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Dispersion of nematodes (Rhabditida) in the guts of slugs and snails

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Abstract

A survey was carried out to find non-parasitic nematodes associated with slugs and snails in order to elucidate the initial phase of endophoresis and necromeny in gastropods. 78% of the specimens of the 12 terrestrial gastropod species surveyed carried nematodes. A total of 23 nematode species were detected alive and propagable in gastropod faeces, with 16 different species found in *Arion rufus* alone. Most were saprobiontic rhabditids, with species of *Caenorhabditis*, *Oscheius* and *Panagrolaimus* appearing with some regularity. The nematodes were accidentally ingested with food and survived the passage through the digestive tract, allowing them to be transported to suitable microhabitats such as decaying fruits or fungi. The intestines of snails and slugs taken from hibernation or aestivation were free of nematodes. Seven gastropod species were experimentally infected with eight rhabditid species, all of which were able to persist uninjured in the intestines of the gastropods for two to five days before being excreted with the faeces. A list of nematode species accidentally associated with gastropods is compiled from the literature for comparison. The role of gastropods in spreading nematodes and other small animals (a few observations on rotifers and mites are mentioned) deserves more attention.

Keywords rhabditids | accidental phoresis | endophoresis | necromeny | dispersal | *Phasmarhabditis*

1. Introduction

The finding that bacteriophagous saprobiontic nematodes that were accidentally ingested by gastropods could survive the intestinal passage is of ecological interest. However, also from an evolutionary point of view a better knowledge of these organisms is desirable as they can be regarded as preadapted to closer relationships with gliding transitions to parasitism.

Before Mengert (1953) of the Stammer school started the first systematic survey of nematodes associated with gastropods, various individual records of non-parasitic nematodes in slugs and snails existed. To my knowledge, Cobb (1888), who recorded five free-living and plant-parasitic nematodes (listed in Tab. 1) in the faeces of the edible snail (*Helix pomatia*) in Germany, was the first to notice that nematodes may pass through the digestive tract uninjured. Örley (1886: 30) observed *Poikilolaimus oxycercus* (‘*Rhabditis brevispina*’) in the rectum of slugs and recovered *Rhabditella axei* (= *Rhabditis elongata*) several times on putrefying slugs (p. 32). More than once Maupas (1899, 1919) found the earthworm nematode *Pellioditis pellio* in slugs. Reiter (1928: 59 + 66) noted *Cephaloboides curvicaudatus* and *Rhabditella axei* (= *Rhabditis elongata*) together in the faeces of an unnamed gastropod, and *Pelodera teres* on putrefying gastropods (p. 51). Maupas (1916) found *Rabditis brassicae* (= *sergenti*) on a putrefying limacid. Chitwood & Chitwood (1937) identified two free-living and plant-parasitic nematode species from the intestine of *Philomycus dorsalis* and three from *Polygyra* (*Neohelix*) *albolabris* (listed in Tab. 1). Later, Shinohara (1960) noted a species of the *Rhabditis Maupasi*-group in the alimentary organs of *Limax flavus*. Yasuraoka et al. identified a rhabditid from the snail *Oncomelania hupensis* as *Pelodera cylindrica* (cited from Yokoo

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Table 1. Free-living nematodes accidentally found by various authors in association with gastropods.

slugs	nematode species	n[1]	country	reference
Ambigolimax (*Lehmannia, Limax*) *valentianus*	*Caenorhabditis elegans*	2/313	South Africa	Ross et al. 2012
	Caenorhabditis elegans	15/387	South Africa	Pieterse 2016
	Caenorhabditis elegans	20/761	South Africa	Pieterse et al. 2017a
	Panagrolaimus sp.	1/313	South Africa	Ross et al. 2012
Arion sp.	rhabditid	3/14	USA	Ross et al. 2010
	Caenorhabditis remanei	12/55	Germany	Petersen et al. 2015
	Caenorhabditis elegans	4/55	Germany	Petersen et al. 2015
Arion ater	*Cephaloboides* (= *Curviditis*) sp.	1/68	USA	Ross et al. 2009, 2010
	rhabditid	4/185	Great Britain	Ross et al. 2010
Arion ater (= *empiricorum*)	*Pelodera* '*coarctata*'[2]	1/468	Germany	Mengert 1953
	Pelodera icosiensis	8/468[3]	Germany	Mengert 1953
	Pelodera parateres (= *conica*)	1/468[4]	Germany	Mengert 1953
	Pelodera teres	19/468	Germany	Mengert 1953
	Rhabditis maupasi	8/468	Germany	Mengert 1953
	Rhabditis terricola (= *aspera*)	2/468	Germany	Mengert 1953
	Acrostichus austriacus	3/468	Germany	Mengert 1953
	Panagrolaimus detritophagus	3/468	Germany	Mengert 1953
	Rhabditophanes schneideri	5/468	Germany	Mengert 1953
	Aphelenchoides parietinus	1/468	Germany	Mengert 1953
Arion circumscriptus	*Oscheius dolichura*	2/44	Germany	Mengert 1953
	rhabditid	1/14	Great Britain	Ross et al. 2010
	Pristionchus lheritieri	2/44	Germany	Mengert 1953
	Bunonema reticulatum	1/44	Germany	Mengert 1953
	Panagrolaimus detritophagus	2/44	Germany	Mengert 1953
	Panagrolaimus superbus	1/44	Germany	Mengert 1953
	Rhabditophanes schneideri[5]	3/44	Germany	Mengert 1953
Arion distinctus	*Pelodera* sp.	1/234	Great Britain	Ross et al. 2010
	rhabditid	2/234	Great Britain	Ross et al. 2010
Arion fasciatus	rhabditid	1/5	Great Britain	Ross et al. 2010
Arion lusitanicus	*Caenorhabditis briggsae*	4/194	Germany	Petersen et al. 2015
	Caenorhabditis elegans	4/194	Germany	Petersen et al. 2015
	Caenorhabditis remanei	15/194	Germany	Petersen et al. 2015
Arion owenii	*Choriorhabditis gracilicauda*	1/21	Great Britain	Ross et al. 2010
Arion subfuscus	rhabditid	1/131	Great Britain	Ross et al. 2010
	rhabditid	6/87	USA	Ross et al. 2010
Ariopelta capensis	rhabditid ('*Rhabditis*')	1/1	South Africa	Ross et al. 2012
Deroceras sp.	rhabditid ('*Rhabditis*')	2/258	USA	Gleich et al. 1977
	rhabditid		Australia	Charwat & Davies 1999
Deroceras panormitanum	*Caenorhabditis elegans*	72/1100	South Africa	Pieterse 2016
	Caenorhabditis elegans	80/1636	South Africa	Pieterse et al. 2017a
	rhabditid	1/141	USA	Ross et al. 2010

slugs	nematode species	n[1]	country	reference
Deroceras reticulatum	*Caenorhabditis briggsae*	1/870	USA	Ross et al. 2009, 2010
	Caenorhabditis elegans	10/173	South Africa	Pieterse 2016
	Caenorhabditis elegans	22/429	South Africa	Pieterse et al. 2017a
	Cruznema cf. *tripartitum* (= *Rhabditis* cf. *lambdiensis*)		USA	Arias & Crowell 1963
	Oscheius pseudodolichura	1/177	Germany	Mengert 1953
	Rhabditella axei (= *elongata*)	2/177	Germany	Mengert 1953
	Rhabditis terricola (= *aspera*)	5/177	Germany	Mengert 1953
	rhabditid (‘*Rhabditis*’)	3/69	South Africa	Ross et al. 2012
	rhabditid	9/870	USA	Ross et al. 2010
	Diplogastrellus gracilis	3/177	Germany	Mengert 1953
	Pristionchus lheritieri	6/177	Germany	Mengert 1953
	diplogastrid (‘*Diplogaster*’)	1/581	Great Britain	Ross et al. 2010
	diplogastrid (‘*Diplogaster*’)		USA	Arias & Crowell 1963
	diplogastrid (‘*Diplogaster*’)	2/870	USA	Ross et al. 2009, 2010
	Panagrolaimus superbus[6]	12/177	Germany	Mengert 1953
	Panagrolaimus sp.		USA	Arias & Crowell 1963
Laevicaulis alte	*Caenorhabditis briggsae*	3/26	USA	Ross et al. 2009, 2010
Lehmannia flava	*Caenorhabditis elegans*[7]		Australia	Charwat & Davies 1999
	rhabditid		Australia	Charwat & Davies 1999
	diplogastrid		Australia	Charwat & Davies 1999
Lehmannia (*Limax*) *marginata*	rhabditid (*‘Rhabditis’*)		Egypt	Azzam 2006
	rhabditid	4/332	USA	Ross et al. 2010
	Pristionchus lheritieri	5/7	Germany	Mengert 1953
Limax cinereoniger	*Pelodera teres*	1/27	Germany	Mengert 1953
Limax flavus	*Caenorhabditis elegans*	1/32	South Africa	Ross et al. 2012
	Caenorhabditis elegans	2/66	South Africa	Pieterse et al. 2017a
	rhabditid (*‘Rhabditis’*)		Egypt	Azzam 2006
	Panagrolaimus sp.	2/23	USA	Ross et al. 2010
	Panagrolaimus sp.	1/32	South Africa	Ross et al. 2012
Limax maximus	*Oscheius dolichura*	1/4	Germany	Mengert 1953
	Pristionchus maupasi	1/4	Germany	Mengert 1953
	Aphelenchoides parietinus[8]	1/4	Germany	Mengert 1953
	Caenorhabditis elegans	1/1	Germany	Petersen et al. 2015
	Caenorhabditis remanei	1/1	Germany	Petersen et al. 2015
Malacolimax (*Limax*) *tenellus*	*Caenorhabditis elegans*	2/35	Germany	Mengert 1953
	Pristionchus lheritieri	1/35	Germany	Mengert 1953
	Bunonema reticulatum	1/35	Germany	Mengert 1953
	Panagrolaimus detritophagus	2/35	Germany	Mengert 1953
	Rhabditophanes schneideri	3/35	Germany	Mengert 1953
	Criconemoides informis	1/35	Germany	Mengert 1953
	Plectus cirratus	1/35	Germany	Mengert 1953

slugs	nematode species	n[1]	country	reference
Milax gagates	*Caenorhabditis elegans*	2/112	South Africa	Pieterse 2016
	Caenorhabditis elegans	2/163	South Africa	Pieterse et al. 2017a
	rhabditid		Australia	Charwat & Davies 1999
	Panagrolaimus sp.	1/44	South Africa	Ross et al. 2012
Pallifera dorsalis	rhabditid (‘*Rhabditis*’)	99/225	USA	Gleich et al. 1977
Philomycus dorsalis	*Heterocephalobus elongatus*		USA	Chitwood & Chitwood 1937
	Aphelenchoides parietinus		USA	Chitwood & Chitwood 1932, '34, 1937
snails				
Achatina achatina	*Rhabditella axei*	30/30	Nigeria	Odaibo et al. 2000
	Rhabditella axei	45/45	Nigeria	Olofintoye & Olorunniyi 2016
Archachatina marginata	*Rhabditella axei*	75/75	Nigeria	Odaibo et al. 2000
	Rhabditella axei		Nigeria	Awharitoma & Edo-Taiwo after Olofintoye & Olorunniyi 2016
Archachatina marginata ovum	*Rhabditella axei*	40/40	Nigeria	Olofintoye & Olorunniyi 2016
Archachatina papyracea	*Rhabditella axei*		Nigeria	Awharitoma & Edo-Taiwo after Olofintoye & Olorunniyi 2016
Bellamya unicolor	rhabditid (‘*Rhabditis*’ 2)		Egypt	Azzam & Belal 2006
Biomphalaria alexandrina	rhabditid (‘*Rhabditis*’ 1)		Egypt	Azzam & Belal 2006
	rhabditid (‘*Rhabditis*’ 2)		Egypt	Azzam & Belal 2006
Biomphalaria glabrata	rhabditid (‘*Rhabditis*’ 1)		Egypt	Azzam & Belal 2006
Bulinus truncatus	rhabditid (‘*Rhabditis*’ 2)		Egypt	Azzam & Belal 2006
Cepaea (Helix) hortensis	*rhabditid (‘Rhabditis’)*		USA	Chitwood & Chitwood 1934
	Cephalobus persegnis		USA	Chitwood & Chitwood 1934
Cernuella virgata	*Oscheius sp.*		Australia	Charwat & Davies 1999
	diplogastrid		Australia	Charwat & Davies 1999
	Panagrolaimus sp.		Australia	Charwat & Davies 1999
Cleopatra bulimoides	rhabditid (‘*Rhabditis*’ 2)		Egypt	Azzam & Belal 2006
	Mononchus sp.		Egypt	Azzam & Belal 2006
Cochlicella barbara	*Caenorhabditis elegans*[9]		Australia	Charwat & Davies 1999
Cornu (Helix) aspersum	*Rhabditis ‘maupasi’*[10]		Morocco	Ratanarat-Brockelman & Jackson 1974
	rhabditid *(‘Rhabditis’)*		USA	Chitwood & Chitwood, 1934
	rhabditid *(‘Rhabditis’)*		Egypt	Azzam 2006
	Cephalobus sp.		Egypt	Azzam 2006
	Dolichodorus sp.		Morocco	Ratanarat-Brockelman & Jackson 1974
Discus cronkhitei	rhabditid (‘*Rhabditis*’)	3/412	USA	Gleich et al. 1977
	Criconema sp.	1/412	USA	Gleich et al. 1977
Eobania vermiculata	rhabditid (‘*Rhabditis*’)		Egypt	Azzam 2006
	Diploscapter sp.		Egypt	Azzam 2006
	Cephalobus sp.		Egypt	Azzam 2006
Euconulus sp.	rhabditid (‘*Rhabditis*’)	2/14	USA	Gleich et al. 1977
Helix pomatia	*Choriorhabditis gongyloides*	4/102[11]	Germany	Mengert 1953
	Oscheius dolichura		Germany	Cobb after Chitwood & Chitwood 1937

slugs	nematode species	n[1]	country	reference
	Pelodera teres	12/102	Germany	Mengert 1953
	Heterocephalobus elongatus		Germany	Cobb after Chitwood & Chitwood 1937
	Aphelenchoides parietinus		Germany	Cobb after Chitwood & Chitwood 1937
	Aphelenchoides parietinus	5/102	Germany	Mengert 1953
	Filenchus filiformis		Germany	Cobb after Chitwood & Chitwood 1937
	Tylenchorhynchus lamelliferus		Germany	Cobb after Chitwood & Chitwood 1937
	Plectus rhizophilus	6/102	Germany	Mengert 1953
Lanistes boltenianus (= *carinatus*)	rhabditid (‘*Rhabditis*’ 2)		Egypt	Azzam & Belal 2006
Limicolaria sp.	*Rhabditella axei*		Nigeria	Awharitoma & Edo-Taiwo after Olofintoye & Olorunniyi 2016
Melanoides tuberculata	rhabditid (‘*Rhabditis*’ 1)		Egypt	Azzam & Belal 2006
	rhabditid (‘*Rhabditis*’ 2)		Egypt	Azzam & Belal 2006
Monacha cartusiana	*Diploscapter* sp.		Egypt	Azzam 2006
Monacha obstructa	rhabditid (*‘Rhabditis’*)		Egypt	Azzam 2006
Neohelix (*Polygyra*) *albolabris*	*Mesorhabditis monhystera*		USA	Chitwood & Chitwood 1934, 1937
	Acrobeloides buetschlii		USA	Chitwood & Chitwood 1934
	Acrobeloides nanus (= *minor*)		USA	Chitwood & Chitwood 1937
	Aphelenchus avenae		USA	Chitwood & Chitwood 1934, 1937
‘Opeas’ goodalli	*Mesorhabditis* sp.[12]		USA	Chitwood & Chitwood 1934
Planorbella (*Helisoma*) *duryi*	rhabditid (‘*Rhabditis*’ 1)		Egypt	Azzam & Belal 2006
Planorbella (Helisoma) trivolvis	*Actinolaimus* sp. (dead)		USA	Chitwood & Chitwood 1934
Polgyra thyroides	rhabditid *(‘Rhabditis’)*		USA	Chitwood & Chitwood 1934
Rumina decollata	*Rhabditella axei*		Turkey (impor-ted from USA)	D. Sturhan (pers. comm. 1995)
Striatura sp.	rhabditid *(‘Rhabditis’)*	2/179	USA	Gleich et al. 1977
Succinella (*Succinea*) *oblonga*	*Oscheius dolichura*	3/15	Germany	Mengert 1953
	Pristionchus maupasi[13]	3/15	Germany	Mengert 1953
Theba sp.	*Cephalobus* sp.		Egypt	Azzam 2006
Theba pisana	*Panagrolaimus* spp.		Australia	Charwat & Davies 1999
	Cephalobus sp.		Egypt	Azzam 2006
Triodopsis (Polygyra) juxtidens	*Dorylaimus stagnalis* (dead)		USA	Chitwood & Chitwood 1934
Zonitoides sp.	*rhabditid* (‘Rhabditis’)	88/312	USA	Gleich et al. 1977

1 First number: occurrence of the species. Second number: quantity of investigated gastropod specimens.
2 I question the species identification as Mengert (p. 331) could culture these dung-nematodes quite well on meat.
3 After the text (p. 331) it appears that it was found only once on the cadaver of this slug in a beet field.
4 Found once on a dead slug in the field (p. 331).
5 In the text the author used the synonym *R. quadrilabiatus*.
6 In the text (p. 337) this species is mentioned for *Arion empiricorum* but not for Deroceras.
7 The rhabditid nominated R 954 in that paper could later be identified to *C. elegans* (Kerrie Davies, pers. comm.).
8 According to the text (p. 338) this species was found in the slime of *Limax tenellus* instead of *L. maximus*.
9 The rhabditid R 954 was later identified to *C. elegans* (Kerrie Davies, pers. comm.).
10 Though the species identification was confirmed by J. R. Lichtenfels, I doubt that it was correct. *Rhabditis maupasi* is a characteristic associate of earthworms. It was often named incorrectly *Rhabditis pellio* (now *Pellioditis*), and from ecology here a species of *Pellioditis* would be more likely. Voucher specimens have not been deposited in Beltsville (Z. Handoo, pers. comm.).
11 Somewhat contradictory to these data is that this author (p. 332) says she found this species once on a *Helix pomatia* from a terrarium.
12 The authors say *Rhabditis monhystera* juvenile.
13 The author reported also *Pristionchus lheritieri* associated with this snail species (p. 338).

& Okabe 1968), though if the given number of nine rays in the male is correct this identification must be doubted. Without reference, but probably on the basis of findings by Arias & Crowell (1963) for *Deroceras reticulatum*, Godan (1983: 43) mentioned *Cruznema tripartitum* (= *Rhabditis lambdiensis*), '*Diplogaster*' and *Panagrolaimus* in association with *Deroceras reticulatum* and *D. laeve*. Cook et al. (1989) showed that *D. reticulatum* could disseminate ingested *Ditylenchus dipsaci.* In a survey of gastropods in California De Ley et al. (2014, 2017) isolated *Caenorhabditis elegans, C. briggsae, Oscheius dolichura, O. tipulae, Koerneria* sp., *Protodiplogasteroides* sp. and *Pseudodiplogasteroides* sp. An interesting relationship might be hidden behind the association between 'Rhabditoidea' and the snail *Assiminea grayana* in the supralittoral zone of Brazil (Marcus & Marcus 1963).

Most of these random findings indicate that various free-living and plant-parasitic nematodes are ingested by gastropods with their food and can pass through their digestive tract uninjured and thus be disseminated. This was the point at which our investigation started.

2. Material and methods

Gastropods from different locations and habitats were efficiently cleaned under running water to remove any adhering nematodes. They were then placed on moist paper towels inside little plastic boxes with ventilation holes, provided with nematode-free food (cucumber slices, fresh lettuce, different types of vegetables, apple) and water ad libitum, and kept at room temperature. The gastropods were transferred daily to a clean box. Their faeces were collected, mixed with tap water and spread out on agar in a petri dish. These samples were investigated daily with a dissecting microscope for one to three weeks for the presence of living nematodes and other small animals that sometimes founded new populations on this substratum. The nematodes were microscopically identified as specifically as possible.

38 actively feeding specimens of seven gastropod species (*Arianta arbustorum, Arion rufus, Cepaea nemoralis, Cornu* (*Helix) aspersum, Deroceras* sp., *Helix pomatia* and *Limax maximus*) were used in infection studies and exposed to definite nematode species from cultures. These gastropods were kept for longer in the laboratory to ascertain that they were not already excreting nematodes with their faeces. In most cases a culture of nematodes on agar in a small petri dish was covered with a thin slice of cucumber so that the gastropod eating the cucumber would also eat some of the agar and ingest the nematodes on its surface. As snails like *Helix pomatia* mostly refused this food, pieces of lettuce, Chinese leaves or pureed carrots inoculated with nematodes were used instead. It was possible to infest *Cepaea nemoralis* by adding nematodes to their drinking water.

As soon as the gastropods started to become active in the late afternoon or evening, their feeding behaviour was stimulated by spraying them with lukewarm water before they were placed in a box containing bait prepared with a special nematode culture. It was ensured by observation that the gastropods were actually feeding from the bait. By feeding coloured vegetables such as red peppers, tomatoes and carrots we were able to establish that passage through the intestines took 14 – 18 hours. After 17 – 24 hours, then, the gastropods were cleaned under running water to remove any nematodes that may have been attached and transferred to a new box containing plenty of food. Each gastropod was cleaned and transferred to a new box every day for six days, and the faeces produced were examined daily for two weeks. Nematodes from the faeces were investigated microscopically.

The following eight species of 'Rhabditidae' were utilised in the infection trials (their strain number is given): *Caenorhabditis remanei* (Sudhaus, 1974) SB111 and SB146*, Mesorhabditis irregularis* (Körner in Osche, 1952) SB321, *Pelodera strongyloides dermatitica* (Sudhaus & Schulte, 1988) SB204, *Poikilolaimus micoletzkyi* Fuchs, 1930 SB352, *Poikilolaimus oxycercus* (de Man, 1895) DF5206, *Reiterina typica* (Stefański, 1922) SB405, *Teratorhabditis palmara* Gerber & Giblin-Davis, 1990 DF5019, and a species of the *Oscheius Insectivora*-group JU761.

3. Results

3.1 Surveys of nematodes associated with terrestrial gastropods

In looking for *Pellioditis* I examined the faeces of slugs and snails and killed and dissected slugs to see whether nematodes developed on the cadavers (Tab. 2). 70 slugs and 2 snails were investigated in total (37 *Arion*, 7 *Deroceras*, 16 *Limax*, 2 *Helix*, 1 *Lehmannia*, 9 slugs of unknown genus). Nematodes were found in only 54% of the gastropods. The percentages varied with respect to the gastropod species and the habitats. Most nematodes came from the intestine, but a few specialists such as *Alloionema* and *Pellioditis* were able to invade the body tissue and were frequently detected developing on the cadaver (Tab. 2). These 'slug nematodes' are not specialised for specific slug taxa, although *Alloionema* was only recorded from *Arion*.

With these preliminary results in mind, we started an investigation specifically to document the transportation of saprobiontic nematodes in the intestine of gastropods (Bretschneider 2007). The faeces of 156 specimens of 12 gastropod species were examined. (To the 148 investigated specimens of 10 gastropod species listed in Tab. 3, four *Cornu aspersum* and four *Succinea putris* must be added, where no nematodes were found in the faeces.) In these 156 gastropods at least 23 nematode species were detected (Tab. 3). The highest number of different species isolated from one gastropod was four. At least 35 gastropods did not excrete any nematodes. So 78 % of the specimens investigated contained non-parasitic nematodes. The proportion of nematode-containing individuals differed from species to species and habitat to habitat. 16 was the maximum number of nematode species documented from one gastropod species (*Arion rufus*) (Fig. 1). Typical associates of gastropods were found in only a few cases (*Alloionema appendiculatum* 8 times, *Pellioditis hermaphrodita* 2 times). It is striking that in this survey in comparison with the previous sample (Tab. 2) *Pellioditis papillosa* was missing. The most commonly occurring nematodes were saprobiontic rhabditids that must have been ingested with decomposing substances. Species of *Panagrolaimus* and the *Oscheius Dolichura*-group (perhaps *O. tipulae*) were the most frequently represented, occurring in various gastropod species. The aphelenchids, tylenchids, plectids, mononchids and dorylaimids (at the end of Tab. 3) indicate that moss, algae and soil were consumed by the gastropods, as does the presence of certain other small animals such as rotifers (found several times in faeces of *Arion rufus, Limax maximus, Arianta* and *Cepaea*), Oribatidae and other mites, Collembola, various protists and even a small snail in the faeces of *Arion rufus*. Like the nematodes, all these animals survived the rasping of the radula and the intestinal passage, and were thus able to be dispersed.

In the faeces of four specimens of *Helix pomatia* and two *Cepaea nemoralis* sealed with an epiphragm when collected in winter rest in January 2007, no nematodes were observed after food intake in the laboratory. The same happened with ten specimens of *Arion rufus* that were awaked in the laboratory after being collected in summer rest from a hiding place in moss in July 2006.

Table 2. Casual records of nematodes in slugs over 45 years. Most records were from Freiburg (Germany) and its surroundings. First number: nematode species present. In parenthesis: number of samples.

	Arion rufus	***Arion ater***	***Arion* sp.**	***Deroceras* sp.**	***Limax cinereoniger***	***Limax maximus***	***Limacidae* genus?**	***Lehmannia marginata***	**small slugs; genus?**
from the body of the slug (including the intestine)									
specimens with nematodes (in parenthesis number of samples)	12 (17)	6 (9)	3 (11)	3 (7)	8 (10)	6 (6)	3 (7)	1 (1)	2 (2)
number of nematode species	4-5	2	~6	2	4	1	2	1	2
Alloionema appendiculata	2	4	1						
Pellioditis papillosa	2		1	1	8			1	
Pellioditis hermaphrodita	2								2
Caenorhabditis remanei	1								
Panagrolaimus			1				1		1
not identified		1	1	2					
from the faeces of the slug									
Alloionema appendiculata		1 (1)	2 (6)						
Pellioditis papillosa				1 (2)	1 (6)				
Rhabditis cf. *terricola*			1 (6)						
Rhabditis cf. *maupasi*					1 (6)				
Oscheius Dolichura-group						1 (1)			
Panagrolaimus							1 (3)		
Cephalobidae			1 (6)				2 (3)		
Plectus sp.					1 (6)				
not identified	1 (2)		2 (6)		2 (6)				

This could mean that the gastropods had emptied their intestines as far as possible before entering dormancy, or that individual nematodes were not able to survive such a long period and were not able to propagate in the intestine either. This would imply that saprobiontic nematodes do not hibernate and cannot bridge an extended period of drought in the gastropod intestine. However, in the faeces of five *Cepaea nemoralis* found on a wire fence approx. 1 m high which were awaked from an aestivation period of unknown length, four different nematode species were recorded (*Diploscapter coronatus, Oscheius Dolichura*-group, *Panagrolaimus* cf. *rigidus, Plectus*).

Table 3. Nematodes found in faeces of gastropods mostly in Berlin. Minimum numbers of documented species are given (as gastropods were sometimes kept more than one to a box).

	Arion rufus	***Arion ater***	***Arion* cf. *fasciatus***	***Limax maximus***	***Deroceras* sp.**	***Helix pomatia***	***Arianta arbustorum***	***Cepaea nemoralis***	***Aegopinella* sp.**	***Discus ruderatus***
specimens with nematodes (in parenthesis: number of specimens examined)	23 (29)	1 (1)	? (5)	1 (6)	1 (4)	18 (24)	<12 (13)	<47 (~55)	? (10)	1 (1)
minimum number of nematode species documented[14]	16	3	5	1	1	3	7	9	3	1
Alloionema appendiculatum	7		>1							
Caenorhabditis sp.	3						>3			
Caenorhabditis elegans	1						1			
Caenorhabditis remanei	2				1					
Diploscapter cf. *coronatus*								>1		
Mesorhabditis cf. *monhystera*	1									
Mesorhabditis spiculigera								>1		
Oscheius Dolichura-group	5		>1			4	1	>6		1
Oscheius tipulae						1[15]				
Oscheius cf. *tipulae*							>1			
Oscheius Insectivora-group	1									
Oscheius cf. *wohlgemuthi*								>1		
Pellioditis hermaphrodita	1		>1							
Rhabditis sp.	1			1				>1		
'tube waving' rhabditid	1									
Diplogastrellus gracilis							1			
Pristionchus sp.		1	>1							
Cephalobidae genus?	1									
Acrobeloides buetschlii							>1			
Panagrolaimus sp.	6					8	>2	>8	>1	
Panagrolaimus cf. *rigidus*						4		>2		
Rhabditophanes sp.			>1							
Aphelenchidae genus?	1									
Aphelenchus avenae	1									
Tylenchidae genus?	1							>1		
Plectus sp.	1	1					>1	>2	>1	
Mononchidae genus?		1							>1	
Dorylaimidae genus?							>1			
not identified	2					1		1		

[14] *Panagrolaimus* sp. and *P.* cf. *rigidus* might be the same, just as species of the *Oscheius Dolichura*-group and *O.* cf. *tipulae* (or *O. tipulae*) and *Caenorhabditis* sp. and *C. elegans*.

[15] Confirmed with sequence data by K. Kiontke (pers. comm.).

3.2 Infection attempts

Infection experiments using well-known rhabditid species were performed to find out whether the species in question could survive the intestinal passage, and if so, for how long they could stay alive in the intestine. Various cultured rhabditids were used, none of which were recorded from gastropods in the field except *Caenorhabditis remanei* and perhaps the species of *Oscheius.* For reasons unknown, *Arianta arbustorum* and *Deroceras* sp. could not be infected. The other five species of gastropods were successfully infected with nematode species they never usually come into contact with under natural conditions. Nematodes were recorded in the faeces of 25 of the 38 gastropods used in the infection experiments. In most gastropods the ingested nematodes only survived for two days. After five days the percentage of gastropods excreting viable nematodes declined to zero (Fig. 2). It was not determined which ontogenetic stages survived the intestinal passage.

The duration of survival in the gastropod gut differed between the nematode species tested (Fig. 3): *Poikilolaimus micoletzkyi* survived for 1 day, *Poikilolaimus oxycercus* and *Teratorhabditis palmara* for 1–3 days, *Mesorhabditis irregularis* and *Reiterina typica* for 2–3 days, *Pelodera strongyloides* for 2–4 days and *Caenorhabditis remanei* and *Oscheius* sp. for 2–5 days. Apparently it is not by chance that the last two taxa which survived up to 5 days in the gastropod intestine were known from natural infections. In infection experiments conducted by Shinohara (1960) in which *Fruticicola sieboldiana* snails were exposed to a nematode he called *Rhabditis inermis*[1], the nematode was present in faeces after 12 hours, but no longer after 24 hours. Although our experiments did not involve *Panagrolaimus,* nematodes of this taxon were sometimes egested for 2–3 days by field-collected *Helix pomatia*. In one case *Panagrolaimus* did not appear until the fourth day, and *Oscheius* even took 10 to 21 days to appear in faeces.

4. Discussion

4.1 A nomenclaturial note

There is a large body of literature on nematodes called *Phasmarhabditis* because some species are promising agents for controlling slugs. The clade *Pellioditis* Dougherty, 1953 (= '*Papillosa-group*'), whose type species is *P. pellio,* includes *P. papillosa,* the type species of *Phasmarhabditis* Andrássy, 1976. Therefore, *Phasmarhabditis* is a junior synonym of *Pellioditis* (Sudhaus 2011). However, Andrássy (e.g. 2007) in his influential books ignored the cladogram of the *Papillosa*-group put forward by Sudhaus (1976) and excluded *P. pellio*, which caused some confusion. The following sentences in a new species description are symptomatic: 'The nomenclature "*Pellioditis*" has priority over "*Phasmarhabditis*", however, both generic names assigned to a synonymous group of rhabditids were simply indicative of diverse perspectives of revisions by Sudhaus and Andrássy respectively. To avoid taxonomic confusion, the new species is herein named as *Phasmarhabditis huizhouensis* sp. nov.' (Huang et al. 2015: 2; nearly in the same words in Pieterse et al. 2017b). By no means the synonymy of both genus taxa is rejected by Nermut' et al. (2016), which in their molecular

[1] On the basis of the photo on p. 2815 I have doubts that the identification was correct.

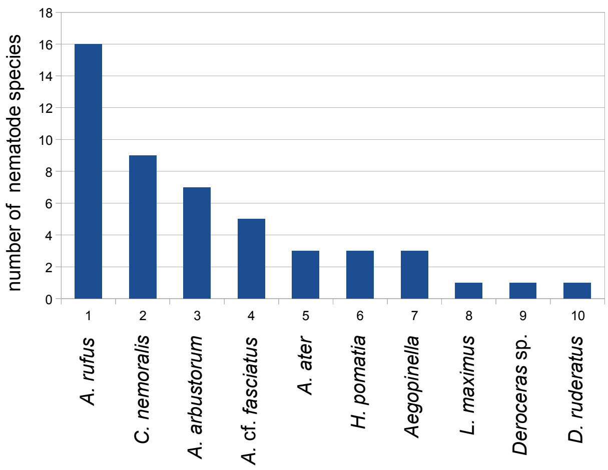

Figure 1. The minimum number of nematode species documented in the ten gastropod species investigated: *Arion rufus, Cepaea nemoralis, Arianta arbustorum, Arion* cf. *fasciatus, Arion ater, Helix pomatia, Aegopinella* sp., *Limax maximus*, *Deroceras* sp., and *Discus ruderatus.*

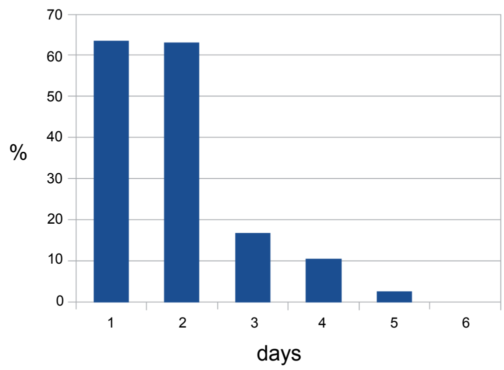

Figure 2. Percentage of 38 gastropods of 7 species that excreted viable nematodes in their faeces over five days after infection, declining from 64% in the beginning to 3% on day five and then to zero.

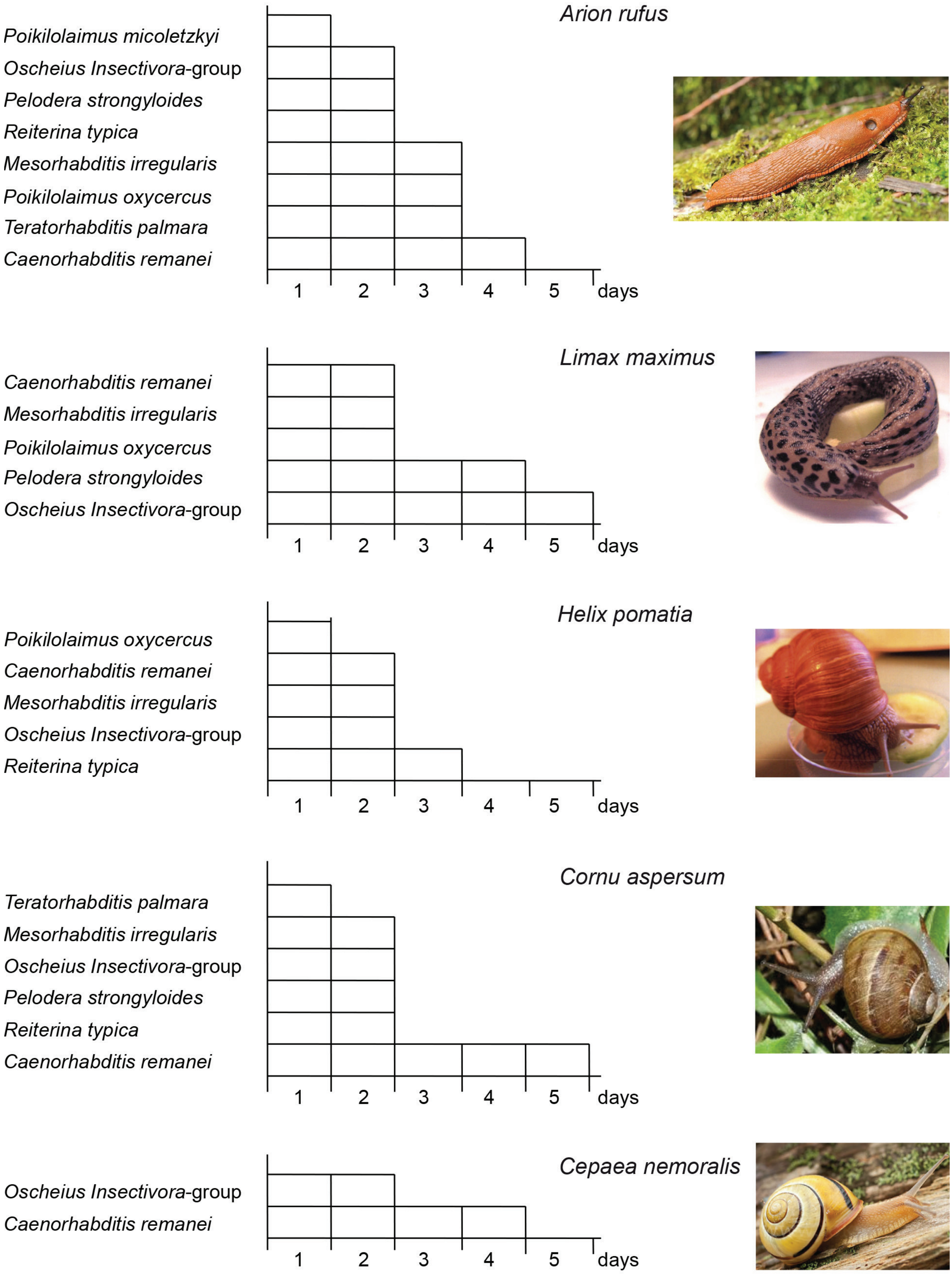

Figure 3. Egestion of different rhabditids by five gastropod species in the days after experimental infection.

analysis compare species of the *Papillosa*-group with two species of *Litoditis* (formerly members of the *Pellioditis Typica*-group of Sudhaus 1976) instead of *Pellioditis pellio.* According to nomenclaturial rules, however, the name of the *Papillosa*-group must remain *Pellioditis* as long as the monophyly hypothesis of this group has not been falsified. – If we regard the amount of literature in which the name *Phasmarhabditis* has appeared in the last 25 years as a putative problem, the situation is comparable to when *Neoaplectana* was shown to be a junior synonym of *Steinernema* by Wouts et al. (1982).

4.2 Comparison with other surveys

While larval-parasitic and/or necromenic *Alloionema appendiculatum, Pellioditis hermaphrodita* and *P. papillosa* have long been recorded in association with putrefying slugs (Schneider 1866 and others) and sporadic records of free-living and plant-parasitic nematodes have existed since Cobb (1888) (see introduction), systematic surveys of gastropod associates began very late. Investigating 1277 gastropods of 22 species in Germany, Mengert (1953) found 23 different nematode species that can be classified as accidental (Tab. 1). Most live in compost-like material, a few in the soil. Mengert thought that these nematodes were attached to the slimy gastropod body, though she once observed a *Pelodera teres* female alive and pregnant in the stomach of a slug (*Limax cinereoniger*). However, in the light of our results it is likely that most of the observed species came from the intestine. Examining 1700 gastropods of 25 different species in the USA, Gleich et al. (1977) found rhabditids which they called '*Rhabditis*' (almost always juveniles) in 6 different gastropod species, and one adult *Criconema* in *Discus cronkhitei.* During parasitological investigations in Great Britain, Ross et al. (2010) examined 1469 slugs of 23 species and found one species each of *Choriorhabditis, Pelodera* and Diplogastridae. The same authors surveyed 2126 slugs of 18 species in the USA and detected *Caenorhabditis briggsae, Cephaloboides* sp., juvenile rhabditids and *Panagrolaimus* sp. (Tab. 1). In South Africa Ross et al. (2012) examined 521 slugs of 12 species and repeatedly registered *Caenorhabditis elegans*, an unidentified rhabditid, and *Panagrolaimus*. In South Africa as well, 5% of 1944 slugs of five species were infested with *C. elegans* and two specimens with species of *Pellioditis* (Pieterse 2016). In Egypt, Azzam (2006) collected 18 species of gastropods and isolated *Cephalobus, Diploscapter* and at least one rhabditid species. The presence of various nematode taxa in slugs was also noted by Petersen et al. (2015), but these authors specifically focussed on species of *Caenorhabditis*. Highly unusually, the gastrointestinal tract of 100% of the giant snails *Archachatina marginata* and *Achatina achatina* investigated in Nigeria was infected with *Rhabditella axei.* These nematodes were mostly found in the rectum, but some were also noted in the crop, stomach and intestine (Odaibo et al. 2000, Olofintoye & Olorunniyi 2016).

In Australia, Charwat & Davies (1999) isolated soil-inhabiting nematodes from the cadavers of various snails (*Cernuella virgata, Cochlicella acuta, Theba pisana*) that were buried alive as bait in soil samples for a week and died during that time. Species of *Cephalobus, Panagrolaimus, Oscheius* and Diplogastridae were found, but it was not determined whether these bacterivorous nematodes were attracted by the living snail or by the cadaver. In southern Australia, Wang et al. (2015) used the same method taking *Cernuella virgata* as bait and obtained the entomoparasitoid *Heterorhabditis bacteriophora* and 11 species of free-living nematodes: rhabditids (*Mesorhabditis* sp., *Oscheius* sp., *O. tipulae* and *Rhabditis Maupasi*-group sp.), diplogastrids (*Mononchoides striatus, Pristionchus americanus, P. lheritieri* and *P. pacificus*) and cephalobids (*Acrobeloides bodenheimeri, A. buetschlii* and *Cephalobus persegnis*). Again, as the nematodes were isolated from the cadavers of the snails they are at most potential associates of snails.

4.3 Internal phoresis

Our experiments showed that saprobiontic nematodes are ingested passively by gastropods during feeding, that they can survive for two or more days in the intestine and that they are egested alive and fertile to found a new population if carried to a suitable substrate. Though we did not focus on the respective developmental stages of the surviving nematodes, Félix & Duveau (2012) and Petersen et al. (2015) observed that various developmental stages of *Caenorhabditis elegans* (respectively *C. briggsae*) were able to persist in the intestines of slugs, but that dauerlarvae were the most frequent. Different stages of *Rhabditella axei* also occurred in the faeces of African giant snails (Odaibo et al. 2000). Shinohara (1960) observed dauerlarvae of *Caenorhabditis fruticicolae* in the intestine of a dissected snail (*Fruticicola sieboldiana*) six days after exposure. He also found them in the intestine during dormancy in winter or a period of drought. Dauerlarvae do not feed and are adapted to cope with various adverse conditions. Other stages would need to feed on something during an extended stay in the intestine, which would be a further step towards intestinal parasitism. As the passage of coloured substances through the intestinal tract took 14 – 18 hours it would be reasonable to expect all ingested nematodes to be egested after one day. However, our experiments showed that, for whatever reason, rhabditids are often retained for a few days and able to survive for an extended period in the gut. This is a further precondition for intestinal parasitism.

The capacity of free-living nematodes to survive the passage through the intestine of slugs and snails enables them to be dispersed by gastropods. Chitwood & Chitwood (1932) assumed this to be true of certain plant-parasitic nematodes, and it would appear to be even more obvious in the case of saprobiontic nematodes living in ephemeral biochores (= short-lived microhabitats) such as composting material, rotting fruits or fungi used as food by certain gastropods. Evidence for the dissemination of saprobiontic nematodes by gastropods is provided by the discovery of the slug-specific *Pellioditis papillosa* in decaying plant material (Schneider 1866, Andrássy 2007) and frequently on putrefying fungi (Reiter 1928: 55). Similarly, *P. hermaphrodita* (= *Rhabditis caussaneli*) was once introduced into rotten wood (Körner 1954). The extent of the area of dissemination of nematodes depends on the length of their stay in the intestine. A slug can cover a distance of 4 – 10 m in one night (data from different authors).

As well as finding live nematodes in the faeces of gastropods, we also observed live oribatid and other mites, springtails, rotifers, protists, and once a small snail. This ties in with results obtained by Türke et al. (2018), who found 25 species of oribatid mites, two species each of Uropodina and Collembola, nematodes and protists surviving the gut and being dispersed to new habitat patches. Similarly, Fox & García-Moll (1962) found various stages of the tardigrade *Echiniscus molluscorum* in faeces of the snail *Bulimulus exilis*. Türke et al. (2018) call this mode of dispersal 'endozoochory', a term borrowed from botany for the dispersal of spores or seeds via ingestion by animals, while Sudhaus (2010), describing the transportation of nematodes in gastropods, called it internal phoresis or 'endophoresis', happening passively along with food consumption in this case.

Species of *Caenorhabditis* are in the evolutionary transition zone from endophoresis to a necromenic (entering a host and waiting for the cadaver) or enteroparasitic mode of life. Isolates for the description of the four species *C. formosana, C. fruticicolae, C. oncomelaniae* and *C. remanei* came from gastropods. *Caenorhabditis briggsae* and *C. elegans* have also repeatedly been reported in association with gastropods (Kiontke & Sudhaus 2006). From these findings it was cautiously inferred that the stemspecies of the *Elegans*-group (in the narrow sense) was already loosely associated with terrestrial gastropods (Sudhaus & Kiontke 1996). However, the waving behaviour of the dauerlarvae in these species indicates a more opportunistic exploitation of carriers for phoresis. *Caenorhabditis remanei* pursues a multipath strategy to ensure transportation, the more passive endophoresis in gastropods and the more active phoresis on isopods and sometimes on myriapods (Kiontke & Sudhaus 2006). Compared with the initial phase of endophoretic behaviour – that in which species of *Oscheius* and *Panagrolaimus* currently find themselves – the preparasitism of species of the *Caenorhabditis Elegans*-group is more advanced.

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