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Host–parasite relations and seasonal occurrence of *Paragordius tricuspidatus* and *Spinochordodes tellinii* (Nematomorpha) in Southern France

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Abstract

Paragordius tricuspidatus (Dufour, 1828) and *Spinochordodes tellinii* (Camerano, 1888) are two sympatric species of horsehair worms in southern France. *Paragordius tricuspidatus* was found in only one host species, *Nemobius sylvestris* (Bosc, 1792), while *Spinochordodes tellinii* was found in nine different hosts belonging to Orthoptera Caelifera. Size of nematomorphs varied strongly, but is additionally influenced by host size (in *Spinochordodes tellinii*) or number of parasites per host (in *Paragordius tricuspidatus*). Both species have a clear seasonality with *Paragordius tricuspidatus* occurring from June to early August and *Spinochordodes tellinii* occurring in August and September.

Keywords: Nematophora; Host species; Host-parasite relationships; Seasonal occurrence

1. Introduction

Horsehair worms (Nematomorpha) typically develop in arthropods (mainly terrestrial species) until they are ready to exit the host (Schmidt-Rhaesa 2001). Because nematomorphs are usually found when they have emerged from their host and started the aquatic free-living phase of their life cycle, numerous aspects of their biology remain poorly documented (but see Hanelt and Janovy 1999, 2003, 2004). Recently, the two hairworm species *Paragordius tricuspidatus* (Dufour, 1828) and

Spinochordodes tellinii (Camerano, 1888) from Southern France have proven to be valuable model systems to examine whether (and potentially how, see Thomas et al. 2003) hairworms manipulate their host behaviour to increase their probability of reaching a suitable aquatic place for reproduction (Thomas et al. 2002). Indeed, insects harbouring these hairworms display a behaviour originally not present in the host's repertoire: they seek water and jump into it (Thomas et al. 2002). The adult worms then emerge from their host and actively leave it by swimming away, beginning the search for a sexual partner.

The parasitic phase of nematomorphs remains enigmatic, because hardly any systematical approach has been performed on larger numbers of specimens per reveal their host specificity, numbers of parasites per

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host and the influence of host size or parasite number for the development of the parasite. Based on collections in Avènes les Bains in Southern France, where *Paragordius tricuspidatus* and *S. tellinii* occur sympatrically, we provide such data.

2. Material and methods

All specimens were captured around a private swimming pool in Avènes les Bains (Southern France, 70 km north of Montpellier). Capture took place mostly between 10 p.m. and 1 a.m. The swimming pool is located between a forest and a small stream in which free adult nematomorphs can be found (see also Thomas et al. 2002, 2003 for description of the location). Hosts were observed to jump into water (the swimming pool) or were set in a container with water, so that parasites and hosts could be assigned to each other. In some cases, hosts were dissected. Hosts and parasites were fixed in ethanol (70%). Length measurements were made with a ruler, diameter measurements with a caliper ruler. Determination of species was based on intensive preliminary investigations including scanning electron microscopy which confirmed that only two species were present in the location investigated. Both species are easy to distinguish from each other under the dissecting microscope due to different shapes of the anterior and posterior end.

3. Results

3.1. Host species

In all cases where *Paragordius tricuspidatus* has been found in association with its host ($n > 400$), the host was the small cricket *Nemobius sylvestris* (Bosc, 1792) (Gryllidae) (Fig. 1B). Infected *N. sylvestris* can be observed in the field and in laboratory experiments (see Thomas et al. 2002) to approach water and enter this by jumping into it. *Paragordius tricuspidatus* starts to emerge from the posterior region of the crickets with its head first very soon after the contact of the host with water. Emergence takes about 1 min and is aided, especially towards the last phase, by undulating movements by the worm. The crickets survive the parasitization and emergence, if they are able to escape from the water, but no long-term investigations according to the fitness of parasitized hosts were performed.

In contrast to *Paragordius tricuspidatus*, *S. tellinii* was found in a total of nine different hosts (see Table 1; Fig. 1D–F). Most worms were found in adult hosts (one exception is a larva of probably *Eupholidoptera chabrieri* (Charpentier, 1825)). With more than 100 cases,

Meconema thalassinum (de Geer, 1773) is the most abundant host (Fig. 1D), followed by 11 cases, in which *Pholidoptera griseoptera* (de Geer, 1773) was host, while the remaining species were found in few or single cases.

In three cases, a specimen of *S. tellinii* was found in a swimming pool in Avignon, France, close to a potential host. These were a praying mantis (*Mantis religiosa* Linnaeus, 1758), a large locust (*Tettigonia viridissima* Linnaeus, 1758) and a scorpion (*Euscorpium flavicaudis* de Geer, 1778) (Fig. 2A–C). The emergence was not observed in these cases. All three specimens of *S. tellinii* were large females with measurements of (*Mantis/Tettigonia/Euscorpium*): 280, 305 and 345 mm in length and 1, 0.9 and 1 mm in diameter.

3.2. Measurements of free-living and parasitic nematomorphs

In *Paragordius tricuspidatus*, the length of free-living females ($n = 51$) ranges from 60 to 135 mm (mean 92.35 ± 16.41 mm), with diameters between 0.5 and 0.8 mm (mean 0.61 ± 0.08 mm). Males ($n = 47$) measure between 65 and 145 mm in length (mean 82.57 ± 16.25 mm) (50 and 60 mm are two further, exceptional measurements from two males together with two further specimens in one host specimen), their diameter ranges between 0.4 and 0.6 mm (mean 0.46 ± 0.06 mm) (see Fig. 1C for two males of different sizes and, additionally, different colouration patterns). Therefore, females are generally larger than males (Fig. 1A).

In free-living *S. tellinii*, females ($n = 60$) measure between 110 and 305 mm in length (mean 141.67 ± 39.85 mm), and between 0.5 and 1.2 mm in diameter (mean 0.73 ± 0.16 mm). Males ($n = 74$) range from 75 to 245 mm in length (mean 116.55 ± 43.59 mm), and from 0.4 to 0.7 mm in diameter (mean 0.48 ± 0.09 mm).

In 65 cases, measurements of the parasite stages within hosts were taken (Table 2). In 57 cases, *N. sylvestris* was parasitized by a single nematomorph, while in eight cases, multiple infections occurred. In six cases, two specimens of *Paragordius tricuspidatus* were found in one host, while one time three (two males and one female) and another time four (three males and one female) *Paragordius tricuspidatus* were found in one cricket. In the cases of two specimens within one host, both specimens were males in one occasion, while in all seven other cases a male and a female occurred together.

In the single infections (one nematomorph per host), males (mean 82.8 mm) are slightly shorter than females (mean 88.3 mm) (see Table 2). In cases with two or three parasite specimens in one host specimen, all measurements were within the range of single infections (length: 70–90 mm in females and in males; diameter: 0.5–0.6 mm in females, 0.4–0.5 mm in males; Table 2), but mean values of cases with two parasites were lower than in

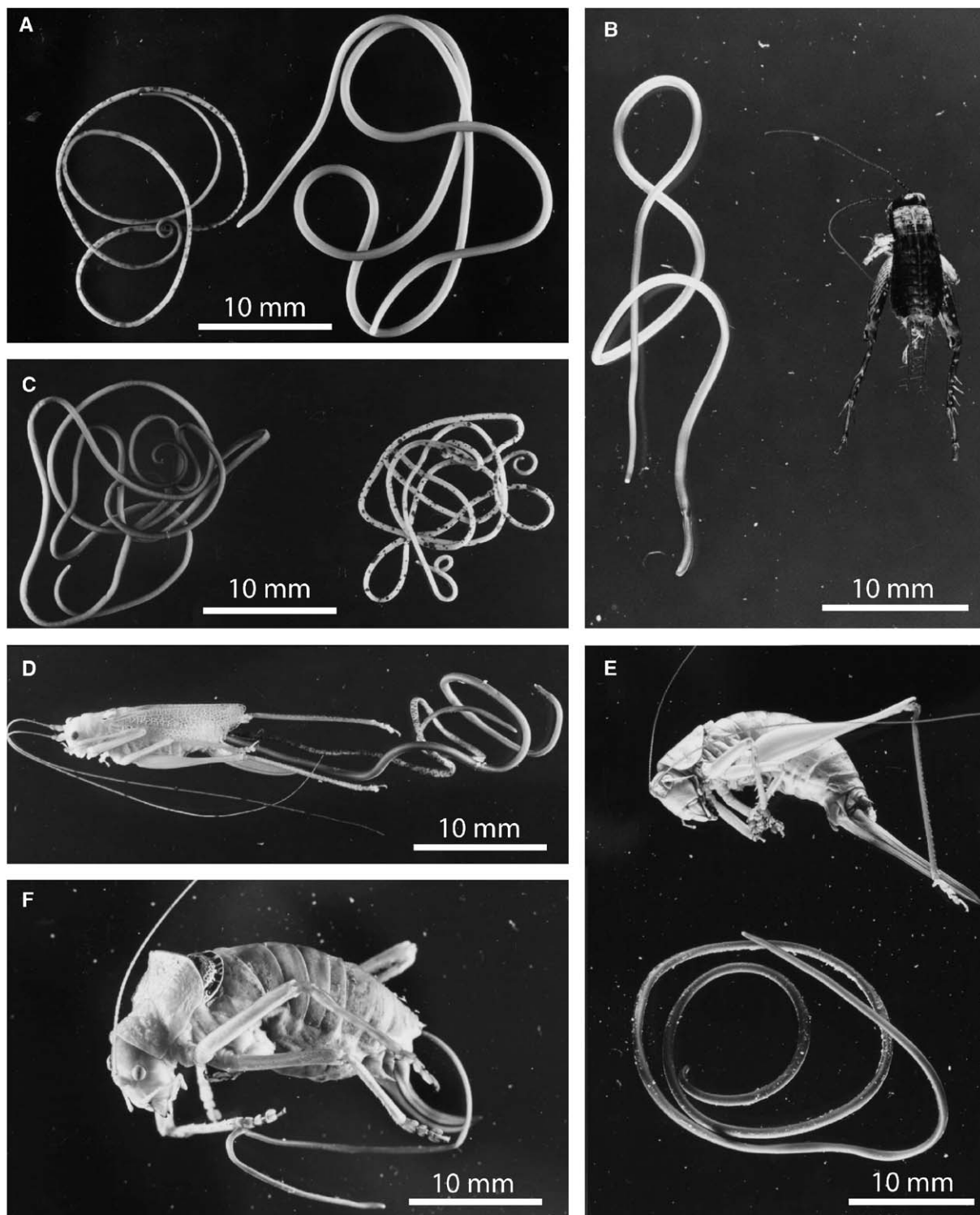


Fig. 1. (A) Male (left) and female (right) from *Spiniochordodes tellinii*. Females are often larger than males, the posterior end of males is curved inwards. (B) *Paragordius tricuspoidatus* with host, *Nemobius sylvestris*. C. Two males of *S. tellinii*, showing different colouration patterns with “leopard pattern” present (right) or absent (left). (D–F) Hosts of *S. tellinii*: *Meconema thalassinum* (D), *Antaxius pedestris* (E) and *Uromenus rugosicollis* (F).

single infections (females: mean length 80 mm, mean diameter 0.56 mm; males: mean length 77.1 mm, mean diameter 0.44 mm). Only in the case where four parasites

were found in one host specimen, the length of two males was less than the shortest male from all other infections (50 and 60 mm), while all diameters

Table 1. Hosts of *Spinochordodes tellinii*

Host	Sex of host	Cases of parazitation
<i>Meconema thalassinum</i> (de Geer, 1773)	Males and females	> 100
<i>Pholidoptera griseoptera</i> (de Geer, 1773)	Males	2
	Females	9
<i>Uromenus rugosicollis</i> (Serville, 1839)	Males	4
	Female	1
<i>Yersinella raymondi</i> (Yersin, 1860)	Males	3
	Females	4
<i>Antaxius pedestris</i> (Fabricius, 1787)	Female	1
<i>Ephippiger cunii</i> (Bolivar, 1877)	Male	1
<i>Barbitistes serricauda</i> (Fabricius, 1798)	Female	1
<i>Leptophyes punctatissima</i> (Bosc, 1792)	Female	1
probably <i>Eupholidoptera chabrieri</i> (Charpentier, 1825)	Larva	1

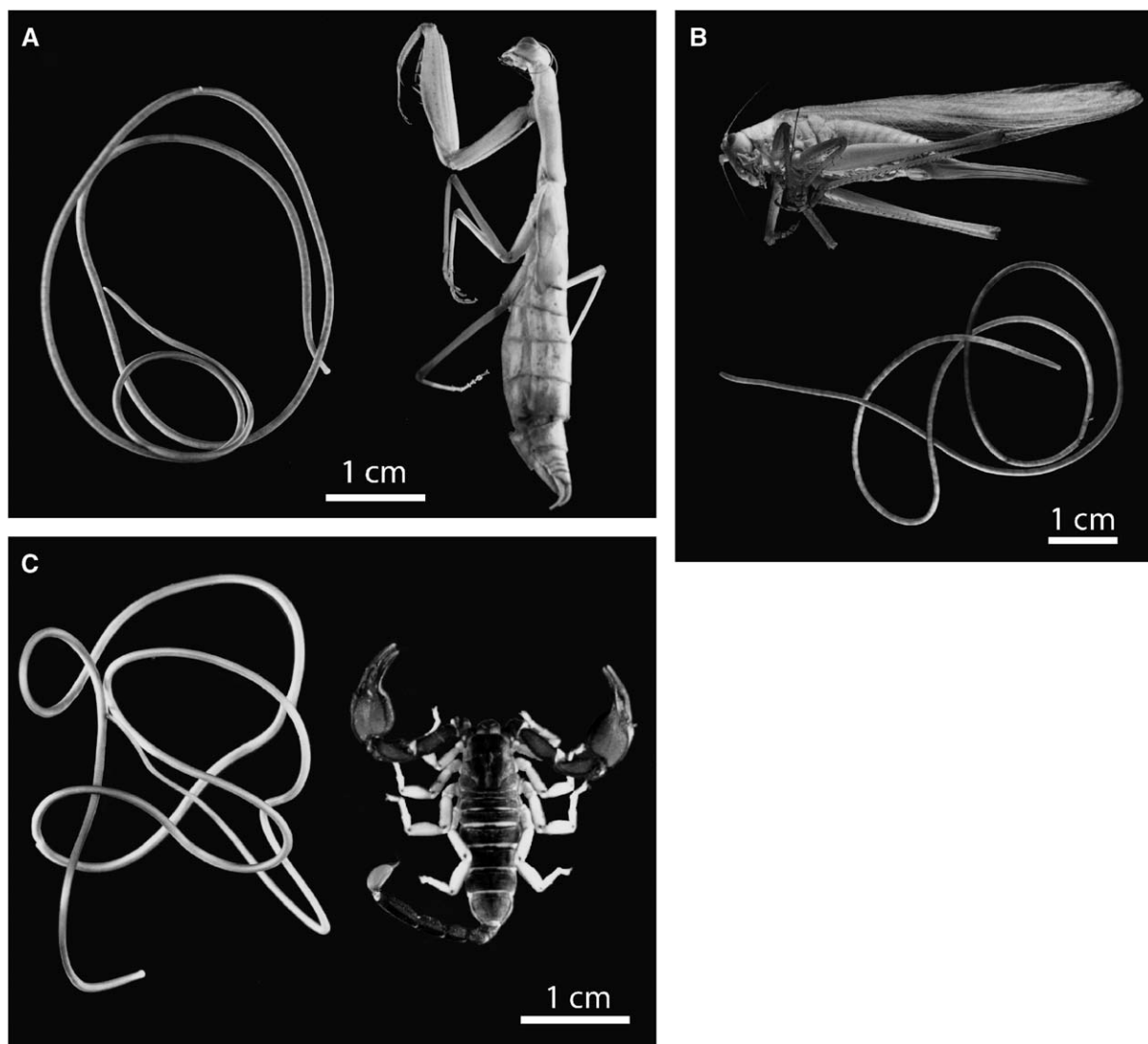


Fig. 2. Probable hosts found close to female specimens of *Spinochordodes tellinii* in a swimming pool in Avignon, France. (A) *Mantis religiosa*. (B) *Tettigonia viridissima*. (C) *Euscorpilus flavicaudis*.

Table 2. Measurements from infections of *Nemobius sylvestris* with different numbers of specimens from *Paragordius tricuspidatus*

Single infections			
Females (n = 32)		Males (n = 25)	
Length in mm	Occurrence	Length in mm	Occurrence
60	1	65	1
65	1	70	3
70	—	75	4
75	4	80	6
80	3	85	2
85	5	90	4
90	9	95	3
95	3	100	2
100	3		
105	2		
110	1		
Diameter in mm	Occurrence	Diameter in mm	Occurrence
05.	5	0.4	13
0.6	14	0.5	10
0.7	12	0.6	2
0.8	1		
Infection with two <i>Paragordius tricuspidatus</i> (n = 6; total of 5 females and 7 males)			
Length in mm	Occurrence	Length in mm	Occurrence
70	1	70	2
75	1	75	3
80	1	80	—
85	1	85	1
90	1	90	1
Diameter in mm	Occurrence	Diameter in mm	Occurrence
0.5	2	0.4	4
0.6	3	0.5	3
Infection with three <i>Paragordius tricuspidatus</i> (n = 1)			
Length in mm	Occurrence	Length in mm	Occurrence
70	1	75	2
Diameter in mm	Occurrence	Diameter in mm	Occurrence
0.6	1	0.4	2
Infection with four <i>Paragordius tricuspidatus</i> (n = 1)			
Length in mm	Occurrence	Length in mm	Occurrence
75	1	50	1
		60	1
		70	1
Diameter in mm	Occurrence	Diameter in mm	Occurrence
0.5	1	0.4	3

and the length of one female (75 mm) and one male (70 mm) were within the range of other infections (see Table 2).

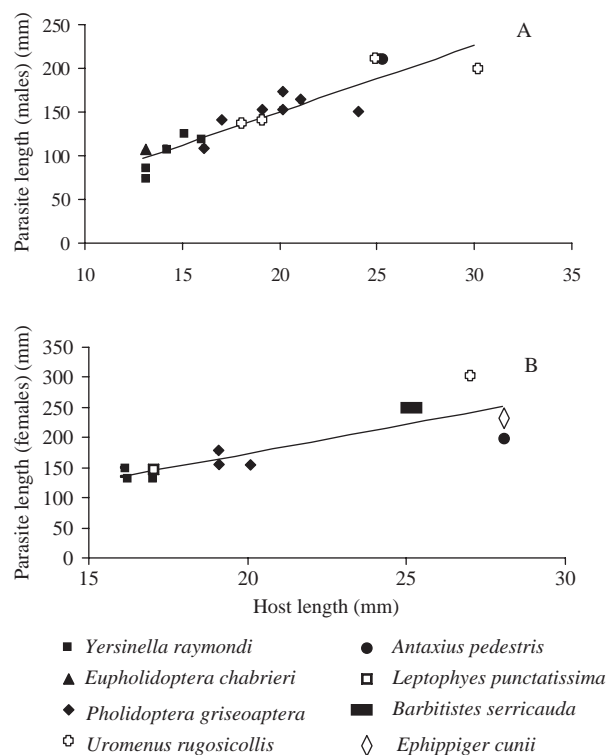


Fig. 3. Relationship between hairworm length and host length. (A) Male hairworms (hairworm length = $7.58 \times$ host size - 1.20, $r^2 = 0.83$, $n = 18$, $P < 0.0001$). (B) Female hairworms (hairworm length = $9.70 \times$ host size - 20.41, $r^2 = 0.72$, $n = 11$, $P = 0.001$).

The size of the hosts of *S. tellinii* varies considerably, from small species such as *Yersinella raymondi* (Yersin, 1860) with 13–17 mm body length (all measurements without ovipositor) to large species such as *Uromenus rugosicollis* (Serville, 1839) with 18–30 mm or *Antaxius pedestris* (Fabricius, 1787) with 25–28 mm. There is a linear relationship between host size (measured as body length exclusive ovipositor) and parasite length (Fig. 3). Small hosts with 13–16 mm length (*Y. raymondi*, small *Pholidoptera griseoptera*) include smaller parasite specimens and large hosts (body sizes > 20 mm: *A. pedestris*, *Barbitistes serricauda* and *U. rugosicollis*) have largest parasites. The length of *S. tellinii* ranged from 75 to 150 mm in hosts < 17 mm, from 130 to 175 mm in hosts from 17 to 20 mm and from 150 to 305 in hosts > 20 mm.

3.3. Seasonal occurrence

There is a clear difference in the seasonal occurrence of *Paragordius tricuspidatus* and *S. tellinii* (see Table 3). *Paragordius tricuspidatus* can be found in June, but has its maximum in July. In August, only few specimens can be found. *S. tellinii* is found in August and, as the

Table 3. Total number of recorded infected species of *Nemobius sylvestris* and *Meconema thalassinum*

Month	<i>Nemobius sylvestris</i> / <i>Paragordius tricuspidatus</i>	<i>Meconema thalassinum</i> / <i>Spinichordodes tellinii</i>
September 1999	3	26
July 2000	95	—
August 2000	5	50
September 2000	—	53
June 2002	12	—
July 2002	331	8
August 2002	19	92

exclusive species, in September. Therefore, August is the only overlapping month for both species. If further specified, the overlapping period becomes even smaller. From the five specimens of *Paragordius tricuspidatus* found in August 2000, three were found in the first half of the month and the two further until 23rd. During the same period, *S. tellinii* occurred with only five specimens in the first half of the month, while all remaining 45 specimens were collected in the second half.

4. Discussion

Paragordius tricuspidatus seems to be restricted to one host species, *N. sylvestris*, in the investigated region, whereas *S. tellinii* has a broader host spectrum with different representatives of Caelifera (Orthoptera). The three potential hosts would raise the range of hosts even further. Mantids are regular hosts for representatives of the genus *Chordodes* (Schmidt-Rhaesa and Ehrmann 2001), but scorpions (and chelicerates in general) have only rarely been reported as hosts for nematomorphs. The only previous record is a scorpion of the family Vaejovidae parasitized by an undetermined nematomorph (no location indicated) (Poinar 2001). The host of *S. tellinii* was previously unknown, whereas Heinze (1941) reported for *Paragordius tricuspidatus* the hosts *Decticus albifrons* (Fabricius, 1775) and probably *Eumedicogryllus bordigalensis* (Latreille, 1804). Both reports seem to go back to reports by Siebold (1842) and Diesing (1851), but at that time no distinction was made between *Paragordius tricuspidatus* and the second European species, *Paragordius stylosus* (Linstow, 1883). Therefore, these hosts are not reliable reports for *Paragordius tricuspidatus*.

The life cycle of all European nematomorph species is unknown. It can be suspected from experiments with the Japanese species *Chordodes japonensis* (Inoue 1960, 1962) and laboratory life cycle experiments with the

Nearctic *Gordius robustus* and *Paragordius varius* (Hanelt and Janovy 1999, 2003, 2004) that a paratenic host is utilized in the life of these species. However, this requires a carnivorous final host that ingests parasitized paratenic hosts. This is the case for most of the hosts of *Paragordius tricuspidatus* and *S. tellinii* (Detzel 1998), but there are exceptions. *B. serricauda* and *Leptophyes punctatissima* are reported to be exclusively herbivorous (Detzel 1998). This corresponds with some reports of short-horned grasshoppers (Orthoptera, Ensifera) in North America (see Schmidt-Rhaesa 2001) and these species might become infected without a paratenic host, e.g. by drinking water or eating vegetation with larvae or cysts of nematomorphs.

It is remarkable that the hosts of *S. tellinii* exhibit a wide range of size. Measurement of the length does even underestimate these differences, because short species such as *Y. raymondi* have a slender abdomen, whereas the abdomen appears almost inflated in some large species such as *A. pedestris* and *Ephippiger cunii*. The size of *S. tellinii* varies strongly (range in free-living males and females more than twofold), but host size has an additional effect on body size with small hosts supporting small parasites and large hosts supporting large parasites. A broad range of size is also present in free-living *Paragordius tricuspidatus*. Spatial effects on development could be investigated in this species not by different host sizes (as in *S. tellinii*), but by different numbers of parasites developing in one host. Development together with other specimens does have significant effects on size only when four parasites are together in one host, in all other cases, body sizes were comparable with lengths from single infections, although in the lower range.

The clear predictability of occurrence of *Paragordius tricuspidatus* and *S. tellinii* has not been reported in the literature before. It is, however, probable that this seasonal occurrence depends much on the occurrence of the hosts. Adults of *N. sylvestris* appear in July and lay eggs until during fall (Campan 1966; Detzel 1998). Adults of *Meconema thalassinum* appear from July to November, but the maximal abundance is in August (Detzel 1998).

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