

Genus *Heligmosomoides* HALL, 1916
(Heligmosomidae: Nematoda) from the Japanese
wood mice, *Apodemus* spp.

II. A review of the genus *Heligmosomoides* with the establishment
of the phylogenetic lines of known species

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Introduction

The taxonomy and the phylogenetic system of heligmonellids and heligmosomids, which occur specifically in the Far Eastern small mammals, have been studied with regard to the phylogenetic system and the zoogeographical movement of hosts.^{2~9)} In the preceding paper (part I), the author reported four species and/or subspecies of *Heligmosomoides* which parasitized the Japanese wood mice, *Apodemus* spp.⁶⁾ In this paper, the genus *Heligmosomoides*, which has been confused taxonomically, is reviewed on the basis of morphologic studies (mainly on the synlophe and spicule). And the zoogeographic and phylogenetic data of the hosts are considered in order to systematize taxonomic and phylogenetic status of the species belonging to this genus including the taxa parasitizing *Apodemus* as the basic research for the future studies.

1. Taxonomic problems of the genus *Heligmosomoides*

The genus *Heligmosomoides* HALL, 1916³⁴⁾ belongs to the family Heligmosomidae CRAM, 1927, and has the following key characteristics:²⁵⁾ Comparatively long (5~10 mm in length) nematode. Body red in color when alive and coiled several times. Cuticle with continuous and longitudinal ridges (synlophe). Axis inclination of orientation of ridges to sagittal axis frontal. Careane absent. Monodelphic. Parasites of holarctic Arvicolidae (=Microtidae), Cricetidae and Muridae.

This genus includes many species and has been confused because of the presence of the synonyms (*H. polygyrus*, *H. laevis* etc.)^{10, 12, 19, 27, 46, 54, 55, 58, 60)} and the subspecies (*H. kurilensis*, *H. bullosus*, *H. desportesi*, *H. polygyrus*, *H.*

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tatricus etc.)^{7,14,19,20,29,30,37,49,56)} and the confusion with other genera (*Heligmosomum* and *Dessetia*).

Up to the present, the author has considered that at least 28 species belong to the genus *Heligmosomoides sensu stricto* (Tab. 1). In this paper, the author agrees with GENOV and JANCHEV'S³²⁾ proposition that *H. moldovensis* (ANDREIKO, 1963)^D belongs to the genus *Dessetia* GENOV & JANCHEV, 1981.

Furthermore, the author proposes that *H. spalacis* (KIRSHENBLAT,

Table 1. List of known species of genus *Heligmosomoides*

SPECIES & SUBSPECIES	REFERENCES	HOSTS	LOCALITIES	SPICULE LENGTH (mm)	NUMBER OF RIDGES
a) <i>travassosi-douglasi</i> line					
<i>travassosi</i>	Schulz, 1926	<i>Cr. cricetus</i>	France	0.6	34
<i>yorkei</i>	Schulz, 1926	<i>Cr. migratorius</i>	USSR	1.7	30
<i>juvenus</i>	Kirshenblat, 1949	<i>Meso. auratus</i>	USA	0.4	?
<i>douglasi</i>	D.-D. <i>et al.</i> , 1972	<i>R. raviventris</i>	USA	1.0	32
<i>turgidus</i>	Walton, 1923	<i>M. arvalis</i>	USA	0.5	34
b) relic group					
<i>polygyrus</i>					
<i>americanus</i>	D.-D. <i>et al.</i> , 1972	<i>P. intermedius</i>	USA	0.9	24
<i>hudsoni</i>	Cameron, 1937	<i>D. hudsonius</i>	Canada	1.4	14
<i>johnsoni</i>	Rausch & Rausch, 1973	<i>P. intermedius</i>	USA	2.4	12
c) <i>laevis-carolinensis</i> line					
<i>laevis</i>	Dujardin, 1845	<i>M. arvalis</i>	France	0.6	15
<i>grareoli</i>	Baylis, 1928	<i>Cl. glareolus</i>	G. Bri	0.9	20
	(Mishra <i>et al.</i> , 1976)	(<i>Cl. glareolus</i>)	(France)	(1.0)	(16)
<i>longispiculus</i>	Tokobaev & Erkulov, 1966	<i>M. gregalis</i>	USSR	1.9	?
<i>tatricus</i>	Erhardova, 1955	<i>M. nivalis</i>	Czecko.	1.3	17
<i>schulzi</i>	Nadtochii, 1966	<i>M. oeconomus</i>	USSR	2.3	?
<i>protobullosus</i>	Asakawa & Ohbayashi, 1987	<i>M. montebelli</i>	Japan	1.9	15
<i>bullosus</i>					
<i>bullosus</i>	D.-D., 1968 b	<i>M. oeconomus</i>	Alaska	1.9	17
<i>matthewensis</i>	D.-D., 1968 b	<i>M. abbreviatus</i>	Alaska	1.7	18
<i>microti</i>	Kuns & Rausch, 1950	<i>M. montanus</i>	USA	0.4	16
<i>wisconsinensis</i>	D.-D., 1968 b	<i>M. pennsylvanicus</i>	USA	2.0	16
<i>carolinensis</i>	Dikmans, 1940	<i>Cl. gapperi</i>	USA	1.8	19
<i>desportesi</i>					
<i>desportesi</i>	Schulz, 1926	<i>A. sylvaticus</i>	France	0.6	?
<i>japonicus</i>	Chabaud <i>et al.</i> , 1963	<i>A. argenteus</i>	Japan	0.6	23
<i>shikokuensis</i>	Asakawa & Ohbayashi, 1986 c	<i>A. speciosus</i>	Japan	0.4	25
<i>ussuriensis</i>	Lubimov, 1932	<i>E. sibiricus</i>	USSR	0.9	18

Cr.: *Cricetus*, *Meso.*: *Mesocricetus*, *R.*: *Reithrodontomys*, *M.*: *Microtus*, *P.*: *Phenacomys*,
D.: *Dicrostonyx*, *Cl.*: *Clethrionomys*, *A.*: *Apodemus*, *E.*: *Eutamias*, D.-D.: Durette-Desset.

Table 1. Continued

SPECIES & SUBSPECIES	REFERENCES	HOSTS	LOCALITIES	SPICULE LENGTH (mm)	NUMBER OF RIDGES
d) <i>longicirratum</i> - <i>longispiculatus</i> line					
<i>longicirratum</i>	Skrjabin <i>et al.</i> , 1954	<i>M. sp.</i>	USSR	2.9	20
<i>simirnovae</i>	D.-D. <i>et al.</i> , 1980	<i>L. sibiricus</i>	USSR	3.1	25
<i>tenorai</i>	D.-D., 1968 b	<i>L. sibiricus</i>	Alaska	2.9	23
<i>montanus</i>	D.-D., 1968 b	<i>M. longicaudus</i>	Alaska	3.9	17
<i>longispiculatus</i>	Dikmans, 1940	<i>M. pennsylvanicus</i>	USA	4.0	?
<i>kurilensis</i>					
<i>kurilensis</i>	Nadtochii, 1966	<i>A. sp.</i>	USSR	3.0	20
<i>kobayashii</i>	Ishimoto, 1974	<i>A. speciosus</i>	Japan	3.0	28
e) <i>polygyrus</i> line					
<i>polygyrus</i>					
<i>polygyrus</i>	Dujardin, 1845	<i>Mus musculus</i>	Europe	0.5	29
<i>corsicus</i>	D.-D., 1968 a	<i>Mus musculus</i>	France	0.5	40
<i>bakeri</i>	D.-D. <i>et al.</i> , 1972	<i>Mus musculus</i>	USA	0.5	37
<i>neopolygyrus</i>	Asakawa & Ohbayashi, 1986 c	<i>A. peninsulac</i>	Japan	0.5	29

M.: *Microtus*, *A.*: *Apodemus*, *L.*: *Lemmus*, D.-D.: Durette-Desset.

1965)³⁹⁾ from *Spalax graecus* belongs also to the genus *Dessetia* because of the morphological characteristics of the externo-dorsal and dorsal rays, and the host family. Nadtochii *et al.*⁴⁹⁾ reported "*Heligmosomum ryjikovi*", which was similar to *H. yorkei* and *H. juvenium*, although was characterized by the structure of the dorsal ray with 6 ramuli instead of 4 in the specimen, from *Microtus oeconomus* in Kamchatka Peninsula, U. S. S. R.. In this paper, however, no determination of the taxonomical status of "*H. ryjikovi*" was possible, because the description of Nadtochii *et al.* (*op. cit.*) lacks a figure and was inadequate. Judging from the morphological characteristics of an aspect of bursa (especially, externo-dorsal rays and dorsal ray) and from the measurements, *Heligmosomum glomerophilus* CHERTKOVA & TARZHIMANOVA, 1973¹⁵⁾ which was found in nodules of the mucous membrane of the small intestine of *Microtus arvalis* (non-endemic host), is considered as a synonym of *H. travassosi*.

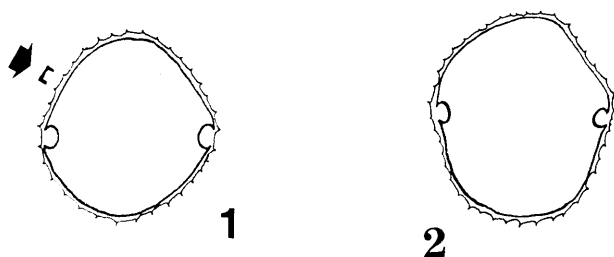
2. Establishment of phylogenetic lines of *Heligmosomoides*

In order to systematize the species of the genus *Heligmosomoides*, the author divided these species into five categories (probably, subgeneric levels) and established phylogenetic lines of the known species belonging to the genus *Heligmosomoides*, namely "*travassosi-douglasi* line", "relic group", "*laevis-carolinensis* line", "*longicirratum-longispiculatus* line" and "*polygyrus* line". For this purpose the morphological characteristics and the zoogeo-

graphical distribution of the parasites, and the phylogenetical data and the zoogeographical movements of hosts were taken into consideration.

a) The *travassosi-douglasi* line

The species of this line are adapted principally to the cricetid rodents. Therefore, the origin of this group seems to be ancient because these heligmosomids occur in the cricetid rodents which are considered to be an ancient form of all vole type rodents.⁴⁰⁾ However, the ancestor of this line is obscure because the members of this line show remarkable characteristics of the number of ridges and the morphology of synlophe. The spicule is usual in length, 0.4 mm~1.7 mm. The number of ridges is 30~34 and each interval between ridges is very narrow (arrow in Fig. 1). Furthermore, there is no gradient in the size of the ridges and each ridge is very small in size (Figs. 1 & 2). The author considers that *H. turgidus* which has 32~36 aretes and has the morphological characteristics mentioned above, is also descended secondarily from this line and is adapted to the genus *Microtus*.



Figures 1-2. Synlophe of the *travassosi-douglasi* line.

Fig. 1. Cross-section of *H. travassosi* (after Durette-Desset, 1973).

Fig. 2. Cross-section of *H. douglasi* (after Durette-Desset, et al., 1972).

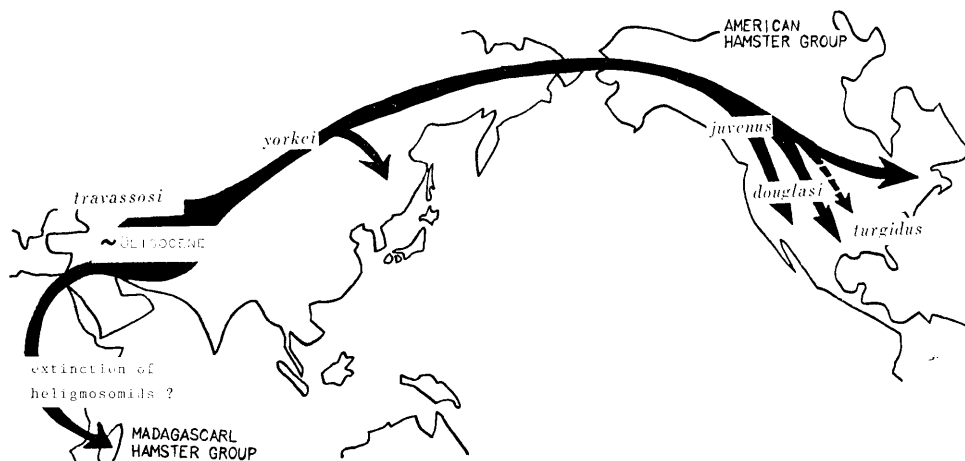
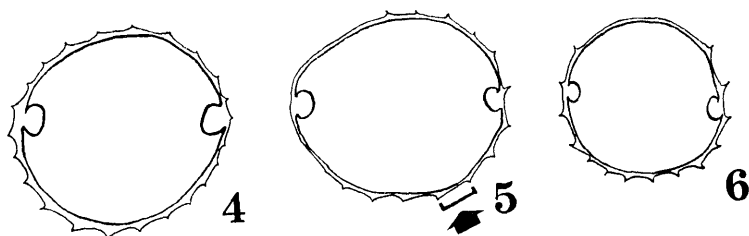


Figure 3. Movement of cricetids and speciation of *travassosi-douglasi* line (---> : adapted secondarily to non-cricetid hosts)

b) The relic group

The species belonging to this group occur in North American mountainous microtids (*Phenacomys* and *Dicrostonyx*) as relic species. The morphological characteristics of the ridges and the bursal rays are variable and specialized (Figs. 4-6), especially *H. hudsoni* and *H. johnsoni*^{50, 51, 53} lack dorsal ridges and parasitize the cecum or colon.



Figures 4-6. Synopse of the relic group.

Fig. 4. Cross-section of *H. polygyrus americanus* (after Durette-Desset *et al.*, 1972).

Fig. 5. Cross-section of *H. johnsoni* (after Rausch & Rausch, 1973).

Fig. 6. Cross-section of *H. hudsoni* (after Durette-Desset, 1968 b).

The author considers the origin of this line also ancient and this line is probably descended from the prototype of the "*laevis-carolinensis* line" because of the morphological characteristics {spicule length is usually (0.9 mm~2.4 mm), wide interval between ridges (arrow in Fig. 5), size of ridges, etc}, the zoogeographical distribution (relic) and the host group (old microtid group). The author suggests that *H. polygyrus americanus*, which was reported by Durette-Desset *et al.*²⁷ from American *Phenacomys*, as Rausch & Rausch^{52, 53} proposed, also belongs to this line, judging from the form of the ridges, the zoogeographical distribution and the host belonging to the family Microtidae.

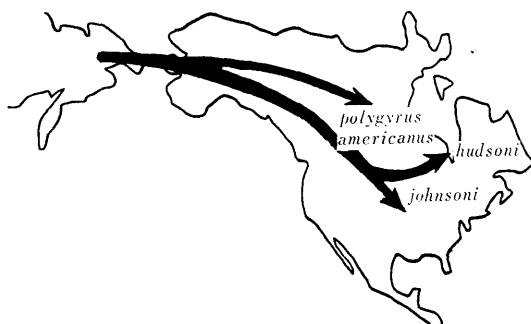
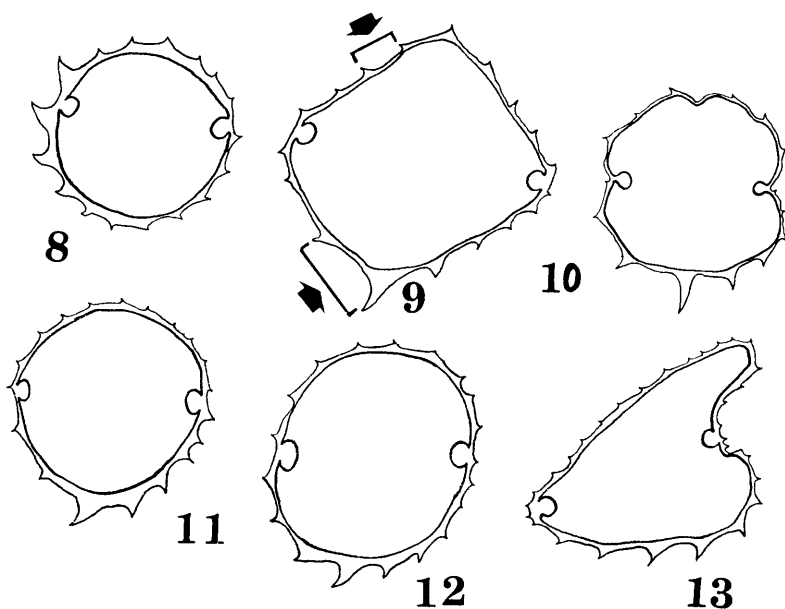


Figure 7. Speciation of the relic group.

c) The *laevis-carolinensis* line

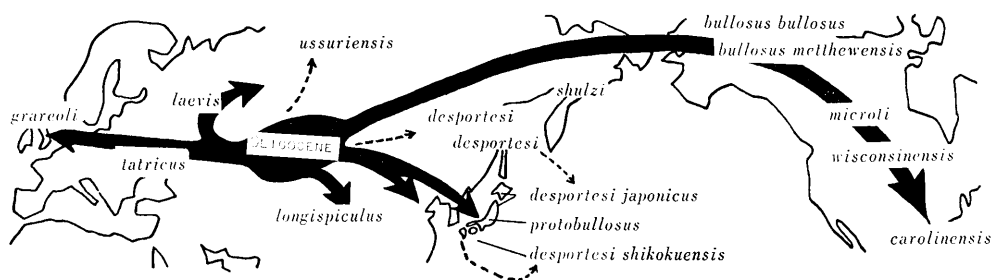
This line shows the typical (*viz.* non-specialized) and common characteristics; spicule length (0.6 mm~2.3 mm), wide or very wide intervals between ridges (arrow in Fig. 9), well-developed ridges, etc. This line contains many species occurring in parallel with the adaptive radiation of hosts. Some species are adapted subsequently to non-microtid hosts, however, this line shows adaptation principally to the microtid rodents, *Microtus* and *Clethrionomys*.

The morphological characteristics of this line appears to be ancient because of the ridges well-developed on the ventral side, gradual decrease in number on the ventral side, *viz.* gradient in size of ridges from dorsal side to ventral side bilaterally.^{22,25,26)} Probably, this line or its progenitor was



Figures 8-13. Synlophe of the *laevis-carolinensis* line.

- Fig. 8.** Cross-section of *H. laevis* (after Durette-Desset, 1968 a).
- Fig. 9.** Cross-section of *H. tatricus* (after Durette-Desset & Tenora, 1974).
- Fig. 10.** Cross-section of *H. protobullosus* (Asakawa & Ohbayashi, 1987).
- Fig. 11.** Cross-section of *H. bullosus* (after Durette-Desset, 1968 b).
- Fig. 12.** Cross-section of *H. wisconsinensis* (after Durette-Desset, 1968 b).
- Fig. 13.** Cross-section of *H. desportesi* (after Asakawa & Ohbayashi, 1986 c).



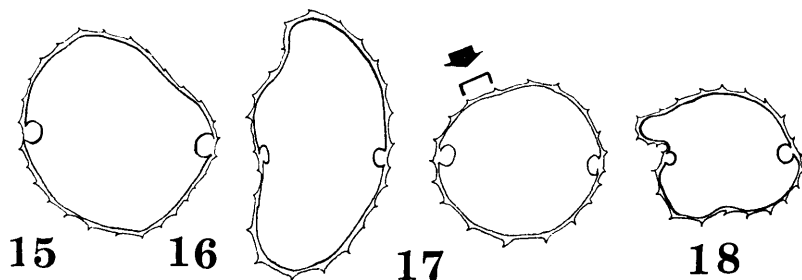
Figures 14. Movement of microtids and speciation of *laevis-carolinensis* line (---): adapted secondarily to non-microtid hosts).

the progenitor of the other lines or group of *Heligmosomoides* and also other genera (*Ohbayashinema sensu stricto* and *Heligmosomum*). Furthermore, the author also proposes that this line is the primary group having the relationship between microtids and heligmosomids.

Some species of this line are adapted secondarily to the murid and sciurid rodents, and *H. desportesi* subsp.^{7,14)} and *H. ussuriensis*⁴⁵⁾ occur in these hosts (Fig. 14).

d) The *longicirratum-longispiculatus* line

This line occurs in the recent microtid genera, *Microtus* and *Lemmus*. This line is recently descended from the *laevis-carolinensis* line, showing lengthening of the spicule and decreasing in size of the ventral ridges (especially, in *H. kurilensis kobayashii*, all ridges in mid- and/or posterior body region gradually vanished and not obvious).⁶⁾ The spicule length is remarkably long, 3.0 mm~4.0 mm. The number of ridges is 17~25 and the intervals between ridges are wide (arrow in Fig. 17). All ridges are almost the same in size (no gradient in size of ridges) and small (Figs. 15-18). *H. kurilensis*



Figures 15-18. Synlophe of the *longicirratum-longispiculatus* line.

Fig. 15. Cross-section of *H. simirnovae* (after Durette-Desset *et al.*, 1980).

Fig. 16. Cross-section of *H. tenorai* (after Durette-Desset, 1968 b).

Fig. 17. Cross-section of *H. momtanus* (after Durette-Desset, 1968 b).

Fig. 18. Cross-section of *H. kurilensis* (after Asakawa & Ohbayashi, 1986 c).

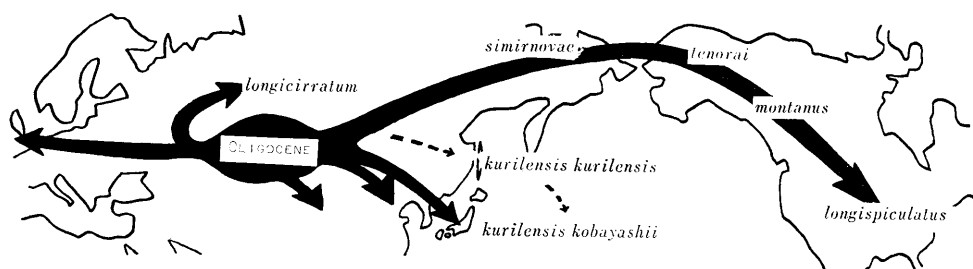


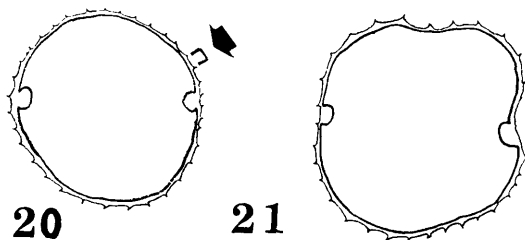
Figure 19. Movement of microtids and speciation of *longicirratum*-*longispiculatus* line (---): adapted secondarily to non-microtid hosts).

subsp.^{6,35,46)} are adapted secondarily to the genus *Apodemus* (Muridae) (Fig. 19).

e) The *polygyrus* line

The line shows perfect adaptation to the murid genera, *Apodemus* and *Mus*. The spicule length is very short, 0.5 mm in length. The number of ridges is 28~40 and the intervals between ridges are very narrow (arrow in Fig. 21). There is no gradient in the size of ridges, and the ridges are the same in size and small (Figs. 20 & 21). The origin of this line appears to be most recent among all lines, since this line appeared after the occurrence of the murid rodents (It is proposed that the murids diversified from its progenitor in the Miocene to the Pliocene in Southeast Asia).^{40,43)} However, the ancestor of this line remains unclear, though this line seems to be descended from the “*laevis-carolinensis* line” because the murids generated in the Old World.

The morphological characteristics of ridges of the “*travassosi-douglasi* line” is similar to those of the ridges of this line (especially, size of ridges and intervals between ridges). However, the author considers that this similarity is a result from the parallelism (*viz.* each line was descended independently from the *laevis-carolinensis* line?) because the hosts groups



Figures 20-21. Synlophs of the *polygyrus* line.

Fig. 20. Cross-section of *H. polygyrus bakeri* (after Hasegawa *et al.*, 1983).

Fig. 21. Cross-section of *H. neopolygyrus* (after Asakawa & Ohbayashi, 1986 c).

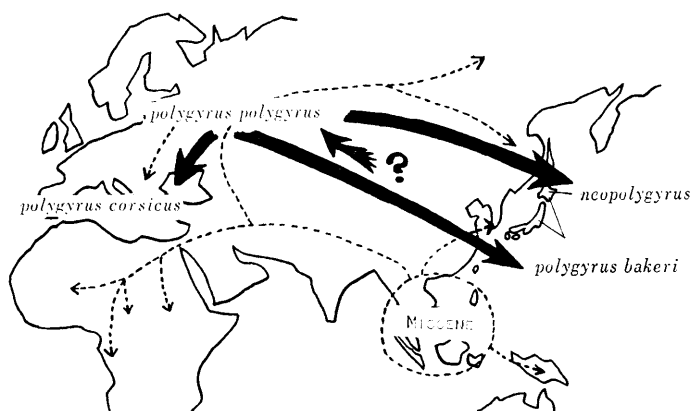


Figure 22. Movement of murids (---) and speciation of *polygyrus* line (—).

could not encounter each other.

The house mouse, *Mus musculus*, appears to have had many opportunities for movement due to human activities. Hence, the author considers that the occurrence of *H. polygyrus* in North America²⁷⁾ and in Japan^{30,64)} is the artifacts derived from the such activities. Therefore, it appears to be difficult to discuss the precise zoogeographical consideration of *H. polygyrus* occurring in such regions.

3. Phylogenetic problems in *Heligmosomoides* and other genera of Heligmosomidae

Durette-Desset^{18,22,26)} proposed that the family Heligmosomidae arose in soricoid insectivores and its evolution continued in the ground squirrels and lagomorphs and later the family passed to the Arvicolidae (=Microtidae) and the genera *Heligmosomoides* and *Heligmosomum* occurred in the Pliocene. Her hypothesis was based on the hypotheses by Kowalski⁴¹⁾ and Thaler⁶¹⁾ that the microtid rodents arose from the cricetid line near at the end of the Pliocene.

However, Hinton³⁶⁾ clarified that the microtids arose in the Oligocene and that the explosive speciation of this group occurred in Mongolia during the Pliocene.^{40,43)} Therefore, the author considers that the geological period in which the genus *Heligmosomoides* appeared was probably prior to the epoch of Durette-Desset's hypothesis.^{20,22)} If the Oligocene theory is correct, the author has to postulate that the phylogenetic origin of the known species belonging to the genus *Heligmosomoides* is not monophyllic as proposed as it arose from *H. laevis*, but is polyphylic (at species level), since the genus can be divided into several morphological (and/or probably, phylogenetical) lines as mentioned above. This speculation might elucidate the

origin of the *travassosi-douglasi* line, which occurs specifically in the criceted rodents (their origin prior to the microtids) and the morphological variety of the relic group.

Ohbayashinema abei is a very interesting taxon. This species is a parasite of the northern pika, *Ochotona hyperborea*, Japan, reported by Fukumoto *et al.*³¹⁾ *O. abei* is similar to the members of *laevis-carolinensis* line and different from another species of the genus *Ohbayashinema* Durette-Desset, 1974,²⁴⁾ because in *O. abei*: 1) gradient in size of ridges from dorsal side to ventral side bilaterally, 2) number of aretes 12~14, 3) spicule length 0.9 mm~1.4 mm. However, judging from absence of bilateral ridges and the host (*Ochotona*: Lagomorpha), *O. abei* accorded partly with the genus *Ohbayashinema*. Fukumoto *et al.*³¹⁾ concluded that "the genus *Ohbayashinema* might be the direct ancestor of the genus *Heligmosomoides* because *O. abei* is the taxon which is located between the genus *Heligmosomoides* and the genus *Ohbayashinema*". The present author, however, considers that *O. abei* was diversified from the progenitor of the "*laevis-carolinensis* line". And a taxon closely related with *O. abei* corresponded to the progenitor of the genus *Ohbayashinema sensu stricto* because the present author obeys the rule that the present taxon should not be descended from other taxon at present.

The genus *Heligmosomum* occurs only in the microtid rodents, especially the genera *Clethrionomys*, *Eothenomys* and *Microtus*.⁹⁾ It can be considered that the parallel evolution (or co-speciation) occurred in the *Heligmosomum* during the speciation of heligmosomid species and microtid rodents.^{9, 18, 20, 3, 46)} The species of *Heligmosomum* have the oblique ridges on the body. However, this group seems to be descended from the progenitor of the "*laevis-carolinensis* line" of *Heligmosomoides*, and adapted, and highly specialized, to the microtids.^{22, 26)} The phylogenetic relationships between the heligmosomids

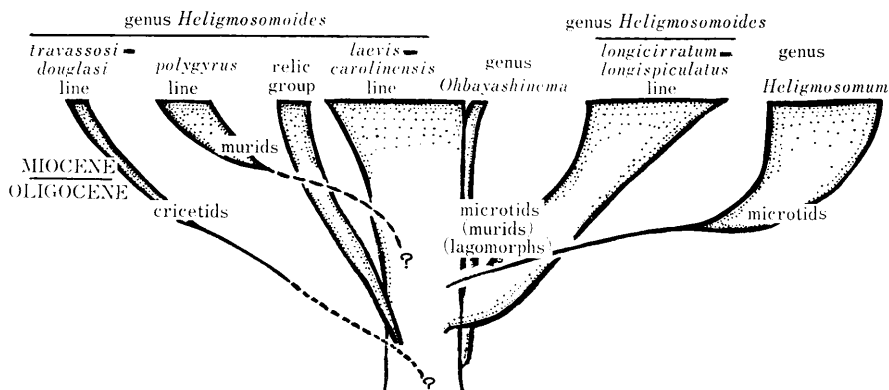


Figure 23. A phylogenetic tree showing phylogenetic relationships between *Heligmosomoides* and other heligmosomoid groups.

mentioned above and the phylogenetic tree of the lines of *Heligmosomoides* are shown in fig. 23. However, hitherto, there are no taxa locating between the *laevis-carolinensis* line and a part of the other lines (*travassosi-douglasi* line and *polygylus* line) or the sciurid heligmosomids (genera *Citellinema* and *Citellinoides*) which were proposed as the progenitors of *Heligmosomoides* by Durette-Desset.^{22,26)} The author can not determine all of the ancestors of the genus *Heligmosomoides sensu lato*.

Summary

In order to systematize the species belonging to the genus *Heligmosomoides*, which has been confused taxonomically, the author divided these species into five categories (probably, subgenus level) with regard to the morphological characteristics (spicule length, number of ridges, intervals between ridges, etc.), zoogeographical distribution of the heligmosomids, and the phylogenetic data and the zoogeographical movements of hosts.

1) The *travassosi-douglasi* line (five species), which is adapted to cricetid rodents. The origin of this line appears to be ancient, but no exact conclusion can be settled yet. 2) The relic group (three species) which occurs in North American mountainous microtids (*Phenacomys* and *Dicrostonyx*). The morphological characteristics of ridges and bursal rays are variable, but this group was descended from the "*laevis-carolinensis* line". This line has a common spicules and wide intervals between ridges. 3) The *laevis-carolinensis* line (twelve species and five subspecies) is adapted principally to the microtids (*Microtus* and *Clethrionomys*) and has the "typical (=non-specialized)" morphological characteristics. This line or its progenitor appears to be the progenitor of the some lines and group belonging to *Heligmosomoides* and additional genera (*Ohbayashinema* and *Heligmosomum*). 4) The *longicirratum-longispiculatus* line (six species and two subspecies) is characterized by remarkably long and specialized spicules (3.0 mm~4.0 mm) and is adapted to the microtids (*Microtus* and *Lemmus*). This line arose from the *laevis-carolinensis* line with the diminution of ventral ridges and lengthening of spicules. 5) The *polygyrus* line (two species and three species) is adapted perfectly to the murids (*Mus* and *Apodemus*). This line occurred recently but the origin is obscure. The parallelism occurred in the morphological characteristics of the ridges (especially, narrow intervals between ridges and small size) between the "*travassosi-douglasi* line" and the "*polygylus* line".

Judging from the geological epoch of the origin of microtids (Oligocene), *Heligmosomoides* appeared also in the Oligocene prior to the epoch proposed by Durette-Desset.^{20,22,26)} Furthermore, the author postulated that the phylogenetic origin of the species of *Heligmosomoides sensu stricto* is not "mon-

ophyly", but is the "polyphyly" at species level with some individual phylogenetic lines.

Key words: Evolution, Morphology, Taxonomy, *Heligmosomoides*, Phylogenetic line

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要 旨

Heligmosomoides 属 (Trichostrongyloidea 上科) は全北区のゲッ歯類 (特にハタネズミ科) において適応放散したグループで、小腸 (時に大腸) に寄生する体長 5 から 10 ミリメートルの小線虫である。現在までのところ、本属には少なくとも 28 種 (本文中にて総括) が知られているが、種類が豊富なため分類学的に混乱していた。そこで著者は *Heligmosomoides* 属各種の系統を考察するために線虫の形態学的特徴 (交接刺長、シンローフの隆起線の数・大きさ、隆起線の間隔など) と宿主の系統・動物地理学的な移動・分布を基に、本属を五つの系統学的グループ (おそらく亜属レベル) に分けた。

1) *travassosi-douglasi* 系列。キスゲネズミ科 (ハムスター類) に適応した 5 種を含む。この系列は宿主の系統からすると古い起源を持つと思われるが、その祖型は不明であった。2) 遺残種 (relic) グループ。北米の山岳地帯の遺残種 (*Phenacomys* や *Dicrostonyx*) に寄生・適応した 3 種で、形態 (ブルザの肋、隆起線の背側での欠如) や寄生部位 (大腸) で特殊化した性質を示す。しかし、宿主がいずれもハタネズミ科 (古いタイプではあるが) であること、隆起線の間隔が比較的に広いことなどで、本グループは *laevis-carolinensis* 系列から古い時代に分かれたものと推定された。3) *laevis-carolinensis* 系列。最も種を多く含む (12 種 5 亜種)、また典型的な形態を残す *Heligmosomoides* で、おもにハタネズミ科 (*Microtus* と *Clethrionomys*) に適応した系列。本系列もしくは本系列の祖型は他の *Heligmosomoides* の系列や近縁の属 (*Ohbayashinema* や *Heligmosomum*) を生じせしめた幹種を含むと思われる。4) *longicirratum-longispiculatus* 系列。非常に長い交接刺 (3.0 mm~4.0 mm) をもち、おもにハタネズミ科 (*Microtus* や *Lemmus*) に適応した 6 種 2 亜種が存在する。この系列は *laevis-carolinensis* 系列より腹側隆起線の縮小化、交接刺の特殊化を伴って生じたと思われる。なお、3) 及び 4) の系列にはネズミ科とリス科 (おそらくウサギ科にも) に二次的に適応したタクサを含んでいると思われる。5) *polygyrus* 系列。ネズミ科 (*Mus* と *Apodemus*) に完全に適応した 2 種 3 亜種を含む。この系列の起源は不

明であるが、宿主出現の時代を考慮にいれると比較的新しい時代に（中新世以降？）生じたと思われる。この系列の隆起線の間隔は非常に狭く、*travassosi-douglasi* 系列に似るが、宿主の系統・動物地理学上の移動等を考え合わせると両者は近縁とは思われず、むしろ両系列は共通の祖先型である *laevis-carolinensis* 系列(?)よりそれぞれ独立に分化したと結論をくだした。おそらく、両系列の類似は平行性 (parallelism) に由来したものと思われる。

ハタネズミ科の初めての出現が漸新世 (2800 万年から 3800 万年前) であることから {Hinron の仮説; この科は鮮新世 (200 万年から 1200 万年前) に爆発的種分化}, この科と平行進化した *Heligmosomoides* 属線虫の起源も漸新世にまで遡るものと推定した。さらに, *Heligmosomoides* 各種は, 従来, *H. laevis* ただ一種を幹種とした単系統の種群とされていたが (Durette-Desset の仮説), 今回の検討によりいくつかの系統分類学的系列の存在が示唆されたため, 多系統 (種のレベルで) の種群と思われた。

NOTE ADDED

The author considered that the recently reported taxon, *Heligmosomoides thomomyos* Gardner & Jasmer, 1983 (after Proc. Helminthol. Soc. Wash., 52: 278-284), belongs to the longicirratum-longispiculatus line because of the spicule length (3.42 mm-3.73 mm) and the morphological type of synlophe, although this taxon parasitized pocket gophers (*Thomomys*: Geomyidae) and had the complex dorsal ray. Probably, the progenitor of *H. thomomyos* was a taxon of the longicirratum-longispiculatus line of microtids which occupy the same habitat as geomyids in North America, and, as Gardner & Jasmer proposed, the progenitor was adapted secondarily to the geomyid host in a recent geological period (Pleistocene).