

## Various evolutionary avenues of Nematoda to parasitism in Gastropoda

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Received 30 September 2018 | Accepted 12 November 2018

Published online at [www.soil-organisms.de](http://www.soil-organisms.de) 1 December 2018 | Printed version 15 December 2018

DOI 10.25674/1yds-c108

### Abstract

The various associations between nematodes and gastropods, which range from random transportation to endophoresis, necromeny, larval parasitism and an entire parasitic or parasitoidic life-style with and without intermediate or paratenic hosts, are discussed in an evolutionary context. Ten to eleven lineages have accomplished the transition to a life at the expense of gastropods, three via a detour of parasitism in vertebrates (Metastrongyloidea, *Nemhelix* and within *Cosmocercoides*). In the lineage to *Agfa* the sequence endophoretic, necromenic, parasitic in the intestine to parasitic in salivary glands of gastropods is reconstructed.

**Keywords** necromeny | parasitoidism | larval parasitism | paratenic host | host switch

### 1. Review on preparasitic and parasitic relationships with gastropods

The associations between nematodes and terrestrial and limnic gastropods range from accidental phoresis to parasitic or pathogenic relationships (Grewal et al. 2003, Nermet' & Půža 2017). Gastropods serve as intermediate and definitive hosts for parasitic nematodes of varying systematic position. Monoxenous parasites in gastropods are *Agfa*, *Alaninema*, Angiostomatidae (*Angiostoma*, *Aulacnema*), several species of Cosmocercidae (*Cosmocercoides*, *Nemhelix*), *Daubaylia* and *Hugotdiplogaster*. In addition, Alloionematidae (*Alloionema*, *Neoalloionema*) and occasionally Mermithidae (species of *Hexameremis* and *Mermis*) and *Marimermithida* (in marine gastropods) are parasitic in juvenile stages only. In the mammal-parasitic Metastrongyloidea, most taxa use gastropods as intermediate hosts, while aquatic gastropods such as *Lymnaea stagnalis* serve as facultative paratenic (transport) hosts to *Spiroxys contortus* (Gnathostomatoidea) and likely to *Serpinema trispinosum* (Camallanoidea), both parasites of water

turtles (Bartlett & Anderson 1985). *Lymnaea (Galba) corvus* was found to act as a paratenic host to the eel parasite *Anguillicola crassus* (Dracunculoidea) under experimental conditions (Moravec 1996), and various snails (Baruš 1964) and slugs experimentally infected with the bird-parasitic *Syngamus trachea* (Strongylidae) 'may also serve as paratenic hosts ... under natural conditions' (Anderson 2000: 79). The snail *Physastra* sp. could act as paratenic host for the ascarid *Amplichaecum robertsi*, a parasite in python (J. F. A. Sprent mentioned in Morley 2010). Terrestrial snails presumably also exhibit a paratenic relationship with certain Rhabdiasidae, particularly those parasitic in lizards which feed on snails (Anderson 2000: 26–27). In the experimental study by Langford & Janovy (2009) various species of *Rhabdias* were able to use snails of *Physella (Physa) gyrina* as paratenic hosts to infest anurans and snakes as final host. In the rhabdiasid *Pneumonema tiliquae*, the exsheathment of third stage juveniles was found to be stimulated by mucus from the snails they invaded. These included *Lymnaea lessoni*, where they were infective for the definitive lizard host (Ballantyne 1991).

The same phenomenon occurs in the marine environment, where *Haliotis corrugata* and *H. fulgens* serve as a paratenic or even intermediate host for *Echinocephalus pseudouncinatus* (Gnathostomatoidea), whose definitive hosts are elasmobranch fishes (Millemann 1963). *Echinocephalus 'uncinatus'* juveniles were reported in *Hemifusus pugilinus* (Anantaraman 1964) and by T. H. Johnston and P. M. Mawson in the gastropods *Polinices conicus* and *Katylisia scalarina* (Cheng 1978). Along with marine bivalves, gastropods also appear to be involved in the life-cycle of *Sulcascaris sulcata* (Ascaridoidea), a parasite of marine turtles with which Berry & Cannon (1981) experimentally infected the snail *Polinices sordidus* and whose third stage juveniles occurred in *Busycotypus (Busycon) canaliculatus* and *Euspira (Lunatia) heros* (after J. R. Lichtenfels in Cheng 1978). Marine gastropods were also found to harbour juveniles of other ascarids (*Contracaecum* sp., *Pseudoterranova decipiens*) (Anderson 2000). Thus, D. E. Norris and R. M. Overstreet reported the occurrence of *Hysterothylacium (Thynnascaris)* sp. in the gastropods *Cantharus cancellarius* and *Thais haemastoma*, and A. Dolgikh *Hysterothylacium (Thynnascaris) aduncum* in *Tritia (Cyclonassa) neritea* and *Tritia (Nassa) reticulata*, a species with which E. D. Valter experimentally infected *Margarites groenlandicus* (Cheng 1978). A. V. Tchesunov reported Marimermithida from gastropods (Miljutin 2014), and a remarkable epibiotic relationship is known from the marine environment, where the chromadorid *Endeolophos skeneae* settled on 47 of 50 shells of the gastropod *Skenea profunda* (Holovachov et al. 2011).

Obligatory associations with terrestrial gastropods are found not just among the parasites mentioned above, but in necromenic species, too (Tab. 1). Necromeny denotes a relationship, where juvenile stages infest a host and wait inside its body until it dies, at which point they develop and complete their life-cycle on the cadaver, feeding on growing bacteria (Sudhaus 2010). Infection occurs for instance when slugs come into contact with the cadavers of conspecifics and feed on them. Most species of *Pellioiditis* (= *Phasmarhabditis*) exhibit a necromenic life history, but *P. hermaphrodita* and perhaps other species of *Pellioiditis* have evolved to a pathogenic stage which causes the premature death of the host and the decomposition of the cadaver. Whether *P. hermaphrodita* behaves like a necromenic or a parasitoidic species depends on the host species. When its dauerlarvae actively enter a slug and introduce compatible bacteria (such as *Moraxella osloensis*) certain slugs are killed while others are resistant (Tan & Grewal 2001). In *P. papillosa* the dauerlarvae invade the host as well (Mengert 1953), a behaviour that was presumably already present in the stemspecies of *Pellioiditis*.

The evolution of all these life histories started from bacteriophagous saprobiontic nematodes that were accidentally ingested with food by slugs or snails and – benefiting from adaptations to a life in saprobious substrates – able to survive in the digestive tract (Sudhaus 2010). As this chance method of transportation was advantageous for the dispersal of the nematodes, some species may have evolved traits that supported it (Petersen et al. 2015). A large number of facultative associates of gastropods have been recorded over the years (Sudhaus 2018). These nematodes are of special interest as they determine the preadaptive plateau for the creation of a new species niche in association with gastropods (Sudhaus 2010) which must be assumed for the respective stemspecies of the clades discussed in the following chapter.

## 2. Multiple avenues to parasitism in gastropods

Ten to eleven species or stemspecies of clades developed a parasitic association with gastropods at which it is worth taking a closer look. For easier comparison the sequence of the discussion is according to the diagram (Fig. 1) from left to right.

- The knowledge about Marimermithida is meagre. They are larval parasites in various marine invertebrate groups, once reported from a gastropod (A. V. Tchesunov after Miljutin 2014).
- Within Mermithidae, which are parasitic or parasitoidic in all but the adult stage, a transition occurred from parasitism in insects to parasitism in slugs and snails perhaps via aberrant hosts or facultative paratenic hosts. This applies to *Mermis nigrescens* (Nermut' & Půža 2017) and first and foremost to *Hexameris 'albicans'* (Hagmeier 1912, Chitwood & Chitwood 1937, Mienis 1986, Juhász 2014). *Hexameris albicans* is known from different insects, and the species from gastropods is presumably different (data by B. Rathke according to Kaiser 1977). Juvenile mermithids from the host could not be identified (Dundee 1977, Thiengo 1995, Pieterse 2016).
- *Daubaylia* belongs to the Cephalobidae and is closely related to *Pseudacrobeles* (Holovachov et al. 2015). The ecological transition undergone by the ancestral lineage of *Daubaylia* is remarkable as cephalobids live in soil and exhibit no notable preadaptations to parasitism. *Daubaylia* species are nearly always parasitic in freshwater snails of Planorbidae, and the same can be presumed for

**Table 1.** Gastropod typical nematodes with a free-living phase that are larval-parasitic, parasitoidic or necromenic.

| slugs                                      | nematode species                 | n <sup>1</sup> | country       | reference               |
|--|----------------------------------|----------------|---------------|-------------------------|
| <i>Ambigolimax (Lehmannia) valentianus</i> | <i>Pellioditis neopapillosa</i>  | 3/3            | France        | Morand et al. 2004      |
| <i>Arion ater</i>                          | <i>Alloionema appendiculatum</i> | 50/90          | France        | Morand et al. 2004      |
|  | <i>Alloionema appendiculatum</i> | 26/68          | USA           | Ross et al. 2009, 2010a |
|  | <i>Alloionema appendiculatum</i> | 10/185         | Great Britain | Ross et al. 2010a       |
|  | <i>Alloionema appendiculatum</i> | 4/33           | Norway        | Ross et al. 2016        |
|  | <i>Pellioditis hermaphrodita</i> | 7/185          | Great Britain | Ross et al. 2009, 2010a |
|  | <i>Pellioditis hermaphrodita</i> | 6/33           | Norway        | Ross et al. 2016        |
|  | <i>Pellioditis neopapillosa</i>  | 4/185          | Great Britain | Ross et al. 2009, 2010a |
| <i>Arion ater (= empiricorum)</i>          | <i>Alloionema appendiculatum</i> | 238/468        | Germany       | Mengert 1953            |
|  | <i>Pellioditis papillosa</i>     | 7/468          | Germany       | Mengert 1953            |
| <i>Arion circumscriptus</i>                | <i>Alloionema appendiculatum</i> | 2/44           | Germany       | Mengert 1953            |
|  | <i>Alloionema appendiculatum</i> | 3/6            | France        | Morand et al. 2004      |
|  | <i>Pellioditis papillosa</i>     | 1/44           | Germany       | Mengert 1953            |
| <i>Arion distinctus</i>                    | <i>Pellioditis neopapillosa</i>  | 1/234          | Great Britain | Ross et al. 2009, 2010a |
| <i>Arion flagellus</i>                     | <i>Alloionema appendiculatum</i> | 2/?            | Great Britain | Ross et al. 2009        |
| <i>Arion fuscus</i>                        | <i>Alloionema appendiculatum</i> | 11/70          | Norway        | Ross et al. 2016        |
|  | <i>Pellioditis hermaphrodita</i> | 1/70           | Norway        | Ross et al. 2016        |
| <i>Arion fuscus X A. ater</i>              | <i>Alloionema appendiculatum</i> | 2/6            | Norway        | Ross et al. 2016        |
|  | <i>Pellioditis hermaphrodita</i> | 2/6            | Norway        | Ross et al. 2016        |
| <i>Arion hortensis</i>                     | <i>Pellioditis hermaphrodita</i> | 4/16           | France        | Morand et al. 2004      |
| <i>Arion intermedius</i>                   | <i>Alloionema appendiculatum</i> | 5/49           | Germany       | Mengert 1953            |
|  | <i>Alloionema appendiculatum</i> | 3/14           | Great Britain | Ross et al. 2010a       |
| <i>Arion lusitanicus</i>                   | <i>Alloionema appendiculatum</i> | 1/?            | Belgium       | Ross et al. 2009        |
|  | <i>Alloionema appendiculatum</i> | 1/?            | Norway        | Ross et al. 2009        |
|  | <i>Alloionema appendiculatum</i> | 1/?            | Slovenia      | Ross et al. 2009        |
|  | <i>Pellioditis hermaphrodita</i> | 5/?            | Norway        | Ross et al. 2009        |
| <i>Arion silvaticus</i>                    | <i>Alloionema appendiculatum</i> | 4/4            | France        | Morand et al. 2004      |
| <i>Arion subfuscus</i>                     | <i>Alloionema appendiculatum</i> | 2/21           | Germany       | Mengert 1953            |
|  | <i>Alloionema appendiculatum</i> | 1/4            | France        | Morand et al. 2004      |
|  | <i>Alloionema appendiculatum</i> | 3/131          | Great Britain | Ross et al. 2010a       |
| <i>Arion vulgaris</i>                      | <i>Alloionema appendiculatum</i> | 38/204         | Norway        | Ross et al. 2016        |
|  | <i>Pellioditis hermaphrodita</i> | 27/204         | Norway        | Ross et al. 2016        |
| <i>Ariostalis nebulosa</i>                 | <i>Pellioditis</i> sp. 1         | 3/4            | South Africa  | Ross et al. 2012        |
| <i>Deroceras</i> sp.                       | <i>Alloionema appendiculatum</i> |                | Australia     | Charwat & Davies 1999   |
| <i>Deroceras laeve</i>                     | <i>Pellioditis papillosa</i>     | 2/11           | Germany       | Mengert 1953            |
| <i>Deroceras panormitanum</i>              | <i>Pellioditis neopapillosa</i>  | 4/109          | Great Britain | Ross et al. 2009, 2010a |
|  | <i>Pellioditis papillosa</i>     | 1/109          | Great Britain | Ross et al. 2010a       |
|  | <i>Pellioditis</i> sp. SA3       | 1/1100         | South Africa  | Pieterse 2016           |
|  | <i>Pellioditis</i> sp. SA3       | 1/1636         | South Africa  | Pieterse et al. 2017    |
| <i>Deroceras reticulatum</i>               | <i>Pellioditis hermaphrodita</i> | 6/581          | Great Britain | Ross et al. 2009, 2010a |

| slugs                                 | nematode species   | n <sup>1</sup> | country       | reference                 |
|---------------------------------------|--|----------------|---------------|---------------------------|
| <i>Deroceras reticulatum</i>          | <i>Pellioditis hermaphrodita</i>                           | 3/7            | France        | Morand et al. 2004        |
|                                       | <i>Pellioditis hermaphrodita</i>                           | 6/260          | Norway        | Ross et al. 2016          |
|                                       | <i>Pellioditis hermaphrodita</i>                           | 1/?            | Chile         | Ross et al. 2009          |
|                                       | <i>Pellioditis neopapillosa</i>                            | 4/581          | Great Britain | Ross et al. 2009, 2010a   |
|                                       | <i>Pellioditis</i> sp. 2                                   | 3/69           | South Africa  | Ross et al. 2012          |
|                                       | <i>Pellioditis</i> sp. SA4                                 | 1/173          | South Africa  | Pieterse 2016             |
|                                       | <i>Pellioditis</i> sp. SA4<br>(=> <i>P. safricana</i> )    | 1/429          | South Africa  | Pieterse et al. 2017      |
| <i>Lehmannia marginata</i>            | <i>Pellioditis hermaphrodita</i>                           |                | Egypt         | Azzam 2006                |
|                                       | <i>Pellioditis tawfiki</i> <sup>2</sup>                    |                | Egypt         | Azzam 2006                |
| <i>Limax cinereoniger</i>             | <i>Pellioditis neopapillosa</i>                            | 2/27           | Germany       | Mengert 1953              |
|                                       | <i>Pellioditis neopapillosa</i>                            | 10/31          | France        | Morand et al. 2004        |
|                                       | <i>Pellioditis papillosa</i>                               | 10/27          | Germany       | Mengert 1953              |
|                                       | <i>Pellioditis papillosa</i>                               | 31/31          | France        | Morand et al. 2004        |
| <i>Limax flavus</i>                   | <i>Pellioditis hermaphrodita</i>                           |                | Egypt         | Azzam 2006                |
|                                       | <i>Pellioditis tawfiki</i>                                 |                | Egypt         | Azzam 2006                |
| <i>Limax maximus</i>                  | <i>Pellioditis neopapillosa</i>                            | 4/4            | France        | Morand et al. 2004        |
|                                       | <i>Pellioditis papillosa</i>                               | 3/4            | Germany       | Mengert 1953              |
| <i>Malacolimax (Limax) tenellus</i>   | <i>Pellioditis papillosa</i>                               | 9/35           | Germany       | Mengert 1953              |
| <i>Milax</i> sp.                      | <i>Pellioditis hermaphrodita</i>                           | 1/3            | France        | Morand et al. 2004        |
| <i>Tandonia sowerbyi</i>              | <i>Pellioditis papillosa</i>                               | 1/16           | Great Britain | Ross et al. 2010a         |
| <b>snails</b>                         |  |                |               |                           |
| <i>Bulinus truncatus</i>              | <i>Pellioditis</i> sp.                                     |                | Egypt         | Azzam & Belal 2006        |
| <i>Cantareus (Helix) aspersus</i>     | <i>Alloionema appendiculatum</i>                           | 1/699          | France        | Morand et al. 2004        |
| <i>Cepaea nemoralis</i>               | <i>Pellioditis hermaphrodita</i>                           | 4/285          | France        | Morand et al. 2004        |
| <i>Cochlicella barbara</i>            | <i>Alloionema appendiculatum</i>                           |                | Australia     | Charwat & Davies 1999     |
| <i>Discus rotundatus</i>              | <i>Pellioditis hermaphrodita</i>                           | 19/49          | France        | Morand et al. 2004        |
| <i>Eobania vermiculata</i>            | <i>Pellioditis hermaphrodita</i>                           |                | Egypt         | Azzam 2006                |
|                                       | <i>Pellioditis tawfiki</i>                                 |                | Egypt         | Azzam 2006                |
| <i>Euomphalia strigella</i>           | <i>Pellioditis hermaphrodita</i>                           | 3/12           | France        | Morand et al. 2004        |
| <i>Helix pomatia</i>                  | <i>Pellioditis hermaphrodita</i>                           | 3/50           | France        | Morand et al. 2004        |
| <i>Monacha cartusiana</i>             | <i>Pellioditis hermaphrodita</i>                           | 5/24           | France        | Morand et al. 2004        |
| <i>Neohelix (Polygyra) albolabris</i> | <i>Pellioditis hermaphrodita</i><br>(= <i>caussaneli</i> ) |                | USA           | Chitwood & Chitwood, 1934 |
| <i>Oxychilus deilus</i>               | <i>Pellioditis neopapillosa</i>                            | 1/3            | Crimea        | Ivanova et al. 2013a      |
| <i>Oxychilus draparnaudi</i>          | <i>Pellioditis hermaphrodita</i>                           | 2/11           | France        | Morand et al. 2004        |
| <i>Pomatias elegans</i>               | <i>Pellioditis hermaphrodita</i>                           | 2/8            | France        | Morand et al. 2004        |
| <i>Succinea putris</i>                | <i>Pellioditis hermaphrodita</i>                           | 7/11           | France        | Morand et al. 2004        |
| <i>Theba</i> sp.                      | <i>Pellioditis tawfiki</i>                                 |                | Egypt         | Azzam 2006                |
| <i>Theba pisana</i>                   | <i>Pellioditis tawfiki</i>                                 |                | Egypt         | Azzam 2006                |
| <i>Zonites algirus</i>                | <i>Pellioditis neopapillosa</i>                            | 39/40          | France        | Morand et al. 2004        |

<sup>1</sup> First number: occurrence of the species. Second number: quantity of investigated gastropod specimens.

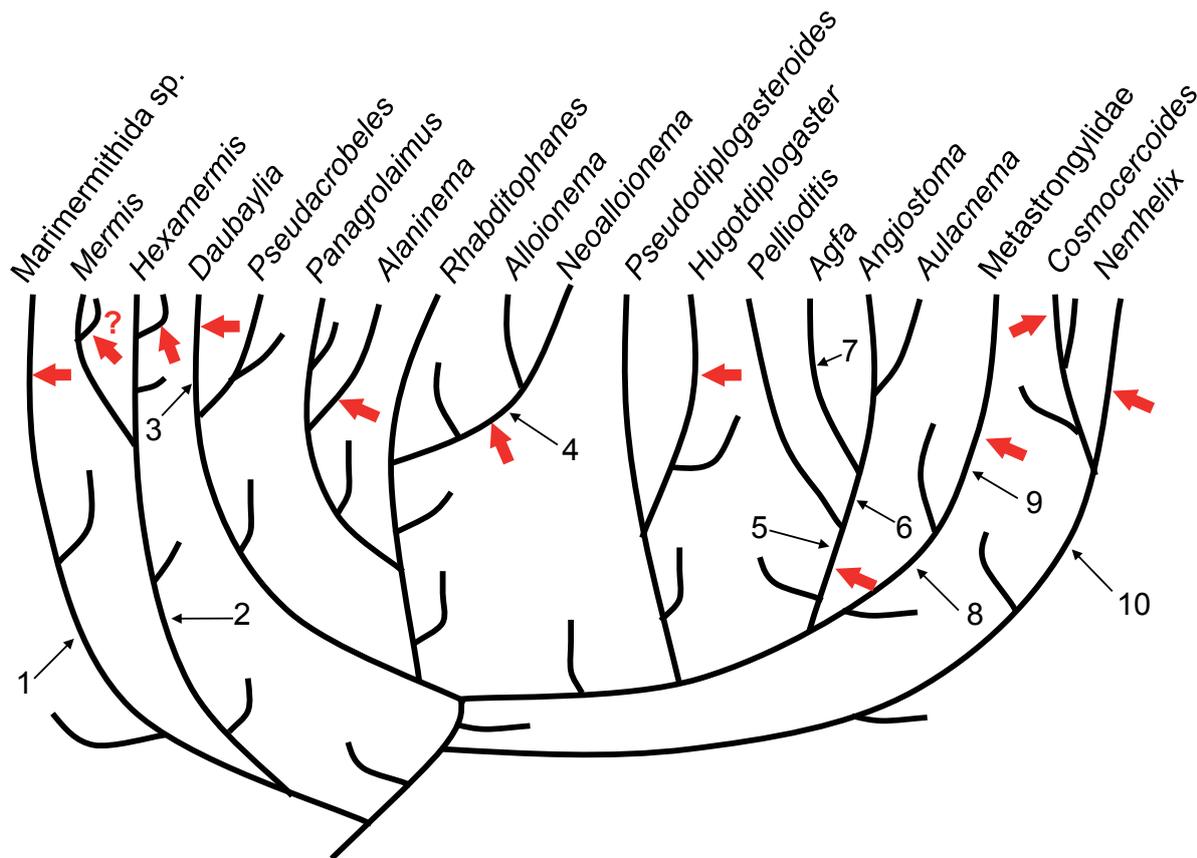
<sup>2</sup> This species was described as *Phasmarhabditis tawfiki* by Azzam (2003). On the basis of the description the assignment to this group must be questioned. Perhaps it is a species of *Pelodera*.

their stemspecies. *Daubaylia olsoni* appears to be in the process of switching to a leech predaceous on planorbids (Poinar 1984). Exceptional records so far are *D. bonaerensis* in '*Helix*' *aspersa* (Camino & González 2011) and *Daubaylia* sp. juveniles in the slug *Philomycus carolinensis* (Chitwood & Chitwood 1934). Because *D. pearsoni* kills its host, Anderson & Bartlett (1993) proposed that it should better be called a parasitoid.

- *Alaninema* belongs to the Panagrolaimorpha (Ivanova et al. 2013b), within which free-living species of *Panagrolaimus* have often been observed in association with gastropods (Sudhaus 2018).
- Alloionematidae (*Alloionema*, *Neoalloionema*) are closely related to the free-living *Rhabditophanes* (Ross et al. 2010b), which were only encountered in accidental contact with slugs (Mengert 1953, Sudhaus 2018). Though the life-cycle of *Neoalloionema* species has not been elucidated,

we can suppose that the stemspecies of Alloionematidae was associated with gastropods and had already acquired both a larval-parasitic and a necromenic life style.

- Most Diplogasteridae that were isolated from gastropods so far were not identified and can not help us to elucidate *Hugotdiplogaster*'s first steps to parasitism in the genital tract of slugs (Morand & Barker 1995), especially as its more exact phylogenetic position and life cycle are uncertain.
- Most species of *Pellioiditis* were isolated from gastropods. Though *Pellioiditis huizhouensis* (Huang, Ye, Ren & Zhao, 2015) n. comb. was found in decaying organic substances, an association with gastropods is suspected here too. Two *Pellioiditis* species (*P. pellio* and its sister species *P. mairei*) exhibit a necromenic association with earthworms, while the unnamed *P. sp.* described by Zaborski et al. (2001) appears to be more a parasitoid of earthworms. The stemspecies of *Pellioiditis* established a relationship with soft-



**Figure 1.** Incomplete phylogenetic diagram showing the position of nematode taxa obligately associated with gastropods in relation to closely related free-living taxa to illustrate, how many times gastropod parasitism was acquired (thick arrow). Thin arrows indicate transitions to new modes of life: 1) larval-parasitic in marine invertebrates, 2) parasitoidic in arthropods, 3) parasitic or parasitoidic, 4) larval-parasitic and necromenic, 5) necromenic, 6) parasitic in intestine, 7) parasitic in salivary glands, 8) parasitic in tetrapods, 9) acquisition of intermediate host, 10) parasitic in amphibians.

bodied animals which were entered actively by the dauer juveniles. I argue that *Pellioiditis* was primarily adapted to a necromenous association with slugs. This means that in the lineage to *P. pello/P. mairei* a switch to earthworms occurred.

- Because of the sister group relationship between *Agfa*/Angiostomatidae and *Pellioiditis* it can be suggested that their last common ancestor was always associated with gastropods and pursued necromeny as most species of *Pellioiditis* do. Then, in the course of evolution, the stemspecies of *Agfa* and Angiostomatidae (*Angiostoma* + *Aulacnema*) shifted to an entirely parasitic life in gastropods.
- According to the analysis of ribosomal RNA gene sequences (Carreno & Nadler 2003), the mammal-parasitic Metastrongyloidea are monophyletic and initially had a heteroxenous life-cycle using terrestrial gastropods as intermediate hosts, as seen in most species today. Gastropods were replaced with earthworms in the stemspecies of *Metastrongylus* and with fishes in the lineages to *Otostrongylus* and *Parafilaroides*, while species in some lineages (*Andersonstrongylus*, *Filaroides*, *Oslerus*) became secondarily monoxenous (Anderson 2000).
- While within *Angiostoma* a host switch occurred to amphibians that fed on gastropods (Dougherty 1951), in the ascarid Cosmocercidae it was the other way round (Sudhaus 2010). This is inferred by outgroup comparison as the species of different genus taxa of Cosmocercidae are parasitic in amphibians and reptiles. Within *Cosmocercoides* and in the evolutionary line to *Nemhelix*, parasites adapted to amphibians exploited terrestrial gastropods that lived in the same habitats and sometimes were 'found under the same rocks and logs' (Baker 1978). Cross-transmission experiments and a thorough comparative morphological study indicated that instead of one and the same species there exist the separate siblings *Cosmocercoides dukae* in slugs and *C. variabilis* in toads (Vanderburgh & Anderson 1987). However, a transfer from snails to frogs was possible, which temporary could acquire *C. dukae* when feeding on terrestrial gastropods. This fact only seemingly supports the contrary view of Poinar (2015: 57) 'that molluscs were the original host of *Cosmocercoides*'. The fossil juvenile nematodes in contact with a small snail of Punctidae in Early Cretaceous Burmese amber he considers to be a member of cosmocercids (Poinar 2011) provides a minimum date for the existence of these parasites also in amphibians.

### 3. Conclusions

One conclusion that can be drawn from this discussion is that throughout the phylogeny of Nematoda, necromenic, parasitoidic, facultative parasitic, hemiparasitic and finally obligate parasitic relationships with gastropods were established in ten or eleven lineages (Fig. 1). The transitions from endophoresis to necromeny and larval parasitism with a free-living phase (*Alloionema*), and finally parasitism through the entire life-cycle are smooth. Some species of *Daubaylia* and *Pellioiditis* behave like parasitoids, killing their 'host' such as Mermithidae. In the course of evolution the monoxenous ancestor of Metastrongylidae, which lived parasitically in mammals, coopted gastropods as intermediate hosts and thus became heteroxenous. This presumably occurred via a paratenic host for which some Rhabdiasidae may serve as a model. Gastropod-parasitic Cosmocercidae result from major host switches by parasites in amphibians. On the other hand, *Angiostoma* is secondarily parasitic in amphibians and turtles, while its adaptations towards parasitism occurred in co-evolution with gastropods. Based on the cladogram of *Pellioiditis*, Angiostomatidae and *Agfa* it can be inferred that in the evolution til *Agfa* there was a sequence of endophoresis, necromeny, parasitism in the intestine and finally (following Ivanova et al. 2013a) in the salivary glands of gastropods (Fig. 1).

### 4. Acknowledgement

Several authors helped me to gain the literature. The suggestions of the reviewer were useful to improve the manuscript. Lucy Cathrow improved the manuscript linguistically.

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