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Taxonomic revision of the Nippostrongylinae (Nematoda, Heligmonellidae) parasitic in Oriental Muridae. The genus *Paraheligmonelloides* Fukumoto, Kamiya & Suzuki, 1980

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Abstract

The genus *Paraheligmonelloides* Fukumoto, Kamiya and Suzuki, 1980 (Nippostrongylinae) is revised and split into four genera, mainly based on characters of the synlophe not previously considered at the supraspecific level. These characters mainly include the homology of the left ridge with ridge 1', the relative size of the right ridge to the left ridge and to ridge 1' and the distribution of the largest ridges. *Paraheligmonelloides sensu stricto*, characterized by the homology of the left ridge with ridge 1', contains only the type species, *Paraheligmonelloides kenyensis* Fukumoto, Kamiya and Suzuki, 1980, parasitic in a lagomorph from Kenya. *Krishnasamyos* n. gen., characterized by ridge 1' forming a comarete, two minute left ventral ridges and ridge 1 larger than other dorsal ridges, only includes the species *Krishnasamyos triangulus* n. comb., parasitic in Malaysian murids. *Hughjonestrongylus* n. gen., characterized by numerous ridges markedly unequal in size, with the largest ridges grouped in relation to the lateral fields, includes *Hughjonestrongylus ennisae* n. comb., *Hughjonestrongylus amplicaudae* n. comb., *Hughjonestrongylus mirzai* n. comb., and *Hughjonestrongylus singauwaensis* n. comb., all parasitic in murids from Papua Indonesia and Papua New Guinea. *Syafruddinema* n. gen., characterized by ridge 1 as long as other dorsal ridges and a gap associated with the left lateral field, between ridges 2' and 3', includes *Syafruddinema paruromyos* n. comb., *Syafruddinema annandalei* n. comb., and *Syafruddinema eropeplios* n. comb., parasitic in murids from Malaysia and Indonesia. A key to the proposed genera is provided.

Key words: Trichostrongylina; synlophe, *Paraheligmonelloides s. str.*, *Krishnasamyos* n. gen., *Hughjonestrongylus* n. gen., *Syafruddinema* n. gen., Kenya; Indonesia, Malaysia, Papua Indonesia, Papua New Guinea.

Introduction

The taxonomy of the Trichostrongylina and particularly of the Heligmonellidae is defined essentially by the synlophe (Durette-Desset 1971, 1985; Durette-Desset *et al*. 1994), a complex cuticular structure in which numerous characters are involved. Moreover, the continuous discovery of new species within this group is constantly providing new elements which are incorporated into the descriptions, but some of them also providing useful characters to be considered in the taxonomy at the supraspecific level. In reviewing the definition and specific composition of certain genera of Nippostrongylinae (Digiani & Durette-Desset 2013), it was found that some generic definitions are too general and not accurate enough in defining the characters provided by the synlophe, a fact which is not consistent with the complexity of this structure. This means that, in certain genera, the inclusion of species with very different synlophes is sometimes allowed by ambiguous generic definitions.

The genus *Paraheligmonelloides* Fukumoto, Kamiya & Suzuki, 1980 (Heligmonellidae, Nippostrongylinae) was erected to classify a species parasitic in a leporid from Kenya, although the species subsequently described in the genus are parasitic in Muridae from South East Asia and the Australasian Region. Fukumoto *et al*. (1980) defined *Paraheligmonelloides* as follows: "Synlophes (sic) consist of 15 aretes, 2 lateral ones comparatively larger,

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in the cross section at middle region of the body. Dorsal synlophes continuous. Externodorsal rays arise from the base of dorsal rays (sic). Dorsal rays divided at their base. Spicules well sclerotized. Gubernaculum large. Female unknown."

This is one example in which the generic definition is too superficial with respect to the characters of the synlophe. As a result, the present species composition of the genus is rather heterogeneous: besides the type species, it includes eight other species from Malaysia, Indonesia and Papua New Guinea (Ow-Yang *et al*. 1983, Hasegawa *et al*. 1999, Smales 2009, Smales & Heinrich 2010), species in which the synlophe shows considerable variability.

In a revision of the Heligmonellidae, it seemed necessary to us to review the specific composition of the genus *Paraheligmonelloides*, and to attempt to group its species into new possible supraspecific taxa. This was based mainly on the characters of the synlophe.

Material and methods

The data were compiled from the published descriptions. The species whose synlophe could be analyzed were: *Paraheligmonelloides kenyensis* Fukumoto, Kamiya & Suzuki, 1980 (type species), *Paraheligmonelloides amplicaudae* Smales & Heinrich, 2010, *Paraheligmonelloides annandalei* Ow-Yang, Durette-Desset & Ohbayashi, 1983, *Paraheligmonelloides ennisae* Smales & Heinrich, 2010, *Paraheligmonelloides eropeplios* Hasegawa, Miyata & Syafruddin, 1999, *Paraheligmonelloides paruromyos,* Hasegawa, Miyata & Syafruddin, 1999, *Paraheligmonelloides singauwaensis* Smales, 2009, *Paraheligmonelloides triangulus* Ow-Yang, Durette-Desset & Ohbayashi, 1983 and *Paraheligmonelloides* sp. Smales, 2011. *Paraheligmonelloides rajah* Ow-Yang, Durette-Desset & Ohbayashi, 1983, whose synlophe at mid-body was not described or illustrated, was not included in the study.

The methods for the study and description of the synlophe follow the terms and criteria provided by Durette-Desset (1985) and Durette-Desset and Digiani (2005). The description of the bursa follows Durette-Desset and Digiani (2012). The terms "right ridge" and "left ridge" when used in the singular indicate the single ridge situated in front of the right and left lateral fields, respectively. "Right ridge" and "left ridge" are then morphological concepts. When an axis of orientation of the ridges (AO) is present, the ridges are numbered from left to right and in relation to this axis: from 1 to *n* for the ridges dorsal to the AO, from 1' to *n*' for the ridges ventral to the AO. The AO corresponds in fact to an imaginary plane which separates the cuticular ridges into two groups with tips pointing in opposing directions. "ridge 1" and "ridge 1'" are then functional concepts.

The main synlophe characters analyzed and eventually used to separate the different genera were the following: (1) homology of ridge 1' with the left ridge (2) development of the left ridge and right ridge, (3) relative size of ridge 1' and the right ridge, (3) relative size of the left ridge and right ridge, (4) presence or absence of gradients in ridge size, (5) position of the largest ridges (6) presence or absence of symmetry of the ridges (in number and/or size) with respect to the axis of orientation.

Other characters, especially of the bursa and spicules were included in the new generic definitions. The abbreviation SpL/BL stands for the proportion (in percentage) of the spicule length on the body length. The nomenclature of the hosts and their taxonomy at suprageneric level follows Wilson & Reeder (2005).

Results

Main synlophe characters

Homology of ridge 1' with the left ridge. Ridge 1' is the left ridge in *P. kenyensis* (Fig. A). In all the other species ridge 1' is distinct from the left ridge and it is situated above, on the left dorsal quadrant (Figs. B, C, D).

Development of ridge 1'. It is small in *P. amplicaudae,* medium-sized in *P. ennisae*, *P. kenyensis*, *P. singauwaensis*, and *Paraheligmonelloides* sp. (Figs. A, C), and small and thin in *P. annandalei, P. eropeplios* and *P. paruromyos* (Fig. D). It appears thick in *P. triangulus*, ridge 1' forming a comarete (Fig. B).

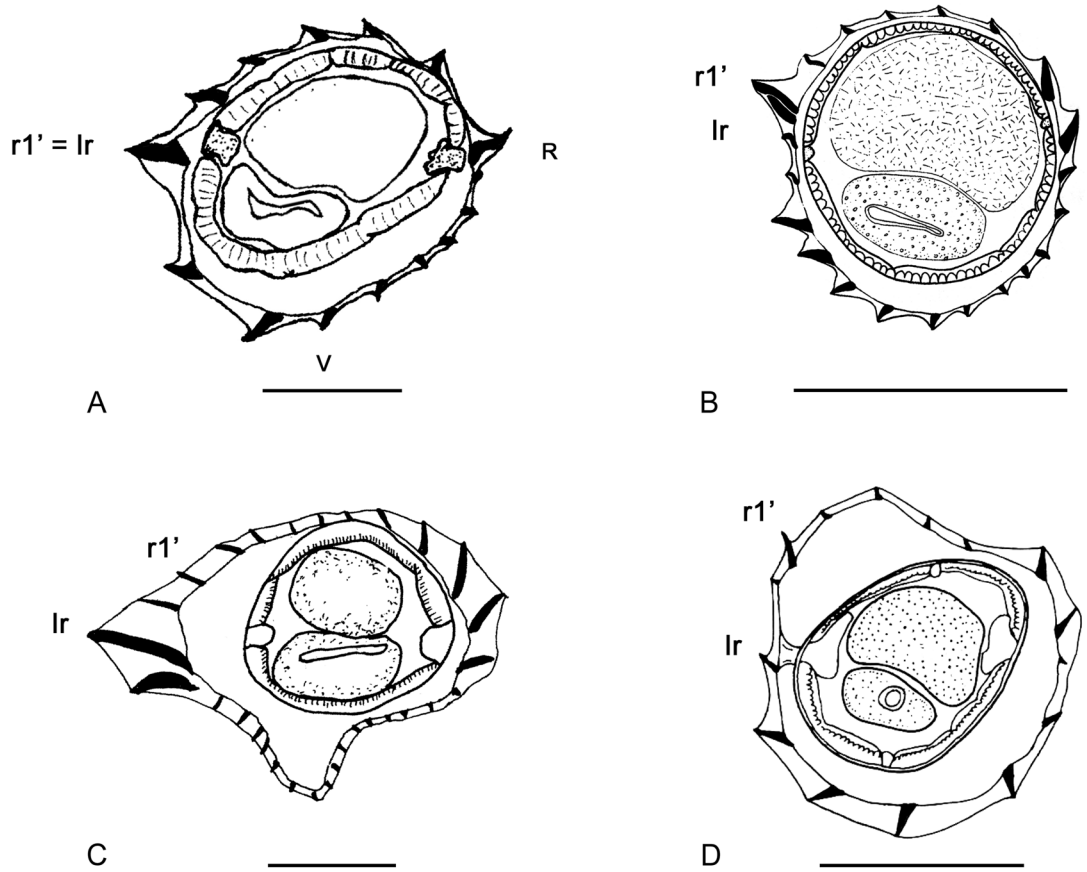
Relative size of the right ridge to ridge 1'. In *P. amplicaudae*, *P. ennisae*, *P. singauwaensis* and *Paraheligmonelloides* sp., the right ridge is larger than ridge 1' (Fig. C). It is just slightly longer in *P. annandalei*. In the remaining species, both ridges are of comparable size, the right ridge can even be slightly smaller (*P. kenyensis*, *P. triangulus*, *P. eropeplios* and *P. paruromyos*) (Figs. A, B, D).

Development of the left ridge. The left ridge is large (usually the largest ridge) in *P. amplicaudae*, *P. ennisae*, *P. singauwaensis* and *Paraheligmonelloides* sp. (Fig. D). It is medium sized (though still the largest ridge) in *P. kenyensis* (Fig. A). It is minute and one of the smallest ridges of the synlophe in *P. triangulus* (Fig. B). There is no left ridge in *P. annandalei* and *P. eropeplios,* where the left lateral field is opposite to a gap between ridges 2' and 3' In *P. paruromyos* the left ridge is minute and situated in the position 3' in the male section (Fig. D) and 2' in the female section.

Relative size of the right ridge to the left ridge. The right ridge is large but smaller than the left ridge in *P. amplicaudae*, *P. ennisae, P. singauwaensis*, and *Paraheligmonelloides* sp. It is medium sized and slightly thinner than the left ridge in *P. kenyensis*. In *P. triangulus*, *P. eropeplios*, *P. paruromyos* and *P. annandalei* the right ridge is usually larger than the left ridge, the latter being small to minute (Fig. D).

Position of the largest ridges. Some of the species analyzed have ridges which are unequal in size but not markedly so. In such species the largest ridge is usually ridge 1', followed by the right ridge (plus 1–2 adjacent ridges), and then the group of ventral left ridges; the other ridges are smaller. This pattern is observed in *P. kenyensis, P. triangulus, P. eropeplios* and *P. paruromyos* (Figs. A. B, D). In *P. annandalei* the ridges are not markedly unequal but the largest are those of the ventral left quadrant.

In *P. amplicaudae*, *P. ennisae, P. singauwaensis,* and *Paraheligmonelloides* sp., the difference in ridge size is more marked and the largest ridges are grouped in relation to the lateral fields: three to four ridges on the right field and one to two ridges on the left field, depending on the species (Fig. C).



FIGURES A–D. Synlophes at mid-body. A, *Paraheligmonelloides kenyensis* Fukumoto, Kamiya & Suzuki, 1980. Male. B, *Krishnasamyos triangulus* n. comb. Female. C, *Hughjonestrongylus ennisae* n. comb. Female. D, *Syafruddinema paruromyos* n. comb. Female. Abbreviations: R, right; r1', ridge 1'; lr, left ridge, V, ventral. All sections oriented as in Fig. A. Scale bars: 50 mm. A, after Fukumoto *et al*. (1980), modified. B, after Ow-Yang *et al*. (1983) modified. C, after Smales and Heinrich (2010), modified. D, after Hasegawa *et al*. (1999), modified.

Size of other ridges/ Presence of gradients in ridge size. In all the species analyzed the right ventral and the median dorsal ridges are always small. The smallest ridges are the right ventral ridges in *P. kenyensis* (Fig. A), all ventral ridges in *P. amplicaudae, P. ennisae*, *P. singauwaensis* and *Paraheligmonelloides* sp. (Fig. D); the right ventral and the median dorsal ridges in *P. eropeplios* and *P. paruromyos*, *P. triangulus, P. annandalei* (Figs. B, D). Ridge 1' is separated from the group of larger ventral left ridges by a minute left ridge (ridge 2') and a gap in *P. annandalei*, *P. eropeplios* and *P. paruromyos* (Fig. D) and by two minute ridges (2' and 3') in *P. triangulus* (Fig. B). There is not a well defined gradient in ridge size in the species considered.

Symmetry of the ridges in relation to the axis of orientation. In *P. triangulus, P. annandalei, P. eropeplios* and *P. paruromyos*, a certain symmetry is established in relation to the axis of orientation, between the ridges of the ventral left quadrant and those of the dorsal right quadrant. Ridges of both groups are larger than the other ridges, they often occur in the same number, and show a convergent orientation with respect to the axis of orientation (Figs. B, D).

The fact that some of the characters analyzed were frequently associated, allowed us to group the species treated in four groups:

(1) species with ridge 1' homologous with left ridge, with left ridge and right ridge medium- sized (Fig. A). One species: *P. kenyensis.*

(2) species with ridge 1' distinct from left ridge and forming a comarete, with ridge 1' and right ridge medium-sized and left ridge minute (Fig. B). One species: *P. triangulus*.

(3) species with ridge 1' small, distinct from left ridge and not forming a comarete, ridges markedly unequal in size, with largest ridges grouped in relation to lateral fields and smallest ridges on the entire ventral surface (Fig. D). Four species: *P. amplicaudae*, *P. ennisae*, *P. singauwaensis* and *Paraheligmonelloides* sp.

(4) species with ridge 1' small, distinct from left ridge, comparable in size to or slightly smaller than right ridge, with ridges unequal in size but not markedly, left ridge absent or minute, ridge 2' minute, and a gap present between ridges 2' and 3' (Fig. D). Three species: *P. annandalei, P. eropeplios, P. paruromyos.*

Four genera representing the four supraspecific groups mentioned above are proposed: (1) *Paraheligmonelloides sensu stricto* (2) *Krishnasamyos* n. gen. (3) *Hughjonestrongylus* n. gen. (4) *Syafruddinema* n. gen.

Paraheligmonelloides Fukumoto, Kamiya & Suzuki, 1980 (Fig. A)

Definition: Heligmonellidae, Nippostrongylinae. Female unknown. At mid-body, 15 cuticular ridges in male. Ridges medium-sized. Ridge 1' is the left ridge. Left ridge and right ridge of similar size, left ridge thicker. Other ridges smaller. On dorsal side, ridges of equivalent size, with ridge 1 slightly larger. On ventral side, left ridges larger than right ridges. Axes of orientation oblique. Bursa dissymmetrical with right lobe larger. Characteristic bursal pattern of type 2–3 tending to 2-2-1. Dorsal ray divided near base. Spicules ending in one tip. SpL/BL 5%.

Type and sole species: *Paraheligmonelloides kenyensis* Fukumoto, Kamiya & Suzuki, 1980.

Hosts: Lagomorpha: Leporidae.

Host site*:* Small intestine.

Distribution*:* Kenya.

Krishnasamyos n. gen. (Fig. B)

Definition: Heligmonellidae, Nippostrongylinae. At mid-body, 19–21 ridges in both sexes. Ridge 1' distinct from left ridge, forming a comarete (fusion of two ridges). Left ridge minute, in position 2'. Ridge 1' and right ridge medium-sized but ridge 1' larger. Two minute ridges (including left ridge) ventral to comarete. Two large left ventral ridges, symmetrical to two dorsal right ridges in relation to axis of orientation. Bursa dissymmetrical with left lobe larger. Characteristic bursal pattern of type 2-2-1. Ventral rays short. Dorsal ray divided at proximal third of length. Spicules undivided. SpL/BL 3 %.

Type species: *Krishnasamyos triangulus* (Ow-Yang, Durette-Desset & Ohbayashi, 1983) n. comb.

Hosts*:* Rodentia: Muridae: Murinae.

Host site*:* Small intestine.

Distribution: Malaysia.

Etymology: The genus is named in honour of Mr. M. Krishnasamy (University of Kuala Lumpur, Malaysia) in recognition of his valuable contribution to the knowledge of the Malaysian Nippostrongylinae.

Hughjonestrongylus n. gen. (Fig. C)

Definition: Heligmonellidae, Nippostrongylinae. At mid-body, 20–30 ridges in both sexes. Ridges markedly unequal in size. Ridge 1' distinct from left ridge, left ridge is ridge 2' or 3'. At mid-body, left ridge and right ridge very large, left ridge larger than right one. Largest ridges grouped in relation to lateral fields: one to three ridges on left side; three to four ridges on right side. Remaining dorsal ridges small and of similar size. Ventral ridges of similar size, smaller than dorsal ones. Bursa dissymmetrical. Characteristic bursal pattern of types 1–4 and 2–3. Dorsal ray divided within distal half. Spicules thick ending in one or three tips. SpL/BL 10–15%.

Type species: *Hughjonestrongylus ennisae* (Smales & Heinrich, 2010) n. comb.

Hosts: Rodentia: Muridae: Murinae.

Host site: Small intestine.

Distribution: Papua New Guinea, Papua Indonesia.

Etymology: This genus is named in honour of Pr. Hugh I. Jones (University of Western Australia), in recognition of his significant contribution to the study of Australian parasites.

Other species: *Hughjonestrongylus amplicaudae* (Smales & Heinrich, 2010) n. comb., *Hughjonestrongylus mirzai* (Smales, 2009) n. comb., *Hughjonestrongylus singauwaensis* (Smales & Heinrich, 2010) n. comb., *Hughjonestrongylus*. sp. (= *Paraheligmonelloides* sp. of Smales (2011).

Syafruddinema n. gen. (Fig. D)

Definition: Heligmonellidae, Nippostrongylinae. At mid-body 14–17 ridges in both sexes. Ridges small to minute, unequal in size but not markedly. Ridge 1' distinct from left ridge. Left ridge minute or absent. Ridge 1' and right ridge of similar size. Largest ridges: ridge 1', left ventral and right dorsal ridges. Left dorsal and right ventral ridges small. Ridge 2' and ridge situated ventrally to right ridge, minute. Gap between ridges 2' and 3'. Ridges 4', 5' or 3'–6', symmetrical to ridges 5, 6, or 5–7 in relation to axis of orientation. Bursa subsymmetrical. Characteristic bursal pattern of type 2-2-1. Dorsal ray divided within proximal third. Spicules ending in one or two tips. SpL/BL: 10–15%.

Type species: *Syafruddinema paruromyos* (Hasegawa, Miyata & Syafruddin, 1999) n. comb.

Hosts: Rodentia: Muridae: Murinae.

Host site: Small intestine.

Distribution: Indonesia, Malaysia.

Etymology: The genus is named in honour of Pr. Syafruddin (University of Hasanuddin, Indonesia) in recognition of his contribution to the study of Indonesian parasites.

Other species: *Syafruddinema annandalei* (Ow-Yang, Durette-Desset & Ohbayashi, 1983) n. comb., *Syafruddinema eropeplios* (Hasegawa, Miyata & Syafruddin, 1999) n. comb.

Discussion

Paraheligmonelloides kenyensis, the only species of *Paraheligmonelloides sensu stricto*, is similar to species of *Taranchonema* Digiani & Durette-Desset, 2013 (Nippostrongylinae), parasitic in Ethiopian Muridae, by certain characters of the synlophe, i.e. left ridge homologous with ridge 1', left ridge and right ridge most developed, ventral left ridges larger than right ones, and a similar number of ridges (13–14 ridges vs. 15). However in the species of *Taranchonema* the left ridge and the right ridge are very large; the dorsal ridges are the smallest and subequal in size, and there is a gradient in ridge size on the ventral left quadrant (Digiani & Durette-Desset 2013). In *Paraheligmonelloides* the left ridge and the right ridge are just medium sized, the right ventral ridges are the smallest, ridge 1 is larger than the other dorsal ridges and there is no gradient in ridge size.

Durette-Desset and Digiani (2010) had temporarily considered the species *Heligmonoides mirzai* Smales, 2009 parasitic in the Black-tailed Melomys *Melomys rufescens* (Alston) from Papua New Guinea, as a Nippostrongylinae

incertae sedis since its synlophe did not match that of *Heligmonoides* Baylis, 1918, characterized by a careen supported by four large ridges (Durette-Desset 1983, Durette-Desset & Digiani 2005). The synlophe of *H. mirzai* is now found to match that of the species here grouped in *Hughjonestrongylus* n. gen. (more than 20 ridges markedly unequal, largest ridges grouped in relation to lateral fields, ventral ridges smallest). On the other hand, the lateral bursal pattern (type 1–4) and the morphology of the dorsal ray of *H. mirzai* also match those found in the species grouped in the new genus. This allows us to propose the new combination *Hughjonestrongylus mirzai* n. comb. for this species.

Smales (2011) described from the Lesser Chiruromys *Chiruromys vates* (Thomas) from Papua New Guinea, some specimens which were considered as *Paraheligmonelloides* sp. These specimens, deposited at the Bernice P. Bishop Museum, Honolulu, Hawaii, under the number BBM NG 103141 (Smales, pers. comm.), also have a synlophe with 27 ridges markedly unequal, with largest ridges in front of the lateral fields (two on the left, four on the right), matching that of the concerned species, grouped in *Hughjonestrongylus* n. gen. Among these species, it is closest to *H. ennisae* by the synlophe and also by the lateral bursal pattern, with rays 2–3 diverging at mid-length and rays 4–6 apparently joined up to the distal extremities (rays 6 are not illustrated in Smales (2011, Fig. 7). However, *H. ennisae* is well characterized by a right spicule with a trifid tip, whereas the spicules of *Paraheligmonelloides* sp. differ from those of *H. ennisae* and of the other species in the genus by having a simple tip strongly bent forming a distal right angle (Smales 2011, Fig. 5).

The characters mentioned above are sufficient to consider *Paraheligmonelloides* sp. as belonging to *Hughjonestrongylus* n. gen. Temporarily, the species will be considered as *Hughjonestrongylus* sp., even when the characters are also sufficient to consider it as different from the other species described in the genus.

Table 1 provides a list of the species included in the former genus *Paraheligmonelloides*, plus *Heligmonoides mirzai*, with their new systematic position, host-spectrum and biogeographic distribution.

TABLE 1: List of the species previously belonging to the genus *Paraheligmonelloides* Fukumoto, Kamiya & Suzuki, 1980 plus *Heligmonoides mirzai* Smales, 2009 with their new generic attribution, host-spectrum and biogeographical distribution.

Species	Reference(s)	Systematic position after this work	Host(s)*	Distribution
Paraheligmonelloides amplicaudae	Smales & Heinrich (2010)	*Hughjonestrongylus amplicaudae* n. comb.	*Paramelomys*	Indonesia
P. annandalei	Ow-Yang *et al*. (1983)	*Syafruddinema annandalei* n. comb.	*Rattus*	Malaysia
P. ennisae	Smales & Heinrich (2010)	*Hughjonestrongylus ennisae* n. comb.	*Paramelomys*	Papua N. Guinea Indonesia
P. eropeplios	Hasegawa *et al*. (1999)	*Syafruddinema eropeplios* n. comb.	*Eropeplus*	Indonesia
P. kenyensis	Fukumoto *et al*. (1980)	*Paraheligmonelloides kenyensis*	*Pronolagus***	Kenya
Heligmonoides mirzai	Smales (2009)	*Hughjonestrongylus mirzai* n. comb.	*Melomys*	Papua N. Guinea
P. paruromyos	Hasegawa *et al*. (1999)	*Syafruddinema paruromyos* n. comb.	*Paruromys*	Indonesia
P. rajah	Ow-Yang *et al*. (1983)	sp. *incertae sedis*	*Maxomys*	Malaysia
P. singauwauensis	Smales (2009) Smales & Heinrich (2010)	*Hughjonestrongylus singauwaensis* n. comb.	*Melomys* *Paramelomys*	Papua N. Guinea
P. triangulus	Ow-Yang *et al*. (1983)	*Krishnasamyos triangulus* n. comb.	*Leopoldamys* *Maxomys* *Chiropodomys*	Malaysia
Paraheligmonelloides sp.	Smales (2011)	*Hughjonestrongylus* sp.	*Chiruromys*	Papua N. Guinea

* Rodentia: Muridae: Murinae, except when indicated.
** Lagomorpha: Leporidae.

Key to the proposed genera

1 Ridge 1 larger than adjacent dorsal ridges 2
- Ridge 1 of same size as adjacent dorsal ridges. 3

2 Ridge 1' situated in front of left lateral field. No minute ridges on left ventral quadrant. Parasites of Leporidae from Kenya. . . . . *Paraheligmonelloides*
- Ridge 1' situated on left dorsal quadrant. Two minute ridges in front of left lateral field. Parasites of Muridae from Malaysia. . . . . *Krishnasamyos* n. gen.

3 Ridges 20–30, markedly unequal in size (very large to minute). Largest ridges grouped in relation to the lateral fields. Parasites of Muridae from Indonesia and Papua New Guinea . . . . . *Hughjonestrongylus* n. gen.
- Ridges 14–17, unequal in size but not markedly (small to minute). Left ventral and right dorsal ridges symmetrical in relation to axis of orientation (similar size and number). Parasites of Muridae from Indonesia. . . . . *Syafruddinema* n. gen.

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