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REVIEWS IN Aquaculture

REVIEW

A global review of problematic and pathogenic parasites of farmed tilapia

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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

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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

Species	Common name	Aquaculture tonnes (2019)	Producing countries (2019)	Number of countries 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*.

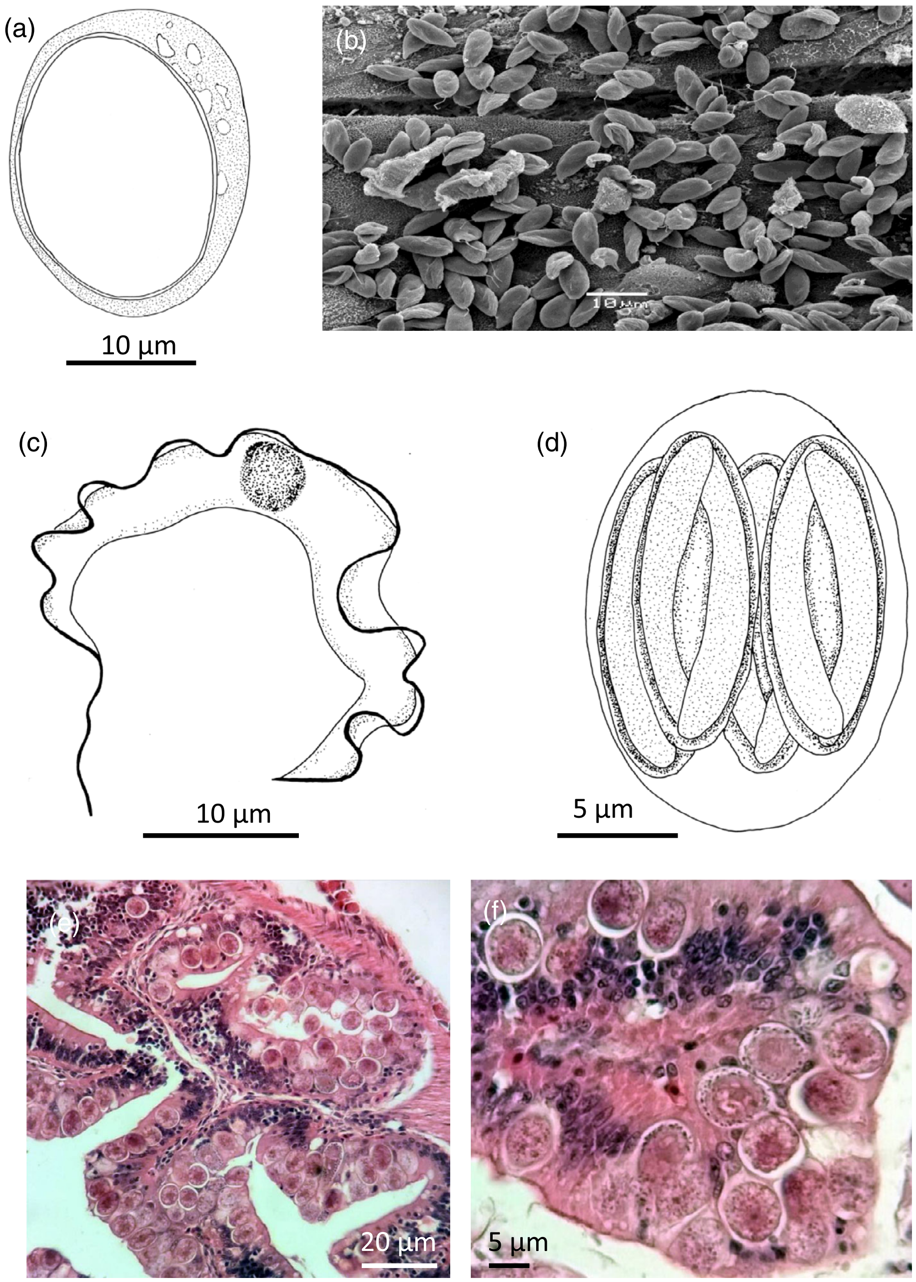

FIGURE 1 Protista. (a) Line drawing of *Dermocystidium aegyptiacus* reported from the intestines of *Oreochromis niloticus* cultured in Egypt. (b) Scanning electron microscope image of *Ichthyobodo necator* on epithelial surfaces. (c) Line drawing of *Trypanosoma mukasai* reported from the blood of a 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

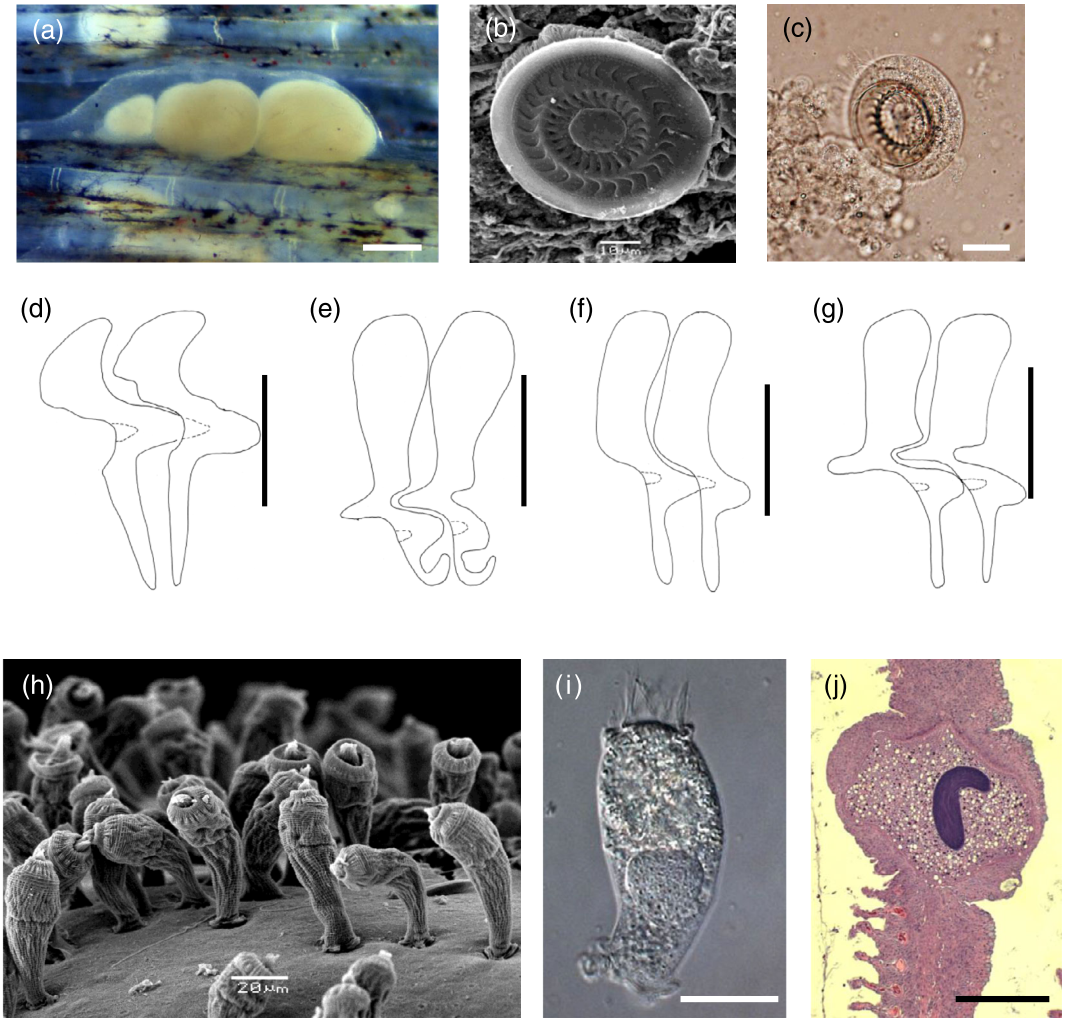

FIGURE 2 Ciliophora. (a) Photomicrograph of *Ichthyophthirius multifiliis* Fouquet, 1876 trophonts in the fin epithelium and (b) scanning electron microscopy image of the aboral surface of an unnamed *Trichodina* sp. collected from farmed *O. niloticus* from Veracruz, Mexico. Note the denticles in a 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,

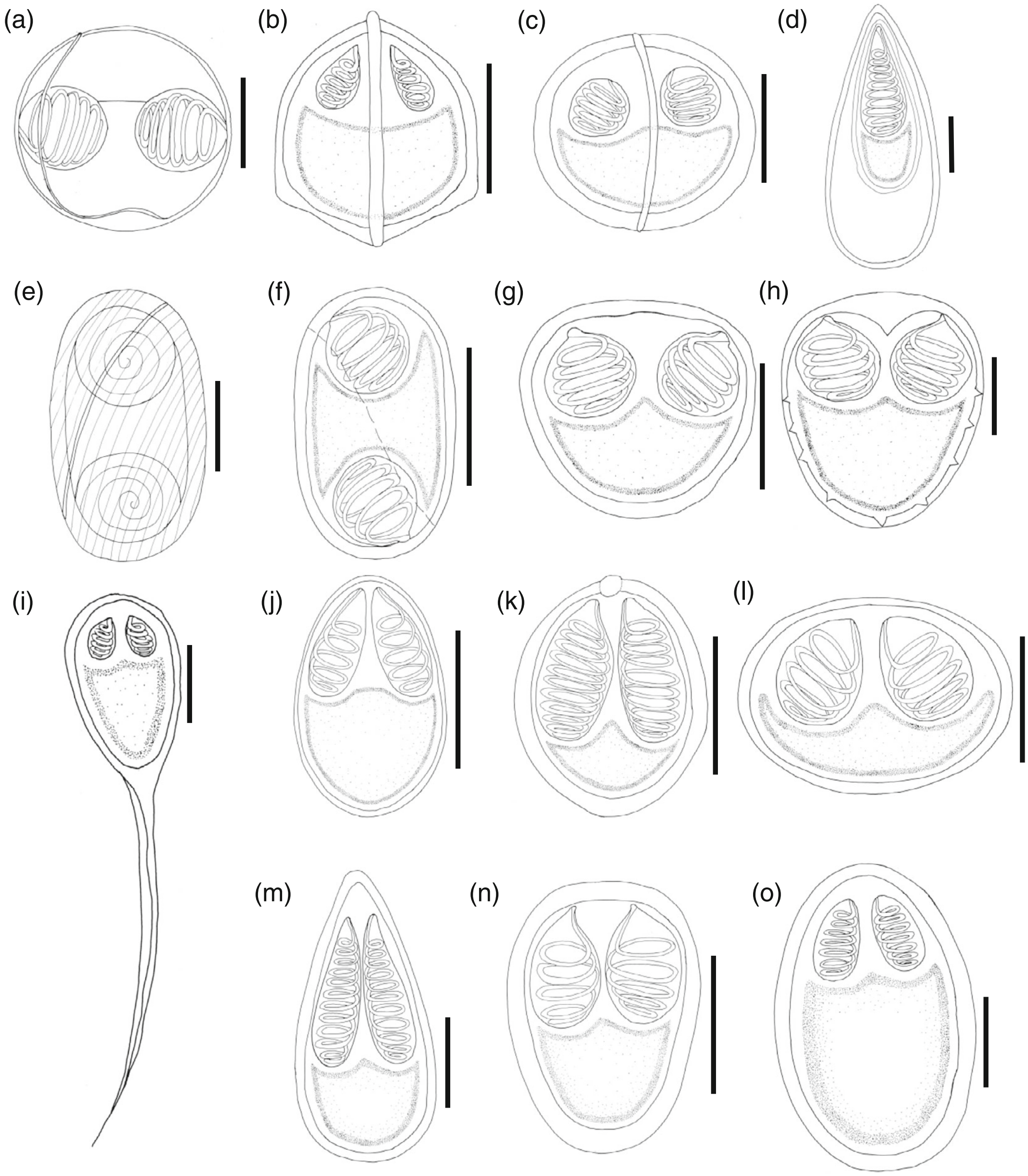

FIGURE 3 Myxozoa. Line drawings of various myxozoan spores reported in tilapia. (a) *Sinuolinea niloticus*, (b) *Sphaerospora melensis*, (c) *Sphaerospora tilapiae*, (d) *Thelohanellus talipiae*, (e) *Zschokkella tilapiae*, (f) *Z. nilei*, (g) *Ortholinea africanus*, (h) *Triangula egyptica*, (i) *Henneguya 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

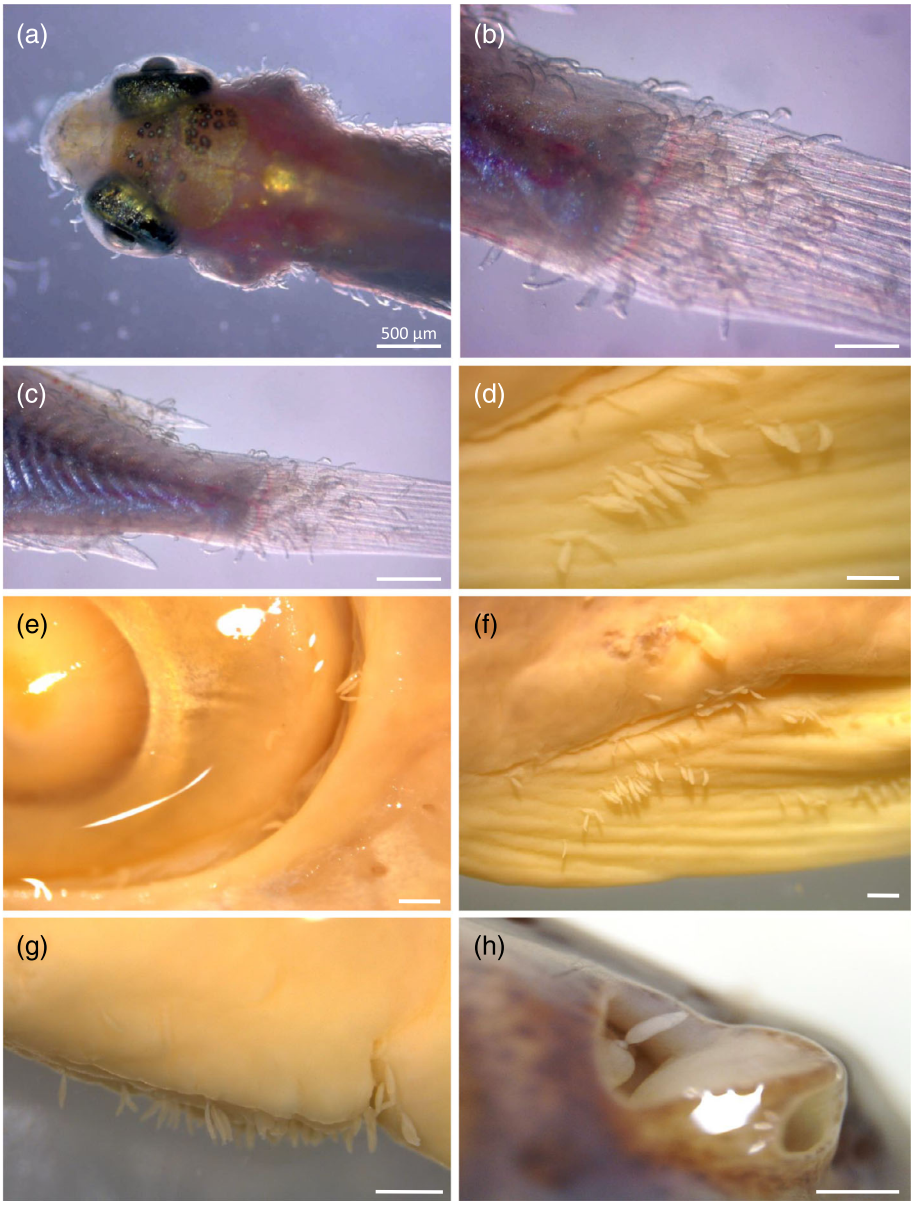

FIGURE 5 Light microphotographs of *Oreochromis niloticus* larvae (~2 cm) with a heavy infection of *Gyrodactylus cichlidarum* Paperna, 1968. (a) Head, (b) Caudal fin, (c) Caudal peduncle, (d, f), Eye, (e), Anal fin, (g) Ventrum and (h) Nares. All scale bars = 500 μm

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

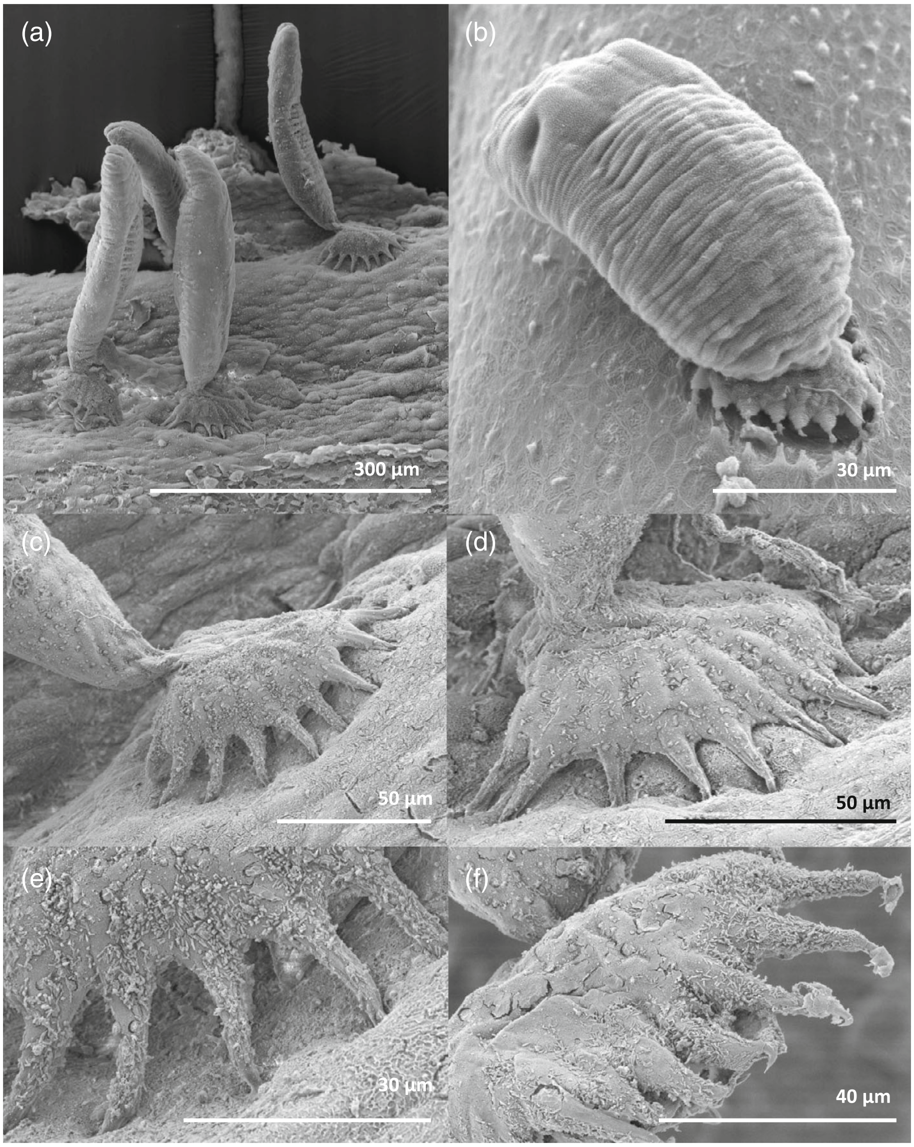

FIGURE 6 Scanning electron micrograph of *Gyrodactylus cichlidarum* Paperna, 1968. (a–e) Attachment on fish skin; (f) Haptoral structure of the worm after detachment from *Oreochromis niloticus*. Images a, c-f courtesy of Mrs Greta Hanako Rosas Saito, Instituto de Ecología A.C., Xalapa, Mexico. Image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

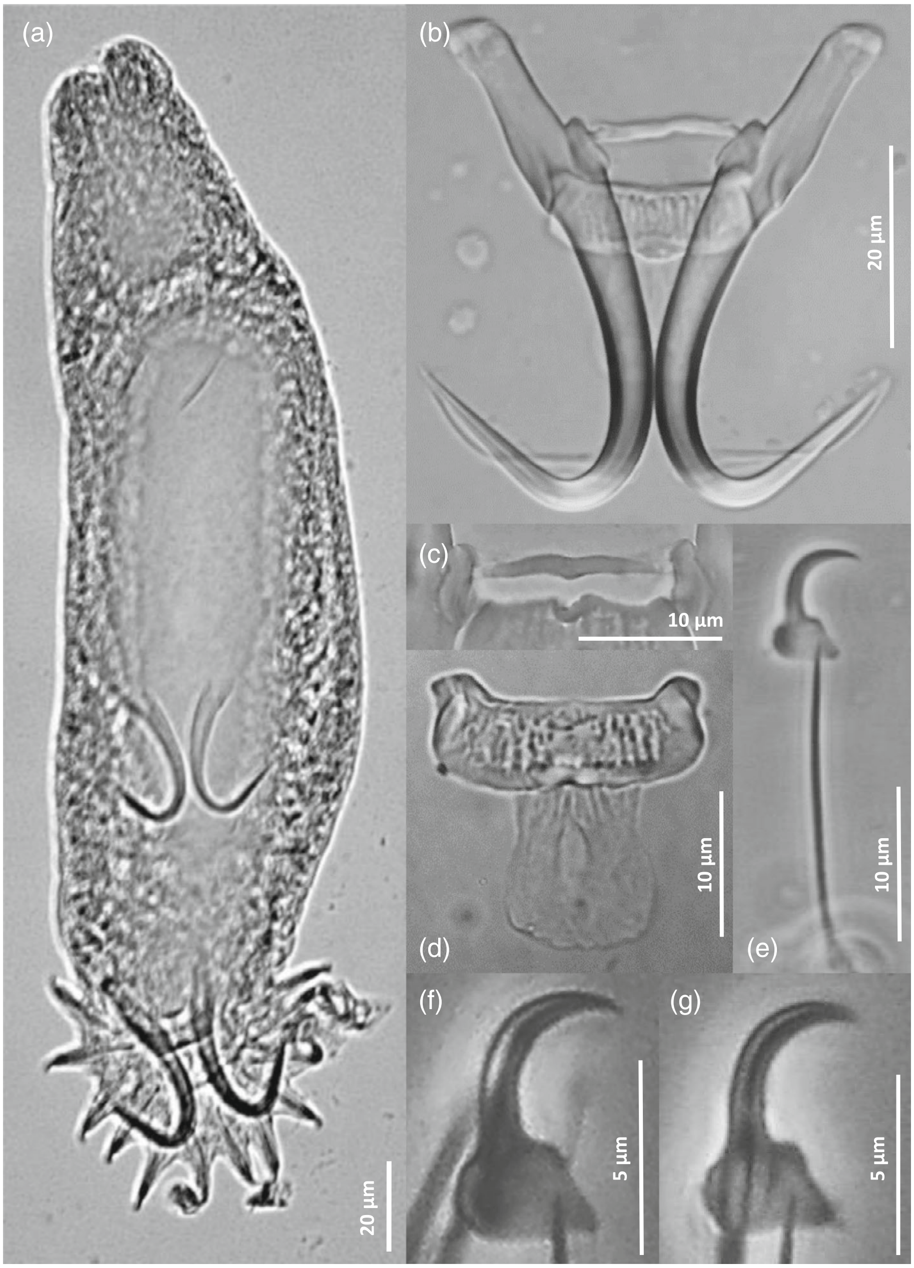

FIGURE 7 Light microphotographs of *Gyrodactylus cichlidarum* from *Oreochromis niloticus*. (a) Whole mount, (b) Hamuli, Ventral and dorsal bars, (c) Dorsal bar, (d) Ventral bar, (e) Marginal hook and (f, g) Marginal hook sickles

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

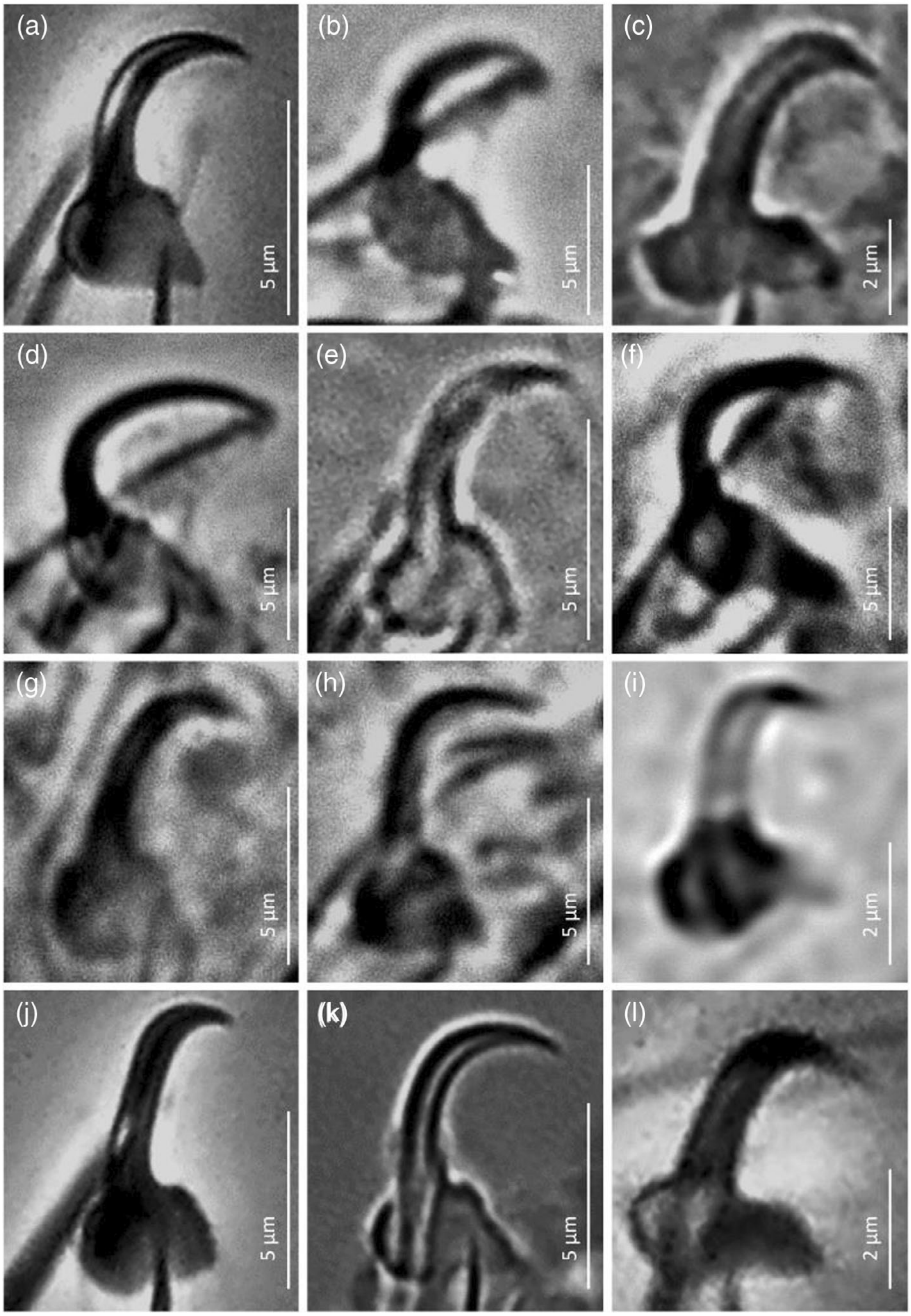

FIGURE 8 Light microphotographs under phase contrast of the marginal hook sickles of *Gyrodactylus* species infecting different species of tilapia. (a) *Gyrodactylus cichlidarum* Paperna, 1968. (b) *Gyrodactylus ergensi* Prikřylová, Matějusová, Musilová et Gelnar, 2009. (c) *Gyrodactylus hildae* García-Vásquez, 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

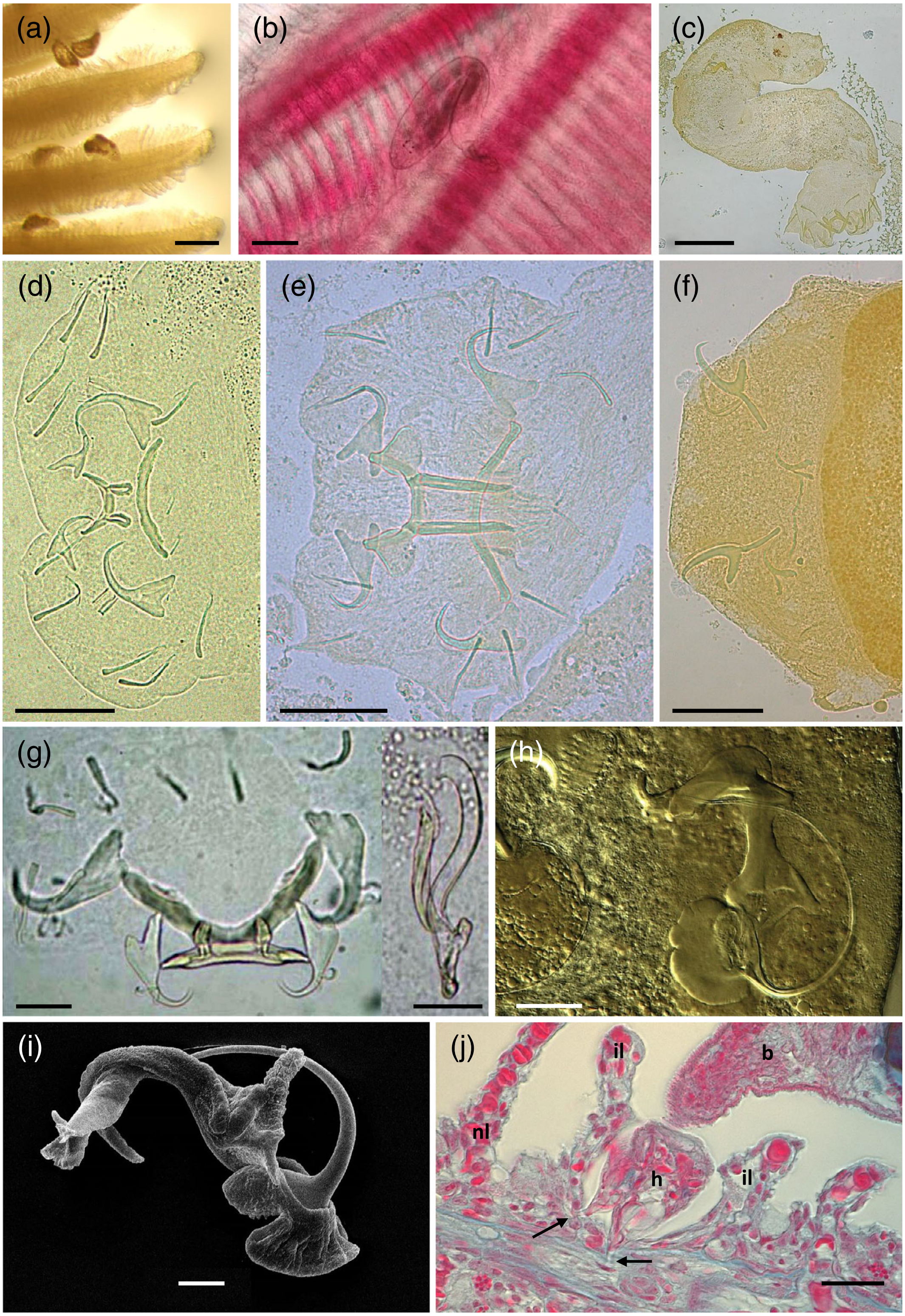

FIGURE 9 (a) *Cichlidogyrus* spp. on the gills of *Sarotherodon melanotheron* (photo A. Pariselle). (b) *Cichlidogyrus* Paperna, 1960 sp. on the gill of *Oreochromis niloticus* from Thailand (photo T. Limakom). (c) *Cichlidogyrus dossoui* Douellou, 1993 (in toto, glycerine ammonium picrate (GAP) medium) (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

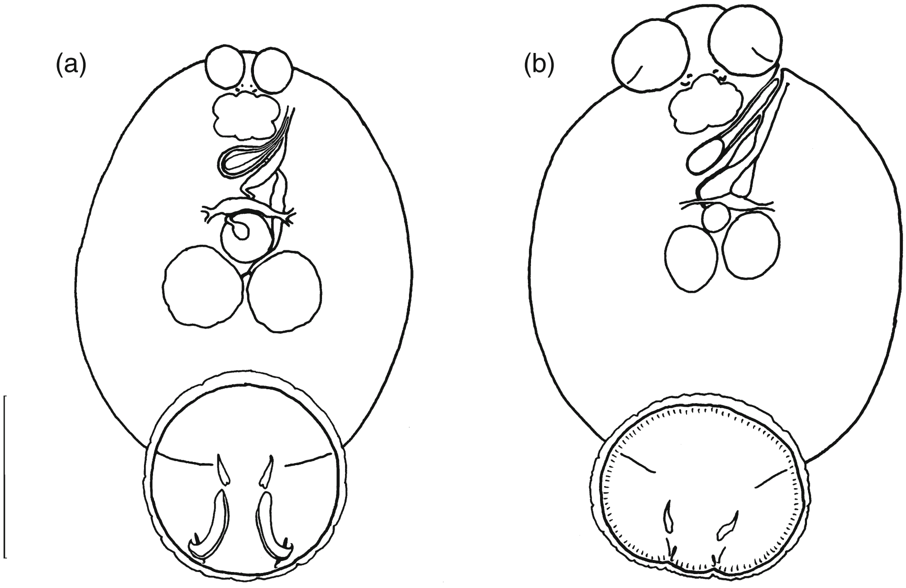

FIGURE 10 Capsalids from tilapia. (a) *Neobenedenia girellae* drawn from Queensland Museum specimen G218281 showing circular haptor, small anterior attachment organs and absence of a vagina. (b) *Benedenia monticellii* drawn from specimens on Hebrew University of Jerusalem slide HUJ-MONO1.0 showing laterally 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

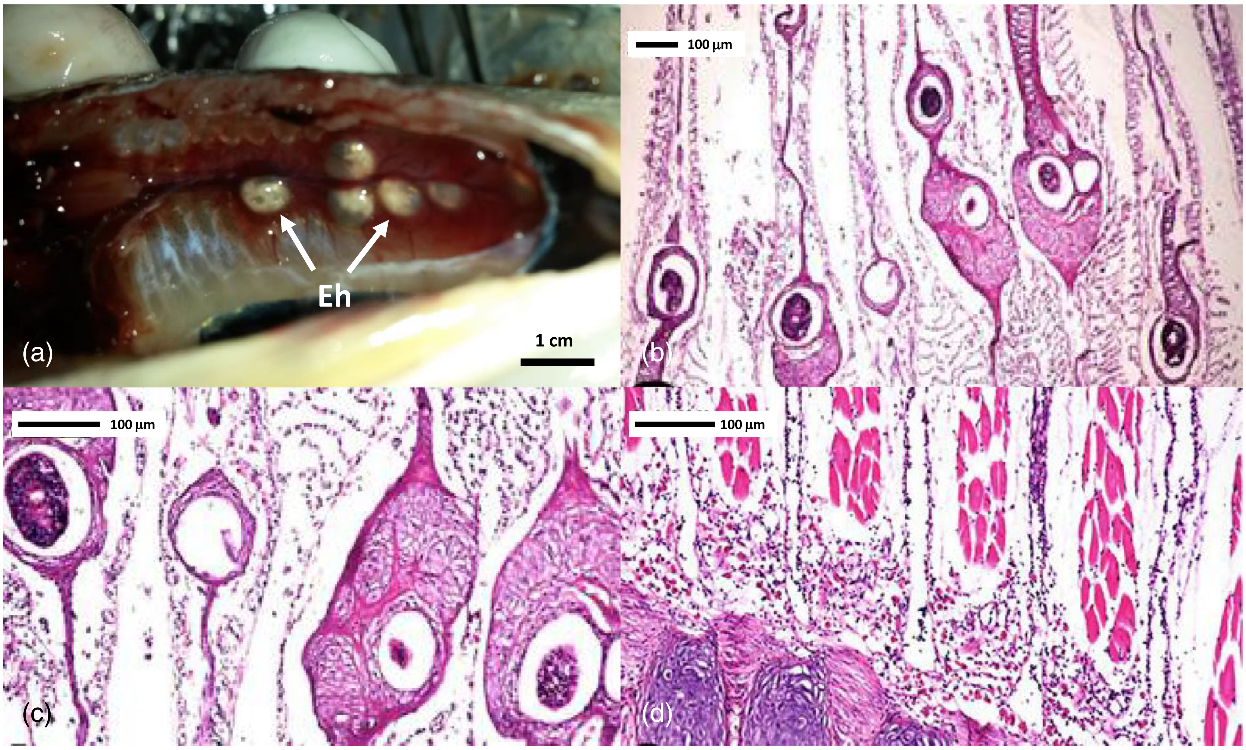

FIGURE 11 (a) Encysted metacercariae of *Euclinostomum heterostomum* (Rudolpi, 1809) (Eh) in the body cavity of *Oreochromis niloticus* (image courtesy of Liesl Van As and Andri Grobelaar from the Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein, Republic of South 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

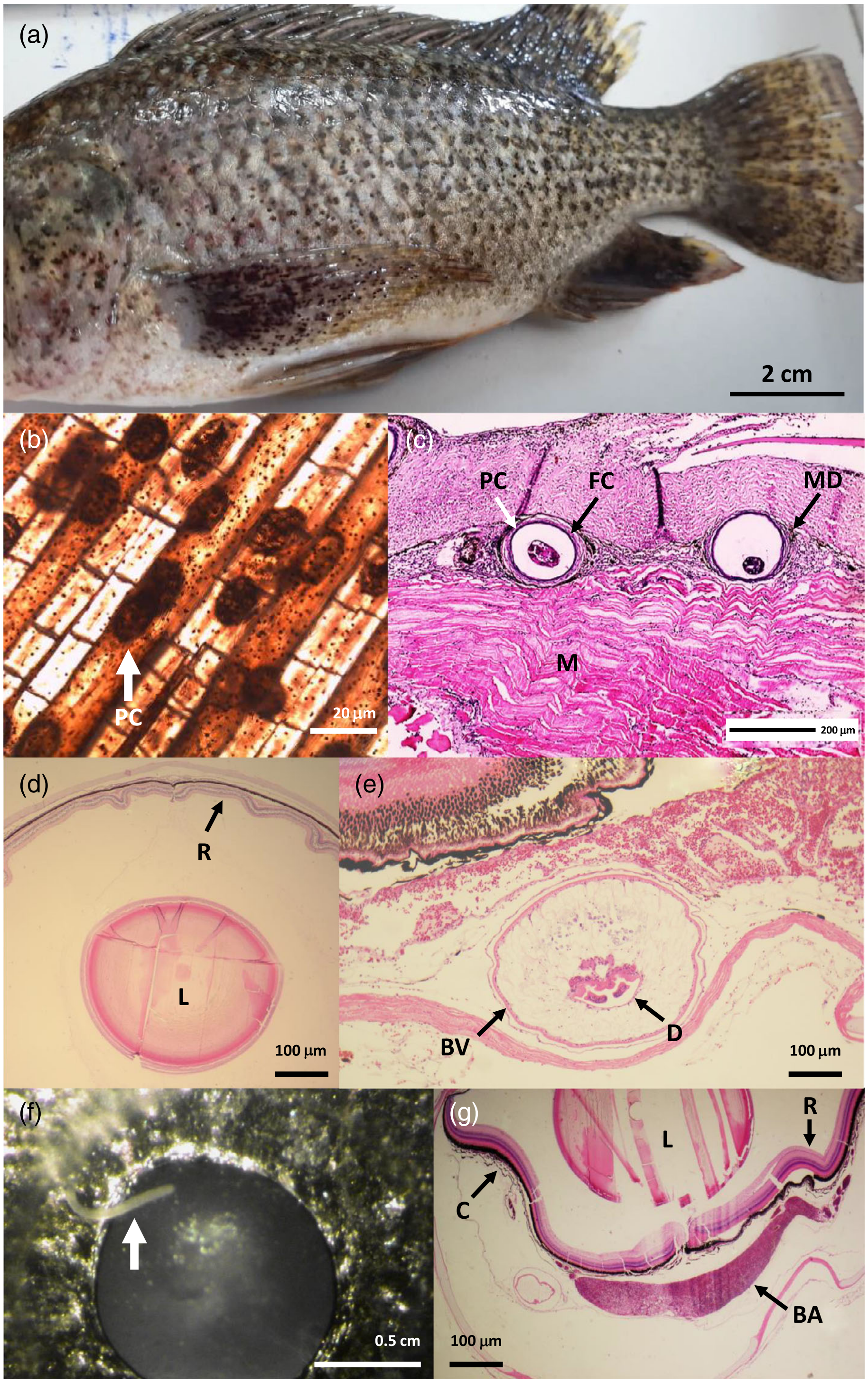

FIGURE 12 (a, b) Gross and microscopic examination of *Oreochromis niloticus* heavily infected with metacercariae of *Uvulifer* sp. (Trematoda: Diplostomidae) (black spot disease). (c) Photomicrograph of a histopathological section of *O. niloticus* skin and muscle infected with *Uvulifer* sp. showing 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.

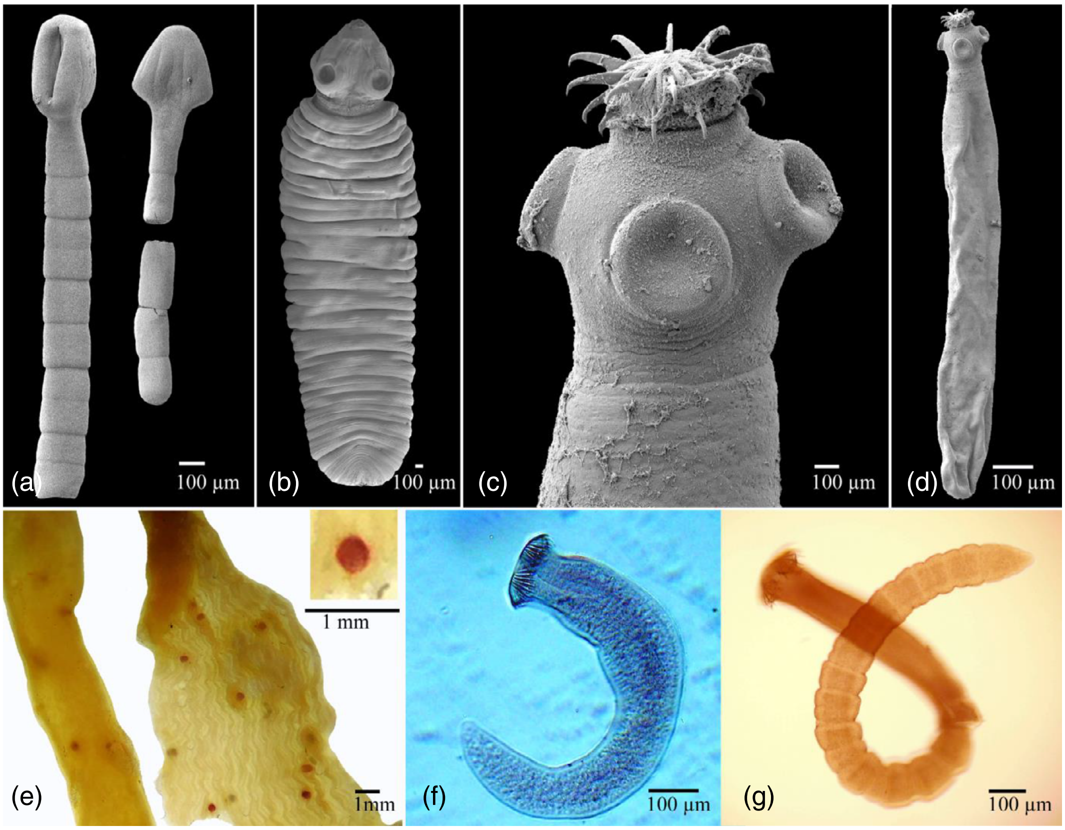

FIGURE 13 Cestodes of tilapias. (a) Immature *Schyzocotyle acheilognathi* (Yamaguti, 1934) from *Symphysodon aequifasciatus* from culture in the Czech Republic. (b) Larval *Amirthalingamia macracantha* (Joyeux et Baer, 1935) from tilapia hybrids in Israel. (c, d) Scolex and whole larva of *Neogryporhynchus 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.

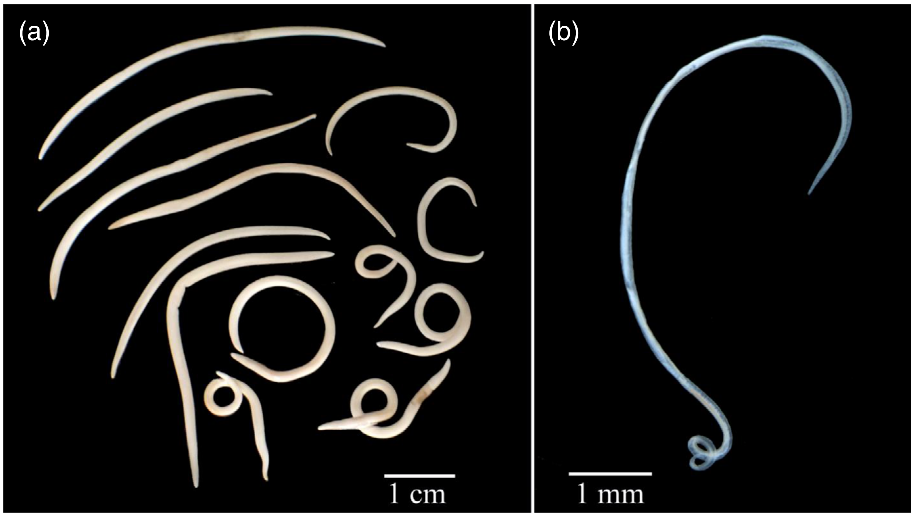

FIGURE 14 Nematodes of tilapias. (a) *Contracaecum* Type 2 larvae from *Oreochromis niloticus* from Egypt. (b) Stage L4 larva of *Rhabdochona* (*Globochona*) *paski* Baylis, 1928 from *O. niloticus* from Lake Victoria, Kenya

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

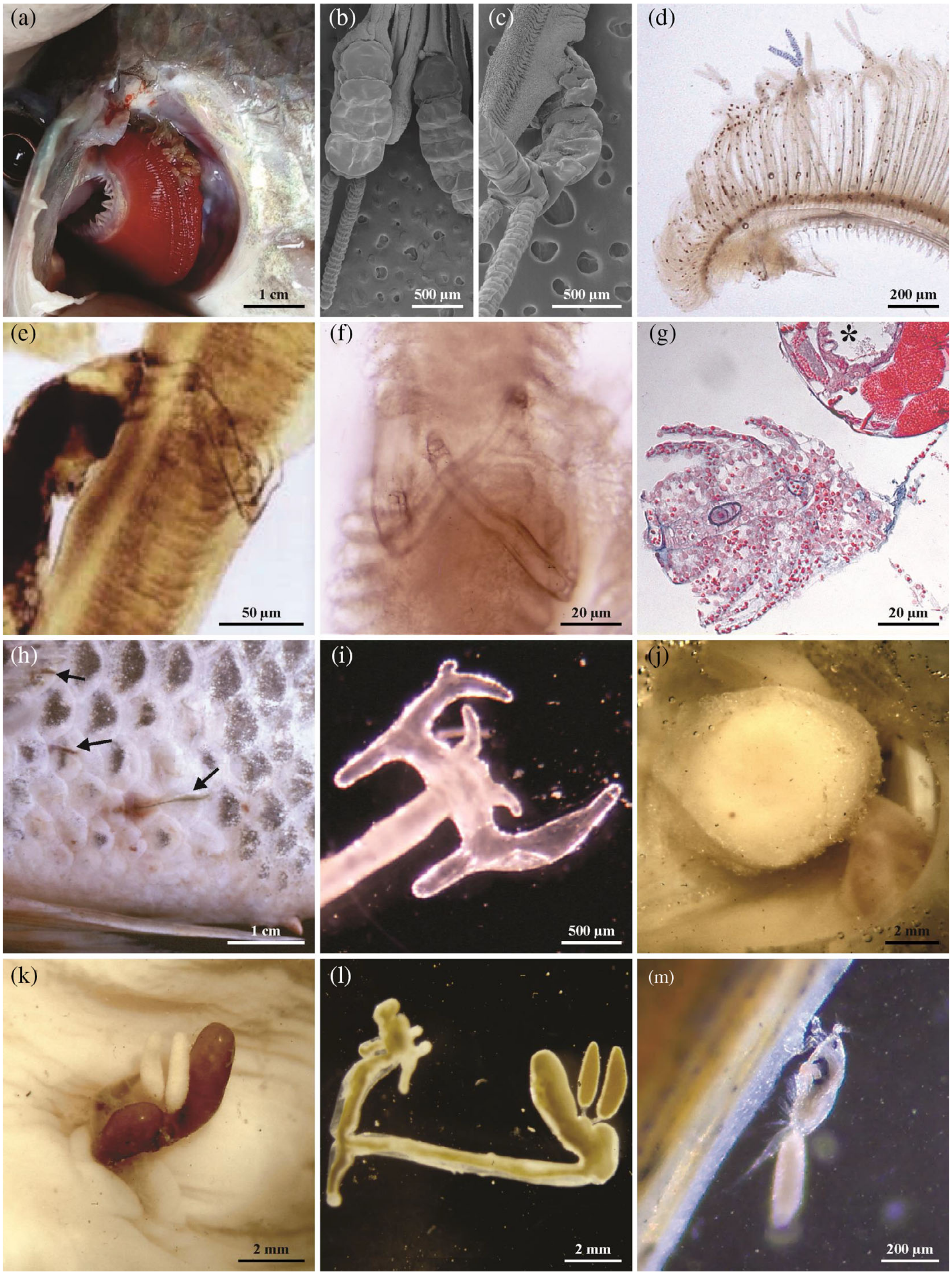

FIGURE 15 Crustacean copepod parasites of cultured tilapias. (a) Macrograph of *Lamproglena monodi* Capart, 1944 females on the gills of *Oreochromis niloticus*. (b) Scanning electron micrograph of *L. monodi* with paired egg sacs on the gills of *O. niloticus*. (c) Scanning electron micrograph of *L. 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.

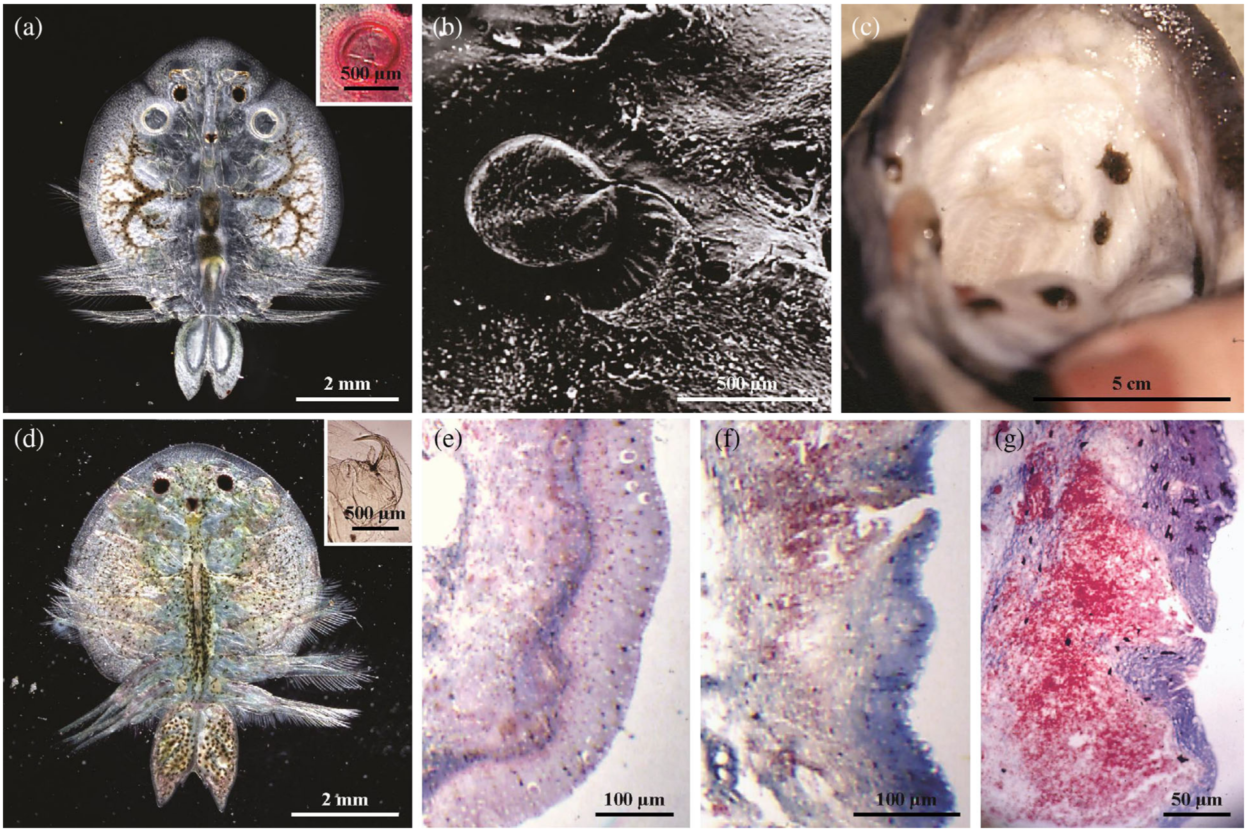

FIGURE 16 Crustacean branchiuran parasites of cultured tilapias. (a) Male *Argulus japonicus* Thiele, 1900. The inlay shows an enlarged image of an attachment sucker. (b) Scanning electron micrograph of the damage to host tissue inflicted by *A. japonicus*. The image shows an imprint of the suckers, 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

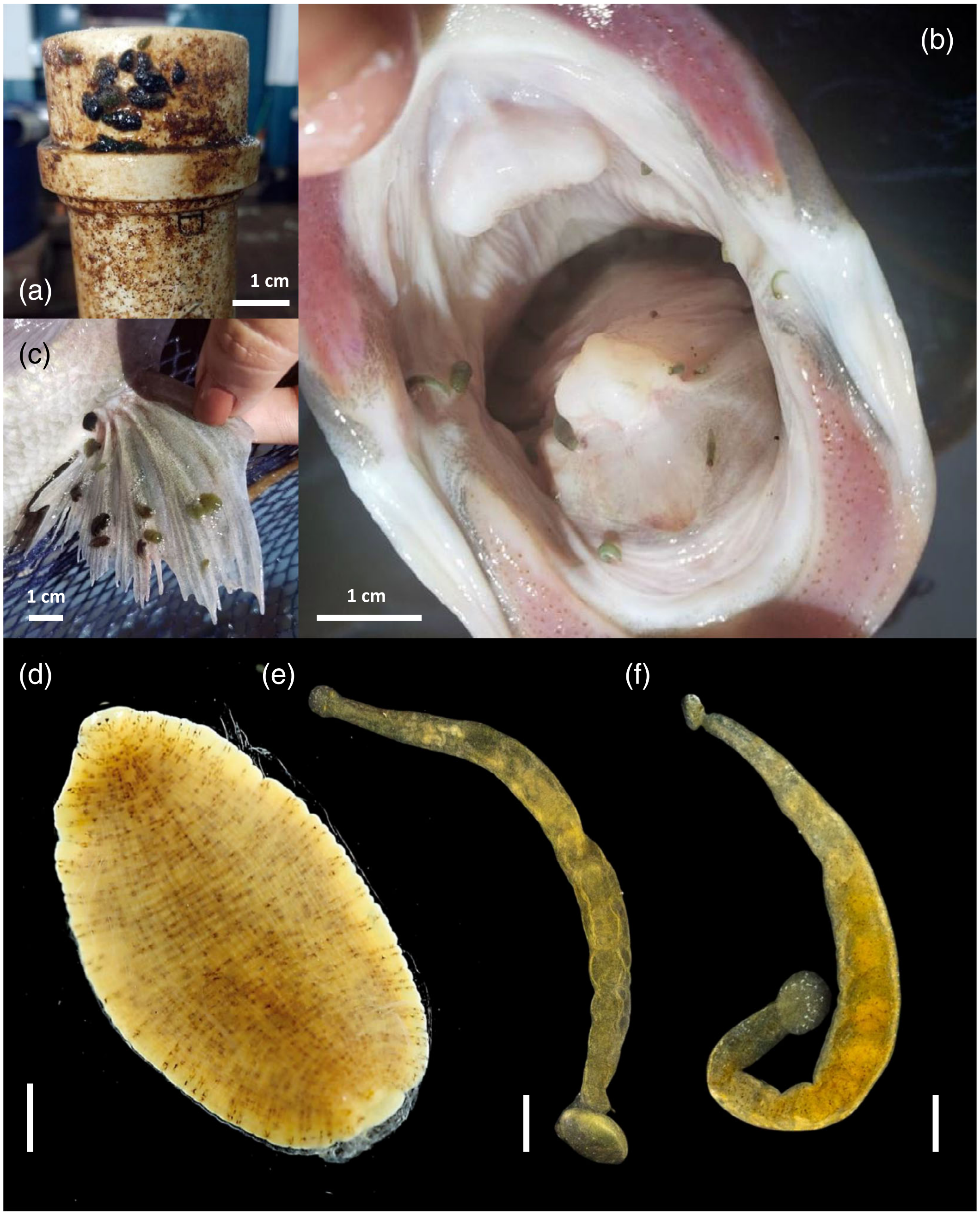

FIGURE 18 Leech infections of *Oreochromis niloticus*. (a–d) *Helobdella* sp. from stock cultured in Brazil showing leeches on (a) the system pipework, (b) attached to the inner lining of the oral cavity, (c) attached to the pectoral fin and (d) an ethanol fixed specimen of *Helobdella* sp. and (e,f)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

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DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

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

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