Taxonomic revision of the genus *Neoheligmonella* Durette-Desset, 1971 (Nematoda, Heligmonellidae) parasitic in Muridae mainly from the Ethiopian Region

María Celina DIGIANI
CONICET. División Zoología Invertebrados,
Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata (Argentina)
mdigiani@fcnym.unlp.edu.ar

Marie-Claude DURETTE-DESSET
Muséum national d'Histoire naturelle,
Département de Systématique et Évolution,
UMR 7138, associée au CNRS
case postale 52, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
mcdd@mnhn.fr

Digiani M. C. & Durette-Desset M.-C. 2013 — Taxonomic revision of the genus *Neoheligmonella* Durette-Desset, 1971 (Nematoda, Heligmonellidae) parasitic in Muridae mainly from the Ethiopian Region. *Zoosystema* 35 (4): 479-488. http://dx.doi.org/10.5252/z2013n4a2

ABSTRACT
The genus *Neoheligmonella* Durette-Desset, 1971 (Nippostrongylinae) is revised and split into three genera, one of them with two subgenera. The new genera can be discriminated mainly by characters of the synlophe which had been not considered previously at the supraspecific level. These characters include the presence of a careen, the size of the right ridge relative to the left ridge, and the presence of gradients in the ridge size. The genus *Neoheligmonella sensu stricto* is proposed to include species with a careen, and it is divided into two subgenera: *Neoheligmonella* (*Neoheligmonella*) characterized by a right ridge measuring more than 45% of the ventral ridge of the careen, and *Neoheligmonella* (*Duplantierus*) n. subgen. with a right ridge measuring less than 45% of the ventral ridge of the careen. *Dioufnema* n. gen. includes one species with neither a careen nor hypertrophied ridges and having a bursa of type 1-3-1. *Taranchonema* n. gen. includes species without a careen, with the left ridge and the right ridge hypertrophied, and without a dorsal gradient in ridge size. A dichotomous key to the new genera and subgenera is provided. Five species of unknown synlophe, originally placed in the former genus *Neoheligmonella* and validated by other characters, are considered as Nippostrongylinae *incertae sedis*.

KEY WORDS
Taxonomic revision,
synlophe,
careen,
Heligmosomoidea,
Muridae,
Ethiopian region,
new combinations,
new genera,
new subgenera.

RÉSUMÉ
Révision taxonomique du genre Neoheligmonella *Durette-Desset, 1971 (Nematoda, Heligmonellidae) parasite de Muridae principalement de la Région éthiopienne.*
Le genre *Neoheligmonella* Durette-Desset, 1971 (Nippostrongylinae) est révisé et scindé en trois genres, dont un avec deux sous-genres. Les nouveaux genres peuvent être principalement différenciés par des caractères du synlophe qui n'avaient pas été considérés jusqu'à présent au niveau supra-spécifique. Ces caractères incluent la présence d'une carène, la taille relative de la crête droite par rapport à la crête gauche, et la présence de gradients de la taille des crêtes. Le genre *Neoheligmonella sensu stricto* est proposé pour inclure des espèces possédant une carène et il se divise en deux sous-genres: *Neoheligmonella* (*Neoheligmonella*) caractérisé par une crête droite mesurant plus du 45 % de la crête ventrale de la carène et *Neoheligmonella* (*Duplantierus*) n. subgen. avec une crête droite mesurant moins du 45 % de la crête ventrale de la carène. *Dioufnema* n. gen. inclut une espèce sans carène ni crêtes hypertrophiées et possédant une bourse caudale du type 1-3-1. *Taranchonema* n. gen. inclut des espèces sans carène, avec la crête gauche et la crête droite hypertrophiées et sans gradient dorsal des crêtes. Une clé dichotomique des nouveaux genres et sous-genres est fournie. Cinq espèces dont le synlophe est inconnu, placées jusqu'à présent dans le précédent genre *Neoheligmonella* et validées par d'autres caractères, sont considérées comme des Nippostrongylinae *incertae sedis*.

MOTS CLÉS
Révision taxonomique,
synlophe,
carène,
Heligmosomoidea,
Muridae,
Région éthiopienne,
combinaisons nouvelles,
genres nouveaux,
sous-genres nouveaux.

INTRODUCTION

The genus *Neoheligmonella* Durette-Desset, 1971 belongs to the subfamily Nippostrongylinae Durette-Desset & Chabaud, 1977 (Heligmonellidae Skrjabin & Schikhobalova, 1952). When the genus was erected it included eleven species, five of which lacked any description of the synlophe. The type species is *Neoheligmonella houini* (Durette-Desset, 1970), a parasite of *Arvicanthis niloticus* (E. Geoffroy, 1803) from Ethiopia.

The genus was defined by the following main elements: 1) synlophe with an axis of orientation of the ridges directed from the right ventral line, to the left dorsal line; hypertrophied lateral ridges; a latero-median gradient in ridge size oriented from right to left on dorsal surface and from left to right on ventral surface; about thirteen cuticular ridges. 2) bursa subsymmetrical; rays 8 arising proximally on dorsal ray, often parallel to it (Durette-Desset 1971).

Since 1971, twelve other species have been assigned to the genus *Neoheligmonella*, all of them parasites of murids from the Ethiopian Region, with the exception of one species from the Philippines. However, the species composition of the genus is at present very heterogeneous, mainly due to considerable variability in the synlophe. Thus it seems that the generic definition was sufficiently ambiguous to allow the inclusion of species with very different synlophes: for instance some species show striking different characters, such as the presence of a careen, whereas in other species it is absent. However both groups of species could fit into the original definition of the genus, in which the presence or absence of a careen had not been taken into account. In other cases the specific characters simply do not match the generic definition (species with lateral ridges not hypertrophied and/or without gradient of size).

The taxonomy of the Trichostrongylina Durette-Desset & Chabaud, 1993 and particularly of the Heligmonellidae is defined essentially by the synlophe (Durette-Desset 1971, 1985; Durette-Desset

et al. 1994). The characters provided by this structure are numerous. However, some of them have not been utilised in the taxonomy at the supraspecific level. In a revision of the Heligmonellidae, it seemed to us necessary to review the specific composition of the genus *Neoheligmonella*, and to attempt to group its species into new possible supraspecific taxa. This was based mainly on characters of the synlophe, the bursa being relatively uniform within the group.

MATERIAL AND METHODS

Methodology

The data were taken from published descriptions, since 21 of the 23 species treated in this work were studied previously on the original material by at least one of the authors (see Table 1). The species of which the synlophe could be analyzed were the following (with reference to type material in parentheses): *N. houini* (MNHN 127 JJ), *N. acomysi* Durette-Desset & Gibson, 1990 (MNHN 943 MC); *N. bai* Diouf & Durette-Desset, 2002 (MHHN 404 HFa); *N. bainae* Durette-Desset, 1970 (MNHN 766 M); *N. capensis* (Ortlepp, 1939) (NCAH, accession number not provided); *N. dielmensis* Diouf, Bâ & Durette-Desset, 1997 (MNHN 391 HFa); *N. dossoi* Durette-Desset & Cassone, 1986 (MNHN 155 KG); *N. granjoni* Durette-Desset, Brouat, Diouf & Duplantier, 2008 (MNHN 599 KXa); *N. heimi* (Desset, 1964) (MNHN 190S); *N. lamaensis* Diouf, Daouda & Durette-Desset, 2005 (MNHN 668 KQc); *N. lemniscomysi* (Durette-Desset, 1970) (MNHN 76 Sa); *N. mastomysi* Diouf, Bâ & Durette-Desset, 1998 (CS B6); *N. orientalis* Asakawa, Kamiya & Ohbayashi, 1986 (Dept. of Parasitology, Faculty of Veterinary Medicine, Hokkaido, Japan, accession number not provided); *N. pseudospira* (Durette-Desset, 1970) (MNHN 127 JJ); *N. schauenbergi* Vaucher & Durette-Desset, 1984 (MHNG 982.1562/3); *N. skirringi* Diouf, Bâ & Durette-Desset, 1998 (CS A20); *N. tranieri* Durette-Desset & Cassone, 1986 (MNHN 155 KG); *N. zera* Diouf, Duplantier & Durette-Desset, 2005 (ZIT/IFAN 051). Species of which the synlophe could not be described were: *N. kenyae* (Yeh, 1958) (Helminthological Collection, London School of Hygiene and Tropical Medicine, UK, accession number not provided), and four species deposited in the Helminthological Collections of the NHM: *N. affinis* (Baylis, 1928) ex *Mastomys erythroleucus* without no.; *N. gracilis* (Baylis, 1928) ex *Mus* (*Nannomys*) *musculoides* no. 411, slides 104, 105, 106, 108; *N. impudica* (Baylis, 1928) ex *Gerbilliscus* (*Taterona*) *kempi* no. 404, slide 77; *Neoheligmonella moennigi* (Baylis, 1928) ex *Praomys tullbergi* no. 189, slides 63, 64.

The methods for the study and the description of the synlophe follow the criteria provided by Durette-Desset (1985) and Durette-Desset & Digiani (2005a) and the description of the bursa follows Durette-Desset & Digiani (2012). The main synlophe characters used to separate the different genera were the following: 1) presence or absence of a careen; 2) relative size of the ridges of the careen and the right ridge; 3) size of the left ridge relative to the right ridge (if careen was absent); and 4) presence or absence of gradients in ridge size. The terms "right ridge" and "left ridge" when used in the singular indicate the single ridge situated in front of the right and the left lateral fields, respectively. The lateral fields surround the lateral hypodermal chords and may be more or less well developed according to the genera.

Abbreviations

Institutions

CS	Collection de Biologie Animale, Université Cheikh Anta Diop, Dakar;
MHNG	Muséum d'Histoire naturelle, Genève;
MNHN	Muséum national d'Histoire naturelle, Paris;
NCAH	National Collection of Animal Helminths, Onderstepoort;
NHM	Natural History Museum, London;
ZIT/IFAN	Laboratoire de Zoologie des Invertébrés Terrestres/Institut fondamental d'Afrique noire Cheikh Anta Diop, Dakar.

Other abbreviations

SpL/BL	proportion of the spicule length on the body length;
Ut/BL	proportion of the uterus length on the body length.

MAIN SYNLOPHE CHARACTERS

Presence or absence of a careen

All known synlophes of *Neoheligmonella* spp. with the exception of *N. lemniscomysi* (Fig. 1C) show a hypertrophied or large left ridge (Fig. 1A, B, D). In several species this ridge, together with the adjacent dorsal ridge form a careen supporting a left dorsal dilatation of the cuticle (Fig. 1A, B). The dorsal ridge of the careen is large but generally smaller than the ventral ridge. Species having a careen are: *N. houini* (type species), *N. bai*, *N. bainae*, *N. capensis*, *N. dielmensis*, *N. granjoni*, *N. heimi*, *N. lamaensis*, *N. mastomysi*, *N. schauenbergi*, *N. skirringi*, *N. tranieri,* and *N. zera*.

Development of the right ridge

The right ridge shows disparate degrees of development in the different species: in a first group (*N. acomysi*, *N. dossoi* and *N. pseudospira*) (Fig. 1D) it is hypertrophied to the same size as the left ridge; in a second group (*N. houini*, *N. bai*, *N. capensis*, *N. dielmensis*, *N. heimi*, *N. schauenbergi*) (Fig. 1A) it is well developed and larger than the adjacent dorsal ridges; in a third group (*N. bainae*, *N. granjoni*, *N. lamaensis*, *N. lemniscomysi, N. mastomysi*, *N. skirringi*, *N. tranieri*) (Fig. 1B) it is developed to about the same size as the adjacent dorsal ridges. It is even smaller than the adjacent dorsal ridges in *N. zera.* The dorsal right ridges are small in *N. zera* and in species of the first and third groups; they are better developed in species of the second group.

Presence of gradients in ridge size

Gradient(s) in the ridge size may be present or absent among the different species. On the right dorsal quadrant a latero-median gradient is present in *N. houini*, *N. bai*, *N. capensis*, *N. dielmensis*, *N. granjoni*, *N. heimi*, *N. lamaensis* (female), *N. mastomysi* (male) and *N. schauenbergi* (Fig. 1A). This gradient is absent in *N. acomysi, N. bainae, N. dossoi, N. lemniscomysi, N. pseudospira, N. skirringi, N. tranieri* and *N. zera* (Fig. 1B-D). On the left ventral quadrant, a latero-median gradient is absent in *N. lemniscomysi* (Fig. 1C), *N. mastomysi* (male), *N. pseudospira,* and *N. tranieri*, but it is present in the other species (Fig. 1A, B, D).

Remarks

Some of the characters mentioned above appear to be associated. An example includes the presence of a hypertrophied right ridge, which is associated with the lack of a dorsal gradient and the absence of a careen. On the other hand, in the species having a careen, the right ridge may be more or less well developed but it is never hypertrophied. This is also generally associated with the presence/absence of a dorsal gradient in ridge size: when the right ridge is larger, usually a dorsal gradient is present. The presence of a ventral size gradient is, on the contrary, more variable.

SYSTEMATICS

Genus *Neoheligmonella* Durette-Desset, 1971

Diagnosis. — Heligmonellidae, Nippostrongylinae. Synlophe with 13-15 ridges at mid-body in both sexes (except *Neoheligmonella* (*Duplantierus*) *tranieri*, with 13 ridges in proximal part and 22-29 at mid-body). Careen made up of two ridges of which ventral longer. On dorsal right quadrant, latero-median gradient in ridge size present or absent. On ventral left quadrant, latero-median gradient in ridge size present. Ridges of right ventral quadrant smallest. Axis(es) of orientation oblique. Bursa subsymmetrical. Characteristic bursal pattern of type 2-3 tending to 2-2-1. Dorsal ray generally divided within distal half. Spicules ending in one tip. SpL/BL 5-16%. Ut/BL 14-26%. Parasites mainly of Ethiopian Muridae.

Subgenus *Neoheligmonella* (*Neoheligmonella*) Durette-Desset, 1971 (Fig. 1A)

Diagnosis. — Careen present along whole body. Right ridge measuring 45% or more (usually 45%-80%) of the ventral ridge of the careen. On right dorsal quadrant, latero-median gradient in ridge size present.

Type species. — *Longistriata houini* (Durette-Desset, 1970).

Hosts. — Muridae.

Host site. — Small intestine.

Distribution. — Central African Republic, Ethiopia, Republic of South Africa, Senegal, Philippines.

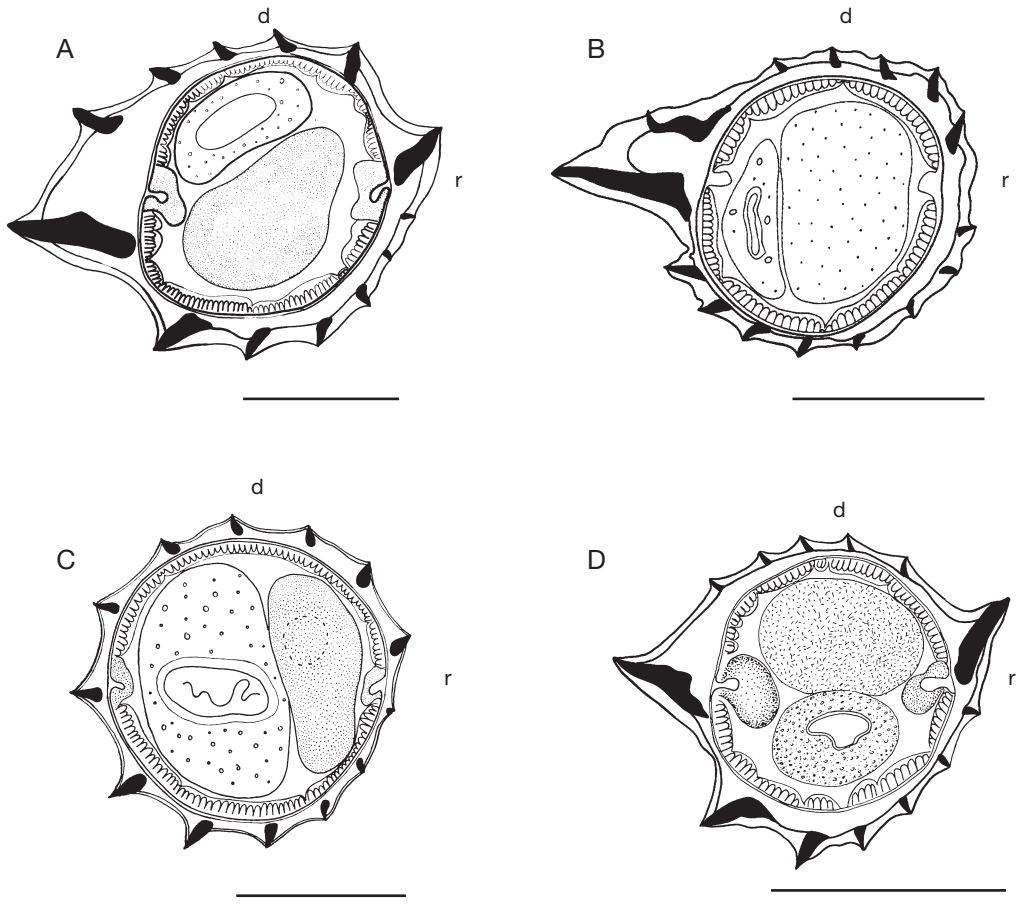

FIG. 1. — Synlophes of females at mid-body: **A**-**C**, after Durette-Desset (1970), modified; **A**, *Neoheligmonella* (*Neoheligmonella*) based on *Neoheligmonella* (*Neoheligmonella*) *houini* (Durette-Desset, 1970); **B**, *Neoheligmonella* (*Duplantierus*) n. subgen. based on *Neoheligmonella* (*Duplantierus*) *bainae* (Durette-Desset, 1970); **C**, *Dioufnema* n. gen. based on *Dioufnema lemniscomysi* (Durette-Desset, 1970) n. comb.; **D**, after Durette-Desset & Cassone (1986) modified, *Taranchonema* n. gen. based on *Taranchonema dossoi* (Durette-Desset & Cassone, 1986) n. comb. Abbreviations: **r**, right side; **d**, dorsal side. Scale bars: 50 µm.

OTHER SPECIES. — *N.* (*N.*) *bai* Diouf & Durette-Desset, 2002; *N.* (*N.*) *capensis* (Ortlepp, 1939); *N.* (*N.*) *dielmensis* Diouf, Bâ & Durette-Desset, 1997; *N.* (*N.*) *heimi* (Desset, 1964); *N.* (*N.*) *schauenbergi* Vaucher & Durette-Desset, 1984.

Subgenus *Duplantierus* n. subgen. (Fig. 1B)

DIAGNOSIS. — Careen present at least within proximal part of body. Right ridge measuring less than 45% (usually 25-45%) of the ventral ridge of the careen. On right dorsal quadrant, latero-median gradient in ridge size present or absent.

TYPE SPECIES. — *Longistriata bainae* Durette-Desset, 1970, by original designation.

HOSTS. — Muridae, Nesomyidae.

HOST SITE. — Small intestine.

DISTRIBUTION. — Benin, Burkina Faso, Cameroon, Senegal.

ETYMOLOGY. — This subgenus is named in honour of Dr. Jean-Marc Duplantier (Campus International

TABLE 1. — List of the species belonging to the former genus *Neoheligmonella* Durette-Desset, 1971 with their new systematic position, host-spectrum and biogeographical distribution. Symbols: *, Muridae, except where indicated; **, Nesomyidae; ***, Cricetidae; †, Republic of South Africa; ‡, Central African Republic.

Species	Reference(s)	Position after this work	Host(s)*	Distribution
N. acomysi Durette-Desset & Gibson, 1990	Durette-Desset & Gibson (1990)	*Taranchonema acomysi* n. comb.	*Acomys*	Somalia
N. affinis (Baylis, 1928)	Baylis (1928) Durette-Desset & Digiani (2010)	sp. incertae sedis	*Mastomys*	Nigeria
N. bai Diouf & Durette-Desset, 2002	Diouf & Durette-Desset (2002)	*N.* (*Neoheligmonella*) *bai*	*Arvicanthis*	Senegal
N. bainae (Durette-Desset,1970)	Durette-Desset (1970)	*N.* (*Duplantierus*) *bainae*	*Steatomys***	Burkina Faso
N. capensis (Ortlepp, 1939)	Ortlepp (1939) Durette-Desset & Digiani (2005b)	*N.* (*Neoheligmonella*) *capensis*	*Rhabdomys*	RSA†
N. dielmensis Diouf, Bâ & Durette-Desset, 1997	Diouf *et al.* (1997)	*N.* (*Neoheligmonella*) *dielmensis*	*Arvicanthis*	Senegal
N. dossoi Durette-Desset & Cassone, 1986	Durette-Desset & Cassone (1986)	*Taranchonema dossoi* n. comb.	*Uranomys*	Ivory Coast
N. gracilis (Baylis, 1928)	Baylis (1928) Durette-Desset & Digiani (2010)	sp. incertae sedis	*Mus* (*Nannomys*)	Nigeria
N. granjoni Durette-Desset, Brouat, Diouf & Duplantier, 2008	Durette-Desset *et al.* (2008)	*N.* (*Duplantierus*) *granjoni*	*Mastomys*	Senegal
N. heimi (Desset,1964)	Desset (1964)	*N.* (*Neoheligmonella*) *heimi*	*Praomys*	CAR‡
N. houini (Durette-Desset,1970)	Durette-Desset (1970)	*N.* (*Neoheligmonella*) *houini*	*Arvicanthis*	Ethiopia
N. impudica (Baylis, 1928)	Baylis (1928) Durette-Desset & Digiani (2010)	sp. incertae sedis	*Gerbilliscus* *Arvicanthis*	Nigeria
N. kenyae (Yeh, 1958)	Yeh (1958)	sp. incertae sedis	*Rattus*	Kenya
N. lamaensis Diouf, Daouda & Durette-Desset, 2005	Diouf *et al.* (2005a)	*N.* (*Duplantierus*) *lamaensis*	*Mastomys*	Benin
N. lemniscomysi (Durette-Desset,1970)	Durette-Desset (1970)	*Dioufnema lemniscomysi* n. comb.	*Lemniscomys*	Gabon
N. mastomysi Diouf, Bâ & Durette-Desset, 1998	Diouf *et al.* (1998)	*N.* (*Duplantierus*) *mastomysi*	*Mastomys*	Senegal
N. moennigi (Baylis, 1928)	Baylis (1928) Durette-Desset & Digiani (2010)	sp. incertae sedis	*Praomys* *Malacomys* *Cricetomys***	Nigeria
N. orientalis Asakawa, Kamiya & Ohbayashi, 1986	Asakawa *et al.* (1986)	Close to *Yatinema* Asakawa & Ohbayashi, 1986	*Eothenomys****	Thailand
N. pseudospira (Durette-Desset,1970)	Durette-Desset (1970)	*Taranchonema pseudospira* n. comb.	*Arvicanthis*	Ethiopia
N. schauenbergi Vaucher & Durette-Desset, 1984	Vaucher & Durette-Desset (1984)	*N.* (*Neoheligmonella*) *schauenbergi*	*Phleomys*	Philippines
N. skirringi Diouf, Bâ & Durette-Desset, 1998	Diouf *et al.* (1998)	*N.* (*Duplantierus*) *skirringi*	*Mastomys*	Senegal
N. tranieri Durette-Desset & Cassone, 1986	Durette-Desset & Cassone (1986)	*N.* (*Duplantierus*) *tranieri*	*Uranomys*	Ivory Coast
N. zera Diouf, Duplantier & Durette-Desset, 2005	Diouf *et al.* (2005b)	*N.* (*Duplantierus*) *zera*	*Arvicanthis*	Cameroon

Baillarguet, Montpellier, France) in recognition of his valuable contribution to the knowledge of the Ethiopian murids.

OTHER SPECIES. — *N.* (*Duplantierus) granjoni* Durette-Desset, Brouat, Diouf & Duplantier, 2008; *N.* (*Duplantierus) lamaensis* Diouf, Daouda & Durette-Desset, 2005; *N.* (*Duplantierus) mastomysi* Diouf, Bâ & Durette-Desset, 1998; *N.* (*Duplantierus) skirringi* Diouf, Bâ & Durette-Desset, 1998; *N.* (*Duplantierus) tranieri* Durette-Desset & Cassone, 1986; *N.* (*Duplantierus) zera* Diouf, Duplantier & Durette-Desset, 2005.

Genus *Dioufnema* n. gen.
(Fig. 1C)

DIAGNOSIS. — Heligmonellidae, Nippostrongylinae. Synlophe with 13 ridges at mid-body in both sexes. Careen absent. No ridges hypertrophied or especially developed. Left ridge and right ridge small, of similar size to dorsal ridges. Gradients in ridge size absent. Ridges on left ventral quadrant largest, ridges on ventral right quadrant smallest. Axis of orientation oblique. Bursa slightly dissymmetrical. Characteristic bursal pattern of type 1-3-1. Dorsal ray divided at mid-length. Spicules ending in one tip. SpL/BL 10%. UtL/BL 12%. Parasites of Ethiopian Muridae.

TYPE SPECIES. — *Longistriata lemniscomysi* Durette-Desset, 1970 by monotypy.

HOSTS. — Muridae.

HOST SITE. — Small intestine.

DISTRIBUTION. — Central African Republic.

ETYMOLOGY. — This genus is named in honour of Dr. Malick Diouf (University of Dakar, Senegal) in recognition of his valuable contribution to the knowledge of the Ethiopian Nippostrongylinae.

Dioufnema lemniscomysi
(Durette-Desset, 1970) n. comb.

Longistriata lemniscomysi Durette-Desset, 1970: 133.

Neoheligmonella lemniscomysi – Durette-Desset 1971: 67.

Genus *Taranchonema* n. gen.
(Fig. 1D)

DIAGNOSIS. — Heligmonellidae, Nippostrongylinae. Synlophe with 13-14 ridges at mid-body in both sexes. Careen absent. Left ridge and right ridge very large. On dorsal side, ridges of similar size. On ventral left quadrant, latero-median gradient in ridge size present or absent, ridges on right ventral quadrant smallest. Axis of orientation oblique. Bursa subsymmetrical. Characteristic bursal pattern of type 2-3 tending to 2-2-1. Dorsal ray divided within distal third. Spicules ending in one tip. SpL/BL 7.4-8.7%. Ut/BL 12.8-18.9%. Parasites of Ethiopian Muridae.

TYPE SPECIES. — *Neoheligmonella acomysi* Durette-Desset & Gibson, 1990, by original designation.

HOSTS. — Muridae.

HOST SITE. — Small intestine.

DISTRIBUTION. — Ethiopia, Ivory Coast, Somalia.

ETYMOLOGY. — This genus is named in honour of Mr Pierre Taranchon (MNHN) for his gracious help in the management of the Helminthological Collections of the MNHN during ten years.

Taranchonema acomysi
(Durette-Desset & Gibson, 1990) n. comb.

Neoheligmonella acomysi Durette-Desset & Gibson, 1990: 111.

Taranchonema dossoi
(Durette-Desset & Cassone, 1986) n. comb.

Neoheligmonella dossoi Durette-Desset & Cassone, 1986: 566.

Taranchonema pseudospira
(Durette-Desset, 1970) n. comb.

Longistriata pseudospira Durette-Desset, 1970: 131.

Neoheligmonella pseudospira – Durette-Desset 1971: 67.

DISCUSSION

The different associations of characters observed allowed us to group the species treated in four groups: 1) species with a careen, with the right ridge well developed and larger than the adjacent dorsal ridges but not hypertrophied, and with a dorsal gradient in ridge size (six species, including the type species); 2) Species with a careen, with the right ridge of similar size to the adjacent dorsal ridges, and the absence of a dorsal gradient in ridge size (seven species); 3) Species without a careen, with the left ridge and the right ridge hypertrophied and a dorsal size gradient in ridge size absent (three species); and 4) Species without a careen, with the right ridge poorly developed and a dorsal size gradient in ridge size absent (one species). This lead us to propose the splitting of the former genus *Neoheligmonella* into three genera: *Neoheligmonella* Durette-Desset, 1971 with two subgenera: *Neoheligmonella* (*Neoheligmonella*) and *Neoheligmonella* (*Duplantierus*) n. subgen., *Taranchonema* n. gen. and *Dioufnema* n. gen. We proposed two subgenera in *Neoheligmonella* rather than recognizing them as genera since they are differentiated by only one character of the synlophe.

Key to the new genera and subgenera

1. Careen absent 2
— Careen present 3

2. Left ridge and right ridge small. 13 ridges in both sexes. Bursal pattern of type 1-3-1. Bursa dissymmetrical. Rays 8 arising at base of dorsal ray. Parasites of *Lemniscomys* from Gabon ..... *Dioufnema* n. gen.
— Left ridge and right ridge large to about the same size. 13-14 ridges in both sexes. Bursal pattern of type 2-3 tending to 2-2-1 or 2-2-1. Bursa subsymmetrical. Rays 8 arising within median third of dorsal ray. Parasites of *Acomys, Uranomys, Arvicanthis* from Somalia, Ivory Coast, Ethiopia ..... *Taranchonema* n. gen.

3. Right ridge measuring at maximum 45% of ventral ridge of careen. Dorsal gradient absent. Parasites of *Steatomys, Mastomys, Arvicanthis, Uranomys* from Benin, Burkina Faso, Senegal, Ivory Coast, Cameroon ..... *Neoheligmonella* (*Duplantierus*) n. subgen.
— Right ridge measuring at least 45% of ventral ridge of careen. Dorsal gradient generally present. Parasites of *Arvicanthis, Rhabdomys, Praomys, Phloeomys* from Central African Republic, Ethiopia, Senegal, Republic of South Africa, Philippines .... *Neoheligmonella* (*Neoheligmonella*)

The Table 1 provides a list of the species belonging to the former genus *Neoheligmonella*, along with their new proposed generic position, host spectrum and biogeographical distribution. The list also includes species *incertae sedis* of which the synlophe is unknown. These species cannot be placed in the generic arrangement proposed above, however their validity was confirmed by Durette-Desset & Digiani (2010), based on other diagnostic characters at the specific level, such as the spicule length, SpL/BL or characters of the ovejector in females. For this reason we also provide a key to these species awaiting knowledge of their synlophes.

The species described as *Neoheligmonella orientalis* Asakawa, Kamiya & Ohbayashi, 1986, parasitic in *Eothenomys melanogaster* (Milne-Edwards, 1871) from Thailand is characterized by 15-25 ridges at mid-body, a very large careen and three right ridges larger than the dorsal and ventral ridges. It was not possible to relate this species to any of the genera defined above. It is probably related to the genus *Yatinema* Asakawa & Ohbayashi, 1986, mainly parasitic in *Eothenomys* spp. from Japan and its systematic position will be treated in another work.

KEY TO SPECIES INCERTAE SEDIS PLACED IN THE FORMER GENUS *NEOHELIGMONELLA*

1. SpL/BL 12-14%. Parasites of *Mastomys erythroleucus* from Nigeria ..... *N. affinis* (Baylis, 1928)
— SpL/BL less than 12% or more than 14% 2

2. Bursal pattern of type 2-2-1 Parasites of *Rattus rattus* from Kenya ..... *N. kenyae* (Yeh, 1958)
— Bursal pattern of type 2-3 tending to 2-2-1 3

3. Dorsal ray medium-sized, divided within median length, rays 9 not curved, female tail thin. Parasite of *Mus* (*Nannomys*) *musculoides* from Nigeria ..... *N. gracilis* (Baylis, 1928)
— Dorsal ray long, divided within distal extremity, rays 9 curved, female tail thick 4

4. SpL/BL less than 10%. Parasites of *Gerbilliscus* (*Taterona*) *kempi* and *Arvicanthis* spp. from Nigeria ..... *N. impudica* (Baylis, 1928)
— SpL/BL more than 20%. Parasites of *Praomys tullbergi, Malacomys edwardsi* and *Cricetomys emini* from Nigeria ..... *N. moennigi* (Baylis, 1928)

Acknowledgements

To Didier Kuriyama (Pôle Dessin, UMS 2700, MNHN) for the iconography. We are also grateful to Dr Agustín Jiménez and other anonymous reviewer for the constructive comments and suggestions.

REFERENCES

ASAKAWA M., KAMIYA M. & OHBAYASHI M. 1986. — Studies on the parasite fauna of Thailand 6. Three new heligmonellid nematodes from Père David's vole, *Eothenomys melanogaster* (Milne-Edwards). *Japanese Journal of Veterinary Research* 34: 219-231.

BAYLIS H. A. 1928. — On a collection of nematodes from Nigerian mammals (chiefly rodents). *Parasitology* 20: 280-304.

DESSET M.-C. 1964. — Les systèmes d'arêtes cuticulaires chez les Nématodes Héligmosomes. Étude de cinq espèces parasites de Rongeurs de La Maboké. *Cahiers de La Maboké* 2: 39-78.

DIOUF M. & DURETTE-DESSET M.-C. 2002. — Two new species of Nippostrongylinae (Nematoda, Trichostrongylina) parasites of *Cricetomys gambianus* and *Arvicanthis niloticus* (Muridae) from Senegal. *Parassitologia* 44: 97-101.

DIOUF M., BÀ C. T. & DURETTE-DESSET M.-C. 1997. — Deux nouveaux Nippostrongylinae (Nematoda-Trichostrongylina) parasites de Muridés du Sénégal. *Zoosystema* 19 (2-3): 223-231.

DIOUF M., BÀ C.T. & DURETTE-DESSET M.-C. 1998. — Deux nouveaux *Neoheligmonella* (Nematoda-Trichostrongylina) parasites de *Mastomys erythroleucus* au Sénégal. *Zoosystema* 20 (1): 23-30.

DIOUF M., DAOUDA I. & DURETTE-DESSET M.-C. 2005a. — Two new species of Nippostrongylinae (Nematoda, Trichostrongylina, Heligmonellidae) coparasites of *Mastomys natalensis* (Muridae, Murinae) from Benin. *Zoosystema* 27 (1): 27-35.

DIOUF M., DUPLANTIER J. M. & DURETTE-DESSET M.-C. 2005b. — Description of two new species of Nippostrongylinae (Nematoda, Trichostrongylina, Heligmosomoidea) coparasites of *Arvicanthis ansorgei* (Muridae). *Parasite* 12: 195-202.

DURETTE-DESSET M.-C. 1970. — Les systèmes d'arêtes cuticulaires chez les Nématodes Héligmosomes. IV. Cinq nouvelles espèces, parasites de Rongeurs africains. *Cahiers de La Maboké* 8: 125-137.

DURETTE-DESSET M.-C. 1971. — Essai de classification des Nématodes Héligmosomes. Corrélation avec la paléobiogéographie des hôtes. *Mémoires du Muséum national d'Histoire naturelle*, nouvelle série, A, Zoologie 49: 1-126.

DURETTE-DESSET M.-C. 1985. — Trichostrongyloid nematodes and their Vertebrate hosts: reconstruction of the phylogeny of a parasitic group. *Advances in Parasitology* 24: 239-306.

DURETTE-DESSET M.-C. & CASSONE J. 1986. — Sur deux Nématodes Trichostrongyloïdes parasites d'un Muridé africain. I. Description des adultes. *Annales de Parasitologie Humaine et Comparée* 61: 565-574.

DURETTE-DESSET M.-C. & GIBSON D. I. 1990. — *Neoheligmonella acomysi* n. sp. (Trichostrongyloidea, Nippostrongylinae), parasite d'*Acomys dimidiatus* (Muridae) de Somalie. *Systematic Parasitology* 17: 109-113.

DURETTE-DESSET M.-C. & DIGIANI M. C. 2005a. — The axis of orientation of the synlophe in the Heligmosomoidea (Nematoda, Trichostrongylina): a new approach. *Parasite* 12: 195-202.

Durette-Desset M.-C. & Digiani M. C. 2005b. — The systematic position of some Ethiopian Nippostrongylinae (Nematoda, Trichostrongylina, Heligmosomoidea) from the National Collection of Animal Helminths, Onderstepoort, South Africa. *Onderstepoort Journal of Veterinary Research* 72: 55-65.

Durette-Desset M.-C. & Digiani M. C. 2010. — Taxonomic revision of the type specimens of Ethiopian Nippostrongylinae (Nematoda) deposited at the Natural History Museum of London. *Zootaxa* 2494: 1-28.

Durette-Desset M.-C. & Digiani M. C. 2012. — The caudal bursa in the Heligmonellidae (Nematoda:Trichostrongylina). Characterization and hypothesis on its evolution. *Parasite* 19: 3-18.

Durette-Desset M.-C., Beveridge I. & Spratt D. 1994. — The origin and evolutionary expansion of the Strongylida (Nematoda). *International Journal for Parasitology* 24: 1077-1344.

Durette-Desset M.-C., Brouat C., Diouf M. & Duplantier J. M. 2008. — Description of two new species of Nippostrongylinae (Nematoda, Heligmonellidae) coparasites in three sympatric species of *Mastomys* spp. (Rodentia, Muridae) from Senegal. *Parasite* 15: 539-551.

Ortlepp R. J. 1939. — South African Helminths, Part VI. Some helminths, chiefly from rodents. *Onderstepoort Journal of Veterinary Science and Animal Industry* 12: 75-101.

Vaucher C. & Durette-Desset M.-C. 1984. — *Neoheligmonella schauenbergi* n. sp. (Nematoda: Trichostrongyloidea) parasite du Rat de Cuming *Phloeomys cumingi* Waterhouse. *Revue Suisse de Zoologie* 90: 935-938.

Yeh L. S. 1958. — On a new bursate nematode, *Longistriata kenyae* sp. nov. from the house rat, *Rattus rattus kijabius* in Kenya and the erection of a new genus *Longistrioides*. *Journal of Helminthology* 32: 89-92.

Submitted on 17 April 2013;
accepted on 9 August 2013;
published on 27 December 2013.