

# DESCRIPTION OF A NEW SPECIES OF *HELIGMONINA* BAYLIS, 1928 (NEMATODA: HELIGMONELLIDAE) A PARASITE OF *MASTOMYS NATALENSIS* (RODENTIA: MURIDAE) FROM SWAZILAND AND NEW DATA ON THE SYNLOPHE OF *HELIGMONINA CHABAUDI* (DESSET, 1966)

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## Summary:

A new species of heligmosomoid nematode belonging to the subfamily Nippostrongylinae Durette-Desset, 1970 is described: *Heligmonina wakelini* n. sp., a parasite from the small intestine of the commensal rodent *Mastomys natalensis* (Smith, 1834) from Swaziland. It differs from the most closely related species *H. boomkeri* Durette-Desset & Digiani, 2005 by the number of the cuticular ridges in the female synlophe (10 vs 12), the width of the left ala, larger than the body diameter in the male, and the inclination of the axis of orientation of the ridges in both sexes (53° vs 70°). New morphological data (head and synlophe) on *Heligmonina chabaudi* (Desset, 1964), also a parasite of *Mastomys natalensis* in the Republic of Congo, are provided in order to compare with the new species.

**KEY WORDS :** *Heligmonina wakelini* n. sp. Nematoda, Trichostrongylina, Heligmosomoidea, Heligmonellidae, Muridae, Swaziland.

**Résumé :** DESCRIPTION D'UNE NOUVELLE ESPÈCE D' *HELIGMONINA* BAYLIS, 1928 (NEMATODA : HELIGMONELLIDAE) PARASITE DE *MASTOMYS NATALENSIS* (RODENTIA : MURIDAE) AU SWAZILAND ET NOUVELLES DONNÉES SUR LE SYNLOPHE D' *HELIGMONINA CHABAUDI* (DESSET, 1966)

Une nouvelle espèce de Nématode Heligmosomoïde appartenant à la sous-famille des Nippostrongylinae Durette-Desset, 1970 est décrite: *Heligmonina wakelini* n. sp., parasite de l'intestin grêle du rongeur commensal *Mastomys natalensis* (Smith, 1834) au Swaziland. Elle diffère de l'espèce la plus proche *H. boomkeri* Durette-Desset & Digiani, 2005 par le nombre de crêtes cuticulaires du synlophe chez la femelle (10 vs. 12 in *H. boomkeri*), par la largeur de l'aile gauche supérieure au diamètre du corps (limité à l'hypoderme) chez le mâle et par une inclinaison différente de l'axe d'orientation chez les deux sexes (53° au lieu de 70°). De nouvelles données morphologiques (tête et synlophe) d'*H. chabaudi* (Desset, 1964), également parasite de *Mastomys natalensis* en République du Congo sont fournies pour comparaison avec la nouvelle espèce.

**MOTS CLÉS :** *Heligmonina wakelini* n. sp. Nematoda, Trichostrongylina, Heligmosomoidea, Heligmonellidae, Muridae, Swaziland.

## INTRODUCTION:

The rodent genus *Mastomys* is found throughout Africa, but mostly in Sub-Saharan Africa, where some species are important pests of crops, and regularly show population explosions that result in significant losses to agriculture (Granjon *et al.*, 1997; Lima *et al.*, 2003; Stenseth *et al.*, 2003). Species such as *M. natalensis* are commensal and regularly invade human habitation whilst others are restricted to the grasslands, fields and the bush (Duplantier & Granjon, 1988; Brouat *et al.*, 2007). *Mastomys* is one of the genera comprising the *Praomys* group of murine rodents, but their exact relationships to other genera

within this grouping and to each other within the genus, have been the subject of debate (Granjon *et al.*, 1997), until recently when the molecular phylogeny was established (Lecompte *et al.*, 2002).

Whilst rodents of the genus *Mastomys* are known to carry a number of important bacterial and viral diseases that are transmissible to humans (Leirs, 1994), and some of their metazoan parasites have been reported (Ugbomoiko & Obiamiwe, 1991), including new species (Diouf *et al.*, 1998, 2005), their helminth communities have only recently attracted attention (Brouat *et al.*, 2007). Such studies are dependent on the accurate identification of the helminths infecting hosts, and in the case of *Mastomys* spp. the full spectrum of helminths from all regions of Africa where these rodents occur, is still poorly documented. *Mastomys* spp. are known to be hosts of several species of the Ethiopian branch of the Nippostrongylinae (Heligmonellidae), which are parasites of Muridae and represented by two genera in particular: *Neobeligionella* Durette-Desset 1970 and *Heligmonina* Baylis, 1928. To-date, three species of *Neobeligionella* (Diouf *et al.*, 1998, 2005) and one of *Heligmonina*, *H. bignonensis* Diouf, Bâ & Durette-Desset, 1997 have been described from *Mastomys erythroleucus* (Temminck, 1853). In *Mastomys*

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*natalensis* (Smith, 1834), two species of *Heligmonina* have been described: *H. chabaudi* (Desset, 1964) and *H. kotoensis* Diouf *et al.*, 2005, the latter being a co-parasite with *Neobeligionella lamaensis* Diouf *et al.*, 2005. All of these species originate from Western Africa (Benin, Senegal, Congo and Central African Republic). Despite the wide distribution of *M. natalensis* throughout Sub-Saharan Africa, and the occurrence of closely related *Mastomys* spp. in specific regions (Leirs, 1994), no other species *Heligmonina* have been recorded so far from this host from either East or South Africa.

In the present paper, a new species of *Heligmonina*, a parasite of *Mastomys natalensis* is described offering the first record of *Heligmonina* from South-Eastern Africa. A description of the head and a re-description of the synlophe of *H. chabaudi* from *M. natalensis* from the Central African Republic are also provided in order to compare with the features of the new species.

## MATERIAL AND METHODS

### CAPTURE OF RODENTS AND STUDY SITES

The identity, distribution and population ecology of wild rodents in Swaziland are all well known (Monadjem, 1998, 1999; Monadjem & Perrin, 2003) and their demography has been studied intensively in other parts of Africa (Lima *et al.*, 2003). Despite the known sympatric occurrence of *M. coucha* (Smith, 1836) in S. Africa, from available evidence only *Mastomys natalensis* is believed to occur in our study sites in Swaziland (Monadjem, pers. com.). Wild rodents were caught in Sherman traps set out in the afternoon and inspected the following morning. The animals for this study were caught at two locations in Swaziland during June 2004. The first site was in the Middleveld region, represented in this case by fields of the Faculty of Agriculture of the University of Swaziland at Luyengo (S 26° 34.453', EO 31° 10.665'). Here traps were set around the periphery of plots where maize was growing. The second site was in the NE of the country, the Lowveld region, in Vuvulane. The site used was a fallow field immediately adjacent to fields with mature sugar cane on an industrial sugar cane plantation (S 26° 04.181', EO 31° 52.186'). Animals were recovered from traps and transported live to the laboratory at the University of Swaziland within a day or two, where they were killed with chloroform, dissected and the worms were recovered from the small intestine by incubation in Hanks' saline. Worms were then transferred to 70 % ethanol, transported to Nottingham (UK) and eventually sent to Paris (France) for examination.

### EXAMINATION OF WORMS AND NOMENCLATURE

The nomenclature used above the family group follows Durette-Desset & Chabaud (1993). The synlophe was studied according to the method of Durette-Desset (1985). The nomenclature used for the study of the synlophe follows Durette-Desset & Digiani (2005a) and that of the caudal bursa Durette-Desset & Chabaud (1981). The curve of the strut of the left ala is not included in the measurement of its length. The caudal bursae of 10 males from the type material (427 MQ) and 20 males from voucher material (10 males 428 MQ and 10 males 430 MQ) were examined in order to determine the relative disposition of rays 3 to 6 and the symmetrical/asymmetrical arising of rays 8 on the dorsal ray. Measurements are in micrometers except where otherwise stated. The material (types and voucher material) is deposited in the Collections of the Muséum national d'Histoire naturelle (MNHN) of Paris (France). The nomenclature of the hosts follows Musser & Carleton (1993).

## DESCRIPTION

### *HELIGMONINA WAKELINI* N. SP.

(Figs 1-15)

Type material: 52 males, 41 females MNHN 427 MQ. Studied material: holotype male, allotype female MNHN 427 MQa, 15 males, 15 females paratypes MNHN 427 MQb.

Host: *Mastomys natalensis* (Smith, 1834) (Muridae, Murinae).

Site: small intestine.

Geographic origin: Middleveld, Luyengo, Swaziland.

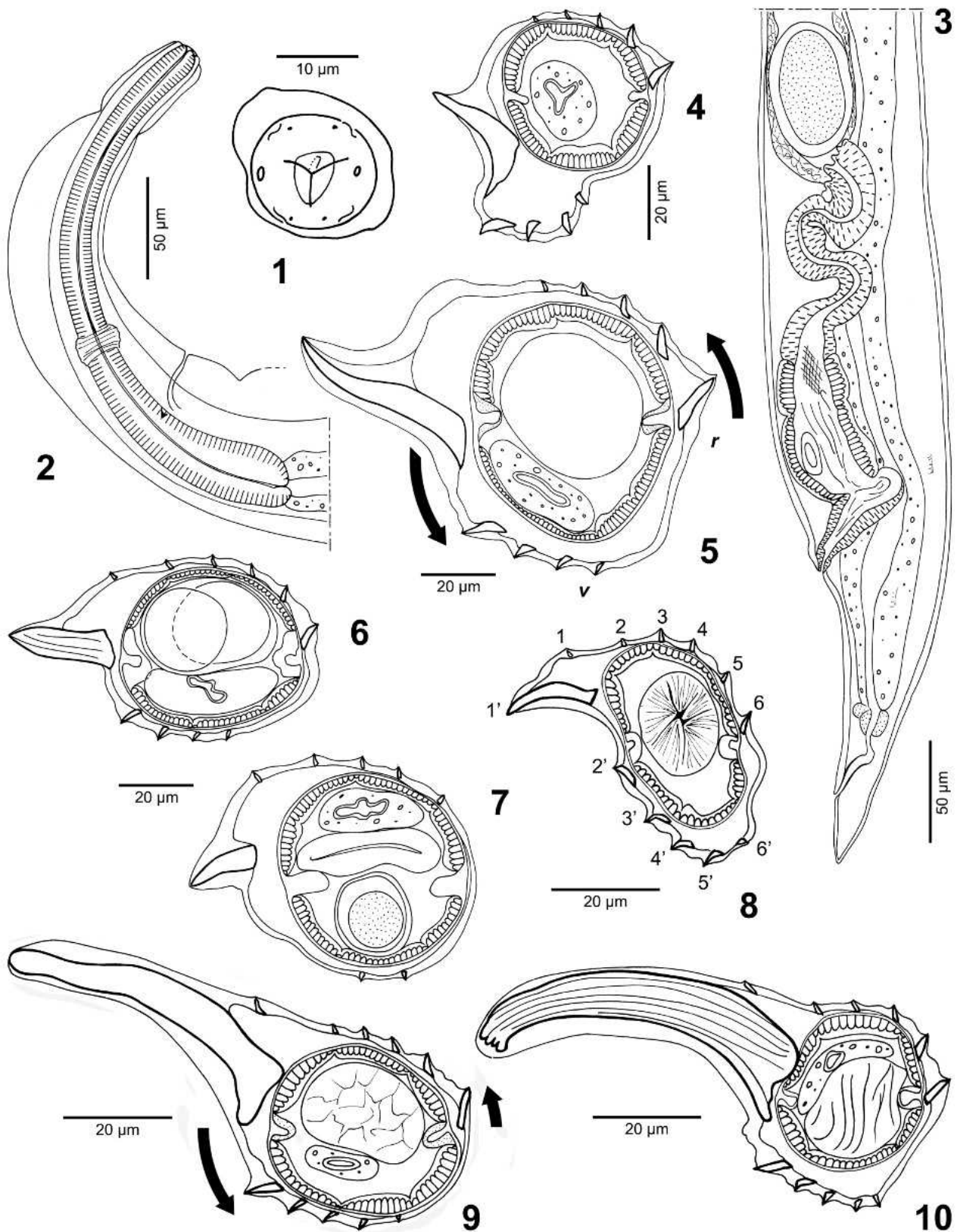
Voucher material: from the small intestine of three *Mastomys natalensis*; 69 specimens MNHN 428 MQ, same locality as type material; 10 specimens MNHN 429 MQ, 81 specimens 430 MQ MNHN from Vuvulane in the Lowveld region of Swaziland.

### GENERAL

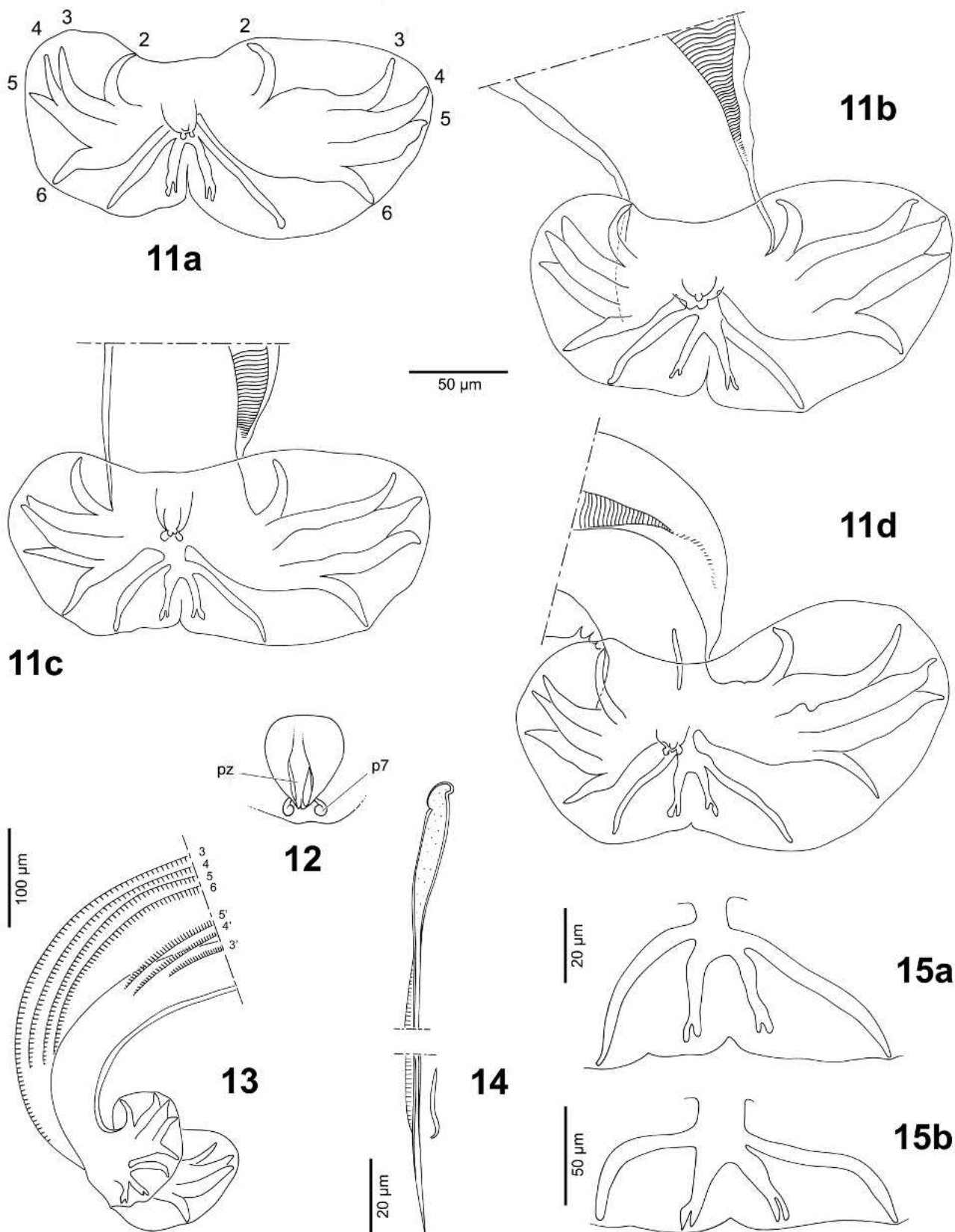
Small nematodes with body sinistrally coiled along ventral side with two spires in male, three in female. Excretory pore situated within posterior third of oesophagus. Deirids generally situated at same level as excretory pore or just posterior to it (Fig. 2). Oesophagus length/body length less than 10 % on average in male and 9 % in female. Uterus very short less than 20 % of body length.

Head: cephalic vesicle present. In apical view, triangular oral opening surrounded by two amphids, four external papillae and four cephalic papillae (Fig. 1).

Synlophe (studied in one male and two female paratypes): in both sexes, body bearing uninterrupted cuti-



Figs 1-10. – *Heligmonina wakelini* n. sp. 1-3. Female. 1 - head, apical view. 2 - anterior extremity, right lateral view. 3 - posterior extremity, left lateral view. 4-10. Transverse sections of the body. 4-7. Female paratype 3.1 mm long. 4 - at 220 µm posterior to cephalic vesicle. 5 - at mid-body (1.9 mm from apex). 6 - At 900 µm anterior to vulva. 7 - at level of *vagina vera*. 8-10. Male paratype 3.3 mm long. 8 - just anterior to oesophageal intestinal junction. 9 - at mid-body (1.8 mm from apex). 10 - within posterior part of body. All sections are orientated as 5. Abbreviations: v: ventral side, r: right side.



Figs 11-15. – *Heligmonina wakelini* n. sp. Male. 11a-d. Different patterns of the caudal bursa. 11a, Type A; 11b, Type B, 11c, Type C; 11d, Type D. 12 - Genital cone, ventral view. 13 - Caudal bursa, disappearance of cuticular ridges, right lateral view. 14 - Gubernaculum, ventral view and spicules (proximal part and tips). 15a-b. Arising of rays 8 on dorsal ray, dorsal view. 15a - asymmetrical. 15b - symmetrical. Abbreviations: pz: papilla zero; p7: papilla 7.

cular ridges except right ventral side free of ridges. All ridges arising just posterior to cephalic vesicle (Figs 4, 8) and disappearing just anterior to caudal bursa in male (Fig. 10) and at vulvar opening in female (Fig. 7). Presence of left hypertrophied ala, straight in female, strongly curved towards ventral side in male. In male, size of ala increasing progressively from cephalic vesicle to posterior part of body, reaching 60 anterior to caudal bursa (Fig. 10). In female, ala reaching maximum size (45) at mid-body (Fig. 5) and decreasing progressively down to 20 anterior to vulva (Fig. 7).

Number of ridges: 12 (ala, six dorsal, five ventral) in male all along body (Figs. 8-10); 10 (ala, five dorsal, four ventral) in female at oesophageal region (Fig. 4) and at mid-body (Fig. 5). At about 1 mm anterior to vulva 11 (ala, six dorsal, four ventral) with arising of ridge n° 1 (Fig. 6), then at level of *vagina vera* 8 (ala, five dorsal, two ventral) with disappearance of ridges n° 6, 2' and 3' (Fig. 7).

At mid-body, double gradient of size from left to right on ventral side and from right to left on dorsal side (with exception of ridge n° 1 in male very thin and longer than ridge n° 2 (Figs 4-6, 8-10). In posterior region of female ridges of equivalent size, except ala (Fig. 7). At mid-body, axis of orientation directed from right ventral quadrant to left dorsal quadrant, inclined at 53° to sagittal axis in both sexes.

- Holotype male: 2.4 mm long and 130 wide at mid-body, including left ala. Cephalic vesicle 51 long and 28 wide. Nerve-ring, excretory pore and deirids situated at 150, 210 and 210 from apex, respectively. Oesophagus 260 long.

Caudal bursa strongly asymmetrical with left lateral lobe most developed. Pattern of caudal bursa of type 1-3-1 for right lobe and 1-4 for left lobe (Fig. 11 a-d). Prebursal papillae not observed. In both lobes, rays 3 arising more distally than rays 6 on common trunk. In right lobe, rays 3 to 5 arising at same level and extremities of rays 3 and 4 closer to each other than those of rays 4 and 5; in left lobe ray 3 arising first from common trunk of rays 3 to 5 and extremities of rays 3 and 4 more distant from each other than those of rays 4 and 5. Small rays 6. Rays 8 longer than dorsal ray arising asymmetrically at its base, first left ray 8 (Fig. 15a). Dorsal ray deeply divided just posterior to arising of rays 8 into two branches. Each branch divided into two small twigs, rays 9 (external branches) slightly thicker than rays 10 (internal branches) (Fig. 15a, b). Filiform spicules 390 long, with sharp tips (Fig. 14). Spicule length/body length: 16.2 %. Semi-circular genital cone 40 long and 20 wide at base with small rounded papilla 0 on ventral lip and papillae 7 on dorsal lip (Fig. 12). Gubernaculum not observed.

Measurements (average and range) of 10 paratypes: 2.8 (2.1-3.3) mm long and 140 (110-160) wide at mid-body;

cephalic vesicle, 51 (42-60) long and 26.5 (21-32) wide; nerve ring (n = 8), excretory pore and deirids (n = 8) situated at 152 (130-170), 220 (180-250) and 228 (205-260) from apex, respectively; oesophagus 270 (250-300) long; spicules 406 (310-445) long, spicules length/body length 14.5 % (13.3-17.1) %. Very thin gubernaculum observed only in some paratypes (Figs 11d, 14).

Examination of several male specimens in the material studied indicated some variations in the relative arrangement of rays 3-4-5 in both lobes of the caudal bursa. These variations are as follows:

- In the right lobe, rays 3, 4 and 5 arising at the same level from their common trunk (Figs 11a, 11b) or rays 3 and 4 arising more distally than ray 5 from common trunk of rays 3 to 5 and diverging only at their extremities (Figs 11c, 11d).

- In the left lobe, rays 3, 4 and 5 arising at the same level from their common trunk (Figs 11b, 11c) or rays 3 arising first from common trunk of rays 3 to 5 and rays 4 and 5 diverging only at their extremities (Figs 11a, 11d). Similarly, the relative distances between the extremities of rays 3 to 5 showed some variations linked to the arising of the rays. When rays 3, 4 and 5 arise at same level, their extremities are approximately equidistant (both left and right lobes). When rays 3 and 4 arise more distally than rays 5 on their common trunk, the extremities of rays 3 and 4 are closer to each other than those of rays 4 and 5 (right lobe). When rays 4 and 5 arise more distally than rays 3, the extremities of rays 4 and 5 are closer to each other than those of rays 3 and 4 (left lobe).

The combination of the relative arising of rays 3-5 and the relative distances between their extremities provides the four different patterns of caudal bursae (types A-D) observed in the material studied:

- Type A (Fig. 11a): in the right lobe, rays 3, 4 and 5 arising at the same level from their common trunk and extremities of rays 3 and 4 closer to each other than those of rays 4 and 5. In the left lobe ray 3 arising first from common trunk of rays 3 to 5, and extremities of rays 4 and 5 closer to each other than those of rays 3 to 4.

- Type B (Fig. 11b): in the right lobe, rays 3, 4 and 5 arising at the same level from their common trunk, extremities of rays 3, 4 and 5 almost equidistant. In the left lobe: same pattern as in the right lobe.

- Type C (Fig. 11c): in the right lobe, ray 5 arising first from the common trunk of rays 3 to 5, extremities of rays 3 and 4 closer to each other than those of rays 4 and 5. In the left lobe rays 3, 4 and 5 arising at the same level from their common trunk, extremities of rays 3, 4 and 5 almost equidistant.

- Type D (Fig. 11d): in the right lobe, ray 5 arising first from the common trunk of rays 3 to 5, extremities of rays 3 and 4 closer to each other than those of rays 4 and 5. In the left lobe ray 3 arising first from the

| Pattern of rays 8 and 9 | Material n° | Pattern of rays 3-5  |         |            |            |
|-------------------------|-------------|----------------------|---------|------------|------------|
|                         |             | Type A               | Type B  | Type C     | Type D     |
| Symmetrical             | 427 MQ      | 6 paratypes          |         |            |            |
|                         | 428 MQ      | 5 males              |         |            |            |
|                         | 430 MQ      | 2 males              |         |            | 1 male     |
| Asymmetrical            | 427 MQ      | Holotype, 1 paratype |         | 1 paratype | 1 paratype |
|                         | 428 MQ      | 2 males              | 3 males |            |            |
|                         | 430 MQ      | 1 male               | 1 male  | 2 males    | 3 males    |

Table I. – The combination of the relative arising of rays 3-5 and the relative distance between their extremities provide four different patterns of caudal bursae in *Heligmonina wakelini* n. sp. These, together with the symmetrical/asymmetrical of rays 8 on the dorsal ray may be considered as infra-specific variations.

common trunk of rays 3 to 5, extremities of rays 4 and 5 closer to each other than those of rays 3 and 4.

Notably, the arising origin of rays 8 on the dorsal ray of the caudal bursa may be asymmetrical (AS) as in the holotype (15 cases) (Fig. 15a) or symmetrical (S) (14 cases) (Fig. 15b). This character was independent of the pattern of the lateral lobes (see Table I).

- Allotype female: 3 mm long and 90 wide at mid-body including left ala. Cephalic vesicle 48 long and 30 wide. Nerve-ring, excretory pore and deirids situated at 150, 220 and 230 from apex, respectively. Oesophagus 270 long (Fig. 2).

Monodelphic (Fig. 3). Vulva situated at 150 from caudal extremity, *vagina vera* 40 long. Ovejector 229 long with vestibule 46 long, sphincter 23 long and 35 wide, infundibulum 160 long. Uterus 480 long with six eggs at morula stage, 65 long and 40 wide. Uterus length/body length 16.2 %. Conical tail 36 long (Fig. 3).

Measurements (average and range) of 10 paratypes: 3.25 (2.9-3.5) mm long and 82 (60-100) wide at mid-body, left ala included, cephalic vesicle 48 (43-55) long and 22 (18-30) wide; nerve ring (n = 7), excretory pore (n = 7) and deirids (n = 5) situated at 144 (110-180), 206 (158-235) and 219 (200-235) from apex, respectively; oesophagus (n = 9) 258 (210-290) long; vulva situated at 146 (130-160) from caudal extremity; *vagina vera* 34 (30-40) long; vestibule 52 (40-65) long, sphincter 29 (23-31) long and 35.5 (30-45) wide, infundibulum (n = 5) 125 (100-150) long; uterus 485 (350-600) long with 8 (2-14) eggs, 60.5 (52-70) long and 34 (30-46) wide; uterus length/body length 14.9 % (10-19) %; tail 49 (30-70) long.

#### DIAGNOSIS

The specimens described above possess the main features of the genus *Heligmonina* as outlined by Baylis (1928) (Heligmonellidae, Nippostrongylinae) and redefined by Durette-Desset (1971). This genus is characterised mainly by the pattern of the synlophe with a hypertrophied left ala and the absence of cuticular ridges totally or pro parte on the right ventral quadrant of the body. The pattern of the caudal bursa varies

greatly among species and generally differs for each lobe.

To date, 23 species have been described in this genus, all parasites of Muridae, 18 in Africa and five in Madagascar.

Concerning the synlophe, the females in the material described in this paper are the only species amongst all known *Heligmonina* having a synlophe with a left ala, five dorsal and four ventral ridges. Whereas the males share a synlophe characterised by the left ala, six dorsal and five ventral ridges with three species: *Heligmonina albignaci* Quentin & Durette-Desset, 1974 and *Heligmonina tanala* Durette-Desset, Lehtonen & Haukisalmi, 2002, parasitic respectively in *Brachyuro-mys betsileoensis* (Bartlett, 1880) and *Eliurus tanala* Major, 1896, both from Madagascar; and with *H. boomkeri* Durette-Desset & Digiani, 2005b, parasitic in *Aethomys chrysophilus* (de Winton, 1897) from South Africa. *H. albignaci* is mainly distinguished from these specimens by the development of the dorsal ridge n° 1, which induces the presence of a carene. It is distinguished on the other hand by the pattern of the caudal bursa, with the left ray 3 arising before ray 6 on the common trunk of rays 3 to 6. *H. tanala* resembles our material through the similar synlophe in males, but it differs by the pattern of the caudal bursa, with the left ray 3 arising at the same level as ray 6 on the common trunk of rays 3-6, and by the strong development of the dorsal lobe. The most similar species is *H. boomkeri*, which has the same pattern of the caudal bursa, with the left ray 6 arising anteriorly to ray 3 from their common trunk. More exactly, the bursal pattern of *H. boomkeri* corresponds best to the type C observed in our material. However, some differences were found between both species in the female synlophe and in some body measurements. The female of *H. boomkeri* has a synlophe with 12 cuticular ridges: ala, six dorsal, five ventral and all ventral ridges disappear at vestibular level. In addition, the ovejector is shorter than that of the new species. In males, the length of the left ala at mid-body does not exceed the body diameter limited by the hypodermis.

We consider the specimens collected in *Mastomys natalensis* as belonging to a new species that we have named *Heligmonina wakelini* n. sp. in honour to Professor Derek Wakelin who retired in 2002 from the University of Nottingham, after an eminent career in research on the genetics of the immune response to intestinal nematodes in rodents.

*HELIGMONINA CHABAUDI* (DESSET, 1964)  
DURETTE-DESSET, 1971  
= *LONGISTRIATA CHABAUDI* DESSET, 1964  
(Figs 16-25)

Studied material: one male, one female MNHN 230 CU.  
Host: *Mastomys natalensis* (Smith, 1834) (Muridae, Murinae).

Site: small intestine.

Geographical origin: Boukoko, Central African Republic.

Head: cephalic vesicle present. In apical view, circular oral opening surrounded by two amphids, six externo-labial papillae of which lateral ones joined to amphids and four submedian cephalic papillae (Fig. 25).

Synlophe (studied in one male, one female): in both sexes, body bearing uninterrupted cuticular ridges except on right ventral side, all arising just posterior to cephalic vesicle (Fig. 16) and disappearing anterior to caudal bursa in male (Fig. 20) and at vulvar opening in female (Fig. 24).

Presence of left hypertrophied ala, at mid-body with sinuous strut in male, straight in female. In male, size increasing progressively from cephalic vesicle to mid-body, reaching 100 at this level (Fig. 18). At about two-thirds of body length, ala still same width and strongly sinuous. At about 100 anterior to caudal bursa, size decreasing down to 40 (Fig. 20). In female, width of ala reaching 80 at mid-body (Fig. 22) and decreasing progressively down to 20 anterior to vulva (Fig. 24). Number of ridges: in both sexes 11 (left ala, six dorsal, four ventral) except in posterior region. In male, at 80 anterior to caudal bursa, nine (left ala, four dorsal, four ventral) with disappearance of ridges n° 1 and n° 2 (Fig. 19), then posteriorly, seven ridges (left ala, three dorsal, three ventral) with disappearance of ridges n° 3 and 2' (Fig. 20). In female, at about 200 anterior to vulva, 10 (left ala, six dorsal, three ventral) with disappearance of ridge n° 5' (Fig. 23), then at about 100 anterior to vulva, nine (left ala, five dorsal, three ventral) with disappearance of ridge n° 6 (Fig. 24). At mid-body, double gradient of size from left to right on ventral side and from right to left on dorsal side (with exception of ridge n° 1 very thin and longer than ridge n° 2). Double gradient distinct at mid-body (Figs 18, 22). In posterior region, except ala, ridges of equivalent size (Figs 19, 20, 23, 24). Axis of orientation directed from right ventral quadrant to left dorsal qua-

drant and at mid-body inclined at 45° to sagittal axis in both sexes (Figs 18, 22).

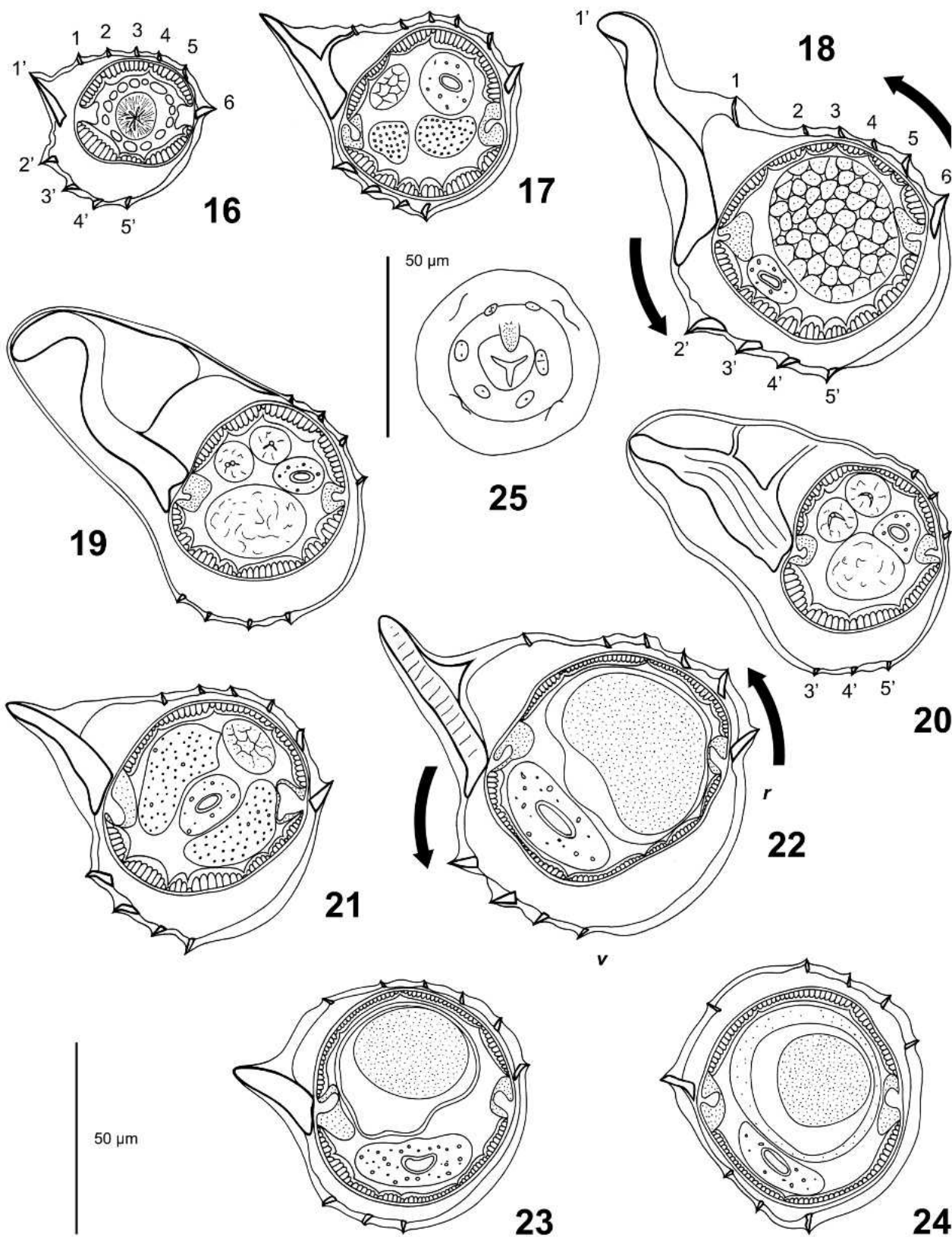
#### REMARKS

As stated above, the genus *Heligmonina* is characterised by the presence of a hypertrophied left ala supported by a sole cuticular ridge. However, in contrast to this relative uniformity among species, the pattern of the caudal bursa and especially the relative arrangement of rays 2 to 6 vary greatly among species and within each lobe.

In *H. wakelini*, the pattern for the right lobe is of type 1-3-1 i.e. rays 2 and 6 arising at the same level from their common trunk. For the left lobe the pattern is of type 1-4 (ray 2 arising first from the common trunk of rays 2 to 6). In both lobes rays 3 always arising more distally to rays 6 on their common trunk in all the specimens studied. This relative arrangement of rays 2, 3 and 6 may be considered as specific, whereas the variations concerning the relative arising of rays 3 to 5 on their common trunk, as well as the relative distances of their extremities may be considered as infra-specific, along with the symmetrical/asymmetrical arising of rays 8 on the dorsal ray.

Currently, three species of *Heligmonina* have been described from the genus *Mastomys*: *H. bignonensis* Diouf *et al.*, 1997 in *M. erythroleucus* from Senegal, *H. chabaudi* (Desset, 1964) from Congo and Central African Republic and *H. kotoensis* Diouf *et al.*, 2005 in *M. natalensis* from Benin. These three species are morphologically closely related to each other and parasitize closely related hosts (Lecompte *et al.*, 2002). Although they have different patterns of caudal bursae, they are very similar in respect of their synlophes, with 11 cuticular ridges arranged as: left ala, six dorsal and four ventral. This type of synlophe is shared with two other species in the genus but only in the males: *H. possompesi* (Durette-Desset, 1966), parasitic in *Mus (Leggada) minutoides* Smith, 1834 from Congo and *H. thamnomysi* (Durette-Desset, 1966), parasitic in *Grammomys rutilans* (Peters, 1876) (= *Thamnomys rutilans*) and *Cricetomys gambianus* Waterhouse, 1840 from Central African Republic. A fourth species, *Heligmonina praomyos* Baylis, 1928, a parasite of *Praomys tullbergi* from Nigeria was reported by Ugbomoiko & Obiamiwe (1991) in *Mastomys natalensis* from the same country but the authors gave no description nor illustration. Given the difficulties of identifying any *Heligmonina*, especially at the specific level (a transverse section of the body must be studied closely) this report should be taken with caution.

*Heligmonina wakelini* n. sp., which parasitizes a host belonging to this group but from South Eastern Africa, is morphologically closer to a South African and two Malagasy species (see Diagnosis), all four species having a synlophe with 12 cuticular ridges arranged as: left ala, six dorsal and five ventral at least in males.



Figs 16-25. – *Heligmonina chabaudi* (Desset, 1964). 16-24. Transverse sections of the body. 16-20. Male 2.2 mm long. 16 - at level of the nerve ring. 17 - at level of the oesophago-intestinal junction. 18 - at mid-body (1.3 mm from apex). 19 - at about 150 μm anterior to caudal bursa. 20 - at 50 μm anterior to caudal bursa 21-24. Female 2.5 mm long. 21 - at level of oesophago-intestinal junction. 22 - at mid-body (1.3 mm from apex). 23 - at proximal level of the uterus. 24 - just anterior to vulva. 25 - Female, head, apical view. All sections are orientated as 22. Abbreviations: v: ventral side, r: right side.



As in western Africa, besides *M. natalensis*, there are other closely related species of *Mastomys* endemic to South Africa (e.g. *M. coucha* (Smith, 1836) and *M. shortridgei* (St. Leger, 1933); Granjon *et al.*, 1997), but their parasites have not yet been reported, and it is quite conceivable that new species of *Heligmonina* will be discovered when these hosts are examined. These may eventually help to explain better the evolution of the genus *Heligmonina*. However, from the available evidence it appears that the geographical location of the *Heligmonina* spp. parasitic in *Mastomys* spp. may be of greater significance than the host spectrum because the hosts of the *Heligmonina* spp. most closely related to *H. wakelini* in south-eastern Africa are not even in the same host genus (*Mastomys*) as the species from western Africa. Thus, host capture may have been an important element in the evolution of this genus with species transferring between sympatric rodents, rather than following a strict co-evolutionary route. *H. wakelini* may represent a lineage of *Heligmonina* in *Mastomys* which diversified from those species in western Africa and spread to and diversified in the other genera of rodents in South Africa and Madagascar, or alternatively invaded *M. natalensis* in South Africa from one of the other rodents. The eventual resolution of the evolutionary history of both rodent hosts and the genus *Heligmonina* will require examination of more specimens from eastern and South Africa, most likely also the recognition and description of new species, and the application of molecular tools to construct a robust molecular phylogeny in support of the relationships that have been suggested based on morphology.

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