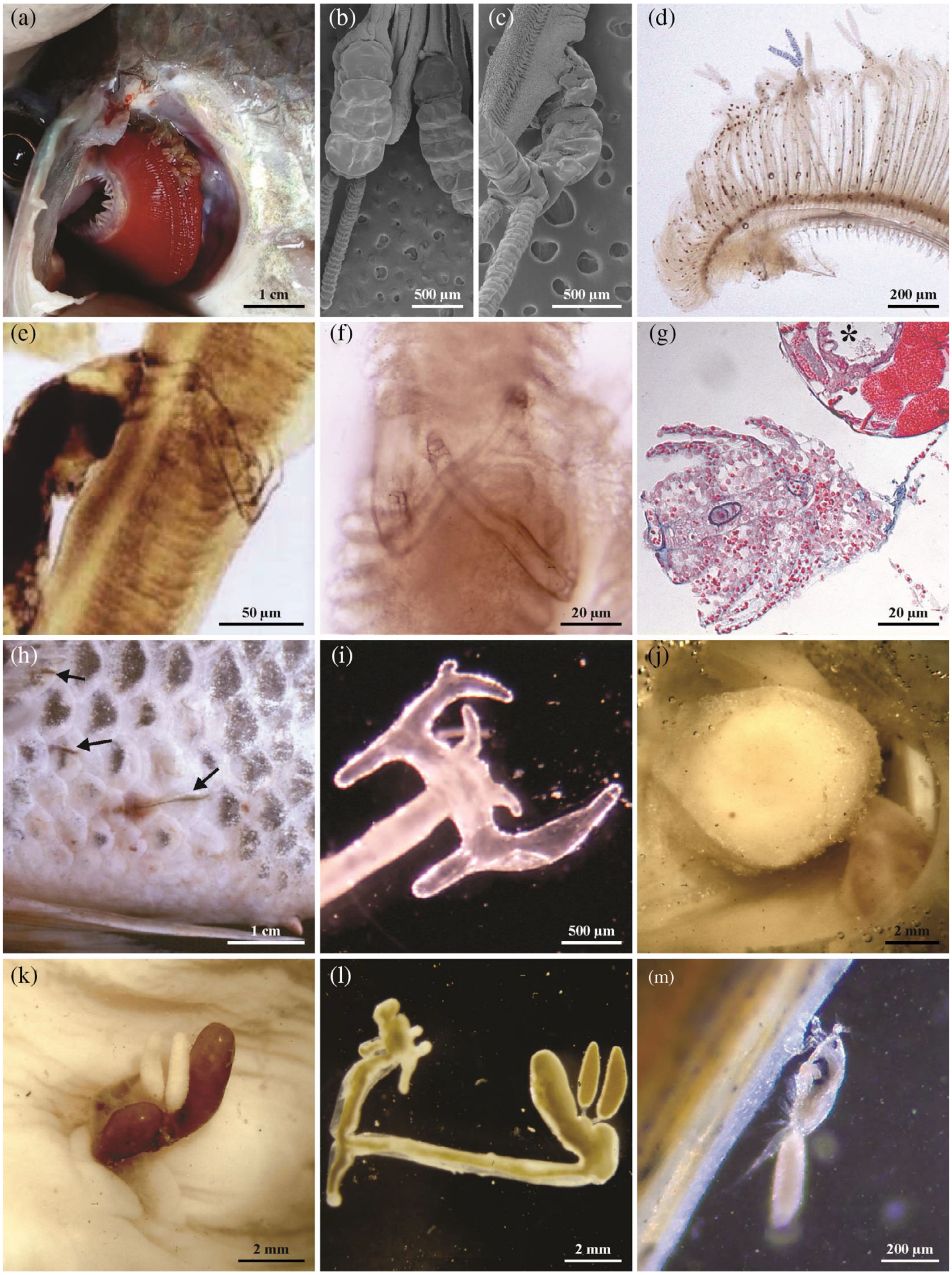

FIGURE 15 Crustacean copepod parasites of cultured tilapias. (a) Macrograph of *Lamproglena monodi* Capart, 1944 females on the gills of *Oreochromis niloticus*. (b) Scanning electron micrograph of *L. monodi* with paired egg sacs on the gills of *O. niloticus*. (c) Scanning electron micrograph of *L. monodi* feeding on the gills of *O. niloticus*. (d) Adult *Ergasilus sarsi* Capart, 1944 females attached to the gill filaments of its host. (e) *Ergasilus mirabilis* Oldewage et Van As, 1987 using their modified antennae in attachment to their host's gill filaments. (f) The antennae of *E. mirabilis* as seen from a different aspect. (g) Cross-section through a gill filament with *E. sarsi* with evident proliferation of the epithelia of the gill lamellae as well as the host tissue (*) in the parasite's intestinum. (h) Adult females of *Lernaea cyprinacea* L., 1758 (arrowed) on the skin of *Oreochromis mossambicus*. (i) Anterior of *L. cyprinacea* displaying its anchors. (j) Capsule housing the anterior of *Opistholernaea* Yin, 1960. (k) The posterior region of *Opistholernaea laterobranchialis* (Fryer, 1959) protruding into the buccal cavity. (l) *Opistholernaea laterobranchialis* released from the enclosing tissues of its host. (m) *Neoergasilus japonicus* (Harada, 1930) attached to the gills of *O. mossambicus* using their modified antennae. Images (a) and (b) are provided courtesy of Nehemiah Rindoria; images (i)–(k) are provided courtesy of Johan Theron and image (m) courtesy of Dr Quinton Dos Santos

become secondarily infected by bacteria and fungi. Blood may ooze into the water behind the parasite from the attachment lesion.[526,528] Larval infections can occur on the gills and cause respiratory distress, epithelial hyperplasia and telangiectasis.[334] Decreased haematocrit is caused by intense lymphocytopenia, neutrophilia and infiltration of immature leucocytes, haemorrhaging and haemodilution because of the ingress of water through the permanently open wound created by the parasite.[528] In small fish this parasite can penetrate the internal organs and cause mortality.[334] Fish that recover resist infection and if infected, the lesions are markedly smaller, probably due to an anamnestic immune response elicited by memory cells.[528]

The pathology associated with *Opistolernaea laterobranchialis* was described by Grobler.[522] The head and thorax, up to the level of the second pair of thoracopods, are surrounded by a large (0.7 mm diameter) bulbous granuloma consisting of three layers; areolar tissue, granular connective tissue and a multilayered epithelium. The remainder of the parasite thorax is covered by a simple, thin connective tissue sleeve containing melanocytes.[522]

2.18.2 | Treatment

Embedded *Lernaea* females are difficult to treat; eradication can require the use of products with strong negative environmental effects. Insecticides are effective but, in many countries, their use is not permitted due to the environmental effects of discharge; they are non-specific, kill non-target organisms and leave residues that can affect human health.[529] Infections can be managed by eradicating copepodite stages with organophosphate trichlorphon at 0.25 ppm with repeated treatments at the duration of the infective larval stages; trichlorphon kills copepodites but not nauplii.[334] Treatment with the carbamate 2-isopropoxyphenyl-N-methylcarbamate (Baygon™) elicited the emergence of resistance in four generations.[530] Sodium chloride eradicates all *Lernaea* at 20–40 mg/L at pH >6, is non-residual and is relatively environmentally benign; conditions for its use may be defined by local regulatory authorities including timing of treatments, volume and concentration used, discharge conditions, dilution and so forth. In recirculation systems, sodium chloride also kills the bacterial populations in biofilters, leading to nitrate build-up that needs to be managed while the bacterial population in the biofilter re-establishes.[531]

Woo and Shariff[532] reported that 50% of parasite eggs collected from fish that recovered from infection with *Lernaea* were viable, indicating a reduction in parasite viability when reinfection occurs. Fish recovering from infection recovered from subsequent infections faster, while parasites on fish that had recovered lost more egg sacs than *Lernaea* on first infection fish. If no naïve fish are introduced into closed aquaculture systems, infective larvae will decline with time and eventually the system should be safe for restocking. This indicates acquired immunity in the recovered fish. Shariff et al.[530] recommend that the parasite could be managed by removing all fish from a pond for 7–9 days because the absence of hosts would result in the loss of all larval stages of the parasite.

2.18.3 | Global translocations

Lernaea cyprinacea L., 1758 is one of the most invasive fish parasites and has spread to all continents,[533] and it is reported from *O. mossambicus* in South Africa[534] and *O. mossambicus*, *Oreochromis placidus* and *T. rendalli* in Zimbabwe.[535]

Neoergasilus japonicus (Harada, 1930) attaches predominantly to the base of the fins of their hosts but also on the operculum (Figure 15m). It was originally described from Asia,[536] but Hudson and Bowen[537] noted that it spread through aquaculture and the aquarium trade over 20 years. Its occurrence is recorded in Alabama, USA,[538] Cuba,[539] Mexico,[540] Peru[541] and South Africa.[542] It displays little host specificity and has been recorded from a wide variety of freshwater fish including cyprinids, percids, centrarchids, ictalurids and cichlids. In Japan *N. japonicus* is reported from redbelly tilapia (*C. zillii*), Mozambique tilapia (*O. mossambicus*) and Nile tilapia (*O. niloticus*).[543]

2.18.4 | Research

Parasitic copepod research focuses on parasite taxonomy, biodiversity and distribution. Research on *Lernaea* and other copepod parasites is complicated by their taxonomy being based on the limited morphological traits. In *Lernaea* the morphology of the anchor is used as a taxonomic character and many nominal species are probably synonyms; experimental infections show that anchor morphology and growth are affected by host anatomy.[544,545] Pallavi et al.[546] found that 18S and 28S sequences from four *Lernaea* specimens assigned to four different morphological species showed that all specimens were *L. cyprinacea*. Hua et al.[547] similarly concluded that *L. cyprinacea* and *L. cruciata* Lesueur, 1824 are conspecific based on their molecular data.

Copepod parasites are good bioindicators of metal and organic pollution.[548,549] Crustacean parasites can be collected from living hosts without harming them, providing further advantages over helminths and fish as indicators of pollution. It may also be possible to use data on the effect of adverse water quality to inform treatment of crustacean parasites provided safety margins are understood.

Development of treatment for crustacean parasites is focusing on natural compounds and application of nanocomposites. The *Lernaea* 1 h/LC_{50} for chitosan-silver was 5.495 ppm. When infected fish were exposed to the LC_{50} concentration for 24 h, it caused pathological changes to the *Lernaea* cuticle that dislodged all females and was followed by rapid healing of parasite-induced wounds.[526]

2.19 | Branchiura Thorell, 1864 (Obazoa: Opisthokonta: Metazoa: Ecdysozoa: Pancrustacea)

The Branchiura (fish lice) are covered by a dorsal carapace that is round to oval, with two carapace lobes and a bilobed abdomen. On average they are 3–7 mm in length, although gravid females may reach 10 mm. Females are larger than males and the sexes can be distinguished by the presence of two round spermathecae in the abdomen of females, whereas males have one testis per abdomen lobe and peg and socket copulatory structures are present on the third and fourth thoracopods. The mouth is carried on a mouth tube, which extends ventrally, with the mandibles situated just inside the opening.

Males and females of *Argulus* Müller, 1785 and *Dolops* Audouin, 1837, as well as all life stages apart from the eggs, are parasitic on fish hosts. Branchiurans attach with maxillules that are modified to form suckers (*Argulus*; Figure 16a) or strong hooks (*Dolops*; Figure 16c) to the skin, in the buccal cavity or in the gill chamber (*Dolops*; Figure 16c). These parasites retain their ability to swim through life and can switch hosts; adults and larvae can survive without a host for up to 9 days.[550] Many species have been reported to have low host specificity.[512,551] *Argulus japonicus* Thiele, 1900, *A. foliaceus* (Linnaeus, 1758) and *A. coregoni* Thorell, 1866 are pathogenic and can reach high numbers in impoundments[552,553] or aquaculture.[551,554] Branchiurans deposit their eggs in rows on a substrate. A single female can deposit hundreds of eggs[555] which typically hatch within 21 days at 25°C, but the time to hatching is temperature dependent.[556]

Dolops spp. are recorded from South America, Africa, and Tasmania. *Dolops ranarum* (Figure 16c) occurs in Africa and infects *O. mossambicus* in the Zambezi River (Fryer, 1960), various rivers in the Limpopo River system in South Africa (Avenant and Van As, 1985) and the Okavango River, Botswana,[557] *Oreochromis variabilis* and *Oreochromis esculentus* (Graham, 1928) in Lake Victoria, Uganda[558] and *Serranochromis* sp. in the Kafue River, Zambia.[558] It was also recorded from *O. niloticus* in Lake Tana, Ethiopia (Fryer, 1965).

The *Argulus* species reported from tilapia are *Argulus africanus* Thiele, 1900, *A. cunningtoni* Fryer, 1965, *A. fryeri* Rushton-Mellor, 1994, *A. jollymani* Fryer, 1956, *A. kosus* Avenant-Oldewage, 1994, *A. monodi* Fryer, 1959, *A. rhipidiophorus* Monod, 1931, *A. striatus* Cunnington, 1913 and *A. tristramellae* Paperna, 1967 is recorded from *Tristramella* sp.[559] *Argulus japonicus* was introduced into Africa with cyprinids and is also reported from *O. mossambicus*.[552,560]

Argulus species transmit viruses, skrjabillanid and daniconematid nematodes.[519,561–563] In Mexico, Moravec et al.[447] reported *Argulus mexicanus* Pineda, Paramo et del Rio, 1995 collected from the cichlid *Mayaheros urophthalmus* (Günther, 1862; syn. *Cichlasoma urophthalmus*) as an intermediate host for daniconematid nematodes. The prevalence of infection was low at 1.29% with an intensity of 1–6 nematode larvae/*Argulus*. This highlights the role of argulids in the transmission of nematodes and the need for a detailed examination of *Argulus* specimens collected from the commercial species of tilapia.

2.19.1 | Pathology

Branchiuran parasites feed on the blood and tissue of their hosts.[512] Avenant-Oldewage[564] described the pathology caused by *Dolops ranarum* (Stuhlmann, 1891). *Dolops* spp. attach by inserting the hooks on the maxillules (Figure 16c), which causes local inflammation, disrupting osmotic control and providing a route of entry for secondary pathogens such as *Aeromonas* Stanier 1943 and opportunistic fungi. Avenant-Oldewage[564] showed that feeding by *D. ranarum* removes the epidermis of the host, leaving the dermis exposed (Figure 16d–f). Tavares-Dias et al.[565] reported that in *D. carvalhoi*, parasite intensity of 3–30 was not correlated to reduced haematocrit but was associated with increased thrombocyte and white blood cell counts and lower plasma glucose and serum electrolyte levels in infected fish.

In *Argulus*, the pre-oral and buccal spines are supplied by glands.[566] The parasites release digestive enzymes onto the host surface,[567] subsequently ingesting the predigested host tissue and blood. The process of feeding creates open wounds and although fish tolerate low and moderate levels of *Argulus* with few signs of disease, localised inflammation and damage at the affected site may lead to secondary infections. The parasite's high reproductive rate,[556] gravid females laying between 1 and 9 strings of eggs with 5–226 eggs per string, and the ability of eggs to overwinter two seasons[568] can quickly escalate an infection. Severe infections (i.e., hundreds of parasites per fish) cause extensive skin damage and inflammation which debilitates the host and reduces the ability of the host to osmoregulate.[569] Although the records of Kruger et al.[552] and Avenant-Oldewage[560] refer to the infection of wild tilapia in the Olifants River System, argulids are noted pathogens of fish held under culture conditions. *Argulus africanus* infection was common on *O. niloticus* in tanks at Kigera Dam, Lake Kainji, Nigeria (prevalence of 15%) and their presence resulted in disruption to the gill rakers.[156]

2.19.2 | Treatment

Fish remove and consume *Dolops* specimens from each other[519] and occasionally prey on free-swimming *Argulus* individuals.[570] Mechanical removal of parasites was suggested as a control method by Benz et al.[571] but is impractical for large-scale aquaculture. Hakalathi et al.[572] successfully reduced the number of parasites in ponds by deploying wooden egg laying plates in fishponds and removing them before the *Argulus* hatched, reducing the number of juvenile parasites in the ponds. Parvez et al.[573] painted chlorinated rubber onto the plates, which attracted more females to the plates, and increased removal of eggs and improved reduction in infection intensities.

The effect of pesticides on the environment prompted a focus on natural treatments. Sahoo et al.[574] analysed the full transcriptome of *Argulus siamensis*, which could direct development of plant-derived targeted treatments. The number of eggs per oviposition and their hatching success in *Argulus bengalensis* was decreased by exposure to 15 mg/L of an aqueous extract of neem, *Azadirachta indica* A. Juss (Meliaceae).[575] Development of *A. japonicus* eggs was disrupted after exposure to *Moringa oleifera* Lam. (Moringaceae) extract.[576]

Essential oil of lemon grass, *Cymbopogon citratus* (de Candolle) (Poaceae) against adult *Argulus* sp. and *Dolops discoidalis* was maximally effective at 140 μg/L. The LC50-24 h for *Argulus* sp. was 83.98 μg/L and the LC50-24 h for *D. discoidalis* was 82.48 μg/L,[577] suggesting that plant products have promise for management of these parasites. They, furthermore, reported that the eggs also lost their sticky cover after 30 days, dislodged from the substrate, sunk to the bottom and that altered anatomy of the ommatidia (eyes) occurred. These studies show promise for alternatives that consider the environmental impact.

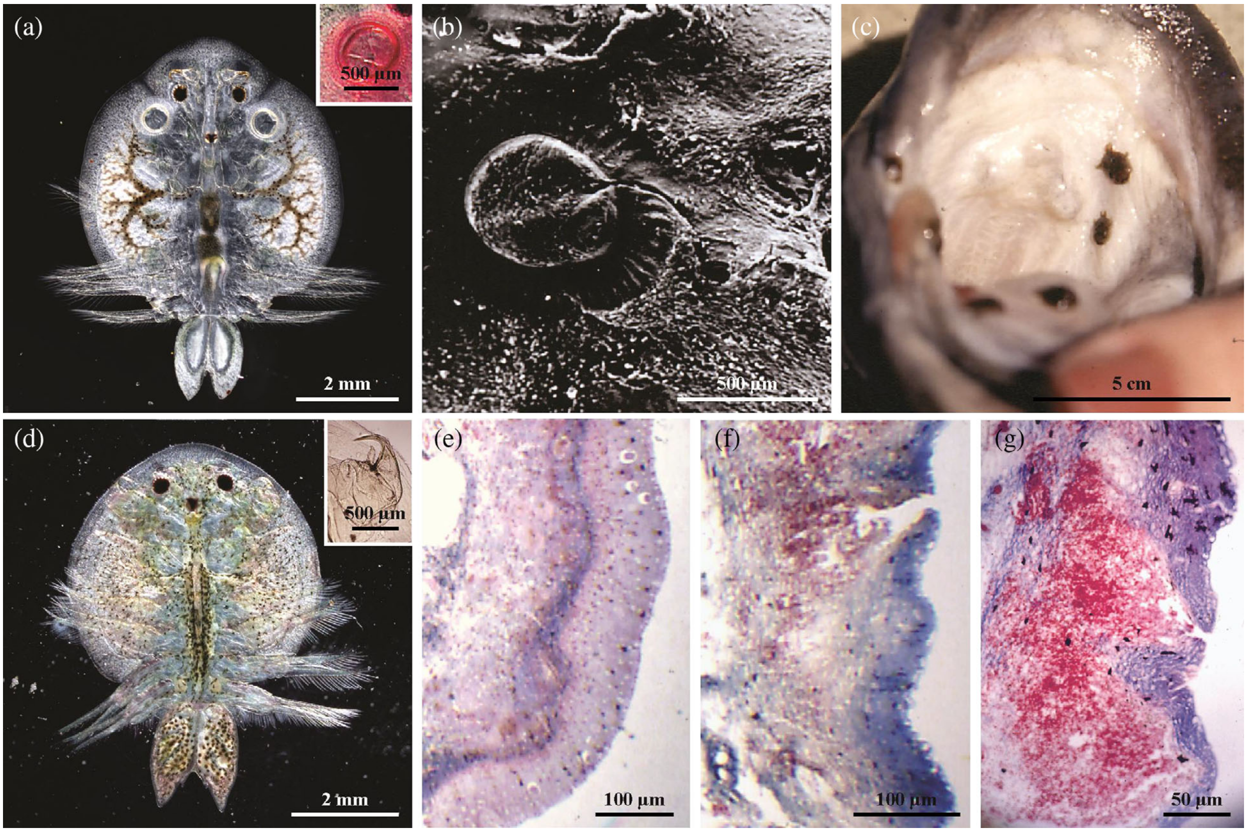

FIGURE 16 Crustacean branchiuran parasites of cultured tilapias. (a) Male *Argulus japonicus* Thiele, 1900. The inlay shows an enlarged image of an attachment sucker. (b) Scanning electron micrograph of the damage to host tissue inflicted by *A. japonicus*. The image shows an imprint of the suckers, destruction of the epithelium and open feeding wounds. (c) *Dolops ranarum* (Stuhlmann, 1891) in situ within the buccal cavity of *Oreochromis mossambicus*. (d) *Dolops ranarum*. The inlay shows the enlarged hook on the maxillulae. (e) Normal skin condition of *Clarias gariepinus* Burchell, 1822. (f) The skin of *C. gariepinus* showing denudement of the epithelium and inflammation as a consequence of *D. ranarum* attachment and activity. (g) The attachment of *D. ranarum* has resulted in extensive damage and haemorrhaging of the host's epithelium

2.19.3 | Global translocations

It is unclear if branchiurans have been translocated with tilapia, but several spillback infections have occurred from the environments to which tilapia are translocated. *Argulus japonicus* is a cosmopolitan species.[578] It infects *O. mossambicus* in South Africa,[552,560] while *A. coregoni* infects red *Oreochromis niloticus* × *Oreochromis mossambicus* in Malaysia[579] and *Argulus indicus* Weber, 1892, red *Oreochromis niloticus* × *Oreochromis mossambicus* in Thailand.[580] There is only one report of an introduction of *Dolops*, that is from Brazil to Japan and is that of *Dolops carvalhoi* Lemos de Castro, 1949 with gulper catfish, *Asterophysus batrachus* Kner, 1858.[581]

2.19.4 | Research

Research on Branchiura investigates biodiversity and new or improved treatment regimes. Morphological differences in descriptions of branchiurans are not conclusive and frequently poorly documented. There is, therefore, a drive to clarify the taxonomy[582] concurrent with the description of new species[583–585] and new hosts in South America.[586] If described species are sequenced, synonymies can be identified provided DNA sequences are included more frequently in descriptive studies. Saurubh et al.[587] reported that *Argulus* infection suppresses alpha-2 macroglobulin, serum complement activity response and ceruplasmin levels, indicative of stress. Ruane et al.[588] reported a humoral response to *Argulus foliaceus* antigens in trout and effective vaccines for *Argulus* are a focus for development.

2.20 | Pentastomida Diesing, 1836 (Obazoa: Opisthokonta: Metazoa: Ecdysozoa: Pancrustacea)

Pentastomids are dioecious flattened, segmented crustaceans ranging from 1 to 16 cm in length (males 1–2 cm; females 2–16 cm), and are covered in a chitinous cuticle, with five anterior appendages: a mouth and four hook-bearing appendages. The members of the order Cephalobaenida Heymons, 1935 have two pairs of appendages that lie behind one another while in Porocephalida Heymons, 1935 have hooked appendages aligned in a single row beside the mouth. Adult pentastomids are obligate parasites of the respiratory tract of vertebrates where they feed on blood or mucus and epithelial cells. Fish are common intermediate hosts that are infected by ingesting eggs or are actively infected by free-living larvae such as in *Subtriquetra subtriquetra* (Diesing, 1835) Sambon, 1922 which attach to the skin, break through the epithelium, and ultimately encyst in the target organ. Larval development in *S. subtriquetra* includes seven moults over 70+ days. The final host is infected by ingesting the intermediate host, after which the pentastomid then crawls into the respiratory tract.

2.20.1 | Taxonomic identity

Four porocephalid pentastomid genera are recorded from tilapias.[589,590] *Alofia* Giglioli in Sambon, 1922, *Leiperia* Sambon, 1922, *Sebekia* Sambon, 1922 (Sebekidae Sambon, 1922), and *Subtriquetra* Sambon, 1922 (Subtriquetridae Fain, 1961), which use freshwater fish as their intermediate hosts and typically crocodilians as their final hosts. In South Africa, *Alofia* sp. Giglioli in Sambon, 1922 is recorded from the swimbladder of *O. mossambicus*,[590] *Leiperia cincinnalis* Sambon, 1922 from the mesentery of *C. rendalli* and *O. mossambicus*,[589] *Sebekia minor* (Wedl, 1861) (syn. *S. wedli*) from the swimbladder of *C. rendalli* and *O. mossambicus*,[589] and *Subtriquetra rileyi* Junker, Boomker et Booyse, 1998 from the swimbladder of *C. rendalli*[589] and *O. mossambicus*.[590] *Leiperia cincinnalis* is also recorded from *O. niloticus* from Africa (unspecified locality)[591] and from the Upper Nile.[592]

2.20.2 | Pathogenicity

Detailed descriptions of pathology in tilapias are lacking, notably of those associated with non-encysted infective *Sebekia* larvae within the swimbladder. Boyce et al.[593] observed that encapsulated nymphs in *Gambusia affinis* (Baird et Girard, 1853) tissues surrounding the gastrointestinal tract, liver, pancreas and mesentery caused a mild inflammatory response whereas nymph infections in *Xiphophorus helleri* Heckel, 1848, caused extensive traumatic damage, granulomatous inflammation with haemorrhage, myositis and myodegeneration. It should be noted that the observed pathologies in the latter resulted from encapsulated larvae and the trauma associated with migrating larvae. Infections are rarely reported from the swimbladder and mesentery of wild *O. niloticus*, *O. mossambicus* and *C. rendalli* from South Africa (Table S2).[590] This group has little impact on tilapias and appears to have no impact on farmed tilapias.

2.20.3 | Global translocation

There is no evidence that pentastomes have been translocated with tilapia.

2.21 | Isopoda Latreille, 1817 (Obazoa: Opisthokonta: Metazoa: Ecdysozoa: Pancrustacea)

2.21.1 | Taxonomic identity

Isopods are crustaceans that are dorsoventrally flattened with the body composed of a head, thorax and an abdomen. The head, containing paired eyes, antennae, antennules, mandible, maxillae and maxillipeds, is fused to the first thoracic somite. The thorax is comprised of six or seven somites, each possessing a pair of swimming legs while the abdomen is made up of five pleonites and a pleotelson that possesses a pair of uropods. All isopods reported from tilapia (Figure 17) are members of the superfamily Cymothoidea and include the families Aegidae, Corallanidae, Cymothoidae and Gnathiidae. Six species are reported from tilapia, including *Alitropus typus* H. Milne Edwards, 1840 (family Aegidae) from *O. niloticus* cultivated in the Philippines[16,594] India[595–598] and Thailand[599] and from *O. mossambicus* from India,[595,598] *Corallana nodosa* Schioedte et Meinert, 1879 (family Corallanidae) from *O. mossambicus* and *O. niloticus* hybrids cultivated in Malaysia,[600] *Braga* syn. *Philostomella cigarra* (Szidat et Schubart, 1960) experimentally transmitted to *O. niloticus* in Brazil,[601] *Nerocila bivittata* (Risso, 1816) and *Nerocila orbignyi* (Guérin-Méneville, 1832) on wild *C. zillii* in Egypt,[602–604] *Renocila thresherorum* Williams et Bunkley-Williams, 1980 (family Cymothoidae) on wild *C. zillii* from Egypt[604,605] and unidentified larval forms from the family Gnathiidae on *O. niloticus* from the Philippines.[13,16] Adult members of this group are typically identified using morphological methods.

2.21.2 | Pathogenicity

Although parasitic isopods can be pathogenic to their host, there are few examples of pathogenic isopods on tilapia. Typically, they are parasites of the surface and fins, but some species also invade the buccal and gill cavities, which can have negative effects on the host, including mortality and some species can attach to the tongue of the fish.[16] Mass mortality associated with *A. typus* on farmed Nile tilapia from the Philippines[594] and from Thailand[599] are reported; in Thailand, mortalities were estimated more than 50% of tilapia measuring 50 g each. Mortalities were noted in wild *C. zillii* from Egypt infected with *N. orbignyi* associated with erosion and haemorrhaging of the gills.[602]

2.21.3 | Global translocations

There is no evidence of translocation; *A. typus* has a wide distribution throughout Indo-China and the infection of tilapia appears to be opportunistic.

2.21.4 | Research

Given the relatively large size and ease of identification of parasitic isopods, it is assumed that the low number of records of isopods on tilapia reflect a genuine rarity of infections on these hosts. Caution should be exercised, however, because isopods can be transient on their host and caution should be exercised to minimise loss during examination of potential hosts. Targeted studies, designed to minimise

FIGURE 17 Infection of *Nerocila orbignyi* in the opercular cavity of *Oreochromis mossambicus* from Egypt. Image courtesy of Shimaa El Sayed Mohamed Ali and Mamdouh Yousif Abd Elaziz Elgendy from WorldFish, Egypt

parasite loss, may increase the number of records. Despite few reports of pathogenic species, studies to identify mechanisms to control infections should be considered.

2.22 | Hirudinea Lamarck, 1818 (Obazoa: Opisthokonta: Metazoa: Lophotrochozoa: Annelida: Clitellata: Hirudinea)

There are few reports of leech infections of tilapia (Table S2) and/or their treatment. This is probably driven by low prevalence and impacts.

Leeches are segmented, muscular, clitellum-bearing, hermaphroditic, parasitic hematophagous or predatory annelids possessing an anterior and posterior sucker. The possession of a proboscis, the number of eyes, gastric and intestinal caeca, testisacs, body annulation, patternation, presence of papillae and whether species produce cocoons or eggs that are brooded are features that are used to classify species.

2.22.1 | Taxonomic identity

Blood-feeding leeches belong to two orders, the Arhynchobdellida Blanchard, 1894 (proboscis-less leeches) and the order Rhynchobdellida Blanchard, 1894 (proboscis-bearing leeches). The Rhynchobdellida contains three families, the Ozobranchidae Pinto, 1921 (leeches of turtles), the Glossiphoniidae Vaillant, 1890 (leeches of freshwater fish) and the Piscicolidae Johnston, 1865 (leeches of freshwater and marine fish). Glossiphoniid and piscicolid leeches are vectors of several viral, bacterial and flagellated protistan pathogens of fish.[606]

Of the glossophoniid leeches infecting farmed tilapia, *Batracobdelloides tricarinata* (Blanchard, 1897) is recorded from *O. niloticus* in Egypt,[607] and a species of *Helobdella* Blanchard, 1896 is recorded from *O. niloticus* in Brazil (M. Metselaar pers. obs.; Figure 18). Two piscicolid leeches infect *O. niloticus*: a species of *Myzobdella* Leidy, 1851 in Malaysia[608] and *Piscicola geometra* (L., 1761) from Nigeria.[609] The ozobranchid, *Ozobranchus branchiatus* (Menzies, 1791) is reported from *O. aureus* in Puerto Rico from a public aquarium and probably infected the tilapia from a turtle that was also held in the system.[610] Arhynchobdellid leeches are recorded from farmed tilapia: *Hirudo michaelseni* Augener, 1936 and an unidentified species of *Hirudo* L., 1758, and a species of *Limnatis* Moquin-Tandon, 1827 was described from freshwater *O. niloticus* farms in south-eastern Côte d'Ivoire.[611] Unidentified leeches are reported to infect farmed *O. mossambicus* in Indonesia[334] and *O. niloticus* in Tanzania.[612] Given that leeches display low host specificity,[613,614] it is likely that species additional to those documented here and in Table S2 can also infect tilapia. *Zeylanicobdella arugamensis* de Silva, 1963 (Piscicolidae) is reported from invasive *O. mossambicus* in brackish water in Japan[615] and Sri Lanka,[616] a species of *Placobdella* Blanchard, 1893 (Piscicolidae) was recorded from invasive freshwater populations of *O. mossambicus* and *O. niloticus* in Thailand,[334] and *Piscicolaria reducta* Meyer, 1940 (Piscicolidae) is reported from invasive populations of *O. aureus* in freshwater in the USA.[617]

2.22.2 | Pathogenicity

The abundance of leech parasites is often inversely proportional to the size of the host.[607,609] Leeches are often considered to not be pathogenic, but infections can, however, cause mortality from physical trauma and blood loss, predisposing hosts to secondary infections, and transmitting pathogenic viruses, bacteria and flagellated haemoprotistans.[334] Leeches are more common in earth pond systems that more sophisticated aquaculture systems. Some leeches attach to their hosts temporarily and leave after taking a blood meal, while others attach for an extended period and take successive blood meals before detaching to lay their cocoons. Leeches that attach for extended periods can elicit a substantial host tissue response at the attachment site, and severe epidermal erosion may occur in heavy infections. Feeding by rhynchobdellid leeches can cause localised petechial haemorrhages and blood loss from damage to epithelia by the proboscis.

Williams et al.[610] described mortality of *O. mossambicus* in Puerto Rico infected with *Myzobdella lugubris* Leidy, 1851, but this was complicated by bacterial infections including *Vibrio vulnificus* (Reichelt et al., 1976). Pathology associated with *Myzobdella* infections was detailed by Volonterio et al.[618] who found that an infection (av. 12.5 leeches per fish) of *M. uruguayensis* (Mañé-Garzón et Montero, 1977) on the gills of *Rhamdia quelen* (Quoy et Gaimard, 1824; av. wt. 633 g) in Uruguay caused haemorrhages and formation of fibrin plaques at the sites of leech attachment. Gill infections were associated with oedema, hyperplasia and telangiectasis of nearby lamellae.

Glossiphoniid and piscicolid leeches are noted vectors of a range of fish pathogens. Feeding by *Piscicola geometra* can

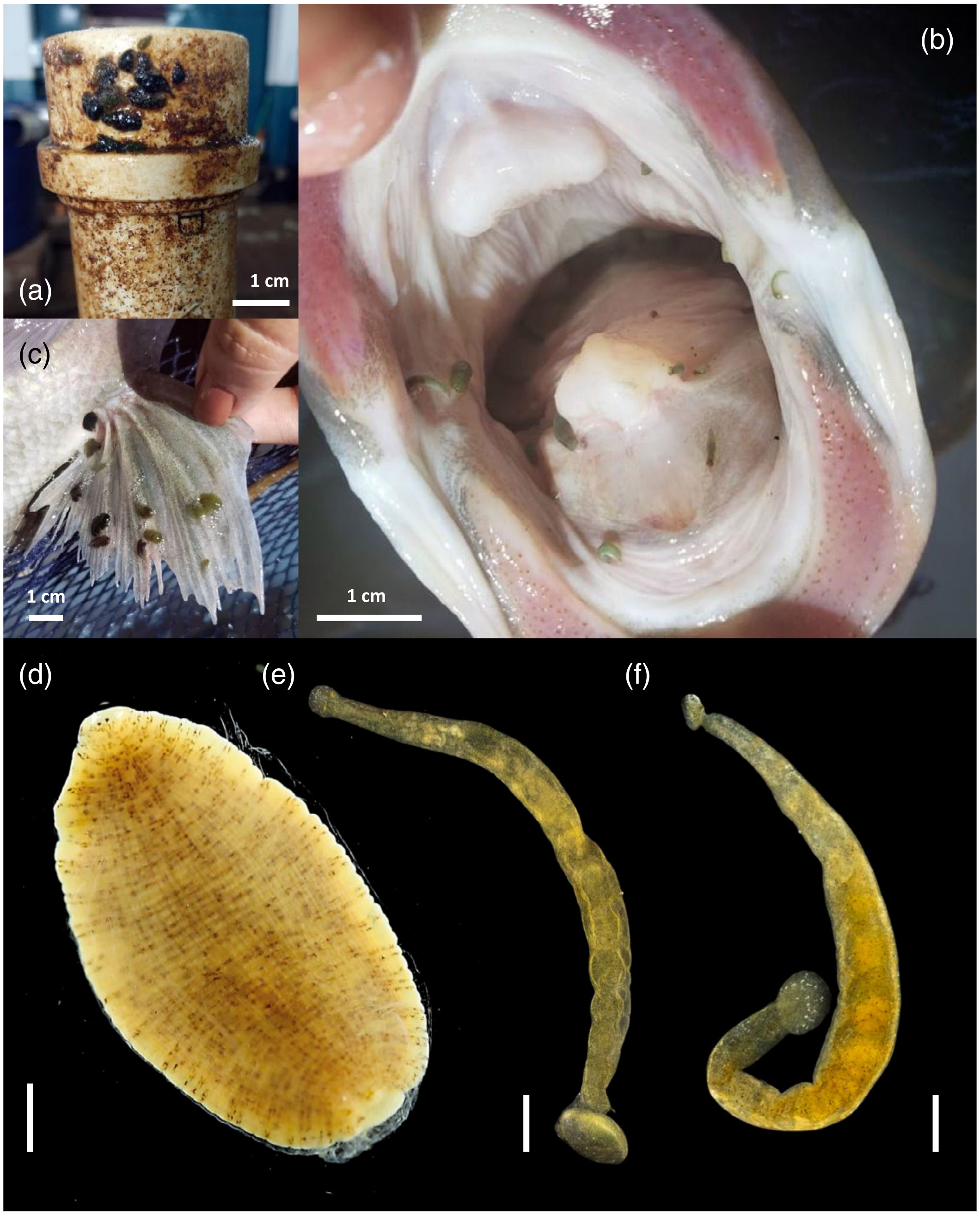

FIGURE 18 Leech infections of *Oreochromis niloticus*. (a–d) *Helobdella* sp. from stock cultured in Brazil showing leeches on (a) the system pipework, (b) attached to the inner lining of the oral cavity, (c) attached to the pectoral fin and (d) an ethanol fixed specimen of *Helobdella* sp. and (e,f) *Zeylanicobdella arugamensis* de Silva, 1963. Scale bar = 1 mm

mechanically transmit spring viraemia of carp virus (SVCV) which causes an acute, contagious haemorrhagic viraemia.[619] *Piscicola geometra* has a wide distribution throughout freshwaters across the Holarctic and Neotropic regions; Soliman et al.[620] reported isolating SVCV from *O. niloticus* from Egypt[621] but did not describe if leeches may have transmitted the virus. A range of bacterial pathogens are isolated from leeches: *Streptococcus* sp. was isolated from *B. tricarinata* in Natal, South Africa[613]; *Pseudomonas punctata* (Zimmermann, 1890) was isolated from *P. geometra*,[622] and Negele[623] reported *Aeromonas hydrophila* (Chester, 1901) from *P. geometra*. *Streptococcus agalactiae* Lehmann et Neumann, 1896 and *A. hydrophila* are significant pathogens of farmed tilapia with large economic impacts.[624] Negm-Eldin and Davies[32] demonstrated in an experiment that *B. tricarinata* could transmit the apicomplexans *Babesiosoma mariae* (Hoare, 1930) and *Cyrilia nili* Wenyon, 1909 from *O. niloticus* to *Clarias gariepinus* (Burchell, 1822).

Leeches are also common vectors of trypanosomes. Davies et al.[38] isolated *Trypanosoma mukasai* from *O. andersonii* from Botswana. Smit et al.[34] subsequently characterised trypanosomes isolated from the blood of South African fish including *C. rendalli* and *O. mossambicus* and from *B. tricarinata*, and found that the trypanosomes resembled *T. mukasai*, suggesting a link between *T. mukasai*, *B. tricarinata* and tilapia.

Zeylanicobdella arugamensis is a problematic leech of cultured fish in South-East Asia[625,626] and is recorded from *O. mossambicus* reared in brackish water in Japan[615] and Sri Lanka.[616] It is a vector of *Haemogregarina curvata* Hayes, Smit, Seddon, Wertheim et Davis, 2006 and fish trypanosomes in South Africa.[627] This broad distribution and history of vectoring serious pathogens highlights the biosecurity risk this leech may have in brackish and marine water tilapia aquaculture.

2.22.3 | Global translocations

Leeches are unlikely to be translocated with fish, but most pre-export health inspections prescribe a sample size that is too low to detect typical prevalences of <2.5%.[607] While leeches are readily seen on the surface of fish, they frequently attach to the gills, buccal and opercular cavities and may be missed by visual inspection.

2.22.4 | Research

The treatment of leeches in aquaculture has largely been neglected. Much of this is due to the scale of earth culture systems, the large volumes of chemotherapeutant required, the environmental concerns regarding the use of certain products and the resistance of cocoons to treatment and need for repeat treatments.[628] For earth pond systems, leech infections were traditionally controlled using undesirable, regulated products such as metrifonate or trichlorfon or by drying and calcium oxide liming ponds to kill leeches and their cocoons.[334,606,629] Strategies for management and control of leech infections in aquaculture facilities have therefore focused on exploring alternative control strategies including the use of non-chemical traps to remove leeches and their cocoons (B.C. Kua, unpublished), in addition to implementing good basic biosecurity and sanitary practices.

2.23 | Mollusca Linnaeus, 1758 (glochidia) (Obazoa: Opisthokonta: Metazoa: Lophotrochozoa: Mollusca)

Glochidia are a microscopic larval stage of some freshwater mussels (Bivalvia) of the family Unionidae Fleming, 1828 and Margaritiferidae Haas, 1940. These parasitic larvae are armed with hooks that allow them to attach to fish (mainly the gills) for a period before detaching and falling to the substrate. *Cristaria plicata* Leach, 1815 (Unionidae) is listed from *O. niloticus* from the Philippines (Luzon) in the checklist of Arthur and Lumanlan-Mayo.[16] Few details regarding this infection of tilapia are available.

2.24 | Treaties, standards and guidelines in international trade of live aquatic organisms and their products

There are policies, legislation and guidelines, obligatory and voluntary, about health management and movement of live aquatic animals.[630–632] These controls are frequently revised and therefore change constantly. This is necessary to respond to rapid worldwide developments in aquaculture and culture-based fisheries, improved knowledge of diseases of aquatic animals and improved or new diagnostic tools and procedures. Trade patterns change to reflect the political, social, industrial and economic environments of countries and regions and contribute to the dynamics of risk and its sensitivity to assessment.[630]

The World Trade Organisation (WTO) Agreement on the Application of Sanitary and Phyto-Sanitary Measures (SPS)[633] is the main regulatory instrument governing health in relation to international trade. The three main international standard setting bodies are the Codex Alimentarius Commission of FAO/WHO for food safety; the World Organisation for Animal Health (formerly the Office International des Epizooties [OIE]) for animal (including aquatic animal) health; and the International Plant Protection Convention (IPPC) for plant health. Other relevant international agreements are the Convention on Biological Diversity[634] and the Convention on International Trade of Endangered Species (CITES). Voluntary agreements or guidelines include that of the International Convention for the Exploration of the Sea,[635] the European Inland Fisheries Advisory Commission[636] and FAO guidelines such as the Code of Conduct for Responsible Fisheries Technical Guidelines on Responsible Movement of Live Aquatic Animals[637] and regional guidelines.[638] Voluntary international guidelines are often incorporated into national legislation and can therefore become locally mandatory.[632]

Health certification is an element of national strategies for health management and aquaculture biosecurity.[637] The objective of certification is to facilitate trade of live aquatic animals while decreasing the risk of spreading infectious diseases to an acceptable level. It also protects captured fisheries, unexploited species and other natural and built assets managed by governments. Health certification is relevant to reportable or notifiable pathogen lists, risk assessment, diagnostics and surveillance of these strategies.[639]

Application of these instruments often does not capture the relevance of parasites whose inclusion may be warranted as pathogens of concern. National, regional and international lists of aquatic pathogens or diseases include few parasitic and fungal pathogens. This is because these eukaryotic pathogens do not fulfil the criteria for disease listing, despite their economic impacts. Redirecting efforts and studies towards understanding the disease burden, impacts and costs of management of these agents, the risks posed and development and application of better generic approaches to managing their translocation will increase attention to this important group and decrease ongoing costs of management. Implementation of basic biosecurity to farm management can aid in controlling numerous serious and production-affecting pathogens, and its uptake should be encouraged. Taxonomic studies are important, and their value will be more significant, if placed in the context of disease control studies and biosecurity implementation.

3 | DISCUSSION

This review summarises the parasite fauna of tilapias from at least 73 countries and 3 major international lake systems—45 of which are in territories away from the native range of tilapias. These global movements of tilapia are associated with numerous transboundary introductions of parasites and spillback infections where local parasites have infected tilapia in their introduced environments (Table S1). More than 2500 host–parasite records are provided, raising awareness about the distribution of parasites and their capacity to spread with translocated fish. Table S2 presents information on 153 protists and 284 metazoan species summarised by country in Table S3. These distributional data highlight gaps in knowledge of the parasite fauna of tilapias in jurisdictions with large aquaculture industries, notably Cambodia, Guatemala, Lao PDR, Myanmar and Zanzibar (Tanzania), each with annual aquaculture production exceeding 10,000 tonnes in 2019 (Tables S1 and S3).[2] Table S3 further highlights additional countries and regions with limited information about the parasite fauna but with large tonnages (i.e. >10,000 in 2019) of tilapia being landed from aquaculture (e.g. Colombia, Costa Rica, Ecuador, Honduras, Taiwan Province of China and Tanzania) and capture fishery activities (e.g. Niger and Sri Lanka; Tables S1 and S3).[2] Gambia (1814 tonnes) and Togo (4507 tonnes) landed modest volumes from capture fishing activity in 2019, but no parasites are recorded from these countries.

Among the parasites, protists appear to be under-represented, with no reports from 31 of the 73 countries where parasites are documented from tilapia, suggesting that many have been overlooked or ignored. It is, however, appreciated that most diagnosed infections are treated to manage the infection and to prevent stock losses without identifying the species or reporting it scientifically. While we aimed to provide a comprehensive coverage of records, it should be noted that it includes some evident misidentifications[428,429,433,434,436,439,440]; where these were identified they are indicated. The identification of some species requires revisiting to confirm their translocation, mostly notably the records of 'introduced' coccidians and myxosporeans; in the absence of reference material, confirming identification of these must unfortunately await resampling.

There is no evidence of an introduced tilapia parasite having had a serious impact on indigenous fish fauna. Of translocated parasites, the most significant mortality event was caused by *A. ocellatum* from May 1997 to October 1998 in the hypersaline (46 psu) Salton Sea, California with massive mortality of young (1–13 cm TL) *O. mossambicus* in the shallows.[71] Assuming an average mortality of 20%–50% of the total 11 kg ha^{-1} biomass,[640] the value of the loss was estimated at US$ 6.77–16.93 M.[389] Other mortality events are reported but are in small populations of fish where losses due to a fungal infection of c. 200 variously sized juvenile *O. mossambicus* in India[174]; and c. 500 × 80 ± 10 g *O. niloticus* due to an oomycete infection in Egypt.[176]

There is also a paucity of information about the impact on introduced tilapia from endemic pathogens/infectious agents in receiving waters; such events have received less attention and are more likely to be regarded as caused by translocation stress, poor stock quality or mishandling.

Infections of *G. cichlidarum* on juvenile *O. niloticus* are common and associated with substantial losses of nursery and pond-reared tilapia in Egypt, Israel, Mexico, Scotland and Thailand.[286,339] Estimating parasite-associated losses in the early phases of production is complicated by the interplay of numerous environmental and management factors that are all difficult to assess. Shinn et al.,[641] however, estimated that the economic losses of juvenile tilapia attributable to parasites were USD 5.13–7.05 M at the swim-up stage, USD 5.84–8.02 M at the 21-day post-monosex stage, and US$ 4.84–6.66 M at the one-inch post-nursery stage in the 4.82 million metric tonnes per annum industry.

Records of host switching events such as *A. compactum* infecting tilapia from native Mexican cichlids and *A. crassus* infecting tilapia from eels in Belgium, although tilapia may be a paratenic host, highlight the vulnerability of translocated tilapia to infectious organisms in receiving waters. Translocation risks have focussed on obvious exotic pathogen introductions that infect indigenous hosts in environments conducive to establishment and spread. This review, however, has not detailed the 'spread' of specific parasites that have been introduced but instead collates infection records.

3.1 | Parasite species of global concern

A question that naturally emerges from this review, is 'which parasite species pose the greatest threat to the security of sustainable tilapia production?' While the mortality caused by *Amyloodinium ocellatum* in the Salton Sea represents the largest documented parasite-caused fish kill, and although other *A. ocellatum* infections are reported (Table S2),[69,70,72] only 17.40% (c. 1,076,612 tonnes) of tilapia in 2019 were cultured in brackish water and <0.002% (115.2 tonnes) in seawater. Of the parasites infecting tilapias grown in freshwater (c. 5,109,230 tonnes),[2] the monogenean genera *Cichlidogyrus*, *Gyrodactylus* and *Scutogyrus* have a wide geographic distribution, low host specificity and are pathogenic. Numerous species, furthermore, are found outside of their native range: *G. cichlidarum* (13); *C. tilapiae* (12); *C. sclerosus* (11); *C. thurstonae* (8); *S. longicornis* (8); *C. halli* (7); *C. longicornis* (3); *C. dossoui* (2); C. *haplochromii* (2); *C. mbirizei* (2); *C. tiberianus* (2); and *G. shinni* García-Vásquez, Pinacho-Pinacho, Guzmán-Valdivieso, Calixto-Rojas et Rubio-Godoy, 2021 (2); and *G. yacatli* (2). Within tilapia, the broad host specificity of the top six are: *G. cichlidarum* (6 hosts); *C. tilapiae* (9 hosts); *C. sclerosus* (9 hosts); *C. thurstonae* (6 hosts); *S. longicornis* (4 hosts); and *C. halli* (9 hosts) (Table S2). All have been recorded from hosts in *Coptodon*, *Oreochromis* and *Sarotherodon* species, except *S. longicornis* which is known from three *Oreochromis* spp. and one *Sarotherodon* species.

Although there are insufficient data to define the relative successes of each species, the non-obligate ciliated ectocommensals such as the trichodinids, may be among some of the most successful colonisers. It is not a specific parasite that directly poses the greatest risk to tilapia aquaculture, but rather their role in facilitating the infection of pathogens of significance such as *S. iniae* and *A. hydrophila*,[318,320,642] their role in increasing stress and decreasing production efficiency and their effective transmission and increased pathogenicity in aquaculture. *Trichodina* spp. in pond systems serve as an appropriate example. In pond systems with high(er) stocking densities, low-to-zero flush or water exchange rates, or in low-tech input systems without additional aeration and waste management, or in systems where feeding regimes attempt to maximise growth, high organic loads, pronounced fluctuations in daily water chemistry and elevated stress combine to facilitate elevated parasite abundance and prevalence and increases the probability of disease and mortality.

3.2 | Parasites of tilapias: status quo

The parasite fauna of tilapias from Africa is unexplored in many regions and studies that have been made need increased visibility.[44] Much ground-level aquatic parasitology remains unknown. Our knowledge of coccidian, myxosporean and nematode infections of tilapias remains poor, the role of leech infections in parasite life cycles is implied but undefined, and these knowledge gaps remain as threats to production.

The global importance of tilapias (i.e. USD 2000 t^{-1} for Nile tilapia and USD 1721 t^{-1} for tilapias nei) in aquaculture while having a lower farm gate value than cyprinids (i.e. USD 2326 t^{-1} for bighead carp, USD 2050 t^{-1} common carp, USD 2291 t^{-1} grass carp, USD 2147 t^{-1} for silver carp), salmonids (i.e. USD 6524 t^{-1} for Atlantic salmon) and shrimp (i.e. USD 5911 t^{-1} for white leg shrimp)[2,643] creates a self-reinforcing problem in health management where low-profit margins from production reduce the likelihood of thorough investigations and the scope of treatments available to either non-chemical changes to farm practices or to regimes that can be afforded in low-income systems and compete with other needs in health and biosecurity. The investment in point-of-care diagnostics (e.g. microscopes, etc.) and capacity to recognise parasite infections may be lower and ‘acceptable’ levels of stock loss may be higher. Thus, the balance between the costs of health intervention versus profit gain on the number of fish surviving to harvest may be tipped in favour of taking fewer active steps to manage tilapia health. At the same time, there is also a need to develop and manage local, regional, and national fish health strategies to improve diagnostics and veterinary care to support producers.

3.3 | Parasites of tilapias: quo vadis?

Global tilapia production has been growing at 3.73% year-on-year (2015–2019) and applying a logarithmic trend to 2000–2019 production, it is expected to rise to c. 9.6 million tonnes by 2030. Africa has huge potential for aquaculture; tilapias are biologically suitable and socially acceptable and could help meet protein demand for growing populations. With increased African production, an increase in movement of tilapia including genetically improved strains is likely—increasing the risk of parasite translocations, disease events and, indeed, of negative impacts on native fauna and biodiversity in Africa. Over the coming decade, tilapia aquaculture will continue to face risks from known and emerging pathogens.

The discovery since 2000 of 25 new parasites from *O. niloticus* worldwide (*Cichlidogyrus mbirizei*; *C. rognoni*; *Dermocystidium aegyptiacus*; *Diplostomum tilapiae* Zhokhov, 2014; *Gyrodactylus ergensi* Přikrylová, Matejusová, Musilová et Gelnar, 2009; *G. hildae* García-Vásquez, Hansen, Christison, Bron et Shinn, 2011; *G. malalai*; *G. occupatus* Zahradníčková, Barson, Luus-Powell et Přikrylová, 2016; *G. parisellei* Zahradníčková, Barson, Luus-Powell et Přikrylová, 2016; *G. shinni*; *G. yacatli*; *Myxobolus bejeranoi* Lovy et al., 2018; *M. branchiophilus* Abdel-Ghaffar et al., 2008; *M. cichlidarum* Abakar-Ousman et al., 2006; *M. fomenai* Abdel-Ghaffar et al., 2008; *M. mapei* Fonkwa et al., 2017; *M. nounensis* Fomena et Bouix, 2000; *M. saintlouisiensis* Diamanka et al., 2007; *M. tchadanayei* Abakar et al., 2006; *Nucleospora braziliensis*; *Ortholinea africanus*; *Saccocoelioides cichlidorum* (Aguirre-Macedo et Scholz, 2005); *Sinuolinea niloticus*; *Triangula egyptica*; and, *Zschokkella nilei*), highlights that there is still much to discover. Translocations to new locations for aquaculture, without the appropriate biosecurity measures in place, reinforce that new host–parasite interactions will increase health threats to both the introduced tilapia and the native fish in receiving systems.[639]

There is also potential for the growth of Mozambique tilapia in coastal aquaculture. From 2015 to 2019, global production increased 26.5% year-on-year from 37,900 tonnes in 2015 to 74,400 in 2019.[2] Nile tilapia over the same period increased 3.2% year-on-year but the size of the industry was 4,590,300 tonnes in 2019.[2] Given global concerns regarding saltwater encroachment and competition for land and freshwater resources, the expansion of aquaculture of saline-tolerant tilapia may have production and environmental benefits. The potential threat from pathogenic marine species such as *Neobenedenia* spp. (Table S2) needs to be recognised and expanding industries will produce a concomitant need for investment in biosecurity and disease mitigation including selective breeding for parasite resistance, vaccine development and parasite management and control strategies.

The ongoing COVID-19 pandemic and disrupted global supply chains highlight the need for increased local and national food security. The pandemic is likely to drive increased consumption of domestically produced seafood and tilapia likely have a place in providing this, but increased production comes with substantial risks that should be mitigated to achieve the potential improvements in local food production and utilisation.

AUTHOR CONTRIBUTIONS

Andrew P. Shinn: Conceptualization; data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Annemarie Avenant-Oldewage:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Melba G. Bondad-Reantaso:** Conceptualization; formal analysis; writing – original draft. **Armando J. Cruz-Laufer:** Data curation. **Adriana García-Vásquez:** Data curation; formal analysis; resources; writing – original draft. **Jesús S Hernández-Orts:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Roman Kuchta:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Matt Longshaw:** Conceptualization; data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Matthijs Metselaar:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Antoine Pariselle:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Gerardo Pérez-Ponce de León:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Pravata Kumar Pradhan:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Miguel Rubio-Godoy:** Conceptualization; data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Neeraj Sood:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Maarten P.M. Vanhove:** Data curation; formal analysis; resources; writing – original draft; writing – review and editing. **Marty R. Deveney:** Conceptualization; data curation; formal analysis; resources; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

This study was supported by two FAO projects, namely, GCP/GLO/979/NOR: Improving Biosecurity Governance and Legal Framework for Efficient and Sustainable Aquaculture Production and GCP/GLO/352/NOR: Responsible use of fisheries and aquaculture resources for sustainable development, both funded by the Norwegian Agency for Development Cooperation (Norad). We also acknowledge the support from Regular Programme funds under FAO's strategic framework on better production and three relevant programme priority areas, that is Blue Transformation, One Health and Safe Food. The authors gratefully acknowledge the following funding agencies: Annemarie Avenant-Oldewage would like to thank the University of Johannesburg, Faculty, and the Central Research Committee Funding in support of this work. Adriana García-Vásquez and Miguel Rubio-Godoy gratefully acknowledge INECOL Institutional Funds supporting their participation in this study. Roman Kuchta was supported by the Czech Science Foundation (grant no. 19-28399X). Jesús S. Hernández-Orts benefited from a postdoctoral fellowship from the Consejo Nacional de Ciencia y Tecnología, CONACyT, Mexico (no. 177603). Gerardo Pérez-Ponce de León gratefully acknowledges Institutional funds from ENES-Mérida and Instituto de Biología, UNAM. Maarten P. M. Vanhove was mainly supported for tilapia parasite research by the Research Foundation—Flanders (FWO-Vlaanderen) (research grant 1513419N), the Special Research Fund of Hasselt University (BOF20TT06 and BOF21INCENT09), and the Belgian Federal Science Policy Office (BRAIN-be Pioneer Project BR/132/PI/TILAPIA). Pravata Kumar Pradhan and Neeraj Sood would like to thank the Director of ICAR—National Bureau of Fish Genetic Resources, Lucknow for kindly providing the facilities for aspects of this work to be undertaken. Melba G. Bondad-Reantaso gratefully acknowledges the Food and Agriculture Organisation of the United Nations (FAO). In addition, we would like to extend our grateful thanks to the following for their kind permission to use selected images in this study: Liesl Van As and Andri Grobbelaar from the Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein, Republic of South Africa and the Editorial Office of African Zoology; Harrison Charo-Karisa, Shimaa Ali and John Benzie from WorldFish, Abbassa, Egypt and Penang, Malaysia and the Editorial Office of Aquaculture (Elsevier); Heba Hassan Mahboub and Adel A. Shaheen, Zagazig University, Egypt; Kwanprasert Panchai, Nakhon Ratchasima Rajabhat University and Chutima Hanjavanit, Khon Kaen University, Thailand; Mahmoud Abou-Okada from the Faculty of Veterinary Medicine, Cairo University, Egypt; Ha Thanh Dong, Asian Institute of Technology, Pathum Thani, Thailand; Supranee Chinabut, Bangkok, Thailand; Tarinee Limakom, Fish Vet Group Asia, Thailand; Nehemiah Rindoria, Kisii University, Kenya; Johan Theron from the University of Limpopo, South Africa; Patience Chwe Igeh and Quinton Dos Santos from the University of Johannesburg, South Africa; Wouter Fannes, Royal Museum for Central Africa, Tervuren, Belgium; Volodimir Sarabeev, Zaporizhzhia National University, Ukraine; Radmila Řepová, Institute of Parasitology, BC, CAS, České Budějovice, Czech Republic; Leo Galli, Uruguay; and, to Giuseppe Paladini from the Institute of Aquaculture, University of Stirling, Scotland, UK. We are indebted to Greta Hanako Rosas Saito BSc, Scanning Electron Microscopy Technician, Red de Estudios Moleculares Avanzados, and to Mrs Gina Gallo Cadena, Graphic Designer, Red TIC's, Instituto de Ecología, A.C., Xalapa, Mexico for their invaluable contribution in the preparation and photography of parasite specimens for the figure plates. We would also like to thank Beng-Chu Kua from the National Fish Health Research Division, Fisheries Research Institute, Department of Fisheries Malaysia for kindly donating fixed samples of *Zeylanicobdella arugamensis* and Ratchakorn Wongwaradechkul, INVE (Thailand) Ltd. for photographs of leeches. Wilmien J. Luus-Powell (University of Limpopo), Maarten Van Steenberge (Royal Belgian Institute of Natural Sciences) and Arnaud Collard are cordially thanked for their input. Tim Benson, South Australian Museum, provided comment on the Latin names and parasite taxonomy. Open access publishing facilitated by James Cook University, as part of the Wiley-James Cook University agreement via the Council of Australian University Librarians.

DATA AVAILABILITY STATEMENT

Data is openly available in a public repository that issues datasets with DOIs.

ORCID

Andrew P. Shinn https://orcid.org/0000-0002-5434-2685
Annemarie Avenant-Oldewage https://orcid.org/0000-0001-8820-7679
Melba G. Bondad-Reantaso https://orcid.org/0000-0002-2380-3549
Armando J. Cruz-Laufer https://orcid.org/0000-0003-1370-4739
Adriana García-Vásquez https://orcid.org/0000-0003-1076-2941
Jesús S. Hernández-Orts https://orcid.org/0000-0002-8177-7959
Roman Kuchta https://orcid.org/0000-0002-4219-6924
Matt Longshaw https://orcid.org/0000-0003-0099-284X

Matthijs Metselaar https://orcid.org/0000-0002-5000-9594
Antoine Pariselle https://orcid.org/0000-0002-1591-7423
Gerardo Pérez-Ponce de León https://orcid.org/0000-0001-6472-5113
Pravata Kumar Pradhan https://orcid.org/0000-0002-6793-1972
Miguel Rubio-Godoy https://orcid.org/0000-0002-9743-4416
Neeraj Sood https://orcid.org/0000-0002-2046-7957
Maarten P. M. Vanhove https://orcid.org/0000-0003-3100-7566
Marty R. Deveney https://orcid.org/0000-0001-6528-3601

REFERENCES

1. Froese R, Pauly D. *FishBase*. World Wide Web Electronic Publication. www.fishbase.org, version (06/2022); 2022
2. FAO. FishStatJ, a tool for fishery statistics analysis. In: Berger T, Sibeni F, Calderini F, eds. *Food and Agriculture Organization of the United Nations*. FAO Fisheries Division (NFI); 2021.
3. Atz J. The peregrinating *Tilapia*. *Anim Kingdom*. 1954;57:148-155.
4. Adl SM, Bass D, Lane CE, et al. Revisions to the classification, nomenclature, and diversity of eukaryotes. *J Eukaryot Microbiol*. 2019;66:4-119. doi:10.1111/jeu.12691
5. Burki F, Roger AJ, Brown MW, Simpson AGB. The new tree of eukaryotes. *Trends Ecol Evol*. 2020;35:43-55. doi:10.1016/j.tree.2019.08.008
6. Dyková I, Macháčková B, Pecková H. Amoebae isolated from organs of farmed tilapias, *Oreochromis niloticus*. *Folia Parasitol*. 1997;44:81-90.
7. Taylor PW. Isolation and experimental infection of free-living amebae in freshwater fishes. *J Parasitol*. 1977;63:232-237. doi:10.2307/3280047
8. Milanez G, Masangkay F, Thomas R, et al. Molecular identification of *Vermamoeba vermiformis* from freshwater fish in Lake Taal, Philippines. *Exp Parasitol*. 2017;183:201-206. doi:10.1016/j.exppara.2017.09.009
9. Ranzani-Paiva M, Nunes Felizardo N, Luque J. Parasitological and hematological analysis of Nile tilapia *Oreochromis niloticus* Linnaeus, 1757 from Guarapiranga reservoir, São Paulo State, Brazil. *Acta Sci Biol Sci*. 2005;27:231-237. doi:10.4025/actascibiolsci.v27i3.1334
10. Kostygov AY, Karnkowska A, Votýpka J, et al. Euglenozoa: taxonomy, diversity and ecology, symbioses and viruses. *Open Biol*. 2021;11:200407. doi:10.1098/rsob.200407
11. de Jesus RB, Gallani SU, Valladão GMR, et al. Trypanosomiasis causing mortality outbreak in Nile tilapia intensive farming: identification and pathological evaluation. *Aquaculture*. 2018;491:169-176. doi:10.1016/j.aquaculture.2018.02.002
12. Mandal A. *Trypanosoma choudhuryi* sp. nov. from *Tilapia mossambica* (Peters). *Acta Protozool*. 1977;16:1-5.
13. Natividad J, Bondad-Reantaso M, Arthur J. In: Maclean J, Dizon L, Hosillos L, eds. *Parasites of Nile Tilapia (Oreochromis niloticus) in The Philippines*. Asian Fisheries Forum; 1986:1.
14. Landsberg JH. Parasites and associated diseases of fish in warm water culture with special emphasis on intensification. In: Shilo M, Sarig ES, eds. *Fish Culture in Warm Water Systems: Problems and Trends*. CRC Press; 1989.
15. Bondad-Reantaso M, Arthur J. The parasites of Nile tilapia (*Oreochromis niloticus* (L.)) in The Philippines, including an analysis of changes in the parasite fauna of cultured tilapia from fry to marketable size. In: Hirano R, Hanyu I, eds. *The Second Asian Fisheries Forum*. *Asian Fisheies Society*, Manila; 1990.
16. Arthur J, Lumanlan-Mayo S. *Checklist of the Parasites of Fishes of The Philippines*. FAO; 1997.
17. Florio D, Gustinelli A, Caffara M, et al. Veterinary and public health aspects in tilapia (*Oreochromis niloticus niloticus*) aquaculture in Kenya, Uganda and Ethiopia. *Ittiopatologia*. 2009;6:51-93. doi:10.4314/evj.v22i2.6
18. Otachi E. *Studies on Occurrence of Protozoan and Helminth Parasites in Nile Tilapia (Oreochromis niloticus L.) from Central and Eastern Provinces, Kenya*. Egerton University; 2009:90.
19. Akoll P, Mwanja W. Fish health status, research and management in East Africa: past and present. *Afr J Aquat Sci*. 2012;37:117-129. doi:10.2989/16085914.2012.694628
20. Ojwala R, Otachi E, Kitaka N. Effect of water quality on the parasite assemblages infecting Nile tilapia in selected fish farms in Nakuru County, Kenya. *Parasitol Res*. 2018;117:3459-3471. doi:10.1007/s00436-018-6042-0
21. Kolia W, Sunarto S, Widiyani T. The infection of ectoparasitic protozoa on farmed Nile tilapia (*Oreochromis niloticus*) at three reservoirs in Central Java, Indonesia. *Biodivers J Biol Divers*. 2021;22:1975-1980. doi:10.13057/biodiv/d220445
22. Afifi S, Al-Thobiati S, Hazaa M. Parasitic gill lesions in Nile tilapia *Oreochromis niloticus* from fish farms in Saudi Arabia. *Assiut Vet Med J*. 2000;42:183-194. doi:10.21608/avmj.2000.180486
23. Akoll P, Konecny R, Mwanja W, Nattabi J, Agoe C, Schiemer F. Parasite fauna of farmed Nile tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*) in Uganda. *Parasitol Res*. 2012;110:315-323. doi:10.1007/s00436-011-2491-4
24. Akoll P, Konecny R, Mwanj W, Schiemer F. Risk assessment of parasitic helminths on cultured *Nile tilapia* (*Oreochromis niloticus*, L.). *Aquaculture*. 2012;356:123-127. doi:10.1016/j.aquaculture.2012.05.027
25. Arguedas D, Ortega C, Martínez S, Astroza A. Parasites of Nile tilapia larvae *Oreochromis niloticus* (Pisces: Cichlidae) in concrete ponds in Guanacaste, northern Costa Rica. *UNED Res J*. 2017;9:313-319. doi:10.22458/urj.v9i2.1904
26. Keremah RI, Inko-Tariah MB. Comparative study of ectoparasites on *Nile tilapia* (*Oreochromis niloticus*) cultured under integrated and unintegrated pond systems. *Afr J Biotechnol*. 2013;12:2711-2714. doi:10.5897/AJB10.1238
27. Sánchez B, Jiménez-Estrada M, Ocampo A. Evaluation of the parasiticide effect of aqueous and methanol *Buddleja cordata* HBK (Tepozan) extracts on *Costia necatrix* in tilapia (*Oreochromis* sp.). *Vet Mex*. 2000;31:189-194.
28. Mhaisen F, Al-Rubaie A. Checklists of fish parasites of Al-Najaf Al-Ashraf province Iraq. *Al-Kufa Univ J Biol*. 2016;2016:86-95. doi:10.26842/binhm.7.2019.15.3.0293
29. Bunkley-Williams L, Williams E. *Parasites of Puerto Rican freshwater sport fishes*. Puerto Rico Department of Natural and Environmental Resources, San Juan, PR and Department of Marine Sciences, University of Puerto Rico; 1994.
30. Sinha C. Occurrence of *Trypanosoma mukasai* Hoare, 1932 in *Tilapia mossambica* (Peters) from India. *Acta Protozool*. 1986;25:449-452.
31. Baker J. Trypanosomes and dactylosomes from the blood of freshwater fish in East Africa. *Parasitology*. 1960;50:515-526.
32. Negm-Eldin M, Davies R. Simultaneous transmission of *Trypanosoma mukasai*, *Babesiosoma mariae* and *Cyrilia nili* to fish by the leech *Batracobdelloides tricarinata*. *Dtsch Tierarztl Wochenschr*. 1999;106:526-527.
33. Ferreira ML, Avenant-Oldewage A. Notes on the occurrence of *Trypanosoma* sp. (Kinetoplastida: Trypanosomatidae) in freshwater fishes from South Africa. *Onderstepoort J Vet Res*. 2013;80:1-4.
34. Smit N, Joubert A, Lawton S, Hayes P, Cook C. Morphological and molecular characterization of an African freshwater fish trypanosome, including its development in a leech vector. *Int J Parasitol*. 2020;50:921-929. doi:10.1016/j.ijpara.2020.06.004
35. Abu El-Wafa SA. Protozoan parasites of some freshwater fishes in Behera Governorate. MSc thesis. Alexandria University, Egypt; 1988:146.

36. El-Gayar A, Aly S. Studies on some protozoan parasites and encysted metacercarial infection of freshwater fishes in Egypt. *Egypt Vet Med Soc Parasitol*. 2013;9:31-43.
37. Hamid S, Babiker E. Prevalence of trypanosome infection in *Oreochromis niloticus* and *Clarias lazera* from fish farms and reservoir of Jebel Aulia Dam in Sudan. *World's Vet J*. 2011;1:14-16.
38. Davies A, Gibson W, Ferris V, Basson L, Smit N. Two genotypic groups of morphologically similar fish trypanosomes from the Okavango Delta, Botswana. *Dis Aquat Organ*. 2005;66:215-220. doi:10.3354/dao066215
39. McHugh K, Weyl O, Smit N. Parasites of fishes in the recently inundated ephemeral Lake Liambezi, Namibia. *Afr J Aquat Sci*. 2016;41:505-509. doi:10.2989/16085914.2016.1238338
40. Reda E. A review of some ecto-and endo protozoan parasites infecting *Sarotherodon galilaeus* and *Tilapia zillii* from Damietta branch of River Nile, Egypt. *J Am Sci*. 2011;7:362-373.
41. Kamundia P, Mbuthia P, Waruiru R, et al. Occurrence of *Trypanosoma* in Nile tilapia in Lake Victoria, Kenya. In: Mdegela R, Rutaisire J, Obua J, Okoth S, eds. *Fisheries & Aquaculture Cluster Proceeding*. Inter-University Council for East Africa Lake Victoria Research Initiative, Mwanza; 2008:83-87.
42. Supamattaya K, Phromkunthong W, Suanyuk N, Soliman H, El-Matbouli M. Spironucleosis in cultured red tilapia. *Vet Rec*. 2012;171:274. doi:10.1136/vr.100809
43. El-Khatib N, El-Hady M. Some epizootological aspects of hole in the head disease affecting cultured *Oreochromis niloticus*. *Zag Vet J*. 2009;37:155-166.
44. Scholz T, Vanhove MPM, Smit N, Jayasundera Z, Gelnar M. *A Guide to the Parasites of African Freshwater Fishes*. *Abc Taxa*. 2018;18:1-425.
45. Poynton S, Fard M, Jenkins J, Ferguson H. Ultrastructure of *Spironucleus salmonis* n. comb. (formerly *Octomitus salmonis* sensu Moore 1922, Davis 1926, and *Hexamita salmonis* sensu Ferguson 1979), with a guide to *Spironucleus* species. *Dis Aquat Organ*. 2004;60:49-64. doi:10.3354/dao060049
46. Williams C, Lloyd D, Poynton SL, Jorgensen A, Millet C, Cable J. *Spironucleus* species: economically-important fish pathogens and enigmatic single-celled eukaryotes. *J Aquac Res Dev*. 2011;S2:002. doi:10.4172/2155-9546.S2-002
47. Ghoneim NH, Abdel-Moein KA, Saeed H. Fish as a possible reservoir for zoonotic *Giardia duodenalis* assemblages. *Parasitol Res*. 2012;110:2193-2196. doi:10.1007/s00436-011-2748-y
48. El-Mansy A. New exogenous stages of oocysts, sporocysts, and sporozoites of *Goussia cichlidarum* Landsberg and Paperna, 1985 (Sporozoa: Coccidia) and impact of endogenous stages on the swim bladder of tilapias in Egypt. *Parasitol Res*. 2008b;102:233-241. doi:10.1007/s00436-007-0752-z
49. Landsberg JH, Paperna I. *Goussia cichlidarum* n. sp. (Barrouxiidae, Apicomplexa), a coccidian parasite in the swimbladder of cichlid fish. *Z Parasitenkd*. 1985;71:199-212.
50. Landsberg JH, Paperna I. Intestinal infections by *Eimeria* (s. l.) *vanasi* n. sp. (Eimeriidae, Apicomplexa, protozoa) in cichlid fish. *Ann Parasitol Hum Comp*. 1987;62:283-293. doi:10.1051/parasite/1987624283
51. Kim H, Paperna I. Fine structure of epicytoplasmic stages of *Eimeria vanasi* from the gut of cichlid fish. *Dis Aquat Organ*. 1992;12:191-197.
52. Paperna I. Fine structure of *Eimeria* (S.l.) *vanasi* merogony stages in the intestinal mucosa of cichlid fishes. *Dis Aquat Organ*. 1991;10:195-201.
53. Vilenkin M, Paperna I. Development of sporozoites of the piscine coccidium *Eimeria* (sensu lato) *vanasi* in gut intraepithelial lymphocyte-like cells. *Folia Parasitol*. 1997;44:91-98.
54. Molnár K, Avenant-Oldewage A, Székely C. A survey of coccidian infection of freshwater fishes in South Africa, with the description of *Goussia anopli* n. sp. (Apicomplexa: Eimeriidae). *Syst Parasitol*. 2004;59:75-80. doi:10.1023/B:SYPA.0000038445.92194.fc
55. Delan G, Rosales R, Rica R, Corrales C, Ilano A. Parasite infestation on *Oreochromis niloticus* (Linnaeus, 158) from selected fish farms in Cebu, Philippines. *Trop Technol J*. 2015;18:1-9.
56. Mhaisen F, Al-Mayali H, Al-Abodi H. Checklists of parasites of fishes of Al-Diwaniyah Province, Iraq. *Bull Iraq Nat Hist Mus*. 2019;15:293-318.
57. Koinari M, Karl S, Ng-Hublin J, Lymbery AJ, Ryan UM. Identification of novel and zoonotic *cryptosporidium* species in fish from Papua New Guinea. *Vet Parasitol*. 2013;198:1-9. doi:10.1016/j.vetpar.2013.08.031
58. Ammar M, Arafa M. *Cryptosporidium* and other zoonotic parasites in *Oreochromis niloticus* in Assiut governorate. *Assiut Vet Med J*. 2013;59:142-151.
59. Landsberg J, Paperna I. Ultrastructural study of the coccidian *cryptosporidium* sp. from stomachs of juvenile cichlid fish. *Dis Aquat Organ*. 1986;2:13-20. doi:10.3354/dao002013
60. Paperna I, Vilenkin M. Cryptosporidiosis in the gourami *Trichogaster leeri*: description of a new species and a proposal for a new genus, *Piscicryptosporidium*, for species infecting fish. *Dis Aquat Organ*. 1996;27:95-101. doi:10.3354/dao027095
61. Palenzuela O, Alvarez-Pellitero P, Sitja-Bobadilla A. Molecular characterization of *Cryptosporidium molnari* reveals a distinct piscine clade. *Appl Environ Microbiol*. 2010;76:7646-7649. doi:10.1128/AEM.01335-10
62. Golomazou E, Malandrakis EE, Panagiotaki P, Karanis P. *Cryptosporidium* in fish: implications for aquaculture and beyRond. *Water Res*. 2021;201:117357. doi:10.1016/j.watres.2021.117357
63. Hoare CA. On a new *Dactylosoma* occurring in fish of Victoria Nyanza. *An Trop Med Parasitol*. 1930;24:241-248.
64. Smit NJ, Van As JG, Davies AJ. Observations on *Babesiosoma mariae* (Apicomplexa: Dactylosomatidae) from the Okavango Delta, Botswana. *Folia Parasitol*. 2013;50:85-86. doi:10.14411/fp.2003.015
65. El-Asely A, El-Gawad E, Soror E, Amin A, Shaheen A. Studies on some parasitic diseases in *Oreochromis niloticus* fish hatchery with emphasis to life stages. *J Adv Vet Res*. 2015;5:99-108.
66. Lua D, Te B, Thanh N. A study on parasites in different stages of three strains of cultured Nile tilapia (*Oreochromis niloticus*): Thai strain, GIFT strain and Viet strain in North Vietnam. Paper Presented at 4th Symposium on Diseases in Asian Aquaculture (DAA IV), Cebu City; 1999.
67. Arthur JR, Bui QT. Checklist of the parasites of fishes of Viet Nam. *FAO Fish Tech Pap*. 2006;369(2):1-133.
68. Bamidele A, Abiodun K, David U, Kayode S. Gastrointestinal parasites of *Sarotherodon melanotheron* (Ruppel, 1852) histopathological alterations and organochlorine pesticides pollution from Lagos, lagoon, Nigeria. *Egypt Acad J Biol Sci E Med Entomol Parasitol*. 2018;10:15-29.
69. Landsberg JH, Smith SA, Noga EJ, Richards SA. Effect of serum and mucus of blue tilapia, *Oreochromis aureus* on infectivity of the parasitic dinoflagellate, *Amyloodinium ocellatum* in cell culture. *Fish Pathol*. 1992;27:163-169. doi:10.3147/jsfp.27.163
70. Smith S, Noga E, Levy M, Gerig T. Effect of serum from tilapia *Oreochromis aureus* immunized with the dinospore *Amyloodinium ocellatum* on the motility, infectivity and growth of the parasite in cell culture. *Dis Aquat Organ*. 1993;15:73-80. doi:10.3354/DAO015073
71. Kuperman B, Matey V. Massive infestation by *Amyloodinium ocellatum* (Dinoflagellida) of fish in a highly saline lake, Salton Sea, California, USA. *Dis Aquat Organ*. 1999;39:65-73. doi:10.3354/dao039065
72. Kuperman BI, Matey VE, Hurlbert SH. Parasites of fish from the Salton Sea, California, U.S.A. *Hydrobiologia*. 2001;466:195-208. doi:10.1023/A:1014555904968

73. Paladini G, Longshaw M, Gustinelli A, Shinn A. Parasitic diseases in aquaculture: their biology, diagnosis and control. In: Austin B, Newaj-Fyzul A, eds. *Diagnosis and Control of Diseases of Fish and Shellfish*. John Wiley & Sons, Ltd; 2017.
74. Martins M, Moraes F, Fujimoto R, et al. Parasitic infections in cultivated freshwater fishes: a survey of diagnosticated cases from 1993 to 1998. *Rev Bras Parasitol Vet*. 2000;9:23-28.
75. Ghiraldelli L, Martins M, Jeronimo G, Yamashita M, Adamante W. Ectoparasites communities from *Oreochromis niloticus* cultivated in the state of Santa Catarina, Brazil. *J Fish Aquat Sci*. 2006;1:181-190. doi:10.3923/jfas.2006.181.190
76. Jerônimo GT, Speck GM, Cechinel MM, Goncalves ELT, Martins ML. Seasonal variation on the ectoparasitic communities of *Nile tilapia* cultured in three regions in southern Brazil. *Braz J Biol*. 2011;71:365-373. doi:10.1590/s1519-69842011000300005
77. Zago AC, Franceschini L, Garcia F, Sérgio HCS, Kátia SG, Reinaldo JS. Ectoparasites of Nile tilapia (*Oreochromis niloticus*) in cage farming in a hydroelectric reservoir in Brazil. *Rev Bras Parasitol Vet*. 2014;23:171-178. doi:10.1590/s1984-29612014041
78. Penprapai N, Chumchareon M. Biodiversity of parasites in red tilapia fishes (*Oreochromis niloticus* Linn.) cultured cage in Trang River at Trang Province. *J Appl Sci Res*. 2013;9:6059-6062.
79. Ramesh KS, Mohan CV, Shankar KM, Ahmed I. *Piscinoodinium* sp. infection in juveniles of common carp (*Cyprinus carpio*), mahseer (*Tor khudree*) and tilapia (*Oreochromis mossambicus*). *J Aquac Trop*. 2000;15:281-288.
80. Burkholder J, Marshall H. Toxigenic Pfiesteria species – updates on biology, ecology, toxins, and impacts. *Harmful Algae*. 2012;14:196-230. doi:10.1016/j.hal.2011.10.022
81. Burkholder J, Glasgow J, Hobbs C. Fish kills linked to a toxic ambush-predator dinoflagellate: distribution and environmental conditions. *Mar Ecol Prog Ser*. 1995;124:43-61.
82. Steidinger KA, Burkholder JM, Glasgow HB Jr, et al. *Pfiesteria piscicida* gen. Et sp. nov. (Pfiesteriaceae fam. Nov.), a new toxic dinoflagellate with a complex life cycle and behavior. *J Phycol*. 1996;32:157-164. doi:10.1111/j.0022-3646.1996.00157.x
83. Wilson JR, Sauders RJ, Hutson KS. Parasites of the invasive tilapia *Oreochromis mossambicus*: evidence for co-introduction. *Aquat Invasions*. 2019;14:332-349. doi:10.3391/ai.2019.14.2.11
84. Van As JG, Basson L. Checklist of freshwater fish parasites from southern Africa. *S Afr J Wildl Res*. 1984;14:49-61.
85. Paperna I, Van As JG. The pathology of *Chilodonella hexasticha* (Kiernik). Infections in cichlid fishes. *J Fish Biol*. 1983;23:441-450. doi:10.1111/j.1095-8649.1983.tb02924.x
86. Alaş A, Öktener A. Different parasitic phyla of fish from Turkey excluding helminths and Crustacea. *J Entomol Zool Stud*. 2015;2:24-41. doi:10.1007/s11160-006-9005-y
87. Doulah M, Islam S, Rahman M, Islam M, Rashid M, Razzak M. Investigation of parasite and diseases at cage culture Nile tilapia (*Oreochromis niloticus*) in southern region of Bangladesh. *Res Agric Livest Fish*. 2019;6:431-437. doi:10.3329/ralf.v6i3.44809
88. Pádua SB, Martins ML, Carrijo-Mauad JR, et al. First record of *Chilodonella hexasticha* (Ciliophora: Chilodonellidae) in Brazilian cultured fish: a morphological and pathological assessment. *Vet Parasitol*. 2013;191:154-160. doi:10.1016/j.vetpar.2012.07.030
89. Marzouk M, Mahdy O, El-Khati N, Yousef N. A contribution in ectoparasitic infection and its control in cultured *Oreochromis niloticus* in Egypt. *Am J Res Commun*. 2013;1:326-338.
90. Jimenez-Garcia I, Rojas-Garcia C, Castro-Jose C, Pavon-Suriano S, Lango-Reynoso F, Castaneda-Chavez M. Growth enhancement, survival and decrease of ectoparasitic infections in masculanized *Nile tilapia* fry in a recirculating aquaculture system. *Trop Subtrop Agroecosystems*. 2012;15:S51-S56.
91. Abdel-Baki A, Al-Quraishy S. First record of *Chilodonella* spp. (Ciliophora: Chilodonellidae) in cultured Nile tilapia (*Oreochromis niloticus*). *Pak J Zool*. 2014;46:657-660.
92. Bastos Gomes G, Jerry D, Miller T, Hutson K. Current status of parasitic ciliates *Chilodonella* spp. (Phyllopharyngea: Chilodonellidae) in freshwater fish aquaculture. *J Fish Dis*. 2017a;40:703-715. doi:10.1111/jfd.12523
93. Bastos Gomes G, Miller T, Vaughan D, et al. Evidence of multiple species of *Chilodonella* (protozoa, Ciliophora) infecting Australian farmed freshwater fishes. *Vet Parasitol*. 2017b;237:8-16. doi:10.1016/j.vetpar.2017.03.004
94. Hatai K, Chukanhom K, Lawhavinit O, Hanjavanit C, Kunitsune M, Imai S. Some biological characteristics of *Tetrahymena corlissi* isolated from guppy in Thailand. *Fish Pathol*. 2001;36:95-199.
95. Astrofsky KM, Schech JM, Sheppard BJ, et al. High mortality due to *Tetrahymena* sp. infection in laboratory-maintained zebrafish (*Brachydanio rerio*). *Comp Med*. 2002;52:363-367.
96. Leibowitz MP, Zilberg D. *Tetrahymena* sp. infection in guppies, *Poecilia reticulata* Peters: parasite characterization and pathology of infected fish. *J Fish Dis*. 2009;32:845-855. doi:10.1111/j.1365-2761.2009.01062.x
97. Simon EM, Nanney DL, Doerder FP. The "*Tetrahymena pyriformis*" complex of cryptic species. *Biodivers Conserv*. 2008;17:365-380.
98. Misumi I, Lewis T, Takemura A, Leong J. Elicited cross-protection and specific antibodies in Mozambique tilapia (*Oreochromis mossambicus*) against two different immobilization serotypes of *Cryptocaryon irritans* isolated in Hawaii. *Fish Shellfish Immunol*. 2011;30:1152-1158. doi:10.1016/j.fsi.2011.03.004
99. Misumi I, Leong J, Takemura A, Lewis T. Immune protection of Mozambique tilapia (*Oreochromis mossambicus*) exposed to different infectious doses of ectoparasite (*Cryptocaryon irritans*). *Parasitol Res*. 2012;110:363-372. doi:10.1007/s00436-011-2500-7
100. El-Sayed A. *Tilapia Culture*. CABI Publishing; 2006.
101. Straus DL, Griffin BR. Prevention of an initial infestation of *Ichthyophthirius multifiliis* in channel catfish and blue tilapia by potassium permanganate treatment. *N Am J Aquac*. 2001;63:11-16.
102. Constantino Casas F, Armijo Ortiz A, Osorio Sarabia D, Chavez SL. Infection due to *Aeromonas hydrophila* and *Ichthyophthirius multifiliis* in rainbow trout (*Oncorhynchus mykiss*, Walbaum) and tilapia (*Oreochromis aureus*, L) in Morelos, Mexico. Pathological study and review of treatment. *Vet Mex*. 1997;28:59-62.
103. Aguilar-Aguilar R, Islas-Ortega A. A checklist of ciliate parasites (Ciliophora) of fishes from Mexico. *Zootaxa*. 2015;4027:270-280. doi:10.11646/zootaxa.4027.2.6
104. Carvalho ED, de Silva RJ, Ramos IP, et al. Ecological features of large neotropical reservoirs and its relation to health of cage reared fish. In: Carvalho E, David G, Silva R, eds. *Health and Environment in Aquaculture*. INTECH; 2012.
105. Pantoja MFW, Neves L, Dias M, Marinho R, Montagner D, Tavares-Dias M. Protozoan and metazoan parasites of Nile tilapia *Oreochromis niloticus* cultured in Brazil. *Rev MVZ Córdoba*. 2012;17:2812-2819.
106. Steckert LD, Cardoso L, Jerônimo GT, de Pádua SB, Martins ML. Investigation of farmed Nile tilapia health through histopathology. *Aquaculture*. 2018;486:161-169. doi:10.1016/j.aquaculture.2017.12.021
107. Mahmoud MA, Abdelsalam M, Mahdy OA, et al. Infectious bacterial pathogens, parasites and pathological correlations of sewage pollution as an important threat to farmed fishes in Egypt. *Environ Pollut*. 2016;219:939-948.
108. Nofal M, Abdel-Latif H. Ectoparasites and bacterial co-infections causing summer mortalities among cultured fishes at Al-Manzala with special reference to water quality parameters. *Life Sci J*. 2017;14:72-83.
109. Abu-Elala N, Attia M, Abd-Elsalam R, Gamal A, Younis N. Peracetic acid treatment of *Ichthyophthirius multifiliis* (Ciliophora: Ichthyophthiriidae) and *Trichodina* spp. reduces the infection by *Aeromonas hydrophila* and improves survival in Nile tilapia (*Oreochromis niloticus*). *Aquaculture*. 2021;538:736591. doi:10.1016/j.aquaculture.2021.736591

110. Athanassopoulou F, Billinis C, Prapas T. Important disease conditions of newly cultured species in intensive freshwater farms in Greece: first incidence of nodavirus infection in *Acipenser* sp. *Dis Aquat Organ*. 2004;60:247-252. doi:10.3354/dao060247
111. Xu DH, Shoemaker CA, Klesius PH. Enhanced mortality in Nile tilapia *Oreochromis niloticus* following coinfections with ichthyophthiriasis and streptococcosis. *Dis Aquat Organ*. 2009;85:187-192. doi:10.3354/dao02073
112. Nguyen V, Dong HT, Senapin S, et al. Synergistic infection of *Ichthyophthirius multifiliis* and *Francisella noatunensis* subsp. *orientalis* in hybrid red tilapia (*Oreochromis* sp.). *Microb Pathog*. 2020;147:104369. doi:10.1016/j.micpath.2020.104369
113. Islas-Ortega AG, Marcotegui PS, Basson L, Aguilar-Aguilar R. A checklist of trichodinid species (Ciliophora: Trichodinidae) on tilapia fishes (Cichlidae), with new records from Mexico and the first data from Argentina. *Zootaxa*. 2020;4896:451-484. doi:10.11646/zootaxa.4896.4.1
114. Basson L, Van As JG. Differential diagnosis of the genera in the family Trichodinidae (Ciliophora: Peritrichida) with the description of a new genus ectoparasitic on freshwater fish from southern Africa. *Syst Parasitol*. 1989;13:153-160. doi:10.1007/BF00015224
115. Van As JG, Basson L. A further contribution to the taxonomy of the Trichodinidae (Ciliophora: Peritrichia) and a review of the taxonomic status of some fish ectoparasitic trichodinids. *Syst Parasitol*. 1989;14:157-179. doi:10.1007/BF02187051
116. Valladão GMR, Pádua SB, Gallani SU, et al. *Paratrichodina africana* (Ciliophora): a pathogenic gill parasite in farmed Nile tilapia. *Vet Parasitol*. 2013;197:705-710. doi:10.1016/j.vetpar.2013.04.043
117. Pádua S, Menezes Filho R, Martins M, et al. A survey of epitheliocystis disease in farmed Nile tilapia (*Oreochromis niloticus* Linnaeus, 1758) in Brazil. *J Appl Ichthyol*. 2015;31:927-930.
118. Rodrigues F, Assane I, Valladão G, et al. First report of *Trichodinella* and new geographical records of trichodinids in Nile tilapia (*Oreochromis niloticus*) farmed in Brazil. *Res Bras Parasitol Vet*. 2019;28:229-237.
119. Jiang Y, Zhao Y, Tang F. Studies on the taxonomy and biodiversity of ectoparasitic trichodinids from cultured tilapia in Guangxi. *Sichuan J Zool*. 2015;34:584-593.
120. Younis NA, Attia MM, Saleh NMK. Analysis of TNF alpha and interlukin-1β genes in *Oreochromis niloticus*: inflammatory responses induced by *Myxobolus* spp. and *Trichodina* spp, Iranian. *J Ichthyol*. 2021;8:30-40. doi:10.22034/iji.v8i1.450
121. de Jager G, Basson L. Taxonomic assessment of three north American trichodinids by reevaluating the taxon validity of *Trichodina heterodentata* Duncan, 1977 (Peritrichia). *Acta Protozool*. 2019;58:125-139.
122. Van As JG, Basson L. Trichodinids (Ciliophora: Peritricha) ectoparasites of cultured cichlids from Taiwan. *Bull Inst Zool Acad Sin*. 1986;25:135-139.
123. Bondad-Reantaso M, Arthur J. Trichodinids (protozoa: Ciliophora: Peritrichida) of Nile tilapia (*Oreochromis niloticus*) in The Philippines. *Asian Fish Sci*. 1989;3:27-44.
124. Valladão GMR, Alves LO, Pilarski F. Trichodiniasis in Nile tilapia hatcheries: diagnosis, parasite:host-stage relationship and treatment. *Aquaculture*. 2016;451:444-450.
125. Duncan B. Urceolariid ciliates, including three new species, from cultured Philippine fishes. *Trans Am Microsc Soc*. 1977;96:76-81.
126. Abdel-Baki A, Gewik M, Al-Quraishy S. First records of *Ambiphrya* and *Vorticella* spp. (protozoa, Ciliophora) in cultured Nile tilapia (*Oreochromis niloticus*) in the central region of Saudi Arabia. *Saudi J Biol Sci*. 2014;21:520-523.
127. Gonzáles Fernández JG. Parasitofauna of tilapia cause mortalities in fingerlings in two fishfarms, Lima, Peru. *Neotrop Helminthol*. 2012;6:219-229.
128. Viljoen S, Van As JG. *Sessile peritrichs* (Ciliophora: Peritricha) from freshwater fish in the Transvaal, South Africa. *S Afr J Zool*. 1985;20:79-96.
129. Paredes-Trujillo A, Velázquez-Abunader I, Torres-Irineo E, Romero D, Vidal-Martínez V. Geographical distribution of protozoan and metazoan parasites of farmed Nile tilapia *Oreochromis niloticus* (L.) (Perciformes: Cichlidae) in Yucatán, México. *Parasit Vectors*. 2016;9:66. doi:10.1186/s13071-016-1332-9
130. Valladão GMR, Levy-Pereira N, Viadanna PHO, Gallani SU, Farias THV, Pilarski F. Haematology and histopathology of Nile tilapia parasitised by *Epistylis* sp., an emerging pathogen in South America. *Bull Eur Assoc Fish Pathol*. 2014;35:14-20.
131. Adly M, El-Galil M, Soliman F, Ahmed F. Histopathological studies on trichodinosis of farmed *Oreochromis niloticus*. *Am J Life Sci*. 2015;3:30-37.
132. Aly S, Fathi M, Youssef E, Mabrok M. Trichodinids and monogeneans infestation among Nile tilapia hatcheries in Egypt: prevalence, therapeutic and prophylactic treatments. *Aquacult Int*. 2020;28:1459-1471. doi:10.1007/s10499-020-00537-w
133. Diamant A, Ram S, Paperna I. Experimental transmission of *Enteromyxum leei* to freshwater fish. *Dis Aquat Organ*. 2006;72:171-178. doi:10.3354/dao072171
134. Sutarni PA, Herawati E, Budiharjo A. Prevalence of endoparasites and histopathological evaluation of intestine in Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) from aquaculture pond in Janti, Polanharjo District, Klaten Regency. *J Iktiologi Indones*. 2021;21:1-10.
135. Rodrigues M, Francisco C, Biondi G, Júnior J. *Sinuolinea niloticus* n. sp., a myxozoan parasite that causes disease in Nile tilapia (*Oreochromis niloticus*). *Parasitol Res*. 2016;115:4307-4316. doi:10.1007/s00436-016-5214-z
136. Battazza A, da Silva Brasileiro FC, Machado EF, et al. Identification and characterization of *Sinuolinea niloticus* from Nile tilapia (*Oreochromis niloticus*) farmed in Botucatu, Brazil. *Aquac Int*. 2020;28:1899-1906. doi:10.1007/s10499-020-00565-6
137. Fomena A, Marques A, Bouix G. Myxosporidea (Myxozoa) of *Oreochromis niloticus* (Linnaeus 1757) (teleost Cichlidae) in fish-farming pools at Melen (Yaounde, Cameroon, Central Africa). *J Afr Zool*. 1993;107:45-56.
138. Fall M, Fomena A, Kostoïngué B, Diebakate C, Faye N, Toguebaye B. Myxosporidies (Myxozoa, Myxosporea) parasites des poissons cichlidae du Cameroun, du Sénégal et du Tchad avec la description de deux nouvelles espèces. *Ann Sci Nat*. 2000;21:81-92.
139. Matsche MA, Yurakhno V, Zhang J, Sato H. Synopsis of the species of the genus *Zschokkella* Auerbach, 1910 (Myxozoa: Bivalvulida: Myxidiidae). *Syst Parasitol*. 2021;98:25-55. doi:10.1007/s11230-020-09960-2
140. Abdel-Ghaffar F, El-Toukhy A, Al-Quraishy S, et al. Five new myxosporean species (Myxozoa: Myxosporea) infecting the Nile tilapia *Oreochromis niloticus* in Bahr Shebin, Nile tributary, Nile Delta, Egypt. *Parasitol Res*. 2008;103:1197-1205. doi:10.1007/s00436-008-1116-z
141. Abdel-Gaber R, Abdel-Ghaffar F, Maher S, El-Mallah A, Al Quraishy S, Mehlhorn H. Morphological re-description and phylogenetic relationship of five myxosporean species of the family Myxobolidae infecting Nile tilapia. *Dis Aquat Organ*. 2017;124:201-214. doi:10.3354/dao03118
142. Ali M. Light and scanning electron microscopy (SEM) of *Ortholinea africanus* Abdel-Ghaffar et al., 2008 (Myxozoa: Myxosporea) infecting tilapia fish *Oreochromis niloticus* (Osteichthyes: Cichlidae) with description of preparation of coelozoic Myxosporea for SEM. *Acta Protozool*. 2009;48:185-190.
143. Eiras J, Molnár K, Lu Y. Synopsis of the species of *Myxobolus* Bütschli, 1882 (Myxozoa: Myxosporea: Myxobolidae). *Syst Parasitol*. 2005;61:1-46. doi:10.1007/s11230-004-6343-9

144. Fonkwa G, Tchuinkam T, Nana Towa A, Tchoumboue J. Prevalence of Myxosporidiosis in *Oreochromis niloticus* Linnaeus, 1758 (Cichlidae) at Mapé reservoir dam (Adamawa-Cameroon). *J Appl Biosci*. 2018b;123:12332-12345.
145. Fonkwa G, Marc K, Timoléon T, Eyango M, Joseph T. *Myxobolus* (Myxosporea: Myxobolidae) polyinfection patterns in *Oreochromis niloticus* in Adamawa-Cameroon. *Int J Fish Aquat Stud*. 2021;9: 123-130.
146. Rocha S, Azevedo C, Oliveira E, et al. Phylogeny and comprehensive revision of mugiliform-infecting myxobolids (Myxozoa, Myxobolidae), with the morphological and molecular redescription of the cryptic species *Myxobolus exiguus*. *Parasitology*. 2019;146:479-496. doi:10.1017/S0031182018001671
147. El-Sayed N. Ultrastructural morphology of the *Myxobolus dermatobius* Ishii 1915 (Mixosporea: Myxobolideae) microspores infecting eyes of Nile tilapia (*Oreochromis niloticus*) in Egypt. *Vet Ital*. 2020;56: 251-255.
148. Longshaw M, Frear PA, Feist SW. Descriptions, development and pathogenicity of myxozoan (Myxozoa: Myxosporea) parasites of juvenile cyprinids (Pisces: Cyprinidae). *J Fish Biol*. 2005;28:489-508. doi:10.1111/j.1365-2761.2005.00656.x
149. Fonkwa G, Benoit L, Timoleon T, Ahmad I, Joseph T. Effect of season on myxosporean infections in *Oreochromis niloticus* Linnaeus, 1758 (Cichlidae) at MAPE Dam in Adamawa, Cameroon. *J Aquac Res Dev*. 2018;9:5. doi:10.4172/2155-9546.1000533
150. Nchoutpouen E, Benoicirc G, Folefack L, Fomena A. Structure and population dynamics of myxobolus infections in wild and cultured *Oreochromis niloticus* Linnaeus, 1758 in the Noun division (West-Cameroon). *J Cell Anim Biol*. 2011;5:254-264. doi:10.5897/JCAB.9000138
151. Lekeufack Folefack GB, Mala Kengne C, Feudjio Dongmo B, Fomena A. Prevalence and mean intensity of *Myxobolus* spp. parasitizing *Oreochromis niloticus* in Cameroon. *Int*. *J Biol*. 2019;11:1-35. doi:10.5539/ijb.v11n2p35
152. Landsberg JH. Myxosporean infections in cultured tilapias in Israel. *J Protozool*. 1985;32:194-120. doi:10.1111/j.1550-7408.1985.tb03038.x
153. Lövy A, Smirnov M, Brekhman V, Ofek T, Lotan T. Morphological and molecular characterization of a novel myxosporean parasite *Myxobolus bejeranoi* n. sp. (Cnidaria: Myxosporea) from hybrid tilapia in Israel. *Parasitol Res*. 2018;117:491-499. doi:10.1007/s00436-017-5725-2
154. Abolarin M. *Myxobolus tilapiae* sp. nov. (Protozoa: Myxosporidia) from three species of freshwater tilapia in Nigeria. *J West Afr Sci Assoc*. 1974;19:109-114.
155. Fomena A, Bouix G. Myxosporea (Protozoa: Myxozoa) of freshwater fishes in Africa: keys to genera and species. *Syst Parasitol*. 1997;37: 161-178. doi:10.1023/A:1005839220014
156. Okaeme AN, Obiekezie AI, Lehman J, Antai EE, Madu CT. Parasites and diseases of cultured fish of Lake Kainji area, Nigeria. *J Fish Biol*. 1988;32:479-481. doi:10.1111/j.1095-8649.1988.tb05383.x
157. Gbankoto A, Pampoulie C, Marques A, Sakiti G. *Myxobolus dahomeyensis* infection in ovaries of *tilapia* species from Benin (West Africa). *J Fish Biol*. 2001a;58:883-886. doi:10.1111/j.1095-8649.2001.tb00539.x
158. Gbankoto A, Pampoulie C, Marques A, Sakiti G. Occurrence of myxosporean parasites in the gills of two tilapia species from Lake Nokoue (Benin, West Africa): effect of host size and sex, and seasonal patterns of infection. *Dis Aquat Organ*. 2001b;44:217-222. doi:10.3354/dao044217
159. Eissa AE, Mourad A, Ibrahim T. A contribution on myxosoma infection in cultured *Oreochromis niloticus* in lower Egypt. *Nat Sci*. 2006; 4:40-46.
160. Eissa AE, Zaki MM, Aziz AA. *Flavobacterium columnare* / *Myxobolus tilapiae* concurrent infection in the earthen pond reared Nile tilapia (*Oreochromis niloticus*) during the early summer. *Interdiscipl Bio Central*. 2010;2:1-10.
161. Eissa AE, Doaa GM, Ismail MM, Qorany R. Diseases caused by helminthes in cultured *Oreochromis niloticus* and *Clarias gariepinus*, in Ismailia province. *Int J Fish Aquat Res*. 2021;6:17-25.
162. Soror EI, Mahrous KF. Epizotiological studies on proliferative kidney disease in tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*). *Benha Vet Med J*. 2012;23:150-158.
163. El-Mansy A-S. Effect of processing steps and aqueous extracts of some medicinal plants on controlling fish parasites in Egypt. *Acta Parasitol Global*. 2016;7:27-53. doi:10.5829/idosi.apg.2016.7.2.103106
164. Ahmed Mahgoub H, Elnaggar A, Sadeyen JR. Implementation of tissue histopathology and parasitic morphometric analysis in the diagnosis of *Myxobolus fomenai* infection in the skeletal muscles Nile tilapia. *Am J Infect Dis Microbiol*. 2017;5:137-142.
165. Abdelkhalek N, El-Adl M, Hamed M, Al-Araby M. Myxosporidiosis in *Oreochromis niloticus*; molecular identification and oxidative stress biomarkers. *Mansoura Vet Med J*. 2017;18:347-363.
166. Younis NA, Laban SE, Al-Mokaddem AK, Attia MM. Immunological status and histopathological appraisal of farmed *Oreochromis niloticus* exposed to parasitic infections and heavy metal toxicity. *Aquac Int*. 2020;28:2247-2262. doi:10.1007/s10499-020-00589-y
167. Verner-Jeffreys DW, Wallis TJ, Cejas IC, et al. *Streptococcus agalactiae* multilocus sequence type 261 is associated with mortalities in the emerging Ghanaian tilapia industry. *J Fish Dis*. 2018;41:175-179. doi:10.1111/jfd.12681
168. Boungou M, Kabre G, Sakiti N, Marques A, Sawadogo L. Description of four new myxosporean species (Myxozoa: Myxosporea) from genus *Myxobolus*, fish parasites of Burkina Faso, West Africa. *Aust J Biol Sci*. 2006;6:861-867.
169. Okaeme AN, Obiekezie A, Okojie P, Agbontale J. Histopathology of normal and infected organs of tilapia by *Myxobolus ovariae*. *Annu Rep Natl Inst Freshwat Fish Res*. 1989;37-40.
170. Cavalier-Smith T. The Kingdom Chromista: Origin and systematics. *Progress Phycol Res*. 1986;4:309-347.
171. Phillips AJ, Anderson VL, Robertson EJ, Secombes CJ, van West P. New insights into animal pathogenic oomycetes. *Trends Microbiol*. 2008;16:13-19. doi:10.1016/j.tim.2007.10.013
172. Goodwin A. 4.2.1 Branchiomycosis. *Fish Health Section Blue Book*. American Fisheries Society (AFS); 2012.
173. Hussein MMA, Hassan WH, Mahmoud MA. Pathogenicity of *Achlya proliferoides* and *Saprolegnia diclina* (Saprolegniaceae) associated with saprolegniosis outbreaks in cultured Nile tilapia (*Oreochromis niloticus*). *World J Fish Mar Sci*. 2013;5:188-193. doi:10.5829/idosi.wjfms.2013.05.02.7212
174. Chauhan R. Fungal attack on *Tilapia mossambicus* in culture pond, leading to mass mortality of fishes. *Int J Pharma Sci Res*. 2014;5:425-428.
175. Zahran E, Hafez EE, Ferdaus Hossain M, Elhadidy M, Shaheen A. Saprolegniosis in Nile tilapia: identification, molecular characterization, and phylogenetic analysis of two novel pathogenic *Saprolegnia* strains. *J Aquat Anim Health*. 2017;29:43-49. doi:10.1080/08997659.2016.1259691
176. Noor El-Deen A, Osman H, Zaki M, AlyAbo-State H. Mass mortality in cultured Nile tilapia *Oreochromis niloticus* in Kafr El-Sheikh province, Egypt due to saprolegniosis with emphasis on treatment trials. *Aust J Biol Sci*. 2018;18:39-45. doi:10.3923/jbs.2018.39.45
177. FAO. *What You Need to Know About Epizootic Ulcerative Syndrome (EUS)*. FAO, Fisheries and Aquaculture Management Division; 2020.
178. Pradhan PK, Rathore G, Sood N, et al. Emergence of epizootic ulcerative syndrome: large-scale mortalities of cultured and wild fish species in Uttar Pradesh, India. *Curr Sci*. 2014;106:1711-1718. doi:10.18520/CS/V106/I12/1711-1718
179. Herbert B, Jones JB, Mohan CV, Perera RP. Impacts of epizootic ulcerative syndrome on subsistence fisheries and wildlife. *Rev Sci Tech*. 2019;38:459-475. doi:10.20506/rst.38.2.2998

180. Yanong RPE. Fungal diseases of fish. *Vet Clin North Am Exot Anim Pract*. 2003;6:377-400. doi:10.1016/s1094-9194(03)00005-7
181. Walker CA, van West P. Zoospore development in the oomycetes. *Fungal Biol Rev*. 2007;21:10-18. doi:10.1016/j.fbr.2007.02.001
182. Bruno DW, van West P, Beakes GW. *Saprolegnia* and other oomycetes. In: Woo P, Bruno D, eds. *Fish Diseases and Disorders*. CABI Publishing; 2011.
183. Gonçalves AA, Gagnon GA. Ozone application in recirculating aquaculture system: an overview. *J Int Ozone Assoc*. 2011;33:345-367. doi:10.1080/01919512.2011.604595
184. Noga E. Fungal diseases of marine and estuarine fishes. In: Couch J, Fournie J, eds. *Pathology of Marine and Estuarine Organisms*. CRC Press; 1992.
185. Gozlan RE, Marshall WL, Lilje O, Jessop CN, Gleason FH, Andreou D. Current ecological understanding of fungal-like pathogens of fish: what lies beneath? *Front Microbiol*. 2014;5:62. doi:10.3389/fmicb.2014.00062
186. Ogbonna C, Alabi R. Studies on species of fungi associated with mycotic infections of fish in a Nigerian freshwater fish pond. *Hydrobiologia*. 1991;220:131-135. doi:10.1007/BF00006545
187. Panchai K, Hanjavanit C, Kitacharoen N. Characteristics of *Achlya bisexualis* isolated from eggs of Nile tilapia (*Oreochromis niloticus*). *KKU Res J*. 2007;12:195-202.
188. Panchai K, Hanjavanit C, Rujinanont N, Wada S, Kurata O, Hatai K. Freshwater oomycete isolated from net cage cultures of *Oreochromis niloticus* with water mold infection in the Nam Phong river, Khon Kaen province Thailand. *Aquac Aquar Conserv Legis Bioflux*. 2014;7:529-542.
189. Ali E, Hashem M, Al-Salahy M. Pathogenicity and oxidative stress in Nile tilapia caused by *Aphanomyces laevis* and *Phoma herbarum* isolated from farmed fish. *Dis Aquat Organ*. 2011;94:17-28. doi:10.3354/dao02290
190. Carraschi S, Garlich N, de Souza-Pollo A, Brayer D. Isolation of *Saprolegnia aenigmatica* oomycetes and protocol for experimental infection of pacu (*Piaractus mesopotamicus*). *Acta Sci Biol Sci*. 2018;40:e38186. doi:10.4025/actascibiolsci.v40i1.38186
191. Zahran E, Awadin W. Experimental pathogenicity of two *Saprolegnia* spp. to Nile tilapia (*Oreochromis niloticus*) in Egypt, with emphasis on histopathological alterations. Paper presented at 8th International Science Conference on MANSOURA 2014; 2014 pp. 81–93.
192. Noor El-Deen A, Zaki M, Razin A, Shalaby S. Field study on the use of *Artemisia cina* (Sheih Baladi) and Humates (Humapol-Fis) in the control of saprolegniosis in fingerlings of Nile tilapias and *Mugil cephalus* in freshwater fish farms. *Life Sci J*. 2010;7:125-128.
193. FAO. *Report of the International Emergency Disease Investigation Task Force on a Serious Fish Disease in Southern Africa*. FAO; 2009.
194. World Organisation for Animal Health. OIE epizootic ulcerative syndrome. *Manual of Diagnostic Tests for Aquatic Animals*. World Organisation for Animal Health; 2021.
195. Khalil R, Talaat T, Saad T, Abo Selema H, Abdel-Latif M. Branchiomyces demigrans infection in farm-reared common carp (*Cyprinus carpio* L.) and Nile tilapia (*Oreochromis niloticus*) at different localities in Egypt, with special emphasis to the role of environmental stress factors. *Int J Innov Stud Aquat Biol Fish*. 2015;1:15-23.
196. Mahboub H, Shaheen A. Mycological and histopathological identification of potential fish pathogens in Nile tilapia. *Aquaculture*. 2021;530:735849. doi:10.1016/j.aquaculture.2020.735849
197. Paperna I, Smirnova M. Branchiomyces-like infection in a cultured tilapia (*Oreochromis* hybrid, Cichlidae). *Dis Aquat Organ*. 1997;31:233-238. doi:10.3354/dao031233
198. Mendoza L, Taylor J, Ajello L. The class Mesomycetozoea: a group of microorganisms at the animal-fungal boundary. *Annu Rev Microbiol*. 2002;56:315-344. doi:10.1146/annurev.micro.56.012302.160950
199. Rowley J, Gleason F, Andreou D, Marshall W, Lilje O, Gozlan R. Impacts of mesomycetozoean parasites on amphibian and freshwater fish populations. *Fungal Biol Rev*. 2013;27:100-111. doi:10.1038/emi.2015.52
200. Paperna I. Parasites, infections and diseases of fishes in Africa—an update. *CIFA Tech Pap*. 1996;31:1-220. http://www.fao.org/docrep/008/v9551e/V9551E00.HTM
201. Paperna I, Kim S, Hammerschlag E. Liver lesions in cultured *Oreochromis* hybrids caused by amoeboid organisms similar to the aetiological agent of goldfish kidney granuloma. *Dis Aquat Organ*. 1996;25:151-153. doi:10.3354/dao025151
202. Steckert LD, Cardoso L, Tancredo KR, Martins ML, Jerônimo GT. *Dermocystidium* sp. in the gills of farmed *Oreochromis niloticus* in Brazil. *An Acad Bras Ciênc*. 2019;91:e20180959. doi:10.1590/0001-3765201920180959
203. Mahboub H, Shaheen A. Prevalence, diagnosis and experimental challenge of *Dermocystidium* sp. infection in Nile tilapia (*Oreochromis niloticus*) in Egypt. *Aquaculture*. 2020;516:734556. doi:10.1016/j.aquaculture.2019.734556
204. El-Mansy A. A new finding of *Dermocystidium*-like spores in the gut of cultured *Oreochromis niloticus*. *Global Vet*. 2008a;2:369-371.
205. Fuller M, Jaworski A. *Zoosporic Fungi in Teaching and Research*. Southeastern Publishing Corporation; 1987.
206. van West P. *Saprolegnia parasitica*, an oomycete pathogen with a fishy appetite: new challenges for an old problem. *Mycologist*. 2006;20:99-104. doi:10.1016/j.mycol.2006.06.004
207. Beakes G. Oomycete phylogeny: ultrastructural perspectives. In: Rayner A, Brasier C, Moore D, eds. *Evolutionary Biology of the Fungi*. Cambridge University Press; 1987.
208. El-Feki M, Hatai K, Hussein M. Chemotactic and chemokinetic activities of *Saprolegnia parasitica* toward different metabolites and fish tissue extracts. *Mycoscience*. 2003;44:159-162.
209. Jones E, Hyde K, Pang K-L, eds. Sarowar M. Infection strategies of pathogenic oomycetes in fish. *Freshwater Fungi and Fungal-Like Organisms*. de Gruyter; 2014.
210. Wawra S, Bain J, Durward E, et al. Host-targeting protein 1 (SpHtp1) from the oomycete *Saprolegnia parasitica* translocates specifically into fish cells in a tyrosine-sulphate-dependent manner. *Proc Natl Acad Sci USA*. 2012a;109:2096-2101. doi:10.1073/pnas.1113775109
211. Wawra S, Belmonte R, Löbach L, Saraiva M, Willems A, van West P. Secretion, delivery and function of oomycete effector proteins. *Curr Opin Microbiol*. 2012b;15:685-691. doi:10.1016/j.mib.2012.10.008
212. Jiang RHY, de Bruijn I, Haas BJ, Belmonte R, Löbach L, Christie J. Distinctive expansion of potential virulence genes in the genome of the oomycete fish pathogen *Saprolegnia parasitica*. *PLoS Genet*. 2013;9:e1003272. doi:10.1371/journal.pgen.1003272
213. Majeed M, Kumar G, Schlosser S, El-Matbouli M, Saleh M. *In vitro* investigations on extracellular proteins secreted by *Aphanomyces invadans*, the causative agent of epizootic ulcerative syndrome. *Acta Vet Scand*. 2017;59:78.
214. Iberahim NA, Trusch F, van West P. *Aphanomyces invadans*, the causal agent of epizootic ulcerative syndrome, is a global threat to wild and farmed fish. *Fungal Biol Rev*. 2018;32:118-130. doi:10.1016/j.fbr.2018.05.002
215. Pradhan PK, Verma DK, Peruzza L, et al. Molecular insights into the mechanisms of susceptibility of *Labeo rohita* against oomycete *Aphanomyces invadans*. *Sci Rep*. 2020;10:19531. doi:10.1038/s41598-020-76278-w
216. Thoen E, Evensen O, Skaar I. Pathogenicity of *Saprolegnia* spp. to Atlantic salmon, *Salmo salar* L., eggs. *J Fish Dis*. 2011;34:601-608. doi:10.1111/j.1365-2761.2011.01273.x
217. Cao H, Zheng W, Xu J, Ou R, He S, Yang X. Identification of an isolate of *Saprolegnia ferax* as the causal agent of saprolegniosis of

yellow catfish (*Pelteobagrus fulvidraco*) eggs. *Vet Res Commun*. 2012; 36:239-244. doi:10.1007/s11259-012-9536-8

218. Lilley JH, Callinan RB, Chinabut S, Kanchanakhan S, MacRae IH, Phillips MJ. *Epizootic Ulcerative Syndrome (EUS) Technical Handbook*. The Aquatic Animal Health Research Institute (AAHRI); 1998.
219. Kiryu Y, Shields J, Vogelbein W, Zwerner D, Kator H, Blazer V. Induction of skin ulcers in Atlantic menhaden by injection and aqueous exposure to the zoospores of *Aphanomyces invadans*. *J Aquat Anim Health*. 2002;14:11-24. doi:10.1577/1548-8667(2002)0142.0.CO;2
220. Pradhan P, Mohan C, Shankar K, Mohana KB. Susceptibility of fingerlings of Indian major carps to *Aphanomyces invadans*. *Asian Fish Sci*. 2008;21:369-375.
221. Sen K, Mandal R. Fresh-water fish diseases in West Bengal, India. *Int J Fish Aquat Stud*. 2018;6:356-362.
222. Peeler E, Oidtmann B, Midtlyng P, Miossec L, Gozlan R. Non-native aquatic animals introductions have driven disease emergence in Europe. *Biol Invasions*. 2010;13:1291-1303. doi:10.1007/s10530-010-9890-9
223. Cameron SA, Lozier JD, Strange JP, et al. Patterns of widespread decline in north American bumble bees. *Proc Natl Acad Sci USA*. 2011;108:662-667. doi:10.1073/pnas.1014743108
224. Balasuriya L. Epizootic ulcerative syndrome in fish in Sri Lanka, country status report. In: Roberts R, Campbell B, MacRae I, eds. *Proceedings of the ODA Regional Seminar on Epizootic Ulcerative Syndrome*. Aquatic Animal Health Research Institute; 1994: 39-47.
225. Rodgers C, Mohan C, Peeler E. The spread of pathogens through trade in aquatic animals and their products. *Rev Sci Tech*. 2011;30: 241-256. doi:10.20506/rst.30.1.2034
226. Huchzermeyer CF, Huchzermeyer KDA, Christison KW, et al. First record of epizootic ulcerative syndrome from the upper Congo catchment: an outbreak in the Bangweulu swamps. *Zambia J Fish Dis*. 2018;41:87-94.
227. Sibanda S, Pfukenyi D, Barson M, Hang'ombe B, Matope G. Emergence of infection with *Aphanomyces invadans* in fish in some main aquatic ecosystems in Zimbabwe: a threat to national fisheries production. *Transbound Emerg Dis*. 2018;65:1648-1656.
228. Boys CA, Rowland SJ, Gabor M, et al. Emergence of epizootic ulcerative syndrome in native fish of the Murray-Darling river system, Australia: hosts, distribution and possible vectors. *PLoS One*. 2012;7: e35568. doi:10.1371/journal.pone.0035568
229. Huchzermeyer KDA, Van der Waal BCW. Epizootic ulcerative syndrome: exotic fish disease threatens Africa's aquatic ecosystems. *J S Afr Vet Assoc*. 2012;83:1-6.
230. Oidtmann B. Review of biological factors relevant to import risk assessments for epizootic ulcerative syndrome (*Aphanomyces invadans*). *Transbound Emerg Dis*. 2012;59:26-39.
231. Iberahim NA, Sood N, Pradhan PK, van den Boom J, van West P, Trusch F. The chaperone Lhs1 contributes to the virulence of the fish pathogenic oomycete *Aphanomyces invadans*. *Fungal Biol*. 2020; 124:1024-1031. doi:10.1016/j.funbio.2020.09.003
232. Verma DK, Peruzza L, Trusch F, et al. Transcriptome analysis reveals immune pathways underlying resistance in the common carp *Cyprinus carpio* against the oomycete *Aphanomyces invadans*. *Genomics*. 2021;113:944-956. doi:10.1016/j.ygeno.2020.10.028
233. Derevnina L, Petre B, Kellner R, et al. Emerging oomycete threats to plants and animals. *Philos Trans R Soc B*. 2016;371:20150459. doi: 10.1098/rstb.2015.0459
234. Copp G, Villizi L, Gozlan R. Fish movements: the introduction pathway for top mouth gudgeon *Pseudorasbora parva* and other non-native fishes in the UK. *Aquat Conserv*. 2010;20:269-273.
235. Kocan R. Transmission models for the fish pathogen *Ichthyophonus*: synthesis of field observations and empirical studies. *Can J Fish Aquat Sci*. 2019;76:636-642.
236. Oztürk T, Özer A, Taşkaya G, Öz M, Aral O. Japon Balığında (*Carassius auratus*) *Ichthyophonus Hoferi* Enfeksiyonu. *J Fish Sci*. 2010;4: 304-309.
237. Abd El-Ghany N, El-Ashram H. Diagnosis of ichthyophoniasis in *Oreochromis niloticus* in Egypt by polymerase chain reaction (PCR). *Proceedings of the 8th International Symposium on Tilapia in Aquaculture*. American Tilapia Association; 2008:1307-1328.
238. Hershberger P, Gregg J, Dykstra C. High prevalence and low intensity *Ichthyophonus* infections in Pacific halibut (*Hippoglossus stenolepis*). *J Aquat Anim Health*. 2018;30:13-19.
239. Oskarsson G, Palsson J, Gudmundsdottir A. An ichthyophoniasis epizootic in Atlantic herring in marine waters around Iceland. *Can J Fish Aquat Sci*. 2018;75:1106-1116. doi:10.1139/cjfas-2017-0219
240. Plaul S, Andrés Laube P, Montes M, Topa E, Martorelli S, Barbeito C. Dermocystidiosis induced by the parasite *Dermocystidium* sp. in the ornamental fish *Paracheirodon axelrodi*. *Bull Eur Assoc Fish Pathol*. 2018;38:73-78.
241. Tooba B, Khalil B, Hadi R, Mehwish M. Skin and gill parasites of fish *Oreochromis niloticus* from Karashi. *Pakistan J Parasitol*. 2018;65: 51-60.
242. Fisher M, Henk D, Briggs C, et al. Emerging fungal threats to animal, plant and ecosystem health. *Nature*. 2012;484:186-194. doi:10.1038/nature10947
243. Salter C, O'Donnell K, Sutton D, et al. Dermatitis and systemic mycosis in lined seahorses *Hippocampus erectus* associated with a marine-adapted *Fusarium solani* species complex pathogen. *Dis Aquat Organ*. 2012;101:23-31. doi:10.3354/dao02506
244. Cutuli M, Gibello A, Rodriguez-Bertos A, et al. Skin and subcutaneous mycoses in tilapia (*Oreochromis niloticus*) caused by *Fusarium oxysporum* in coinfection with *Aeromonas hydrophila*. *Med Mycol Case Rep*. 2015;12:7-111.
245. Chen YY, Chao CC, Liu FC, et al. Dynamic transcript profiling of *Candida albicans* infection in zebrafish: a pathogen-host interaction study. *PLoS One*. 2013;8:e72483. doi:10.1371/journal.pone.0072483
246. Iqbal Z, Sheikh U, Mughal R. Fungal infections in some economically important freshwater fishes. *Pakistan Vet J*. 2012;32:422-426.
247. Urquhart K, Collins C, Monte M, Sokolowska J, Secombes C, Collet B. Individual measurement of gene expression in blood cells from rainbow trout *Oncorhynchus mykiss* (Walbaum). *J Exp App Anim Sci*. 2016;2:1-9.
248. Bruno D. Observations on a swim bladder fungal infection of a farmed Atlantic salmon, *Salmo salar* L. *Bull Eur Assoc Fish Pathol*. 1989;9:7-8.
249. Lee SC, Corradi N, Brynes EJ, et al. Microsporidia evolved from ancestral sexual fungi. *Curr Biol*. 2008;18:1675-1679. doi:10.1016/j.cub.2008.09.030
250. Capella-Gutierrez S, Marcet-Houben M, Gabaldon T. Phylogenomics supports microsporidia as the earliest diverging clade of sequenced fungi. *BMC Biol*. 2012;10:47. doi:10.1186/1741-7007-10-47
251. Canning E, Lom J. *The Microsporidia of Vertebrates*. Academic Press; 1986.
252. Lom J, Dyková I. *Protozoan Parasites of Fishes*. Elsevier; 1992.
253. McClymont H, Dunn A, Terry R, Rollinson D, Littlewood D, Smith J. Molecular data suggest that microsporidian parasites in freshwater snail are diverse. *Int J Parasitol*. 2005;35:1071-1078. doi:10.1016/j.ijpara.2005.05.008
254. Winters AD, Langohr IM, Souz MDEA, Colodel EM, Soares MP, Faisal M. Ultrastructure and molecular phylogeny of *Pleistophora hyphessobryconis* (Microsporidia) infecting hybrid jundiara (*Leiarius marmoratus* × *Pseudoplatystoma reticulatum*) in a Brazilian aquaculture facility. *Parasitology*. 2016;143:41-49. doi:10.1017/S0031182015001420
255. Garcia L. Laboratory identification of the Microsporidia. *J Clin Microbiol*. 2002;40:1892-1901.

256. Aldama-Cano D, Sanguanrut P, Munkongwongsiri N, et al. Bioassay for spore polar tube extrusion of shrimp *Enterocytozoon hepatopenaei* (EHP). *Aquaculture*. 2018;490:156-161.
257. Zhao RH, Gao W, Qiu L, et al. A staining method for detection of *Enterocytozoon hepatopenaei* (EHP) spores with calcofluor white. *J Invertebr Pathol*. 2020;172:107347. doi:10.1016/j.jip.2020.107347
258. Dezfuli BS, Giari L, Simoni E, Shinn AP, Bosi G. Immunohistochemistry, histopathology and ultrastructure of tissue of the *Gasterosteus aculeatus* (L.) due to infection with *Glugea anomala* (Moniez 1887). *Dis Aquat Organ*. 2004;58:193-202. doi:10.3354/dao058193
259. Lee SJ, Yokoyama H, Ogawa K. Rapid in situ hybridization technique for the detection of fish microsporidian parasites. *Fish Pathol*. 2003;38:117-119.
260. Tang KFJ, Pantoja CR, Redman RM, Han JE, Tran LH, Lightner DV. Development of in situ hybridization and PCR assays for the detection of *Enterocytozoon hepatopenaei* (EHP), a microsporidian parasite infecting penaeid shrimp. *J Invertebr Pathol*. 2015;130:37-41.
261. Weli SC, Dale OB, Hansen H, Gjessing MC, Rønneberg LB, Falk K. A case study of *Desmozoon lepeophtherii* infection in farmed Atlantic salmon associated with gill disease, peritonitis, intestinal infection, stunted growth, and increased mortality. *Parasit Vectors*. 2017;10:370.
262. Fomena A, Coste F, Bouix G. *Loma camerounensis* sp. nov. (protozoa, Microsporida) a parasite of *Oreochromis niloticus* Linnaeus, 1757 (teleost, Cichlidae) in fish-rearing ponds in Melen, Yaounde, Cameroon. *Parasitol Res*. 1992;78:201-208.
263. Sakiti NG, Bouix G. *Nosemoides tilapiae* sp. n., microsporidie parasite de poissons Cichlidae des eaux saumatres du Benin: implantation et caracteres ultrastructuraux. *Parasitol Res*. 1987;73:203-212.
264. Faye N, Toguebaye BS, Bouix G. Ultrastructure and development of *Neonosemoides tilapiae* (Sakiti and Bouix, 1987) n.g., n. comb. (Protozoa, Microspora) from African cichlid fish. *Eur J Protistol*. 1996;32:320-326.
265. Rodrigues M, Francisco C, David G, da Silva R, Araújo J Jr. A new microsporidium species, *Nucleospora braziliensis* n. sp. infecting Nile tilapia (*Oreochromis niloticus*) from Brazilian aquaculture. *Int J Fish Aquat Stud*. 2017;5:496-505.
266. Nur I, Yusnaini Idris M, Sari A. Study on the impact of environmental pollution: parasitic infestation and conditions factor of fish living in amalgamation ponds. *International Conference: Improving Tropical Animal Production for Food Security. IOP Conference Series on Earth Environmental Sciences*. Vol 465. Atlantis Press; 2020:012042.
267. Paperna I. Occurrence of *Cnidospora* infections in freshwater fishes in Africa. *Bull Inst Fondam Afr Noire*. 1973;35:509-521.
268. Larsson JIR. Identification of microsporidian genera (Protozoa, Microspora)—a guide with comments on the taxonomy. *Arch Protistenkd*. 1988;136:1-37.
269. Larsson JIR. Identification of Microsporidia. *Acta Protozool*. 1999;38:161-197.
270. Sprague V, Becnel JJ, Hazard EI. Taxonomy of phylum Microspora. *Crit Rev Microbiol*. 1992;18:285-395.
271. Canning E, Vávra J. Phylum Microsporidia. In: Lee J, Leedale G, Bradbury P, eds. *The Illustrated Guide to the Protozoa*. Allen Press; 2000.
272. Cali A, Becnel J, Microsporidia TP. Microsporidia. In: Archibald J, Simpson A, Slamovits C, eds. *Handbook of the Protists*. Springer International Publishing; 2016.
273. Ramsay J, Watral V, Schreck C, Kent M. *Pseudoloma neurophilia* infections in zebrafish *Danio rerio*: effects of stress on survival, growth, and reproduction. *Dis Aquat Organ*. 2009;88:69-84.
274. Ahmed NH, Caffara M, Sitjà-Bobadilla A, et al. Detection of the intranuclear microsporidian *Enterospora nucleophila* in gilthead sea bream by in situ hybridization. *J Fish Dis*. 2019;42:809-815.
275. Picard-Sánchez P, Piazzon MC, Estensoro I, et al. Experimental horizontal transmission of *Enterospora nucleophila* (Microsporea: Enterocytozoonidae) in gilthead sea bream (*Sparus aurata*). *Animals*. 2021;11:362. doi:10.3390/ani11020362
276. Speare DJ, Athanassopoulou F, Daley J, Sanchez JG. A preliminary investigation of alternatives to fumagillin for the treatment of *Loma salmonae* infection in rainbow trout. *J Comp Pathol*. 1999;121:241-248.
277. Guselle N, Speare D, Markham R, Patelakis S. Efficacy of intraperitoneally and orally administered ProVale, a yeast beta-(1,3)/(1,6)-D-glucan product, in inhibiting xenoma formation by the microsporidian *Loma salmonae* on rainbow trout gills. *N Am J Aquac*. 2010;72:65-72.
278. Becker J, Speare D, Daley J, Dick P. Effects of monensin dose and treatment on xenoma reduction in microsporidial gill disease in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *J Fish Dis*. 2002;25:673-680.
279. Speare D, Ritter G, Schmidt H. Quinine hydrochloride treatment delays xenoma formation and dissolution in rainbow trout challenged with *Loma salmonae*. *J Comp Pathol*. 1998;119:459-465.
280. Schmahl G, El Toukhy A, Ghaffar F. Transmission electron microscopic studies on the effects of toltrazuril on *Glugea anomala*, Moniez, 1887 (Microsporidia) infecting the three-spined stickleback *Gasterosteus aculeatus*. *Parasitol Res*. 1990;76:700-706.
281. Rychen G, Aquilina G, Azimonti G, et al. Safety and efficacy of Monimax®(monensin sodium and nicarbazin) for turkeys for fattening. *EFSA J*. 2017;15:5094. doi:10.2903/j.efsa.2017.5094
282. Speare D, Markham R, Guselle N. Development of an effective whole-spore vaccine to protect against microsporidial gill disease in rainbow trout (*Oncorhynchus mykiss*) by using a low-virulence strain of *Loma salmonae*. *Clin Vaccine Immunol*. 2007;14:1652-1654.
283. Přikrylová I, Matějusová I, Musilová N, Gelnar M. *Gyrodactylus* species (Monogenea: Gyrodactylidae) on the cichlid fishes of Senegal, with the description of *Gyrodactylus ergensi* n. sp. from mango tilapia, *Sarotherodon galilaeus* L. (Teleostei: Cichilidae). *Parasitol Res*. 2009;106:1-6. doi:10.1007/s00436-009-1600-0
284. Přikrylová I, Vanhove MPM, Janssens SB, Billeter PA, Huyse T. Tiny worms from a mighty continent: high diversity and new phylogenetic lineages of African monogeneans. *Mol Phylogenet Evol*. 2012;67:43-52. doi:10.1016/j.ympev.2012.12.017
285. Zahradníčková P, Barson M, Luus-Powell W, Přikrylová I. Species of *Gyrodactylus* von Nordmann, 1832 (Platyhelminthes: Monogenea) from cichlids from Zambezi and Pimpopo river basins in Zimbabwe and South Africa: evidence for unexplored species richness. *Syst Parasitol*. 2016;93:679-700. doi:10.1007/s11230-016-9652-x
286. García-Vásquez A, Hansen H, Christison KW, Bron JE, Shinn AP. Description of three new species of *Gyrodactylus* von Nordmann, 1832 (Monogenea) parasitising *Oreochromis niloticus niloticus* (L.) and *O. mossambicus* (Peters) (Cichlidae). *Acta Parasitol*. 2011;56:20-33. doi:10.2478/s11686-011-0005-2
287. García-Vásquez A, Pinacho-Pinacho CD, Guzmán-Valdivieso I, Calixto-Rojas M, Rubio-Godoy M. Morpho-molecular characterization of *Gyrodactylus* parasites of farmed tilapia and their spillover to native fishes in Mexico. *Sci Rep*. 2021;11:13957. doi:10.1038/s41598-021-93472-6
288. García-Vásquez A, Hansen H, Christison KW, Rubio-Godoy M, Bron JE, Shinn AP. *Gyrodactylids* (Gyrodactylidae, Monogenea) infecting *Oreochromis niloticus niloticus* (L.) and *Oreochromis mossambicus* (Peters) (Cichlidae): a pan-global survey. *Acta Parasitol*. 2010;55:215-229. doi:10.2478/s11686-010-0042-2
289. Cruz-Laufer A, Artois T, Koblmüller S, et al. Explosive networking: The role of adaptive host radiations and ecological opportunity in a species-rich host-parasite assembly. *Ecol Lett*. 2021;27:1-27. doi:10.22541/au.163274253.31016446/v1

290. Li H, Chen W, Man G, Yi Z. Research on alien fish's Monogenea in Pearl River water system (part one): four species of Ancyrocephalidae parasitising in the gills of *Tilapia niloticus* (including three new records). *J Guangzhou Univ*. 2009;8:54-57.
291. Douëllou L. Monogenean of the genus *Cichlidogyrus* Paperna, 1960 (Dactylogyridae: Ancyrocephalinae) from cichlid fishes of Lake Kariba (Zimbabwe) with description of five new species. *Syst Parasitol*. 1993;25:159-186. doi:10.1007/bf00007007
292. Jorissen MWP, Pariselle A, Huyse T, et al. Six new dactylogyrid species (Platyhelminthes, Monogenea) from the gills of cichlids (Teleostei, Cichliformes) from the lower Congo Basin. *Parasite*. 2018;25:64. doi:10.1051/parasite/2018059
293. Pariselle A, Bilong CF, Euzet L. Four new species of *Cichlidogyrus* Paperna, 1960 (Monogenea, Ancyrocephalidae), all gill parasites from African mouthbreeder tilapias of the genera *Sarotherodon* and *Oreochromis* (Pisces, Cichlidae), with a redescription of *C. thurstonae* Ergens, 1981. *Syst Parasitol*. 2003a;56:201-210. doi:10.1023/B:SYPA.0000003807.27452.bd
294. Garcia DAZ, Orsi ML, Silva-Souza AT. From Africa to Brazil: detection of African *Oreochromis niloticus* parasites in Brazilian fish farms. *Acta Limnol Bras*. 2019;31:e202. doi:10.1590/S2179-975X6218
295. Pariselle A, Euzet L. Systematic revision of dactylogyridean parasites (Monogenea) from cichlid fishes in Africa, the Levant and Madagascar. *Zoosystema*. 2009;31:849-898. doi:10.5252/z2009n4a6
296. Luus-Powell WJ, Madanire-Moyo GN, Matla MM, Přikrylová I. Monogenean parasites from the stomach of *Oreochromis mossambicus* from South Africa: two new species of *Enterogyrus* (Dactylogyridae: Ancyrocephalinae). *Parasitol Res*. 2020;119:1505-1514. doi:10.1007/s00436-020-06650-2
297. Jerônimo GT, Speck GM, Martins ML. First report of *Enterogyrus cichlidarum* Paperna 1963 (Monogenoidea: Ancyrocephalidae) on Nile tilapia *Oreochromis niloticus* cultured in Brazil. *Neotrop Helminthol*. 2010;4:75-80.
298. Assane IM, Prada-Mejia KD, Gallani SU, Weiser NF, Valladão GMR, Pilarski F. *Enterogyrus* spp. (Monogenea: Ancyrocephalinae) and *Aeromonas jandaei* co-infection associated with high mortality following transport stress in cultured Nile tilapia. *Transbound Emerg Dis*. 2021;69:e276-e287. doi:10.1111/tbed.14295
299. Mendoza-Franco E, Caspeta-Mandujano J, Osorio M. Ecto- and endo-parasitic monogeneans (Platyhelminthes) on cultured freshwater exotic fish species in the state of Morelos, South-Central Mexico. *ZooKeys*. 2018;776:1-12. doi:10.3897/zookeys.776.26149
300. Zhang S, Zhi T, Xu X, et al. Monogenean fauna of alien tilapias (Cichlidae) in South China. *Parasite*. 2019;26:4. doi:10.1051/parasite/2019003
301. Prats León F, Martínez Pérez M, Silveira R. Primer reporte de monogeneos del género *Enterogyrus* Paperna, 1963 (Monogenea: Ancyrocephalidae) en tilapias de cultivo en Cuba. *Rev Electrón Vet*. 2012;13:1-12.
302. Cruz-Laufer AJ, Artois T, Pariselle A, Smeets K, Vanhove MPM. The cichlid-*Cichlidogyrus* network: a blueprint for a model system of parasite evolution. *Hydrobiologia*. 2021;848:3847-3863. doi:10.1007/s10750-020-04426-4
303. Muterezi Bukinga F, Vanhove MPM, Van Steenberge M, Pariselle A. Ancyrocephalidae (Monogenea) of Lake Tanganyika: III: *Cichlidogyrus* infecting the world's biggest cichlid and the non-endemic tribes Haplochromini, Oreochromini and Tylochromini (Teleostei, Cichlidae). *Parasitol Res*. 2012;111:2049-2061. doi:10.1007/s00436-012-3052-1
304. Lerssutthichawal T, Maneepitaksanti W, Purivirojkul W. Gill monogeneans of potentially cultured tilapias and first record of *Cichlidogyrus mbirizei* Bukinga et al., 2012, in Thailand. *Walailak J Sci Tech*. 2016;13:543-553.
305. Lim SY, Ooi AL, Wong WL. Gill monogeneans of Nile tilapia (*Oreochromis niloticus*) and red hybrid tilapia (*Oreochromis* spp.) from the wild and fish farms in Perak, Malaysia: infection dynamics and spatial distribution. *SpringerPlus*. 2016;5:1609. doi:10.1186/s40064-016-3266-2
306. Geraerts M, Muterezi Bukinga F, Vanhove MPM, et al. Six new species of *Cichlidogyrus* Paperna, 1960 (Platyhelminthes: Monogenea) from the gills of cichlids (Teleostei: Cichliformes) from the Lomami River basin (DRC: middle Congo). *Parasit Vectors*. 2020;13:187. doi:10.1186/s13071-020-3927-4
307. Pouyaud L, Desmarais E, Deveney M, Pariselle A. Phylogenetic relationships among monogenean gill parasites (Dactylogyridea, Ancyrocephalidae) infesting tilapiine hosts (Cichlidae): systematic and evolutionary implications. *Mol Phylogenet Evol*. 2006;38:241-249. doi:10.1016/j.ympev.2005.08.013
308. Jorissen MWP, Pariselle A, Huyse T, et al. Diversity, endemicity and host-specificity of monogenean gill parasites (Platyhelminthes) of cichlids in the Bangweulu-Mweru ecoregion. *J Helminthol*. 2018b;92:417-437. doi:10.1017/S0022149X17000712
309. Jorissen M, Vanhove MPM, Pariselle A, et al. Molecular footprint of parasite co-introduction with Nile tilapia in the Congo Basin. *Org Divers Evol*. 2022. doi:10.1007/s13127-022-00563-x
310. Vanhove MPM, Tessens B, Schoelinck C, et al. Problematic barcoding in flatworms: a case-study on monogeneans and rhabdocoels (Platyhelminthes). *ZooKeys*. 2013;365:355-379. doi:10.3897/zookeys.365.5776
311. Ek-Huchim J, Jimenez-Garcia I, Pérez-Vega J, Rodríguez-Canul R. Non-lethal detection of DNA from *Cichlidogyrus* spp. (Monogenea, Ancyrocephalinae) in gill mucus of the Nile tilapia *Oreochromis niloticus*. *Dis Aquat Organ*. 2012;98:155-162. doi:10.3354/dao02435
312. Ek-Huchim J, Jiménez-García I, Rodríguez-Canul R. DNA detection of *Gyrodactylus* spp. in skin mucus of Nile tilapia *Oreochromis niloticus*. *Vet Parasitol*. 2019;272:75-78. doi:10.1016/j.vetpar.2019.07.004
313. Buchmann K, Bresciani J. Parasitic infections in pond-reared rainbow trout *Oncorhynchus mykiss* in Denmark. *Dis Aquat Organ*. 1997;28:125-138. doi:10.3354/dao028125
314. Kristmundsson A, Bambir SH, Helgason S. *Gyrodactylus anarhichatis* Mo & Lile (Monogenea: Gyrodactylidae) infection of farmed spotted wolffish, *Anarhichas minor* Olafsen, in Iceland. *J Fish Dis*. 2006;29:365-370. doi:10.1111/j.1365-2761.2006.00706.x
315. Van Oosterhout C, Mohammed RS, Hansen H, et al. Selection by parasites in spate conditions in wild Trinidadian guppies (*Poecilia reticulata*). *Int J Parasitol*. 2007;37:805-812. doi:10.1016/j.ijpara.2006.12.016
316. Ali N, Aboyadak I. Tail erosion an emerging disease affecting tilapia fry in Kafrelsheikh hatcheries. *Aust J Biol Sci*. 2018;18:280-288. doi:10.3923/jbs.2018.280.288
317. Pettersen R, Hytterød S, Vøllestad L, Mo T. Osmoregulatory disturbances in Atlantic salmon, *Salmo salar* L., caused by the monogenean *Gyrodactylus salaris*. *J Fish Dis*. 2013;36:67-70. doi:10.1111/j.1365-2761.2012.01441.x
318. Abdel-Latif H, Khafaga A. Natural co-infection of cultured Nile tilapia *Oreochromis niloticus* with *Aeromonas hydrophila* and *Gyrodactylus cichlidarum* experiencing high mortality during summer. *Aquacult Res*. 2020;51:1880-1892. doi:10.1111/are.14538
319. Soler-Jiménez L, Paredes-Trujillo A, Vidal-Martínez V. Helminth parasites of finfish commercial aquaculture in Latin America. *J Helminthol*. 2017;91:110-136. doi:10.1017/S0022149X16000833
320. Xu DH, Shoemaker CA, Klesius PH. Evaluation of the link between gyrodactylosis and streptococcosis of Nile tilapia, *Oreochromis niloticus* (L.). *J Fish Dis*. 2007;30:233-238. doi:10.1111/j.1365-2761.2007.00806.x
321. Madanire-Moyo GN, Avenant-Oldewage A. The histopathology of *Enterogyrus coronatus* Pariselle, Lambert & Euzet, 1999

(Monogenoidea) in the stomach of the southern mouthbrooder *Pseudocrenilabrus philander* (weber, 1897) (Cichlidae). *Afr Zool*. 2015; 50:1-6. doi:10.1080/15627020.2015.1048729

322. Igeh PC, Avenant OA. Pathological effects of *Cichlidogyrus philander* Douëllou, 1993 (Monogenea, Ancyrocephalidae) on the gills of *Pseudocrenilabrus philander* (Weber, 1897) (Cichlidae). *J Fish Dis*. 2020; 43:177-184. doi:10.1111/jfd.13121
323. El-Naggar M, Hagras A, Ogawa K, Hussein A, El-Naggar A. Attachment of *Cichlidogyrus* monogenean species to the gills of the Nile fish *Oreochromis niloticus* and their local pathological impact on them. *J Egypt Ger Soc Zool*. 2001;35:143-155.
324. Sandoval-Gío J, Rodrıíguez-Canul R, Vidal-Martínez V. Humoral antibody response of the tilapia *Oreochromis niloticus* against *Cichlidogyrus* spp. (Monogenea). *J Parasitol*. 2008;94:404-409. doi:10.1645/GE-1382.1
325. Sandoval-Gío J, Rosado-Vallado M, Rodríguez-Canul R. Efectos individuales de la ciclidogiriasis y estreptococosis inducidas en la bioquímica sanguínea de la tilapia *Oreochromis niloticus*. *Hidrobiológica*. 2013;23:328-339.
326. El-Naggar M, Kearn G. Haptor glands in the gill-parasitic, ancyrocephaline monogenean *Cichlidogyrus halli typicus* and the report of a possible prokaryotic symbiont. *Int J Parasitol*. 1989;19:401-408. doi:10.1016/0020-7519(89)90096-9
327. El-Mansy A, Hamada S, Hasan S, El-Sarnagawy D. Histopathology of farmed freshwater fish infested with different helminthes. *Egypt J Aquac Biol Fish*. 2011;15:1-13.
328. Noga E, Flowers J. Invasion of *Tilapia mossambica* (Cichlidae) viscera by the monogenean *Enterogyrus cichlidarum*. *J Parasitol*. 1995;81: 815-817.
329. Zhi T, Xu X, Chen J, et al. Expression of immune-related genes of Nile tilapia *Oreochromis niloticus* after *Gyrodactylus cichlidarum* and *Cichlidogyrus sclerosus* infections demonstrating immunosuppression in coinfection. *Fish Shellfish Immunol*. 2018;80:397-404. doi:10.1016/j.fsi.2018.05.060
330. Martins MI, Shoemaker SA, Xu D, Klesius PH. Effect of parasitism on vaccine efficacy against *Streptococcus iniae* in Nile tilapia. *Aquaculture*. 2011;314:18-23. doi:10.1016/j.aquaculture.2011.01.022
331. Paredes-Trujillo A, Velázquez-Abunader I, Papiol V, del Río-Rodríguez R, Vidal-Martínez V. Negative effect of ectoparasite burdens on the condition factor from farmed tilapia *Oreochromis niloticus* in the Yucatan, Mexico. *Vet Parasitol*. 2021;292:109393. doi:10.1016/j.vetpar.2021.109393
332. Michel C. Pathology of tilapias. *Aquat Living Resour*. 1989;2:117-126. doi:10.1051/alr:1989014
333. Robinson R, Khalil L, Hall R, Steele R. Infection of red hybrid tilapia with a monogenean in coastal waters off southern Jamaica. *Proc Gulf Caribb Fish Inst*. 1989;42:441-447.
334. Kabata Z. *Parasites and Diseases of Fish Cultured in the Tropics*. Taylor & Francis; 1985.
335. Aguirre-Fey D, Benítez-Villa G, Pérez-Ponce de León G, Rubio-Godoy M. Population dynamics of *Cichlidogyrus* spp. and *Scutogyrus* sp. (Monogenea) infecting farmed tilapia in Veracruz, Mexico. *Aquaculture*. 2015;443:11-15. doi:10.1016/j.aquaculture.2015.03.004
336. Salgado-Maldonado G, Rubio-Godoy M. Helmintos parásitos de peces de agua dulce introducidos. In: Mendoza R, Koleff P, eds. *Especies Acuáticas Invasoras en México*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad; 2014.
337. Šimková A, Řehulková E, Rasoloariniaina JR, et al. Transmission of parasites from introduced tilapias: a new threat to endemic Malagasy ichthyofauna. *Biol Invasions*. 2019;21:803-819. doi:10.1007/s10530-018-1859-0
338. García-Vásquez A, Razo-Mendivil U, Rubio-Godoy M. Triple trouble? Invasive poeciliid fishes carry the introduced tilapia pathogen *Gyrodactylus cichlidarum* in the Mexican highlands. *Vet Parasitol*. 2017; 235:37-40. doi:10.1016/j.vetpar.2017.01.014
339. Garcia-Vasquez A, Hansen H, Shinn AP. A revised description of *Gyrodactylus cichlidarum* Paperna, 1968 (Gyrodactylidae) from the Nile tilapia, *Oreochromis niloticus niloticus* (Cichlidae), and its synonymy with *G. niloticus* Cone, Arthur et Bondad-Reantaso, 1995. *Folia Parasitol*. 2007;54:129-140. doi:10.14411/fp.2007.018
340. Jorissen MWP, Huyse T, Pariselle A, et al. Historical museum collections help detect parasite species jumps after tilapia introductions in The Congo Basin. *Biol Invasions*. 2020;22:2825-2844. doi:10.1007/s10530-020-02288-4
341. Outa J, Dos Santos Q, Avenant-Oldewage A, Jirsa F. Parasite diversity of introduced fish *Lates niloticus*, *Oreochromis niloticus* and endemic *Haplochromis* spp. of Lake Victoria, Kenya. *Parasitol Res*. 2021;120:1583-1592. doi:10.1007/s00436-021-07095-x
342. Jiménez-García MI, Vidal-Martínez VM, López-Jiménez S. Monogeneans in introduced and native cichlids in Mexico: evidence for transfer. *J Parasitol*. 2001;87:907-909. doi:10.1645/0022-3395(2001)087[0907:MIIANC]2.0.CO;2
343. Fannes W, Vanhove MPM, Huyse T. Redescription of *Cichlidogyrus tiberianus* Paperna, 1960 and *C. dossoui* Douëllou, 1993 (Monogenea: Ancyrocephalidae), with special reference to the male copulatory organ. *Syst Parasitol*. 2017;94:133-144. doi:10.1007/s11230-016-9685-1
344. Combes C, Toft CA, Aeschlimann A, Bolis L. Evolution of parasite life cycles. In: Toft CA, Aeschlimann A, Bolis L, eds. *Parasite-Host Associations: Coexistence or Conflict?* . Oxford University Press; 1991.
345. Firmat C, Alibert P, Mutin G, Losseau M, Pariselle A, Sasal P. A case of complete loss of gill parasites in the invasive cichlid *Oreochromis mossambicus*. *Parasitol Res*. 2016;115:3657-3661. doi:10.1007/s00436-016-5168-1
346. Chen J, Zhi T, Xu X, Zhang S, Zheng Y, Yang T. Molecular characterization and dynamic expressions of three Nile tilapia (*Oreochromis niloticus*) complement genes after *Gyrodactylus cichlidarum* (Monogenea) infection. *Aquaculture*. 2019;502:176-188. doi:10.1016/j.aquaculture.2018.12.018
347. Chen J, Zheng Y, Zhi T, et al. MHC II α polymorphism of Nile tilapia, *Oreochromis niloticus*, and its association with the susceptibility to *Gyrodactylus cichlidarum* (Monogenea) infection. *Aquaculture*. 2021; 539:736637. doi:10.1016/j.aquaculture.2021.736637
348. Caña-Bozada V, Chapa-López M, Díaz-Martín R, et al. In silico identification of excretory/secretory proteins and drug targets in monogenean parasites. *Infect Genet Evol*. 2021;93:104931. doi:10.1016/j.meegid.2021.104931
349. Vanhove MPM. Evolutionary parasitology of African freshwater fishes—and its implications for the sustainable management of aquatic resources. In: Scholz T, Vanhove M, Smit N, Jayasundera Z, Gelnar M, eds. *A Guide to the Parasites of African Freshwater Fishes*. Abc Taxa; 2018.
350. Messu Mandeng FD, Bilong Bilong CF, Pariselle A, Vanhove MPM, Bitja Nyom AR, Agnèse JF. A phylogeny of *Cichlidogyrus* species (Monogenea, Dactylogyridea) clarifies a host switch between fish families and reveals an adaptive component to attachment organ morphology of this parasite genus. *Parasite Vector*. 2015;8:582. doi:10.1186/s13071-015-1181-y
351. Rahmouni C, Van Steenberge M, Vanhove MPM, Šimková A. Intraspecific morphological variation in *Cichlidogyrus* (Monogenea) parasitizing two cichlid hosts from Lake Tanganyika exhibiting different dispersal capacities. *Hydrobiologia*. 2021;848:3833-3845. doi:10.1007/s10750-020-04429-1
352. Kmentová N, Gelnar M, Mendlová M, Van Steenberge M, Koblmüller S, Vanhove MPM. Reduced host-specificity in a parasite infecting non-littoral Lake Tanganyika cichlids evidenced by intraspecific morphological and genetic diversity. *Sci Rep*. 2016;6:39605. doi:10.1038/srep39605
353. Vanhove MPM, Hablützel PI, Pariselle A, Šimková A, Huyse T, Raeymaekers JAM. Cichlids: a host of opportunities for evolutionary

parasitology. *Trends Parasitol*. 2016;32:820-832. doi:10.1016/j.pt.2016.07.002

354. Shechonge A, Ngatunga BP, Bradbeer SJ, et al. Widespread colonisation of Tanzanian catchments by introduced *Oreochromis tilapia* fishes: the legacy from decades of deliberate introduction. *Hydrobiologia*. 2019;832:235-253. doi:10.1007/s10750-018-3597-9
355. Vanhove MPM, Kmentová N, Luus-Powell WJ, Netherlands EC, de Buron I. Barger MA a snapshot of parasites in tropical and subtropical freshwater wetlands: modest attention for major players. In: Dalu T, Wasserman RJ, eds. *Fundamentals of Tropical Freshwater Wetlands: from Ecology to Conservation Management*. Elsevier; 2022.
356. Elumalai P, Kurian A, Lakshmi S, Faggio C, Esteban M, Ringø E. Herbal immunomodulators in aquaculture. *Rev Fish Sci Aquac*. 2021;29:33-57. doi:10.1080/23308249.2020.1779651
357. Adeshina I, Tiamiyu L, Akpoilih B, Jenyo-Oni A, Ajani E. Dietary *Mitracarpus scaber* leaves extract improved growth, antioxidants, non-specific immunity, and resistance of Nile tilapia, *Oreochromis niloticus* to *Gyrodactylus malalai* infestation. *Aquaculture*. 2021;535:736377. doi:10.1016/j.aquaculture.2021.736377
358. Compean-Martínez J, Salazar-Ulloa M, Chávez-Soriano L, Muñoz-Córdoba G, von Son-de FE. Anthelmintic-like activity of *Leucaena leucocephala aqueous* extract against *Gyrodactylus* spp. in naturally infected tilapia fingerlings. *N Am J Aquac*. 2021;83:354-362. doi:10.1002/naaq.10206
359. Dotta G, Brum A, Jeronimo G, Maraschin M, Martins M. Effect of dietary supplementation with propolis and *Aloe barbadensis* extracts on hematological parameters and parasitism in Nile tilapia. *Braz J Vet Parasitol*. 2015;24:66-71. doi:10.1590/S1984-29612015004
360. de Oliveira HG, Neto F, Ruiz M, et al. Essential oils of *Lippia sidoides* and *Mentha piperita* against monogenean parasites and their influence on the hematology of Nile tilapia. *Aquaculture*. 2016;450:182-186. doi:10.1016/j.aquaculture.2015.07.029
361. Pariselle A, Morand S, Deveney M, Pouyaud L. Parasite species richness of closely related hosts: historical scenario and "genetic" hypothesis. In: Combes C, Jourdane J, eds. *Taxonomy, Ecology and Evolution of Metazoan Parasites*. Presses Universitaires de Perpignan; 2003.
362. Pariselle A, Bitja Nyom A, Bilong Bilong C. Checklist of the ancyrocephalids (Monogenea) parasitizing *Tilapia* species in Cameroon, with the description of three new species. *Zootaxa*. 2013;3599:78-86. doi:10.11646/zootaxa.3599.1.7
363. Vanhove MPM, Briscoe AG, Jorissen MWP, Littlewood DTJ, Huyse T. The first next-generation sequencing approach to the mitochondrial phylogeny of African monogenean parasites (Platyhelminthes: Gyrodactylidae and Dactylogyridae). *BMC Genomics*. 2018;19:520. doi:10.1186/s12864-018-4893-5
364. Caña-Bozada V, Llera-Herrera R, Fajer-Ávila E, Morales-Serna F. Mitochondrial genome of *Scutogyrus longicornis* (Monogenea: Dactylogyridea), a parasite of Nile tilapia *Oreochromis niloticus*. *Parasitol Int*. 2021;81:102281. doi:10.1016/j.parint.2020.102281
365. Kmentová N, Hahn C, Koblmüller S, et al. Contrasting host-parasite population structure: morphology and mitogenomics of a parasitic flatworm on pelagic deepwater cichlid fishes from Lake Tanganyika. *Biology*. 2021;10:797. doi:10.3390/biology10080797
366. Whittington ID. The Capsalidae (Monogenea: Monopisthocotylea): a review of diversity, classification and phylogeny with a note about species complexes. *Folia Parasitol*. 2004;51:109-122. doi:10.14411/fp.2004.016
367. Kaneko JJK, Yamada R, Brock JA, Nakamura R. Infection of a tilapia *Oreochromis mossambicus* (Trewavas), by a marine monogenean, *Neobenedenia melleni* (MacCallum, 1927) Yamaguti, 1963 in Kaneohe Bay, Hawaii, USA, and its treatment. *J Fish Dis*. 1988;11:295-300. doi:10.1111/j.1365-2761.1988.tb01225.x
368. Prieto A, Fajer E, Cartaya R, Vinjoy M. *Benedenia* sp. (Monogenea: Capsalidae) in tilapia (*Oreochromis aureus*) grown in a marine environment: preliminary report. *Rev Salud Anim*. 1986;8:141-145.
369. Whittington ID, Deveney MR, Wyborn SJ. A revision of *Benedenia* Diesing, 1858 including a redescription of *B. sciaenae* (van Beneden, 1856) Odhner, 1905 and recognition of *Menziesia* Gibson, 1976 (Monogenea: Capsalidae). *J Nat Hist*. 2001;35:663-777. doi:10.1080/00222930152023090
370. Trujillo AAP. *Monogeneos (Platyhelmintes) parasitos de peces de interes comercial sometidos a cultivo intesivos en Cuba: Sistematica, patologia y control*. Instituto Superior de Ciencias Agropecuarias de la Habana; 1987.
371. Kishimori JM, Takemura A, Leong JAC. *Neobenedenia melleni*-specific antibodies are associated with protection after continuous exposure in *Mozambique tilapia*. *J Immunol Res*. 2015;2015:635387. doi:10.1155/2015/635387
372. Gallet De Saint Aurin D, Raymond JC, Vianas V. Marine finfish pathology: specific problems and research in the French West Indies. *Advances in Tropical Aquaculture*. Actes de colloques Ifremer; 1989:143-160.
373. Robinson R, O'Connor N, Steele R. Interactions between cage-cultured hybrid tilapia and a marine monogenean, *Neobenedenia melleni*, in Jamaica. *N Am J Aquac*. 2008;70:68-73. doi:10.1577/A06-037.1
374. Ernst DH, Ellingson LJ, Olla BL, Wichlund RI, Watanabe WO, Grover JJ. Production of Florida red tilapia in seawater pools: nursery rearing with chicken manure and growout with prepared feed. *Aquaculture*. 1989;80:247-260. doi:10.1016/0044-8486(89)90173-7
375. Mueller K, Watanabe W, Head W. Effect of salinity on hatching in *Neobenedenia melleni*, a monogenean ectoparasite of seawater-cultured tilapia. *J World Aquac Soc*. 1992;23:199-204. doi:10.1111/j.1749-7345.1992.tb00769.x
376. Cowell L, Watanabe W, Head W, Grover J, Shenker J. Use of tropical cleaner fish to control the ectoparasite *Neobenedenia melleni* (Monogenea: Capsalidae) on seawater-cultured Florida red tilapia. *Aquaculture*. 1993;113:189-200. doi:10.1016/0044-8486(93)90473-C
377. Ellis E, Watanabe W. The effects of hyposalinity on eggs, juveniles and adults of the marine monogenean, *Neobenedenia melleni* treatment of ecto-parasitosis in seawater-cultured tilapia. *Aquaculture*. 1993;117:15-27. doi:10.1016/0044-8486(93)90119-J
378. Rubio-Godoy M, Montiel-Leyva A, Martínez-Hernández J. Comparative susceptibility of two different genetic types of tilapia to *Neobenedenia* sp. (Monogenea). *Dis Aquat Org*. 2011;93:171-177. doi:10.3354/dao02287
379. Deveney MR, Whittington ID. Three new species of *Benedenia* Diesing, 1858 from the great barrier reef, Australia, with a key to species of the genus. *Zootaxa*. 2010;2348:1-22. doi:10.11646/zootaxa.2348.1.1
380. Whittington ID, Horton MA. A revision of *Neobenedenia* Yamaguti, 1963 (Monogenea: Capsalidae) including a redescription of *N. melleni* (MacCallum, 1927) Yamaguti, 1963. *J Nat Hist*. 1996;30:1113-1156. doi:10.1080/00222939600770611
381. Brazenor AK, Bertozzi T, Miller TL, Whittington ID, Hutson KS. DNA profiling reveals *Neobenedenia girellae* as the primary culprit in global fisheries and aquaculture. *Mol Phylogenet Evol*. 2018;129:130-137. doi:10.1016/j.ympev.2018.05.012
382. Li AX, Wu XY, Ding XJ, et al. PCR-SSCP as a molecular tool for the identification of Benedeniinae (Monogenea: Capsalidae) from marine fish. *Mol Cell Probes*. 2005;19:35-39. doi:10.1016/j.mcp.2004.09.002
383. Deveney MR, Chisholm LA, Whittington ID. First published record of the pathogenic monogenean parasite *Neobenedenia melleni*

(Capsalidae) from Australia. *Dis Aquat Organ*. 2001;46:79-82. doi:10.3354/dao046079

384. Dinh Hoai T, Hutson K. Reproductive strategies of the insidious fish ectoparasite *Neobenedenia* sp. (Capsalidae: Monogenea). *PLoS One*. 2014;10:e0117881. doi:10.1371/journal.pone.0117881
385. Trujillo-González A, Constantinoiu C, Johnson L, Hutson K. Histopathology associated with haptor attachment of the ectoparasitic monogenean *Neobenedenia* sp. (Capsalidae) to Asian sea bass, *Lates calcarifer* (Bloch). *J Fish Dis*. 2015;38:1063-1067. doi:10.1111/jfd.12320
386. Whittington ID. *Benedenia seriolae* and *Neobenedenia* species. In: Woo P, Buchmann K, eds. *Fish Parasites: Pathobiology and Protection*. CAB International; 2012.
387. Hirayama T, Kawano F, Hirazawa N. Effect of *Neobenedenia girellae* (Monogenea) infection on host amberjack *Seriola dumerili* (Carangidae). *Aquaculture*. 2009;288:159-165. doi:10.1016/j.aquaculture.2008.11.038
388. Ogawa K, Bondad-Reantaso M, Fukudome M, Wakabayashi H. *Neobenedenia girellae* (Hargis, 1955) Tamaguti, 1963 (Monogenea: Capsalidae) from cultured marine fishes of Japan. *J Parasitol*. 1995;81:223-227.
389. Shinn A, Pratoomyot J, Bron J, Paladini G, Brooker E, Brooker A. Economic impacts of aquatic parasites on global finfish production. *Glob Aquac Advocate*. 2015;2015:82-84.
390. Brazenor A, Hutson K. Effects of temperature and salinity on the lifecycle of *Neobenedenia* sp. (Monogenea: Capsalidae) infecting farmed barramundi (*Lates calcarifer*). *Parasitol Res*. 2015;114:1875-1876. doi:10.1007/s00436-015-4375-5
391. Valles-Vega I, Ascencio F, Sicard-González T, et al. Effects of temperature on the life cycle of *Neobenedenia* sp. (Monogenea: Capsalidae) from *Seriola rivoliana* (Almaco jack) in Bahía de La Paz, BCS Mexico. *Parasitol Res*. 2019;118:3267-3277. doi:10.1007/s00436-019-06460-1
392. Dinh Hoai T, Trang T, Nguyan T. The effects of short freshwater bath treatments on the susceptibility of different stages of *Neobenedenia girellae* infecting barramundi (*Lates calcarifer*). *Vietnam J Agric Sci*. 2019;2:409-417. doi:10.31817/vjas.2019.2.3.01
393. Morales-Serna F, Chapa-López M, Martínez-Brown J, Ibarra-Castro L, Medina-Guerrero R, Fajer-Áila E. Efficacy of praziquantel and a combination anthelmintic (Adecto®) in bath treatments against *Tagia ecuadori* and *Neobenedenia melleni* (Monogenea), parasites of Bullseye puffer fish. *Aquaculture*. 2018;492:361-368. doi:10.1016/j.aquaculture.2018.04.043
394. Hirazawa N, Hagiwara H, Tsubone S, Takano R. Investigation of the toxicological effects of hydrogen peroxide bath treatments at different concentrations on *Seriola* species and the effectiveness of these treatments on *Neobenedenia girellae* (Monogenea) infestations. *Aquaculture*. 2017;479:217-224. doi:10.1016/j.aquaculture.2017.05.019
395. Hutson KS, Mata L, Paul NA, de Nys R. Seaweed extracts as a natural control against the monogenean parasite *Neobenedenia* sp. infecting farmed barramundi (*Lates calcarifer*). *Int J Parasitol*. 2012;42:1135-1141. doi:10.1016/j.ijpara.2012.09.007
396. Shirakashi S, Hirano C, binti Asmara A, Ishimaru K, Miyashita S. Shading reduces *Neobenedenia girellae* infection on cultured greater amberjack *Seriola dumerili*. *Fish Pathol*. 2013a;48:25-28. doi:10.3147/jsfp.48.25
397. Shirakashi S, Hirano C, Ishitana H, Ishimaru K. Diurnal pattern of skin fluke infection in cultured amberjack *Seriola dumerili*, at different water depths. *Aquaculture*. 2013b;402:19-23. doi:10.1016/j.aquaculture.2013.03.014
398. Simon-Oke IA. Diversity, intensity and prevalence of parasites of cichlids in polluted and unpolluted sections of Eleyele Dam, Ibadan, Nigeria. *UNED Res J*. 2017;9:45-50.
399. Salgado-Maldonado G. Checklist of helminth parasites of freshwater fishes from Mexico. *Zootaxa*. 2006;1324:1-357. doi:10.11646/zootaxa.1324.1.1
400. Salgado-Maldonado G, Cabanas-Carranza G, Soto-Galera E, et al. Helminth parasites of freshwater fishes of the Pánuco River basin, east Central Mexico. *Comp Parasitol*. 2004;71:190-202. doi:10.1654/4088
401. Aguirre-Macedo ML, Scholz T. *Culuwiya cichlidorum* n. sp. (Digenea: Haploporidae) from the black-belt cichlid *Vieja maculicauda* (Pisces: Cichlidae) from Nicaragua. *J Parasitol*. 2005;91:1379-1384. doi:10.1645/GE-3490.1
402. Abou-Okada M, AbuBakr HO, Hassan A, et al. Efficacy of acriflavine for controlling parasitic diseases in farmed Nile tilapia with emphasis on fish health, gene expression analysis, oxidative stress, and histopathological alterations. *Aquaculture*. 2021;541:736-791. doi:10.1016/j.aquaculture.2021.736791
403. Chai JY. *Human Intestinal Flukes*. Springer Nature; 2019.
404. Grobbelaar A, Van As LL, Van As JG, Butler HJB. Pathology of eyes and brain of fish infected with diplostomids, southern Africa. *Afr Zool*. 2015;50:181-186. doi:10.1080/15627020.2015.1055701
405. Charo-Karisa H, Ali S, Marijani E, et al. Genetic parameters for black spot disease (diplostomiasis) caused by *Uvulifer* sp. infection in Nile tilapia (*Oreochromis niloticus* L.). *Aquaculture*. 2021;541:736039. doi:10.1016/j.aquaculture.2020.736039
406. García-Márquez L, Osorio-Sarabia D, Constantino F. Prevalencia de los parásitos y las alteraciones histológicas que producen a las tilapias de la Laguna de Amela, Tecomán, Colima. *Vet Mex*. 1993;24:199-205.
407. Hamouda A, Younis A. Characterization of *Clinostomum cutaneum* and *Clinostomum phalacrocoracis* in tilapia species of Aswan governorate, Egypt: a morphological, molecular and histopathological study. *Aquacult Res*. 2021;52:6726-6740. doi:10.1111/are.15543
408. Huston D, Worsham M, Huffman D, Ostrand K. Infection of fishes, including threatened and endangered species by the trematode parasite *Haplorchis pumilio* (Looss, 1896) (Trematoda: Heterophyidae). *Bioinvasions Rec*. 2014;3:189-194. doi:10.3391/bir.2014.3.3.09
409. Martínez-Aquino A, ChanMartin A, García-Teh J, Ceccarelli F, Aguirre-Macedo M. Metacercariae of *Haplorchis pumilio* (Looss, 1896) in *Carassius auratus* (Linnaeus, 1758) from Merida City, Yucatán, Mexico: a cointroduced parasite. *Bioinvasions Rec*. 2019;8:712-728. doi:10.3391/bir.2019.8.3.29
410. Lopes AS, Pulido-Murillo EA, Melo AL, Pinto HA. *Haplorchis pumilio* (Trematoda: Heterophyidae) as a new fish-borne zoonotic agent transmitted by *Melanoides tuberculata* (Mollusca: Thiaridae) in Brazil: a morphological and molecular study. *Infect Genet Evol*. 2020;85:104495. doi:10.1016/j.meegid.2020.104495
411. Pérez-Ponce de León G, Mandoza-Garfias B, García-Prieto L. Trematode parasites (Platyhelminthes) of wildlife vertebrates in Mexico. *Zootaxa*. 2007;1534:1-247. doi:10.11646/zootaxa.1534.1.1
412. Violante-González J, García-Varela M, Rojas-Herrera A, Gil-Guerrero S. Diplostomiasis in cultured wild tilapia *Oreochromis niloticus* in Guerrero State, Mexico. *Parasitol Res*. 2009;105:803-807. doi:10.1007/s00436-009-1458-1
413. Pinto HA, Mati VLT, Melo AL. Metacercarial infection of wild Nile tilapia (*Oreochromis niloticus*) from Brazil. *Sci World J*. 2014;2014:807492. doi:10.1155/2014/807492
414. Hoogendoorn C, Smit NJ, Kudlai O. Molecular and morphological characterisation of four diplostomid metacercariae infecting *Tilapia sparrmanii* (Perciformes: Cichlidae) in the North West Province, South Africa. *Parasitol Res*. 2019;118:1403-1416. doi:10.1007/s00436-019-06285-y
415. Hoogendoorn C, Smit NJ, Kudlai O. Resolution of the identity of three species of *Diplostomum* (Digenea: Diplostomidae) parasitising freshwater fishes in South Africa, combining molecular and morphological evidence. *Int J Parasitol Parasit Wildl*. 2020;11:50-61. doi:10.1016/j.ijppaw.2019.12.003
416. Mahdy O, Abdel-Maogood S, Abdelsalam M, Shaalan M, Abdelrahman H, Salem M. Epidemiological study of fish-borne

zoonotic trematodes infecting Nile tilapia with first molecular characterization of two heterophyid flukes. *Aquacult Res*. 2020;52:4475-4488. doi:10.1111/are.15286

417. Wiriya B, Clausen JH, Inpankaewa T, et al. Fish-borne trematodes in cultured Nile tilapia (*Oreochromis niloticus*) and wild-caught fish from Thailand. *Vet Parasitol*. 2013;198:230-234. doi:10.1016/j.vetpar.2013.08.008
418. Kuchta R, Choudhury A, Scholz T. Asian fish tapeworm: the most successful invasive parasite in freshwaters. *Trends Parasitol*. 2018;34:511-523. doi:10.1016/j.pt.2018.03.001
419. Woodland WNF. Some cestodes from Sierra Leone. I. On *Wenyonia longicauda*, sp. n., and *Proteocephalus bivitellatus*, sp. n. *Proc Zool Soc*. 1937;106:931-937. doi:10.1111/j.1469-7998.1936.tb06293.x
420. Mariaux J, Tkach VV, Vasileva GP, et al. Cyclophyllidea. In: Caira J, Jensen K, eds. *Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth*. University of Kansas, Natural History Museum; 2017.
421. Chervy L. The terminology of larval cestodes or metacestodes. *Syst Parasitol*. 2002;52:1-33. doi:10.1023/A:1015086301717
422. Scholz T, Bray R, Kuchta R, Řepová R. Larval gryporhynchid cestodes (Cyclophyllidea) from fish: a review. *Folia Parasitol*. 2004;51:131-152. doi:10.14411/fp.2004.018
423. Scholz T, Tavakol S, Uhrová L, et al. An annotated list and molecular data on larvae of gryporhynchid tapeworms (Cestoda: Cyclophyllidea) from freshwater fishes in Africa. *Syst Parasitol*. 2018;95:567-590. doi:10.1007/s11230-018-9796-y
424. Scholz T, Davidovich N, Aflalo O, Hadar S, Mazuz ML, Yasur-Landau D. Invasive *Amirthalingamia macracantha* (Cestoda: Cyclophyllidea) larvae infecting tilapia hybrids in Israel: a potential threat for aquaculture. *Dis Aquat Organ*. 2021;145:185-190. doi:10.3354/dao03611
425. Diab A. The execution of specific assessments in the coastal areas of Port Said: fishery. Paper presented at *The European Union's short and medium-term priority environmental. Action programme (SMAP) "Plan of Action" for an Integrated Coastal Zone Management in the area of Port Said (Egypt)*; 2007.
426. Ramadan MR. On the biology of *Polyonchobothrium clarias* parasitizing cultured *Clarias gariepinus*, with special emphasis on parasite-induced host behavioral changes. *Parassitologia*. 2007;49(Suppl.2):355.
427. Ramadan MR, Ghobashy MA, Taeleb AA. Establishing cause effect of multistressor environments on *Oreochromis niloticus* and its parasite communities. *Afr J Microbiol Res*. 2014;8:3038-3043. doi:10.5897/AJMR2014.6782
428. Eissa AM, Gado MS, Laila AM, Mona SZ, Noor El-Deen AE. Field studies on prevailing internal parasitic diseases in male and hybrid tilapia relation to monosex tilapia at Kafr El-Sheikh governorate fish farms. *J Am Sci*. 2011;7:722-728.
429. Eissa AM, Mona MI, Doaa GMS, Rehab AQ. Diseases caused by helminthes in cultured *Oreochromis niloticus* and *Clarias gariepinus*, in Ismailia province. *Int J Fish Aquat Res*. 2011;6:17-25.
430. Kuchta R, Burianová A, Jirků M, et al. Bothriocephalidean tapeworms (Cestoda) of freshwater fish in Africa, including erection of *Kirstenella* n. gen. and description of *Tetracampos martinae* n. sp. *Zootaxa*. 2012;3309:1-35. doi:10.11646/zootaxa.3309.1.1
431. Scholz T, de Chambrier A, Beletew M, Mahmoudet Z. Redescription of *Proteocephalus glanduligerus* (Cestoda: Proteocephalidea), a parasite of clariid catfishes in Africa with a unique glandular apical organ. *J Parasitol*. 2009;95:443-449. doi:10.1645/GE-1715.1
432. Blahoua K, Adou Y, Elité R, Tiho S. Parasite community of *Oreochromis niloticus* from man-made Lake Ayame I, Côte D'ivoire. *Int J Biosci*. 2020;16:193-205. doi:10.12692/ijb/16.4.193-205
433. Khamis HM, Luswet D, Orina PS. Prevalence and diversity of internal cestode parasites infected *Nile tilapia* (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*) in farmers fresh water ponds in Kenya. *Am Acad Sci Res J Engineer Tech Sci*. 2017;34:123-137.
434. Edeh C, Solomon R. Endoparasites of *Oreochromis niloticus* and *Clarias gariepinus* found in Utako flowing gutter. *Direct Res J Agric Food Sci*. 2016;4:361-373.
435. Scholz T, Kuchta R, Brabec J. Broad tapeworms (Diphyllobothriidae), parasites of wildlife and humans: recent progress and future challenges. *Int J Parasitol Parasit Wildl*. 2019;9:359-369. doi:10.1016/j.ijppaw.2019.02.001
436. Maguza-Tembo F, Mfitilodze M. Occurrence (incidence) of parasites in three fish species (*Clarias gariepinus*, *Oreochromis shiranus* and *Haplochromis*) from Bunda reservoir. *Bunda J Agric Environ Sci Technol*. 2008;3:3-7.
437. Kuchta R, Pearson R, Scholz T, Ditrich O, Olson PD. Spathebothriidea: survey of species, scolex and egg morphology, and interrelationships of a non-segmented, relictual tapeworm group (Platyhelminthes: Cestoda). *Folia Parasitol*. 2014;61:331-346.
438. Barčák D, Oros M, Hanzelová V, Scholz T. A synoptic review of *Caryophyllaeus* Gmelin, 1790 (Cestoda: Caryophyllidea), parasites of cyprinid fishes. *Folia Parasitol*. 2017;64:27. doi:10.14411/fp.2017.027
439. Nmor J, Egwunyenga A, Ake J. Observations on the intestinal helminth parasites of cichlids in the upper reaches of River Orogodo, a freshwater body in Delta State, Southern Nigeria. *Trop Freshw Biol*. 2003;12:131-136. doi:10.4314/tfb.v12i1.20883
440. Schaeffner B, Jirků M, Mahmoud Z, Scholz T. Revision of *Wenyonia* Woodland, 1923 (Cestoda: Caryophyllidea) from catfishes (Siluriformes) in Africa. *Syst Parasitol*. 2011;79:83-107. doi:10.1007/s11230-011-9290-2
441. Pineda-López R, González-Enriquez C. *Bothriocephalus acheilognathi*: Presencia e importancia de un invasor asiático infectando peces de Querétaro. *Zool Inform*. 1997;35:5-12.
442. Pérez-Ponce de León G, Rosas-Valdez R, Mendoza-Garfias B, et al. Survey of the endohelminth parasites of freshwater fishes in the upper Mezquital River basin, Durango State, Mexico. *Zootaxa*. 2009;2164:1-20. doi:10.11646/zootaxa.2164.1.1
443. Scholz T, Kuchta R, Williams C. *Bothriocephalus acheilognathi*. In: Woo P, Buchmann K, eds. *Fish Parasites: Pathobiology and Protection*. CAB International; 2012.
444. Ogbulie TE, Nwigwe HC, Anyadoh SO. Comparative assessment of bioload of healthy and diseased *Oreochromis niloticus* as means of food security. *An Univ Oradea Fasc Biol*. 2011;18:10-14.
445. Scholz T, Cestoda KR. In: Scholz T, Vanhove M, Smit N, Jayasundera Z, Gelnar M, eds. *A Guide to the Parasites of African Freshwater Fishes*. Abc Taxa; 2018.
446. Osorio-Sarabia D. Descripción de una nueva especie del género *Goezia* Zeder, 1800 (Nematoda: Goeziidae) en peces de agua dulce de México. *An Inst Biol, Univ Nat Autonom México*. 1982;52:71-87.
447. Moravec F. *Nematodes of Freshwater Fishes of the Neotropical Region*. Academia; 1998.
448. Prieto A, Fajer E, Vinjoy M, Martiínez M. Parasitos de peces cultivados en aguas interiores claves para su dignostico diferencial. *Proyecto AQUILA II, FAO*. 1993;15:1-62.
449. Moravec F. *Parasitic Nematodes of Freshwater Fishes of Africa*. Academia; 2019.
450. Opara K, Okon A. Studies on the parasites of cultured *Oreochromis niloticus* (Cichlidae) in a rainforest fish pond in south eastern Nigeria. *J Aquat Sci*. 2002;17:17-20.
451. Bienvenu ZT, Darius TN, Ignance TA, et al. General survey on metazoan parasites infecting *Oreochromis niloticus* L. (Teleostei, Cichlidae) from two different fish ponds systems in southern Benin. *Int J Fish Aquat Stud*. 2019;7:26-30.
452. Madanire-Moyo GN, Luus-Powell WJ, Olivier P. Diversity of metazoan parasites of the Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), as indicators of pollution in the Limpopo and Olifants

river systems. *Onderstepoort J Vet Res*. 2012;79:E1-E9. doi:10.4102/ojvr.v79i1.362

453. Abro M, Birmani N, Bhutto M. Observations on the occurrence of subgenus *Procamallanus* (*Spirocamallanus*) (Nematoda: Camallanidae) parasitizing two species of freshwater fishes from Sindh, Pakistan. *J Innov Sci*. 2021;7:98-102. doi:10.17582/journal.jis/2021/7.1.98.102
454. Deardorff T, Overstreet R. Review of *Hysterothylacium* and *Iheringascaris* (both previously = *Thynnascaris*) (Nematoda: Anisakidae) from the northern Gulf of Mexico. *Proc Helminthol Soc Wash*. 1981;93:1035-1079.
455. Chen P. *Aplectana chamaeleonis* (Baylis, 1929) from a frog and a freshwater fish in Ethiopia. *Ann Mag Nat Hist*. 1966;9:103-105. doi:10.1080/00222936608651653
456. Tavakol S, Smit WJ, Sara JR, Halajian A, Luus-Powell WJ. Distribution of *Contracaecum* (Nematoda: Anisakidae) larvae in freshwater fish from the northern regions of South Africa. *Afr Zool*. 2015;50:133-139. doi:10.1080/15627020.2015.1052302
457. Elseify M, El Shihawy I, Metwally A, Fawaz M. Studies on nematode parasites infecting freshwater fish in Qena governorate. *Kafr El-Sheikh Vet Med J*. 2015;13:19-34.
458. Moravec F, Scholz T. Some nematodes, including two new species, from freshwater fishes in The Sudan and Ethiopia. *Folia Parasitol*. 2015;64:010. doi:10.14411/fp.2017.010
459. Chebon B, Matolla G, Ngeiywa M, Edwine Y. Influence of rainfall seasonality on endohelminth parasites of *Oreochromis niloticus baringoensis* (Trewavas, 1983) at River Molo inlet in Lake Baringo, Rift Valley, Kenya. *J Aquat Sci Mar Biol*. 2018;1:34-41.
460. Barson M, Bray R, Ollevier F, Huyse T. Taxonomy and faunistics of the helminth parasites of *Clarias gariepinus* (Burchell, 1822), and *Oreochromis mossambicus* (Peters, 1852) from temporary pans and pools in the save-Runde River floodplain, Zimbabwe. *Comp Parasitol*. 2008;75:228-240.
461. Hernández-Martínez M. Estudio helmintológico de tres especies de peces cultivados en dos centros acuícolas del estado de Sonora, México. *Univ Ciencia*. 1992;9:111-115.
462. Chiclla-Salazar A, Tantas-García D. Infection of *Contracaecum* sp. larvae (Nematoda: Anisakidae) in tilapia *Oreochromis niloticus* of Peru. *Biologist (Lima)*. 2015;13:419-427.
463. Awosolu OB, Simon-Oke IA, Oyelere AA. Studies on the prevalence and distribution of parasites of tilapia fish (*Oreochromis niloticus*) from Igbokoda River, Ondo State, Nigeria. *Mol Pathogens*. 2018;9:1-4. doi:10.5376/mp.2018.09.0001
464. Pérez-Álvarez Y, Garcia-Prieto L, Osorio-Sarabia D, Lamothe-Argumedo R, León-Règagnon V. Present distribution of the genus *Gnathostoma* (Nematoda: Gnathostomatidae) in Mexico. *Zootaxa*. 2008;1930:39-55. doi:10.11646/zootaxa.1930.1.3
465. Thomas K, Ollevier F. Paratenic hosts of the swimbladder nematode *Anguillicola crassus*. *Dis Aquat Organ*. 1992;13:165-174. doi:10.3354/dao027237
466. Selim KM, El-Ashram AM. Studies on anguillicoliasis of cultured eel (*Anguilla Anguilla*) in Egypt. Paper presented at Fifth International Conference on Global Fisheries and Aquaculture Research, Faculty of Agriculture, Cario University, Cario; 2012: 409–425.
467. Moyo D, Chimbira C, Yalala P. Observations on the helminth parasites of fish in Insukamini Dam, Zimbabwe. *Res J Agric Biol Sci*. 2009;5:782-785.
468. Mbahinzireki GB. Observations on some common parasites of *Bagrus docmac* Forskahl (Pisces: Siluroidea) of Lake Victoria. *Hydrobiologia*. 1980;75:273-280. doi:10.1007/BF00006493
469. Molnár K, Buchmann K. Székely C Phylum Nematoda. In: Woo P, ed. *Fish Diseases and Disorders*. CABI Publishing; 2012.
470. Liu GH, Sun MM, Elsheikha HM, et al. Human gnathostomiasis: a neglected food-borne zoonosis. *Parasit Vectors*. 2020;13:616. doi:10.1186/s13071-020-04494-4
471. Wey-Fabrizius AR, Herlyn H, Rieger B, et al. Transcriptome data reveal Syndermatan relationships and suggest the evolution of endoparasitism in Acanthocephala via an epizoic stage. *PLoS One*. 2014;9:e88618. doi:10.1371/journal.pone.0088618
472. Amin OM. Occurrence of the subgenus *Acanthosentis* Verma & Datta, 1929 (Acanthocephala: Quadrigyridae) in Japan, with the description of *Acanthogyrus* (*Acanthosentis*) *alternatspinus* n. sp. and *A.* (*a.*) *parareceptaclis* n. sp. from Lake Biwa drainage fishes and a key to the species of the subgenus. *Syst Parasitol*. 2005;60:125-137. doi:10.1007/s11230-004-1386-5
473. Amin OM, Hendrix SS. Acanthocephala of cichlids (Pisces) in Lake Malawi, Africa, with a description of *Acanthogyrus* (*Acanthosentis*) *malawiensis* sp. n. (Quadrigyridae) from *Labeo cylindricus* Peters, 1852 (Cyprinidae). *J Helminthol*. 1999;66:47-55.
474. Sures B, Kvach Y, Kuchta R. Acanthocephala. In: Scholz T, Vanhove M, Smit N, Jayasundera Z, Gelnar M, eds. *A Guide to the Parasites of African Freshwater Fish*. Abc Taxa; 2018.
475. Okaeme AN, Obiekezie AI, Ogbondeminu FS. The economic impact of diseases and parasitic problems in freshwater fish production. Proceedings of the 5th Annual Conference of the Fisheries Society of Nigeria (FISON) Ilorin, Lagos; 1987: 368–374.
476. El-Shahawi G, Al-Bassel D. A general survey of the helminth parasites infecting the common fishes in some inland water in Egypt. *Proc Zool Soc A R Egypt*. 1992;23:227-241.
477. Otachi E, Szostakowska B, Jirsa F, Fellner-Frank C. Parasite communities of the elongate tigerfish *Hydrocynus forskahlii* (Cuvier 1819) and redbelly tilapia *Tilapia zillii* (Gervais 1848) from Lake Turkana, Kenya: influence of host sex and size. *Acta Parasitol*. 2015;60:9-20. doi:10.1515/ap-2015-0002
478. Amin OM, Van Oosterhout C, Blais J, Robinson RL, Cable J. On the ecology and host relationships of *Acanthogyrus* (*Acanthosentis*) *tilapiae* (Acanthocephala: Quadrigyridae) from cichlids in Lake Malawi. *Comp Parasitol*. 2008;75:278-282. doi:10.1654/4321.1
479. Amin O, Heckmann R. An SEM study of *Acanthogyrus* (*Acanthosentis*) *tilapiae* (Acanthocephala: Quadrigyridae) from Africa documenting previously unreported features and host parasite interface. *Sci Parasitol*. 2012;13:57-63.
480. Eissa AE, Attia MM, Elgendy MY, et al. *Streptococcus*, *Centrocestus formosanus* and *Myxobolus tilapiae* concurrent infections in farmed Nile tilapia (*Oreochromis niloticus*). *Microb Pathog*. 2021;158:105084. doi:10.1016/j.micpath.2021.105084
481. Bayoumy ME, El-Hady OKA, Osman HAM. Site adaptations of *Acanthogyrus* (*Acanthosentis*) *tilapiae*: observations through light and scanning electron microscopy. *J Vet Sci*. 2006;7:339-342. doi:10.4142/jvs.2006.7.4.339
482. Onwuliri C, Mgbemena M. The parasitic fauna of some fresh water fish from Jos Plateau, Nigeria. *Nigeria J Appl Fish Hydrobiol.* 1987;2:33-37.
483. Ajala O, Olatunde F. Diets and enteroparasitic infestation of *Oreochromis niloticus* (Linné, 1757) (Cichlidae) in Oba Reservoir Ogbomoso, Nigeria. *Elixir Appl Zool*. 2015a;83:32983-32988.
484. Ajala O, Olatunde F. Diets and enteroparasitic infestation in *Sarotherodon galilaeus* (Linnaeus, 1758) (Cichlidae) in Oba reservoir Ogbomoso, Nigeria. *Int J Fish Aquat Stud*. 2015b;2:3-10.
485. Briones J, Papa R, Cauyan G, Urabe M. The first report of three acanthocephalan parasites species isolated from Philippine fishes. *Helminthologia*. 2015;52:384-389. doi:10.1515/helmin-2015-0061
486. de la Cruz CPP, Paller VGV. Occurrence of *Neoechinorhynchus* sp. (Acanthocephala: Neoechinorhynchidae) in cultured *tilapia* [*Oreochromis niloticus* (L.), Perciformes: Cichlidae] from Sampaloc Lake, Philippines. *Asia Life Sci*. 2012;21:287-298.
487. de la Cruz CPP, Bandal MZ, Avila ARB, Paller VGV. Distribution pattern of *Acanthogyrus* sp. (Acanthocephala: Quadrigyridae) in *Nile tilapia* (*Oreochromis niloticus* L.) from Sampaloc Lake, Philippines. *J Nat Stud*. 2013;12:1-10.

488. Paller VGV, Resurreccion DJB, de la Cruz CPP, Bandal MZ. Acanthocephalan parasites (*Acanthogyrus* sp.) of Nile tilapia (*Oreochromis niloticus*) as biosink of lead (Pb) contamination in a Philippine freshwater lake. *Bull Environ Contam Toxicol*. 2016a;96:810-815. doi:10.1007/s00128-016-1790-y
489. Paller V, Sy R, Bandal M. Hematology and histopathology of Nile tilapia (*Oreochromis niloticus* L.) infected with *Acanthogyrus* sp. (Acanthocephala: Quadrigyridae). *Ecol Environ Conserv*. 2016b;22:497-504.
490. Amin O. Revision of *Neoechinorhynchus* Stiles & Hassall, 1905 (Acanthocephala: Neoechinorhynchidae) with keys to 88 species in two subgenera. *Syst Parasitol*. 2002;53:1-18. doi:10.1023/A:1019953421835
491. Van Cleave J, Lynch JE. The circumpolar distribution of *Neoechinorhynchus rutili*, an acanthocephalan parasite of fresh-water fishes. *Trans Am Microsc Soc*. 1950;69:156-171. doi:10.2307/3223404
492. Tingbao Y, Xianghua L. Seasonal population dynamics of *Neoechinorhynchus qinghaiensis* in the carp, *Gymnocypris przewalskii przewalskii*, from Qinghai Lake, China. *J Helminthol*. 2001;75:93-98. doi:10.1079/joh200030
493. Alam M, Alam M. A comparative study of endoparasite infestation of *Oreochromis niloticus* (Linnaeus, 1758) in polluted and non-polluted water bodies of Bangladesh. *Int J Fauna Biol Stud*. 2014;4:4-9.
494. Amin O, Heckmann R, Chaudhary A, Rubtsova N, Singh H. Redescription and molecular analysis of *Pallisentis* (*Pallisentis*) *nandai* Sarkar, 1953 (Acanthocephala: Quadrigyridae) in India. *J Helminthol*. 2021;95:e3. doi:10.1017/S0022149X20001005
495. Aloo P, Dezfuli B. Occurrence of cystacanths of *Polyacanthorhynchus kenyensis larvae* (Acanthocephala) in four teleostean fishes from a tropical lake, Lake Naivasha, Kenya. *Folia Parasitol*. 1997;44:233-238.
496. Aloo P. A comparative study of helminth parasites from the fish *Tilapia zillii* and *Oreochromis leucostictus* in Lake Naivasha and Oloidien Bay, Kenya. *J Helminthol*. 2002;76:95-102. doi:10.1079/JOH2001105
497. Amin O, Heckmann R, Peňa C, Castro T. On the larval stages of *Polymorphus spindlatus* (Acanthocephala: Polymorphidae) from a new fish host, *Oreochromis niloticus*, in Peru. *Neotrop Helminthol*. 2010;4:81-85.
498. Amin O, Heckmann R. Description and host relationships of *Polymorphus spindlatus* n. sp. (Acanthocephala: Polymorphidae) from the heron *Nycticorax nycticorax* in Peru. *J Parasitol*. 1991;77:201-205. doi:10.2307/3283081
499. Schmidt GD. Resurrection of *Southwellina* Witenberg, 1932, with a description of *Southwellina dimorpha* sp. n., and a key to genera in Polymorphidae (Acanthocephala). *J Parasitol*. 1973;59:299-305. doi:10.2307/3278821
500. Fonseca M, Knoff M, Felizardo N, et al. Acanthocephalan parasites of the flounder species *Paralichthys isosceles*, *Paralichthys patagonicus* and *Xystreurys rasile* from Brazil. *Rev Bras Parasitol Vet*. 2019;28:346-359. doi:10.1590/S1984-29612019031
501. Abdallah E, Al Tayip A, Nasr S, Sayed G, Elkamel A. *Acanthogyrus tilapiae* infections in wild and cultured Nile tilapia *Oreochromis niloticus*. *Assiut Vet Med J*. 2017;63:44-50.
502. Bazh EKA, Hamouda AH. Scanning morphology, prevalence and histopathology of some acanthocephalans infecting some river Nile fish. *Bulg J Vet Med A*. 2021;24:239-250. doi:10.15547/bjvm.2019-0087
503. Taraschewski H. *Acanthocephalus anguillae* in intra- and extraintestinal positions in experimentally infected juveniles of goldfish and carp and in sticklebacks. *J Parasitol*. 1989;75:108-118. doi:10.2307/3282947
504. Golvan YJ. Acanthocéphales de Madagascar recoltés par E. R. Brygoo. *Ann Parasitol*. 1965;40:303-316.
505. Pinacho-Pinacho CD, García-Varela M, Sereno-Uribe AL, Pérez-Ponce de León G. A hyper-diverse genus of acanthocephalans revealed by tree-based and non-tree-based species delimitation methods: ten cryptic species of *Neoechinorhynchus* in middle American freshwater fishes. *Mol Phylogenet Evol*. 2018;127:30-45.
506. Reier S, Sattmann H, Schwaha T, Fuehrer H-P, Haring E. Unravelling the hidden biodiversity—the establishment of DNA barcodes of fish-parasitizing Acanthocephala Koehlreuther, 1771 in view of taxonomic misidentifications, intraspecific variability and possible cryptic species. *Parasitology*. 2020;147:1499-1508. doi:10.1017/S0031182020001316
507. Kennedy CR. *Ecology of the Acanthocephala*. Cambridge University Press; 2006.
508. Scheifler M, Ruiz-Rodríguez M, Sanchez-Brosseau S, et al. Characterization of ecto- and endoparasite communities of wild Mediterranean teleosts by a metabarcoding approach. *PLoS One*. 2019;14:e0221475. doi:10.1371/journal.pone.0223392
509. Elsaied HE, Soliman T, Abu-Taleb HT, Goto H, Jenke-Kodam H. Phylogenetic characterization of eukaryotic and prokaryotic gut flora of Nile tilapia, *Oreochromis niloticus*, along niches of Lake Nasser, Egypt, based on rRNA gene high-throughput sequences. *Ecol Genet*. 2019;11:100037. doi:10.1016/j.egg.2019.100037
510. Hamouda A, Abd Alkareem O. Insight into the correlation between parasitic infestation and heavy metal concentrations in tilapia species inhabiting Lake Nasser, Egypt. *Aquac Res*. 2021;52:3425-3437. doi:10.1111/are.15187
511. Oldewage WH, Avenant-Oldewage A. *Checklist of the Parasitic Copepoda (Crustacea) of African Fishes*. Musee Royal de l'Afrique Centrale; 1993.
512. Neethling L, Avenant-Oldewage A. Branchiura—a compendium of the geograpical distribution and a summary of their biology. *Crustaceana*. 2016;89:1243-1446. doi:10.1163/15685403-00003597
513. Capart A. Notes sur les copépodes parasites. III. Copépodes parasites des poissons d'eau douce du Congo Belge. *Bul Mus R d'Hist Nat Belgique*. 1944;20:1-24.
514. Gobbin TP, Vanhove MPM, Seehausen O, Maan ME. Microhabitat distributions and species interactions of ectoparasites on the gills of cichlid fish in Lake Victoria, Tanzania. *Int J Parasitol*. 2021;51:201-214. doi:10.1016/j.ijpara.2020.09.001
515. Ibraheem MH, Izawa K. On the morphology of *Lamproglena monodi* Capart, a parasitic copepod on the gills of tilapia in Egypt. *Zool Middle East*. 2000;21:103-108. doi:10.1080/09397140.2000.10637837
516. Martins M, Azevedo T, Ghiraldelli L, Bernardi N. Can the parasitic fauna on Nile tilapias be affected by different production systems? *An Acad Bras Cienc*. 2010;82:493-500. doi:10.1590/S0001-37652010000200024
517. Azevedo R, Abdallah V, Silva R, Pegado de Azevedo T, Martins M, Luque J. Expanded description of *Lamproglena monodi* (Copepoda: Lernaeidae), parasitizing native and introduced fishes in Brazil. *Rev Bras Parasitol Vet*. 2010;21:263-269. doi:10.1590/s1984-29612012000300015
518. Yambot AV, Lopez EA. Gill parasite *Lamproglena monodi* Capart, infecting the Nile tilapia, *Oreochromis niloticus* L. cultured in Philippines. In: Flegel T, Mac Rae I, eds. *Diseases in Asian Aquaculture III. Fish Health Section*. Asian Fisheries Society; 1997.
519. Piasecki W, Avenant-Oldewage A. Diseases caused by Crustacea. In: Eiras J, Segner H, Wahli T, Kapoor GB, eds. *Fish Diseases*. CRC Press; 2008.
520. Fryer G. A report of the parasitic Copepoda and Branchiura of the fishes of Lake Bangweulu (Nothern Rhodesia). *Proc Zool Soc Lond*. 1959;132:517-550.
521. Fryer G. Parasitic crustaceans of African freshwater fishes from the Nile and Niger systems. *Proc Zool Soc Lond*. 1965;145:285-303. doi:10.1111/j.1469-7998.1965.tb02018.x
522. Grobler JM. *Visektoparasitiese Lernaeidae van die Oos-Caprivi (MSc thesis)*. Rand Afrikaans University; 1989:215.

523. Ibraheem MH. *Lamproglena monodi* Capart, 1944, attachment scheme and associated pathology on the gills of *Oreochromis niloticus niloticus*, with a special reference to thoracic appendages. *Arab Gulf J Sci Res*. 2008;26:123-132.
524. Oldewage WH, Van As JG. Observations on the attachment of a piscine gill parasitic ergasilid (Crustacea: Copepoda). *S Afr J Zool*. 1987;22:313-317. doi:10.1080/02541858.1987.11448063
525. Kilian E, Avenant-Oldewage A. Observations on the pathology of *Ergasilus* (Crustacea: Copepoda) from Lake Tanganyika on the gills of *Lamprichtys tanganicanus*. *Suid-Afrik Tydskr Nat Wet Tegnol*. 2013;32:803. doi:10.4102/satnt.v32i1.803
526. Abu-Elala N, Attia M, Abd-Elsalam R. Chitosan-silver nanocomposites in goldfish aquaria: a new perspective in *Lernaea cyprinacea* control. *Int J Biol Macromol*. 2018;111:614-622. doi:10.1016/j.ijbiomac.2017.12.133
527. Pérez-Bote JL. *Barbus comizo* infestation by *Lernaea cyprinacea* (Crustacea: Copepoda) in the Guadiana River, southwestern Spain. *J Appl Ichthyol*. 2010;26:592-595. doi:10.1111/j.1439-0426.2010.01461.x
528. Shariff M, Roberts R. The experimental histopathology of *Lernaea polymorpha* Yu, 1938, infection in naïve *Aristichthys nobilis* (Richardson) and a comparison with the lesion in naturally infected clinically resistant fish. *J Fish Dis*. 1989;12:405-414. doi:10.1111/j.1365-2761.1989.tb00553.x
529. Woo PTK, Buchmann K, eds. Avenant Oldewage a *Lernaea cyprinacea* and related species. *Fish Parasites: Pathobiology and Protection*. CABI; 2012.
530. Shariff M, Kabata Z, Sommerville C. Host susceptibility to *Lernaea cyprinacea* L. and its treatment in a large aquarium system. *J Fish Dis*. 1986;9:393-401. doi:10.1111/j.1365-2761.1986.tb01032.x
531. Dempster RP, Morales P, Glennon FX. Use of sodium chlorite to combat anchor worm infestation of fish. *Progress Fish Cult*. 1988;50:51-55.
532. Woo P, Shariff M. *Lernaea cyprinacea* L. (Copepoda: Caligidae) in *Heliostoma temminck*i Cuvier and Valenciennes: the dynamics of resistance in recovered and naïve fish. *J Fish Dis*. 1990;13:485-494. doi:10.1111/j.1365-2761.1990.tb00807.x
533. Piasecki W, Goodwin A, Eiras J, Nowak B. Importance of Copepoda in freshwater aquaculture. *Zool Stud*. 2004;43:193-205.
534. Robinson J, Avenant-Oldewage A. Aspects of the morphology of the parasitic copepod *Lernaea cyprinacea* Linnaeus, 1758 and notes on its distribution in Africa. *Crustaceana*. 1996;69:610-626. doi:10.1163/156854096X00628
535. Barson M, Mulonga A, Nhiwatiwa T. Investigation of a parasitic outbreak of *Lernaea cyprinacea* Linnaeus (Crustacea: Copepoda) in fish from Zimbabwe. *Afr Zool*. 2008;43:175-183.
536. Harada I. Studies on the freshwater fauna of Formosa (I). A new copepod species parasitic on Formosan freshwater fish. *Pertanika J Trop Agric Sci*. 1930;2:71-76.
537. Hudson PL, Bowen CA. First record of *Neoergasilus japonicus* (Poecilostomatoida: Ergasilidae), a parasitic copepod new to the Laurentian Great Lakes. *J Parasitol*. 2002;88:657-663. doi:10.2307/3285339
538. Hayden KJ, Rogers WA. *Neoergasilus japonicus* (Poecilostomatoida: Ergasilidae), a parasitic copepod new to North America. *J Parasitol*. 1998;84:88-93. doi:10.2307/3284535
539. Prieto A, Fajer E, Vinjoy M. *Neoergasilus japonicus* (Copepoda: Ergasilidae) en peces en cultivo intensivo en Cuba. *Rev Salud Animal*. 1985;7:407-410.
540. Suárez-Morales E, Paredes-Trujillo A, González-Solís D. The introduced Asian parasitic copepod *Neoergasilus japonicus* (Harada) (Cyclopoida: Ergasilidae) from endangered cichlid teleosts in Mexico. *Zool Sci*. 2010;27:851-855. doi:10.2108/zsj.27.851
541. Mendes Marques T, Murrieta MG. First record of *Neoergasilus japonicus* (Harada, 1930) (Copepoda: Cyclopoida) infecting a fish species in South America. *Folia Amazon*. 2018;27:111-117. doi:10.24841/fa.v27i1.460
542. Smit W, Luus-Powell W, Kunutu K, et al. *Neoergasilus japonicus*: an alien invasive dispersing at an alarming rate in South Africa. Paper presented at 14th International Congress of Parasitology (ICOPA), Daegu; 2018.
543. Nagasawa K, Uyeno D. Utilization of alien freshwater fishes by the parasitic copepod *Neoergasilus japonicus* (Ergasilidae) on Okinawa-Jima Island, Japan, with a list of its known hosts. *Zoosymposia*. 2012;8:81-96. doi:10.11646/zoosymposia.8.1.11
544. Harding JP. On some species of *Lernaea*, Crustacea, Copepoda, parasites of freshwater fish. *Bull Br Mus Nat Hist*. 1950;1:1-27. doi:10.5962/p.314117
545. Fryer G. Variation and systematic problems in a group of lernaeid copepods. *Crustaceana*. 1961;2:275-285. doi:10.1163/156854061X00400
546. Pallavi B, Shankar KM, Abhiman PB, Ahmed I. Molecular identification of the fish parasite *Lernaea*. *Indian J Fish*. 2017;64:76-82. doi:10.21077/ijf.2017.64.2.60131-12
547. Hua CJ, Hong DZ, Zou L, et al. Morphology is not a reliable taxonomic tool for the genus *Lernaea*: molecular data and experimental infection reveal that *L. cyprinacea* and *L. cruciata* are conspecific. *Parasit Vectors*. 2019;12:579.
548. Pretorius M, Avenant-Oldewage A. Parasites as biological indicators: the impact of environmental quality on the infections of *Lamproglena clariae* (Crustacea) on *Clarias gariepinus* along the Vaal River, South Africa. *Biol Trace Elem Res*. 2021;200:2937-2947. doi:10.1007/s12011-021-02899-5
549. Ndaba J, Gilbert B, Avenant-Oldewage A. Metallothionein expression in a parasitic crustacean, *Lamproglena clariae* (Crustacea: Copepoda), on *Clarias gariepinus* (Teleostei: Clariidae) corresponds to water quality. *J Parasitol*. 2022;108:10-21. doi:10.1645/21-62
550. Walker PD, Russon IJ, Haond C, Van Der Velde G, Wendelaar Bonga SE. Feeding in adult *Argulus japonicus* Thiele, 1900 (Maxillopoda, Branchiura), an ectoparasite on fish. *Crustaceana*. 2011;84:307-318. doi:10.2307/29779502
551. Walker PD, Harris JE, van der Velde G, Bonga SEW. Effect of host weight on the distribution on *Argulus foliaceus* (L.) (Crustacea, Branchiura) within a fish community. *Acta Parasitol*. 2008;53:165-172. doi:10.2478/s11686-008-0020-0
552. Kruger I, Van As JG, Saayman J. Observations on the occurrence of the fish louse *Argulus japonicus* Thiele, 1900 in the western Transvaal. *Afr Zool*. 1983;18:408-410. doi:10.1080/02541858.1983.11447848
553. Mikheev V, Pasternak A, Valtonen E. Behavioural adaptations of argulid parasites (Crustacea: Branchiura) to major challenges in their life cycle. *Parasit Vectors*. 2015;8:394. doi:10.1186/s13071-015-1005-0
554. Walker P, Flik G, Bonga S. The biology of parasites from the genus *Argulus* and a review of the interactions with its host. In: Wiegertjes G, Flik G, eds. *Host-Parasite Interactions*. Taylor & Francis Group; 2004.
555. Shafir A, Oldewage WH. Dynamics of a fish ectoparasite population: opportunistic parasitism in *Argulus japonicus* (Branchiura). *Crustaceana*. 1992;62:50-64.
556. Shafir A, Van As JG. Laying, development and hatching of eggs of the fish ectoparasite *Argulus japonicus* (Crustacea: Branchiura). *J Zool*. 1986;210:401-414. doi:10.1111/j.1469-7998.1986.tb03645.x
557. Van As LL, Van As JG. Branchiuran parasites (Crustacea: Branchiura) from fishes in the Okavango (Botswana) and Zambezi (Namibia) systems. *Afr J Aquat Sci*. 2015;40:9-20. doi:10.2989/16085914.2015.1014995
558. Fryer G. Further studies on the parasitic Crustacea of African freshwater fishes. *Proc Zool Soc London*. 1964;143:79-102. doi:10.1111/j.1469-7998.1968.tb08578.x

559. Paperna I. Parasitic crustacea (Copepoda and Branchiura) from inland water fishes of Israel. *Isr J Ecol Evol*. 1964;13:58-68. doi:10.1080/00212210.1964.10688189
560. Avenant-Oldewage A. *Argulus japonicus* in the Olifants River system—possible conservation threat? *S Afr J Wildl Res*. 2001;31:59-63.
561. Tikhomirova VA. On nematodes of the family Skrjabillanidae (Nematoda: Camallanata). *Parazitologiya*. 1980;14:258-262.
562. Molnár K, Székely C. Occurrence of skrjabillanid nematodes in fishes of Hungary and in the intermediate host, *Argulus Foliaceus* L. *Acta Vet Hung*. 1998;46:451-463.
563. Moravec F, Vidal-Martinez V, Aguirre-Macedo L. Branchiurids (*Argulus*) as intermediate hosts of the Daniconematid nematode *Mexiconema cichlasomae*. *Folia Parasitol*. 1999;46:79.
564. Avenant-Oldewage A. Integumental damage caused by *Dolops ranarum* (Stuhlmann, 1891) (Crustacea: Branchiura) to *Clarias gariepinus* (Burchell), with reference to normal histology and wound-inflicting structures. *J Fish Dis*. 1994;17:641-647. doi:10.1111/j.1365-2761.1994.tb00262.x
565. Tavares-Dias M, De Moraes FR, Onaka EM, Rezende PCB. Changes in blood parameters of hybrid tambacu fish parasitized by *Dolops carvalhoi* (Crustacea, Branchiura), a fish louse. *Veti Arhiv*. 2007;77:355-363.
566. Swanepoel JH, Avenant-Oldewage A. Comments on the morphology of the pre-oral spine in *Argulus* (Crustacea: Branchiura). *J Morphol*. 1992;212:155-162. doi:10.1002/jmor.1052120206
567. AmbuAli A, Monaghan S, Al-Adawi K, Al-Kindi M, Bron J. Histological and histochemical characterisation of glands associated with the feeding appendages of *Argulus foliaceus* (Linnaeus, 1758). *Parasitol Int*. 2019;69:82-92. doi:10.1016/j.parint.2018.12.002
568. Mikheev V, Pasternak A, Valtonen E, Lankinen Y. Spatial distribution and hatching of overwintered eggs of a fish ectoparasite, *Argulus coregoni* (Crustacea: Branchiura). *Dis Aquat Organ*. 2001;46:123-128. doi:10.3354/dao046123
569. Tavares-Dias M, Martins ML, Kronka SN. Evaluation of the haematological parameters in *Piaractus mesopotamicus* Holmberg (Osteichthyes, Characidae) with *Argulus* sp. (Crustacea, Branchiura) infestation and treatment with organophosphate. *Rev Bras Zool*. 1999;16:553-555. doi:10.1590/S0101-81751999000200019
570. Bandilla M, Hakalahti-Sirén T, Valtonen E. Patterns of host switching in the fish ectoparasites *Argulus coregoni*. *Behav Ecol Sociobiol*. 2008;62:975-982. doi:10.1007/s00265-007-0523-y
571. Benz GW, Bullard SA, Dove ADM. Metazoan parasites of fishes: synoptic information and portal to the literature for aquarists. Paper presented at Regional Conference Proceedings of the American Zoo and Aquarium Association, Silver Spring, MD; 2001: 1–15.
572. Hakalahti T, Pasternak AF, Valtonen ET. Seasonal dynamics of egg laying and egg-laying strategy of the ectoparasite *Argulus coregoni* (Crustacea: Branchiura). *Parasitology*. 2004;128:655-660. doi:10.1017/s0031182004004986
573. Parvez MM, Bhuyain MAB, Shahabuddin AM, Farque AR, Shinn AS. Environmentally sustainable control measure of *Argulus* in freshwater ponds in Bangladesh. *Int J Sust Agricult Technol*. 2013;9:64-70.
574. Sahoo P, Kar B, Mohapatra A, Mohanty J. *De novo* whole transcriptome analysis of the fish louse, *Argulus siamensis*: first molecular insights into characterization of toll downstream signalling molecules of crustaceans. *Exp Parasitol*. 2013;135:629-641. doi:10.1016/j.exppara.2013.09.018
575. Banerjee A, Manna S, Saha S. Effect of aqueous extract of *Azadirachta indica* a. Juss (neem) leaf on oocyte maturation, oviposition, reproductive potentials and embryonic development of a freshwater ectoparasite *Argulus bengalensis* Ramakrishna, 1951 (Crustacea: Branchiura). *Parasitol Res*. 2014;113:4641-4650. doi:10.1007/s00436-014-4155-7
576. Kismiyati IF, Mahasri G. Different concentration influence of *Moringa oleifera* leaf aqueous extract immersion against *Argulus japonicus* egg damage. *IOP Conf Ser Earth Environ Sci*. 2020;441:012131. doi:10.1088/1755-1315/441/1/012131
577. Pereira EC, Oliveira C, Sousa EMO, et al. Lethal concentration of *Cymbopogon citratus* (Poaceae) essential oil for *Dolops discoidalis* and *Argulus* sp. (Crustacea: Argulidae). *J Fish Dis*. 2020;43:1497-1504. doi:10.1111/jfd.13250
578. Poly W. Global diversity of fishlice (Crustacea: Branchiura: Argulidae) in freshwater. *Hydrobiologia*. 2008;595:209-212. doi:10.1007/s10750-007-9015-3
579. Everts L, Avenant-Oldewage A. First record of *Argulus coregoni*: a fish ectoparasitic crustacean from Malaysia and additional notes on the morphology. *Malays Appl Biol*. 2009;38:61-71.
580. Sriwongpuk S. A new report of *Argulus indicus* (Crustacea: Branchiura) infestation in red tilapia (*Oreochromis niloticus* × *Oreochromis mossambicus*) in Thailand. *Int J Geomate*. 2020;18:182-187.
581. Moller OS, Olesen J. First description of larval stage 1 from a non-African fish parasite *Dolops* (Branchiura). *J Crust Biol*. 2012;32:231-238. doi:10.2307/41497028
582. Van As LL, Smit NJ, Hadfield KA. Description of life stages, molecular characterisation as well as a new host and locality record of *Chonopeltis lisikili* Van As and Van As (1996) from Phongolo River, South Africa. *Int J Parasitol: Parasit Wildl*. 2021;14:248-259. doi:10.1016/j.ijppaw.2021.02.012
583. Aguiar JC, Rosim DF, Santos SMC, et al. A new species of *Argulus* (Crustacea, Branchiura, Argulidae) from the skin of catfish, with new records of branchiurans from wild fish in the Brazilian Pantanal wetland. *Zootaxa*. 2017;4320:447-469. doi:10.11646/zootaxa.4320.3.3
584. Silva AKS, Malta JCO. A new species of *Branchiura* (Crustacea: Argulidae) parasites of *Arapaima gigas* Schinz, 1822 from Brazilian Amazon. *Neotrop Helminthol*. 2018;12:187-193.
585. Souza AKS, Porto DB, Malta JCO. A new species of *Argulus*, a fish parasite from the Brazilian Amazon (Crustacea, Branchiura). *Spixiana*. 2019;41:7-14.
586. Oliveira MSB, Corrêa LL, Ferreira DO, Neves LR, Tavares-Dias M. Records of new localities and hosts for crustacean parasites in fish from the eastern Amazon in northern Brazil. *J Parasitol*. 2017;41:565-570. doi:10.1007/s12639-016-0852-8
587. Saurubh S, Sahoo P, Mohanty B, et al. Modulation of the innate immune response of rohu *Labeo rohita* (Hamilton) by experimental freshwater lice *Argulus siamensis* (Wilson) infection. *Aquacult Res*. 2010;41:326-335. doi:10.1111/j.1365-2109.2010.02538.x
588. Ruane N, McCarthy TK, Reilly P. Antibody response to crustacean ectoparasites in rainbow trout, *Oncorhyncus mykiss* (Walbaum), immunized with *Argulus foliaceus* L. antigen extract. *J Fish Dis*. 1995;18:529-537. doi:10.1111/j.1365-2761.1995.tb00357.x
589. Junker K, Boomker J, Booyse DG. Pentastomid infections in cichlid fishes in the Kruger Natioanl Park, and description of the infective larva of *Subtriquetra rileyi* n. sp. *Onderstepoort J Vet Res*. 1998;65:159-167.
590. Luus-Powell WJ, Jooste A, Junker K. Pentastomid parasites in fish in the Olifants and Incomati River systems, South Africa. *Onderstepoort J Vet Res*. 2008;75:322-329.
591. Fain A. Les pentastomides de l' Afrique Central. *Ann Mus R Afr Centr*. 1961;92:1-115.
592. Southwell T, Pillers AWN. A note on a nymphal Linguatulidae *Leiperia cincinnalis* Sambon from the musculature of the fish *Tilapia nilotica*. *Ann Trop Med Parasitol*. 1929;23:130. doi:10.1080/00034983.1929.11684599
593. Boyce WM, Kazacos EA, Kazacos KR, Engelhardt JA. Pathology of pentastomid infections (*Sebekia mississippiensis*) in fish. *J Widl Dis*. 1987;23:689-692. doi:10.7589/0090-3558-23.4.689
594. Lopez NC. Parasitic crustaceans in fishes from some Philippine lakes. In: Santiago CB, Cuvin-Aralar M, Basiao ZU, eds. *Conservation and*

Ecological Management of Philippine Lakes in Relation to Fisheries and Aquaculture. Aquaculture Department, Southeast Asian Fisheries Development Center; 2001:75-79.

595. Rameshkumar G, Ravichandran S. *Cymothoa indica* (isopoda; Cymothoidae) and *Alitropus typus* (Isopoda; Aegidae) on freshwater fish *Tilapia mossambica* (Cichlidae) in Vellar estuary, Southeast Coast of India. *Biotemas*. 2010;23:67-70. doi:10.5007/2175-7925.2010v23n3p67
596. Kavanat Beerahassan R, Dileep N, Pillai D. Changes in the proximate and elemental composition of *Alitropus typus* (Crustacea: Flabellifera: Aegidae) exposed to lethal dose of bacterial consortium. *J Parasit Dis*. 2021;45:859-868. doi:10.1007/s12639-021-01374-1
597. Bhakta D, Das BK, Kamble SP, Das SK, Samanta S, Mitra S. New record of two isopods *Alitropus typus* and *Tachaea spongillicola* from riverine freshwater fishes in the river Tapti. *J Parasit Dis*. 2022;46:18-23. doi:10.1007/s12639-021-01449-z
598. Ray D, Mohapatra P, Ghorai N, Seth JK, Mohapatra A. Infection of the parasitic isopods on commercial fishes of the northern part of the east coast of India. *J Parasit Dis*. 2022;46:440-453. doi:10.1007/s12639-021-01463-1
599. Chinabut S. *A Case Study of Isopod Infestation in Tilapia Cage Culture in Thailand*. FAO Fish Tech Paper; 2002.
600. Chu KB, Jaapar MZ, Bruce NL. *Corallana nodosa* (Schioedte and Meinert, 1879) (Crustacea: Isopoda; Corallanidae), attacking freshwater fish at the durian Tunggal dam, Melaka, Malaysia. *Asian Fish Sci*. 2010;23:116-124. doi:10.33997/j.afs.2010.23.1.010
601. Oliveira AAN. *Parasitismo por Philostomella cigarra Szidat e Schubart, 1960 (Isopoda: Cymothoidae) em tilápia-do-Nilo (Oreochromis niloticus)*. Universidade Federal de Lavras; 2007:47.
602. Abdel-Latif HMR. Cymothoid parasite, *Nerocila orbigni* inflicts great losses on *Tilapia zilli* in Lake Qarun at El-Fayoum Province. *Int J Innovat Stud Aquat Biol Fish*. 2016;2:1-9. doi:10.20431/2454-7670.0203001
603. Elgendy MY, Hassan AM, Zaher MFA, Abbas HH, Soliman WSE-D, Bayoumy EM. *Nerocila bivittata* massive infestations in *Tilapia zillii* with emphasis on hematological and histopathological changes. *Asian J Sci Res*. 2018;11:134-144. doi:10.3923/ajsr.2018.134.144
604. Mahmoud N, Abd Elwahab A, Abouwarda M, Khattab M, Ramadan R. Further studies on cymothoid isopods of some fish species from Lake Qarun, Egypt. *Egypt Vet Med Soc Parasitol J*. 2017a;13:15-24. doi:10.21608/evmspj.2017.37456
605. Abdelkhalek NK, El-Adl M, Salama M, Al-Araby MA. *Mass Mortalities Associated with Isopoda Infestation as a Result of Uncontrolled Biosecurity Measures in Lake Qarun, Egypt*. World Aquaculture Society; 2017. https://www.was.org/MeetingAbstracts/ShowAbstract/47509.
606. Burreson E. Phylum Annelida: Hirudinea as vectors and disease agents. In: Woo P, ed. *Fish Diseases and Disorders*. CABI Publishing; 2006.
607. Negm Eldin M. Preliminary observation on leech (Hirudinea) infections in tilapia fish. *Alex J Vet Sci*. 1995;11:67-74.
608. Aidala S. *Ectoparasites on freshwater fish Oreochromis niloticus Linnaeus, 1758 (Tilapia Merah) in fish farms at Penampang, Kota Kinabalu, Sabah*. Universiti Teknologi Mara; 2017:30.
609. Opara K. Population dynamics of *Piscicola geometra* (Hirudinea: Rhynchobdellida) on *Oreochromis niloticus* (cichlidae) cultured in a rainforest pond, South Eastern Nigeria. *J Environ Sci*. 2002;14:536-540.
610. Williams EHJ, Bunkley-Williams L, Burreson EM. Some new records of marine and freshwater leeches from Caribbean, southeastern U.S.A., eastern Pacific, and Okinawan animals. *J Helminthol Soc Wash*. 1994;61:133-138.
611. Kone M. Biosécurité en pisciculture et traitements contrôle le parasite *Argulus* sp. pour une amélioration de la production du tilapia du Nil *Oreochromis niloticus* (Linnaeus, 1758) de Côte d'Ivoire. Thèse de doctorat, Université de Nangui Abrogoua, Cote d'Ivoire; 2015.
612. Nyamete F, Chacha M, Msagati T, Raymond J. Prevalence of fish parasites in Nile tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*) and physicochemical characteristics of pond water in Arusha and Morogoro, Tanzania. *Int. J Biosci*. 2020;7:76-91. doi:10.12692/ijb/17.6.76-91
613. Bragg R, Oosthuizen J, Lordan S. The leech *Batracobdelloides tricarinata* (Blanchard, 1897) (Hirudinea: Glossiphoniidae) as a possible reservoir of the rainbow trout pathogenic *Streptococcus* species. *Onderstepoort J Vet Res*. 1989;56:203-204.
614. Oosthuizen J. Redescription of the African fish leech *Batracobdelloides tricarinata* (Blanchard, 1897) (Hirudinea: Glossiphoniidae). *Hydrobiologia*. 1989;184:153-164. doi:10.1007/BF02392951
615. Nagasawa K, Uyeno D. *Zeylanicobdella arugamensis* (Hirudinida, Piscicolidae), a leech infesting brackish-water fishes, new to Japan. *Biogeography*. 2009;11:125-130.
616. de Silva P. *Zeylanicobdella arguamensis* gen. nov. and sp. nov. from Arguam Kalapu, Eastern Province, Ceylon. *Spolia Zeylan*. 1963;30:47-53.
617. Price W, Nadolny J. *Piscicolaria reducta* (Hirudinea: Piscicolidae) from fishes in a subtropical Florida stream. *J Helminthol Soc Wash*. 1993;60:130-134.
618. Volonterio O, López-de León E, Ponce de León R. Infestation dynamics and histopathology of two species of freshwater leeches (Hirudinea: Piscicolidae) on teleost fish from Uruguay. *Comp Parasitol*. 2004;71:21-28. doi:10.1654/4087
619. Ahne W. *Argulus foliaceus* L. and *Piscicola geometra* L. as mechanical vectors of spring viraemia of carp virus (SVCV). *J Fish Dis*. 1985;8:241-242. doi:10.1111/j.1365-2761.1985.tb01220.x
620. Soliman MK, Aboeisa MM, Mohamed SG, Saleh WD. First record of isolation and identification of spring viraemia of carp virus from *Oreochromis niloticus* in Egypt. *Paper presented at 8th International Symposium on Tilapia in Aquaculture*. American Tilapia Association; 2008:1287-1306.
621. OIE. Spring viraemia of carp. *Manual of Diagnostic Tests for Aquatic Animals*. World Organisation for Animal Health; 2019.
622. Dombrowski H. Die nahrungsmenge des fischegels *Piscicola geometra* L. (Zugleich ein beitrage zur physiologie des blutes des karpfens *Cyprinus carpio* L.). *Biol Zentralbl*. 1953;72:311-314.
623. Negele R. Fish leeches as pests and vectors of disease. *Fisch Umwelt*. 1975;1:123-126.
624. Shinn A, Pratoomyot J, Metselaar M, Bastos GG. Diseases in aquaculture—counting the costs of the top 100. In: Binder E, Rigl A, Hines R, eds. *SCOPE—Scientific Challenges and Opportunities in the Protein Economy*. Biomin World Nutrition Forum; 2018:227-262.
625. Cruz-Lacierda E, Toledo J, Tan-Fermin J, Burreson E. Marine leech (*Zeylanicobdella arugamensis*) infestation in cultured orange-spotted grouper, Epinephelus Coioides. *Aquaculture*. 2000;185:191-196. doi:10.1016/S0044-8486(99)00356-7
626. Kua BC, Azila A, Siti Zahrah A, Ramley AB. A case study on the mortality outbreak of cobia *Rachycentron canadum* cultured in traditional floating cages. *Trop Life Sci Res*. 2013;24:77-84.
627. Hayes PM, Smit NJ, Seddon AM, Wertheim DF, Davies AJ. A new fish haemogregarine from South Africa and its suspected dual transmission with trypanosomes by a marine fish. *Folia Parasitol*. 2006;53:241-248. doi:10.14411/fp.2006.031
628. Kozlovskaya VI, Chukyo GM, Lapkina LN, Nepomnyashchikh VA. Resistance of aquatic animals to organophosphorus pesticides and its mechanisms. In: Ryans RC, ed. *Problems of Aquatic Toxicology, Biotesting and Water Quality Management. Proceedings of the USA-USSR Symposium*. Environmental Research Laboratory Office of Research and Development, U.S. Environmental Protection Agency; 1984:227.

629. Prost M, Studnicka M, Niezgoda J. Efficacy of some methods controlling leeches in water. *Aquaculture*. 1974;3:287-294. doi:10.1016/0044-8486(74)90078-7
630. FAO/NACA. *Manual of Procedures for the Implementation of the Asia Regional Technical Guidelines on Health Management for the Responsible Movement of Live Aquatic Animals*. FAO, Fisheries and Aquaculture Management Division; 2001.
631. Subasinghe RP, Bondad-Reantaso MG. Biosecurity in aquaculture: international agreements and instruments, their compliance, prospects and challenges for developing countries. In: Scarfe A, Lee C, O'Bryen P, eds. *Aquaculture Biosecurity: Prevention, Control and Eradication of Aquatic Animal Disease*. Blackwell Publishing; 2006.
632. Bondad-Reantaso M, Lem A, Subasinghe R. International trade in aquatic animals and aquatic animal health: what lessons have we learned so far in managing the risks? *Fish Pathol*. 2009;44:109-144. doi:10.3147/jsfp.44.107
633. World Trade Organization (WTO). *Agreement on the Application of Sanitary and Phytosanitary Measures (SPS Agreement)*. WTO; 1994. https://www.wto.org/english/tratop_e/sps_e/spsagr_e.htm#fntext1.
634. CBD. *Convention on Biological Diversity*. United Nations; 1992.
635. ICES. *ICES Code of Practice on the Introductions and Transfers of Marine Organisms*. International Energy Agency; 2005.
636. Turner GE. *Codes of Practice and Manual of Procedures for Consideration of Introductions and Transfers of Marine and Freshwater Organisms. EIFAC/CECPI Occasional Paper No. 23*. Food and Agriculture Organization of the United Nations; 1988:44.
637. FAO. *Aquaculture Development. Health Management for Responsible Movement of Live Aquatic Animals*. Food and Agriculture Organization; 2007.
638. FAO/NACA. *Asia Regional Technical Guidelines on Health Management for the Responsible Movement of Live Aquatic Animals and the Beijing Consensus and Implementation Strategy*. FAO, Fisheries and Aquaculture Management Division; 2000.
639. Department of Agriculture, Water and the Environment, Australian Government. *National Policy Guidelines for the Translocation of Live Aquatic Animals*. Department of Agriculture, Water and the Environment, Australian Government; 2020.
640. Riedel R, Caskey L, Costa-Pierce B. Fish biology and fisheries ecology of the Salton Sea, California. In: Barnum D, Elder J, Stephens D, Friend M, eds. *Developments in Hydrobiology: The Salton Sea*. Kluwer Academic Publishers; 2002.
641. Shinn A, Pratoomyot J, Bron J, Paladini G, Brooker E, Brooker A. Economic costs of protistan and metazoan parasites to global marine mariculture. *Parasitology*. 2015a;142:196-270. doi:10.1017/S0031182014001437
642. Abdel-Latif H, Dawood M, Menanteau-Ledouble S, El-Matbouli M. The nature and consequences of co-infections in tilapia: a review. *J Fish Dis*. 2020;43:651-664. doi:10.1111/jfd.13164
643. Jahangiri L, Shinn A, Pratoomyot J, Bastos GG. Unveiling associations between ciliate parasites and bacterial microbiomes under warm-water fish farm conditions—a review. *Rev Aquac*. 2021;13:1097-1118. doi:10.1111/raq.12514

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Shinn AP, Avenant-Oldewage A, Bondad-Reantaso MG, et al. A global review of problematic and pathogenic parasites of farmed tilapia. *Rev Aquac*. 2023;15(Suppl. 1):92-153. doi:10.1111/raq.12742