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ORIGINAL PAPER

# Resistance of an invasive gastropod to an indigenous trematode parasite in Lake Malawi

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**Abstract** Successful establishment and spread of biological invaders may be promoted by the absence of population-regulating enemies such as pathogens, parasites or predators. This may come about when introduced taxa are missing enemies from their native habitats, or through immunity to enemies within invaded habitats. Here we provide field evidence that trematode parasites are absent in a highly invasive morph of the gastropod *Melanoides tuberculata* in Lake Malawi, and that the invasive morph is resistant to indigenous trematodes that castrate and induce gigantism in native *M. tuberculata*. Since helminth infections can strongly influence host population abundances in other host-parasite systems, this enemy release may have provided an advantage to the invasive morph in terms of reproductive capacity and survivorship.

**Keywords** Biological invasion · Enemy release · Non-indigenous species · Exotic species · Fish parasites · African lakes · Thiaridae

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## Introduction

Natural enemies may play a major role in determining success of colonisations of new habitat by invasive lineages. In particular it has been found that colonisers can benefit considerably from the release of life history, ecological and fitness constraints associated with parasitic infection. Release from the regulatory role of parasites may take two forms. Firstly, invaders may benefit by release from parasites that occur within native habitats (Keane and Crawley 2002; Torchin et al. 2003). This is because parasites may not have migrated with host populations, or because parasites are unable to survive in new habitats due to a lack of suitable intermediate or final hosts. Secondly, invaders may benefit through immunity to parasites that are prevalent within the invaded community. Such immunity may occur because parasites are often locally adapted to their hosts (Ebert 1994; 1998), and as a consequence are unable to infect invading taxa (Prenter et al. 2004; Fromme and Dybdahl 2006).

The mollusc-trematode system has been frequently used as a model for investigating the benefits, costs and mechanisms of co-evolution between parasites and hosts (Sorensen and Minchella 2001; Lively et al. 2004). Trematodes affect host molluscs through changes in survivorship, fecundity, growth rates, behaviour and morphology (Sorensen and Minchella 2001), potentially with considerable influences on population abundance and competitive interactions (Byers and Goldwasser 2001). Many trematodes also possess strong selectivity for gastropod intermediate host species (Torchin et al. 2005), suggesting trematode communities have co-evolved with hosts and that introduced species can be resistant to indigenous parasites. Moreover, adaptations of trematodes to geographically localised conspecific host populations have also been shown for some gastropod species, implying mollusc-trematode co-evolution over short evolutionary timescales. This has been shown most clearly in cross-inoculation experiments of the freshwater snail *Potamopyrgus antipodarum* with *Microphallus* trematodes. Several studies have revealed higher infection rates in snail populations from sympatric parasite source sites when compared to snail populations from allopatric sites (Lively and Dybdahl 2000; Lively et al. 2004).

Many studies have demonstrated the importance of local adaptation by parasites for our understanding of ecological and evolutionary dynamics. In particular, with regard to biological invasions, investigations of parasite adaptations and host invasion success have found that parasites can be influential in determining outcomes of competition between indigenous and invasive lineages (MacNeil et al. 2003; Prenter et al. 2004). In this study we report field evidence that a newly colonising lineage of the parthenogenetic freshwater gastropod *Melanoides tuberculata* (Müller) in Lake Malawi is free from trematode infection, including opisthorchid trematodes that sterilise and induce gigantism within an indigenous *M. tuberculata* population. This indicates that the introduced population is not only missing parasites from its original range, but also that it is resistant to trematodes within the invaded community. This enemy release may have afforded a competitive advantage over indigenous taxa, and contributed to rapid population expansion of this highly invasive morph.

## Methods

### Study organisms

*Melanoides tuberculata* is a viviparous freshwater snail common to tropical environments across Asia and Africa. It is highly invasive, and has colonised many non-native subtropical and tropical locations during the last century including the Americas and Australasia (e.g. Samadi et al. 1997). This taxon typically undergoes clonal reproduction and is a direct developer (Heller and Farstay 1990; Samadi et al. 1997). Within Lake Malawi, two lineages of *M. tuberculata* are present on littoral soft-sediments. One is indigenous (Lake Malawi Native—LMN) and present throughout Lake Malawi and several peripheral water bodies. By contrast molecular phylogenetic and museum collection evidence strongly suggests that the other (Lake Malawi Introduced—LMI) has been introduced during the last 25 years from South-East Asia (Genner et al. 2004, 2007). This invasive morph is most abundant in the south of Lake Malawi, Lake Malombe and the Shire River (Genner et al. 2004), but is spreading around the lake; live individuals have been collected in June 2005 at Unaka lagoon (12°23′ S, 34°05′ E) indicate it is ranging north. *Melanoides tuberculata* is often an intermediate host of trematode flukes, and prevalence within populations can reach as high 87.5% of individuals (Ben-Ami and Heller 2005).

### Field survey: abundance of gastropods at Cape Maclear

To compare abundance of the invasive and indigenous lineages of *M. tuberculata* we surveyed the gastropod communities at 17 sites around Cape Maclear (Fig. 1) during August 2004. Using snorkel, three replicates of the gastropod fauna were collected from each site from a depth of 4 m. To collect gastropods a hand net (stretched mesh 2.25 mm, square gape 20 cm) was dredged through the top 3–5 cm of sediment for 50 cm (Genner and Michel 2003). Sediment collected inside the net was shaken through the mesh and residual material was sealed in a labelled ziplock bag. All molluscs were identified to species, and *M. tuberculata* individuals were identified as either LMI or LMN.

### Trematode infection and fecundity of *Melanoides tuberculata*

We examined 146 specimens of LMN and 139 LMI collected from Cape Maclear (14°01′51 S,

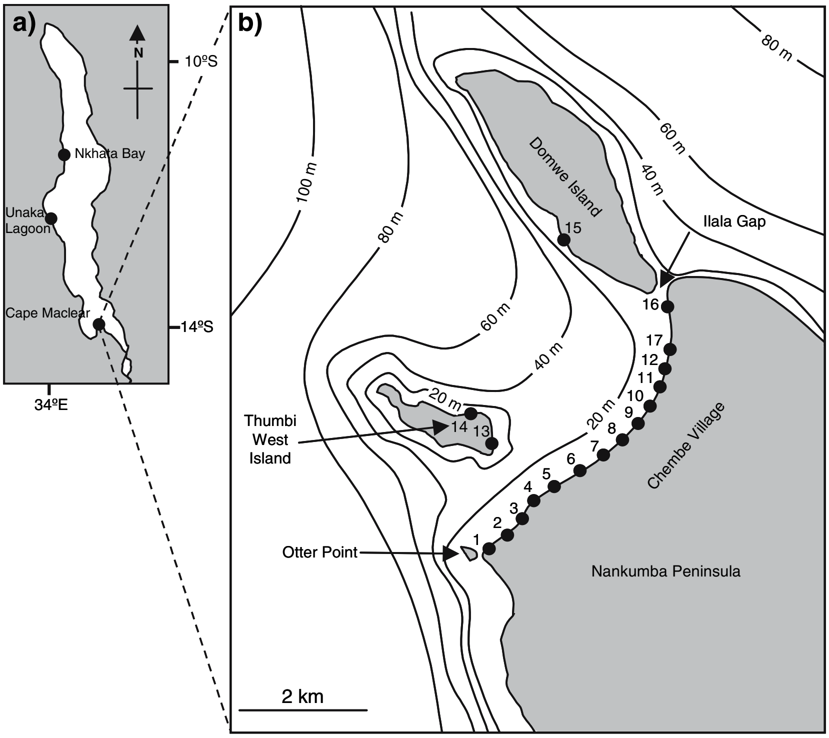


**Fig. 1** (**a**) Lake Malawi; (**b**) Cape Maclear with 20 m depth contour lines and locations of seventeen sites where gastropod abundance was surveyed

34°49′47 E; Site 5 Fig. 1; Table 1) during 2005 and 137 specimens of LMN collected at Nkhata Bay (~11°36′ S, 34°18′ E) during 2002. Each individual was weighed (ethanol wet mass of shell and soft tissue) and the height of each shell was measured using digital callipers. The shell of each

**Table 1** Mean abundance of gastropods (individuals per m$^2$) at each sampling site at Cape Maclear (mean of three samples per site)

| Sampling site | Latitude | Longitude | *Melanoides tuberculata* (LMI) | *Melanoides tuberculata* (LMN) | *Melanoides polymorpha* | *Bulinus nyassanus* | *Bellamya capillata* | *Lanistes nyassanus* | *Gabbiella stanleyi* |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 14°02′19″ S | 34°49′30″ E | 3.3 | 16.7 | 340.0 | 6.7 | – | – | – |
| 2 | 14°02′13″ S | 34°49′34″ E | – | 30.0 | 520.0 | 20.0 | 3.3 | – | – |
| 3 | 14°02′03″ S | 34°49′34″ E | – | 30.0 | 480.0 | 13.3 | 3.3 | – | – |
| 4 | 14°01′55″ S | 34°49′35″ E | 203.3 | 20.0 | 160.0 | 16.7 | 3.3 | – | – |
| 5 | 14°01′51″ S | 34°49′47″ E | 10.0 | 103.3 | 546.7 | 70.0 | – | – | – |
| 6 | 14°01′46″ S | 34°49′47″ E | 293.3 | 76.7 | 30.0 | 10.0 | 6.7 | – | – |
| 7 | 14°01′42″ S | 34°50′07″ E | 136.7 | 103.3 | 310.0 | 110.0 | 10.0 | 3.3 | – |
| 8 | 14°01′35″ S | 34°50′18″ E | 883.3 | 50.0 | 176.7 | 26.7 | 13.3 | 3.3 | 3.3 |
| 9 | 14°01′24″ S | 34°50′28″ E | 4020.0 | 83.3 | – | 6.7 | – | – | 3.3 |
| 10 | 14°01′18″ S | 34°50′37″ E | 3530.0 | 16.7 | 6.7 | 23.3 | – | – | – |
| 11 | 14°01′07″ S | 34°50′47″ E | 520.0 | 76.7 | 1043.3 | 3.3 | – | – | 3.3 |
| 12 | 14°00′59″ S | 34°50′50″ E | 5140.0 | 126.7 | 126.7 | 13.3 | 6.7 | 3.3 | – |
| 13 | 14°01′20″ S | 34°49′25″ E | 496.7 | 56.7 | 13.3 | 26.7 | – | – | 3.3 |
| 14 | 14°01′07″ S | 34°49′10″ E | 20.0 | – | 10.0 | – | – | – | – |
| 15 | 13°59′46″ S | 34°50′15″ E | 20.0 | 10.0 | 226.7 | 6.7 | 10.0 | – | – |
| 16 | 14°00′22″ S | 34°51′00″ E | 23.3 | 20.0 | 110.0 | – | 3.3 | – | – |
| 17 | 14°00′49″ S | 34°50′59″ E | 193.3 | 90.0 | 256.7 | – | – | – | – |
| Mean abundance over all sites | | | 911.4 | 53.5 | 256.3 | 20.8 | 3.5 | 0.6 | 0.8 |
| 95% confidence interval | | | 773.9 | 18.6 | 129.5 | 13.5 | 2.1 | 0.6 | 0.7 |

– indicates absence at the sampling site individual was then broken enabling the individual to be sexed and embryos in brood pouches counted under 10 × magnification. The presence or absence of digenean trematode rediae within gonad and digestive gland tissue was determined by examining tissue compressed between two slides at 40×–100× magnification.

### Trematode identification

Identification of freshwater trematode cercariae and rediae can be difficult using morphological traits alone. To identify the parasite we adopted a DNA barcoding approach. First we amplified a 283 bp section of ITS1 from two infected *M. tuberculata* individuals using the primers ITS HC2 (ATATGCTTAAGTTCAGCGGG) and ITS LC2 (CGAGTATCGATGAAGAACGCAGC) (Navajas et al. 1992). Polymerase chain reaction (PCR) was performed in 25-μl reactions including 1 μl genomic DNA, 2.5 μl 10× PCR buffer, 2.5 μl dNTPs (1 mm); 1 μl each primer (10 mm stock), 1 μl $MgCl_2$ (25 mm stock), 0.5 units SuperTaq (Promega), 1μl bovine serum albumin (20 μg/ml) and 14.9 μl double-distilled water. PCR conditions were as follows: 1 min at 95°C; then 34 cycles of 95°C for 30 s, 43°C for 30 s and 72°C for 1 min, followed by 72°C for 5 min. PCR products were purified, and one clone was sequenced from each using the cloning and sequencing procedure described in Erpenbeck et al. (2002).

The two generated sequences of the unidentified parasites were 283 base-pairs in length, of which two sites were polymorphic. We employed nucleotide-nucleotide BLAST to search Genbank for the 100 closest sequences. All were from digenean trematodes. These data were aligned against an outgroup sequence from the more distantly related trematode *Schistosoma mansoni* and our two unidentified sequences, resulting in a final alignment of 74 sequences of 332 base pairs in length, including 34 genera and at least 55 species. Phylogenetic trees were reconstructed using maximum likelihood in PhyML (Guindon and Gascuel 2003). Prior to analyses, MrModeltest 1.1b http://www.ebc.uu.se/systzoo/staff/nylander.html) was used to determine the best-fitting model of sequence evolution, the GTR + Γ + I model was selected. Branch support was calculated as the percentage of 1000 bootstrap replicates.

## Results

### Field survey: Abundance of gastropods at Cape Maclear

*Melanoides* dominated the gastropod community at all of the seventeen survey sites. *M. tuberculata* morph LMI comprised on average 73.1% of gastropod communities with mean abundance 911.4 $m^2$, *M. tuberculata* morph LMN comprised 4.3% with mean abundance 53.5 $m^2$ while *M. polymorpha* (Smith) comprised 20.6% with mean abundance 256.3 $m^2$. The remaining 2.0% of the communities was made up of *Bellamya capillata* (Frauenfeld), *Bulinus nyassanus* (Smith), *Gabbiella stanleyi* (Smith) and *Lanistes nyassanus* Dohrn (Table 1).

### Trematode infection and fecundity of *Melanoides tuberculata*

Individuals from the introduced morph LMI possessed no trematode rediae, while in the indigenous morph LMN trematode prevalence was significantly associated with body size (Fig. 2). Parasitised individuals of morph LMN were larger in shell height (Cape Maclear, $t = -8.07$, df = 144, $P < 0.001$; Nkhata Bay, $t = -16.07$, df = 135, $P < 0.001$) and weight (Cape Maclear, $t = -11.14$, df = 144, $P < 0.001$; Nkhata Bay, $t = -13.47$, df = 135, $P < 0.001$). All individuals over 26.12 mm and 25.48 mm from Cape Maclear and Nkhata Bay, respectively, were parasitised (Figs. 2, 3). Pooling individuals from both sites for the height range where non-parasitised and parasitised individuals overlap (10.43–26.12 mm), parasitised individuals of morph LMN were heavier per unit shell height than non-parasitised individuals (Homogeneity of Slopes Test on $\log_e x$ transformed data: $F_{1,181} = 6.342$, $P = 0.013$) (Fig. 4). Despite all sampled individuals being female, only 3.7% (2 in 54) and 3.0% (1 in 33) of parasitised LMN individuals possessed embryos at Nkhata Bay and Cape Maclear,

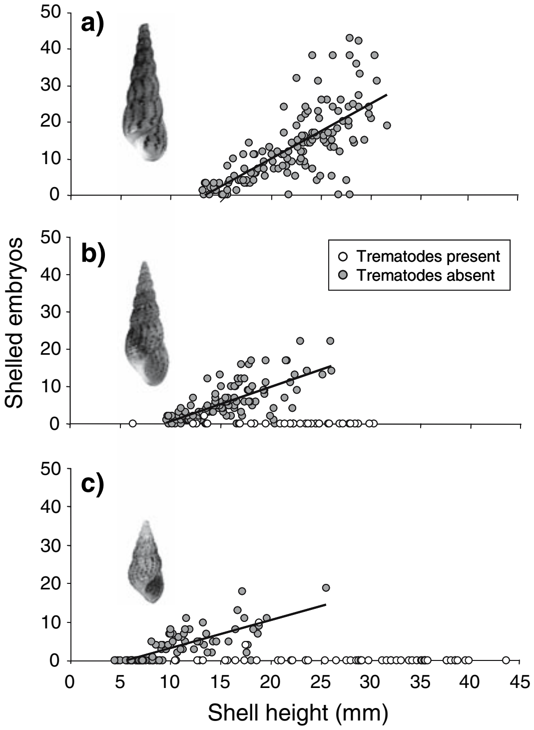


**Fig. 2** Shelled embryos present in brood pouches of parasitised and non-parasitised *M. tuberculata* (**a**) morph LMI Cape Maclear; (**b**) morph LMN Cape Maclear (**c**) morph LMN Nkhata Bay

respectively. Non-parasitised individuals of morph LMN had significant positive relationships between shell height and embryo number (Cape Maclear, $F_{1,111} = 106.79$, $R^2 = 0.49$, $P < 0.001$; Nkhata Bay, $F_{1,81} = 102.62$, $R^2 = 0.55$, $P < 0.001$), and shell weight and embryo number (Cape Maclear, $F_{1,111} = 98.089$, $R^2 = 0.46$, $P < 0.001$; Nkhata Bay, $F_{1,81} = 86.469$, $R^2 = 0.51$, $P < 0.001$) (Fig. 2). Similarly in morph LMI there was a significant positive relationship between shell height and embryo number ($F_{1,137} = 148.77$, $R^2 = 0.52$, $P < 0.001$), and shell weight and embryo number ($F_{1,137} = 115.67$, $R^2 = 0.45$, $P < 0.001$) (Fig. 2).

### Trematode identification

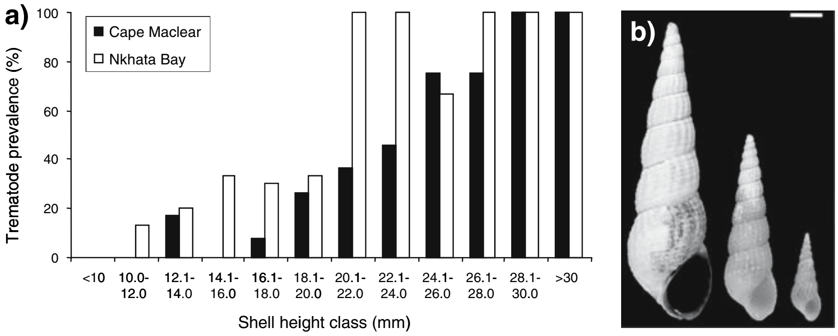
Reconstruction of the molecular phylogeny using the nuclear ITS sequences placed the Lake Malawi digeneans in a clade comprised of Opisthorchiata, and revealed them as a sister lineage to *Haplorchis pumilio* (Looss), a member of the Heterophyidae (Fig. 5).

## Discussion

### Host-parasite co-evolution and competition

At Cape Maclear *M. tuberculata* morph LMI was numerically dominant to the indigenous morph LMN in field samples. This high abundance, combined with the expanding distribution around Lake Malawi, demonstrates that this is a highly invasive lineage. The absence of trematode parasites in morph LMI supports previous phylogenetic evidence that it is new coloniser (Genner et al. 2004). It also suggests that it is missing parasites from its original distributional range, South-East Asia, where trematode infection is commonplace (e.g. Lo and Lee 1996). Trematode parasites have also been found to be absent in other introduced *M. tuberculata* populations, for example the extensively studied introduced *M. tuberculata* morphs on the Caribbean island of Martinique, (Samadi et al. 1997). Thus, absence of trematode infection may be a common feature of invasive gastropods, however there is also evidence to suggest that *M. tuberculata* has

**Fig. 3** (**a**) Prevalence of trematode infection by size class in *M. tuberculata* morph LMN; (**b**) Gigantism in morph LMN at Nkhata Bay, individuals measure 47.6, 29.7 and 14.0 mm in shell height, respectively. Scale bar = 5 mm



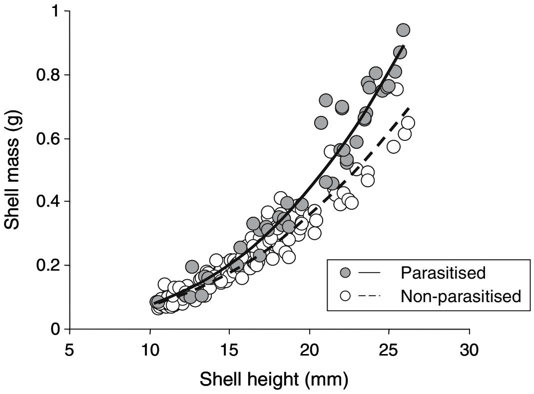


**Fig. 4** Height-mass relationships of parasitised and non-parasitised morph LMN. Data include individuals from both sites from the size range where non-parasitised and parasitised individuals overlap (10.43–26.12 mm). Shell mass is ethanol wet weight of the shell, including the animal

promoted the establishment of heterophyid trematodes on the central American mainland (Scholz et al. 2001).

It has been suggested that non-indigenous taxa should be more susceptible to native enemies than indigenous taxa in the invaded community. This is because invaders may experience bottlenecks that reduce the diversity of genes that promote disease resistance, or because invaders are naïve to native enemies (Colautti et al. 2004). In contrast to these suggestions, our results suggest the invasive morph LMI does not have increased susceptibility to the native parasites. Instead, the absence of trematode parasites in LMI, but prevalence in the indigenous morph LMN, implies that LMI is resistant. Similar resistance of introduced species or genotypes to locally adapted native range trematodes has been recorded in other gastropod-trematode systems (Torchin et al. 2005; Fromme and Dybdahl 2006).

Parasites regulate host population abundance in a broad range of host-parasite systems (Hudson et al. 1998; Albon et al. 2002; Newey and Thirgood 2004), including mollusc-trematode systems (Dillon 2000; Fredensborg et al. 2005). Thus, immunity of introduced morph LMI may provide the lineage with an advantage over the indigenous LMN through greater reproductive output and longevity. Our data show they share habitats, but without abundance data prior to invasion by LMI it is unclear if the LMN population has been significantly affected. Moreover, other factors are also likely to influence competitive outcomes, for example growth rates, body sizes, food utilisation efficiency and interactions with other gastropods including *M. polymorpha*. Field surveys, laboratory assessments of growth and reproduction, and studies of competitive interactions in controlled environments will help to clarify the role of parasites in determining population dynamics of these lineages.

## Trematode identification

Phylogenetic analyses of the sequenced Lake Malawi trematode rediae placed them within a sister lineage to *Haplorchis pumilio*, a member of the Heterophyidae. It is likely that they are either closely related to, or conspecific with, *H. pumilio*. Morphological analyses of adult stages are required to confirm identity. Further study may also reveal a more diverse trematode community within *Melanoides* from Lake Malawi. Nevertheless, this identification is consistent with the known biogeographical distributions and host use of *H. pumilio*. This species has a wide distribution ranging through Africa (Abd el-Kader Saad and Abed 1995) and Asia (Wang et al. 2002), and has recently been introduced into Neotropical America (Scholz et al. 2001). It has a three-stage life history, and has been reported to use thiarid gastropods, including *M. tuberculata*, as first intermediate hosts (Umadevi and Madhavi 1997; Wang et al. 2002), and cichlid fishes as second intermediate hosts (Sommerville 1982; Mahdy and Shaheed 2001). Final hosts include piscivorous birds and mammals (Dzikowski et al. 2004). Cichlid fishes are abundant in Lake Malawi and plausible final hosts are cichlid predators including white-breasted cormorants [*Phalacrocorax carbo* (L.)] and spotted-neck otters (*Lutra maculicollis* Lichtenstein).

## Parasite-induced gigantism

Our results showed that the incidence of parasitism increased with shell size; no LMN specimens with a shell height larger than 27 mm were free from infection and all were sterile. Parasitised snails

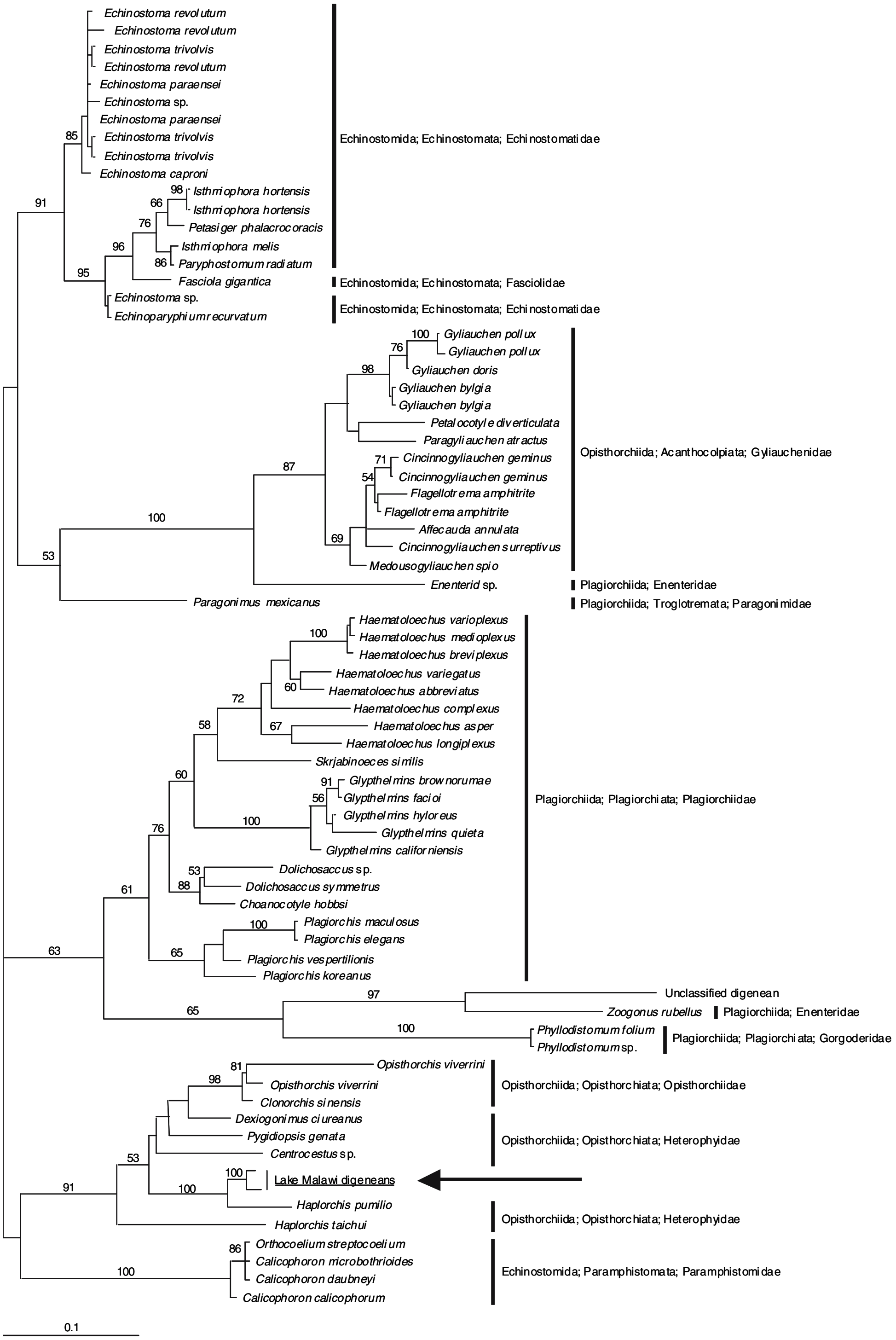


**Fig. 5** Maximum likelihood phylogram of unique ITS sequences closest to the Lake Malawi digeneans revealed from a BLAST nucleotide-nucleotide search on Genbank. Numbers on branches indicate ML percentage bootstrap support, only branches with >50% support are labelled. The Lake Malawi digenean sequences are placed within the Opisthorchiata and form a well-supported clade with *Haplorchis pumilio*. The tree was rooted using a sequence of *Schistosoma mansoni*

were significantly heavier than non-parasitised individuals of equivalent size (Fig. 4), implying that increase is size is not exclusively a consequence of individuals being older and thus having longer exposure to trematode miracidia. Instead, this evidence suggests parasite-induced growth, which has been previously suggested as a consequence of heterophyid infection of *M. tuberculata* (Minchella 1985). Gigantism is thought to take place following castration as a consequence of the diversion of resources used for reproduction into growth (Mouritsen and Jensen 1994; Dillon 2000). This strategy appears to benefit parasites by increasing reproductive output and thus transmission probability to the next host (Ebert et al. 2004). Gigantism may promote this by increasing host tissue mass, but it may also increase the longevity of the host lifespan. In freshwater snails larger body sizes and thicker shells can render individuals less vulnerable to predation (e.g. Seeley 1986). This also seems to be the case in Lake Malawi where the main predators of gastropods are believed to be specialised molluscivorous fish. One of the most common molluscivores is the cichlid *Trematocranus placodon* (Regan), but even large individuals of this species do not consume *Melanoides* larger than 14.6 mm in height (Evers et al. 2006). An alternative perspective on the advantage of gigantism is that it represents a host adaptation selected to promote survival of the host itself; the longer hosts live, the more likely they are to recover from parasite infection and resume reproductive activity (Ballabeni 1995). However this seems unlikely in this system. No parasite-free individuals were present within the largest size classes of LMN (>28 mm shell height; Fig. 3) suggesting hosts never recover from infections.

## Conclusions

Here we provided field evidence that a recent invader is resistant to indigenous parasites. This provides the basis for experimental work investigating how parasites mediate growth rates, fecundity and possibly competition in this system. Studies examining the parasite burden of new colonisers suggest immunity of successful invaders against indigenous parasites may be widespread. For example Torchin et al. (2005) and Krakau et al. (2006) have found the parasite burden of introduced molluscs to be considerably lower than sympatric native molluscs in marine environments. Thus, invasive genotypes may be successful due to widespread indigenous host-parasite adaptation. This fits comfortably with evidence that the most successful invaders are also the most phylogenetically distinct from native taxa (Strauss et al. 2006). However, advantages for parasite-free invaders may not be permanent, as evidence suggests trematode adaptation for new invasive hosts can arise rapidly (Gérard and Le Lannic 2003).

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