

Relations between free-living nematodes and dung-burying *Geotrupes* spp. (Coleoptera : Geotrupini)

Ragnar KÜHNE

Institut für Zoologie, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany.

Accepted for publication 4 May 1995.

Summary – The nematode fauna of more than 300 brood balls of the beetle species *Geotrupes spiniger* and *G. vernalis* was determined. In this context the insect biology was studied, also. The succession of nematodes in nine *G. spiniger* brood balls and six *G. vernalis* brood balls was observed in the course of the entire individual development of the beetles. The results show that *Diplogaster hirschmannae*, *D. henrichae* and *D. labiomorphus* are nematodes which have specialised in phoresy on *Geotrupes* beetles. Experiments on the generation time and number of offspring of these three diplogasterids show adaptations of the reproduction strategies to life in the brood ball. The nematodes are in a position to live on the limited resources of food until the young beetle pupates. Only then many second-stage juveniles develop into dauer larvae. The dauer larvae seek shelter in the genital region of the newly hatched beetle. There they stay until their carrier has started to build a brood burrow.

Résumé – Rapports entre les nématodes libres et les espèces de *Geotrupes* (Coleoptera : Geotrupini) bousiers terricoles – La faune nématologique dans plus de 300 ballots couvés des coléoptères *Geotrupes spiniger* et *G. vernalis* et la biologie des insectes ont été étudiées. La succession des espèces de nématodes dans neuf ballots couvés de *G. spiniger* et dans six ballots couvés de *G. vernalis* a été enregistrée au cours du développement individuel des coléoptères. Les résultats montrent que *Diplogaster hirschmannae*, *D. henrichae* et *D. labiomorphus* sont des nématodes qui se sont spécialisés dans la phorésie avec les coléoptères *Geotrupes*. Les résultats des observations concernant la durée des générations et l'importance de la descendance montrent une adaptation des stratégies de reproduction à la vie dans le ballot couvé. Les nématodes sont en mesure de vivre avec des ressources limitées de nourriture jusqu'à la formation de la larve en chrysalide. C'est ensuite que des dauer larvae sont formées. Les dauer larvae se mettent à l'abri dans la zone génitale du coléoptère nouvellement sorti. Elles y restent jusqu'à ce que l'insecte commence le creusement du terrier pour couvrir.

Key-words : Brood ball, *Diplogaster*, dauer larvae, generation time, offspring, phoresy.

In general, many nematode species living in ephemeral habitats can be transported as dauer larvae into another saprobiotic substrate by insects (Sudhaus, 1976). Such a temporary bond between carrier and carried is called phoresy. The phoretic resting form is a modified third instar juvenile (dauer larva).

Dauer larvae from the genus *Diplogaster* frequently have been found in the genital apparatus of dung-burying *Geotrupes* beetles (Bovien, 1937; Sachs, 1950; Théodoridès, 1955). In the present case of phoretic bond between beetles and nematodes, it was surprising to find that the dauer larvae were not able to develop further even after transferring them onto different kinds of mammal excrements.

Sachs (1950) succeeded in rearing some dauer larvae until they reached their adult stage. He described the species *Diplogaster hirschmannae* Sachs, 1950 which he also detected in the brood balls of beetles. Thus it is a species which seemed to be specialised in living in the *Geotrupes* brood ball. *Diplogaster henrichae* Sachs, 1950 – originally found in cow-pats – and *Diplogaster labiomorphus* Kühne, 1995 also show a strong bond with geotrupinids (Kühne, 1993).

Materials and methods

In order to investigate the life cycles of the nematodes linked to *Geotrupes*, it was necessary to examine the biology of the beetles more closely. The dung-beetle species *Geotrupes spiniger* Marsh., and *G. vernalis* L. were observed in field studies and in the laboratory.

G. spiniger mostly occurred in pairs in droppings in pasture lands. *G. vernalis* could be found in mixed forests – often at a higher number of individuals in the same dung pat. Individuals of both species were collected from spring till autumn. The origin of all beetles cultivated was Berlin and vicinity (Germany). Females and males of *G. spiniger* were kept in special observation cages (Fig. 1). *G. vernalis* formed brood balls only in larger breeding containers ($\varnothing = 25-35$ cm).

After the brood balls (without surrounding soil) and the eggs had been transferred into small breeding boxes ($\varnothing = 8$ cm, $h = 3$ cm), the individual development of *G. spiniger* and *G. vernalis* could be observed until the young beetles were hatched. They were reared at 17-18 °C, and the brood balls were kept moist during this time.

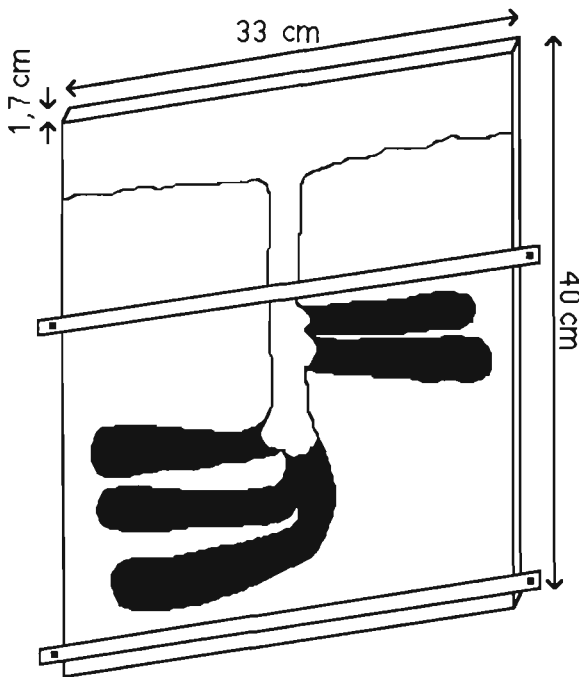


Fig. 1. Observation cage for dung-burying beetles.

The nematode fauna of more than 300 brood balls was determined by the Baermann method in sample tests. Brood balls of *G. spiniger* that had been dug out in the field were compared with brood balls that had been produced by beetles in the laboratory. The beetles put together for breeding in the laboratory had been kept in a dry environment for 1-2 days to dry up the nematodes on their surface (except of the dauer larvae).

Identification of nematodes was made using data of Rehfeld (unpubl.), Sachs (1950), Weingärtner (1955), Meyl (1961), Goodey (1963), and Andrassy (1984).

The succession of nematodes in nine *G. spiniger* brood balls and six *G. vernalis* brood balls was observed throughout the beetle's entire individual development. Substrate samples were taken every 5-7 days from the brood balls, and the nematodes were determined and counted.

To assure comparability of the individual cases, each point in time was related to a certain stage of development of the beetle, e.g., L 50 refers to the point when about 50 % of the larval development of the insect was completed, P0 means pupation just completed (see legend of Fig. 3). This transposition of the time scale into another reference scale was necessary, as the development times of the beetles fluctuated considerably in individual brood balls. The new reference scale made it possible to average the measuring data from different brood balls and to show them in a system of coordinates.

The data were averaged according to the following formula :

$$N_{mean,t} = \frac{1}{n} \left(\frac{N_{1,t}}{N_{1,max}} + \frac{N_{2,t}}{N_{2,max}} + \frac{N_{3,t}}{N_{3,max}} + \dots + \frac{N_{n,t}}{N_{n,max}} \right) \times (N_{1,max} + N_{2,max} + N_{3,max} + \dots + N_{n,max}) / n$$

where :

$N_{mean,t}$ = mean number of individuals of all compared brood balls at the time of development t

$N_{n,t}$ = number of individuals from brood ball n at the time of development t

$N_{n,max}$ = maximum number of individuals in the brood ball n

n = number of brood balls compared

This formula prevents brood balls containing many individuals from excessively influencing the result.

For a more precise understanding of the development of population in the brood balls, further studies were carried out on the generation time and reproduction rates of the nematode species to be compared. Over a period of 16 days at 17-18 °C, the offspring of fifteen females each of the species *D. henrichae*, *D. hirschmannae*, and *D. labiomorphus* were counted daily. For the experiment, one female just turned adult and two males of the same age were put into a small well ($\varnothing = 7$ mm, $h = 6$ mm) with a small amount of cow dung on a 2 % water-agar layer. An indefinite number of dauer larvae of *Rhabditis icostiensis* was also placed into the vessels of *D. hirschmannae*, in order to supply the adults with food. *D. hirschmannae* is predatory in the adult stage, at least optionally, whereas *D. henrichae* and *D. labiomorphus* feed exclusively on bacteria.

Results and discussion

OBSERVATIONS CONCERNING THE BIOLOGY OF GEOTRUPES BEETLES

The geotrupinids practice parental care (v. Lengerken, 1954; Howden, 1955), i.e., the parents build an individual food reserve for each of their offspring (Fig. 2). Often the sexual partners help each other in building brood balls. However, females can carry out all kinds of work on their own, too. In the case of *G. spiniger*, the male helps in excavating the main shaft and the brood chamber and in carrying in dung. The females and the males work the dung together and press it into the horizontal brood chamber. An average of about 90 ml of dung per egg is carried in. The lowest brood ball is made first, the highest one last. Under favourable conditions the female lays about 20 eggs.

Most individuals of *G. spiniger* commenced breeding in the second half of September; the reproductive phase reached its climax in October. *G. vernalis* began breeding in mid-August; most eggs were laid in September.

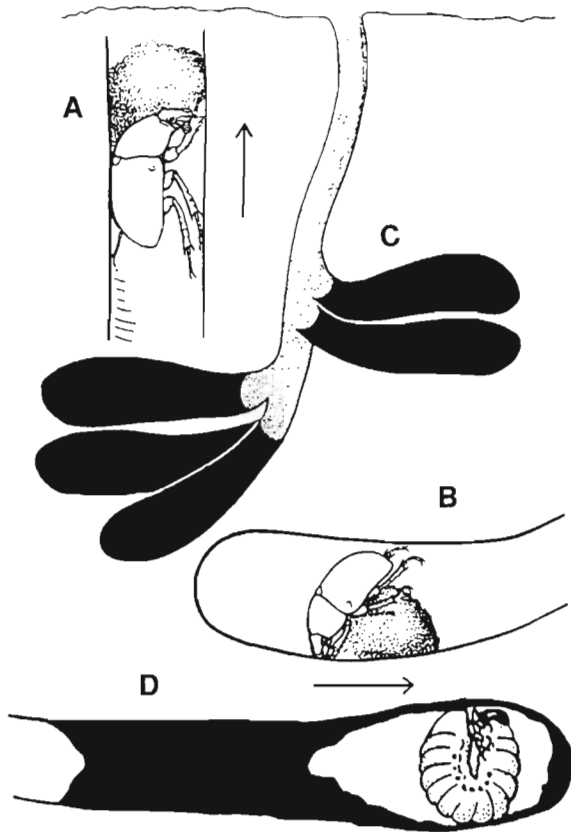


Fig. 2. Brood burrow of *Geotrupes spiniger*. A: Beetle pushing up a load of sand; B: Beetle excavating the brood chamber; C: Completed brood burrow; D: Brood ball with larva. (After Teichert, 1955).

The embryonic phases of both species were equally long, lasting about 2 weeks, but subsequent phases of development up to the emergence of the young beetle lasted longer in *G. vernalis* than in *G. spiniger*. The mean duration of the larval phase of *G. vernalis* was 7.5 months, with the prepupal phase lasting 2.5 weeks, and the pupal stage 4 weeks. In the case of *G. spiniger* the larval development lasted about 3 months on average, the prepupal phase 2 weeks, and the pupal stage 3.5 weeks. The young beetles of both species remained in the pupal cell about 10 days (Klemperer, 1978).

The young beetles of *G. spiniger* are potentially able to appear earlier in the year than the adults of *G. vernalis*. The total period of development until leaving the pupal cell averaged about 5-6 months in the case of *G. spiniger* and 9-10 months in *G. vernalis*.

In the same year, or sometimes only in the following year, the young beetles start breeding after a period of "maturation feeding" (Teichert, 1955; Klemperer, 1979). In the meantime they normally dig short, vertical food shafts weekly, which they fill with dung for their own nutrition (Teichert, 1956; Kühne, 1993).

FAUNA OF NEMATODES IN *GEOTRUPES* BROOD BALLS

The comparison of the frequency of observation of nematodes in field and laboratory brood balls of *G. spiniger* revealed that only a few of the nematode species were able to utilize the beetle efficiently as a distribution vector. Mainly they were *D. henrichae*, *D. hirschmannae*, and *R. icosiensis*. Most other nematode species (Table 1) are only accidentally carried off with the surface dung into the brood balls by the digging activity of the beetles.

Table 1. Nematodes observed in laboratory and field brood balls of *Geotrupes spiniger* and in laboratory brood balls of *G. vernalis*. (++) = species frequently found).

	<i>Geotrupes spiniger</i>	<i>Geotrupes vernalis</i>
<i>Diplogaster affinis</i>	+	+
<i>D. coprophages</i>	++	+
<i>D. faecalis</i>	+	
<i>D. henrichae</i>	++	++
<i>D. hirschmannae</i>	++	+
<i>D. labiomorphus</i>		+
<i>D. lheritieri</i>	+	
<i>D. maupasi</i>		+
<i>D. micrurus</i>	+	+
<i>D. monhysteroides</i>	++	
<i>D. similis</i>	++	++
<i>D. stercorarius</i>	+	+
<i>D. aff. striatus</i>	++	
<i>Diplogasteroides</i> sp.	+	
<i>Tylopharynx foetidus</i>	+	
<i>Diploscapter coronatus</i>	++	++
<i>Rhabditis axei</i>	+	
<i>R. berolina</i>	+	
<i>R. buetschlii</i>	+	
<i>R. coarctata</i>	++	
<i>R. cylindrica</i>	+	
<i>R. dubia</i>	+	
<i>R. icosiensis</i>	++	++
<i>R. longicaudata</i>	+	
<i>R. longispina</i>	+	
<i>R. pellicoides</i>	+	
<i>R. tretzeli</i>	+	
<i>R. voelki</i>	+	
<i>R. (Caenorhabditis)</i> sp.	+	+
Cephalobidae ind.	+	+
<i>Acrobeloides buetschlii</i>		+
Tylenchidae ind.	+	
<i>Aphelenchoides</i> spp.	+	+

In contrast to the brood balls of *G. spiniger*, *D. hirschmannae* was found only rarely in the brood balls of *G. vernalis*, but *D. labiomorphus* was found in 18 % of these dung samples.

Some of the nematodes found in the brood balls were typical cow dung nematodes (Sachs, 1950; Sudhaus, 1981; Rehfeld, 1988; Sudhaus *et al.*, 1988). Only a few of these species were able to make use of the ecological opportunities afforded by the brood ball until the beetle emerged. Most species could no longer be detected after a few weeks (Fig. 3).

Young adults of *G. spiniger* were often used by *D. henrichae* and *D. hirschmannae* as carriers. Only in five of the

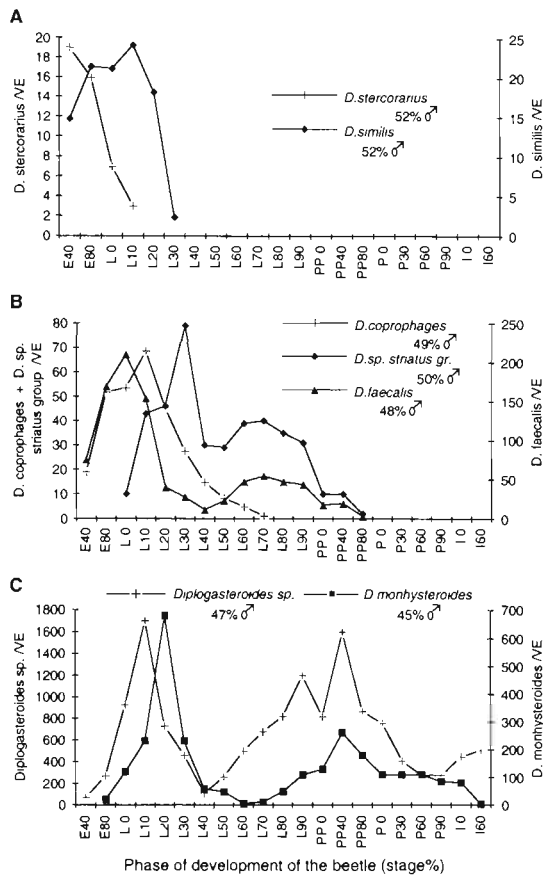


Fig. 3. Density of adult individuals of different diplogasterids during aging of *Geotrupes spiniger* brood balls. The data for *Diplogaster stercorarius*, *D. sp.* of the striatus group, *Diplogasteroides sp.*, and *D. monhystreroides* relate to four different brood balls. The mean value of two brood balls is shown for *D. similis* and *D. faecalis* and the mean value of six brood balls for *D. coprophages*. Age of the brood balls is given as the stage of beetle development (E = egg, L = larva, PP = prepupa, P = pupa, I = imago), VE = Volume equivalent (5 ml sedimentary dung in water).

83 cases studied was another nematode species found on the hatched beetle. The infestation of the young *G. vernalis* beetles was demonstrably achieved only by the species *D. henrichae* and *D. hirschmannae*.

The dauer larvae of these species are, as opposed to the dauer larvae of other nematode species (see also Bovien, 1937; Sachs, 1950; Théodoridès, 1955), exclusively found in the genital region of the beetles. This area of transport is the most favourable for these diplogasterids, as their dauer larvae do not require rapid liberation. Their requirement is only to get into a new brood ball.

D. henrichae, *D. hirschmannae* and probably also *D. labiomorphus* are species especially adapted to the living conditions in the brood balls. Both *D. henrichae* and *D. hirschmannae* were present in 74 % of more than 200 *G. spiniger* brood balls observed. In contrast, 69 % of more than 100 *G. vernalis* brood balls examined were inhabited only by *D. henrichae*. Only 11-13 % of the brood balls were free of these species which are “*Geotrupes* specialists”.

All three species were first found after 1.5-2 weeks of brood ball aging. On average, the first adult specialists occurred during the late egg phase of the beetle.

Where both *D. henrichae* and *D. hirschmannae* are present in the same brood ball, population development and dominance can vary greatly (Fig. 4). In a comparison of seven brood balls, the maximum population of *D. hirschmannae* tended on the average to be slightly higher than that of *D. henrichae*. At 80 vs 130 adults per unit of volume (5 ml sedimentary dung in water), the maximum number of individuals was significantly smaller for *D. hirschmannae* than for *D. henrichae*. Nevertheless, *D. hirschmannae* dominated when the beetle emerged.

In brood balls in which *D. henrichae* was present without *D. hirschmannae*, the average maximum population of *D. henrichae* (700 animals per unit of volume) was over five times greater than in those brood balls it shared with *D. hirschmannae*. It follows from this that the feeding pressure that *D. hirschmannae* exerts on *D. henrichae* is significant.

When adult individuals of the species *D. henrichae*, *D. hirschmannae* and *D. labiomorphus*, shared the same brood ball of *G. vernalis*, they were in an average proportion of 10:6:1. Even in a brood ball where *D. labiomorphus* occurred without possible competition from one of the two other specialists, no high density of individuals of this species was found. However, *D. labiomorphus*, as well as the two species related most closely, has the ability of growing into an adult by the time the beetle hatches.

The ratio between numbers of specialist and “non-specialist” species in different *Geotrupes* brood balls followed a nearly sigmoid curve as a function of time (Fig. 5). The greatest changes in the ratio occurred between the late egg phase and the early larval phase of the

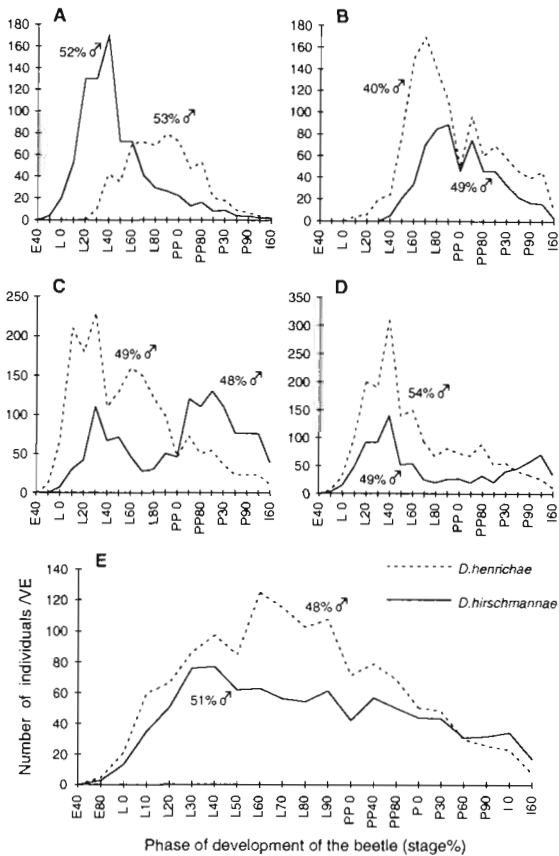


Fig. 4. A-D: Common occurrence of *Diplogaster henrichae* and *D. hirschmannae* in four brood balls of *Geotrupes spiniger*. E: Mean population development of seven brood balls.

beetle. From this time on, the specialist species were dominating.

One of the most important demands for a phoretically bound nematode is the ability to change the normal individual cycle at the right moment and to become a dauer larva able to contact the carrier host. When the beetle hatches, there must be enough offspring of the founder population in the dauer larval stage so that they can be transported into a new habitat.

The number of dauer larvae of the phoretically non-specialised nematode species reached its peak in the brood ball about at the time when the beetle larva left the egg. However, a remarkable number of dauer larvae of *D. henrichae* and *D. hirschmannae* were only formed after the pupation of the beetle (Fig. 6). Their number increased until the imago hatched.

The formation of dauer larvae is induced by the *Geotrupes* pupa. That chemical substances may be responsible for the formation of dauer larvae in nematodes has been shown in *Rhabditis (Caenorhabditis) elegans* (Golden & Riddle, 1982). Here, however, a pheromone,

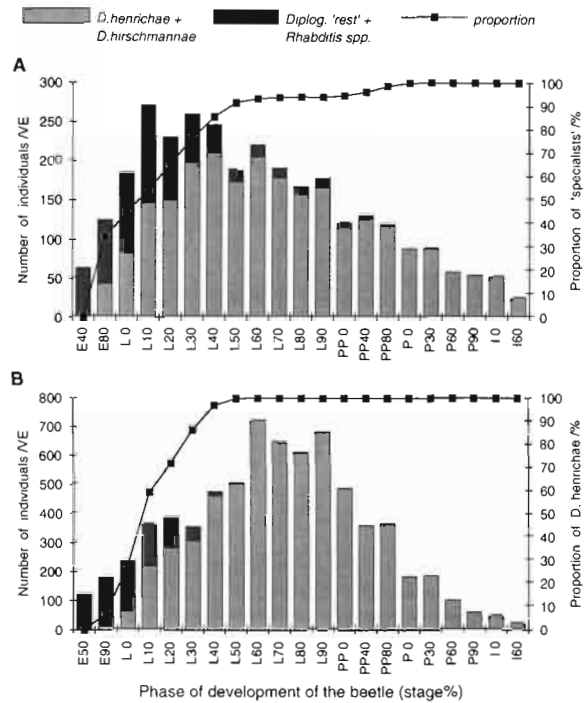


Fig. 5. Mean density of individuals of adult phoresy specialists as well as other *Rhabditis* and *Diplogaster* species in seven laboratory and field brood balls of *Geotrupes spiniger* (A) and in three *G. vernalis* laboratory brood balls (B). Both absolute figures (bar charts) and the ratio of specialist vs "non-specialist" species (polygonal progressions) during the brood ball aging are shown. Age is given as the stage of beetle development.

i.e., a messenger substance emitted by members of the same species is active. Until now, nothing was known about the influence on the formation of dauer larvae by their carrier insects.

The dauer larvae of *D. henrichae* and *D. hirschmannae* specifically search for the newly hatched young beetle in the pupal cell, in order to ascend it. Females and males of beetles are infested with the same rate and intensity. The maximum infestation intensity in laboratory bred beetles was about 1500 dauer larvae in *G. spiniger* and 750 in *G. vernalis*. A maximum of about 2000 dauer larvae was recorded in the genital region of *G. spiniger* beetles caught in the field.

After the completed transport phase, the dauer larvae only descend when the beetles begin building a brood ball. The food shafts of the animals are not frequented. The dauer larvae of at least *D. hirschmannae* can get into the brood ball even before the oviposition. A salivary gland secretion, which the beetles give to the brood ball substrate, might be the stimulus that causes the nematodes to descend (Kühne, 1993).

Sachs (1950) supposed that the excrements from the beetle larvae induce the further development of the

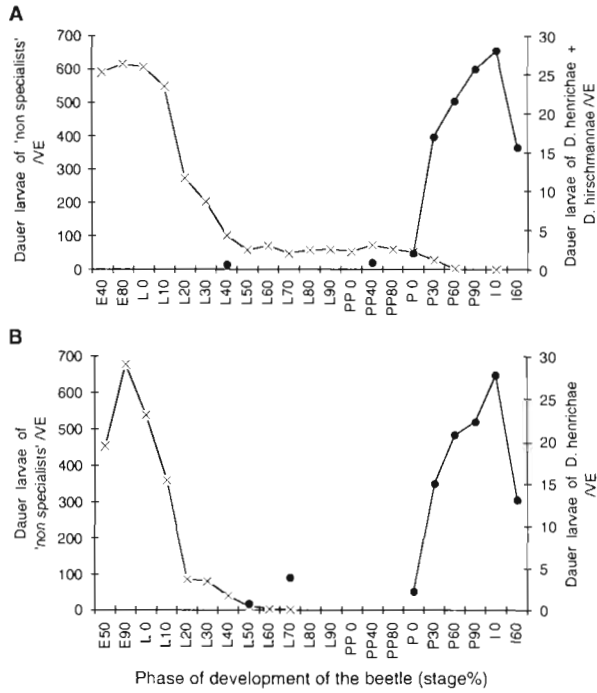


Fig. 6. Mean dauer larvae density of the phoresy specialists *Diplogaster henrichae* and *D. hirschmannae* (points) as well as other species (crosses) in seven brood balls of *Geotrupes spiniger* (A) and in three brood balls of *G. vernalis* (B). The diagrams show the density of individuals depending on the age of the brood balls. The degree of aging is characterized by the corresponding stage of the beetle ontogenesis.

dauer larvae. However, this is not the case, as already reported by Rehfeld (1988). Adults of *D. hirschmannae*, *D. henrichae*, and *D. labiomorphus* were often observed before the beetle larva hatched (see above). Thus the substance inducing the development into an adult must come from the brood ball itself. It is conceivable that the same stimulus makes the nematodes descend.

The dauer larvae transported by a female are relatively evenly distributed into all manufactured brood balls. Five beetle females of *G. spiniger* that were dissected after laying the first eggs were still carrying 130-940 dauer larvae in their genital region. The strategy of dauer larvae dispersion into the brood balls promotes the inclusive fitness of the nematodes.

REPRODUCTIVE BIOLOGY OF DIPLOGASTERIDS BOND-ED TO *GEOTRUPES*

50% of the adults of *D. henrichae*, *D. hirschmannae* and *D. labiomorphus* lived at least 12-14 days after the last molt. Extrapolations on the basis of a Gompertz survival function (see Strehler, 1977) yield a maximum adult life expectancy between 21 and 26 days (Fig. 7). A 12-14 day median life expectancy as an adult is quite

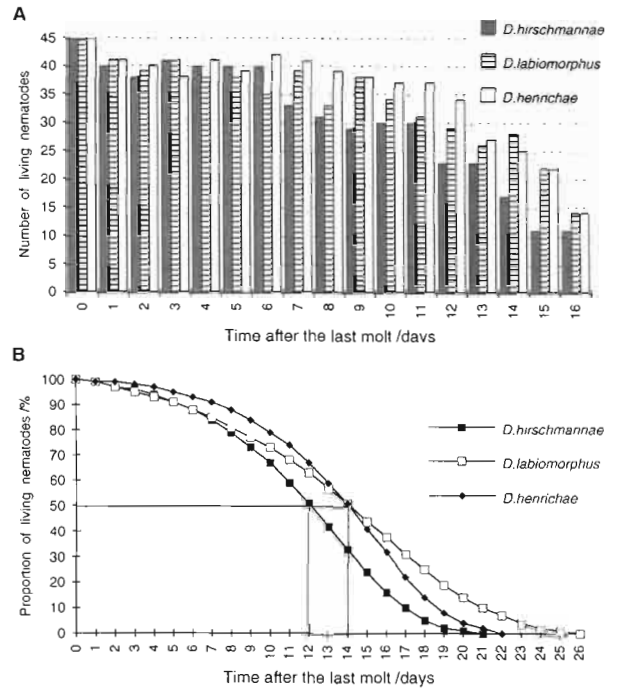


Fig. 7. Survival diagrams of adult *Diplogaster henrichae*, *D. labiomorphus*, and *D. hirschmannae*. A: Empirical data; B: Theoretical approximate functions according to Gompertz (in Strehler, 1977). (The animals were kept at 17-18 °C under mainly natural food conditions.)

high for dung nematodes, as far as it is known. Thus 50% of the individuals of *R. icosiensis* and *R. cylindrica* died at 20 °C only 5-6 days after the last molt (Strauch & Rehfeld, 1989).

No offspring of any of the *Diplogaster* species were detected until the 3rd day. The first young *D. henrichae* were observed 4 days after the adult stage had been reached. Between the 4th and 7th days, half of the females of the three species had begun to lay eggs. This fact can also be interpreted as a mechanism to enhance the generation time for the "purpose" of an improvement of the fitness.

The females of all three species produced about 50% of the offspring within the first 5 days after beginning to deposit eggs. By the 10th day, almost all of the eggs had been deposited. Compared to many other dung nematode species, the reproductive phase is quite long and balanced. The offspring of most other saprobiotic nematodes examined are produced mainly in the first days after the beginning of the oviposition (Pillai & Taylor, 1968; Sudhaus, 1976).

The number of offspring produced by *D. henrichae* was 70 ± 25 , by *D. labiomorphus* it was 30 ± 15 , and by *D. hirschmannae* it was 40 ± 15 individuals (arithmetic mean and standard deviation). These figures are com-

Table 2. Data on the start of different phases of development, the generation time, and the median life expectancy of individuals of *Diplogaster henrichae*, *D. labiomorphus*, and *D. hirschmannae*. The mean time specifications refer to the date of oviposition. Minimum values are put within brackets. The times are given in days. The breeding temperature was 17-18 °C.

Species	Stage of development			Beginning of oviposition	Generation time	50 % dead
	J3	J4	Adult			
<i>D. henrichae</i>	2	4 (3)	7 (6)	11-12 (9)	16	21
<i>D. labiomorphus</i>	3 (2)	5	7 (5-6)	13 (11)	17-18	21
<i>D. hirschmannae</i>	2 (1)	3-4	7-8	14 (12)	18	19-20

paratively low (see Pillai & Taylor, 1968; Sudhaus, 1985; Strauch & Rehfeld, 1989; Sudhaus & Kühne, 1989). With a slightly higher reproduction rate, *D. henrichae* possibly compensates for the feeding pressure exerted by *D. hirschmannae*, in case both occur in the same dung ball.

In all three species, the adult develops within about 7 days (Table 2). By the time *G. spiniger* pupates, *D. hirschmannae* and *D. henrichae* will have completed an average of less than ten generations. In the brood balls of *G. vernalis*, about fifteen generations of *D. henrichae* and *D. labiomorphus* complete their development by the time the beetle reaches pupation.

The results show an adaptation of the reproduction strategy to the life in the brood ball. The generation time of the species is comparatively long, and the numbers of offspring are low. The nematodes specialised in living in the brood ball are subject to K-selection as the food resources are limited.

CHANGE IN SEX RATIO IN THE COURSE OF THE BROOD BALL AGING

To point to a further phenomenon: in older brood balls, the adults of *D. henrichae* were significantly smaller than in younger brood balls, and the proportion of males was significantly lower (Fig. 8). Therefore, it can be concluded that the sex ratio can change in the course of the brood ball aging, as in unfavourable living conditions the mortality of males is higher than the mortality of females. An increased mortality of males in poor living conditions is also described by Strauch (1990) for *R. icosiensis* and *R. cylindrica*. In *Heterodera glycines* (Tylenchida: Heteroderidae), an increased population density has exactly the reverse effect. Here, it is mainly the females that die (Koliopoulos & Triantaphyllou, 1972). Another possible explanation for the density-dependent proportion of males could be a pheromone regulation of the sexual development. In the facultatively parthenogenetic *Diploenteron colobocercus*, sex determination is metabolite-mediated. Here, the production of males increases at times when the probability of finding a mate is high (Yeates, 1970; Clark, 1978).

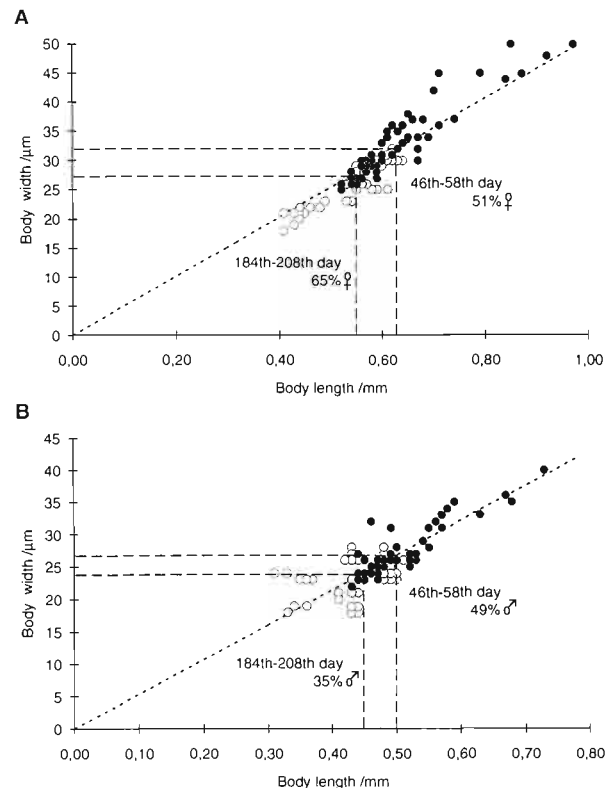


Fig. 8. Body length and width of adult *Diplogaster henrichae* in a brood ball of *Geotrupes vernalis*. The measurements of ($n = 2 \times 60$) females (A) and ($n = 2 \times 60$) males (B) are shown. These were isolated around the 52nd and the 196th day after building the brood ball. The linear regression lines put through the zero point and the mean values of the comparison groups are presented as dotted lines.

The decline of the proportion of *D. henrichae* males in older brood balls influences the production of offspring in a favorable way. The animals are no longer competitors for their sisters and, if available, for their offspring, which results in a possible increase of inclusive fitness.

For the production of dauer larvae, it is useful (in the case of food shortage shortly before the pupation of the beetle) to maintain a high density of the population of females.

Conclusion

As the morphological comparison shows that *D. henrichae*, *D. labiomorphus* and *D. hirschmannae* are closely related to one another (Kühne, 1995), the phoretic bond with geotrupinids has to be viewed as homologous. According to the current state of knowledge, this hypothesis is the most economical one. Thus the adaptations, which enable the phoresy onto dung-beetles, are acquired in the stem lineage of the three species. They include the following abilities: *i*) to be economical with the food resource until the beetle hatches; *ii*) to develop into a dauer larva only after the pupation of the beetle; *iii*) to look for the beetle specifically and to ascend it; *iv*) to seek shelter in the genital region of the beetle, and *v*) not to descend until the beetle has started to build a brood ball.

A nematode population bound to a *Geotrupes* doing parental care is at the same time isolated ecologically from many other species. These individuals only have contact with cow-pat or soil nematodes, which occur occasionally in the same brood ball.

Nematode populations of the same species occurring on different dung-beetle species are separated reproductively, as a genetic exchange is hardly possible. This fact promoted radiation after a geotrupinid beetle was accepted as a carrier.

As similar *Diplogaster* dauer larvae have previously been found in the genital apparatus of at least nine beetle species (Sachs, 1950; Théodoridès, 1955; Poinar, 1975), it must be assumed that there exist other diplogasterids bound to *Geotrupes*. This hypothesis will be tested in the near future.

Acknowledgement

I am grateful to Prof. W. Sudhaus for introducing me to the determination of nematodes and for his helpful criticism, and I would also like to thank Prof. G. W. Yeates for his valuable comments on the manuscript.

References

- ANDRÁSSY, I. (1984). *Klasse Nematoda (Ordnungen Monhysterida, Desmoscolecida, Araeolaimida, Chromadorida, Rhabditida)*. Stuttgart, Germany, Gustav Fischer Verlag, 509 p.
- BOVIEN, P. (1937). Some types of association between nematodes and insects. *Vidensk. Meddr dansk Naturh. Foren.*, 101 : 1-114.
- CLARK, W. C. (1978). Metabolite-mediated density-dependent sex determination in a free-living nematode, *Diplenteron potonikusi*. *J. zool., Lond.*, 184 : 245-254.
- GOODEY, T. (1963). *Soil and Freshwater Nematodes* : 2nd ed., revised by Goodey, J. B., London, UK, Methuen & Co Ltd, 544 p.
- GOLDEN, J. W. & RIDDLE, D. L. (1982). A pheromone influences larval development in the nematode *Caenorhabditis elegans*. *Science*, 218 : 578-580.
- HOWDEN, H. F. (1955). Biology and taxonomy of North American beetles of the subfamily Geotrupinae, with revisions of the genera *Bolbocerosoma*, *Eucanthus*, *Geotrupes*, and *Peltotrupes* (Scarabaeidae). *Proc. U. S. natn. Mus.*, 104 : 151-319.
- KLEMPERER, H. G. (1978). The repair of larval cells and other larval activities in *Geotrupes spiniger* Marsham and other species (Coleoptera, Scarabaeidae). *Ecol. Entomol.*, 3 : 119-131.
- KLEMPERER, H. G. (1979). An analysis of the nesting behaviour of *Geotrupes spiniger* Marsham (Coleoptera, Scarabaeidae). *Ecol. Entomol.*, 4 : 133-150.
- KOLIOPANOS, C. N. & TRIANTAPHYLLOU, A. C. (1972). Effect of infection density on sex ratio of *Heterodera glycines*. *Nematologica*, 18 : 131-137.
- KÜHNE, R. (1993). *Beziehungen zwischen freilebenden Nematoden und Brutfürsorge betreibenden Geotrupes-Arten (Coleoptera : Scarabaeidae)*. Dissertation, Fachbereich für Biologie, Freie Universität Berlin, Germany, 154 p.
- KÜHNE, R. (1995). Nematoden mit phoretischer Bindung an Dung vergrabende *Geotrupes*-Käfer : ein morphologischer Vergleich von *Diplogaster henrichae* Sachs, 1950, *D. hirschmannae* Sachs, 1950, und *D. labiomorphus* sp. n. (Nematoda : Diplogasteridae). *Nematologica*, 41 : 7-34.
- VON LENGERKEN, H. (1954). *Die Brutfürsorge und Brutpflegeinstinkte der Käfer*. 2. Aufl. Leipzig, Germany, Akademische Verlagsgesellschaft, 383 p.
- MEYL, A. H. (1961). Die freilebenden Erd- und Süßwassernematoden (Fadenwürmer). In : Brohmer, P., Erdmann, P. & Ulmer, G. (Eds). *Die Tierwelt Mitteleuropas*. 1 Bd. Leipzig, Germany, Quelle & Meyer, 164 p.
- PILLAI, J. K. & TAYLOR, D. P. (1968). Biology of *Paroigolaimella bernensis* and *Fictor anchicopropha* (Diplogasterinae) in laboratory culture. *Nematologica*, 14 : 159-170.
- POINAR, G. O., Jr. (1975). *Entomogenous Nematodes. A Manual and Host List of Insect-Nematode Associations*. Leiden, The Netherlands, E. J. Brill, 317 p.
- REHFELD, K. (1988). *Experimentelle Untersuchungen zur Sukzession der Nematoden in Kuhfladen*. Dissertation, Fachbereich für Biologie, Freie Universität Berlin, Germany, 174 p.
- SACHS, H. (1950). Die Nematodenfauna der Rinderexkremente. Eine ökologisch-systematische Studie. *Zool. Jb.*, 79 : 209-272.
- STRAUCH, O. (1990). *Zur Populationsbiologie und Konkurrenz von Zwillingarten bakteriophager saprobionter Nematoden (Rhabditis cylindrica & Rhabditis icosiensis)*. Diplomarbeit, Fachbereich für Biologie, Freie Universität Berlin, Germany, 140 p.
- STRAUCH, O. & REHFELD, K. (1989). Untersuchungen zur Populationsökologie, Umweltkapazität und Koexistenzfähigkeit der Zwillingarten *Rhabditis icosiensis* und *Rh. cylindrica* (Nematoda : Rhabditida). *Verhandl. Gesellsch. Ökol. Essen, Deutschland, 1988*, 18 : 807-812.

- STREHLER, B. L. (1977). *Time, Cells, and Aging*, 2nd ed. New York, San Francisco, USA & London, UK, Academic Press, 456 p.
- SUDHAUS, W. (1976). Vergleichende Untersuchungen zur Phylogenie, Systematik, Ökologie, Biologie und Ethologie der Rhabditidae (Nematoda). *Zoologica*, 43 : 1-229.
- SUDHAUS, W. (1981). Über die Sukzession von Nematoden in Kuhfladen. *Pedobiologia*, 21 : 271-297.
- SUDHAUS, W. (1985). Vergleich von Lebenszyklus und Fortpflanzungsstrategie zweier Nematodenarten der Gattung *Rhabditis* (*Teratorhabditis*). *Zool. Jb.*, 112 : 455-468.
- SUDHAUS, W. & KÜHNE, R. (1989). Nematodes associated with Psychodidae : Description of *Rhabditis berolina* sp. n. and redescription of *R. dubia* Boven, 1937 (Nematoda : Rhabditidae), with biological and ecological notes, and a phylogenetic discussion. *Nematologica*, 35 : 305-320.
- SUDHAUS, W., REHFELD, K., SCHLÜTER, D. & SCHWEIGER, J. (1988). Beziehungen zwischen Nematoden, Coleopteren und Dipteren in der Sukzession beim Abbau von Kuhfladen. *Pedobiologia*, 31 : 305-322.
- TEICHERT, M. (1955). Biologie und Brutfürsorgemaßnahmen von *Geotrupes mutator* Marsch., und *Geotrupes stercorarius* L. (Col. Scarab.) *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg*, 5 : 187-217.
- TEICHERT, M. (1956). Nahrungsspeicherung von *Geotrupes vernalis* L. und *Geotrupes stercorosus* Scriba (Coleopt. Scarab.). *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg*, 5 : 669-672.
- THÉODORIDÈS, J. (1955). *Contribution à l'étude des parasites et phorétiques de Coléoptères terrestres*, Saintes, France, Imprimerie Delavaud, 310 p.
- WEINGÄRTNER, I. (1955). Versuch einer Neuordnung der Gattung *Diplogaster* Schulze 1857 (Nematoda). *Zool. Jb.*, 83 : 248-317.
- YEATES, G. W. (1970). Studies on laboratory cultures of dune sand nematodes. *J. nat. Hist.*, 4 : 119-136.