

REVIEW

Phocid seals, seal lice and heartworms: a terrestrial host–parasite system conveyed to the marine environment

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ABSTRACT: Adaptation of pinnipeds to the marine habitat imposed parallel evolutions in their parasites. Ancestral pinnipeds must have harboured sucking lice, which were ancestors of the seal louse *Echinophthirius horridus*. The seal louse is one of the few insects that successfully adjusted to the marine environment. Adaptations such as keeping an air reservoir and the ability to hold on to and move on the host were necessary, as well as an adjustment of their life cycle to fit the diving habits of their host. *E. horridus* are confined to the Northern Hemisphere and have been reported from 9 species of northern phocids belonging to 4 genera, including land-locked seal species. The transmission from seal to seal is only possible when animals are hauled-out on land or ice. Lice are rarely found on healthy adult seals, but frequently on weak and young animals. The seal louse is suggested to play an important role as an intermediate host transmitting the heartworm *Acanthocheilonema spirocauda* among seals. However, the evidence is restricted to a single study where the first 3 larval stages of the heartworm were shown to develop in the louse. The fourth-stage larvae develop in the blood system of seals and eventually transform into the adult stage that matures in the heart. Since all other studies failed to confirm the presence of heartworm larvae in seal lice, other unknown intermediate hosts could be involved in the transmission of the heartworm. Transplacental transmission of microfilariae in seals has been suggested as an additional possibility, but is not likely to be important since the occurrence of heartworms in adult seals is very rare compared with juveniles. Furthermore, there are no findings of the first 3 larval stages in seals. This review shows that the heartworm infects nearly the same species of seals as the seal louse, except for the grey seal *Halichoerus grypus*, where the heartworm is absent. Prevalence and intensity of infection differ among regions in the Northern Hemisphere. As for seal lice, heartworms mainly infect immature seals, and after infection the prevalence seems to decrease with increasing age of the host.

KEY WORDS: *Acanthocheilonema spirocauda* · Heartworm · *Echinophthirius horridus* · Seal louse · Intermediate host · Life cycle · Adaptation

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INTRODUCTION

The pinnipeds derived from carnivore ancestors after the separation of Feliformia and Caniformia about 45 million years ago (MYA) (Kulu 1972). Seals gradually adapted to the marine environment before they split between Phocidae and Otarioidea in the

Oligocene (~33 MYA) (Arnason et al. 2006). The oldest phocid fossil, called the 'Oligocene seal' (28 MYA), was likely accompanied by parasite systems with terrestrial origins (von Sprehn 1966). Some of these parasite systems were probably lost, while others developed together with the seals through evolution. Adaptation of pinnipeds to the marine habitat imposed adaptive

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pressures on their parasites (Tijskens 1969). Pinnipeds are the only marine mammals which have stayed in contact with the terrestrial as well as the marine environment (Ménier 2000). Their parasite fauna is very diverse and includes endo- and ectoparasites. The most common parasites in seals belong to the phyla Nematoda (roundworms), Acanthocephala (spiny-headed worms), and Platyhelminthes (flatworms), with the classes Trematoda (flukes) and Cestoda (tapeworms). Common parasitic arthropods are mites (subclass Acarina) and lice (suborder Anoplura) (Dierauf 2000).

The most frequently reported parasite species in Atlantic harbour seals *Phoca vitulina vitulina/concolor* are summarised in Table 1. Most of the mentioned endoparasites utilise a number of intermediate hosts. Whereas general biology and intermediate hosts are well known for many of the approximately 25 000 trematode species (Sukhdeo & Sukhdeo 2004), details about the life cycles of parasitic nematodes infecting marine mammals are still scarce. Most investigations are confined to anisakid nematodes and their impact on the fishing industry and on human health. The life cycle of the seal worm/cod worm *Pseudoterranova decipiens* has been described in several experimental studies (e.g. McClland 1980a,b, 1982). Eggs are shed with the faeces of the final host (seals), after which eggs hatch to free-living ensheathed larvae (McClland 2002). First intermediate hosts are meiofaunal copepods, gammarids and amphipods, but also macroinvertebrates such as polychaetes, nudibranchs, mysids, isopods, cumaceans and decapods. Later larval stages infect the flesh of numerous marine and euryhaline fish species (>75 species) that mostly act as second intermediate hosts. The life cycle of the seal worm is completed when the second intermediate host is ingested by a

grey seal *Halichoerus grypus*, although the cod worm is common also in harbour seals *Phoca vitulina* (McClland 2002). The cod worm may exemplify a strategy whereby the parasite can have several alternative final hosts.

Klimpel et al. (2004) gave a modified and detailed life cycle for *Anisakis simplex*, in which copepods, euphausiids and cephalopods, as well as planktivorous and piscivorous fishes, acted as intermediate hosts. Toothed whales, such as porpoises and dolphins, constitute primary final hosts, whereas pinnipeds are assumed to provide suboptimal environments, since the prevalence is lower than in odontocetes and the adult size of *A. simplex* is considerably smaller in pinnipeds (B. Berland pers. comm.). Consequently, *A. simplex* is assumed to have co-evolved with small odontocetes, whereas the parasite is less adapted to completion of its life cycle in pinnipeds. Similar parallel evolutions are seen in canoid carnivores and heartworm species, e.g. in *Dirofilaria immitis* that infect terrestrial Canidae (dogs, wolves, foxes, coyotes, dingoes and jackals, etc.) (Lai et al. 2000, Sacks et al. 2002) and in the related heartworm species *Acanthocheilonema spirocauda*, which infects phocid seals in the Northern Hemisphere.

This review is focussed on the taxonomy and morphology, as well as the distribution and host range, of the heartworm *Acanthocheilonema spirocauda* and the seal louse *Echinophthirius horridus*, which is suggested to act as an intermediate host. We further illustrate the adaptation of the seal louse to the marine environment, pathological findings associated with *A. spirocauda* infection and the possible life cycle of *A. spirocauda* based on available information. A comparison with a terrestrial parasite–host system in dogs will also be discussed.

Table 1. Most frequently identified parasite species (larvae, immature or mature form) in Atlantic harbour seals. N: Nematode; C: Cestode; A: Acanthocephala; T: Trematoda

Parasite species	Source	
	West Atlantic	East Atlantic
<i>Cryptocotyle lingua</i> Creplin, 1825 (T)	–	Strauss et al. (1991)
<i>Phagicola septentrionalis</i> van de Broek, 1967 (T)	–	Strauss et al. (1991)
<i>Diphyllobothrium elegans</i> Krabbe, 1865 (C)	–	Strauss et al. (1991)
<i>Diphyllobothrium cordatum</i> Leukart, 1863 (C)	–	Strauss et al. (1991)
<i>Acanthocheilonema spirocauda</i> Leidy, 1858 (N)	Measures et al. (1997)	Claussen et al. (1991)
<i>Anisakis simplex</i> (Rudolphi, 1809) (N)	Stobo et al. (2002)	Ólafsdóttir & Hauksson (1998)
<i>Phocascaris cystophorae</i> /spp. Bergland, 1963 (N)	Bratley & Stenson (1993)	Ólafsdóttir & Hauksson (1998)
<i>Contraecum osculatum</i> (Rudolphi, 1802) (N)	Stobo et al. (2002)	Claussen et al. (1991)
(<i>Pseudo</i> -) <i>Terranova decipiens</i> (Krabbe, 1878) (N)	Stobo et al. (2002)	Claussen et al. (1991)
<i>Otostrongylus circumlitus</i> (Raillet, 1899) (N)	Gosselin et al. (1998)	Claussen et al. (1991)
<i>Parafilaroides gymnuris</i> Raillet, 1899 (N)	Gosselin et al. (1998)	Claussen et al. (1991)
<i>Corynosoma strumosum</i> Rudolphi, 1802 (A)	–	Strauss et al. (1991)
<i>Echinophthirius horridus</i> von Olfers, 1816 (Anoplura)	Hoffmann et al. (2004)	Thompson et al. (1998)

Table 2. *Acanthocheilonema spirocauda* (Leidy, 1858) Anderson, 1992. Taxonomic hierarchy and synonyms of the heartworm

Taxonomic hierarchy (Anderson 2000)	Synonyms
Phylum: Nematoda	= <i>Filaria spirocauda</i> Leidy, 1858
Class: Secernentea	= <i>Filaria cordis phocae</i> Joly, 1858
Order: Spirurida	= <i>Skrjabinaria spirocauda</i> (Leidy) Lubimov, 1927
Suborder: Spirurina	= <i>Skrjabinaria heteromorpha</i> Kreis, 1953
Superfamily: Filarioidea	= <i>Dipetalonema spirocauda</i> Anderson, 1959
Family: Onchocercidae	= <i>Dipetalonema (Acanthocheilonema) spirocauda</i>
Subfamily: Onchocercinae	Anderson and Bain, 1976
Genus: <i>Acanthocheilonema</i> Cobbold, 1870	
Species: <i>spirocauda</i> Anderson, 1992	

THE HEARTWORM ACANTHOICHEILONEMA SPIROCAUDA (LEIDY, 1858) ANDERSON, 1992

Taxonomy and morphology

The heartworm of harbour seals *Phoca vitulina vitulina* was first described by Leidy (1858) as *Filaria spirocauda*, and somewhat later by Joly (1858) as *F. cordis phocae*. The taxonomy has been revised several times, resulting in name changes (Table 2). Railliet & Henry (1910) transferred the heartworm, together with other filarioids, to the new genus *Dipetalonema*. Later, Lubimov (1927) published a similar description in which the worm was named *Skrjabinaria spirocauda*. Chabaud (1952) used the genus name *Dipetalonema* in his taxonomical description, whereas Kreis (1953) described heartworms found in captive harbour seals as *S. heteromorpha*. Using specimens from earlier descriptions as well as new material, Anderson (1959) reviewed the taxonomy of the heartworm and gave a full re-description of *D. spirocauda*. In this process it was noticed that the descriptions of Leidy (1858) and Joly (1858) were so general that the worms could belong either to *Dipetalonema spirocauda* or *Dirofilaria immitis* and that the female worm described by Lubimov (1927) did not belong to the filarioids, but seemed to be a metastrongyle. The descriptions of the male worm of Lubimov (1927) and the worm of Kreis (1953) were identical with those of *D. spirocauda*, and, therefore, *S. spirocauda/heteromorpha* are regarded as synonyms (Anderson 1959). Anderson & Bain (1976) mentioned the heartworm in their keys to the genera of the order Spirurida as *Dipetalonema (Acanthocheilonema) spirocauda*. Later Bain et al. (1982) raised the subgeneric *Acanthocheilonema* to generic status, and 10 yr later Anderson (1959, 1992) presented the

recent name *A. spirocauda* for the heartworm nematode for the first time.

The genus *Acanthocheilonema* belongs to the subfamily Onchocercinae (Table 2). A typical characteristic of this genus is the lamina of the right spicule, which is simple and spoon-shaped, and the lamina of the left spicule that is generally longer than the shaft in contrast to other genera (Anderson & Bain 1976). The glandular oesophagus is much broader than the muscular one. The cephalic extremity is flat or convex in a lateral view. The *A. spirocauda* is a long, slender nematode with a tapering extremity. Anderson (1959) described the anterior end as round, without cuticular structures, but with 4 pairs of submedian papillae and lateral amphids, whereas the oral opening is surrounded by a cuticular ring leading into a cavity with a thick, curved refractory wall (Fig. 1D). The wall and oesophagus are separated by a big cuticular ring. The oesophagus is rather short and is divided into a short anterior muscular part and a broader posterior glandular part (Anderson 1959) (Fig. 1E). The cuticula is thin, often with regular transverse striations. Males and females differ in some specific morphological charac-

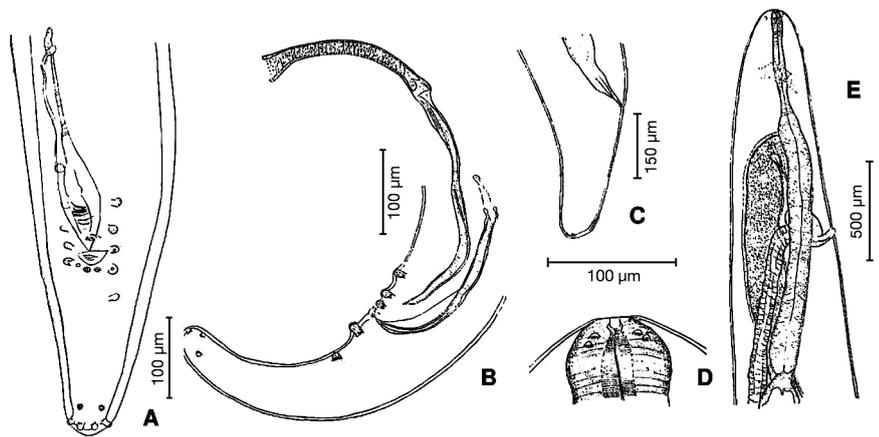


Fig. 1. *Acanthocheilonema spirocauda*. Male caudal end (A) lateral view and (B) ventral view and female (C) caudal end, lateral view, (D) lateral view, anterior end and (E) anterior end, lateral view

teristics. Whereas the female has a single terminal papilla, the male has well-defined and arranged numbers of caudal papillae (Fig. 1A,B): 3 pairs of preanal papillae, 5 smaller papillae in a row behind the anus, a single broad median papilla before the anus, an unpaired papilla on the left side of the ventral surface behind the anus (Fig. 1B), a pair of papillae on the ventrolateral surface of the caudal extremity and 2 pairs of terminal papillae (Fig. 1A) (Anderson 1959). Male spicules differ in size (Wülker 1930). The left spicule, consisting of tubular calornus and membranous lamina, is 0.47 mm in length, whereas the right one is 0.21 to 0.27 mm in length (Anderson 1959). The capitula of the spicules is weakly developed, and a gubernaculum is absent. An excretory pore is distinct in females, but not present in males (Anderson 1959). The female vulva is 1.2 to 1.3 mm from the anterior extremity and has 2 lateral rounded flaps. The anterior of the vagina is sharply bent and bound with ligament, which is typical of the genus *Acanthocheilonema*.

Borgesteede et al. (1991) mentioned entangled worms that were difficult to separate. This is probably the reason why only a few published measurements of the size of adult *Acanthocheilonema spirocauda* are available (Table 3). However, the average length of males is about 9.0 cm and the width 0.37 mm, whereas female worms are larger, with mean lengths and widths at 14.9 cm and 0.66 mm (Anderson 1959).

Female worms shed microfilariae (mf) in the blood of their host (Dailey 1978). Circulating in the blood of seals, mf are unsheathed and have attenuated, pointed tails (Anderson & Bain 1976, Anderson 2000). The life cycle of *Acanthocheilonema spirocauda* is not fully understood, but filarioid mf are known to transform into 4 different larval stages.

Taylor et al. (1961) described the mf of *Acanthocheilonema spirocauda* found in blood smears as

unsheathed and exceedingly slender, with greatly extenuated caudal extremities, $235 \pm 10 \mu\text{m}$ in length and $5.4 \mu\text{m}$ in width. The measurements of Geraci et al. (1981) are significantly greater than those of Taylor: $286 \pm 10 \mu\text{m}$ in length and $5.3 \pm 0.5 \mu\text{m}$ in width (N = 40). The authors suggested that the differences might be explained by differences in used fixation techniques. Whereas Geraci et al. (1981) centrifuged 1 ml of blood with 10 ml of 2% formalin and placed an aliquot of the pellet on a glass slide, Taylor et al. (1961) used the thick blood smear (TBS) technique and stained with Giemsa's stain.

The mf transform into first-stage larvae (Fig. 2A), which Geraci et al. (1981) described as a short, thick 'sausage' stage, which becomes longer, develops a tail and a protruding cephalic knob ($280 \pm 60 \mu\text{m}$ in length; $-8.4 \pm 5.7 \mu\text{m}$ in width; N = 66). After moulting into the

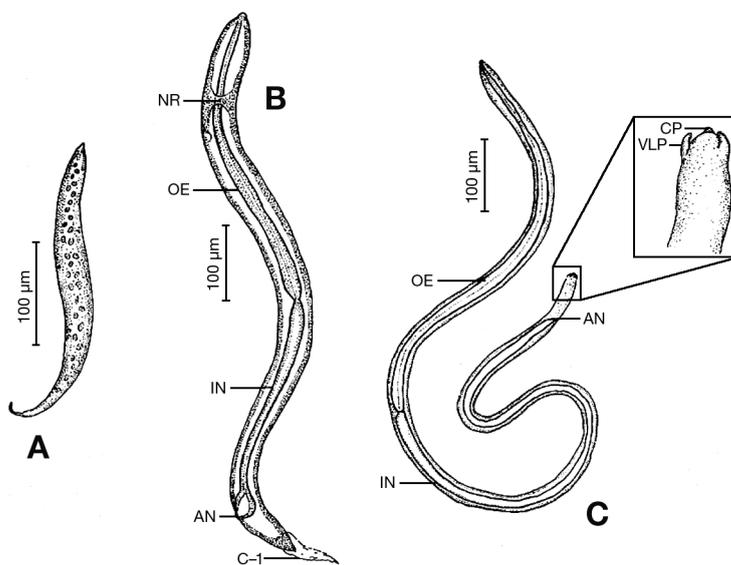


Fig. 2. *Acanthocheilonema spirocauda*. Laval stages of heartworms (lateral view): (A) first-stage, (B) second-stage (AN: anus; C-1: remnant of first-stage cuticle; IN: intestine; NR: nerve ring; OE: oesophagus), (C) third-stage (AN: anus; CP: caudal papilla; IN: intestine; OE: oesophagus; VLP: ventrolateral papilla) (Geraci et al. 1981)

Table 3. *Acanthocheilonema spirocauda*. Number (N) and measurements of adult male and female heartworms found in *Phoca vitulina*. -: no data

N	Male worm		N	Female worm		Source
	Width (mm)	Length (cm) Range Mean		Width (mm)	Length (cm) Range Mean	
4	-	10.4–11.4 10.8	-	-	-	Measures et al. (1997)
-	0.50	- 9.0	-	0.50	- 15.0	Borgesteede et al. (1991)
-	0.50	9.0–15.0 -	-	0.50	9.0–15.0 -	van der Kamp (1987)
-	-	11.0–(18.0) -	-	-	11.0–18.0 -	Wipper (1974)
-	-	- -	-	0.30	- 15.0	van den Broek & Wensvoort (1959)
2	0.33–0.40	8.7–9.3 9.0	2	0.66	14.3–15.5 14.9	Anderson (1959)
4	-	11.0–12.0 -	7	0.70	15.0–17.0 -	Leidy (1858)

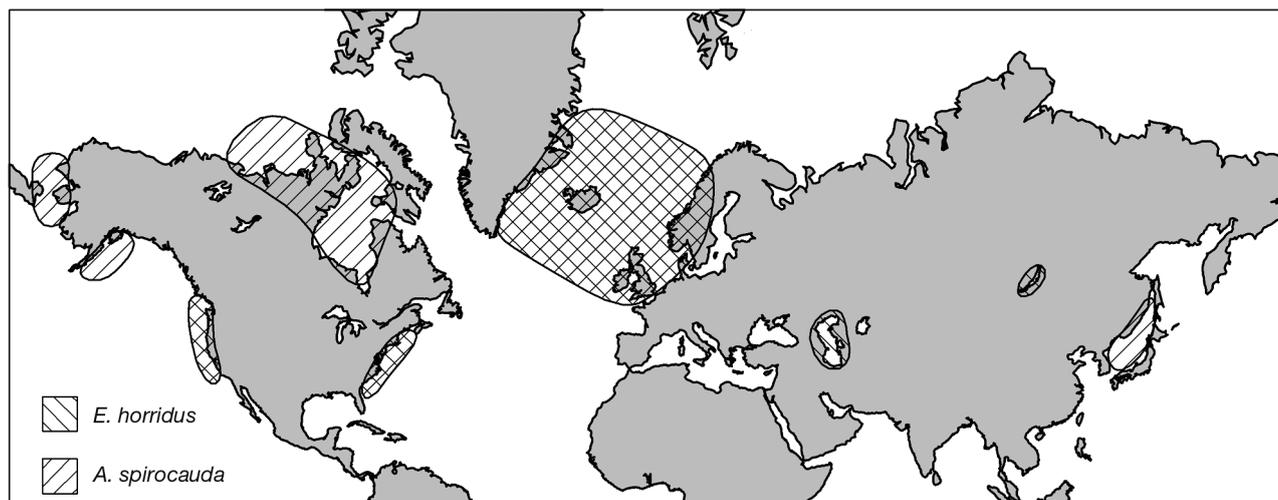


Fig. 3. Map of distribution of *Acanthocheilonema spirocauda* and *Echinophthirus horridus* in the Northern Hemisphere

second larval stage, these structures are lost and the second-stage larva is longer and thicker than the first stage ($923 \pm 202 \mu\text{m}$ in length; $29.7 \pm 3.2 \mu\text{m}$ in width; $N = 7$) (Fig. 2B). The third larval stage is likewise longer, but thinner ($1470 \pm 497 \mu\text{m}$ in length; $23.8 \pm 3.2 \mu\text{m}$ in width; $N = 31$). Larvae in this stage have 1 caudal papilla and 2 ventrolateral 'ears' at the posterior end (Geraci et al. 1981) (Fig. 2C).

No additional larval stages have been described for *Acanthocheilonema spirocauda*, except by Raga (1992), who mentioned a fourth larval stage without giving detailed descriptions.

Epizootiology

Distribution and host range

Most investigations on *Acanthocheilonema spirocauda* have been carried out in the Northern Hemisphere, and only limited information is available for southern pinnipeds. However, since no finds of the heartworm have been reported from the Southern Hemisphere (Lauckner 1985), the spatial distribution of *A. spirocauda* seems to be limited to the Northern Hemisphere, where it has a holarctic distribution (Fig. 3). Although *A. spirocauda* seems to be an ancient species, originating from the parasitic nematodes infecting terrestrial ancestors of seals (von Sprehn 1966, Anderson 1984, Ménier 2000), the heartworm is confined to phocid seals and has not been reported to occur in Otariinae or Monachinae (Dailey 1975).

The filarioid heartworm infects a variety of phocid seals, encompassing 3 genera and 7 species or subspecies. The heartworm does not seem to have any preferred host species within this group of seals, since

adult worms from different phocid species are all of similar size (Measures et al. 1997).

Acanthocheilonema spirocauda is commonly reported in harbour seals *Phoca vitulina* (subspecies *P. v. vitulina*, *P. v. concolor* and *P. v. richardii*). It has also been reported in *P. v. stejnegeri* (Nagasawa 1999) (Table 4, Fig. 3). In addition, the heartworm occurs in hooded seals *Cystophora cristata* (Delamure & Treshchev 1966, Helle & Blix 1973, Pouvreau et al. 1980, Measures et al. 1997), bearded seals *Erignathus barbatus* (Popov 1975a, Eley 1981), ribbon seals *P. fasciata* (Popov 1975b, Eley 1981, Shults & Frost 1988), harp seals *P. groenlandica* (Measures et al. 1997), ringed seals *P. hispida* (King 1964, Delamure & Popov 1974, Dailey 1975, Popov 1975a, Treshchev & Yurakhno 1975, Eley 1981, Measures & Gosselin 1994, Measures et al. 1997) and spotted seals *P. largha* (Popov 1975a, Delamure et al. 1976, Goltsev et al. 1978, Eley 1981, Shults 1982).

Perry (1967) described a related species to *Acanthocheilonema* (*Dipetalonema*) infecting California sea lions *Zalophus californianus* named *Dipetalonema odendhali*. This species differs from *A. spirocauda* in being of a smaller size (male: 4.6 to 6.4 cm length, mean 5.4 cm; female: 10.0 to 15.0 cm length, mean 11.8 cm), having a proportionally longer oesophagus and longer tail in both sexes. A further difference between the species is the location where worms are found. According to Perry's description, *D. odendhali* occurred in subcutaneous and intermuscular sites of *Z. californianus*, and not in the heart. A high infection rate of California sea lions was also noted by Dailey (1975). Lauckner (1985) mentioned that *D. odendhali* does not have as high a zoonotic potential as *A. spirocauda*.

Anderson (1959) mentioned the occurrence of *Acanthocheilonema spirocauda* in northern fur seals *Callo-*

Table 4. *Acanthocheilonema spirocauda*. Records of heartworms found in harbour seals *Phoca vitulina*. P: prevalence; D: cause of seal death; C: captive, H: hunting, N: netting, S: stranded, PDV: phocine distemper virus; –: no data

Subspecies of <i>P. vitulina</i>	Location	Examined/ infected seals	P (%)	D	Source
<i>vitulina</i>	Europe				
	Denmark/North Sea–Limfjord–Kattegat	65/16	24.6	H/N/S/C	Clausen (1978)
	Germany/North Sea	18/2	11.1	–	Menschel et al. (1966)
	Germany/Sylt	25/2	8.0	PDV	Breuer et al. (1988)
	Germany/Wadden Sea	115/37	32.2	PDV	Claussen et al. (1991)
	Germany/Wadden Sea	93/36	38.7	H/S	Wipper (1974)
	Ireland/Irish Sea	76/12	15.8	PDV	Kennedy et al. (1989)
	Iceland/entire coast	15/3	20.0	H	Skirnisson & Ólafsson (1990)
	Netherlands/Texel	24/12	50.0	S	Van den Broek & Wensvoort (1959)
	Netherlands/Terschelling	48/21	43.8	S	van den Broek (1963)
	Netherlands/Wadden Sea	54/4	7.4	H/S	van der Kamp (1982)
	Netherlands/Wadden Sea	363/44	9.5	H/S	van Haafden (1982)
	Netherlands/Wadden Sea	12/8	66.7	–	M. van der Wal & C. Helbergen (unpubl. data) ^a
	Netherlands/Wadden Sea	34/1	2.9	C	van der Kamp (1987)
	Netherlands/Wadden Sea	94/23	24.5	PDV	Borgsteede et al. (1991)
Sweden/Kattegat–Skaggeak–Baltic	158/18	11.4	PDV	Lunneryd (1992)	
<i>concolor</i>	USA east/Canada				
	Canadian Arctic	18/2	11.1	H/N	Measures et al. (1997)
	Nova Scotia/Sable Island	15/2	13.3	C	McClland (1980c)
	Nova Scotia/Sable Island	5/4	80.0	C	Dunn & Spotte (1974)
	Rhode Island/Connecticut	5/5	100	S/C	Dunn & Wolke (1976b)
<i>richardii</i>	USA west				
	California/Los Angeles	5/5	100	C	Brown et al. (1960)
	Southern California	5/5	100	C	Taylor et al. (1961)
	Los Angeles Country	13/2	15.4	S	Schroeder et al. (1973)
	San Diego/California	13/4	30.8	–	Sweeney (1973)
	Oregon coast	18/2	11.1	S	Stroud & Dailey (1978)
	Grays Harbor/Washington	77/36	47.0	C/S	Dailey & Fallace (1989)
	Alaska	99/17	17.2	H	Eley (1981)
<i>stejnegeri</i>	Asia				
	Japan Sea	–	–	–	Nagasawa (1999)

^aUnpubl. report, as cited in Borgsteede et al. 1991

rhinus ursinus, but added that none of the worms were in good enough condition for detailed description. It is therefore likely that the observed nematodes were *Dipetalonema odendhali* as suggested by Perry (1967), since *A. spirocauda* has not been confirmed by later investigations. Further, Perry & Forrester (1971) also found *D. odendhali* in the right thoracic area in the fascia between the muscles and the fascia beneath the blubber in some northern fur seals. Machida (1977) re-assigned the worms he found in 1969 in the subfascia of the cervical and thoracic region of Japanese *C. ursinus* from *A. spirocauda* to *D. odendhali*, because of the organs they infected. The mf of *A. spirocauda* (225 to 296 µm in length; 4.8 to 5.8 µm in width) and *D. odendhali* (225 to 250 µm in length, 3.5 to 4.4 µm in width) are similar in size, but do not infect the same host species (Howard et al. 1983). *D. odendhali* are found in the

blood of the northern fur seal *C. ursinus* and the California sea lion *Zalophus californianus* (Perry 1967, Perry & Forrester 1971, Forrester et al. 1973), whereas *A. spirocauda* seems to infect phocid seals only.

Acanthocheilonema spirocauda had not been reported from grey seals *Halichoerus grypus*. This led Measures et al. (1997) to suggest that a larger sample size of young grey seals from a broad geographic area would be needed to detect heartworm infections in this species. However, no heartworms were found in a sample examined at the Swedish Museum of Natural History (B.-M. Bäcklin pers. comm.), although it encompassed 103 yearlings, 144 aged 1 to 5 yr, and 168 older than 5 yr. Consequently, grey seals seem to escape *A. spirocauda* infection.

Since the vulnerability to heartworm infection could vary among species, we have compared the geograph-

ical patterns in prevalence and intensity of infection of the heartworm in harbour seals, which have a circum-polar distribution, and split the seal species into sub-species. In Europe, the heartworm is found in *Phoca vitulina vitulina* in the whole Wadden Sea region, as well as in the Irish Sea, on the coast of Iceland, in the Kattegat-Skagerrak and in the Baltic region (Table 4). Most examined seals were hunted or collected during the PDV (phocine distemper virus) epidemic. The prevalence of infections ranged between 8.0 and 32.2% among seals collected during the PDV epidemic in 1988. High prevalence (43.8 to 50.0%) was also noted in seals stranded in the Netherlands during the 1960s. The subspecies *P. v. concolor* and *P. v. richardii* have similar prevalence among hunted, netted, or captive seal samples (11.1 to 47.0%). Examined stranded seals of *P. v. richardii* showed prevalence values ranging between 11 and 15.5%. Higher reported prevalence is mostly based on very small sample sizes (Table 4). Since the prevalence and intensity of infection are affected by the general health status of individual seals (Measures et al. 1997), studies of regional differences in the prevalence of heartworms require carefully designed sampling program. Large samples from mass mortality events, by-catches and material from hunted populations are more likely to provide unbiased data, whereas material from captive and stranded animals could be severely biased and not representative of the population.

Microhabitat

Most heartworms are found in the right ventricle of the heart and in the pulmonary arteries, as described for the first time in a harbour seal (Leidy 1858, Anderson 2000). *Acanthocheilonema spirocauda* has been located in the heart in most studies (Leidy 1858, Freund 1933, Anderson 1959, van den Broek & Wensvoort 1959, Menschel et al. 1966, Helle & Blix 1973, Sweeney 1973, Lauckner 1985, Breuer et al. 1988, Kennedy et al. 1989, Skirnisson & Olafsson 1990, Claussen et al. 1991, Lunneryd 1992), more specifically in the right ventricle (Anderson 1959, Brown et al. 1960, Delamure & Treshchev 1966, MacDonald & Gilchrist 1969, Wipper 1974, Dunn & Wolke 1976b, Dailey 1978, Geraci 1978, Conlogue et al. 1980, Eley 1981, Reijnders et al. 1981, Shults 1982, van der Kamp 1987, Measures et al. 1997), but it has also been found in the pulmonary artery (Anderson 1959, Delamure & Treshchev 1966, Menschel et al. 1966, MacDonald & Gilchrist 1969, Dunn & Wolke 1976b, Stroud & Dailey 1978, Conlogue et al. 1980, Eley 1981, Reijnders et al. 1981, van der Kamp 1987, Measures et al. 1997), in the vena cava caudalis (Borgesteede et al. 1991), in the chorda tendineae and

truncus pulmonalis (Wipper 1974), the aorta (McClelland 1980c), the lungs (van den Broek & Wensvoort 1959, Measures et al. 1997), in mesenteries (Dailey 1978) and in testicular sheath (Shults & Frost 1988).

Another interesting aspect is the age structure of infected seals. Delamure & Treshchev (1966), as well as Popov (1975b), observed that *Acanthocheilonema spirocauda* primarily infects pups of the year and immature (1 to 4 yr) seals. They also suggested that severely infected individuals may not survive heartworm infections. Claussen et al. (1991) and Borgsteede et al. (1991) observed high prevalence in younger seals, and Measures et al. (1997) mentioned that *A. spirocauda* was found in 14 of 19 immature seals. This pattern is repeated in other parts of the distribution area of *A. spirocauda* (Dailey & Fallace 1989), and seals younger than 4 yr in the Skagerrak carried 69% of all heartworms examined by Lunneryd (1992). Consequently, the prevalence of infection decreases with increasing age of the host in most studies, whereas this pattern was not found by Dailey & Fallace (1989). We suggest that once infected, a seal cannot escape the heartworm, which eventually will have lethal consequences. This would explain the low prevalence of heartworms in older seals.

It has been suggested that females and males become infected to a similar extent, and that the infection has a seasonal component, where highest infection rates of *Acanthocheilonema spirocauda* occur during the summer, and lowest in the spring (Dailey & Fallace 1989). Claussen et al. (1991) suggested that higher numbers of heartworms could occur in underfed (blubber thickness <11 mm) and ill-fed (11 to 15 mm) seals compared to well-fed (>15 mm) seals, but their results are not clearly presented. Neither Lunneryd (1992) nor Measures et al. (1997) could correlate differences in body conditions with heartworm infection.

Clinical signs and pathology

Attributing specific clinical signs to *Acanthocheilonema spirocauda* infection is difficult, since most examined seals have multiple infections, including the lungworms *Otostrongylus circumlitus* and *Parafilaroides* spp. (Measures 2001). Various signs, such as fatigue, anorexia, emaciation and dehydration, as well as coughing, nasal discharge, bronchospasm, dyspnoea and erratic breathing patterns, are typical for heavy filariasis (Brown et al. 1960, Sweeney 1978, Lauckner 1985, Dailey 2001, Measures 2001). In addition to a high respiratory rate after minimal effort, the animals show listlessness (Brown et al. 1960, Wallach 1972).

Microfilariae are observed in the lumen of vessels, the hepatic and splenic parenchyma, or in acute

lesions, and in the blood (Dunn & Wolke 1976a). *Acanthocheilonema spirocauda* infection in living seals can be confirmed by the presence of mf in TBS (Taylor et al. 1961, Dunn & Spotte 1974, Sweeney 1978, Dailey 2001), but this technique can sometimes miss positive cases (Menschel et al. 1966). A new, more sensitive, simpler and less-time-consuming method used for diagnosis of mf (hematoparasites/filariasis) is the quantitative buffy coat (QBC) technique, e.g. for heartworm infections with *Dirofilaria immitis* in dogs (Wang 1998) or malaria infections in humans (Estacio et al. 1993). Other methods to detect mf in dogs (*D. repens*, *D. immitis*, *A. reconditum*) are Knott's test (Svobodová et al. 2006), a simple molecular method (Casiraghi et al. 2006), the serological (filter) test, and frequently used immunological methods for detecting circulating antibodies or antigens (Sacks et al. 2002). Experience with these modern methods with regard to *A. spirocauda* are still lacking, and such tests must be validated before using them in wildlife populations.

Pathological changes linked to heartworm infection have been observed in the lungs, heart and liver. Severe infection can be detrimental to the host (Howard et al. 1983, van der Kamp 1987). Pathological processes are mainly initiated by endarteritis of the pulmonary artery and its branches due to chronic, mechanical, or metabolic activity of the worms (Otto & Jackson 1969, Stroud & Dailey 1978). The endarteritis progresses into thickening of intima, as a proliferation of the endothelial layer (Dunn & Wolke 1976b). The reduced elasticity of arteries results in increased pressure in the pulmonary artery, the right side of the heart and the venae cavae. Other common signs are obstructions of the pulmonary arteries, inflammation and thrombosis with subsequent infarct in the parenchyma of the lung (Sweeney 1973, Stroud & Dailey 1978, van der Kamp 1987, Breuer et al. 1988, Vercruyssen et al. 2003). Dead adult worms can also form verminous emboli (Otto & Jackson 1969, Dunn & Wolke 1976b). Congestion and oedema in all lobes of the lung have been reported by MacDonald & Gilchrist (1969). The lungs often show hepatisation and diffuse or granulomatous pneumonia (Brown et al. 1960, Menschel et al. 1966, Dunn & Wolke 1976b). Geraci & Aubin (1986) suggested that complications associated with heartworm infection and reduction in lung capacity would reduce the ability to dive and forage.

Cardiac changes are limited to dilatation and hypertrophy of the right chamber of the heart (Taylor et al. 1961, Sweeney 1974, Gulland et al. 2001) as a result of increased pressure caused by partial blockade of the pulmonary artery (Otto & Jackson 1969). The right atrium and venae cavae are noticeably enlarged, resulting from assemblies of worms obstructing blood flow. However, no significant differences in the

weights of hearts of infected seals compared to non-infected animals have been reported (Eley 1981). In addition to macroscopic lesions in the heart and cardiovascular and pulmonary arterial lesions, microscopic lesions in the lungs, liver, spleen and vascular system have been observed (Dunn & Wolke 1976a). Heartworm-infected seals may also be more susceptible to secondary bacterial infections (McDonald & Gilchrist 1969, Dunn & Wolke 1976a,b, Howard et al. 1983, Measures et al. 1997). Hepatic lesions are passive congestion and centrilobular necrosis of the central veins (Otto & Jackson 1969), or vary from acute eosinophilic necrosis to chronic focal granulomas with foreign body giant cells (Dunn & Wolke 1976a,b). Some of the pathological changes may be irreversible, especially after long infections.

THE SEAL LOUSE *ECHINOPHTHIRIUS HORRIDUS* (VON OLFERS, 1816) FAHRENHOLZ, 1919

Taxonomy and morphology

Sucking lice (Anoplura) are obligate, permanent ectoparasites of pinnipeds, and were mentioned in the scientific literature 200 yr ago (von Olfers 1816). Morphological and biological traits and host specificity of echinophthiriids suggest that the lice must have co-evolved with their hosts and been harboured by ancestors to seals before they ventured into the marine environment (Kim 1975, Kim et al. 1975, Ménier 2000). Pinnipeds are infected with a unique group of anoplurid lice, distinct from those found in other carnivores, which has been used as an argument supporting the hypothesis that the pinniped order must have differentiated as a single group from one ancestral canid carnivore (Hopkins 1949). Later the monophyletic origin of pinnipeds was demonstrated by immunological study (Sarich 1969), as well as a molecular one (Arnason et al. 2006).

The family Echinophthiriidae consists of 5 distinct genera and 12 known species (Durden & Musser 1994). The most diverse taxon is the genus *Antarctophthirus*, which includes 6 species and occurs in both hemispheres. The lice infected a wide range of pinniped hosts mainly within the families Otariidae, Odobenidae and Phocidae (Monachinae) (Kim et al. 1975, Durden & Musser 1994). The genus *Echinophthirus* is monotypic with the species *E. horridus* and has a Holarctic distribution in the Northern Hemisphere, where it only infects true seals (Phocidae). The genus *Proechinophthirus* includes 2 species often found on seals within the Otariinae and Arctocephalinae. The genus *Lepidophthirus*, encompassing 2 species, infects monk seals *Monachus monachus* and southern elephant

Table 5. *Echinophthirius horridus* (von Olfers, 1816) Fahrenholz, 1919. Taxonomic hierarchy and synonyms of the seal louse

Taxonomic hierarchy	Synonyms
Phylum: Arthropoda	= <i>Pediculus horridus</i> von Olfers, 1816
Subphylum: Hexapoda	= <i>Pediculus phocae</i> Lucas, 1834
Class: Insecta	= <i>Pediculus setosus</i> Burmeister, 1838
Order: Phthiraptera	= <i>Haematopinus setosus</i> Denny, 1842
Suborder: Anoplura	= <i>Haematopinus annulatus</i> Schilling & Gurlt, 1857
Superfamily: Echinophthirioidea	= <i>Haematopinus (Echinophthirius) setosus</i> Giebel, 1871
Family: Echinophthiriidae	= <i>Echinophthirius setosus</i> Piaget, 1880
Genus: <i>Echinophthirius</i> Giebel, 1871	= <i>Echinophthirius groenlandicus</i> Becher, 1886
Species: <i>horridus</i> (von Olfers 1816) Fahrenholz, 1919	= <i>Echinophthirius sericans</i> Meinert, 1897
	= <i>Echinophthirius phocae</i> Enderlein, 1904

seals *Mirounga leonina* (Kim et al. 1975, Durden & Musser 1994). The genus *Latagophthirus*, which includes a single species, mainly infects mustelids such as *Lontra canadensis* (Durden & Musser 1994).

The seal louse *Echinophthirius horridus* was first described as *Pediculus horridus* by von Olfers (1816). Later descriptions resulted in a number of synonyms cited in the literature (Table 5). Lucas (1834) named the seal louse *P. phocae*, whereas Burmeister (1838) described it as *P. setosus*. Other scientific names that have been used are *Haematopinus setosus* (Denny 1842) and *H. annulatus* (Schilling & Gurlt 1857). The genus *Echinophthirius* was first suggested by Giebel (1871), who used the name *H. (Echinophthirius) setosus* for the seal louse. All lice found on seals were first described as belonging to the genus *Echinophthirius*, i.e. *E. setosus* Piaget, 1880; Osborn (1896), Meinert (1897), Breddin (1901); *E. groenlandicus* Becher, 1886; *E. sericans* Meinert, 1897, until Enderlein (1904) named it *E. phocae* and described 2 new genera: the genus *Lepidophthirus* (1904) and *Antarctophthirus* (1906) within the suborder Anoplura. Enderlein (1906) mentioned that the genus *Echinophthirius* has setae all over the body, in contrast to *Lepidophthirus* and *Antarctophthirus*, which have leaf-like scales on dorsal or ventral sides of the thorax or the abdomen.

The seal louse was subsequently called *Echinophthirius phocae* by Enderlein (1904, 1906, 1909), von Dalla-Torres (1908), Luther (1909), Mjöberg (1910) and Evans (1913) until Fahrenholz (1919) finally named it *E. horridus*. A number of subspecies have been described in the past, but they have not been generally accepted. Ass (1935) suggested *E. h. baikalensis* for the seal louse on Baikal seals *Phoca sibirica*, Kurochkin & Badamshin (1968) reported a louse *E. h. caspicus* on Caspian seals *P. caspica*, and Blagoveshtchensky (1966) named the louse found on bearded seals *Erignathus barbatus* as *E. h. erignathi*.

Both Freund (1928) and Jancke (1938) gave detailed descriptions of adult specimens of *Echinophthirius horridus*, and a more general description is given in the

monograph by Ferris (1934). The first full description, including eggs and the 3 nymphal stages, was given by Scherf (1963a). More details of the developmental stages were observed using scanning electron micrographs of adult (Miller 1971) and nymphal stages of the louse (Beder 1990).

Eggs of *Echinophthirius horridus* resemble small barrels, with even bases and vaulted tops, and are laid in parallel with the hair of the host (Scherf 1963a). An egg is 0.928 mm long and 0.464 mm wide, covered with a brown attachment substance and divided into 7 to 11 chambers.

The 3 nymphal stages are distinguished by size differences. Nymphs undergo heterometabolic metamorphoses (Scherf 1963b): Stage 1 nymphs (N₁) are 1.12 to 1.13 mm long, Stage 2 nymphs (N₂) are 1.44 to 1.49 mm long and third stage nymphs (N₃) are 1.79 to 1.91 mm (Table 6).

The first nymphal stage has a stocky conical head, well distinguishable from the thorax (Scherf 1963a). All nymphs are eyeless, and the antennae have 4 segments like the adult stage (imago) (Fig. 4). The extremities are fully developed and increasingly sclerotised from the tibiotarsus to the tip of the claw. The tibia carry small teeth (Scherf 1963a). For each nymphal stage the extremities become stronger, but show the same basic structures. Scherf (1963a) also described 1 to 2 ventral spines at the basal segment for the third nymphal stage. All nymphal stages have fewer setae than adults do, and numbers of setae increase with each nymphal stage (Scherf 1963a, Beder 1990). Sexual organs are first seen in N₃, where a genital region is discernible at the ninth segment of the abdomen. The imago is reached after the third moult (Scherf 1963b).

Although there are remains of corneal structures (Freund 1928), the imago is eyeless, with a short and wide head (Ferris 1934, present paper Fig. 5). The rostrum is strong and well-developed, with various piercing structures used for sucking blood from the host (Scherf 1963b). The first and second segments of

Table 6. *Echinophthirius horridus*. Number (N) and mean total lengths (mm) of the 3 nymphal stages of sucking lice

Nymph 1			Nymph 2			Nymph 3			Source
N	Length (mm)	Min.–Max. (mm)	N	Length (mm)	Min.–Max. (mm)	N	Length (mm)	Min.–Max. (mm)	
50	1.13	(0.97–1.25)	50	1.49	(1.29–1.62)	50	1.91	(1.74–2.15)	Scherf (1963a,b)
34	1.12	(0.78–1.38)	42	1.44	(1.20–1.83)	53	1.79	(1.58–2.13)	Beder (1990)

antennae show ventral lobes (Ferris 1934, Scherf 1963a,b, Miller 1971). While Freund (1928) and Scherf (1963a) mentioned sensilla basicornia on the terminal antennal segment, Miller (1971) described 2 such structures and 2 pore organs. The sensilla basicornia have 11 to 13 setae forming a ring. The head, thorax and abdomen of a louse are covered with numerous setae of variable lengths. In contrast to other taxa of lice, body spines are only developed in *Echinophthirius* (Kim 1985). The whole body, except for the corneal region (Freund 1928), is covered with setae

(Ferris 1934), but short stout setae are most common on the head (Kim et al. 1975) and on the ventral side of the thorax, whereas longer setae are more common on the abdomen (Miller 1971). Scales are totally absent in *E. horridus* (Freund 1928, Ferris 1934).

The thorax is small compared with the wide, nearly circular abdomen (Figs. 4 & 5). The sternum has an irregular, sclerotic plate (Ferris 1934). Forelegs are smaller than the successively longer midlegs and hindlegs (Kim 1985). The femur carries most of the setae of the leg (Scherf 1963a). The caudal part of the climbing structure is enlarged, and the tibia and the tarsus are fused (Ferris 1934, Scherf 1963b), while the median tibiotarsus has a blunt appendix with 4 small pegs (Freund 1928). The claw has an obvious basal lobe (Ferris 1934).

The abdomen shows separated single segments, slightly furrowed, and is entirely membranous in both sexes except for the ninth tergum and the genital areas (Ferris 1934). The genital region is covered with long and slender setae (Miller 1971). Females lack dorsal setae, but have obvious ventral setae, whereas males have dorsal setae and obvious signs of a genital region on the ventral side of the abdomen (Scherf 1963a) (Fig. 6). Females carry 6 to 7 eggs of different stages of development in their abdomen, as described by Scherf (1963a,b). Females are somewhat longer (2.33 to 3.5 mm) than males (2.12 to 3.0 mm) (Table 7), but the sexes are otherwise quite similar (Ferris 1934, Scherf 1963a,b).

Epidemiology

Distribution and host range

Echinophthirius horridus is confined to northern phocid seals belonging to 4 genera and has been found on 9 species or subspecies. The presence on land-locked seal species in Lake Saimaa, Lake Baikal, and the Caspian Sea suggested that the relationship between lice and seals began at least before the freshwater species were separated by land barri-

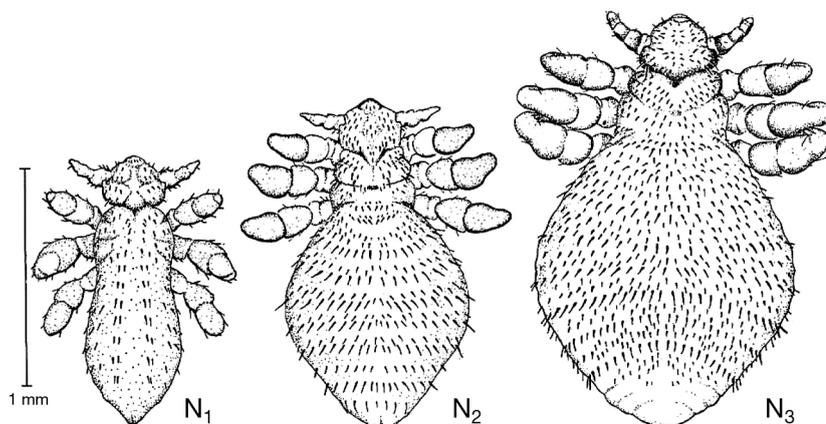


Fig. 4. *Echinophthirius horridus*. Three nymphal stages (N₁, N₂, N₃) of lice, from dorsal views (Scherf 1963a)

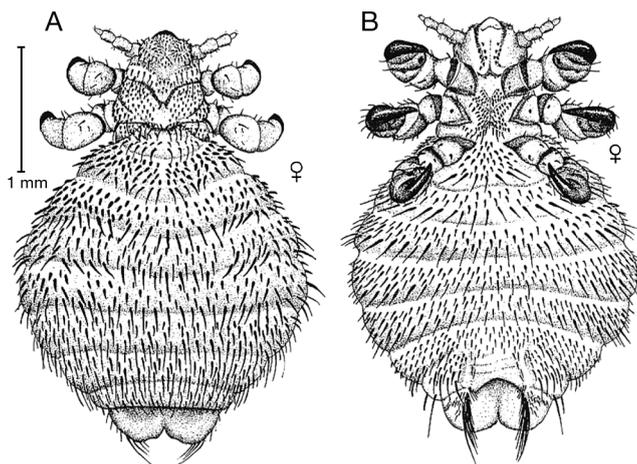


Fig. 5. *Echinophthirius horridus*. Adult female in (A) dorsal and (B) ventral views (Scherf 1963a)

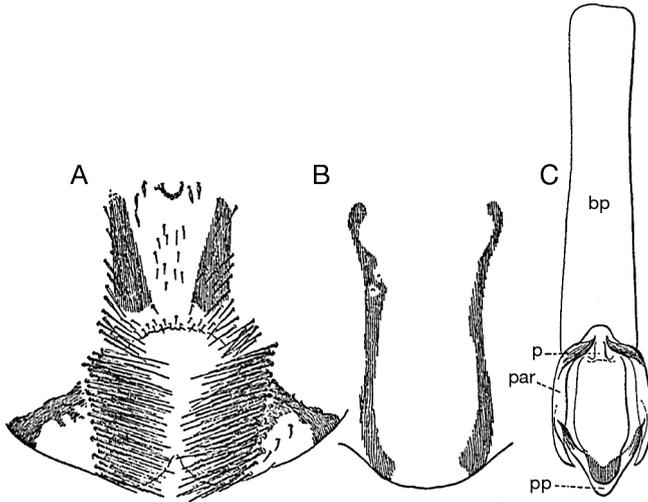


Fig. 6. *Echinophthirius horridus*. Genital regions: (A) female, (B) male and (C) genitalia of male. bp: basal plate; p: penis; par: parameres; pp: v-shaped pseudopenis (von Olfers 1816)

ers (Tijskens 1969). *E. horridus* is common on the harbour seals *Phoca vitulina vitulina*, *P. v. concolor* and *P. v. richardii* (Table 8) and is less frequently reported on Caspian seals (Kurochkin 1975), harp seals (Mjöberg 1910, Freund 1933, Ferris 1934, Hopkins 1949, Scherf 1963a, King 1964, Kim et al. 1975, Durden & Musser 1994), ringed seals (Freund 1933, Ferris 1934, Hopkins 1949, King 1964, Mehl 1970, Miller 1971, Kim et al. 1975, Durden & Musser 1994), the Saimaa ringed seals *Phoca hispida saimensis* (Luther 1909), Baikal seals *P. sibirica* (Freund 1928, Ass 1935, Scherf 1963a, King 1964, Kim et al. 1975, Durden & Musser 1994), grey seals (Ferris 1934, Hopkins 1949, van den Broek & Jansen 1964, King 1964, Bonner 1972, Kim et al. 1975, Durden & Musser 1994, Kadulski 2001), bearded seals (Freund 1933, Hopkins 1949, King 1964, Blagoveshtchensky 1966, Kim et al. 1975, Durden & Musser 1994) and hooded seals (Freund 1933, Hopkins 1949, King 1964, Kim et al. 1975, Durden & Musser 1994) (Fig. 3).

Table 7. *Echinophthirius horridus*. Number (N) and mean total lengths (mm) of male and female lice. -: no data

Males			Females			Source
N	Length (mm)	Min.–Max. (mm)	N	Length (mm)	Min.–Max. (mm)	
–	1.9	–	–	2.35	–	Piaget (1880)
–	3.0	–	–	3.5	–	Ferris (1934)
50	2.36	(2.11–2.60)	50	2.61	(2.34–3.03)	Scherf (1963a,b)
6	2.70–2.90	–	5	3.20–3.40	–	Blagoveshtchensky (1966)
–	–	(2.50–3.00)	–	–	(2.75–3.50)	Lauckner (1985)
150	2.12	(1.75–2.48)	171	2.33	(1.70–2.92)	Beder (1990)
2	–	–	2	2.71	–	Kadulski (2001)

Echinophthirius horridus occurs on harbour seals throughout Europe and on the Atlantic and Pacific coasts of Canada and the USA (Fig. 3). Only 3 quantitative studies have been carried out on louse abundance in harbour seals. The highest prevalence (45.5%) was found in Washington (Dailey & Fallace 1989), followed by 39.0% in northeast Scotland (Thompson et al. 1998) and 36.6% in the Wadden Sea (Wipper 1974). In most other cases, only single animals have been examined or the lice burden is only mentioned vaguely in connection with general pathological investigations or health status reports (Table 8).

The seal louse is rarely found on healthy seals (T. Härkönen unpubl. obs.), but is frequently reported on weak and especially young animals, which seem to be preferentially infected, because they are less resistant to diseases (Turner 1971, Geraci 1978, Reijnders et al. 1981, Lauckner 1985). Great numbers of lice have been reported on specimens from Norway (Mehl 1970), Scotland (Thompson et al. 1998), the Connecticut inlet, USA (Dunn & Wolke 1976b), and from the coast of Florida (Caldwell & Caldwell 1969). A young harbour seal from Danish waters was so heavily infected by lice that this was suspected to be the primary cause of death (Clausen 1978). Thompson et al. (1998) found the prevalence and intensity of lice infections to be greater in years when harbour seals were in poor condition. Weak and sick seals on the beach are sometimes infected with 1000s of lice. Massive infections have been documented on young seals in the Wadden Sea (Scherf 1963a, Schumann 1989) and the North Sea, where one seal had >3 lice cm⁻² body surface (Lauckner 1985), and up to 51 lice cm⁻² body surface have been reported from the coast of Virginia, USA (Conlogue et al. 1980).

Wipper (1974) reported heavy lice burdens mainly on yearlings (N = 27, 7 heavily infected animals), whereas adults (N = 44) and pups (N = 20) were less infected. Only one 4 mo old pup showed heavy infection. The quantitative study by Thompson et al. (1998) showed that only a few harbour seals carried high burdens (100s) of lice. The prevalence was low the first few months after birth, but increased when seals were older than 7 mo. Statistical analyses showed that age, season and year of investigation influenced the intensity of lice found on seals, whereby age and season had the strongest effects. Thompson et al. (1998) observed no seasonal variations for adults, but immature seals had higher prevalence of lice in spring. Contrastingly, Dailey & Fallace (1989) found highest prevalence in autumn and winter,

Table 8. *Echinophthirius horridus*. Reported occurrence of lice on harbour seals *Phoca vitulina*. M: mass burden/heavily infested; P: presence; A: absence. D: cause of seal death. C: captive; H: hunting; N: netting; O: observation; PDV: phocine distemper virus; S: stranded; -: no data

Subspecies of <i>P. vitulina</i>	Location	Examined/infected seals	Lice burden	D	Source
<i>vitulina</i>	Europe				
	Denmark/Kattegat	65/1	M	H/N/S/C	Clausen (1978)
	UK/Shetland Islands	–	P	–	Ferris (1934)
	UK/North Welsh coast	1/1	M	H	Anderson et al. (1974)
	UK/Moray Firth, Scotland	223/87	P	O	Thompson et al. (1998)
	Germany/North Sea Helgoland	1/1	P	–	Mjöberg (1910)
	Germany/North Sea Helgoland	12/2	P	S	Vauk (1973)
	Germany/Wadden Sea Sylt	1/1	M	H	Scherf (1963a)
	Germany/Wadden Sea Sylt	43/11	P	PDV	Schumacher et al. (1990)
	Germany/Wadden Sea	–	P	O	Essink et al. (2005)
	Germany/Wadden Sea	1/1	M	O	Schumann (1989)
	Germany/Wadden Sea	91/34	P	H/S	Wipper (1974)
	Iceland/Western part	–	P	H	Skirnisson & Ólafsson (1990)
	Netherlands/Texel	2/1	P	S	Van den Broek & Wensvoort (1959)
	Netherlands/Wadden Sea	–	P	C	Reijnders et al. (1981)
	Norway	–	P	–	Mehl (1970)
Sweden/Kattegat–Skagge- rak–Baltic	158/0	A	PDV	Lunneryd (1992)	
Sweden/Skagerrak	2140	P	O	T. Härkönen (unpubl. data)	
<i>concolor</i>	USA east/Canada				
	New Jersey coast	1/1	P	C	Hoffmann et al. (2004)
	Virginia coast	1/1	M	S	Conlogue et al. (1980)
	Nova Scotia/Sable Island	15/15	P	C	McClland (1980c)
	Rhode Island/Connecticut	3/1	M	S/C	Dunn & Wolke (1976b)
	New England coast	108	P	S/O	Geraci (1978)
Florida	1/1	M	S	Caldwell & Caldwell (1969)	
<i>richardii</i>	USA west				
	California/Los Angeles	5/3	P	C	Brown et al. (1960)
	Southern California	5/3	P	C	Taylor et al. (1961)
	Grays Harbor/Washington	77/35	P	C/S	Dailey & Fallace (1989)

but no significant differences between examined age classes of seals and their lice burdens. The prevalence of lice differed strongly (20.0 to 81.8%) among the 3 investigated years. The Wadden Sea Quality Status Report (Essink et al. 2005) documented a decline in occurrence of the seal louse on *Phoca vitulina vitulina* from approximately 15% in the early 1980s down to 1.5% around 2000. Thus, seal louse populations seem to be influenced both by many biotic (e.g. age and body condition of the host) and abiotic factors (e.g. temperature).

The prevalence of lice (*Antarctophthirius callorhini* and *Proechinophthirius fluctus*) in the pelage and on the skin of northern fur seals was highest on pups of the year and decreased with the age of the host, and more adult females than males were infected (Kim 1972, 1975). It has been suggested that the higher prevalence in pups is linked to a higher body temperature, thinner dermis, thinner blubber/panniculus adiposus and thinner pelage structure compared with adults (Kim 1975). Additionally, pups spend more time on shore, where transmission is possible.

Clinical signs and pathology

Lice do not normally cause severe pathological changes, but infected patches of skin often show alopecia and skin irritations (Colongue et al. 1980, Raga 1992, Dailey 2001). However, large numbers of lice on a seal can weaken the host, and thereby increase the risk of other parasite or bacterial infections, or lead to severe anaemia (Turner 1971, Sweeney 1978, Lauckner 1985, Dailey 2001). Thompson et al. (1998) reported no significant differences in haematological parameters of infected and non-infected seals, but a significant negative correlation between number of lice on infected seals and their total erythrocyte count, haematocrit and haemoglobin concentration. Consequently, high burdens of lice can impair the diving ability of seals (Thompson et al. 1998).

Microhabitat: adaptation to the marine environment

The fact that lice (suborder Anoplura) belong to the class Insecta and have adapted to the marine environ-

ment is an example of a rare evolutionary event, since few insects have been able to adjust in order to cope with the marine environment. Contrastingly, whale-lice such as *Cyamus* (Cyamidae), which suck blood and destroy the tissue of whales, are not insects but amphipods (Crustacea). Insect parasites on marine hosts require adaptations such as a reservoir of air and an ability to adjust movements and life cycles to the diving pattern of the host (Tijssens 1969). The extremities of the seal louse are strongly built in all developmental stages compared to the rest of the body, and increasingly sclerotised in each developmental stage (Scherf 1963a). Claws are blunt (Kim et al. 1975) and extremely strong (Mjöberg 1910). Scherf (1963a) gave a detailed description of how the tibiotarsus was adapted to cling on to the fur of the host.

Echinophthirius horridus spends its entire life on the seal host (from egg to nymph to imago). Seals can be submerged up to 80% of the time, depending on the seasonal activity patterns of the seal (Teilmann et al. 1999). Consequently, access to air could be a factor limiting survival and reproduction in *E. horridus*. Female lice are suggested to lay eggs only when the host is on land (Scherf 1963b). However, there could be some differences between the genera *Echinophthirius*, *Antarctophthirus* and *Lepidophthirus* in this respect. *Echinophthirius* is mainly found on the head and neck of phocid seals (Lucas 1834, Luther 1909, Mjöberg 1910, Caldwell & Caldwell 1969, Bonner 1972, Wipper 1974, Geraci 1978, Conlogue et al. 1980, Reijnders et al. 1981, Kadulski 2001), especially near the snout (Lucas 1834, Luther 1909, Skirnisson & Ólafsson 1990), but also on the ventrolateral region of the posterior part of the stomach (Caldwell & Caldwell 1969), on the back (Luther 1909), around the tail (Reijnders et al. 1981), on the caudal back including the hind flipper (Mohr 1952, Wipper 1974), around the anus (Bonner 1972), on the sacral and genital region, on the femoral region of the flipper (Conlogue et al. 1980), on the hind flipper (Mjöberg 1910), and on the dorsal surface of the hind flipper (Thompson et al. 1998). *E. horridus* is suggested to prefer skin areas, which the host cannot reach (Mohr 1952).

In contrast, species of the genera *Antarctophthirus* and *Lepidophthirus* found on Otariidae, Odobenidae and Monarchinae are not observed in the head region of seals, but on other parts of the body (Enderlein 1906): the hind flippers (Murray 1958, Murray & Nicholls 1965, Murray et al. 1965, Kim 1975, Mehlhorn et al. 2002), the fore flippers (Murray & Nicholls 1965, Murray et al. 1965, Kim 1972), the tail, ankle and hip (Murray et al. 1965), the nostrils, auditory canal, eyelids and umbilical area (Kim 1972) and around anal and penile orifices (Murray et al. 1965, Kim 1972).

Enderlein (1906) suggested that the region where lice live on the seals, as well as the existence of either

setae (*Echinophthirius*) or leaf-like scales (*Antarctophthirus* and *Lepidophthirus*), are adaptations of the lice to their habitats. *E. horridus* mainly prefer the head region, which is the part of the body most frequently exposed to air in the phocid seals they infect, whereas species of *Antarctophthirus* also live on other parts of the seal's body. Enderlein (1906) also suggested that the leaf-like scales covering the body of *Antarctophthirus* have the physiological property of keeping an air reservoir when submerged. Diving experiments with adults and nymphs of *E. horridus* show that the hydrophilic cuticula of *E. horridus* cannot store air, so they must use the air trapped in the fur of their hosts during diving periods (Messner et al. 1998). The fact that *E. horridus* becomes immobilised as soon as it is submerged reveals the difficulties insects have in adjusting to a marine existence, and that seal lice cannot be termed plastrons, since true plastrons maintain their ability to move (Messner et al. 1998). Whereas the louse species *Lepidophthirus macrorhini* is more morphologically adapted to the marine environment (e.g. leaf-like scales), *E. horridus* has a behavioural adaptation (e.g. to occur near the nose or head region during diving periods of the seal).

Transmission patterns

Transmission of lice from one seal to another is only possible when seals are hauled-out on land or on ice (Kim 1975). Mechanisms and opportunities for lice to spread are likely to differ among genera and are obviously affected by the haul-out substrate of the host, since weaned pups of seals are heavily infected in the Arctic and Antarctic (Murray & Nicholls 1965, Murray et al. 1965, Kim 1972, 1975), which is rarely seen in harbour seals (Thompson et al. 1998). The life cycles of Antarctic lice are completed within 17 to 28 d, but are shorter in warmer air (Murray & Nicholls 1965, Murray et al. 1965, Kim 1975). There is no information about the duration of the life cycle of *Echinophthirius horridus*, but it is suggested to be longer than those of Antarctic lice, since only low numbers of lice are found on adult females and weaned pups (Thompson et al. 1998).

For Arctic and Antarctic lice species the major transmission occurs from females to pups during nursing, since pups are infected 7 to 12 h after birth (Kim 1972). Pup-to-pup transmission also seems to be important in species where pups form close congregations (Kim 1972), whereas transmission among adults may play a minor role since lice densities are low in adults (Kim 1975).

The transmission of *Echinophthirius horridus* is suggested to differ from the patterns shown for Arctic and

Antarctic lice species. Thompson et al. (1998) suggested the possibility that lice must travel several metres to find their next host in herds of seals or, alternatively, that lice can survive some time without a host until a new host appears at the haul-out site. Movements of lice can be triggered by a decreasing host body temperature (Kim 1972), because lice always abandon their hosts at rigor mortis (Mjöberg 1910), but lice may not be able to survive for significant periods without a host (Scherf 1963b). Lunneryd (1992) could not find any lice, although the prevalence of *Acanthocheilonema spirocauda* was 18% in harbour seal samples from the Kattegat–Skagerrak and lice have been observed on seals from this area (T. Härkönen unpubl. data) (Table 6). The total absence of lice in this region reported in earlier studies was suggested to be a consequence of lice having left their hosts before carcasses were recovered (Thompson et al. 1998).

Also, the different haul-out substrates used by seals (sand banks, mud pools, rocks) seem to affect the dispersal of lice. While Wipper (1974) recorded low numbers of lice at haul-out patches of harbour seals on sand banks, Murray & Nicholls (1965) could not observe transmission of lice among seals moulting in mud pools. The period adult pinnipeds spend in mud pools or ashore during moulting time seems to be a limiting factor for the survival of lice (Murray & Nicholls 1965, Kim et al. 1975).

THE SEAL LOUSE AS INTERMEDIATE VECTOR OF THE HEARTWORM

Lice are well-known vectors of serious diseases in terrestrial mammals, e.g. *Rickettsia prowazekii*, which causes epidemic typhus in humans (Hase 1931). Studies on lice-borne pathogens are scarce from the marine environment, but seal lice could potentially be important for spreading epidemic viral or bacterial diseases in seals. However, the only example of this to date is *Salmonella enteritidis* isolated in tissue of lice found on 5 infected fur seal pups at the Pribilof Islands (Jellison & Milner 1958).

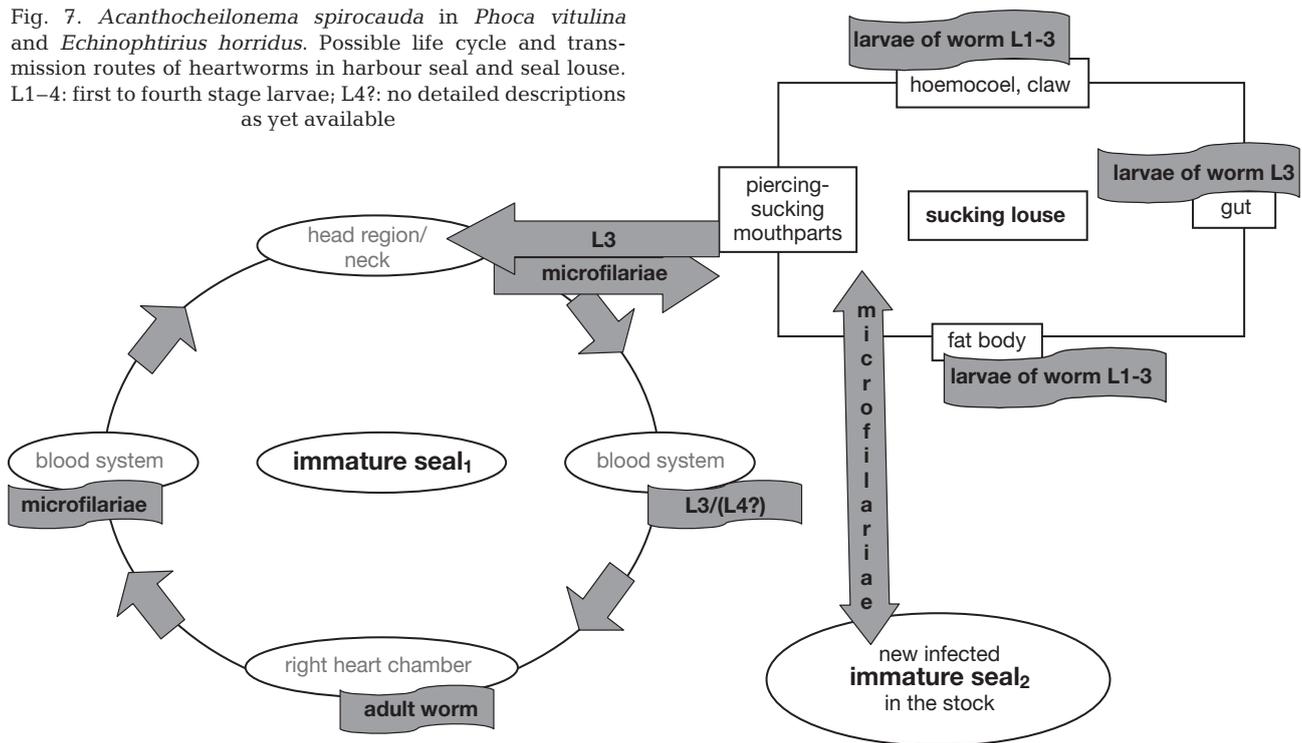
Species within the genus *Acanthocheilonema* use several vectors, such as fleas, ticks, or sucking lice for transmission among terrestrial hosts (Anderson 2000). Wülker (1930) was the first to suggest *Echinophthirius horridus* could play an important role in the transmission of *A. spirocauda* in seals, but found no evidence of mf in lice. The coincidence of simultaneous occurrence of *E. horridus* on seals and *A. spirocauda* in the heart of seals led several investigators to support this hypothesis (e.g. Mohr 1952). Several studies have attempted to find intermediate stages of *A. spirocauda* in *E. horridus* (Taylor et al. 1961, Dunne & Wolke 1976b, Mehlhorn et

al. 2002). However, since no evidence of filariae appeared, some investigators instead suggested other intermediate hosts, such as simuliids and mosquitoes that are often observed around hauled out seals (Taylor et al. 1961). This suggestion seems plausible since well-known heartworm species, such as *Dirofilaria immitis*, infecting dogs and cats, cannot mature into adult worms without first passing through a mosquito (Anderson 2001).

The only current conclusive evidence of filariae of *Acanthocheilonema spirocauda* in *Echinophthirius horridus* was provided by Geraci et al. (1981), who dissected 102 lice collected from a stranded harbour seal held in captivity. Seventy lice were infected with different stages of *A. spirocauda*, and they found an average of 4.6 first-stage larvae per louse in 87% of all infected lice, an average of 1.4 second-stage larvae per louse in 26% of infected lice, and an average of 3.0 third-stage larvae per louse in 54% of the infected lice. The larvae were mainly found in the fat body of the louse, but also in the gut, haemocoel, claws and head. The mf found in the gut were not distinguishable from those found in the blood of the seals. Consequently, the first 3 larval stages seem to develop in the louse, after which third-stage larvae are transmitted back to the final host (Fig. 7). The fourth-stage larvae will develop in the blood system of seals and eventually transform to the adult stage (Raga 1992). Dunn & Wolke (1976b) suggested that *A. spirocauda* reach sexual maturity within 6 mo or less, because they found mf in the blood of young 8 mo old harbour seals. Adult worms seem to mature in the heart, where females shed mf into the blood stream, and these are subsequently transmitted to sucking lice. Geraci et al. (1981) noted the rarity of sucking lice serving as vectors of filariid worms, because there is only one additional known example: the canine louse *Linognathus setosus*, which serves as an intermediate host for *A. reconditum* infecting dogs (Pennington & Phelps 1969).

That the seal louse acts as an intermediate host of the heartworm is also supported by the significant correlation between the occurrence of *Acanthocheilonema spirocauda* and *Echinophthirius horridus* on seals in Washington State, USA (Dailey & Fallace 1989). Although *E. horridus* is the main candidate as an intermediate host of *A. spirocauda*, this has yet to be verified experimentally. The heartworm life cycle (Fig. 7) illustrates the possible transmission of *A. spirocauda* through sucking lice from seal to seal. A transplacental transmission of mf has been described for *Dirofilaria immitis* (Todd & Howland 1983) and *D. repens* in dogs (Guarda & Mandelli 1996). In general, transplacental passage of mf is possible (Loke 1982), but seems to be relatively rare. In a study encompassing 22 mf-positive mothers of *Wuchereria bancrofti* in Haiti, only 2 pla-

Fig. 7. *Acanthocheilonema spirocauda* in *Phoca vitulina* and *Echinophthirius horridus*. Possible life cycle and transmission routes of heartworms in harbour seal and seal louse. L1–4: first to fourth stage larvae; L4?: no detailed descriptions as yet available



centas were infected with mf (Eberhard et al. 1993). To date, there have been no observations of the 3 first larval stages of heartworms in seals. The only observation of mf in 8 mo old pups (Dunn & Wolke 1976b) could be a result of transplacental transmission as well as the first generation of mature worms. Sweeney (1973) reported *A. spirocauda* in 4 of 13 examined pups, all <3 mo. However, the author did not give details about the developmental stage (mf or larvae), but it was taken as evidence for transplacental transmission (Sweeney 1973). Nevertheless, this form of transmission cannot be the main mechanism, since heartworms are much rarer in adult seals compared with juveniles.

In contrast to terrestrial mammals, there is a predominance of heteroxenous forms of parasitic nematodes in marine mammals, using intermediate hosts for transmission (Anderson 1984). Lack of effective swimming stages (such as kinocilia) in aquatic parasitic nematodes means that the dispersal routes of *Acanthocheilonema spirocauda* are limited by the behaviour of its hosts. The seal louse *Echinophthirius horridus* likely became a paratenic host of heartworms, and as the louse became more specialised, *A. spirocauda* is suggested to have adapted its dispersal to the behaviour of the ancestors of the seals (Anderson 1984).

Due to the limited evidence of mf and larval stages in *Echinophthirius horridus*, it cannot be ruled out that alternative intermediate hosts such as mosquitoes or

simuliids could play an important role in the dispersal of *Acanthocheilonema spirocauda* among seals. Heartworms infecting dogs in terrestrial environments and phocid seals in the marine environment are good examples of adaptations among parasites (Ménier 2000). Both heartworms show high pathogenic rates and have similar clinical signs that often end with the death of the host. The fact that *Dirofilaria immitis* has been observed several times in California sea lions (Forrester et al. 1973, Howard et al. 1983, Sato et al. 2002), supports the idea that the 2 heartworms share the ancestor Canoidea.

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