Preadaptive plateau in Rhabditida (Nematoda) allowed the repeated evolution of zooparasites, with an outlook on evolution of life cycles within Spiroascarida[1]

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Abstract

The highly diverse Nematoda are free-living in all marine, freshwater and terrestrial habitats and parasitic in plants or animals from Foraminifera to Vertebrata. At present about 10 % of the estimated existing species might be scientifically known. About 30 parasitic lineages originated independently in different geological periods since Silurian times, most of them in the terrestrial Secernentea and several of them in the "Rhabditidae". Descendants from these lineages also invaded aquatic hosts. Within the primarily marine "Adenophorea" only the rare invertebrate-parasitic Benthimermithida and Marimermithida originated in the marine environment. Nearly all marine animals are free from parasitic "Adenophorea". This ecological "void in the sea" (OSCHE 1966) with respect to parasitic "Adenophorea" and the multiple parasitic lineages of Secernentea can be elucidated by the preadaptation concept, which is illustrated here in detail. This concept implies that crucial problems for life as a parasitic worm are "pre-solved" by manifold physiological and reproductive adaptations as bacterial feeding inhabitants of patchily distributed, rapidly changing and short-lived (ephemeral) saprobious habitats on land. Such saprobiontic nematodes ultimately must contact a larger animal for transport (phoresy) and its dauer larva (evolved in the ancestral lineage of Secernentea) respond to cues of the carrier. A transformed dauer larva initiated special associations like endophoresy, entoecy, necromeny, larval parasitism, accidental, facultative and obligate parasitism in terrestrial gastropods, annelids, arthropods and vertebrates. Some examples for these associations are reported, and the gradual evolutionary transitions are depicted in a diagram. The intergradation from preadapted saprobiontic rhabditids is not only evidenced in parasites retaining a free-living saprobiontic phase like Strongylida and Rhabdiasidae, but is also plausible for the exclusively parasitic Spiroascarida originating at the base of Secernentea encompassing most parasitic nematodes in vertebrates. The evolution of life cycles of clades within the Spiroascarida (Ascaridida, Gnathostomatida, Oxyurida, Rhigonematida, Spirurida) are explored in a phylogenetic context starting with the suggestion that the stem-species of Spiroascarida lived endo-saprobiontically in the hindgut of a terrestrial, saprophagous arthropod. Thus, an arthropod-parasitic state preceded vertebrate parasitism in Ascaridida, Gnathostomatida, Spirurida and part of the Oxyurida. Cutaneous penetration by the infective larva and a lung route of migration via the circulatory system are conspicuous convergences in the life cycles of different parasites in tetrapods.

K e y w o r d s : Parasitic "Adenophorea", preadaptation concept, life cycles of stemspecies, Ascaridida, Gnathostomatida, Oxyurida, Rhigonematida, Spirurida.

Zusammenfassung

Nematoden zeigen eine große Mannigfaltigkeit, freilebend in sämtlichen Lebensstätten im marinen, limnischen und terrestrischen Bereich und parasitisch an Pflanzen und in Tieren von Foraminiferen bis zu Wirbeltieren. Derzeit dürften erst ca. 10 % der geschätzten Arten wissenschaftlich bekannt sein. Aus freilebenden Formen entstanden seit dem Silur unabhängig und zu verschiedenen Zeiten der Erdgeschichte etwa 30 parasitische Linien, die meisten von ihnen innerhalb der terrestrischen Secernentea und etliche davon innerhalb der „Rhabditidae". Abkömmlinge dieser Parasitenlinien erschlossen auch wasserlebende Wirte. Im marinen Bereich entstanden innerhalb der „Adenophorea" als Parasiten nur die seltenen Benthimermithida und Marimermithida. Parasitische „Adenophorea" in Meerestieren gibt es sonst fast nicht. Diese „Lücke im Meer" (OSCHE 1966) sowie der Tatbestand vielfacher Parasitwerdung innerhalb der Secernentea kann durch das näher erläuterte Präadaptations-Konzept erklärt werden. Dieses Konzept beinhaltet, dass entscheidende Probleme für ein Leben als Parasit bereits gelöst sind durch verschiedene physiologische und reproduktive Anpassungen an eine Lebenssituation als Bakterienfresser in saproben terrestrischen Lebensstätten, die disjunkt verteilt sowie kurzlebig (ephemer) sind und rascher Zersetzung unterliegen. Saprobionte Nematoden müssen durch größere Bewohner dieser Lebensstätten transportiert werden, wobei die in der Ahnenlinie der Secernentea evolvierte Dauerlarve als phoretisches Stadium auf verschiedene Signale reagieren muss. Eine Abänderung der Dauerlarve ermöglichte spezielle Assoziationen wie Endophoresie, Entoecie, Necromenie, Larvalparasitismus, zufälligen, fakultativen und obligaten Parasitismus in terrestrischen Gastropoden, Anneliden, Arthropoden und Wirbeltieren. Diese werden beispielhaft und in einem Diagramm als graduelle evolutionäre Übergänge dargestellt. Überzeugend ist der allmähliche Übergang präadaptierter saprobionter „Rhabditidae" für Parasitenlinien wie Strongylida und Rhabdiasidae, die eine freilebende saprobiontische Phase beibehalten haben.

Offensichtlich ist er aber auch bei den ausschließlich parasitischen und an der Basis der Secernentea entspringenden Spiroascarida, welche die meisten wirbeltier-parasitischen Nematoden-Taxa enthalten. Ausgehend von der Annahme, dass die Stammart der Spiroascarida endo-saprobiont im Enddarm eines terrestrischen saprophagen Arthropoden lebte, sowie auf der Basis eines phylogenetischen Diagramms wird die Evolution der Lebenszyklen der dazugehörigen Ascaridida, Gnathostomatida, Oxyurida, Rhigonematida und Spirurida untersucht. Danach ging dem Parasitismus von Ascaridida, Gnathostomatida, Spirurida und einem Teil der Oxyurida in Wirbeltieren jeweils eine arthropoden-parasitische Phase voraus. Auffällige Konvergenzen im Lebenszyklus verschiedener Parasiten in Tetrapoden sind das Eindringen der Infektionslarve durch die Haut und eine Wanderung über Kreislauf und Lunge.

Contents

1. Introduction

Since SYDNEY BRENNER started his research on the developmental biology and genetics of *Caenorhabditis elegans* about 40 years ago and convinced more and more other scientists to join his efforts, this nematode species advanced quickly to become a famous model organism for many branches of biology. Because *C. elegans* is a nematode, this research has also brought the rest of the Nematoda into the limelight for comparative research. Cautiously, it must be noted that *C. elegans* is at most a model for *Caenorhabditis*, which currently has 37 known species (only 20 of which have been scientifically described so far), but not a very good model for the more encompassing group "Rhabditidae", which has about 360 known species. It would be completely misleading to take *C. elegans* as a model for the Nematoda, which is as diverse as such a species-rich, ancient group (existing since Precambrian times) could be. We think that more than half a million different species of nematodes exist on the globe and that, at a maximum, only 5–10 % of them are described with a name and thus scientifically known. Only a fraction of the biodiversity is described. We still find new species in such well-explored places as European countries. In Berlin, we discovered 14 new species in the last 25 years, one of them *(Myolaimus xylophilus)* in rotten wood in a tree in front of our house (SUDHAUS 2010).

So, despite about 150 years of nematology, we are only at about the beginning of taxonomic and systematic research on nematodes. Accordingly, we possess only provisional knowledge on ecology, life cycle and the role of already described species as "elements" of different ecosystems. Nematodes are the most abundant metazoan organisms in marine, freshwater and terrestrial environments. They exist in all the habitats one may imagine: from the deep sea to spaces in arctic ice or in thermal springs, from seaweed deposits on the shores to exudates of trees, from associates of very different insects to parasites of plants and animals. It is much easier to realize the only two biotopes in which nematodes are nearly always missing: they only accidentally occur in the air and in the pelagic zone.

Only a few points shall be addressed regarding the diversity of major groups of Nematoda and their supposed relationships as visualised in a very rough diagram (Fig. 1). "Rhabditidae" belongs to a species-rich monophylum called Secernentea. The paraphyletic taxon that includes all the rest is the "Adenophorea". The first radiations of nematodes took place in the marine environment during Precambrian times (other authors suggest the Cambrian period: VAN MEGEN et al. 2009) and resulted in the main branches of "Adenophorea", a group that has as great a divergence among species as that of crustaceans. From the oceans, different lineages invaded freshwater at
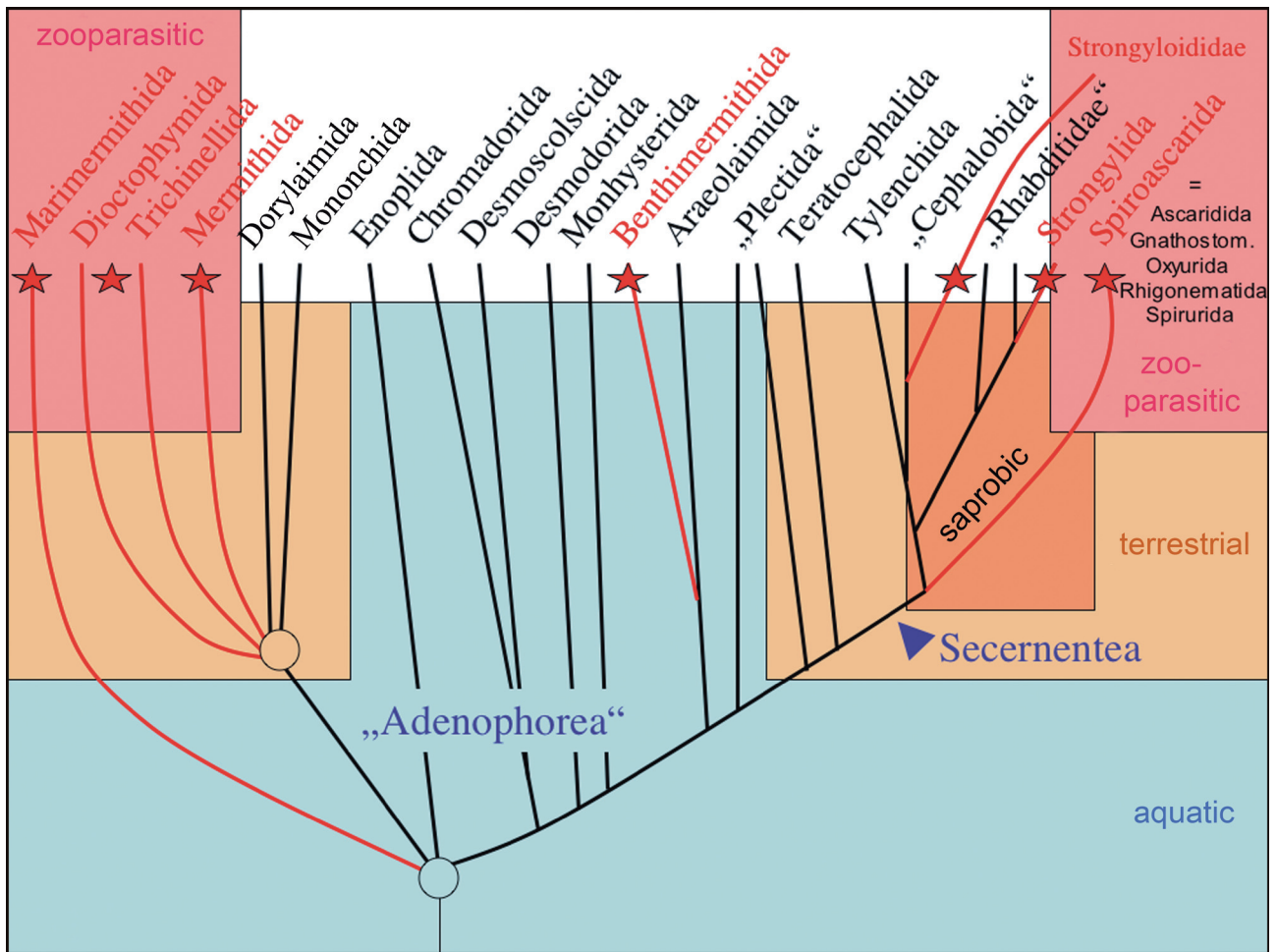
Fig. 1. Fragmentary phylogenetic tree showing the radiation of Nematoda (combined from different authors) with a rough consideration of the environment of high-ranked taxa and with a focus on zooparasitic groups.

different historical periods via estuaries; the terrestrial environment was presumably inhabited since Silurian times (about 430 million years ago). The Secernentea is one of these lineages that originated in a terrestrial environment. Perhaps more precisely, the ancestors of Secernentea lived in saprobious habitats, where organic matter is decaying. In three or more lineages, terrestrial nematodes became plant-parasitic, of which the most important are the Dorylaimida in the "Adenophorea" and Tylenchida in the Secernentea. Finally, as stated by several authors since 70 years (BAYLIS 1938: 256), parasites in animals originated in several lineages independently and at various times in the evolutionary history of nematodes (alone more than 20 insect-parasitic lineages: SUDHAUS 2008), which illustrates the great diversity in the life cycles of parasitic taxa, which cannot be derived from each other (compare Table 1). Therefore, "a single mechanism for the evolution of parasitism is an unnecessary and unlikely simplification"

(DORRIS et al. 1999: 192). Even if the point of origin might have been very similar, multiple evolutionary pathways and unconstrained solutions would be possible. Here, I focus on the evolution of parasitic lineages within the Rhabditida and discuss the theory that living as saprobionts in ephemeral habitats on land constitutes the transitional ecological zone from free-living terrestrial to parasitic life cycles in invertebrate and vertebrate animals. Finally, hypotheses are formulated to derive the ancestral life cycles of clades within the exclusively parasitic Spiroascarida (= Spirurina of other authors). In this overview, special parasitic taxa must be excluded, such as *Daubaylia* in gastropods or Drilonematoidea in earthworms.

2. Animal parasitic lineages in nematodes

Hardly more than four lineages within the paraphyletic "Adenophorea" adapted to a parasitic life in animals (Fig. 1): the Dioctophymida (e. g. *Dioctophyme*, *Eustrongylides*, *Soboliphyme*) and Trichinellida (e. g. *Capillaria*, *Muspicea*, *Trichinella*, *Trichuris*) in vertebrates (together forming a clade: VAN MEGEN et al. 2009), the Mermithida predominantly in insects, and the convergently similar Marimermithida and Benthimermithida in various benthic marine invertebrates mainly of the deep sea (TCHESUNOV 1997; MILJUTIN 2004). The first two clades arose within terrestrial "Adenophorea" (not "from freshwater ancestors" as suggested by MALAKHOV 1994: 191); however, the transition to parasitism has not been consistently worked out. SUDHAUS (1974) discussed their possible origin by entoecy in the gill chamber of semi-terrestrial crustaceans, while MAGGENTI (1981: 248) suggested that in this lineage "vertebrate parasitism may have had some of its development through associations with annelid worms", having in mind that several Dioctophymida and Trichinellida use oligochaetes as paratenic or intermediate hosts. Only Benthimermithida and Marimermithida should have originated in the marine environement, although no molecular data are available to confirm this.

On the other hand, the primarily terrestrial Secernentea generated a multiplicity of parasitic lineages. "The possibility of establishing parasitic lines certainly existed to an abundant degree for the Nematoda from the beginning of their saprobiontic way of life, and we must assume that these opportunities were exploited very early" (OSCHE 1963: 299). Though predicted by MALAKHOV (1994), it was a rather unexpected result of the reconstructions of phylogeny from DNA sequence data (starting with BLAXTER et al. 1998) that the first split brought about an exclusively zooparasitic lineage. Following MALAKHOV (1994: 196), who called it the "spiroascarid branch", I refer here to this group as the Spiroascarida. This clade (Fig. 1) includes such important and well-known parasitic nematode groups like Ascaridida (with *Ascaris*), Gnathostomatida, Oxyurida (with *Enterobius*), Rhigonematida and Spirurida (with *Brugia*, *Dracunculus*, *Onchocerca* and other human-parasitic taxa). Some of them are parasites of arthropods, others of vertebrates, and many change during their life cycles between an arthropod intermediate host and a definitive vertebrate host. Within the paraphyletic "Rhabditidae" arose the Strongylida, which is exclusively parasitic in tetrapod vertebrates. The Strongyloididae, also parasites of vertebrates, arose close to species of Panagrolaimidae ("Cephaloboidea"). Later, I present further parasitic taxa in the sister group of Spiroascarida, which MALAKHOV (1994: 200) called the "rhabditostrongylid branch" or the "Rhabditostrongylida" and for which I prefer the new name Rhabditylenchida.

From this overview, it is noteworthy that, with exception of the Benthimermithida and Marimermithida, nearly no animal parasitic nematodes originated in the marine environment. "Zooparasitism originated under terrestrial conditions" (ANDERSON 1984: 319; see also MAGGENTI 1981: 248–250), even though in this context terrestrial in no way means "soil". The paraphyletic "Adenophorea" include a wide range of marine, freshwater, soil and plant-parasitic nematodes with some of them living commensalistic in cavities of the body of different marine organisms like Porifera, Echinodermata, Bivalvia or Crustacea. However, it is only exceptional that one of such associates lives at the expense of its host. *Theristus polychaetophilus* (Monhysterida) is temporarily ectoparasitic on the polychaete *Scolelepis squamata* (HOPPER 1966), three species of the Harpagonchinae (Chromadorida) are likewise ectoparasitic on polychaetes of *Aglaophamus* and *Hemipodus* (PLATANOVA & POTIN 1972), two *Domorganus* species (Ohridiidae) are perhaps endoparasitic in the intestine of the marine supralittoral oligochaets *Lumbricillus lineatus* and *Enchytraeus albidus* (VON THUN 1967; TCHESUNOV & STURHAN 2004), and species of Camacolaiminae exist in the body cavity of the polychaete *Syllis* sp. and even in Foraminifera (MILJUTIN 2004). The thousands and thousands of marine molluscs, polychaete worms, crustaceans and many other taxa almost without exception are free from parasitic "Adenophorea". If they possess parasitic nematodes at all, usually juveniles, these are descendants of primarily terrestrial Secernentea groups which secondarily invaded animals of the oceans. For parasitic nematodes, life in water inhabiting invertebrate and vertebrate animals was via a detour of life on land. "The nematode parasites of fish and marine mammals have their ancestral origins among terrestrial nematodes" (MAGGENTI 1981: 248).

With respect to parasitic "Adenophorea", there is an ecological "void in the sea" as was first realized by OSCHE (1966a). The existence of this vacancy is a mystery, as there has been a very long time (since the Precambrian) for nematodes to coevolution with the different clades of metazoa in different ecosystems. The deficiency of nearly all the different lineages of "Adenophorea" to evolve parasites must be explained by evolutionary ecology, and this is part of the "preadaptation concept" formulated by OSCHE (OSCHE 1956, 1962, 1963; MAGGENTI 1981: 259; SUDHAUS 1974, 2008; SUDHAUS & REHFELD 1992: 176; WEISCHER & BROWN 2000: 120). This concept must be illustrated in detail. It implies that special habitats, where nematodes can evolve physiological, ecological and ethological preadaptations for parasitism, are nearly nonexistent in the aquatic environment.

3. The "preadaptation concept" for understanding evolution of parasitism

With their vermiform body, resistant cuticle and internal fertilization, nematodes all in all appear preadapted for a life inside of animals. However, if free-living nematodes are accidentally ingested with some contaminated food, they usually are digested or, in a warm-blooded animal, die because of the heat. If the worms were able to survive for some days under certain physiological circumstances of the host (some cases mentioned below), they would not be able to reproduce and infest a new host with any degree of certainty. Such an "ecological saltation" from free-living to animal parasitic is not possible. There are too many problems for survival and reproduction that must be changed simultaneously by evolution and which would have to result all at once in stabilised attributes in the offspring to facilitate an endoparasitic life. A parasite e. g. in the intestine must tolerate or overcome

– (1) little partial pressure of oxygen,
– (2) high and changing osmotic pressure,
– (3) activity of digestive enzymes
– (4) and higher temperature (37–44 °C), if it is a warm-blooded host.
– (5) Moreover, it has to cope with the risk of failure in trying to infect a new host and therefore needs an infective stage
– (6) as well as a high rate of reproduction
– (7) and in consequence mechanisms that inhibit the development of a subsequent generation in the same host.

The first three or four problems are evolutionarily nearly solved by special adaptations of saprobiontic nematodes of Secernentea for a life in habitats formed by decaying organic matter that are short-lived (ephemeral) and patchily distributed like tiny islands:

– (1) In decomposing situations there is often a deprivation of oxygen. Nematodes living in these habitats can even survive anaerobic conditions for a certain period.
– (2) They have well developed regulatory mechanisms to accommodate changing osmotic pressure in their environment.
– (3) A rich coenosis of bacteria exists on decomposing substances, which release their enzymes into the substratum. The nematode cuticle is resistant to these exoenzymes.
– (4) An increase in temperature as a result of metabolic activity is well-known during composting, and nematodes living in decaying organic matter must tolerate this.
– (5) To live in patchily distributed ephemeral habitats formed by decomposing material requires for nematodes to get in contact (as a rule) with emerging insects of the same habitat that surmount the distance between such "islands" by flight and possess sense organs to find a fresh habitat of the same kind. Such an association for transport is known as "phoresy" or phoresis (see below), and the phoretic stage is the dauer larva. This dauer larva is an alternate third stage juvenile which does not feed, has a closed stoma and retains the moulted cuticle of the previous stage as a protective sheath. It represents an evolutionary novelty of the Secernentea to resist adverse conditions in the terrestrial environment for longer periods. In phoretic dauer larvae, recognition mechanisms to detect and use an insect (or another mobile animal) for transport and to react on triggers from a new habitat to disembark from the carrier are established. These sensoric-neurologic adaptations of the dauer larva in a phoretic association with an insect are preadaptations to the evolution of an infective stage as a parasite, which needs mechanisms to find and select a new host.

– (6) To establish a parasitic life cycle requires two further attributes. An increased reproductive capacity is necessary for parasites to compensate their great risk to colonise a suitable host. To complete their life cycles, they produce thousands or some of them millions of eggs. To reach a fresh habitat is also risky for nematodes inhabiting ephemeral biochores. Thus, we observe an increased number of (hundreds of) offspring compared with soil-inhabiting relatives. In comparing these two ecological groups, saprobiontic nematodes are more *r*-selected.

– (7) One restriction for an endoparasite with its unchanged high reproductive capacity is that it should pass at a maximum one generation within its host. (Rare exceptions include *Gynopoecilia pseudovipara*, some Oxyurida and the capillariid *Aonchotheca philippinensis* with its special facilities to produce two kinds of eggs. In these taxa and in the trichostrongylid *Ollulanus tricuspis*, the ascarid *Probstmayria vivipara* and in *Strongyloides stercoralis* endogenous autoinfection is possible: ANDERSON 2000.) Mechanisms are needed to arrest the development of eggs produced within the same host. Otherwise, with its raised reproductive potential, the parasite would overrun the host and cause its death very soon, thus destroying its environment, which would be the end for the parasite itself. This lineage would go extinct. In fact, parasites develop at the expense of their host which, however, they spare. Surprisingly, we observe in certain saprobiontic nematodes (rhabditids and diplogastrids), that they pass only one generation in the substratum, even though it is not exhausted (SUDHAUS 2008). They produce dauer larvae which need a chemical signal from a carrier (insect) that phoresy occurred, which at once is a cue that the habitat of the elder generation was left.

From the discussion of these seven points, we can conclude that several problems that are essential for a change to a parasitic way of life are "pre-solved" as adaptations to a saprobiontic life in ephemeral habitats. And such a syndrome of adaptations to "old" living conditions might serve as preadaptations to a new mode of life or ecological zone.

Because such saprobious temporary habitats that have to be bridged by a carrier exist only in the terrestrial environment, it is comprehensible why most parasitic lineages of nematodes belong to the primarily terrestrial Secernentea. Apomorphic characters that establish the Secernentea as monophyletic, like a dauer larva or an effective osmoregulatory secretory-excretory system with paired lateral canals within the epidermis, are adaptations to a terrestrial or even saprobiontic life. In contrast, as such a transitional ecological situation favoring the initiation towards parasitism is missing in the marine environment, "Adenophorea" nearly did not generate parasites. This example demonstrates that there exist no "empty niches", but ecological licences that only can be exploited if the organisms first evolved necessary preadaptations. Also, this example is one of the rare occasions in which evolutionary ecology can explain why a certain step did not happen, whilst we are usually satisfied if we can explain what happened in the course of evolution.

However, there exists the so far incomprehensible problem of the Benthimermithida (classified within Chromadoria) and Marimermithida (within Enoplia) mentioned above, where admittedly the knowledge on life cycles and relationships is quite insufficient to approach the question of their evolution, even though MALAKHOV (1994) pointed to related taxa of Marimermithida living as commensals. Convergently, both are parasitic in the juvenile stages in various echinoderms, polychaetes, priapulids and other taxa, obtain nourishment through the cuticle and epidermis (parenteral), and later quit the host in order to copulate and reproduce in the sediment using nutrients stored during the parasitic phase (TCHESUNOV 1997; MILJUTIN 2004). Their life cycle is reminiscent of that of the terrestrial Mermithida, which is the only lineage of invertebrate parasites that transferred into the aquatic (usually freshwater) environment and even reached the deep sea (TCHESUNOV & HOPE 1997).

4. The paraphyly of "Rhabditidae" and parasitic taxa within the Rhabditida

The "Rhabditidae" belong to the Secernentea. It is a diverse group. Nearly all of the 360 species classified in 37 genus-level taxa are saprobiontic and feed on bacteria. The species are characterised by a tubular stoma, a pharynx with a grinder in the terminal bulb and usually a copulatory bursa in the male. From sequence data (SUDHAUS & FITCH 2001; KIONTKE et al. 2007) supported by morphological characters "Rhabditidae" is paraphyletic, because the free-living Diplogastridae and the parasitic Strongylida are excluded on behalf of their completely different bauplan with respect to buccal cavity, pharynx and male caudal region. According to our current knowledge, the sister taxon of Diplogastridae is *Rhabditoides inermis* and the sister

taxon of Strongylida is *Heterorhabditis* (SUDHAUS & FITCH 2001; KIONTKE et al. 2007), both members of the "Rhabditidae". Possibly also *Agfa*, *Angiostoma*, *Carabonema*, *Noteodiplogaster* and certainly Rhabdiasidae originate within "Rhabditidae". At present they cannot be placed with certainty because they are morphologically very distinct and no molecular data are published. The encompassing monophylum of all groups mentioned in this paragraph is called Rhabditida (Fig. 3).

Several descendents of the stemspecies of Rhabditida independently became parasitic. Three taxa belong to the Diplogastridae: all species of *Cephalobium* and *Mehdinema* are parasitic in the intestine of crickets, *Longibucca* species are parasitic in the gut of different tetrapods (SUDHAUS & FÜRST VON LIEVEN 2003). *Carabonema*, *Oryctonema* and *Noteodiplogaster* are parasitic in beetles, *Agfa* in the genital tract of terrestrial gastropods, *Angiostoma* in the gut of slugs and amphibians, Strongylida in tetrapods, primarily in their intestines, and Rhabdiasidae are lung parasites of amphibians and reptiles. Angiostomatidae (*Angiostoma*) "quite possibly … established themselves first in gasteropods [sic!] and then in the amphibians that fed on the latter" (DOUGHERTY 1951: 362). Besides these groups, where all species live as parasites, there are individual parasitic species that have arisen within a mostly free-living group. In the Diplogastridae, this latter situation applies to *Diplogastrellus secundus* and *Mononchoides aphodii* (SUDHAUS & FÜRST VON LIEVEN 2003), both larval-parasitic in the body cavity of dung beetles, and perhaps applies to certain species of *Parasitodiplogaster* in fig wasps (GIBLIN-DAVIS et al. 2006). In the "Rhabditidae", some species of *Parasitorhabditis* and *Oscheius* are larval-parasitic in beetles (SUDHAUS 1976), *Teratorhabditis brevicaudata* in the intestine of a mole-cricket (LATHEEF & SESHADRI 1972), and species of the *Pelodera Strongyloides*-group are larval-parasitic in rodents (see below).

Thus we can summarize, that from the preadaptive plateau established by "Rhabditidae" and retained by Diplogastridae parasitic species arose frequently and nearly at any geological time since the Silurian (Devonian after MALAKHOV 1994: 197). Mentioned are 17 such lineages. "The Rhabditina are a veritable laboratory of evolutionary parasitism" (DOUGHERTY 1951: 362). The questions must be asked: what is the preadaptive plateau for the multiple evolution of parasitism in these nematodes, and what are first steps we might observe today.

5. The preadaptive plateau: special associations of "Rhabditidae" species with different animals represent gliding transitions to parasitism (Fig. 2)

Droppings of cows and other big mammals are patchily distributed saprobious habitats for rhabditids and diplogastrids and are decomposed maximally after two
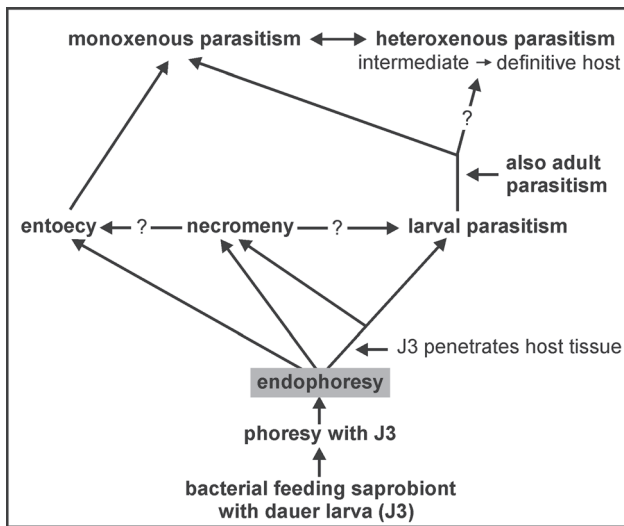
Fig. 2. Different associations of Secernentea with other organisms as intermediate evolutionary steps towards a parasitic habit (modified after SUDHAUS 2008). The starting point was the saprobiontic nematodes that possessed a dauer larva to survive adverse conditions. This stage became the phoretic larva, which was transformed in parasites to the infective larva. Endophoresy (inside the body of the carrier) played a crucial part in evolution and opened different evolutionary alleys: to entoecy (where the life cycle is completed within an animal without living at its expense), necromeny (waiting for the cadaver), and larval parasitism. From entoecy and larval parasitism, it appears to be only a small step to adult parasitism also, when the nematodes develop to the adult stage and reproduce within the host at its expense. The life cycle can be direct, with only a single host (monoxenous), or indirect, with a change between two or more hosts (heteroxenous).

months. Several species adapted to fresh dung only pass through one generation in this substratum. The third juvenile stage is the special dauer larva, which searches for a dung beetle and attaches there, to be transported like with an air-taxi to a fresh cow pat. This behaviour to use a carrier for transportation to a new habitat is generally termed "p h o r e s y" (LESNE). It requires special adaptations of the dauer larva, like recognition mechanisms and behaviour, to find the carrier and a suitable place on or in it and to respond to signals from the surroundings, to leave the carrier in a habitat appropriate to the species to continue its development. As these ephemeral habitats are unpredictable in space and time and distributed like small islands, which cannot be reached by nematodes on their own, to be phoretic is a prerequisite to colonise such habitats. To increase the probability to come into contact with a prospective carrier, many dung-inhabiting nematodes show a special behaviour we call „waving": the dauer larva lifts the anterior body from the substrate, stands on its tail and

waves back and forth. Waving is an adaptation to phoretic behaviour; however, as described below, it has been retained in many nematodes that shifted to a life as a parasite or a parasitoid to come into contact with their host.

The same ecological situation found with dung inhabitants can be observed in saprobiontic nematodes developing on carcasses, in exudates of trees, in tunnels of insects developing in wood or different plants and similar temporary biochores. Here we find many unanticipated life cycles and special adaptations of nematodes resulting from co-evolution with insects in small biocoenoses. Special adaptations of the dauer larvae are abilities to locate specific places for transportation like the intersegmental furrows of the abdomen or between genital structures of special insects or the gill chamber of wood lice (like in *Caenorhabditis remanei*). Others find shelter entering the rectum, sometimes up to the malpighian tubules (*Parasitorhabditis* in bark-beetles), the reproductive system (*Paroigolaimella coprophila* in flies) or the pharyngeal glands in the heads of ants or termites like different rhabditid and diplogastrid species. We specify such a behaviour of transport inside the body of an animal as internal phoresy or "e n d o p h o r e s y" and distinguish it from "ectophoresy" if it is reasonable. Recently, we investigated how slugs and snails act as (slow-going) agents of dispersal of rhabditids. Feeding on rotten fruits, for example, they ingest nematodes like *Caenorhabditis* species and transport them viable over several days inside their intestine to new substrates. Endophoresy adopts a key position in the evolution of associations exemplified in the next paragraphs, like necromeny, "entomo-parasitoidy" (= entomopathogeny) and larval parasitism.

From endophoresy it is only a small step to what we termed "n e c r o m e n y" (SUDHAUS). In this association dauer larvae enter a living animal and wait for the death of the carrier to develop on the decomposing carcass by feeding on growing bacteria. There exist several examples of necromenous rhabditids and diplogastrids in earthworms, slugs, millipedes, and cock chafers.

From endophoresy and particularly from necromeny, it is a small step to "e n t o m o p a t h o g e n y". Entomopathogenic nematodes are not real parasites that only live at expense of a host, but they reproduce inside a host and finally kill it with the aid of insect-pathogenic bacteria, so that in this respect they behave like parasitoids, a term that was already used for mermithid nematodes (KAISER 1986; POINAR & POINAR 1999: 150). Therefore it appears more accurate to call them "entomoparasitoids" and the association "e n t o m o p a r a s i t o i d y". The two secernentean entomoparasitoid taxa *Heterorhabditis* and *Steinernema* independently evolved a parasitoid life cycle mutualistically associated with pathogenic bacteria (*Photorhabdus* and *Xenorhabdus*, respectively) they feed upon and which actually kill the insect.

A possible uncomplex transition from endophoresy is also l a r v a l   p a r a s i t i s m , where the young nematode gets nutrition from the carrier. In some of the examples mentioned under endophoresy are candidates that take in nutritive substances while waiting in glands or the hind gut of an insect to reach a new habitat. Here the life cycle of *Pelodera cutanea* of the *Pelodera Strongyloides*-group shall be portrayed (SUDHAUS et al. 1987). This species lives in the nests of wood mice *(Apodemus)* and feeds on bacteria. To colonise a new nest the "endophoretic" larva uses the rodent. It has been modified to a special infective larva, which is sensitive to heat, thus finds the mouse, invades the skin through a hair follicle and leaves it later in a new nest to join others that initiate a new colony. Meanwhile, however, it uses the tissue to obtain nutrients from the host by assimilating them through the body surface (parenteral). Thus, the species became a parasite only in this infective larva stage, which is formed under certain environmental conditions. Some more species of this group are on the borderline between being saprobiontic and parasitic. In the laboratory it is possible to cultivate them indefinitely without a mouse. The closely related *Pelodera strongyloides dermatitica*, which accidentally was larval parasitic in the skin of a cow, has been bred on agar plates since it was collected 62 years ago (SUDHAUS & SCHULTE 1988).

With the last example of seemingly free-living species, that in the wild ultimately must pass through a larval-parasitic phase from time to time, the Rubicon to a parasitic life is crossed. From larval parasitism it appears only a small step to parasitism as adults that above all reproduce at the expense of the host. Although the *Pelodera Strongyloides*-group is not the sister group of the Strongylida, its species in a certain respect might serve as "models" for incipient steps of strongylid evolution (SCHULTE & SUDHAUS 1988). This appears obvious from the ancestral life cycle of Strongylida as discussed in chapter 6.3.

6. Preparatory stages toward parasitism and obligatory parasites retaining a free-living saprobiontic phase

6.1. Current facultative parasites as models of transitory steps to obligate parasitism

We learned from the marine "Adenophorea" that the ecological licence (opportunity) for parasitism offered only by the presence of diverse potential hosts is not a sufficient condition for the evolution of parasitism. At the same time, organismic licences of the nematodes are required in order to attack a living animal and feed upon it. The preadaptation concept implies that a complex of adaptations was additively established in nematodes evolving toward a life in saprobious and ephemeral substrates, which finally – as

preadaptations – organismically licenced the step to a parasitic life history (SUDHAUS 1976: 143–146). Such preadaptations were, among others, the formation of a dauer larva, its contact with a different species, its ability to penetrate animal tissue and its reaction to specific triggers from an organism and a habitat. In secernentean nematodes, we find all transitionary stages between and including free-living saprobionts and obligatory parasites, such as those that have a tight relationship with a host animal, those capable of living temporarily inside a host, and those that are facultative or partial parasitic forms. Somewhat like a snap shot, these examples serve as "models" to illuminate the different sequences and pathways to endoparasitism that took place again and again during the phylogeny of saprobiontic Nematoda. "Even in our time, many forms … are making the transition to parasitism … and in the future, the saprobionts still will serve as a source of new taxa of parasitic nematodes" (MALAKHOV 1994: 197, 200). From the preadaptive platform, only certain steps are possible; however, these can occur consistently and canalise parallelisms in certain traits. More than pure models for further discussion on transformations in the past, such real organismic models of beginnings and transitions comprise an explanatory principle, particularly because the life cycles of nematodes showing different types of intimate associations with terrestrial arthropods and gastropods can be studied in all details.

Only a few facultative or partial parasitic ("pre-" or "pseudo-parasitic") nematode species should be mentioned, which stand on the borderline between a saprobiontic and a parasitic mode of life in warm-blooded animals. In mammals, different nematodes like *Diploscapter coronatus*, *Panagrellus redivivus* (syn. *Cephalobus parasiticus*), *Rhabditophanes* sp. and others which were occasionally ingested with food, under certain conditions like paucity of gastric acid could persist in the intestine and eventually even develop to the adult stage and multiply there (ATHARI & MAHMOUDI 2008; CHANDLER 1938; SANDGROUND 1939). Adult *Caenorhabditis avicola* were detected in the intestine of a songbird, and *Caenorhabditis bovis* and *Rhabditis blumi* could colonise inflamed outer auditory canals of zebu cattle and propagate there (KIONTKE & SUDHAUS 2006). The rhabditid species erroneously named *"Diplogaster" parasitica* populated a buccal pouch of the bush pig *Potamochoeres porcus* (MARLOW 1955), and on various occasions the panagrolaimid *Halicephalobus gingivalis* was found in tumours of the oral cavity or nares of horses (ANDERSON & BEMRICK 1965). Since 1975 there are four records of *Halicephalobus* even in human (ONDREJKA et al. 2010). Morphologically all these species are not different from their closely related free-living relatives, but they exhibit physiological and biochemical adaptations and withstand environmental temperatures up to 37 °C.

6.2. Alternation of free-living and parasitic generations

Likewise in favour of the hypothesis that life in saprobious and ephemeral organic matter was the starting point for parasitic nematodes are special taxa with an alternation of generations partly or completely within a host and outside the host. In *Alloionema appendiculatum*, third-stage juveniles are parasitic in a slug, but mature outside after quitting the host or developing on the cadaver. It is striking that at least one free-living bisexual generation follows which structurally differs in corresponding stages from that of the parasitic phase (different authors' and my own observations). Very similar complex life cycles exist in Rhabdiasidae and Strongyloididae. Both *Rhabdias* and *Strongyloides* are primarily heterogonic with a free-living generation consisting of bacteria-feeding males and females giving rise to infective larvae, which penetrate the skin of a tetrapod and migrate via the blood system and lungs to start an autogamic parasitic generation. In Rhabdiasidae, protandrous hermaphrodites with female morphology live and reproduce parasitically in the lungs primarily of amphibians, whereas *Strongyloides* exhibits parthenogenetic females living in the gut mostly of mammals. In its sister taxon *Parastrongyloides* however, the parasitic generation (in marsupials and insectivores) also has males and females, which probably is ancestral for Strongyloididae. Based on morphological divergence (the free-living generation of *Rhabdias* is similar to rhabditis and that of *Strongyloides* is similar to *Rhabditophanes* and *Alloionema*; see Dougherty 1951: 362) and presumed ancestral hosts (amphibians versus mammals) indicating different periods of origin of parasitism (presumably Carboniferous and Cretaceous ages, respectively), heterogony should have evolved independently in both lineages.

This is in contrast to the conclusion by Dorris et al. (2002) on the strength of their molecular phylogenetic analysis and a resultant clade consisting of *Steinernema*, *Rhabdias*, *Rhabditophanes* and Strongyloididae (branching in that sequence). In this study, however, there exists a long branch problem in these groups with respect to the gene used, some important relatives are disregarded, and it is difficult to reconcile the consequence that in *Rhabditophanes*, with its exclusively free-living existence, the parasitic generation must have been abandoned ("the first known example of reversal of parasitism in a metazoan": Dorris et al. 2002: 1515). Passing the bisexual generation in soil mixed with faeces of the host indicates that, in both lineages, preadaptations for a parasitic life were evolved in a saprobiontic situation.

6.3. The evolution of Strongylida

Strongylida, whose adults exist in the digestive tract of tetrapods and ingest nutrients through their mouth, can be traced back to saprobiontic rhabditis (see above). Its ecological niche consists of two phases: free-living as juveniles and parasitic in the last two stages. The eggs pass out in the faeces of the host and develop in the droppings, where the juveniles live, having a rhabditoid stoma and pharynx with a grinder to chew the bacteria they feed upon. The two "rhabditiform" stages are nearly indistinguishable from juvenile rhabditis. Instead of a dauer larva, Strongylida exhibit an infective larva, which retains the cuticle and relatively long tail of the second stage and, like many saprobiontic nematodes, performs waving to increase the chance of getting contact to a potential host. Then it enters the host primarily through the skin (like the hookworm *Ancylostoma*), sheds the outer cuticle, invades lymphatic capillaries and is carried via the heart to the lungs, from where it (meanwhile in the fourth stage) migrates along the trachea, is swallowed and reaches the intestine to become an adult and reproduce.

Thus, Strongylida recapitulate the ecological situation and phylogenetic stage we believe was transitional in the ancestral lineage when becoming an endoparasitic nematode. From the percutaneous infection and the common tissue phase in the host we may conclude that the parasitic-living might have started larval parasitic in the skin of the host like in the *Pelodera* spp. discussed before. Then parasitic feeding extended to later stages and was accompanied by a drastic evolutionary change in the bauplan. The main transformations applied to the adult (though starting earlier in ontogeny), where the buccal cavity became much more complicated, the pharynx lost the grinder and muscles invaded the rays of the copulatory bursa, with which the male can grasp the female's body for copulation like closing a hand. This type of mating was an adaptation to the gut motility. Concerning the primary host of Strongylida, it can be supposed that it was an ectothermal animal with a relatively thin skin furnished with many glands, and without a very effective immune system. Also, from the phylogenetic age of the host range, it can be suggested that Strongylida might have originated at least in the Triassic period. It is hardly conceivable that the ancestor could have been primarily parasitic in insects like those in the sister group *Heterorhabditis*. Thus, I disagree with Blaxter (2001) who suggested that penetrating the body wall in Strongylida and *Heterorhabditis* is homologous, which would call for an ancestor of both living parasitically in insects (or tetrapods) and that in one of the lineages the host was totally changed. Even more, the mutualistic association with bacteria, including their transport in the interstine of the infective larva, and the alternation of generations with different modes of reproduction (hermaphroditic and gonochoristic) inside an insect must be judged as evolutionary novelties of *Heterorhabditis*.

Tab. 1. Data to life cycles and hosts in stemspecies of respective groups of Spiroascarida (J1 to J3 = juvenile stages).

	Ascaridida	**Gnathostomatida**	**Oxyurida**	**Rhigonematida**	**Spirurida**
life history	monoxeny	heteroxeny	monoxeny	monoxeny	heteroxeny
only host or intermediate host	tetrapod	copepod	insect (or diplopod?)	diplopod	arthropod
infective stage for that host	free-living J3	hatched J2	egg containing J3	free-living juv. (which stage?)	egg containig J1
manner of entering that host	actively	passively	passively	unknown	passively
external stages	egg and J1 to J3	egg and ensheathed J2	developing egg	at least egg, J1 and J2	developing egg
hatching egg	in the open	in the open	after ingestion	in the open	after ingestion
first moult	in substratum	within egg	within egg	in substratum	in gut of host

6.4. What the Cosmocercidae tell us about the evolution of Ascaridida

Cosmocercidae are basically parasites in the rectum of amphibians and secondarily also in terrestrial gastropods (this transfer occurred several times independently: MORAND 1988). Cosmocercidae belongs to the Spiroascarida and are usually positioned as the first branch of Ascaridida (CHABAUD 1957; NADLER et al. 2007). Therefore the development of three juvenile stages outside the host, infection by the third stage by skin penetration and lung migration in Cosmocercidae occurred convergently to the same traits in Strongylida. Without taking reversions into account, free-living juveniles must be assumed for the ancestral lineage of Ascaridida and at the same time as the initial situation for the other clades of Spiroascarida (Fig. 3). Also in Gnathostomatida and Rhigonematidae exist juveniles outside the egg and a host (Tab. 1). The consequences are discussed in the following chapter.

7. Hypotheses for the Spiroascarida lineage and descendant parasitic groups

> "The life history of parasitic forms constitutes one of the most intricate and interesting subjects in the whole field of biology."
> STUNKARD (1929: 352, 1953: 8)

7.1. The mode of life of the Spiroascarida stemspecies

In comparison to the parasitic groups discussed before, we are more in the dark about initial steps to parasitism in the Spiroascarida. I reject the concept of MALAKHOV (1994: 200) that "the primary hosts of this nematode group

were aquatic (freshwater) ancestors of vertebrates". This must be justified. We can approach the problem hypothetically. In all reconstructions of phylogeny with molecular data (BLAXTER et al. 1998; BLAXTER 2001; VAN MEGEN et al. 2009) Spiroascarida is the first branch of Secernentea, which encompasses not less than five exclusively parasitic taxa (Ascaridida, Gnathostomatida, Oxyurida, Rhigonematida and Spirurida) as surviving clades of the first radiation (Fig. 3). Though adults of Ascaridida, Gnathostomatida, Spirurida and part of the Oxyurida (the Oxyuridae) are parasitic in vertebrates, this cannot apply for the ancestral lineage of the Spiroascarida. The stemspecies of the Spiroascarida crown group lived long before vertebrates became terrestrial in late Devonian times.

The stemspecies of Secernentea must have lived in a terrestrial environment presumably in the Silurian period. In this lineage, a dauer larva was evolved which could be used as an infective larva and thus was one precondition for parasitism. We might speculate that species of the ancestral lineage of Spiroascarida also lived as saprobionts in decaying organic matter and were associated with arthropods for transport, using the dauer larva as a phoretic stage. Since – parallel to the nematodes – arthropod groups emerged on land and offered ecological licences for parasitic habits since Silurian times, it seems self-evident that the first hosts in the Spiroascarida lineage were likely to be arthropods.

There is some evidence on the possible lifestyle of the stemspecies of the Spiroascarida crown group (that is, the stemspecies of exclusively all existing Spiroascarida taxa). The first piece of evidence comes from the phylogenetic tree (Fig. 3). Oxyurida (like Thelastomatidae) primarily live in the rectum of inects and Rhigonematida in the rectum of diplopods, where the faeces are produced and a special biocoenosis of bacteria and fungi exists. Apart from oxygen tension, the conditions here inside a host are not very different from emitted faeces in the environment,
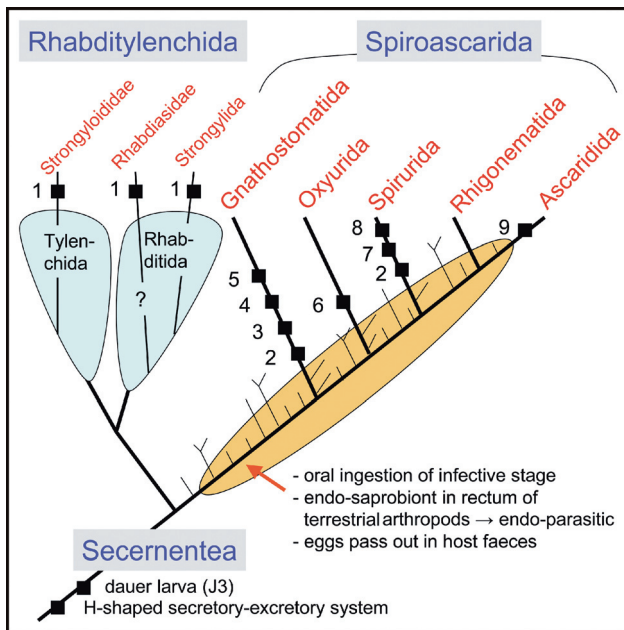
Fig. 3. Branching diagram showing high-ranked taxa of Secernentea (after BLAXTER 2001, NADLER et al. 2007, VAN MEGEN et al. 2009) and the origin of five monophyletic zooparasitic groups of the Spiroascarida by successive speciation. The original life history of the Spiroascarida is characterised in the oval beige field. From the respective ancestral lineages toward the stemspecies of recent (crown) groups, hypothetical blind side branches point to extensive extinction due to a demise of host groups and competition by representatives of the modern nematode groups. Black squares are apomorphic traits of life cycles: 1) skin penetration by the infective larva (J3) and lung migration, 2) heteroxenous (arthropod → vertebrate), 3) copepod as intermediate host, 4) first moult inside egg, 5) J2 retains cuticle of J1, 6) two moults inside egg, 7) J1 hatches in an arthropod, 8) J1 bores through the gut, 9) monoxenous in a tetrapod.

where representatives of the ancestral lineage presumably lived (similarly already in BAYLIS 1938). Even today Oxyurida as well as Rhigonematida can live outside in the faeces of their host for several weeks (ADAMSON & VAN WAEREBEKE 1985; SUDHAUS 2008). Both taxa retained the rhabditoid pharynx with a grinder in all stages and as entoecs or "endo-saprobionts" feed on bacteria and fungi. Only from this sort of nourishment is it explainable that carnivorous species arose both within the Rhigonematida and Thelastomatidae (Oxyurida) living on other nematodes within the host (OSCHE 1966b: 115; VAN WAEREBEKE 1986; HUNT & MOORE 1999; HUNT 1999). In addition some absorption of nutritive substances from the hosts intestine is possible (HOMINICK & DAVEY 1973). If it turns out that the tree is robust and Oxyurida and Rhigonematida are not sister groups as was thought earlier, we may further conclude that the stemspecies of Spiroascarida lived ent-

oecically/endo-saprobiontically or partly endo-parasitically in the hindgut of a terrestrial, saprophagous arthropod (SUDHAUS 2008) and had the dauer larva transformed into an infective larva, which had to be ingested with contaminated food. Such a scenario would be even further supported if it turns out that Rhigonematida is polyphyletic (ADAMSON & VAN WAEREBEKE 1985; NADLER et al. 2007; VAN MEGEN et al. 2009). As discussed before about the Cosmocercidae, the first three juvenile stages should have been free-living, the fourth stage and adult adapted to an anaerobic environment in the rectum of a saprophagous arthropod and the eggs passed in faeces of the host to the external environment. From this supposed basic situation, the alterations in the different lineages shall be discussed (compare Fig. 3).

7.2. Possible derivation of different lineages

The first branch is the G n a t h o s t o m a t i d a containing basically stomach parasites of tetrapods. Its heteroxenic life cycle is hard to derive from that reconstructed for the Spiroascarida stemspecis and thus is challenging for the evolutionary scenario developed here. Many apomorphic traits must have evolved in the ancestral lineage of Gnathostomatida towards the stemspecies of its crown group. Freshwater was invaded, where the eggs develop. The first moult occurs in the egg and is incomplete, so that the hatching second-stage juvenile retains the cuticle of the first stage. This stage must be ingested by a copepod as the intermediate host, where it penetrates the intestine and develops in the haemocoel to the infective third stage. An infested copepode then has to be swallowed by the definitive host or first by a paratenic (transport) host, which serves to tranfer the parasite to the definitive host (ANDERSON 2000).

The O x y u r i d a retained the monoxenous (direct) life cycle as reconstructed for the Spiroascarida stemspecies, but suppressed the free juvenile stages. Only the egg is outside and development occurs under aerobic conditions. Two moults occur inside the egg, the first moult outside the host and the second after the egg has been ingested by an arthropod, triggered by substances in the digestive tract; and shortly afterwards the infective third stage hatches (TODD 1944). Transfer to tetrapods succeeded at least in the Mesozoic.

S p i r u r i d a adults are mainly parasites of the stomach and intestine of vertebrates and in juvenile stages are parasites of arthropods. In the lineage from a species presumably living in the rectum of an arthropod to the stemspecies of the Spirurida crown group, a heteroxenous life cycle was established, where an original arthropod host became the intermediate host while a vertebrate was acquired as definitive host, where the parasite reached maturity. This

new way of life eventually was possible when a certain vertebrate frequently fed on infested arthropods, so that different stages of the nematodes from the arthropod were exposed to conditions inside the gut of the vertebrate over and over again, and the eggs of the parasites leaving the vertebrate host with its faeces were ingested by the same arthropods living as scavengers. In such a predictable scenario, a parasitic cycle could be stabilised by obligatorily separating the life cycle into two parts, in which the third stage played the crucial role for host change, initiated phylogenetically by features of the dauer larva and the infective larva, respectively. The evolution of the life cycle of the Spirurida furthermore required an alteration in behaviour and nutrition of the juveniles. The first juvenile eclosing from an egg (being triggered on ingestion by an arthropod) had to penetrate the wall of the intestine, became larval parasitic in the body cavity, was encapsulated after two moults in the third stage, and waited for signals from the definitive host to continue its development. The other possibility (Sudhaus 2008) is that the ancestors in the lineage of Spirurida, in parallel to certain Oxyuridae, transferred to vertebrate hosts and in a later step acquired an insect as intermediate host, thus becoming heteroxenous. This appears more complicated, and more evidence is still required to decide between these possibilities.

Development of R h i g o n e m a t i d a eggs outside the host and the mode of infection of Diplopoda seems almost unknown (Adamson & van Waerebeke 1985). However, in different species of one clade within this group (the Ransomnematoidea) Spiridonov (1989) observed hatching of the first-stage juvenile and its moulting in water, so that here the second or third stage could be the infective stage. In Rhigonematoidea on the other hand juveniles beginning with the first stage already were found in the gut of diplopods (Hunt & Moore 1999).

7.3. The origin of and evolution within the Ascaridida

From the relationship of Oxyurida and Ascaridida, a transfer from insects to tetrapods in the ancestral lineage of Ascaridida was already postulated by Dougherty (1951). Also, Anderson (1984: 320) presumed that they "first established themselves as monoxenous forms in the earliest land vertebrates". With respect to the Cosmocercoidea, the stemspecies of Ascaridida had three free-living juvenile stages and a parasitic phase in a tetrapod. Also the adults were primarily feeding on bacteria as could be observed in *Cosmocercoides dukae* (Ogren 1953). On this basis, the indirect life cycle within ascarids occurred secondarily by acquiring an arthropod as an intermediate host or as a paratenic host with a different vertebrate as intermediate host. In parallel to the Spirurida, in the Subuluroidea, the first three stages developed in an arthropod intermediate host and continued in a (warm-blooded) vertebrate fi-

nal host after it had eaten the infested arthropod. The eggs hatched in the intestine of an insect, the first stage juvenile penetrated the wall and developed – becoming encapsulated – to the third stage, which retained valves in the terminal bulb of the pharynx (Anderson 2000).

In Ascaridoidea, a heteroxenous life cycle was established in aquatic habitats characterised by several apomorphies. The first moult occurred in the egg, the second-stage juvenile (J2) retained the cuticle of the J1, this stage was ingested by a crustacean and transmitted in the food chain to a fish as intermediate host and finally to a fish-eating vertebrate. In the course of evolution, the intermediate host could be replaced by an invertebrate paratenic host, and certain lineages (e. g. *Ascaris*, *Toxocara*) became secondarily monoxenous (Anderson 2000). Heterakoidea are gut parasites of tetrapods, which are interpreted as secondarily monoxenous (Chabaud 1957). After two moults within the eggshell, the egg contains the infective third-stage larva.

7.4. Concluding remarks

If this scenario comes close to what in fact happened in the past, all possibilities for retaining or changing the primary life cycle of early Spiroascarida were realized.

– (1) The original entoecic/endo-saprobiontic life in the gut of an arthropod was retained in Oxyurida and Rhigonematida.

– (2) A vertebrate was acquired as definitive host and the original host became the intermediate host in Spirurida.

– (3) A transfer to a vertebrate host occurred in Ascaridida.

– (4) From a recent study by Saad et al. (2009) it could be followed that, in the Gnathostomatida, first a transfer to a tetrapod happened and later an intermediate host (a crustacean) was acquired.

This attempt to discuss the knowledge on life cycle features within the framework of phylogeny reconstructed with molecular sequence data demonstrates the immense difficulties in deriving the completely different life cycles of major groups from that reconstructed for the Spiroascarida stemspecies (compare Tab. 1). To get a coherent evolutionary history from different sources of information, much more research is needed, both on the phylogeny and the evolutionary ecology of these different groups, including a number of hitherto neglected taxa.

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