University of South Bohemia in České Budějovice
Faculty of Science

Small but diverse: larval trematode communities in the small freshwater planorbids *Gyraulus albus* and *Segmentina nitida* (Gastropoda: Pulmonata) from the Ruhr River, Germany

RNDr. Thesis

Bc. Tereza Vyhlídalová

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Annotation:

This study reveals the importance of small planorbid snails, in particular *Gyraulus albus*, as first intermediate hosts for a species-rich trematode fauna in European freshwater systems, and highlights the parasite contribution to the ecosystem biodiversity.

Declaration [in Czech]:

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I agree with the statement above.

M.Sc. Jessica Schwelm

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ORIGINAL PAPER

Small but diverse: larval trematode communities in the small freshwater planorbids *Gyraulus albus* and *Segmentina nitida* (Gastropoda: Pulmonata) from the Ruhr River, Germany

J. Schwelm[1,2] · M. Soldánová[2] · T. Vyhlídalová[3] · B. Sures[1,4] · C. Selbach[5,6]

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Abstract

In contrast to the well-studied trematode fauna of lymnaeid snails, only little is known about the role of small planorbid snails as first intermediate hosts for trematodes in temperate freshwater systems. This study aims at closing this gap by assessing the diversity and composition of larval trematode communities in *Gyraulus albus* and *Segmentina nitida* in a Central European reservoir system, and by providing an updated comprehensive review of the published trematode records of these snail hosts. A total of 3691 planorbid snails (3270 *G. albus*; 421 *S. nitida*) was collected in three consecutive years from four reservoirs of the River Ruhr catchment area in Germany. *Gyraulus albus* showed a higher overall trematode prevalence (11.7%) and more diverse trematode fauna (12 species) compared to *S. nitida*, which harboured three species and showed a lower trematode prevalence (1.7%). Altogether, 13 trematode species belonging to four families were identified in both hosts. Seven trematode species encountered in this study represent novel records for these hosts, and/or constitute first records of these larval stages from Germany. Trematode component communities in *G. albus* were stable across seasons and years, indicating excellent conditions for trematodes in this snail host and the continuous presence of the final hosts of the most dominant trematode species. Overall, this study reveals the importance of small planorbid snails, in particular *G. albus*, as first intermediate hosts for a species-rich trematode fauna in European freshwater systems, and highlights the parasites' contribution to the ecosystem's biodiversity.

Keywords Planorbidae · Digenea · Parasite diversity · Community composition · Reservoir · Europe

Introduction

Aquatic snails play a central role in the life cycle of digenean trematodes. They serve as first intermediate hosts to the majority of digenean trematodes, which undergo asexual multiplication within the snail and produce free-swimming larval stages, the cercariae. In European freshwater systems, molluscs of the families Lymnaeidae and Planorbidae represent species-rich and abundant snail families and serve as important first intermediate hosts for a broad spectrum of digenean trematodes (reviewed in Żbikowska and Nowak 2009; Cichy et al. 2011; Faltýnková et al. 2016). So far, attention has been focused mostly on lymnaeid snails (e.g. *Lymnaea stagnalis* Linnaeus, 1785, and *Radix* spp.), which are well-studied hosts with respect to their trematode diversity (e.g. Loy and Haas 2001; Faltýnková et al. 2007; Zikmundová et al. 2014; Selbach et al. 2015), and community composition and structure (Soldánová et al. 2010, 2011, 2012; Brown et al. 2011; Soldánová and Kostadinova 2011). In contrast to the data we

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✉ J. Schwelm
jessica.schwelm@uni-due.de

[1] Aquatic Ecology and Centre for Water and Environmental Research, University of Duisburg-Essen, Universitätsstraße 5, 45141 Essen, Germany

[2] Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic

[3] Faculty of Science, University of South Bohemia in České Budějovice, Branišovská 31, 370 05 České Budějovice, Czech Republic

[4] Department of Zoology, University of Johannesburg, PO Box 524, 2006 Auckland Park, Johannesburg, South Africa

[5] Water Research Group, Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa

[6] Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand

find on trematode larvae in lymnaeid snails, datasets on trematode diversity and community composition in planorbid snails in Europe are scarce and fragmentary, apart from general faunistic trematode overviews (Faltýnková 2005; Faltýnková and Haas 2006; Żbikowska 2007; Faltýnková et al. 2008a).

A notable exception is the great ramshorn snail *Planorbarius corneus* Linnaeus, 1785. Most likely due to its large size and widespread distribution throughout Central Europe, *P. corneus* represents the most extensively studied planorbid snail host with respect to infections with larval trematodes (Brown et al. 2011; Faltýnková 2005; Żbikowska 2007; Faltýnková et al. 2008a). Furthermore, outside Europe, most studies on planorbid snails are performed in Africa, Asia, the Middle East and South America, where planorbid snails act as hosts for pathogens of humans, livestock and wild animals (e.g. Ibikounlé et al. 2009; Attwood et al. 2015; Mohammed et al. 2016; Kariuki et al. 2017). Research focuses mainly on planorbids of the genera *Bulinus*, *Biomphalaria* or *Indoplanorbis*, which act as intermediate hosts for *Schistosoma* spp., the infectious agents of schistosomiasis (Morgan et al. 2002). Although there are studies which include the trematode assemblages of small planorbid snail species in Europe, these studies summarise faunistic data from several snail species collected over an extended period of time and which were pooled from different sampling sites (e.g. Faltýnková and Haas 2006; Żbikowska 2007). Moreover, selected population dynamics of the host were described rather than identifying the parasite species (Gérard et al. 2008), or the studies deal with cryptic diversity within an individual trematode genus (Aldhoun et al. 2012; Georgieva et al. 2014; Selbach et al. 2014; Faltýnková et al. 2015).

Beyond these examples, only little is known about the role of small planorbid snails as first intermediate hosts for trematodes in temperate freshwater systems. To fill that gap, this study aims at assessing the diversity and composition of larval trematode communities in the small freshwater planorbids *Gyraulus albus* O.F. Müller, 1774, and *Segmentina nitida* O.F. Müller, 1774, in Central Europe. To the best of our knowledge, this is the first long-term consecutive sampling approach to study the trematode community composition and diversity in the small planorbids *G. albus* and *S. nitida*. Furthermore, we reviewed the available literature to provide an updated comprehensive overview of the trematode fauna in these so far underestimated host species for digenean trematodes.

Material and methods

Sample collection A total of 3691 planorbid snails of two species (3270 *G. albus* and 421 *S. nitida*) was collected and examined for trematode infections during monthly collections in spring (May), summer (June, July, August) and autumn (September) in the consecutive years 2012, 2013 and 2014. Snails were collected in four reservoirs of the River Ruhr catchment area in North Rhine-Westphalia, Germany: Baldeneysee (51° 24′ 20.08″ N, 7° 2′ 22.47″ E), Hengsteysee (51° 24′ 52.17″ N, 7° 27′ 42.55″ E), Hennetalsperre (51°19′50.97″N, 8°15′46.82″E) and Versetalsperre (51° 10′ 55.71″ N, 7° 40′ 57.12″ E) (Fig. 1). Since only few isolated planorbid snails were found in all lakes except Hennetalsperre, the main sampling focus was on this reservoir, where abundant planorbid snail populations occurred. Here, snails were sampled at one site in 2012 and 2013; an additional sampling site was added in 2014 (Fig. 1). All snails were collected by hand and strainer or sieve from

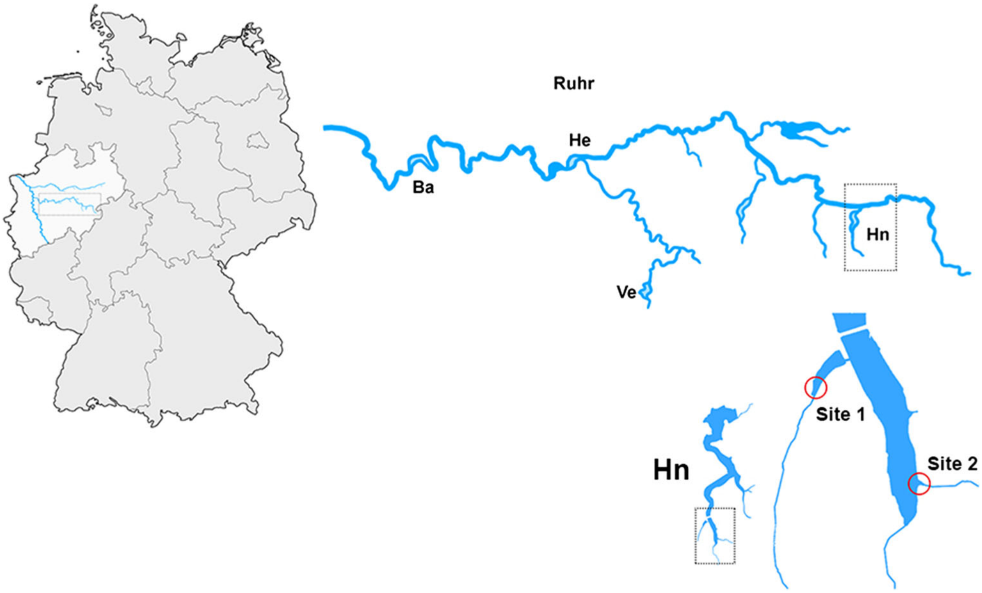


Fig. 1 Map of Germany indicating sampling sites along the Ruhr River system with a detailed map of the two main sampling sites in Hennetalsperre. Abbreviations: Ba, Baldeneysee; He, Hengsteysee; Ve, Versetalsperre; Hn, Hennetalsperre (main sampling sites marked with a circle)

driftwood, stones and floating aquatic vegetation along the shore. In the laboratory, the shell width of all snails was measured following Glöer (2002), and snails were placed in separate containers with filtered lake water under a light source to stimulate cercarial emergence. Snails that did not emit cercariae for several days were dissected and examined for the presence of prepatent infections (sporocysts and/or rediae). Cercariae, sporocysts and rediae were fixed in molecular grade ethanol for DNA isolation and sequencing, and preserved in 4% formaldehyde solution for future morphological analyses.

Morphological analysis Trematode larval stages were identified alive using light microscopy (Olympus BX51). Cercariae were identified to the species level based on the morphological descriptions and the keys of Faltýnková et al. (2008a), Selbach et al. (2014) and Hugghins (1954). Detailed light microscopy photographs of cercariae of all detected species were taken with an Olympus UC30 digital camera attached to the light microscope.

Literature analysis In order to provide an updated overview of the trematodes species in *G. albus* and *S. nitida* in Europe, ISI Web of Science was searched for literature data on trematode infections in these two snail hosts in Europe and the available data was reviewed and compiled. All species classification is according to Gibson et al. (2002), Jones et al. (2005), Bray et al. (2008) and Tkach et al. (2016).

Data analysis Parasite prevalence (p) was calculated for parasite assemblages in *G. albus* und *S. nitida* as the proportion of infected host individuals in relation to the total number of host individuals in a population ($p = n_{\mathrm{inf}} / N * 100$, where n_{inf} is the number of infected snails and N are all snails in a sampled population). Species richness (the total number of parasite species in an assemblage) was calculated to assess the diversity of trematode assemblages.

In order to identify patterns and structure at the trematode component community level (i.e. all parasite species found in one population of one snail species at a certain locality during one sampling trip), temporal and seasonal dynamics and composition of component communities were analysed using Statistica v.7 (Spearman's correlation and ANOVA; StatSoft, Inc., Tulsa, OK, US) and Primer v6 (ANOSIM and SIMPER; Clarke and Gorley 2006). In order to avoid data distortion by small sample size, only samples comprising more than 15 snails were considered as distinct samples and used in the analyses. Trematode component communities found in *S. nitida* were excluded from all analyses due to the low number of infections throughout the study (Table 1). For *G. albus*, a sufficient testable number of communities were available only from Hennetalsperre, leaving a total of 20 and 21 distinct component communities for analyses in Primer and Statistica, respectively (Table 1). Data were transformed in order to meet assumptions for parametric tests. Prevalence, calculated for each snail population sample, was expressed as proportion and arcsin square-root-transformed. Snail size and sample size data were natural-log-transformed and species richness data natural-log $(x + 1)$-transformed. Prepatent infections (sporocysts or rediae) that could not be assigned to a species were excluded from analyses. Due to the generally low prevalence in small planorbid snails, trematode species with a prevalence exceeding 3% in at least one component community were considered dominant.

We used Spearman's rank correlation coefficient (r_s) to test the association between sample size (as a measure of snail density, since the catch per unit effort was comparable during each sampling), mean shell width (as a measure of snail size/age) and overall trematode prevalence as well as the prevalence of the most frequent and dominant trematode species

Table 1 Total numbers of examined snails, overall prevalence of trematode infections (%) and number of samples in the four reservoirs in 2012–2014

		Baldeneysee			Hengsteysee			Hennetalsperre				Versetalsperre			Total
		2012	2013	Total	2012	2013	Total	2012	2013	2014	Total	2012	2013	Total	
Gyraulus albus	No. of snails	5	14	19	2	26	28	1098	830	1289	3217	1	5	6	3270
	Prevalence (%)	0	57.1[a]	42.1	0	7.7	7.1	14.3	13.7	7.8	11.5	100.0[a]	0	16.7[a]	11.7
	No. of samples with snails ≤ 15							6	5	10	21				21
	No. of samples with infected snails							6	4	10	20				20
Segmentina nitida	No. of snails	15		15				127	53	226	406				421
	Prevalence (%)	0		0				1.6	5.7	0.9	1.7				1.7
	No. of samples with snails ≤ 15							3	1	6	10				10
	No. of samples with infected snails							1	1	1	3				3

[a] Sample size small ($n \leq 15$)

present in most communities (Table 2). We also tested the possible correlation between trematode species richness, sample size and mean shell width. We used separate ANOVAs to assess variability in prevalence of infection, species richness and sample size among different seasons (spring, summer and autumn) and years (2012, 2013 and 2014). Since data on snail sizes were available from 1 year, the relationships among trematode prevalence, species richness and mean shell width along with its variation among seasons was examined for 2014 only (10 component communities; Table 1). We used analysis of similarities (ANOSIM) with defined factors ‘year’ and ‘season’ to examine similarity in species composition and structure between pairs of communities by calculation of the Bray-Curtis similarity index. SIMPER analysis was applied to explain which variable contributes most to the dis/similarities in the data.

In all analyses, samples for the factor ‘season’ were grouped as spring (May), summer (June–August) and autumn (September). To avoid a possible effect of the additional sampling site at Hennetalsperre in 2014 on the component community parameters, we first searched for possible differences in a subset of data comprising 10 communities from both sites (five communities each). Infection levels (two-way ANOVA; $F_{(2,\ 4)} = 0.193$, $P = 0.832$), size of samples (two-way ANOVA; $F_{(2,\ 4)} = 3.352$, $P = 0.140$), snail size (two-way ANOVA; $F_{(2,\ 4)} = 0.407$, $P = 0.691$) and species

Table 2 Individual trematode species: overall prevalence (%) per reservoir and year

		Baldeneysee	Hengsteysee	Hennetalsperre				Versetalsperre	Total
		2013	2013	2012	2013	2014	Total	2012	
Gyraulus albus	Diplostomidae								
	Hysteromorpha triloba		3.8	0.6	6.9	0.6	2.24		2.23
	Tylodelphys excavata	7.1[b]							0.03
	Echinostomatidae								
	Cathaemasia hians					0.2	0.06		0.06
	Neopetasiger sp. 1 (Syn. *Petasiger* sp. 1)			0.2	0.1		0.09		0.09
	Neopetasiger sp. 2 (Syn. *Petasiger* sp. 2)			0.1	0.1		0.06		0.06
	Neopetasiger sp. 3 (Syn. *Petasiger* sp. 3)		3.8		0.2	0.1	0.09		0.12
	Petasiger radiatum (Syn. *Paryphostomum radiatum*)	35.7[b]		1.9	2.7	0.2	1.43		1.56
	Schistosomatidae								
	Schistosomatidae gen. sp. 1[a]			0.1			0.03		0.03
	Schistosomatidae gen. sp. 2[a]			0.3		0.2	0.16		0.15
	Strigeidae								
	Apharyngostrigea cornu					0.1	0.03		0.03
	Australapatemon burti			10.7	3.3	6.4	7.03	100[b]	6.94
	Cotylurus sp.	14.3[b]							0.06
	Prepatent infections								
	Echinostome rediae			0.1		0.1	0.06		0.06
	Furcocercariae				0.5		0.12		0.12
	Total	57.1[b]	7.7	14.3	13.7	7.8	11.53	100[b]	11.69
Segmentina nitida	Diplostomidae								
	Hysteromorpha triloba				1.9		0.25		0.24
	Schistosomatidae								
	Schistosomatidae gen. sp. 3[a]			0.8			0.25		0.24
	Strigeidae								
	Australapatemon burti			0.8	1.9	0.9	0.99		0.95
	Prepatent infections								
	Echinostome rediae			1.6	5.7		1.23		1.19
	Furcocercariae				1.9		0.25		0.24
	Total			3.2	11.3	0.9	2.96		2.85

[a] Based on morphological identification; further molecular identification required

[b] Sample size small ($n \leq 15$)

composition of communities were homogeneous among sites and seasons (two-way layout ANOSIM; global $R = -0.037$, $P = 0.800$, and global $R = -0.286$, $P = 0.730$, respectively). Therefore, these two sites were considered as one in the following seasonal and annual temporal community analyses.

Results

Snail populations A total of 3691 small planorbid snails (3270 *G. albus* and 421 *S. nitida*) was collected every 4 weeks during May–September in three consecutive years (2012, 2013 and 2014) at four different reservoirs (Table 1; Fig. 1). *Gyraulus albus* and *S. nitida* were found occasionally in very low numbers at the reservoirs Baldeneysee, Hengsteysee and Versetalsperre. The main sampling focus was on Hennetalsperre, where distinctly more abundant populations of *G. albus* and *S. nitida* occurred. In this reservoir, *G. albus* showed high abundance throughout the years, whereas *S. nitida* could be found in markedly lower quantities (3217 vs. 406 snails, respectively; Table 1). Accordingly, distinctive samples for component community analyses (> 15 snails) were only found for *G. albus* in Hennetalsperre (Table 1).

Populations of *G. albus* were stable over all 3 years at Hennetalsperre. Although the total numbers of sampled snails varied between the years (1094 snails in 2012, 830 snails in 2013 and 1289 snails in 2014) and seasons (476 snails in spring, 2008 snails in summer and 733 snails in autumn),there were no significant differences in sample sizes (as a measure of snail density) of *G. albus* between years and seasons in Hennetalsperre (two-way ANOVA; $F_{(4,\ 12)} = 1.598$, $P = 0.238$), indicating equal density of snail populations throughout the study. Mean snail size in individual communities, reflecting the age of snails, ranged from 3.49 to 5.78 mm in 2014 with generally smaller snails in autumn (mean length 4.15 mm) compared to spring and summer (4.78 and 5.19 mm, respectively). However, differences in snail sizes among seasons were not significant (one-way ANOVA; $F_{(2,7)} = 4.578$, $P = 0.053$). Both sample and snail size of *G. albus* were not associated with overall prevalence ($r_s = 0.276$, $P = 0.226$; and $r_s = -0.321$, $P = 0.365$, respectively), suggesting an effect neither of number of sampled snails nor of mean shell width on the levels of trematode infection.

Larval trematodes in *G. albus* and *S. nitida* A total of 11.7% of all collected *G. albus* had larval trematode infections, while *S. nitida* showed a much lower overall prevalence of 1.7% (Table 1). The overall prevalence in the pooled samples was higher in 2012 and 2013 (14.3 and 13.7%, respectively) compared to 2014 (7.8%) (Fig. 2a). Pooled seasonal samples across the years showed a clear trend of increasing prevalence (2.5% in spring, 11.5% in summer and 17.5% in autumn) (Fig. 2b).

Altogether, 13 different trematode species belonging to four families were identified in both examined hosts (Table 2, Figs. 3, 4, and 5). Five out of these 13 species belong to the family Echinostomatidae. The other eight species represent three families, Diplostomidae, Schistosomatidae and Strigeidae. The populations of *G. albus* were parasitized by 12 species belonging to four trematode families; *S. nitida* was infected with three species belonging to three trematode families. Only two species, *Hysteromorpha triloba* Rudolphi, 1819, and *Australapatemon burti* Miller, 1923, were found in both snail hosts (Table 2). Six prepatent infections (sporocysts or rediae) in *G. albus* and three in *S. nitida* could not be assigned to a certain species. The majority of trematode species (8 out of 13) complete their life cycle in amphibian- and fish-eating birds, and the remaining five mature in anatid birds (Table 3).

Although trematode infections in *G. albus* could be found in all studied lakes, most infections were found at the sampling sites at Hennetalsperre, where the most abundant snail populations were present (Table 1). *Gyraulus albus* populations in Hennetalsperre harboured the most species-rich trematode fauna (10 species) compared with the other reservoirs (1–3 species). Nevertheless, the isolated and small snail populations in Baldeneysee harboured two trematode species (*Tylodelphys excavata* Rudophi, 1803, and *Cotylurus* sp.)

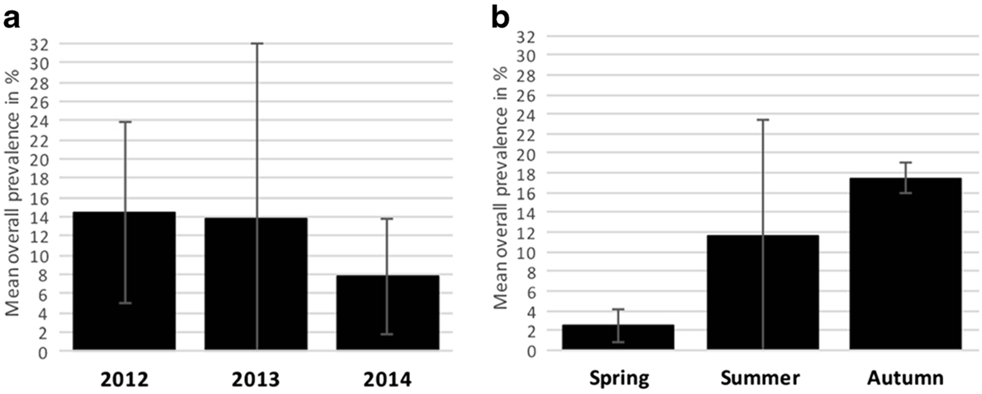


Fig. 2 **a** Annual and **b** seasonal overall trematode prevalence in *G. albus* from Hennetalsperre. Error bars indicate the standard deviation

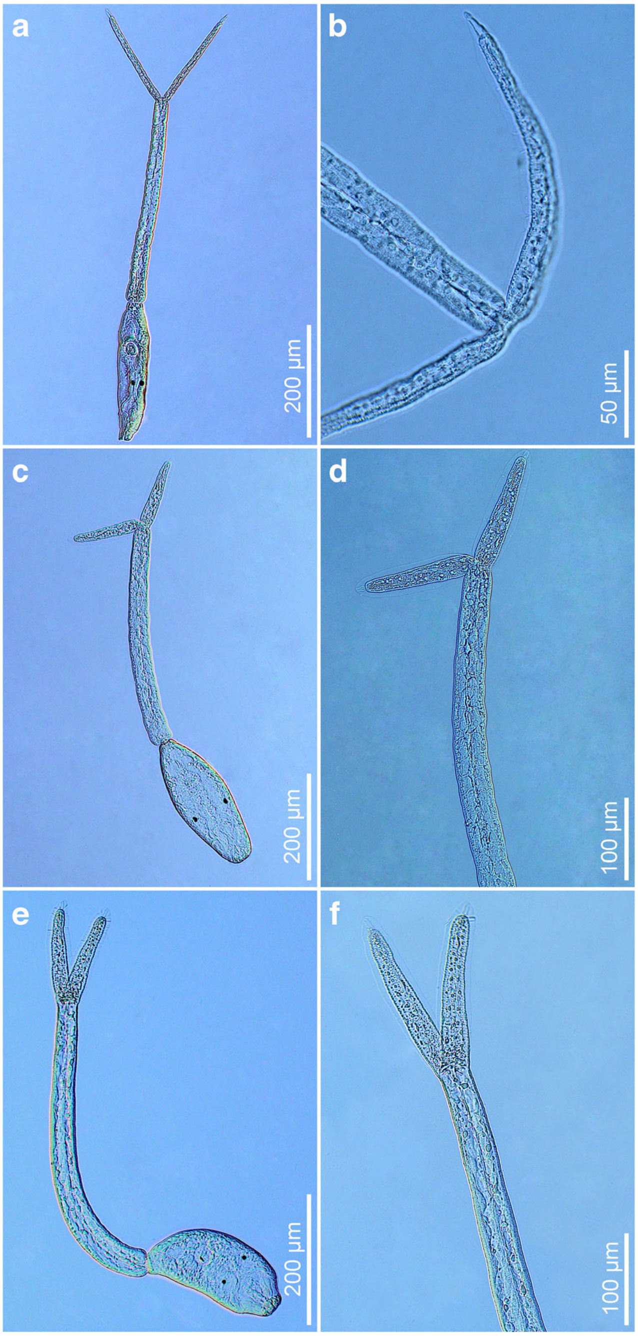


Fig. 3 Microphotographs of live cercariae of the trematode family Schistosomatidae. **a** Schistosomatidae gen. sp. 1., body. **b** Schistosomatidae gen. sp. 1., furcae with finfold. **c** Schistosomatidae gen. sp. 2., body. **d** Schistosomatidae gen. sp. 2., furcae with finfold. **e** Schistosomatidae gen. sp. 3., body. **f** Schistosomatidae gen. sp. 3., furcae with finfold

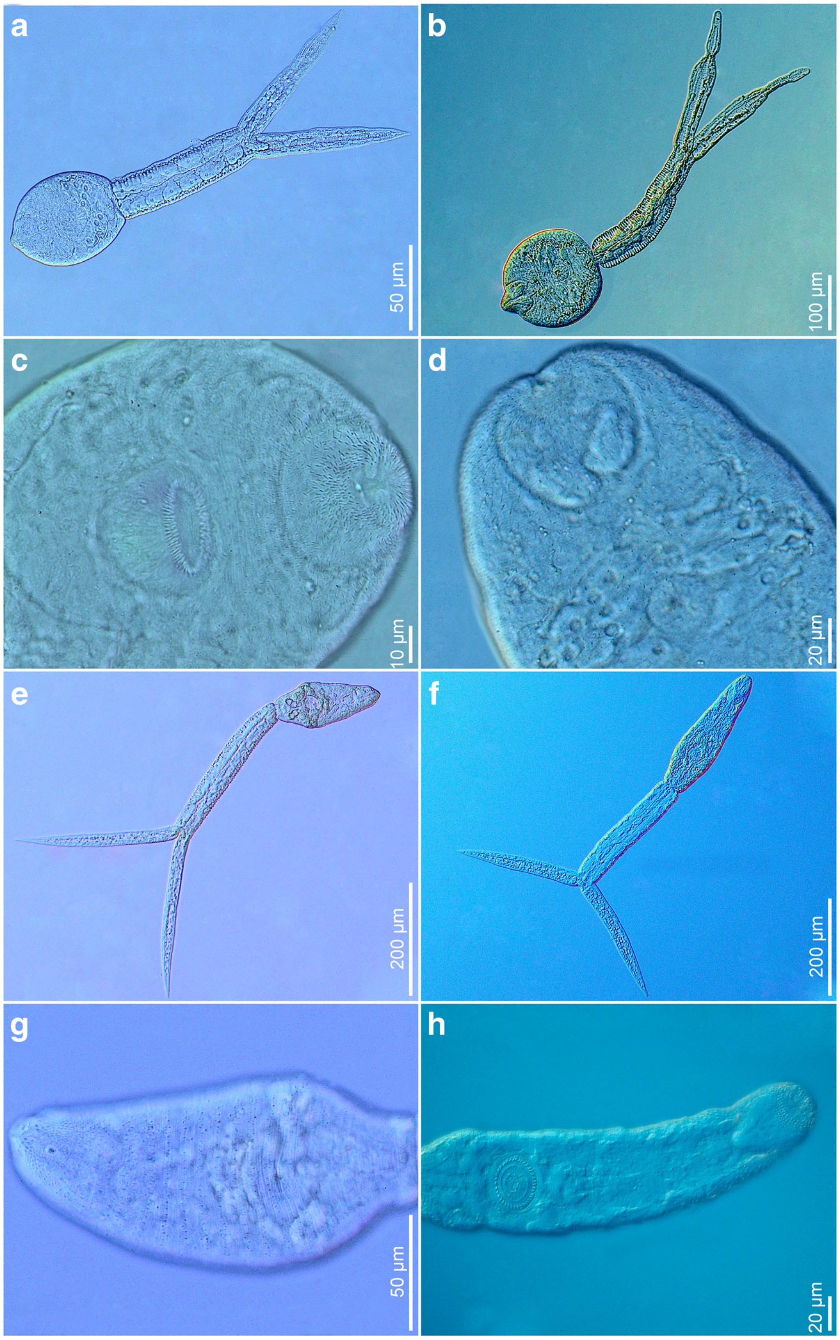
not found in any of the other lakes (Table 2). *Segmentina nitida* only harboured infections in Hennetalsperre (Tables 1 and 2).

Several trematode species found in this study represent novel records for these planorbid snail hosts, and/or constitute first records of these larval stages from Germany (Table 4). Altogether six species from *G. albus* and two species from *S. nitida* represent such new records: *Apharyngostrigea cornu* Zeder, 1800, *Cathaemasia hians* Rudolphi, 1809, *T. excavata* and *Cotylurus* sp. ex *G. albus* and *A. burti* ex *S. nitida* constitute new records for their respective hosts; *C. hians*, *H. triloba*, *Petasiger radiatus* (Syn. *Paryphostomum radiatum* (Dujardin, 1845)) and *Cotylurus* sp. ex *G. albus* and *H. triloba* ex *S. nitida* constitute first records of these larval trematode species from planorbid snails in Germany. Trematode infections of the family Schistosomatidae that could not be identified to species level (Schistosomatidae gen. sp. 1 and Schistosomatidae gen. sp. 2 ex *G. albus*; Schistosomatidae gen. sp. 3 ex *S. nitida*) could either represent further new records or correspond to already described species and are therefore not included in this count. These isolates will require further taxonomic investigation.

Trematode component communities in *S. nitida* comprised only one species each (either *A. burti* or *H. triloba* or Schistosomatidae gen. sp. 3), and were dominated by *A. burti*, a parasite of anatid birds. Prepatent infections with echinostome rediae were found with relatively high prevalence in 2 years (Table 2), but no patent infections were observed during the 3-year sampling. Considering the comparably high prevalence of *P. radiatus* found in *G. albus* in the same years and morphology of rediae distinct from *Neopetasiger* spp., it is possible that these premature infections belong to *P. radiatus*. The low number of trematode component communities from *S. nitida* did not allow further analyses of annual and seasonal structure.

Component communities in *G. albus* comprised one to six species and were dominated by three species (*A. burti*, *H. triloba* and *P. radiatus*). These three species occurred in all examined seasons (spring, summer, autumn) and in all 3 years. No correlation was detected for these species between their prevalence and sample size (*A. burti*, $r_s = 0.197$, $P = 0.392$; *P. radiatus*, $r_s = 0.325$, $P = 0.150$) or snail size (*A. burti*, $r_s = -0.213$, $P = 0.555$; *H. triloba*, $r_s = 0.253$, $P = 0.481$; and *P. radiatus*, $r_s = -0.350$, $P = 0.321$), except for prevalence of *H. triloba* which positively correlated with sample size, indicating higher infection levels in more abundant snail populations ($r_s = 0{,}488$, $P = 0.025$). Although overall annual and seasonal prevalence varied (Fig. 2a, b) and trematode prevalence varied widely between component communities (range 1.4–43.4%), no significant differences in seasonal and annual fluctuations were detected between communities (two-way ANOVA, $F_{(4,12)} = 0.075$, $P = 0.988$). The three most dominant trematode species for which prevalence did not show any significant differences between seasons and years (two-way ANOVA for prevalence of *A. burti*, $F_{(4,12)} = 0.611$, $P = 0.663$; prevalence of *H. triloba*, $F_{(4,12)} = 0.633$, $P = 0.649$; and prevalence of *P. radiatus*, $F_{(4,12)} = 0.335$, $P = 0.849$) are responsible for the general pattern of stable overall prevalence throughout the study (see also results of SIMPER procedure below). Similar to overall trematode prevalence, all three

Fig. 4 Microphotographs of live cercariae of the trematode families Diplostomidae and Strigeidae. **a** *Australapatemon burti*, body. **b** *Apharyngostrigea cornu*, body. **c** *A. burti*, details of body spines. **d** *A. cornu*, details of body spines. **e** *Hysteromorpha triloba*, body. **f** *Tylodelphys excavata*, body. **g** *H. triloba,* details of body spines. **h** *T. excavata*, details of body spines



dominant species followed the same pattern of lower levels of infection in spring with a gradual increase towards autumn. *Australapatemon burti*, with an overall prevalence of 10.7 and 6.4%, was the most dominant species in 2012 and 2014, respectively, while *H. triloba* showed the highest overall prevalence in 2013 (6.9%) (Table 2). *Petasiger radiatus* exhibited similar levels of infection in 2012 and 2013, while distinctly lower in 2014 (Table 2).

The highest trematode species richness in *G. albus* was detected in summer communities (11 species), while comparatively few species were detected in spring and autumn communities (three and five species, respectively). The average number of species per community pooled across years was three species, and two to four species pooled across seasons within each year. The highest number of species was detected once in 2013 with six species, and twice in 2012 with five species. However, no significant differences in species richness between seasons and years were found (two-way ANOVA, $F_{(4,12)} = 0.260$, $P = 0.897$), suggesting stable communities with respect to the number of species detected throughout the study (three species on average). There was a positive correlation between

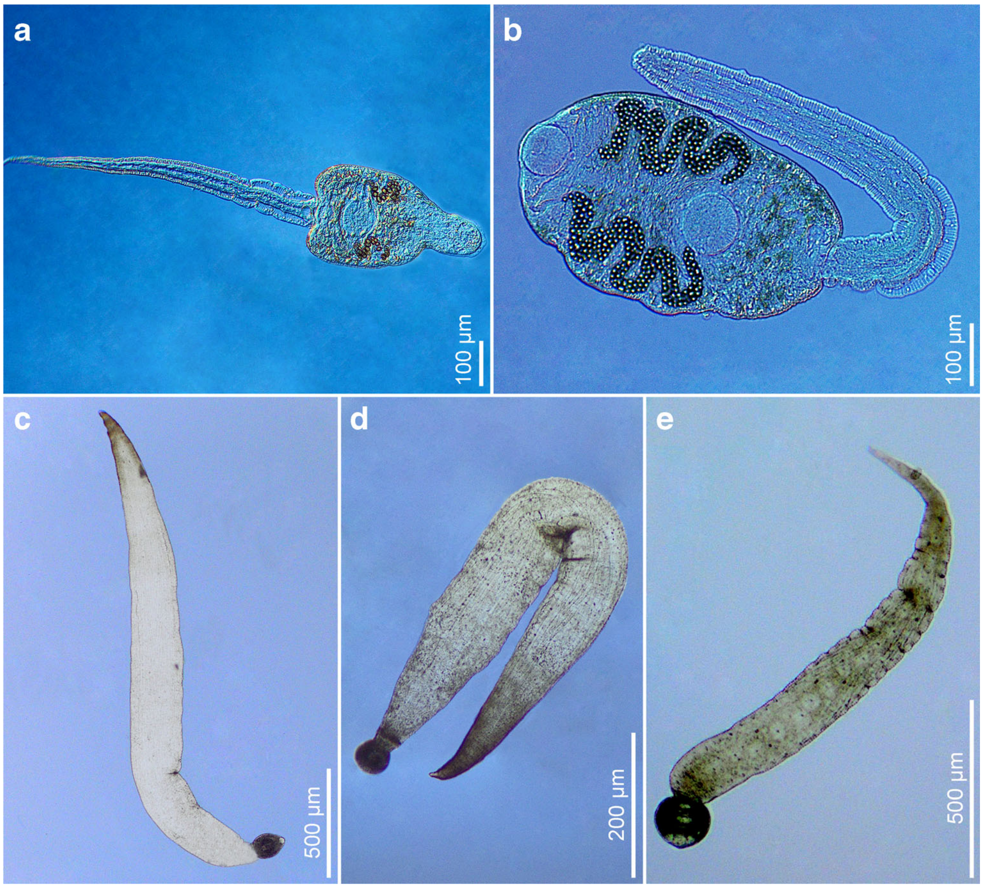


Fig. 5 Microphotographs of live cercariae of the trematode family Echinostomatidae. **a** *Petasiger radiatus*, body. **b** *Cathaemasia hians*, body. **c** *Neopetasiger* sp. 1., body. **d** *Neopetasiger* sp. 2., body. **e** *Neopetasiger* sp. 3, body

species richness with respect to sample size and overall prevalence ($r_s = 0.639$; $P = 0.0018$ and $r_s = 0.770$; $P < 10^{-4}$, respectively), which indicates a higher number of trematode species in more abundant snail populations with higher trematode prevalence. No significant correlation between the number of trematode species and snail size was found ($r_s = -0.157$; $P = 0.625$).

A two-way crossed ANOSIM revealed no significant effects of both ‘year’ and ‘season’ on trematode component community composition in *G. albus* (global $R = -0.247$, $P = 0.917$, and global $R = -0.095$, $P = 0.741$, respectively), indicating similarly homogenous seasonal and annual composition of trematode communities throughout the 3-year study observation. These detected similarities are mainly due to the continuous presence and relatively high prevalence of *A. burti* (Table 2), which occurred in nearly all communities (19 out of 21), with prevalence higher than 3% in eight communities, and exceeding 10% in six communities. Furthermore, *P. radiatus* and *H. triloba* occurred in half of the communities (11 and 9, respectively), however far less frequently, with prevalence higher than 3% in two communities each. In support, the SIMPER analysis revealed nearly half of the similarity (47.5%) between trematode communities in Hennetalsperre based on their species composition. Together, *A. burti* and *P. radiatus* contributed 90.5% (78.6 and 11.9%, respectively) to the similarity of species composition observed in the ecosystem across years and seasons.

Trematode list for *G. albus* and *S. nitida* Table 4 shows the updated list of trematode species for *G. albus* and *S. nitida* in Europe, based on our literature review and the findings of the present study. Altogether, the list comprises a total of 30 trematode taxa in *G. albus* (16 of those to species level) and 20 trematode taxa in *S. nitida* (14 of those to species level).

Discussion

This study examined the diversity and community composition of larval trematodes in the small planorbid snails *G. albus* and *S. nitida*, and provides an updated overview of the trematode diversity in these hosts recorded in Europe. The manmade water bodies of the Ruhr River provide excellent conditions for stable snail populations and diverse and abundant trematode communities in the examined snail hosts. The most abundant snail populations were found at the two sampling sites in the reservoir Hennetalsperre. Consequently, the most species-rich and prevalent trematode communities were discovered in this system. The high abundance of planorbid snails at Hennetalsperre is most likely due to the

Table 3 Trematode species found in this study and their associated hosts

Trematode family and species	First intermediate host	Second intermediate host	Definitive host	Reservoir	Reference
Diplostomidae					
Hysteromorpha triloba	GA, SN	Fishes	Cormorants, Herons, Grebes	Hn, He	Hugghins 1954; Storer 2000; Locke et al. 2011
Tylodelphys excavata	GA	Amphibians	Storks	Ba	Brown et al. 2011
Echinostomatidae					
Cathaemasia hians	GA	Amphibians	Storks	Hn	Brown et al. 2011
Neopetasiger sp. 1 (Syn. *Petasiger* sp. 1)	GA	Fishes	Grebes	Hn	Faltýnková et al. 2008c; Selbach et al. 2014
Neopetasiger sp. 2 (Syn. *Petasiger* sp. 2)	GA	Fishes	Grebes	Hn	Faltýnková et al. 2008c; Selbach et al. 2014
Neopetasiger sp. 3 (Syn. *Petasiger* sp. 3)	GA	Fishes	Grebes	Hn, He	Faltýnková et al. 2008c; Selbach et al. 2014
Petasiger radiatus (Syn. *Paryphostomum radiatum*)	GA	Fishes	Cormorants	Ba, Hn	Brown et al. 2011
Schistosomatidae[a]					
Schistosomatidae gen. sp. 1	GA	–	Anatid birds	Hn	Aldhoun et al. 2012
Schistosomatidae gen. sp. 2	GA	–	Anatid birds	Hn	Aldhoun et al. 2012
Schistosomatidae gen. sp. 3	SN	–	Anatid birds	Hn	Aldhoun et al.(2012
Strigeidae					
Apharyngostrigea cornu	GA	Fishes	Herons	Hn	Navarro et al. 2005; Locke et al. 2011
Australapatemon burti	GA, SN	Leeches	Anatid birds	Hn, Ve	Brown et al. 2011
Cotylurus sp.	GA	Leeches, molluscs	Anatid birds	Ba	Brown et al. 2011

GA Gyraulus albus, *SN Segmentina nitida*, *Hn* Hennetalsperre, *He* Hengsteysee, *Ba* Baldeneysee, *Ve* Versetalsperre

[a] No second intermediate host in the life cycle

characteristics of these sampling sites, which were located in a forebay upstream of the main reservoir. Such forebays act as sediment and debris traps before the water is released into the main reservoir. The large amount of deadwood at the sampling sites provides ideal conditions for small planorbids at these localities that prefer mesotrophic conditions (Costil and Clement 1996).

As reported in previous surveys of trematode infections of planorbid snails in Central Europe (Faltýnková and Haas 2006; Faltýnková et al. 2008a; Faltýnková et al. 2016), trematode prevalence and species richness in most species of small planorbid snails are usually low, as described for *Anisus leucostoma* Millet, 1813, *Anisus vortex* Linnaeus, 1785, *Bathyomphalus contortus* Linnaeus, 1785, and *G. albus* typically showing overall trematode prevalences between 0.4 and 1.8%, and one to seven different trematode species. *Planorbis planorbis* Linnaeus, 1785, and *S. nitida*, the only small planorbids from which relatively high overall trematode prevalences (9.3 and 6.2%, respectively) and species richness (39 and 5 species, respectively) were reported in the surveys, appear to constitute the most important hosts for larval trematodes within the family Planorbidae in Central Europe, alongside the large planorbid snail *P. corneus* (24 species, 35.6%; Faltýnková et al. 2008a, 2016). While the most recent assessment of the biodiversity of trematodes in their intermediate hosts lists a total of four and five trematode species for *G. albus* and *S. nitida*, respectively (Faltýnková et al. 2016), this database only considers records of trematodes identified to the species level. Moreover, it is based on host-parasite records published between 1878 and 2012 and does not include later records (Aldhoun et al. 2012; Selbach et al. 2014; Faltýnková et al. 2015). Our updated list provides a total of 50 records of trematodes (species and genus level identifications) for *G. albus* and *S. nitida* in Europe.

The results of our sampling demonstrate that *G. albus* and *S. nitida* serve as important first intermediate hosts for a diverse trematode fauna in the studied reservoir systems. The total of 13 different trematode species belonging to five families described in this study shows the importance of small planorbids in the Ruhr reservoir system, and in freshwater ecosystems in general. This high overall trematode diversity and prevalence was mainly found in the more abundant *G. albus* populations (12 species, 11.7%). *Segmentina nitida* only harboured three trematode species and showed a low overall trematode prevalence (1.7%).

Table 4 Species composition of larval trematodes for the first intermediate hosts *Gyraulus albus* and *Segmentina nitida* in Europe. Classification according to Gibson et al. 2002; Jones et al. 2005; Bray et al. 2008 and Tkach et al. 2016

Snail species	Trematode species	Comment	Country^a	Literature source
Gyraulus albus	Diplodiscidae Cohn, 1904			
	Diplodiscus subclavatus (Pallas, 1760)		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Diplostomidae Poirier, 1886			
	Alaria alata (Goeze, 1782)		DE	Cichy et al. 2011
	Hysteromorpha triloba (Rudolphi, 1819)	First record from planorbid snails from Germany	RU, DE	Klochkova 1974; Faltýnková et al. 2016; this study
	Neodiplostomum attenuatum (Linstow, 1906)		DE	Cichy et al. 2011
	Tylodelphys excavata (Rudophi, 1803)	New record for snail species	DE	This study
	Echinostomatidae Looss, 1899			
	Cathaemasia hians (Rudolphi, 1809)	New record for snail species First record from planorbid snails for Germany	DE	This study
	Echinostoma nasincovae Faltýnková, Georgieva, Soldánová, Kostadinova, 2015 (Syn. *Echinostoma spiniferum* (La Valette, 1855))		CZ	Našincová 1992; Cichy et al. 2011; Faltýnková et al. 2008a
	Echinostoma sp.		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Neopetasiger sp. 1 (Syn. *Petasiger* sp. 1)		DE	Selbach et al. 2014; this study
	Neopetasiger sp. 2 (Syn. *Petasiger* sp. 2)		DE	Selbach et al. 2014; this study
	Neopetasiger sp. 3 (Syn. *Petasiger* sp. 3)		DE	Selbach et al. 2014; this study
	Petasiger radiatus (Syn. *Paryphostomum radiatum* (Dujardin, 1845))	First record from planorbid snails from Germany	CZ, DE	Cichy et al. 2011; Faltýnková et al. 2008a; Faltýnková et al. 2016; this study
	Haematoloechidae Freitas & Lent, 1939			
	Haematoloechus sp.		CZ	Cichy et al. 2011
	Haematoloechus variegatus (Rudolphi, 1819)		CZ, DE^b	Faltýnková et al. 2008a
	Lissorchiidae Magath, 1917			
	Asymphylodora sp.		CZ	Cichy et al. 2011
	Asymphylodora tincae (Modeer, 1790)		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Leptophallidae Dayal, 1938			
	Paralepoderma sp.		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Notocotylidae Lühe, 1909			
	Catatropis verrucosa (Frölich, 1789)		DE	Cichy et al. 2011; Faltýnková et al. 2016
	Notocotylus ephemera (Nitzsch, 1817)		CZ	Žďárská 1964; Faltýnková et al. 2016
	Notocotylus sp.		CZ	Cichy et al. 2011
	Notocotylus sp. V		RU	Frolova 1975
	Quinqueserialis quinqueserialis (Barker & Laughlin, 1911)		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Schistosomatidae Stiles & Hassall, 1898			
	Gigantobilharzia sp. (Syn. *Trichobilharzia ocellata* (La Valette, 1855))		CZ	Našíncová 1992; Cichy et al. 2011
	Schistosomatidae gen. sp. I1		CZ	Aldhoun et al. 2012
	Schistosomatidae gen. sp. 1^c	?	DE	This study
	Schistosomatidae gen. sp. 2^c	?	DE	This study
	Strigeidae Railliet, 1919			
	Apharyngostrigea cornu (Zeder, 1800)	New record for snail species	DE	This study
	Australapatemon burti (Miller, 1923)		CZ, DE	Cichy et al. 2011; Faltýnková et al. 2008a; this study

Table 4 (continued)

Snail species	Trematode species	Comment	Country[a]	Literature source
	Parastrigea robusta Szidat, 1928		CZ, DE	Combes 1980; Faltýnková et al. 2008a
	Cotylurus sp.	New record for snail species First record from planorbid snails for Germany	DE	This study
Segmentina nitida	Diplodiscidae Cohn, 1904			
	Diplodiscus subclavatus (Pallas, 1760)		CZ, AT, RU, SK, DE[b]	Golikova 1960; Faltýnková et al. 2008a; Faltýnková et al. 2016
	Diplostomidae Poirier, 1886			
	Hysteromorpha triloba (Rudophi, 1819)	First record from planorbid snails from Germany	DE	Klochkova 1974; this study
	Echinostomatidae Looss, 1899			
	Petasiger radiatus (Syn. *Paryphostomum radiatum* (Dujardin, 1845))		CZ	Cichy et al. 2011; Faltýnková et al. 2008a; Faltýnková et al. 2016
	Haematoloechidae Freitas & Lent, 1939			
	Haematoloechus sp.		CZ	Cichy et al. 2011
	Haematoloechus variegatus (Rudolphi, 1819)		CZ, DE[b]	Faltýnková et al. 2008a
	Lissorchiidae Magath, 1917			
	Asymphylodora sp.		CZ	Cichy et al. 2011
	Asymphylodora tincae (Modeer, 1790)		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Leptophallidae Dayal, 1938			
	Paralepoderma sp.		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Notocotylidae Lühe, 1909			
	Catatropis sp.		CZ	Cichy et al. 2011; Faltýnková et al. 2008a
	Catatropis verrucosa (Frölich, 1789)		DE	Cichy et al. 2011; Faltýnková et al. 2016
	Quinqueserialis quinqueserialis (Barker & Laughlin, 1911)		CZ, DE[b]	Cichy et al. 2011; Faltýnková et al. 2008a
	Paramphistomidae Fischoeder, 1901			
	Paramphistomum cervi (Zeder, 1790)		DE	Faltýnková et al. 2008a
	Schistosomatidae Stiles & Hassall, 1898			
	Schistosomatidae gen. sp. I2		CZ	Aldhoun et al. 2012
	Schistosomatidae gen. sp. 3[c]	?	DE	This study
	Strigeidae Railliet, 1919			
	Apatemon gracilis (Rudolphi, 1819)		PL	Cichy et al. 2011
	Apharyngostrigea cornu (Zeder, 1800)		DE	Cichy et al. 2011
	Australapatemon burti (Miller, 1923)	New record for snail species		this study
	Australapatemon minor (Yamaguti, 1933)		CZ, DE[b]	Cichy et al. 2011; Faltýnková et al. 2008a
	Cotylurus brevis Dubois & Rausch, 1950		RU	Cichy et al. 2011; Faltýnková et al. 2016
	Parastrigea robusta Szidat, 1928		CZ, PL, DE	Combes 1980; Faltýnková et al. 2008a; Cichy et al. 2011; Faltýnková et al. 2016

[a] The standard two-letter country code: AT—Austria; CZ—Czech Republic; DE—Germany; PL—Poland; RU—Russia, SK—Slovakia

[b] No clear indication in which of these countries the infection was recorded

[c] Trematode species without molecular identification which can represent new records or concordance with findings of Aldhoun et al. (2012)

? Not identified to species level; further molecular characterisation required

This contrasts sharply with the more dominant role of *S. nitida* and the low infection rates in *G. albus* described in previous studies and surveys from Central Europe (Faltýnková 2005; Faltýnková and Haas 2006; Faltýnková et al. 2008a). The most likely reason for this discrepancy is the different nature of habitats studied. While the data of Faltýnková (2005), Faltýnková et al. (2008a) and Faltýnková and Haas (2006) were derived from small fishponds and standing waterbodies, the present study was undertaken in a large interconnected reservoir system with slowly moving waters. The different habitat preferences of the two snail species described in the literature explains the more abundant *G. albus* populations in the Ruhr River system: *G. albus* has a wide ecological amplitude and tolerates mild pollution, whereas *S. nitida* is more sensitive to pollution and disturbances and prefers shallow, standing water bodies with dense vegetation (Glöer 2002; Watson and Ormerod 2004; Welter-Schultes 2012). Interestingly, a similar relationship was found for trematode communities of *L. stagnalis* and *R. auricularia* sampled from small ponds in the Czech Republic and Poland compared to the Ruhr reservoir system in Germany. While studies registered a poor trematode fauna in *R. auricularia* and a rich one in *L. stagnalis* in small ponds (Faltýnková and Haas 2006; Faltýnková 2005; Żbikowska 2007), Soldánová et al. (2010) observed a reversed faunal richness in the Ruhr reservoir system. As indicated, *R. auricularia* plays a role in the life cycles of trematodes in lakes, similar to that of *L. stagnalis* in ponds (Soldánová et al. 2010). Apparently, these findings are transferable to our study. Thus, in larger, slowly moving and slightly polluted waters, *G. albus* seems to play a dominant role in the life cycle of trematodes, comparable to that of *S. nitida* in small standing waterbodies in Europe.

Even though there is no significant difference in component communities of *G. albus* between seasons, a clear increase in overall prevalence from spring to autumn is apparent. This seasonal trend is in line with other freshwater snail-trematode systems, where highest infection levels usually occur during late summer and autumn (e.g. Brassard et al. 1982; Klockars et al. 2007; Brown et al. 2011; Soldánová et al. 2011). Usually, the probability of infection increases with snail size (Kuris 1990; Faltýnková et al. 2008b), but we did not observe any significant relationship between prevalence and snail size in our dataset. In our case, smaller snails were found in autumn, while comparatively larger snails were found in spring and summer. This pattern is due to the fast reproduction cycle and growth of *G. albus*. First offspring is produced in July and grows quickly through August and September, and produce their own offspring in September (Dussart 1979). Smaller snails in autumn indicate new snail cohorts born in summer, while larger snails in spring represent old snail cohorts born in the previous year. The stable composition of trematode component communities throughout seasons indicates a fast recruitment of trematode infections and a stable and continuous presence of final hosts. Such rapid colonisation patterns by larval trematodes have previously been studied in populations of the large pond snail, *Lymnaea stagnalis* (Soldánová and Kostadinova 2011), where the fast recruitment facilitates inter-specific competition between trematodes that structure the parasite communities (Soldánová et al. 2012). It remains to be tested what structuring role such antagonistic interactions among trematodes might play in small planorbid snails.

The three most frequent and prevalent species across years and seasons were *A. burti*, *P. radiatus* and *H. triloba*. Especially *A. burti* showed a continuously high prevalence across seasons and years. *Australapatemon burti* uses leeches and anatid birds as second intermediate and final hosts, respectively. Both groups are abundant and widespread in the studied area and were constantly encountered during the samplings, showing that ideal conditions for maintaining the life cycle of *A. burti* were present in the ecosystem. *Petasiger radiatus* and *H. triloba*, which develop in fishes and subsequently in fish-eating birds, constitute the second and third most dominant species. Overall, the mesotrophic to eutrophic conditions due to agricultural run-off and the presence of nutrients and food provide a stable habitat for planorbid snails and birds at the sampling sites at Hennetalsperre, which in turn ensures a stable trematode community.

Although the trematode communities were dominated by these three species, which were found in every year of our sampling, new trematode species could still be detected, even in the third year of consecutive sampling. Some of these species, such as *C. hians*, represent new records for small planorbids. In total, we observed six new records in *G. albus* (*C. hians*, *H. triloba*, *T. excavata*, *P. radiatus*, *A. cornu* and *Cotylurus* sp.), and two new records for *S. nitida* (*H. triloba* and *A. burti*). These are either new records for their respective host species, or constitute the first records from planorbid snails in freshwater systems in Germany. The finding of two of these newly reported trematode species, *P. radiatus* and *T. excavata*, from small and patchy snail populations in Baldeneysee underlines the importance of large-scale sampling efforts that include several sampling locations, even where host populations are sparse. Trematode infections that could not be identified to species level (*Cotylurus* sp., Schistosomatidae gen. sp. 1 and 2 ex *G. albus* and Schistosomatidae gen. sp. 3 ex *S. nitida*) but appear to have morphologically distinct cercariae, will require further detailed molecular analyses to determine whether they represent novel species or correspond to already described lineages, such as Schistosomatidae gen. spp. of Aldhoun et al. (2012) from small planorbid snails. Altogether, the detection of new trematode records after several years of consecutive sampling and in small host populations, as well as the potential cryptic species diversity in some groups, highlights the importance of regular long-term sampling approaches to detect relatively rare trematode species.

Due to most trematode species' obligatory multiple-host life cycle, diverse and species-rich trematode communities indicate the presence of a number of other taxa, making trematodes excellent and particularly promising indicators of free-living communities within the ecosystem (Kuris and Lafferty 1994; Huspeni and Lafferty 2004; Huspeni et al. 2005; Hechinger et al. 2007). In many aquatic systems, birds are the most important final hosts for trematodes and sources of larval stages (miracidia) infecting snails (Hechinger et al. 2007). A positive association between trematode diversity and bird diversity and/or benthic communities has been shown for estuarine systems (Hechinger and Lafferty 2005; Hechinger et al. 2007; Byers et al. 2010). Hence, a high diversity of larval trematodes in biotopes indicates a good status of the environment with high abundance and diversity of free-living organisms, so that life cycles of trematodes can be successfully completed (Hechinger et al. 2007). A detailed knowledge about the trematode communities of a certain habitat is therefore of relevance, as it allows to assess the presence of different free-living organisms which serve as second and definitive host for these trematodes in the ecosystem. For example, *T. excavata* and *C. hians* indicate the presence of amphibians and storks, which are used as second intermediate host and final host, respectively. In this instance, trematodes can provide valuable and specific information on the presence of organisms that are of nature conservation interest.

Our findings help to highlight the important role of *G. albus* and *S. nitida* as first intermediate hosts for trematodes in temperate freshwater systems, but also underline the fact that the trematode fauna of small planorbid snails is still understudied and deserves far more attention, as it can reveal important information about parasitic and free-living diversity in aquatic ecosystems.

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Compliance with ethical standards

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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