



# HOKKAIDO UNIVERSITY

Title	MORPHOLOGICAL STUDY OF THE SYNLOPHE OF THE INTESTINAL NEMATODE, HELIGMONELLA LEPORIS (SCHULZ, 1931) DURETTE-DESSET, 1971 (HELIGMONELLIDAE : TRICHOSTRONGYLOIDEA) FROM LAGOMORPHS IN JAPAN
Author(s)	FUKUMOTO, Shin-ichiro; KAMIYA, Masao; OHBAYASHI, Masashi
Citation	Japanese Journal of Veterinary Research, 34(3-4), 203-217
Issue Date	1986-10-31
DOI	<a href="https://doi.org/10.14943/jjvr.34.3-4.203">https://doi.org/10.14943/jjvr.34.3-4.203</a>
Doc URL	<a href="https://hdl.handle.net/2115/3018">https://hdl.handle.net/2115/3018</a>
Type	departmental bulletin paper
File Information	KJ00002374432.pdf



MORPHOLOGICAL STUDY OF THE SYNLOPHE  
OF THE INTESTINAL NEMATODE,  
*HELIGMONELLA LEPORIS* (SCHULZ, 1931)  
DURETTE-DESSET, 1971  
(HELIGMONELLIDAE : TRICHOSTRONGYLOIDEA)  
FROM LAGOMORPHS IN JAPAN

Shin-ichiro FUKUMOTO<sup>1</sup>, Masao KAMIYA<sup>2</sup> and Masashi OHBAYASHI<sup>2</sup>

(Received for publication July 31, 1986)

The morphology of the cuticular ridges (synlophe) of the intestinal nematode of Japanese lagomorphs, *Heligmonella leporis* (SCHULZ, 1931) DURETTE-DESSET, 1971 (Heligmonellidae: Trichostrongyloidea) was examined. There were no morphological differences, except the minute differences of the dorsal and external rays and the distal end of the spicules, among the three populations of *H. leporis* collected from three species of hosts, *Lepus timidus ainu* in Hokkaido, *Lepus brachyurus brachyurus* in Fukuoka Prefecture and *Pentalagus furnessi* in Amami-Oshima Island. The number of ridges at the midbody of *H. leporis* was always 13 in both sexes within the populations of *H. leporis*. In cross sections of the body, the axis of orientation of cuticular ridges was subfrontal, and a small carene supported by two ridges existed on the left lateral aspect. These synlophe characteristics were different from the genus *Heligmonella* MÖNNIG, 1927 classified by DURETTE-DESSET (1971, 1983), suggesting that *H. leporis* should be classified as belonging to subfamily Brevistriatinae. The small but consistent number of cuticular ridges of *H. leporis* seemed to be a consistent and primitive morphologic characteristic within the family Heligmonellidae.

Key words : *Heligmonella leporis*, synlophe

INTRODUCTION

*Heligmonella leporis* (SCHULZ, 1931) DURETTE-DESSET, 1971 was reported from *Lepus timidus* collected in Sakhalin, U. S. S. R., as *Longistriata leporis* SCHULZ, 1931. DURETTE-DESSET (1971) moved *Longistriata leporis* SCHULZ, 1931 into the genus

<sup>1</sup>) Laboratory of Parasitology, Department of Veterinary Medicine, College of Dairying, 582 Bunkyo-dai-Midorimachi, Ebetsu 069, Japan

<sup>2</sup>) Department of Parasitology, Faculty of Veterinary Medicine, Hokkaido University, N-18, W-9, Kita-ku, Sapporo 060, Japan

*Heligmonella* MÖNNING, 1927 with other *Longistriata* spp.

In Japan, *H. leporis* has been reported in Hokkaido (*L. timidus ainu*; in the present study), *L. brachyurus angustidens* in Aomori Prefecture (YAGISAWA, 1978), *L. brachyurus brachyurus* in Mie Prefecture (YAMAGUTI, 1935) and *Pentalagus furnessi* in Amami-Oshima Island (KAMIYA et al., 1979; FUKUMOTO et al., 1983) (fig. 1).

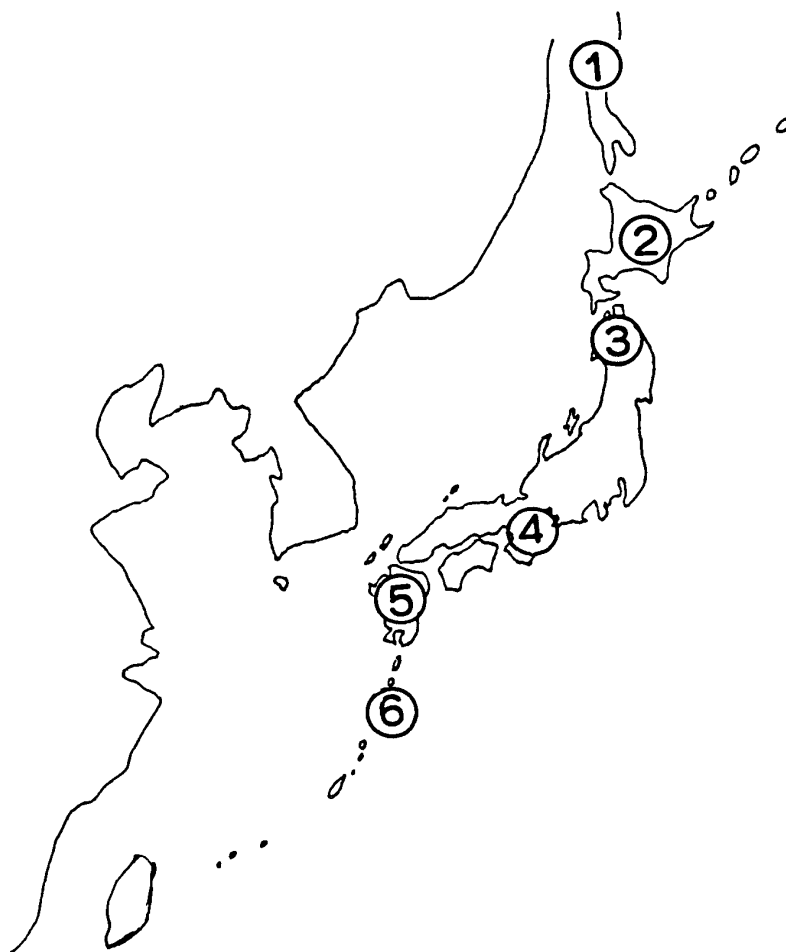


FIGURE 1 Geographical distribution of *H. leporis* (SCHULZ, 1931) reported in Japan and neighbouring areas

- 1 Sakhalin, U. S. S. R. (*Lepus timidus*: SKRJABIN et al., 1954)
- 2 Hokkaido (*L. timidus ainu*: Collected by SARASHINA & OHBAYASHI)
- 3 Aomori Prefecture (*L. brachyurus angustidens*: YAGISAWA, 1978)
- 4 Miki City, Mie Prefecture (*L. b. brachyurus*: YAMAGUTI, 1935)
- 5 Kurume City, Fukuoka Prefecture (*L. b. brachyurus*: collected by Drs. TAKAO & YONEDA, Kurume University)
- 6 Amami-Oshima Island, Kagoshima Prefecture (*Pentalagus furnessi*: KAMIYA et al., 1979 and FUKUMOTO et al., 1983)

Recently the morphology of the cuticular ridges (synlophe) of the trichostrongylid nematodes was utilized as a character for classification to genus, species or subspecies (DURETTE-DESSET, 1971 & 1983; LICHTENFELS, 1983; MEASURES & ANDERSON, 1983).

The present study compared specimens of *H. leporis* from *Lepus timidus ainu* in Hokkaido, *Lepus brachyurus brachyurus* in Fukuoka Prefecture and *Pentalagus furnessi* in Amami-Oshima Island particularly with respect to morphology of the synlophe.

#### MATERIALS AND METHODS

The following specimens of *H. leporis* were examined (fig. 1):

1) *H. leporis* in Hokkaido: This sample is preserved in the parasitological collection of the Department of Parasitology, Faculty of Veterinary Medicine, Hokkaido University, Sapporo, Japan, record number 1862. It was collected from *Lepus timidus ainu* captured in Hokkaido (43°N, 142°E) and identified by Drs. T. SARASHINA & M. OHBAYASHI in 1960.

2) *H. leporis* in Fukuoka Prefecture: This sample was collected from *Lepus brachyurus brachyurus* in Fukuoka Prefecture (33°N 133°E) by Drs. Y. TAKAO & Y. YONEDA, Department of Parasitology, School of Medicine, Kurume University in 1977.

3) *H. leporis* in Amami-Oshima Island: The specimens were collected from *Pentalagus furnessi* in 1979 at Amami-Oshima Island (28°N, 129°E), south Japan, with special permission from the central and the local governments.

All specimens were preserved in 5 or 10% formalin and treated with lactophenol. Drawings and measurement were done with the aid of a camera lucida. The synlophe was examined in wholly mounted nematodes and the number of ridges on cross sections was counted using a microscope. Cross sections cut with a blade using a dissection microscope were made in three body regions, i. e. (1) the esophageal region, (2) the midbody and (3) the prebursal region in males or the prevulval region in females.

#### RESULTS

The major measurements are shown in tables 1 & 2. The number of cuticular ridges is shown in table 3. The number of ridges was consistently 13 at midbody in both sexes and in all three populations.

The morphology of the distal end of the spicules is slightly different among specimens from *Lepus* spp. and *P. furnessi*. The distal end of spicules of *H. leporis* from *Lepus* spp. is slightly inflated and has a blunt end. Two branches are observed distally (fig. 2-G). The distal end of spicules of *H. leporis* from *Pentalagus furnessi* has a simple, sharp end (fig. 2-F).

The dorsal and externo-dorsal rays have a common trunk. Externo-dorsal rays arise one third the distance from the proximal end of the dorsal ray. Externo-dorsal rays arise almost symmetrically in specimens from *L. timidus ainu* and *P. furnessi*

TABLE 1 Major measurements<sup>1)</sup> of male *Heligmonella leporis* (SCHULZ) from different hosts in Japan and the U. S. S. R.

AUTHORS	PRESENT AUTHORS			YAMAGUTI, 1935	SCHULZ, 1931
	<i>Lepus timidus ainu</i>	<i>L. b. brachyurus</i>	<i>Pentalagus furnessi</i>	<i>L. b. brachyurus</i>	<i>L. timidus</i>
Hosts	Sapporo, Hidaka Hokkaido	Kurume Fukuoka Pref.	Amami-Ohsima Is. Kagosima Pref.	Miki Mie Pref.	Sakhalin U. S. S. R.
Number examined	10	10	10	NI <sup>3)</sup>	NI
Body length (mm)	5.0-6.5 (5.7±0.7)	5.3-6.2 (5.5±0.6)	5.2-6.7 (5.4±0.6)	5.8-7.0	6.5-8.12
width	130-161 (144±15)	115-124 (117±7)	110-126 (117±5)	150-170	166-215
Cephalic vesicle					
length	78-87 (81±6)	63-80 (76±8)	57-74 (69±8)	NI	NI
width	45-61 (51±7)	43-56 (46±7)	39-56 (43±7)	45-57	NI
Esophagus length	357-404 (371±22)	337-387 (354±17)	296-339 (322±18)	330-450	460-500
Nerve ring <sup>2)</sup>	183-270 (226±35)	166-215 (185±22)	135-196 (167±20)	210-220	NI
Excretory pore <sup>2)</sup>	361-413 (389±21)	266-351 (303±30)	235-322 (298±33)	320-400	431-535
Spicule length	720-820 (781±34)	670-890 (832±35)	630-970 (853±44)	800-900	830-975
Gubernaculum					
length	74-86 (77±9)	65-85 (73±6)	68-90 (75±8)	60-66	74-86
width	45-61 (53±5)	44-57 (49±6)	47-59 (50±4)	NI	22-33

<sup>1)</sup> In  $\mu\text{m}$  unless otherwise indicated; mean  $\pm$  S. D. in parentheses<sup>2)</sup> Distance from anterior extremity<sup>3)</sup> NI: Not indicated

TABLE 2 Major measurements<sup>1</sup> of female *Heligmonella leporis* (SCHULZ) from different hosts in Japan and the U.S.S.R.

AUTHORS	PRESENT AUTHORS			YAMAGUTI, 1935	SCHULZ, 1931
Hosts	<i>Lepus timidus ainu</i>	<i>L. b. brachyurus</i>	<i>Pentalagus furnessi</i>	<i>L. b. brachyurus</i>	<i>L. timidus</i>
Number examined	10	10	10	NI <sup>4</sup>	NI
Body length (mm)	5.7–8.8(7.3±0.6)	5.5–8.3(6.8±0.7)	5.9–8.5(7.0±0.8)	8.0–9.4	6.96–10.45
width	148–209(166±22)	112–166(141±17)	109–143(122±11)	180	190–200
Cephalic vesicle					
length	76–100( 86± 7)	60– 84( 76± 9)	65– 74( 69± 5)	NI	NI
width	54– 61( 57± 4)	52– 59( 53± 4)	46– 59( 50± 4)	NI	NI
Esophagus length	348–478(415±18)	336–425(407±21)	304–457(375±33)	NI	NI
Nerve ring <sup>2</sup>	239–267(249±14)	182–241(201±20)	139–209(172±28)	NI	NI
Excretory pore <sup>2</sup>	413–500(436±26)	370–431(386±27)	218–348(297±37)	NI	498
Anus <sup>3</sup>	52– 61( 55± 4)	46– 60( 53± 4)	48– 65( 55± 7)	60–70	56–71
Vulva <sup>3</sup>	123–152(129± 9)	99–166(144±20)	139–196(162±20)	75–105	216
Eggs	65– 83( 71± 6)	52– 77( 62± 4)	46– 67( 56± 9)	68–75	NI
	X	X	X	X	
	35– 52( 41± 5)	30– 46( 39± 4)	28– 41( 34± 4)	35–39	NI

<sup>1</sup> In  $\mu\text{m}$  unless otherwise indicated; mean  $\pm$  S.D. in parentheses

<sup>2</sup> Distance from anterior extremity

<sup>3</sup> Distance from posterior extremity

<sup>4</sup> NI: not indicated

TABLE 3 Number of cuticular ridges<sup>1)</sup> in various body regions of *Heligmonella leporis* (SCHULZ) collected from different hosts in Japan

HOST & LOCALITY	MALE			FEMALE		
	Anterior <sup>2)</sup>	Midbody	Posterior <sup>3)</sup>	Anterior <sup>2)</sup>	Midbody	Posterior <sup>3)</sup>
<i>Lepus timidus ainu</i> Hokkaido	10-12 (5)	13 (10)	11-12 (5)	10-11 (5)	13 (8)	8-10 (4)
<i>L. b. brachyurus</i> Fukuoka Pref.	11-12 (5)	13 (10)	10-11 (5)	11-12 (5)	13 (10)	8-11 (5)
<i>Pentalagus furnessi</i> Amami-Ohshima Is.	10-12 (4)	13 (10)	10-11 (5)	10-12 (5)	13 (10)	8-10 (5)

<sup>1)</sup>Number examined in parentheses

<sup>2)</sup>Cross section at esophageal region

<sup>3)</sup>Cross section at prebursal region in males and at anterior region of vulva in females

(fig. 2-D). Asymmetrically derived externo-dorsal rays were observed in some specimens of *L. brachyurus brachyurus* from Fukuoka Prefecture (fig. 2-E).

Redescription of *Heligmonella leporis* (SCHULZ, 1931) DURETTE-DESSET, 1971 from Japanese lagomorphs

Small nematode. Dark reddish in color and coiled while alive and coiled dextrally after fixation. Well developed cephalic vesicle with fine annulations. Pair of cervical papillae situated laterally, each arising at the same level with each other and the excretory pore (fig. 2-A).

Cuticular ridges originate from posterior margin of cephalic vesicle (fig. 3-A). Ridges extend to prebursal region in males and to prevulval region in females (fig. 3-B, C, D). Ridges increase in number posteriorly with the greatest number at midbody. Seven ridges are present dorsally and 6 ridges ventrally at midbody. Gradient in size of ridges is right to left dorsally and left to right ventrally. The axis of orientation of ridges inclines nearly 90° from the sagittal axis (fig. 4). A small carene (after DURETTE-DESSET (1983)), supported by two ridges that are almost equal in size, exists on the left dorsal side of the body.

Male: Lateral lobes of bursa well developed and symmetrical. Pair of minute prebursal papillae present. Antero-ventral and postero-ventral rays with common trunk and distal extremity of each extends to bursal margin. Bursal margin protrudes at region of postero-ventral rays. Lateral rays extend to bursal margin. Antero-lateral rays turn anteriorly at distal extremity. Medio-lateral and postero-lateral rays have a

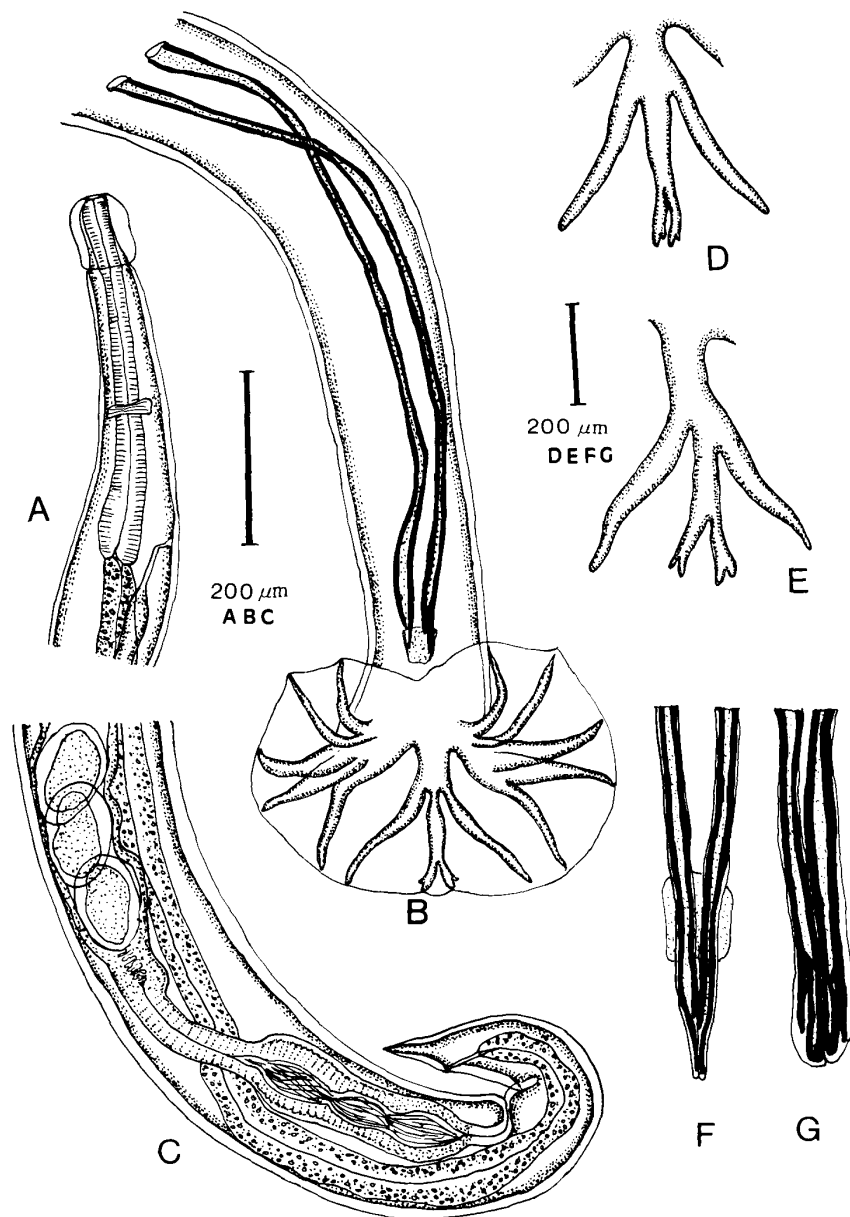


FIGURE 2 *Morphology of Heligmonella leporis* (SCHULZ, 1931) from Japanese lagomorphs

Drawings were based on *H. leporis* from *Lepus timidus ainu* in Hokkaido unless otherwise indicated.

- A. Anterior region of female
- B. Posterior region of male
- C. Posterior region of female
- D. Externo-dorsal and dorsal rays of *H. leporis* from *Pentalagus furnessi* in Amami-Ohshima Island
- E. Externo-dorsal and dorsal rays of *H. leporis* from *Lepus brachyurus brachyurus* in Kurume
- F. Distal end of spicules of *H. leporis* from *P. furnessi*
- G. Distal end of spicules of *H. leporis* from *L. b. brachyurus* in Kurume

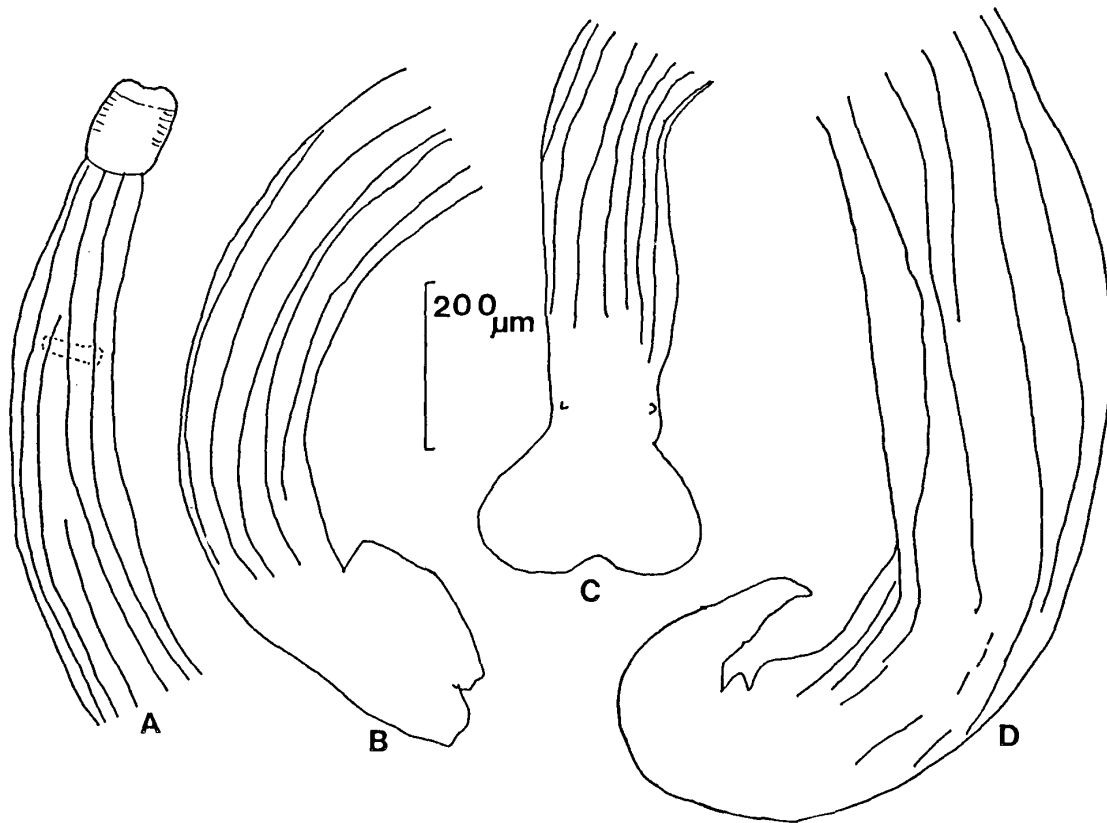


FIGURE 3 *Morphology of cuticular ridges (synlophe) on the body surface of Heligmonella leporis*

Drawings were based on the specimens from *Pentalagus furnessi*

- A Anterior region of female
- B Posterior region of male, lateral view
- C Posterior region of male, ventral view Note prebursal papillae
- D Posterior region of female

common trunk. Externo-dorsal rays arise one-third the distance from the proximal extremity of the dorsal ray, and the distal end of the rays does not extend to the margin of bursa. Dorsal ray thick, with distal end divided into two branches and each branch bifurcated. Inner branches extend to bursal margin. Spicules equal in length and shape, long and slender. The distal end of spicules is slightly inflated and has either a blunt end, or a simple and sharp one. A boat shaped gubernaculum present (fig. 2).

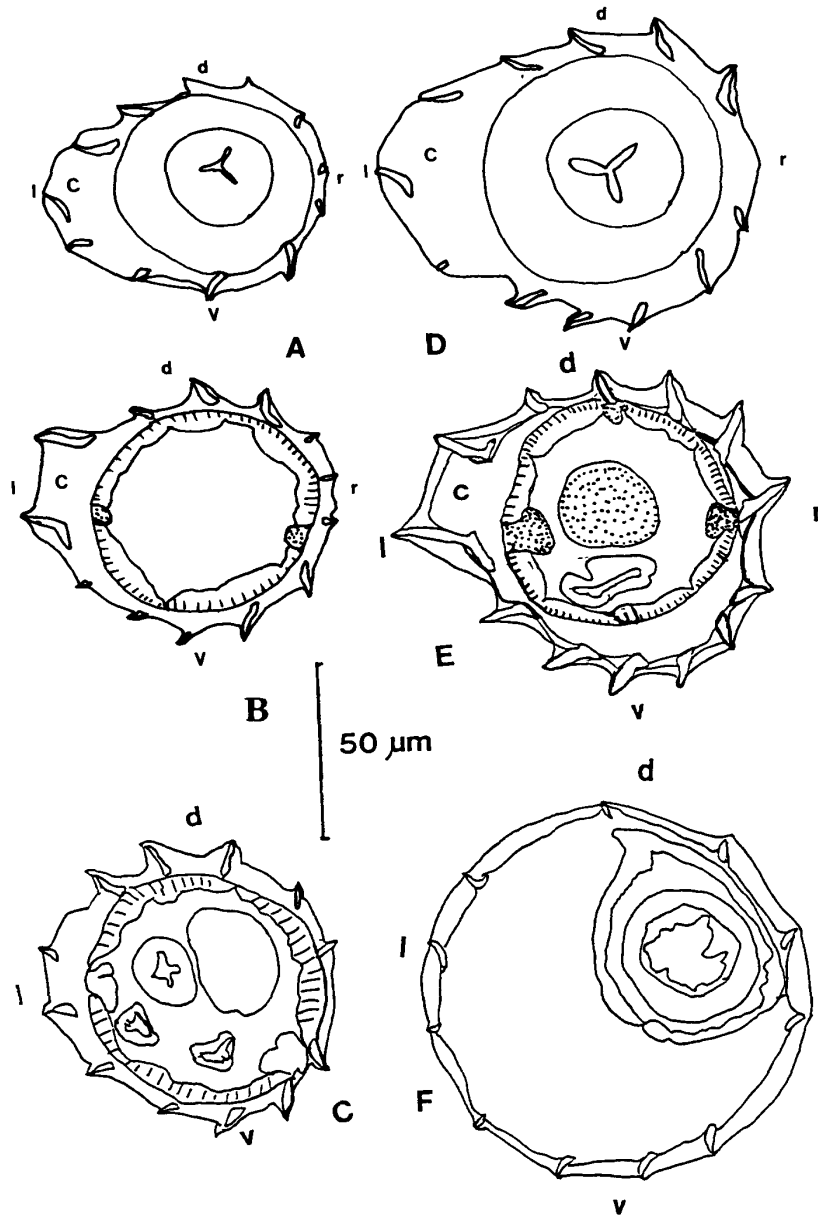


FIGURE 4 Cross sections in various body regions of male and female *Heligmonella leporis* (SCHULZ, 1931) from *Pentalagus furnessi* in Amami-Ohshima Island.

A-C Male

A In the esophageal region

B Midbody

C Near the proximal extremity of spicules

D-F Female

D In the esophageal region

E Midbody

F Near vulva

c: carene, d: dorsal, l: left, r: right, v: ventral

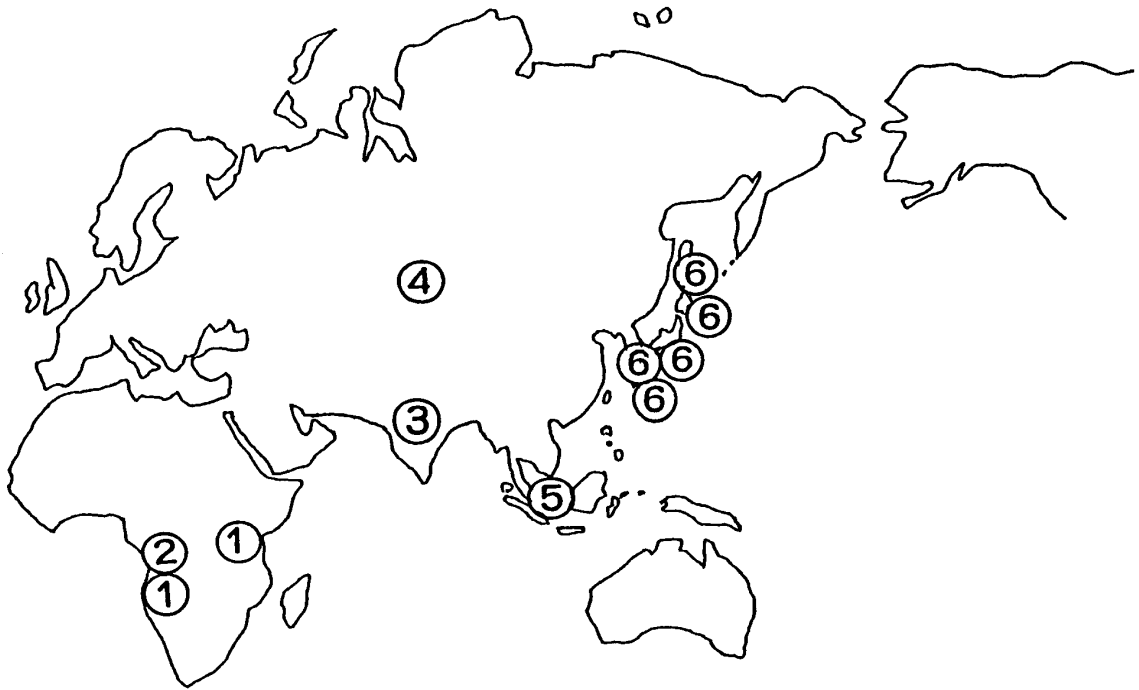


FIGURE 5 Geographical distribution of six species of the genus *Heligmonella* MÖNNIG, 1927

- 1 *H. spira* (MÖNNIG, 1927: South Rhodesia & Kenya)
- 2 *H. asymmetrica* (DURETTE-DESSET, 1969: Congo)
- 3 *H. indica* (SINGH, 1968: India)
- 4 *H. kurenzovi* (SKRJABIN et al., 1954: U. S. S. R.)
- 5 *H. limbooliati* (DURETTE-DESSET et al., 1975: Malaysia)
- 6 *H. leporis* (SKRJABIN et al., 1954, YAMAGUTI, 1935, present authors: Sakhalin, U. S. S. R. & Japan)

Female: Monodelphic. Tail bent ventrally. Tail short and conical. Anus and vulva present near tail extremity (fig. 2). Caudal spine absent.

#### DISCUSSION

At the present time, six species of *Heligmonella* have been reported from rodents collected in Africa and Asia and from lagomorphs collected in Eurasia (DURETTE-DESSET, 1969ab, 1971, 1974, 1983; DURETTE-DESSET et al., 1975; tab. 4 & fig. 5).

DURETTE-DESSET (1971, 1983) classified the genus *Heligmonella* MÖNNIG, 1927 by the following characteristics: all sides of body cuticle with ridges, ridges continuous

over entire body, lateral ridges more developed than adjacent dorsal ridges, carene absent, ray 6 (postero-lateral ray) equal to or shorter than ray 5 (medio-lateral ray), bursa lacking separate dorsal lobe; parasites of *Thryonomys*, palearctic and oriental lagomorphs, ethiopian and oriental Hystricidae (Rodentia).

DURETTE-DESSET (1971) recognized 5 species in the genus *Heligmonella*, but she did not examine the morphology of synlophes of *H. leporis*, *H. kurenzovi* and *H. indica* collected from lagomorphs in Eurasia.

Subsequently, DURETTE-DESSET (1974) recognized *H. dremomysi* from *Dremomys lokriah* in Nepal, and DURETTE-DESSET et al. (1975) identified *H. limbooliati* from *Trichys lipura* in Malaysia.

GIBBONS et al. (1977) transferred *Impalalia dremomys* YEN, 1973 from *Dremomys r. rufigans* in China to the genus *Heligmonella*, and this taxon became *Heligmonella dremomys* (YEN, 1973) (GIBBONS et al. 1977). Because the taxon *H. dremomysi* DURETTE-DESSET, 1974 became a homonym of YEN's species, they proposed a new name *Heligmonella moreli*, for the taxon of DURETTE-DESSET (1974) in Nepal.

In the latest classification, DURETTE-DESSET (1983) proposed a new genus '*Sciuricola*' for *H. dremomys* (YEN, 1973) and *H. moreli* GIBBONS et al., 1977. DURETTE-DESSET (1983) distinguished *Sciuricola* from *Heligmonella* by these points: the form of the dorsal lobe of bursa, synlophe with 17–18 ridges, ray 6 longer than ray 5.

In the present study, morphology of ridges in the cross sections of *H. leporis* showed quite different characteristics from those in the genus *Heligmonella* as defined by DURETTE-DESSET (1971, 1983). The authors consider that *Heligmonella leporis* should be transferred into the subfamily Brevistriatinae according to the classification by DURETTE-DESSET (1971, 1983). Because further bibliographical research on related genera of *Heligmonella* is needed, the authors have retained the name *Heligmonella* for the present species.

*H. leporis*, *H. kurenzovi* and *H. indica* were reported from *Lepus* spp. in Eurasia. *H. leporis* was identical to *H. kurenzovi* in morphology of the externo-dorsal and dorsal rays.

*H. indica* is closely similar to *H. leporis*, but according to the description of the dorsal ray of *H. indica*, SINGH (1986) was able to separate *H. indica* from *H. leporis*.

YAMAGUTI (1935) described *Longistriata leporis* n. sp. from *Lepus brachyurus brachyurus* collected in Mie Prefecture, not knowing SCHULZ's taxon. Consequently, SKRJABIN et al. (1954) and YAMAGUTI (1961) synonymized both taxa. SCHULZ (1931) noted that there were 12 ridges on the body of *H. leporis* from *Lepus timidus* collected in Sakhalin. YAMAGUTI (1935) described 13 ridges in both sexes collected from *L. brachyurus brachyurus* in Japan, and he showed that the cross section of the female and the morphology of the synlophe were similar to the present results. This number of ridges (13) is consistent within populations collected from different species of Japanese lagomorphs captured from geographically separated areas.

TABLE 4 *Comparison of six species of the genus Heligmonella MÖNNIG, 1927*

SPECIES	<i>SPIRA</i>	<i>ASYMMETRICA</i>	<i>LIMBOOLIATI</i>	<i>INDICA</i>	<i>KURENZOVI</i>	<i>LEPORIS</i>		
Authors	MÖNNIG	DURETTE- DESSET	DURETTE- DESSET	SINGH	SADOVSKAJA	SCHULZ	YAMAGUTI	Present authors
Year	1927	1969	1974	1968	1952	1931	1935	
Locality	South Rhodesia Kenya	Congo	Malaysia	India	U. S. S. R.	Sakhalin U. S. S. R.	Mie pref. Japan	Hokkaido Fukuoka Pref. Amami-Ohshima Is.
Host		Rodentia				Lagomorpha		
	<i>Thryonomys swinderianus</i>	<i>Atherurus africans</i>	<i>Trichys lipura</i>	<i>L. r.</i>	<i>L. m.</i>	<i>L. t.</i>	<i>L. b. b.</i>	<i>L. b. b.</i> , <i>L. t. ainu</i> <i>Pentalagus furnessi</i>
No. of ridges ( midbody)								
male	7	10	15	12	12	12	13	13
female	NI	11	NI	12	12	NI	13	13

NI: Not indicated

*L. b. b.*: *Lepus brachyurus brachyurus*    *L. m.*: *Lepus mantschuricus*    *L. r.*: *Lepus ruficaudatus**L. t.*: *Lepus timidus*    *L. t. ainu*: *Lepus timidus ainu*

Few studies have been appeared on the variation of the number of cuticular ridges within species of the family Heligmonellidae.

LICHTENFELS (1974) reported that there is no difference in the number of cuticular ridges of the rat nematode, *Nippostrongylus brasiliensis* (TRAVASSOS, 1914) TRAVASSOS & DARRIBA, 1929 (Heligmonellidae: Nippostrongylinae), from different populations.

FUKUMOTO & OHBAYASHI (1985) described that the number of cuticular ridges of the rat nematode, *Orientostrongylus ezoensis* TADA, 1975 (Nippostrongylinae: Heligmonellidae), was inconsistent among different populations. The number of cuticular ridges also differed within various body regions. They considered all specimens to be the same species.

*Pentalagus furnessi* have been isolated on Amami-Oshima Island for more than one million years from other parts of the Japanese archipelago and Asian continent (KIZAKI & OHSHIRO, 1976, 1980).

It is significant that *H. leporis* is found in a relic host and that the morphology of *H. leporis* is almost the same as that of specimens collected from different species of lagomorphs collected from geographically separated areas.

The results of this study provide further support for the classification of family Heligmonellidae and suggest that fewer ridges and consistency in the number of ridges of the synlophe may be ancestral and invariable characters in the family Heligmonellidae, compared with other morphological characteristics such as the dorsal and externo-dorsal rays and the distal end of the spicules.

#### ACKNOWLEDGEMENTS

The advice of Dr. Lena N. MEASURES, the University of Guelph was invaluable. The authors wish to thank Drs. Y. TAKAO and Y. YONEDA, School of Medicine, Kurume University, for providing the nematodes from Fukuoka Prefecture. We also wish to extend our gratitude to Dr. H. SUZUKI, Institute for Tropical Medicine, Nagasaki University, Dr. T. NOMURA and Prof. Y. TAJIMA, Central Institute for Animals, for their cooperation in collecting Ryukyu rabbits. This study was supported in part by Grant-in-Aid No. 58870119 from the Ministry of Education, Science and Culture of Japan.

#### REFERENCES

- 1) DURETTE-DESSET, M.-C. (1969 a): Nouvelles données morphologiques sur quelques Nématodes Héligmosomes, parasites de Rongeurs *Ann. Parasitol. Hum. Comp.*, **44**, 37-46.
- 2) DURETTE-DESSET, M.-C. (1969 b): Sept nouvelles espèces Nématodes Héligmosomes, parasites d'un *Atherurus africanus* GRAY, et remarques sur leur répartition dans l'intestin *Cah. La Maboke*, **7**, 109-130
- 3) DURETTE-DESSET, M.-C. (1971): Essai de classification des Nématodes

- Héligmosomes. Corrélation avec la paléobiographie des hôtes *Mem. Mus. Natl. Hist. Nat.*, N. Ser. A., Zool., **49**, 1-126
- 4) DURETTE-DESSET, M.-C. (1974): Description de deux nouveaux Nématodes Héligmosomes chez un Sciuride du Nepal *Bull. Mus. Natl. Hist. Nat.*, 3<sup>e</sup> Ser., n 232, Zool., **156**, 819-825
  - 5) DURETTE-DESSET, M.-C. (1983): Keys to genera of the superfamily Trichostrongyloidea In CIH Keys to Nematode Parasites of Vertebrates No. 10 Eds. ANDERSON, R. C. & CHABAUD, M. G. , 1-83, Farnham Royal, Bucks, England: Commonwealth Agricultural Beaureaux
  - 6) DURETTE-DESSET, M.-C., DIAW, O. & KRISHNASAMY, M. (1975): Quatre nouvelles espèces de Nématodes Héligmosomes parasites de l'intestin d'un *Trichys lipura* GÜNTHER malais; Comparaison avec la faune d'*Atherures* congolais *Ann. Parasitol. Hum. Comp.*, **50**, 477-491
  - 7) FUKUMOTO, S.-I., OKU, Y., YAMAGUCHI, K., KAMIYA, M. & SUZUKI, H. (1983): Helminth fauna of the Amami black rabbit, *Pentalagus furnessi* *Jpn. J. Parasitol.*, **28** (Suppl.), 730 (in Japanese)
  - 8) FUKUMOTO, S.-I. & OHBAYASHI, M. (1985): Variations of cuticular longitudinal ridges (synlophe) of rat nematode, *Orientostrongylus ezoensis* TADA, 1975 (Nematoda: Heligmonellidae) among different populations in Japan *Jpn. J. Vet. Res.*, **33**, 27-43
  - 9) GIBBONS, L. M., DURETTE-DESSET, M.-C. & DAYNAS, P. (1977): A review of the genus *Impalaia* MÖNNIG, 1923 (Nematoda: Trichostrongyloidea) *Ann. Parasitol. Hum. Comp.*, **52**, 435-446
  - 10) KAMIYA, M., SUZUKI, H. & HAYASHI, K. (1979): Helminth parasites of *Romerolagus diazi* and *Pentalagus furnessi* *Jpn. J. Parasitol.*, **28**, (Suppl.), 73 (in Japanese)
  - 11) KIZAKI, K. and OHSHIRO, I. (1976): Palaeography of the Ryukyu Islands *Marine Science Monthly*, **9**, 38-45 (in Japanese with English summary)
  - 12) KIZAKI, K. & OHSHIRO, I. (1980): Outline of geohistory of Ryukyu Islands In: The Natural History of the Ryukyu Islands Ed. KIZAKI, K., 8-32, Tokyo: Tsukiji Shokan (in Japanese)
  - 13) LICHTENFELS, J. R. (1974): Number and distribution of ridges in the cuticle of *Nippostrongylus brasiliensis* (Nematoda: Heligmosomatoidea) *J. Parasitol.*, **60**, 285-288
  - 14) LICHTENFELS, J. R. (1983): Synlophe and species determination of Trichostrongyloidea In: Concepts in Nematode Systematics Eds. STONE, A. R. & PLATT, H. M., 273-291, London: Academic Press
  - 15) MEASURES, L. N. & ANDERSON, R. C. (1983): New subspecies of the stomach worm *Obeliscoides cuniculi* (GRAYBILL) of Lagomorphs *Proc. Helminthol. Soc. Wash.*, **50**, 1-14
  - 16) MÖNNIG, H. O. (1927): On a new *Physaloptera* from an eagle and a trichostrongyle from the cane rat, with notes on *Polydelphis quadricornis* and the genus *Spirostrongylus* *Tr. Roy. Soc. S. Africa*, **14.**, 261-265
  - 17) SINGH, K. S. (1968): *Longistriata indica* sp. n. (Heligmosomatidae: Trichostrongyloidea: Nematoda) from a hare from India *Proc. Natl. Inst. Sci. India., Pt. B.*, **35**,

53-59

- 18) SKRJABIN, K. I., SHIKHOBALOVA N. P. & SCHULZ, R. S. (1954): Principles of nematology, Vol. 4, Dictyocaulidae, Heligmosomatidae and Ollulanidae of animals, 1-323, Izdatz, Akad. Nauk SSR: Moscow (in Russian)
- 19) YAGISAWA, M. (1978): Studies on zoonotic helminths from mammals in northern Honshu, Japan *Hirosaki-Igaku*, **30**, 239-284 (in Japanese with English summary)
- 20) YAMAGUTI, S. (1935): Studies on the helminth fauna of Japan Part 13 Mammalian nematodes *Jpn. J. Zool.*, **6**, 433-457
- 21) YAMAGUTI, S. (1961): Systema Helminthum, Vol. 3, the nematodes of vertebrates, 1-1261, Interscience: New York
- 22) YEN, W. C. (1973): Helminths of birds and wild animals from Lin-Tsan Prefecture, Yunnan Province, China II Parasitic nematodes of mammals *Acta Zool. Sinica*, **19**, 354-364