INTRODUCTION

Two previous articles (Durette-Desset et al., 2002a, b) dealt with the trichostrongylid fauna of taxonomical analysis of endemic rodents from Madagascar namely the Nesomyinae with the genera Nesomys Peters, 1870 and Eliurus Milne-Edwards, 1885. The present study describes a new species belonging to the genus Heligmonoides Baylis, 1928, parasitic in Mus musculus (Muridae), a non-native rodent which colonized Madagascar probably from the Arabian Peninsula (Duplantier et al., 2002). A new definition and a dichotomous key of this genus are provided with comments of its host-spectrum and biogeographical distribution. This work is part of a project on the potential effects of endoparasites introduced by the non-native black rat, Rattus rattus, on the endemic small mammals in Madagascar. The conclusions on the Trichostrongylina will be presented when the taxonomic analysis of the fauna is complete. General conclusions and the summary of the project will be published elsewhere when the parasitic fauna has been analysed.

MATERIAL AND METHODS

Eight Mus musculus were collected on the peripheral of Ranomafana National Park (21° 16’ S, 47° 20’ E) in Southeastern Madagascar between October and November, 1998-1999. The gastrointestinal tract was preserved in 70 % ethanol or buffered formalin in the field. Later, the stomach, small intestine, caecum and rectum were examined for helminths. The small intestine was divided into ten sections of similar length, numbered S1 to S10 from the duodenum to the end of the ileum. The worms were stored in 70 % ethanol.

The nomenclature used above the family group level is that of Durette-Desset & Chabaud (1993). The synlophe was studied following the method of Durette-Desset (1985) and for the nomenclature of the axis of

Summary:

Heligmonoides variabilis n. sp. (Heligmososomidea, Nippostrongylinae) a parasite of Mus musculus from Madagascar is related to H. afghanus (Tenora, 1969), H. ikerai Hasegawa, 1990 and H. josephi (Wertheim & Durette-Desset, 1976), all having the dorsal ray divided anterior to the arising of rays 8. H. ikerai a parasite of Tokudaia muenninki (Muridae) from Japan is the most closely related species with rays 8 arising at midlength along the dorsal ray. It is differentiated from the new species by very long spicules (almost half of body length) and by the length of the vestibule (almost one millimeter). A new definition of the genus Heligmonoides Baylis, 1928 is proposed with a dichotomic key of the species. The biogeographic distribution and the host spectrum of the genus are described.

KEY WORDS : Heligmonoides variabilis n. sp., Trichostrongylina, Heligmososomidea, Heligmonellidae, Nippostrongylinae, Mus musculus, Muridae, Madagascar, systematics.

Résumé : Trichostrongylina (Nematoda) parasites de Muridés malgaches. III – Description d’une nouvelle espèce d’Heligmonoides Baylis, 1928 (Heligmonellidae) chez Mus musculus


MOTS CLÉS : Heligmonoides variabilis n. sp., Trichostrongylina, Heligmososomidea, Heligmonellidae, Nippostrongylinae, Mus musculus, Muridae, Madagascar, systématique.
orientation that of Durette-Desset & Digiani (2005). The nomenclature used for the study of the caudal bursa is that of Durette-Desset & Chabaud (1981). Measurements are in micrometers except where stated otherwise. Type specimens have been deposited in the Helminthological Collections of the Muséum national d’Histoire naturelle, Paris, France (MNHN). The names of the hosts were updated according to Musser & Carleton (1993).

**RESULTS**

**Heligmonoides variabilis** N. sp. (Figs 1-16)

Type material: holotype male, allotype female, MNHN 208 MQa, 209 male and female paratypes, MNHN 208 MQb.

Studied material: holotype, allotype, 15 male, 15 female paratypes.

Host: *Mus musculus* (L) Muridae.

Site: SI1 (205 worms), SI5-7 (2 males, 2 females).


Other material: 1,220 males and females collected in Ranomafana National Park, Madagascar, October-November 1998-1999, MNHN 431MQ to 437MQ.

Prevalence: 100 % with mean of 152.5 and range of 2-307.

**DESCRIPTION**

Very small nematodes with body uncoiled or coiled only in anterior part. Excretory pore situated within posterior half of oesophagus between 47.9 % and 92 % of oesophageal length (average: 69.8 %). Deirids situated at same level as excretory pore or slightly posterior to it. Oesophagus length/body length less than 13 % in male, 12 % in females. Spicule length/body length varying from 11.7-19.2 % (average: 14.9 %). Uterus very short: 14.2 % of body length on average.

Head: cephalic vesicle present. In apical view, triangular buccal opening surrounded by two amplics, six externo-labial papillae and four sub-median cephalic papillae (Fig. 12).

Synlophe (studied in one male and two female paratypes): in both sexes, cuticle bearing longitudinally uninterrupted ridges with chitinoid struts. Ridges appearing at different levels between cephalic vesicle and oesophageal junction in male and beginning of intestine in female. Arising of one new ridge between cephalic vesicle and nerve ring (Fig. 2) three ridges at level of nerve ring; all four additional ridges arising on ventral side, adjacent to right lateral field (Figs 2-5). Ridges disappearing anterior to caudal bursa in male and at level of vulva in female.

Carene present extending along body, except in ovejector region, composed of four left ridges, most developed being ventral. Two median ridges of carene appearing first, just posterior to cephalic vesicle (Fig. 1) then dorsal (Fig. 2), then ventral (Fig. 3). In both sexes size of carene decreasing in posterior third of body; in female, carene of equivalent size as other ridges at level of infundibulum (Fig. 6). Number of ridges: in male 19 (carene, 6 dorsal, 9 ventral) all along body (Figs 7-10). In female, 19 (carene, 6 dorsal, 9 ventral) at level of oesophageal junction and at mid-body (Figs 4, 5). In posterior third of body, number decreasing to 16 (8 dorsal, 8 ventral) up to level of vulva (Fig. 6).

At mid-body, in both sexes, gradient of size decreasing from left to right on dorsal side. On ventral side, left ridges more developed than right ones (Figs 5, 8). In female, at level of ovejector, ridges of equivalent size (Fig. 6).

At mid-body, axes of orientation directed from right-ventral to left dorsal side. Right axis inclined at 45° to sagittal axis in male, 60° in female; left axis inclined at 80° in male, 65° in female (Figs 5, 8). In female, at level of ovejector, ridges oriented perpendicularly to body surface (Fig. 6).

Holotype male: 2.0 mm long, 50 wide at mid-body; cephalic vesicle 40 long by 22 wide; nerve ring, excretory pore and deirids situated at 110, 150 and 155 from apex, respectively; oesophagus, 240 long.

Asymmetrical caudal bursa with left lateral lobe more developed. Pattern of caudal bursa of type 2-2-1 (Fig. 16). Rays 2 and 3 separated to base. Rays 4 larger than rays 5 and ventrally curved at extremity. Rays 6 smallest. Rays 8 arising posterior to division of dorsal ray, slightly longer than latter. Dorsal ray divided in anterior half into two branches, each branch giving rise to two small branches, curved rays 9 (external branches) and rectilinear rays 10 (internal branches) (Fig. 15). Spicules filiform alate 310 long with sharp distal extremities (Fig. 14). Spicule length/body length 15.5 %. Elongated triangular genital cone 25 long, 20 wide at base with sharp papilla zero on ventral lip and two rounded papillae 7 on dorsal lip (Fig. 13). Gubernaculum absent.

Main measurements (average and range) of ten paratypes. Body, 2.2 (2.05-2.55) mm long, 59.5 (50-65) wide; cephalic vesicle 39.8 (32-50) long, 21.8 (20-25) wide; nerve ring (n = 8), excretory pore and deirids (n = 5) situated at 122 (90-150), 192 (115-250), 178 (155-215) from apex, respectively; oesophagus 275.5 (190-320) long; spicules 331 (290-390) long, spicules length/body length, 14.9 (11.7-19.2) %.

Allotype female: 2.4 mm long, 50 wide at mid-body; cephalic vesicle 40 long by 20 wide; nerve ring, excretory pore and deirids situated at 120, 170 and 170 from apex, respectively; oesophagus 270 long (Fig. 11).
Figs 1-10. – *Heligmonoides variabilis* n. sp. 1, transverse sections of body. 1-6: paratype female, 2.55 mm long. 1, just posterior to cephalic vesicle; 2, at 80 µm posterior to cephalic vesicle; 3, at level of nerve ring; 4, at level of oesophageal intestinal junction; 5, at mid-body (1.1 mm from apex); 6, at level of infundibulum. 7-10: paratype male, 2.4 mm long. 7, at level of oesophageal intestinal junction; 8, at mid-body (1.2 mm from apex); 9, at 350 µm anterior to caudal bursa; 10, at 200 µm anterior to caudal bursa.

Abbreviations. – c: carene; r: right side; v: ventral side. The long arrows represent the axes of orientation, double in male, single in female. The short arrows directed away from the body indicate the origin of a ridge. The ridges are numbered in relation to the frontal axis (passing through the lateral fields) and not in relation to the axes of orientation.
Figs 11-16.  *Heligmonoides variabilis* n. sp. 11: female, anterior extremity, right lateral view; 12: female, head, apical view. 13-16, male: 13, detail of genital cone, ventral view; 14, tip of a dissected spicule; 15, dorsal ray, dorsal view; 17, L4 male (1.25 mm long), transverse section at mid-body; 18, female, posterior extremity right lateral view.

Abbreviations. – r: right side; v: ventral side; d: deirid. The arrow represents the axis of orientation.
Monodelphic (Fig. 18). Vulva situated at 100 from caudal extremity. Vagina vera 26 long. Ovejector 182 long with vestibule 50 long, sphincter 32 long by 35 wide and infundibulum 100 long. Infundibulum generally twisted (allotype and nine paratypes of out 10). Uterus 365 long with five eggs at morula stage, 70 long by 35 wide on average. Uterus length/body length, 15.2 %. Conical tail 35 long (Fig. 18).

Main measurements (average and range) of ten paratypes. Body, 2.5 (2.3-2.8) long, 56 (50-60) wide; nerve ring, excretory pore and deirids (n = 8) situated at 120 (110-135), 189 (160-210), 178 (155-215) from apex, respectively; oesophagus 268 (245-285) long; vulva situated at 101 (95-110) from caudal extremity; vestibule 53.4 (45-60) long; sphincter 28.8 (22-38) long by 34.4 (28-41) wide; infundibulum (n = 7) 99 (95-170) long; uterus 385 (325-530) long with five (2-8 eggs), 62 (55-70) long by 28.8 (28-40) wide; tail 30.4 (25-40) long; uterus length/body length, 15.2 (11-14.2) %.

L4 male: 950 long, 40 wide, oesophagus 190 long i.e. 20 % of body length. Synlopho: at mid-body, 11 cuticular ridges (5 dorsal, 6 ventral) without chitinoid strut orientated from right ventral side to left dorsal side; axis of orientation inclined at 60° to sagittal axis (Fig. 17).

DIAGNOSIS
The Malagasy specimens possess the main features of the genus Heligmonoides Baylis, 1928 (Heligmonellidae, Nippostrongylinae) redefined by Durette-Desset (1971): synlopho with a carene made up of enlarged four ridges more developed than the other ridges and a caudal bursa pattern generally of type 2-2-1. The eleven species described in the genus are parasites of Murinae, mainly of the genus Mus, and originate from the Old World. In this genus, the division of the dorsal ray occurs at the same level as the arising of rays 8 or more distally except for four species: H. afghanus (Tenora, 1969) a parasite of Mus musculus and other Murinae in Afghanistan, H. ikebarai Hasegawa, 1990, a parasite of Tokudaiia muenninki in Japan, H. josephi (Wertheim & Durette-Desset, 1976), a parasite of Mus musculus in Israel and the Malagasy specimens. In these specimens the dorsal ray is divided anteriorly to the arising of rays 8 or more distally. In H. afghanus and H. josephi, rays 8 arise within anterior third of the dorsal ray. In H. ikebarai and the Malagasy specimens, rays 8 arise within the median third of the dorsal ray. The two latter species are easily distinguished by the length of the spicules (almost half of the body length in H. ikebarai vs 13-19 % in the new species) along with the length of the vestibule (900 µm in H. ikebarai vs 45-60 in the new species).

In the species of the genus Heligmonoides, the left axis of orientation of the ridges is inclined to the sagittal axis between 55° and 65° in the male, 55° and 70° in the female (Durette Desset & Digiani, 2005). The Malagasy specimens differ from the other species on two points: the degree of inclination of the left axis in the male is 80° and, contrary to the other species the inclination of the left axis between sexes is more pronounced in the male.

We consider the specimens from Madagascar as belonging to a new species which we have named Heligmonoides variabilis n. sp. due to the variability of some morphometric features such as the position of the excretory pore and the length of the spicules.

DISCUSSION
The genus Heligmonoides was erected by Baylis (1928) with the type species H. murina, a parasite of Mus (Leggada) musculoides (presently known as Nannomys (Leggada) musculoides) (type host) and Mus musculus, both from Nigeria. In 1970, Durette-Desset erected the genus Tenorastrongylus with T. pavulus (Durette-Desset, 1966) as type-species. She noted that the two genera are closely related but preferred to erect a new genus, the description of the synlopho of H. murina being reduced to approximately 30 ridges. In 1983, Durette-Desset revalidated the genus Heligmonoides because of new data concerning the caudal bursa (dorsal lobe) and transferred the four species belonging to the genus Tenorastrongylus to this genus. Thus Tenorastrongylus became a junior synonym of Heligmonoides.

Since 1983, seven other species have been described in this genus. Due to a new nomenclature of the synlopho in the Heligmosomoidea (Durette-Desset & Digiani, 2005), it seems worthwhile to amend the definition of the genus even if the synlopho of the type species is not well known.

Definition of the genus Heligmonoides Baylis, 1928: Heligmonellidae, Nippostrongylinae. Synlopho at mid-body with 17 to 30 cuticular ridges including a carene made up of four left ridges. Number of dorsal ridges fewer than ventral ridges. Apart from carene, right ridges more developed on dorsal side, left ridges on ventral side. Single or double axis of orientation. Caudal bursa slightly asymmetrical with left lobe more developed than right lobe. Pattern of type 2-3 with tendency to 2-2-1 or else 2-2-1. Small dorsal lobe. Spicules with sharp tips. Female with uterus less than 20 % of body length. Fewer than 10 eggs. Tail without spine.

Parasite of rodents (Muridae, Murinae), particularly the murine and arvicoline rodents).

Type species: Heligmonoides murina Baylis, 1928

**DICHOTOMOUS KEY OF THE SPECIES**

1 - (8) Dorsal ray divided anterior to arising of rays 8
2 - (5) Rays 8 arising within anterior third of dorsal ray
3 - (4) Left ray 3 arising more proximally than ray 6 on their common trunk. Female tail twisted at 90° and invaginated

<table>
<thead>
<tr>
<th>Oriental region</th>
<th>Ethiopian region</th>
<th>Palearctic region</th>
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<tbody>
<tr>
<td><em>H. afghanus</em> (Tenora, 1969)</td>
<td><em>Ninisenter</em></td>
<td><em>Mus, Nesokia, Rattus</em> Afghanistan</td>
</tr>
<tr>
<td><em>H. alishanensis</em> (Hasegawa, 1990)</td>
<td><em>Ninisenter</em></td>
<td><em>Tokudaia</em> Japan</td>
</tr>
<tr>
<td><em>H. bulbosus</em> (Ow-Yang et al., 1983)</td>
<td><em>Rattus</em></td>
<td><em>Mus</em> Israel</td>
</tr>
<tr>
<td><em>H. ikebarai</em> (Hasegawa, 1990)</td>
<td><em>Rattus</em></td>
<td><em>Mus</em> Nigeria</td>
</tr>
<tr>
<td><em>H. josephi</em> (Wertheim &amp; Durette-Desset, 1976)</td>
<td><em>Rattus</em></td>
<td><em>Mus</em> Centrafrican R.</td>
</tr>
<tr>
<td><em>H. lanceolatus</em> (Ow-Yang et al., 1983)</td>
<td><em>Rattus</em></td>
<td><em>Mus</em> Centrafrican R.</td>
</tr>
<tr>
<td><em>H. murina</em> (Baylis, 128)</td>
<td><em>Mus</em></td>
<td><em>Apodemus, Clethrionomys</em> Japan</td>
</tr>
<tr>
<td><em>H. parvulus</em> (Durette-Desset, 1966)</td>
<td><em>Ninisomys</em></td>
<td><em>Apodemus, Clethrionomys</em> Japan</td>
</tr>
<tr>
<td><em>H. ryukyensis</em> (Hasegawa &amp; Otsum, 1982)</td>
<td><em>Mus</em></td>
<td><em>Apodemus, Clethrionomys</em> Japan</td>
</tr>
<tr>
<td><em>H. speciosus</em> (Konno, 1958)</td>
<td><em>Ninisomys</em></td>
<td><em>Apodemus, Clethrionomys</em> Japan</td>
</tr>
<tr>
<td><em>H. taiwanensis</em> (Hasegawa, 1990)</td>
<td><em>Apodemus</em></td>
<td><em>Mus</em> Taiwan</td>
</tr>
<tr>
<td><em>H. variabilis</em> (This work)</td>
<td><em>Mus</em></td>
<td><em>Mus</em> Madagascar</td>
</tr>
</tbody>
</table>

Table 1. – Host spectrum and biogeographic distribution of the species of the genus *Heligmonoides* Baylis, 1928.
14 - (15) Spicule length > 800 µm. Left rays 4 and 5 thick, diverging at mid-length. 
Parasite of Nannomys (Leggada) musculoides and Mus musculus from Nigeria 
H. murina Baylis, 1928

15 - (14) Spicule length < 400 µm. Left rays 4 and 5 thin, diverging at their extremities.

16 - (17) Spicule length more than 20 % of body length. Genital cone poorly developed. 
Parasite of Nannomys (Leggada) spp. from the Central African Republic. 
H. parvulus (Durette-Desset, 1966) Durette-Desset, 1983

17 - (16) Spicule length less than 15 % of body length. Genital cone well developed. 
Parasite of Niviventer confucianus from Taiwan 
H. alishanensis Hasegawa, 1990

18 - (9) Dorsal ray divided posterior to arising of rays 8 
19 - (20) Dorsal ray and rays 8 very thick. Spicule length/body length: 15 % 
Parasite of Maxomys whiteheadi from Malaysia 
H. bulbosus Ow Yang, Durette-Desset & Ohbayashi, 1983

20 - (19) Dorsal ray and rays 8 very thin. Spicules length/body length not 15 % 
21 - (22) Spicules length/body length: 26 %. Female tail invaginated 
Parasite of Maxomys rajab from Malaysia 
H. lanceolatus Ow-Yang, Durette-Desset & Ohbayashi, 1983

22 - (21) Spicule length/body length: 10 %. Female tail not invaginated 
Parasite of Murinae and Arvicolinae from Japan 
H. speciosus (Konno, 1958) Durette-Desset, 1983

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