# Taxonomical and faunistic studies on the nematode parasites from Indonesian murines (Rodentia; Muridae; Murinae) with special reference to *Syphacia* spp. and their biogeography

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## ABBREVIATIONS

*Cox*1; cytochrome *C* oxidase subunit 1 gene

DNA; deoxyribonucleic acid

IUCN; International Union for Conservation of Nature

LE; laterally-elongated

ML; maximum likelihood

MZB; Museum Zoologicum Bogoriense

NJ; neighbor-joining

R; round

S; square

WL; worm length

# Contents

## PREFACE

Rats and/or mice (Rodentia; Muridae) are of special interest due to their role as reservoirs of many important parasitic nematodes of humans and livestock (Kwo and Kwo, 1968; Bhaibulaya and Indrangarm, 1975; Baker, 1998). Human infections with migration of larvae of *Angiostrongylus cantonensis* (Chen, 1950), a nematode of rat, had been reported from North Sumatra and Java (Smit, 1962; Widagdo et al., 1977). Until recently, only *A. cantonensis* has been focused as zoonotic nematode of rat in Indonesia (Margono, 1970; Margono and Ilahude, 1974; Lim Boo Liat et al., 1978, 1986). However, murines have been known to harbor other zoonotic nematodes such as *Calodium hepaticum* (Bancroft, 1893) (syn. *Capillaria hepatica*), *Trichinella spiralis* (Owen, 1835) and *Toxocara* spp. (Beaver et al., 1984). Moreover, rodents participate in transmission of many nematodiases of cattle and pets (Hildebrand et al., 2009). Hence, it is critical to understand the nematode fauna of the murines, many of which are zoonotic organisms and may affect animal and human health (Pisanu et al., 2007). Fortunately, many rodents are easily collected and collection is not regulated by any policies by IUCN and so on. In short, they are ideal materials for the faunal study like the present one.

At first, this thesis focuses on the general faunistic consideration based on the preceding papers and the author's fieldworks since 2007 on nematodes parasitic in murine

rodents in Indonesia. As a result, the author could demonstrate characteristic nematode fauna of murines, including many species of zoonotic importance and some new taxa including two new subgenera of *Syphacia*, one new genus of Heterakidae and a new molineid from the Wallacea. Special attention is paid for *Syphacia* species because they show diversification in Indonesian murines and rather strict host-parasite relationships. Because a unique distributional pattern has been observed in Wallacea according to the faunal studies on various free-living organisms, a biogeographical discussion on the host-parasite relationship between the murines and the genus *Syphacia* will be given (see Chapter 4).

The biogeography is one field of the evolutionary biology, focusing on a historical process of an animal dispersal and evolution. Hasegawa and Asakawa (2003) made a biogeographical discussion on the host-parasite relationship of the Japanese endemic murines and some genera of the parasitic nematodes. However, there has been no such trial in other Asian countries including Indonesia. Based on the findings obtained in this study, a historical scenario was given, although several speculations, which should be tested in the future, are included. Even tentative, a hypothesis would provide a ground for further progress (Asakawa, 1991). Besides the traditional morphological measures, molecular analysis of DNA sequences is also employed partly to depict more robust phylogenetic relationship of *Syphacia* species in Indonesia and surrounding regions.

Nowadays, preventive (veterinary) medicine is needed for suppression of an outbreak of infectious diseases including zoonotic nematodiasis. Ultimately, the preventive measures related to an ecosystem should be connected with the context of the One Health concept (see Chapter 4): the measures are based on the natural history of parasites and hosts, viz., from where the nematode originated, when and how to invade the present locality. Therefore, the taxonomical and faunistic study on the nematode genus has medical importance also. Although *Syphacia* species show host specificity, they have been regarded to possess zoonotic potential (Yamaguti, 1961). Actually, some human cases infested with *Syphacia* have been reported (Riley, 1919; Mahmoud et al., 2009). The author hopes that the present results could provide a model not only for biogeography of nematode parasites, but also for the One Health approach in Indonesia.

# CHAPTER 1

## Faunal study on the nematodes parasitic in Indonesian murines

### Introduction

Faunistic study on the Indonesian murines has already resulted in discovery of many new species and new genera since the early 20th century (see Suyanto et al., 1998). However, the faunal study on the nematodes of the murines has just started since the 1970's, and only limited murine species have been studied till now. It is therefore strongly expected that there are still numerous undescribed species that may provide key information on the zoonotic agents and/or evolution of nematodes in the endemic murines of Indonesia. Hence, the author performed a general survey on nematodes parasitic in murine rodents in Indonesia.

### Materials and methods

This overviewing study was based on the published papers by the preceding researchers, and their papers were cited in the references list of this thesis. Besides this, the author had investigated the murine collections held by researchers in Museum Zoologicum

Bogoriense (MZB) for mammalogical projects. In total, over 10,000 murines from various areas of Indonesia had been deposited in MZB. Among them, approximatly 800 murine individuals were presented for this study. Additional nematode specimens of murines obtained in the medico-zoological survey conducted during the period from 1991 to 1994 (Miyagi, 1994) were also examined. Moreover, some specimens recovered from the carcass of murines preserved in the American Museum of Natural History, New York, USA (Musser, 1987) were examined (see Appendix 1).

The bodies of murines have been kept mainly in 10% formalin solution, and partly in 70% ethanol solution. The alimentary canals and viscera were removed from carcass of the murine specimens and opened with scissors. Contents of each portion of the alimentary canal were rinsed separately and examined for nematodes under a stereomicroscope. Scrapings were also be taken from each portion of the alimentary canal and examined. The worms were fixed and stored in 70% ethanol. Later, the worm specimens were cleared in glycerol–alcohol solution, and were examined using a compound Olympus BH series microscope (Olympus Co. Ltd., Tokyo, Japan). All worm specimens were deposited in MZB.

## Results

**Records between the 1930's and early 2000's;** Before the present study, a total of 51 taxa (38 species and 13 identified nematode up to generic level) belonging to 29 genera and 17 families of nematode parasites were obtained from 32 species of Indonesian murines (Dewi & Purwaningsih, 2013a). The nematodes that parasitize commensal rats are of special interest due to the role of rats as reservoirs for many important parasites of humans. Rats also harbor many zoonotic agents that affect captive animal and human health (Kwo and Kwo, 1968; Bhaibulaya and Indrangarm, 1975; Baker, 1998; Pisanu, 2007).

Besides the discovery of new species, a series of research projects on nematode parasites of Indonesian murines have been conducted. Many nematode parasites of Indonesian murines have been collected, recorded and described. The oldest specimen deposited in MZB was *Nippostrongylus* sp., parasitizing *Rattus sabanus* collected from Jakarta in 1970. However, the study on helminth parasites of rats in Indonesia began much earlier with Vogel and Vogelsang in 1930 (Wiroreno, 1975), and the first publication on nematodes from Indonesian murines by an Indonesian scientist was made by Sri S. Margono, lecturer of the University of Indonesia. She obtained *Angiostrongylus* from laboratory-reared white rats which were given feeding with naturally infected snails in Jakarta. Her paper was

appeared in The Southeast Asian Journal of Tropical Medical and Public Health in 1970 (Margono,1970). In early reports of rat helminths in Indonesia, only medium to large sized worms were dealt, and minute nematodes were presumably overlooked due to insufficient research equipment (Wiroreno, 1975, 1978; Kadarsan et al., 1986; Purwaningsih and Saim, 1988; Saim and Purwaningsih, 1999).

A review of the literature published during the period from the 1970's to today including the present study suggests that most nematological studies of Indonesian rodents focused on biodiversity of the nematodes. Major works on nematode parasites of Indonesian murines as well as the description of many new species and genera were published by Hideo Hasegawa, Oita University, Japan, and his colleagues in 1992–1999. Meanwhile, taxonomic study of nematodes in MZB was begun by Endang Purwaningsih in 1992, who has reported many species of nematode parasites of murines from various islands in Indonesia since then (see 'References' section).

**Present author's records;** Adding to the historical records mentioned above, a total of 20 species including one new genus and two new sub genera have been reported in the publications by the present author. In total, 61 taxa of nematodes (46 identified to species level and 15 to generic level) have been obtained from 35 species and three genera of

Indonesian murines (see Appendix 1). The newly found taxa by the present author were mostly collected from host materials from islands situated in Wallacea. Observation of the murines for nematodes from Sulawesi hitherto had been done only on so-called "new endemic" murines, whereas no nematodes data had been recorded for so-called "old endemic" ones (see Musser, 1987 and Chapter 4 about "old/new endemic"). However, a prominent taxon, *Musserakis sulawesiensis* Hasegawa, Dewi & Asakawa, 2014 (Heterakidae), was described recently from an old endemic rat, *Echiothrix centrosa*. Molineidae gen. sp. collected from *Paruromys dominator*, a new endemic rat of Sulawesi, also showed peculiar morphology (Dewi et al., 2013). These two taxa will be dealt in the following paragraphs.

Other newly found taxa also consisted of *Aspiculuris* sp., *Cyclodontostomum purvisi, Gongylonema neoplasticum, Heterakis spumosa, Nippostrongylus brasiliensis, Pterygodermatities tani, P. whartoni, Subulura andersoni, Syphacia muris, Tikusnema javaense, Trichuris muris* and seven species of the genus *Syphacia*. Among them, seven *Syphacia* species represented new taxa, and two of them belonged to new subgenera. Because each species has faunistic and/or biogeographical peculiarity, they will be dealt in the following chapters. Besides new host records, Sulawesi has been added as new locality for *Tikusnema javaense* from *Bunomys prolatus* and *Rattus hoffmanni*; *Pterygodermatites whartoni* from *Rattus tanezumi, R. xanthurus* and *B. chrysocomus*; *Subulura andersoni* from

*B. chrysocomus*, *B. prolatus, Margaretamys elegans*, *Maxomys bartelsii, R. marmosurus*, *R. hoffmanni*, *R. xanturus* and *B. penitus*; *Cyclodontostomum purvisi* from *R. hoffmanni; Gongylonema neoplasticum* from *R. tanezumi* and *B. chrysocomus*; *Nippostrongylus brasiliensis* from *Taeromys* sp.; *Heterakis spumosa* from *B. andrewsi, B. chrysocomus*, *B. penitus, B. prolatus*, *Crunomys celebensis, Eropeplus canus, Margaretamys elegans, Paruromys dominator, Rattus hoffmanni, R. marmosurus, R. xanthurus, Tateomys macrocercus* and *T. rhinogradoides*; *Pterygodermatities tani* from *R. xanthurus*; *Masthoporus muris* from *B. chrysocomus, R. tiomanicus, R. tanezumi* and *R. xanthurus*; and *Trichuris muris* from *B. chrysocomus.*

**The new genus and species *Musserakis sulawesiensis* (Heterakidae);** This new genus is obtained from an old endemic rat, *Echiothrix centrosa* and readily distinguished from other heterakid genera by having non-recurrent and non-anastomosing cephalic cordons, by lacking papillae between papillae groups around the precloacal sucker and the cloacal aperture and by lacking teeth in the pharyngeal portion (Hasegawa, Dewi and Asakawa, 2014). The spicules are equal but with marked dimorphism among individuals. Other heterakids collected from other old endemic murines examined, i.e., *Crunomys celebensis*, *Tateomys macrocerca* and *T. rhinogratoides* and the new endemic rats of Sulawesi, were *Heterakis spumosa*, a

cosmopolitan nematode of various murines. It is suggested that *M. sulawesiensis* is specific to the shrew rats, *Echiothrix*, of which primary diet component is earthworm (Musser, 1987).

**The superfamily Trichostrongyloidea and its murine hosts;** The family Heligmonellidae (Trichostrongyloidea) is the dominant nematode group in rodents of the world (see Durette-Desset, 1971 and Appendix 3). From Indonesian murines, 16 species in eight heligmonellid genera had been recorded before the present study. This family was obtained from endemic murines in *Mallomys, Mastacomys, Melomys, Mesembriomys, Pseudomys, Uromys, Zyzomys, Paramelomys* and *Bunomys* (Hasegawa et al*.,* 1999; Smales, 2012). The present author collected many heligmonellid specimens during the present study and their data will be analyzed in the future.

All of the species that belong to Heligmonellidae are endemic species except *Nippostrongylus brasiliensis* and *Orientostrongylus tenorai.* Sulawesi is the richest island for heligmonellids and a total of 14 species have been recorded. Most of these heligmonellids are parasitic in endemic murines in each area (Hasegawa and Syafrudin, 1994b; Hasegawa and Tarore, 1995; Hasegawa and Mangali, 1996; Hasegawa et al., 1999). However, helligmonellid genera in the intestine of murine rodents have wider distribution. For example, *Maxomystrongylus* was also proved in *Maxomys* of Kalimantan (Hasegawa and Syafruddin,

1997). *Heligmonelloides*, *Heligmonoides* and *Macrostrongylus* have been also known from both Sunda Shelf and New Guinea (Smales, 2012). Moreover, *Orientostrongylus* is also distributed in Sunda Shelf to Moluccas (Hasegawa and Syafruddin, 1995a). However, these genera have not been recorded from Australia. Meanwhile, *Hasanuddinia* is also shared by endemic rats of Sulawesi, Papua Indonesia/Papua New Guinea, and *Odilia* shows more wider distribution from Sulawesi to Australia, but they have not been demonstrated from Sunda Shelf (Smales, 2010, 2012). Only *Nippostrongylus* has been known from a wide distribution range through Sunda Shelf, Sulawesi, Mollucas, Papua and Australia (Durette-Desset, 1969, 1971, 1983).

Beside the heligmonellids, a species belonging to Molineidae (Trichostrongyloidea) was found from the small intestine of only one individual of *Paruromys dominator* from Sulawesi (Fig. 1-1). It is unique from the morphological and taxonomical point of view (Dewi et al., 2013). Although its copulatory bursa is similar to the heligmonellids, this taxon has specific shape of anterior part and weakly-developed ridges or actually no ridges of synlophe like in the worms of family Molineidae. It is suggested that this was accidental parasitism, and its principal host is other mammalian host (probably the order Chiroptera). The resemblance in the copulatory bursa may be an example of convergence.

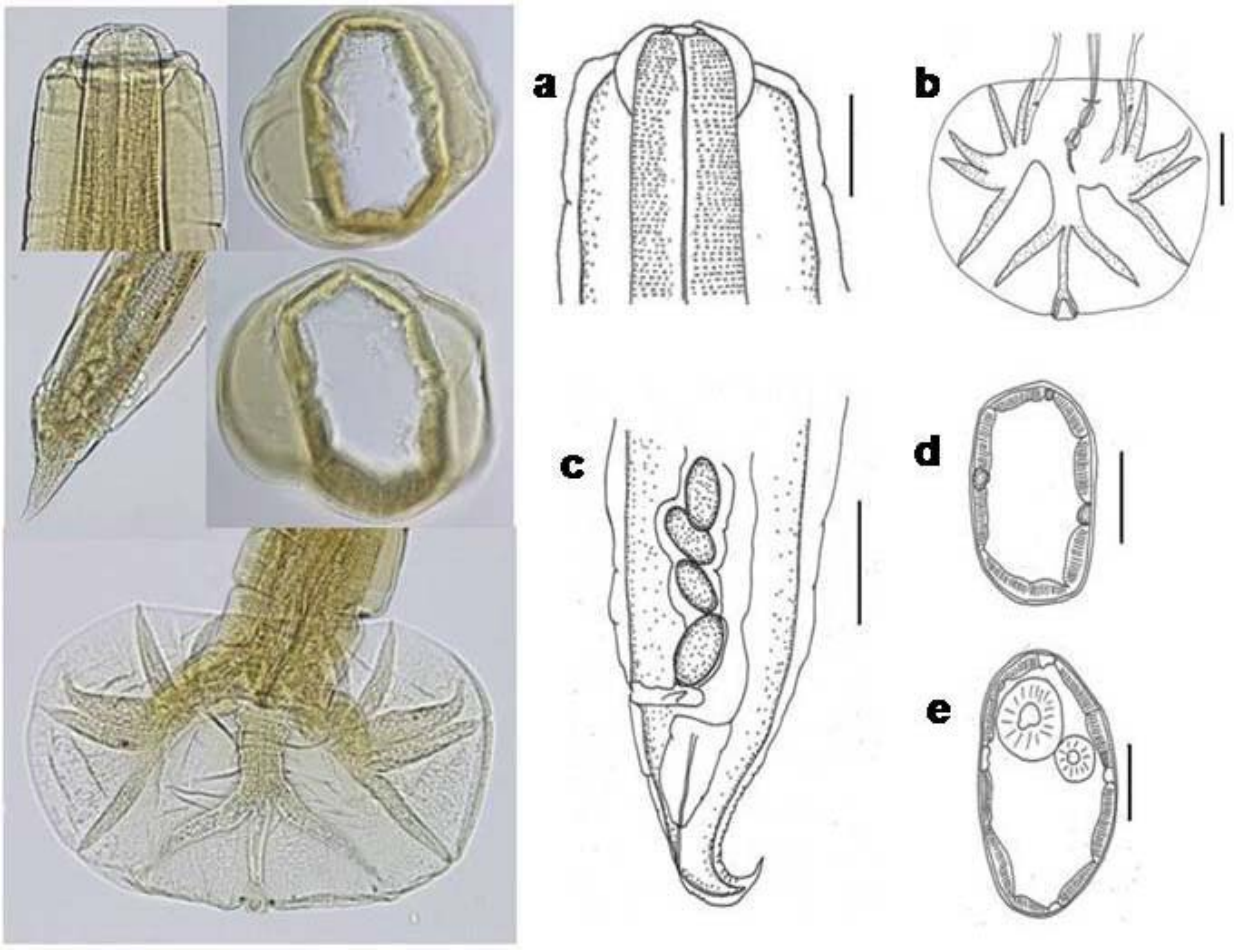



**Fig. 1-1.** Molineidae gen. sp. from *Paruromys dominator* on Sulawesi: (a) anterior portion, lateral view; (b) bursa copulatrix, ventral view; (c) posterior portion of female, left lateral view; (d) cross-section of male through midbody; (d) cross-section of female through midbody (Scale bars: 1: 50µm, 2; 3; 4; 5: 100µm).

**Zoonotic nematodes found from Indonesian murines;** Rodents could act as an intermediate, definitive or paratenic host for many helminth species **(**Hildebrand et al., 2009). Some nematodes parasitizing murines are regarded as zoonotic agents of nematodiasis of humans and/or captive animals (Kwo and Kwo, 1968; Bhaibulaya and Indrangarm, 1975; Baker, 1998). For example, *Angiostrongylus cantonensis* (Chen, 1935) (syn. *Parastrongylus cantonensis*), *Calodium hepaticum* (Bancroft, 1893) (syn. *Capillaria hepatica*), *Trichinella spiralis* (Owen, 1835) and *Gnathostoma* spp. are potential zoonotic pathogens that utilize rodents as final, reservoir or paratenic hosts. *Cyclodontostomum purvisi*, a nematode parasitic in the cecum of murines, has been recorded from human body (Bhaibulaya and Indrangarm, 1975). A case of human infection with *Rictularia* was found in New York (Kenney et al., 1975). The diagnosis was made based on worm sections appeared in the histopathological slides. However, it is impossible to distinguish *Rictularia* from *Pterygodermatites* by sectioned worms as the discrimination of these genera is based on oral structures (Quentin, 1969). Therefore, *Pterygodermatites* of rats could be also regarded as possible zoonotic agent.

Presence of *A. cantonensis* infection in Indonesian murines has been reported since the 1960's (Kwo and Kwo, 1968; Wiroreno, 1978; Cross, 1979). Moreover, human cases of angiostrongyloidiasis were reported from North Sumatra (Smit, 1962) and Java (Widagdo et al., 1977). Distribution of *Trichinella* has been recorded for Bali, and human infections with

*T. spiralis* were also reported from Bali and North Sumatra (Holz, 1962, 1966; Pozio, 2007). In addition, many nematodiasis in cattle and pets caused by the rodent transmission including suspected ones have been reported (Hildebrand et al., 2009), but there have been only limited reports about the direct detection of the nematode agents from the murines in Indonesia (Untung and Nalim, 1982; Dewi, 2011; Dewi and Purwaningsih, 2013a). *Calodium hepaticum* have been recorded from Indonesian murines (Brown et al., 1975). However, from the present survey, some potential agents were recorded and/or newly found, viz., *Cyclodontostomum purvisi*, *Pterygodermatites* sp. and *Syphacia* spp. The former two species are heteroxenous, requiring intermediate hosts and/or paratenic hosts for transmission, on the other hand, nematodes belonging to the genus *Syphacia* are monoxenous, infecting directly to their hosts (Anderson, 2000). Hence, it seems to be quite easy for humans to acquire infection with *Syphacia* by swallowing matured eggs. Actually, *Syphacia obvelata* was collected from a sample of stool of an American child in the Philippines (Riley, 1919; Ashford and Crewe, 2003). Although this record was very old, *Syphacia* nematodes should be regarded to have zoonotic potential. More recently, Mahmoud et al. (2009) reported 25 human cases of *Syphacia* infection in Egypt. They found *Syphacia muris*, *Syphacia* spp. and *Enterobius vermicularis*. Very curiously, only females were found among the worms

identified as *Syphacia*, whereas males and females were observed in *E. vermicularis*. Judging from the photomicrographs presented, the identification may need further confirmation.

**An overview of nematode fauna from Indonesian murines;** The parasitic nematodes collected from Indonesian murines can be classified largely into two groups; viz., cosmopolitan and endemic nematodes. The cosmopolitan nematodes are *Heterakis spumosa, A. cantonensis, M. muris, C. hepaticum*, *Nippostrongylus brasilieneis, Strongyloides ratti, Strongyloides venezuelensis* and *Syphacia muris.* They are distributed worldwide, mostly having spread their geographical distribution range with the dispersal of commensal murine species such as *Mus musculus*, *Rattus norvegicus*, *R. rattus*, *R. tanezumi, R. argentiventer, R. nitidus* and *R. exulans* (for the commensal murine species see Fabre et al., 2013). Whereas, endemic nematodes are those of which geographical distribution is limited and usually found only in specific host murines. *Musserakis sulawesiensis* and the new species of *Syphacia* are examples of the endemic nematodes. The 61 nematode taxa (46 identified to species and 15 to generic level) hitherto recorded belong to 32 genera and 18 families (Appendix 1). They were obtained from 38 Indonesian murine species including three species identified onlyto generic level, of which 23 species are currently regarded as endemic species (see Appendix 1).

The most recent checklist of Indonesian murines recorded 167 species belonging to 47 genera (Suyanto et al., 1998), while catalogue of mammals of MZB in 2012 listed at least 173 species of Muridae. It means that 79% of the murines species remain without any nematode record. Many of the murine species are listed as endangered or extinct. The extinction of hosts means extinction of their parasitic nematodes, especially if they are host-specific or endemic. All of those data are important for documenting biodiversity of nematode parasites, especially from Indonesian murines. Furthermore, these data can be used as a baseline to guide future experimental and survey works.

Most nematodes of Indonesian murines were recorded from western and central Indonesia. The low number of recorded nematodes from eastern Indonesia is due to few expeditions and studies on murine rodents in that region. It seems that large numbers of new species will be discovered with more intensive examination. Further observations of endemic host murines from Indonesia will reveal more new species and/or genera of nematode parasites and demonstrate characteristic distribution. The continuous studies may ultimately provide a model database to study the biodiversity of parasites and their coevolution with their hosts in a geographical area with high levels of endemism.

**Summary**

This study performed a general survey on nematodes parasitic in murine rodents, especially of central islands of Indonesia. About 800 murines deposited in MZB were used. Adding to this, an overview based on the published papers by the preceding researchers was given for a baseline for the present study. In total, 61 species / taxa (46 species identified to species level and 15 taxa assigned up to generic level) including zoonotic agents were recorded from 35 species and three genera of Indonesian murines. A total of 20 nematode species including a new genus and two new subgenera were newly recorded. The new taxa consisted of *Musserakis sulawesiensis* from *Echiothrix centrosa* (Sulawesi), seven new species of the genus *Syphacia* including two new subgenera, *Rumbaisyphacia* and *Segienamsyphacia*. Molineidae gen. sp. from *Paruromys dominator* (Sulawesi) was surmised to represent a new genus. Zoonotic and possibly zoonotic nematodes found were *A. cantonensis, A. malaysiensis, Cyclodontostomum purvisi* and *Pterygodermatities* sp. Furthermore, it was discussed that *Syphacia* spp. could be zoonotic agents. As there are at least 173 murine species in Indonesia, over 130 murine species are waiting for future faunal studies of parasitic nematodes. Unfortunately, many of the murine species are listed as endangered or extinct. The extinction of hosts means extinction of their parasitic nematodes,

especially if they are host-specific or endemic. Hence, the study should be continued to provide a model database to understand the biodiversity of parasites and their coevolution with their hosts ultimately in a geographical area with high levels of endemism.

# CHAPTER 2

## Morphological taxonomy of the genus *Syphacia* from Indonesian murines

### Introduction

Nematodes of the genus *Syphacia* Seurat, 1916 (family Oxyuridae) are pinworms parasitic in various murines all over the world (Hugot, 1988). Their life cycle is typical of the oxyurids in that it actually lacks a period to be exposed to the external environments. The simplicity of the life cycle is likely to provide less opportunity to acquire a new host than for other parasites that require a long period in external environment or in intermediate host to become infective. Therefore, *Syphacia* nematodes are considered to have generally co-evolved with their hosts (Hugot, 1988, 1990). Indeed, the *Syphacia* spp. found in Indonesia seem to be specific to host species or genus (Hasegawa et al., 1992; Dewi et al., 2010, 2014a, b, 2015), and this means that the nematode could provide interesting biogeographical evidence (see Chapter 4).

Moreover, the genus *Syphacia* could be zoonotic because a human case infested with *Syphacia* sp. was reported in the Philippines (Riley, 1919; see Chapter 1). *Syphacia* species are minute and resemble each other, strict taxonomical and morphological study on this nematode genus will become a baseline of an easy and quick diagnosis method. As

mentioned in Chapter 1, the present faunal survey demonstrated new taxa including two new subgenera in central Indonesia. Hence, descriptions of the *Syphasia* taxa are made herein, and a key of all species recorded from the areas Sunda to Sahul including the newly found taxa is proposed.

## Materials and methods

**Collection of materials:** The present study was based largely on the material from various parts of Indonesia that were housed in MZB and some specimens collected in the medico-zoological survey conducted during the period from 1991 to 1994 (Miyagi, 1994) (see Chapter 1). Detailed data (Coll. Date, Loc. and register MZB number etc.) of each host material was shown in a part of description of each nematode species. The viscera were removed from carcass of rodent and opened with scissors. Contents of each portion of the alimentary canal were rinsed separately and examined for nematodes under a stereomicroscope. Scrapings were also be taken from each portion of the alimentary canal and examined. The worms were fixed and stored in 70% ethanol.

**Morphological observation:** Later, the worms were examined using a compound Olympus BH series microscope (Olympus Co. Ltd., Tokyo, Japan) with a drawing tube or a Nikon microscope (Nikon Co., Tokyo, Japan) attached with a Canon PS s5is digital camera (Canon Inc., Tokyo, Japan), and a JEOL JSM5310LV scanning electron microscope (SEM) (JEOL Ltd., Tokyo, Japan). For light microscopy, the specimens were cleared in glycerol–alcohol solution. For scanning electron microscope, the specimens were fixed in glutaraldehyde, dehydrated through an ethanol series, and freeze–dried then coated with gold at 5–8 mA for 5 minutes using an ion coater Eiko IB-2 (Eiko Co., Tokyo, Japan). Characters recorded by light microscope measurements were made with an ocular micrometer. Measurements (range, followed by mean in parentheses) are given in micrometers unless otherwise stated.

## Results and discussion

### Description

***Syphacia (Rumbaisyphacia)* Dewi, Hasegawa and Asakawa, 2014 (new subgenus)**

*Diagnosis* –Cephalic plate round. Cephalic papillae pedunculated. Amphidial pores with porous patches laterally. Cephalic vesicle present. Cervical alae absent. Lateral alae vesicular. Pharynx with setiferous apical margin. Male with three mamelons. Gubernaculum with non-ornamented accessory piece. Parasites of murine rodents.

*Type and only species -Syphacia* (*R.*) *kumis*

***Syphacia* (*R.*) *kumis* Dewi, Hasegawa and Asakawa, 2014 (new species)**

**(Figs. 2-1a, b)**

*General* –Medium sized pinworm with subgeneric chatacteristics defined above. Cuticle with faint transverse striations. Oral aperture surrounded by three triangular lips, one dorsal and two subventral; anterior margin of pharynx setiferous; four large cephalic papillae pedunculated, situated squarely; amphids close to subventral cephalic papillae. Esophagus of typical oxyuroid form with valved bulb. Nerve ring anterior to midlevel of esophageal corpus. Cephalic vesicle extending to nerve ring level. Deirids not seen.

*Male (holotype and 10 paratypes)* –Total length 1.51–1.72 (1.65) mm, maximum width 111–128 (125). Posterior body bent ventrally. Cephalic papillae situated trapezoidally with wider

distance ventrally. Lateral alae large, vesicular. Total esophagus 352–393 (353) long: pharynx 13–17 (16) long and 17–24 (22) wide, corpus 252–278 (273) long and 34–39 (37) wide, isthmus 16–25 (21) wide at narrowest level, and bulb 52–70 (67) long by 68–78 (71) wide. Nerve ring 127–147 (132), and excretory pore far posterior to esophago-intestinal junction, protruded, 568–667 (617) from cephalic end. Three mamelons with prominent annulations developed at ventral posterior body; anterior mamelon 72–103 (92) long, middle mamelon 92–103 (97) long and posterior mamelon 64–100 (80) long. Distance from cephalic end to anterior edges of anterior, middle and posterior mamelons 820–926 (862), 1.04–1.16 (1.07) mm and 1.21–1.37 (1.29) mm, respectively. Spicule single, relatively short, thin, needle-shaped, 79–84 (83) long, i.e. 4.72–8.58 (5.0) % of WL). Gubernaculum, 39–42 (41) long with thin, unornamented accessory piece of 10–12 (11) long. Caudal papillae present in 3 pairs, 2 pairs small, near cloaca and 1 pair, large, protruding posterolaterally. Tail 108–136 (121) long [i.e. 6.4–8.1 (7.4)% of WL].

*Female* (*allotype and 10 paratypes)* –Body slender, relatively stout; length 3.21–4.12 (3.60) mm, width 192–279 (212). Cephalic papillae situated quadrangularly. Distance between amphids 37.7–39.2 (n=2). Lateral alae small, vesicular. Total esophagus 470–537 (500) long: pharynx 17–21 (19) long and 33–38 (36) wide, corpus 369–404 (384) long and 47–56 (50) wide, isthmus 15–21 (18) long, 28–39 (34) wide at narrowest level, and bulb 96–114 (98) long by 97–117 (108) wide. Nerve ring 161–181 (174), and excretory pore 726–861 (795), from cephalic end. Vulva protruded, 0.97–1.16 (1.08) mm from cephalic end; vagina and ovejector directed posteriorly. Distance between excretory pore and vulva 228–295 (270) [i.e. 6.7–8.3 (7.6) % of WL]. Eggs ellipsoidal, asymmetrical with one side flattened, operculated in bubble side, shell surface pitted, embryonated in uteri, 96–102 x 34–40. Uterus extending

anteriorly from just posterior of esophageal bulb and ending posteriorly near anus. Tail relatively long, tapering to pointed end, 500–607 (552) long [i.e. 14.6–16.3 (15.3) % of WL].

*Type host* –*Eropeplus canus* Miller and Hollister, 1921 (Sulawesi soft-furred rat) (Rodentia: Muridae).

*Symbiotype* –The type host was deposited to the American Museum of Natural History with accession number M-267755.

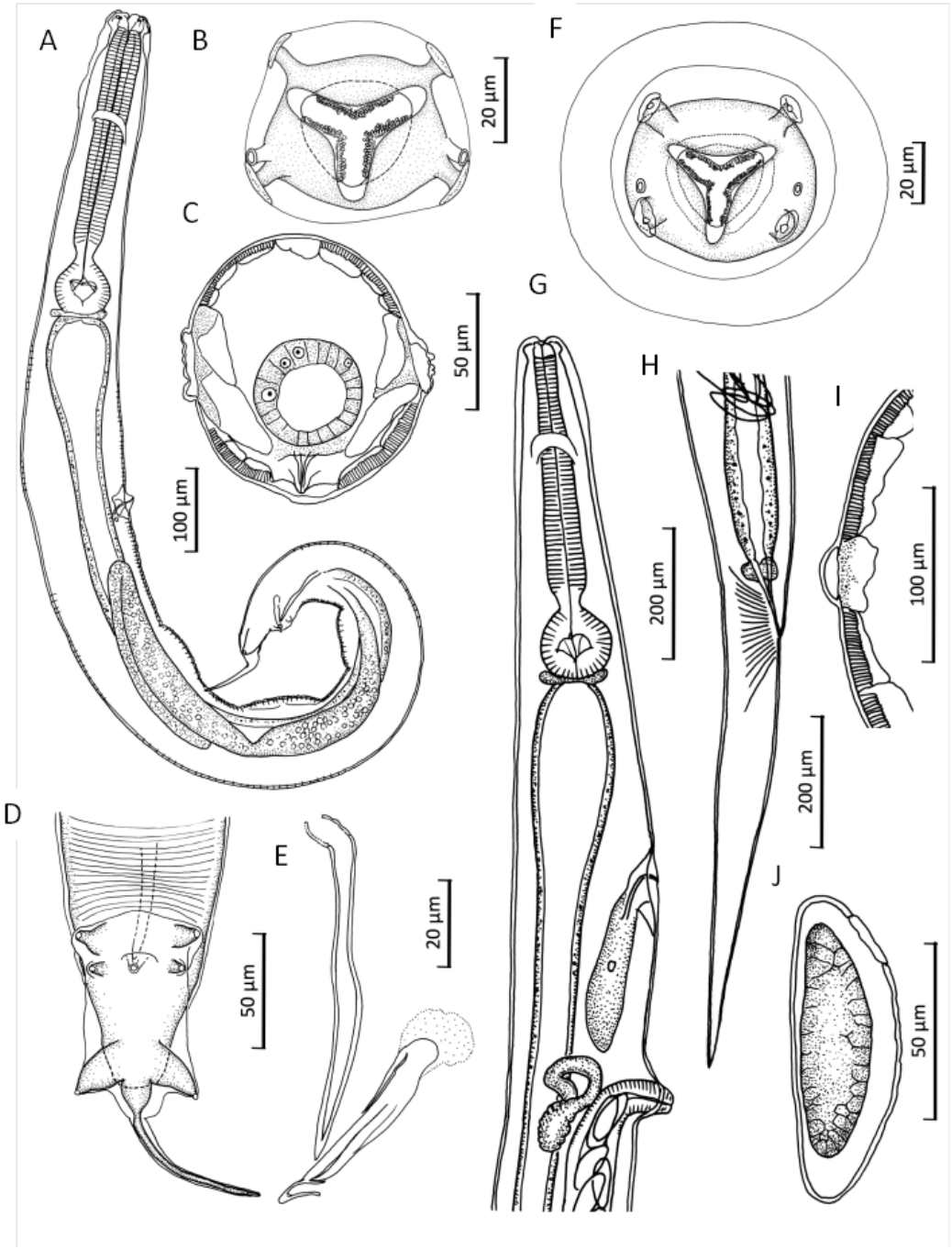
*Site of infection* –Cecum.

*Type locality* –Lambanan, Sulawesi, Indonesia.

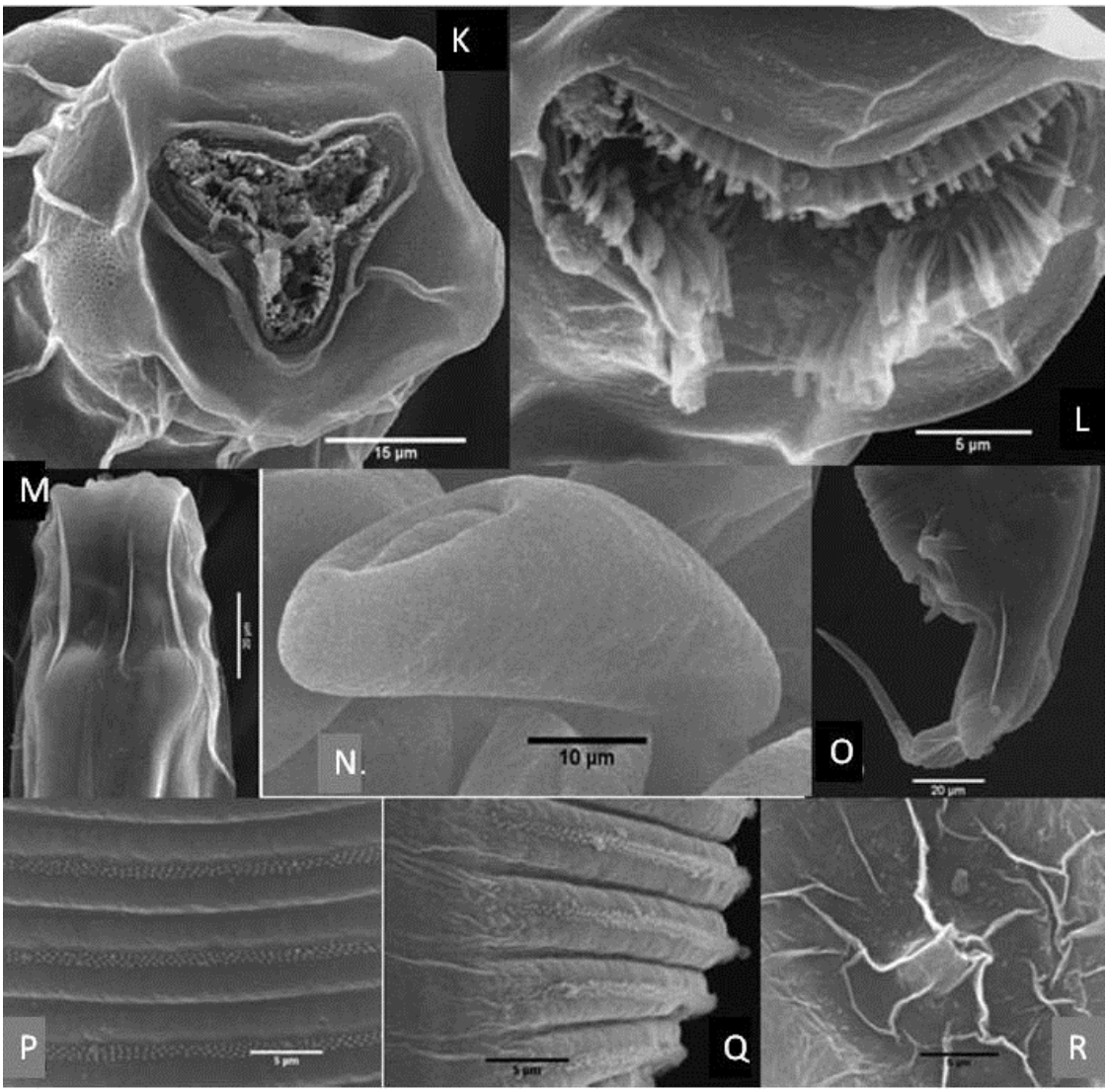
*Specimens deposited* – Holotype male and allotype female (MZBNa 624), 10 males and 10 females paratypes (MZBNa 625*),* Lambanan, Sulawesi, Indonesia, coll. H. Hasegawa, 31 July 1992.

*Etymology* –The subgeneric name was created by combining an Indonesian word 'rumbai', meaning fringe, and *Syphacia*, and the species epithet was derived from an Indonesian word 'kumis', which means moustach. Both words were adopted as the setiferous apical margin of pharynx reminds of fringed edge and moustach.

*Remarks* –This is a typical member of the genus *Syphacia* Seurat, 1914 by having three mamelons in males (Petter and Quentin, 1976; Hugot, 1988). Three subgenera have been recognized: *Syphacia* Seurat, 1914, *Cricetoxyuris* Hugot, 1988 and *Sueratoxyuris* Hugot, 1988 (Hugot, 1988). By lacking cervical alae, developed deirids, and by having an unornamented accessory piece of gubernaculum, and vesicular lateral alae, it resembles subgenus *Syphacia* (Hugot, 1988). Pedunculated cephalic papillae arranged quadrangularly are also seen in *Syphacia (Syphacia) muris* (Yamaguti, 1935) (Quentin, 1971). However, setiferous apical margin of pharynx is a quite peculiar characteristic. A comparable structure has been known only in *Oxyuris* (Schrank, 1788) among the oxyuroids of vertebrates (Petter and Quentin, 1976; Gibbons, 2010). A new subgenus is hence proposed.




Figs. 2−1a. *Syphacia* (*Rumbaisyphacia*) *kumis*, new species from *Eropeplus canus* in south Sulawesi, Indonesia. (A) male, holotype, lateral view; (B) cephalic end of male, apical view; (C) midbody in cross section of male; (D) posterior end of male, ventral view; (E) spicule and gubernaculum, lateral view; (F) cephalic end of female, apical view; (G) anterior portion of female, lateral view; (H) Posterior portion of female; (I) midbody in cross section of female; (J) egg.




Figs. 2–1b. Scanning electron microscopy of *Syphacia* (*Rumbaisyphacia*) *kumis*, new species from *Eropeplus canus* in south Sulawesi, Indonesia. (K) cephalic end, apical view; (L) mouth opening showing setiferous apical margin of pharynx; (M) anterior end, lateral view; (N) egg; (O) posterior end of male; (P) mamelon, ventral view; (Q) mamelon (lateral view); (R) protruded vulva.

### *Syphacia* (*Segienamsyphacia*) Dewi, Hasegawa and Asakawa, 2014 (new subgenus)

*Diagnosis* –Cephalic plate round. Cephalic papillae and amphidial pores forming circle. Amphidial pores with porous patches laterally. Cephalic vesicle present. Oral aperture triradiate, surrounded by 3 lips in male, hexagonal in female. Cervical alae absent. Lateral alae vesicular in male. Male with three mamelons. Accessory piece of gubernaculum unornamented. Parasites of murine rodents.

*Type and only species -Syphacia (Se.) yuniae*

### *Syphacia (Se.) yuniae* Dewi, Hasegawa and Asakawa, 2014 (new species)

**(Figs. 2-2a, b)**

*General* –With subgeneric characteristics defined above. Small sized worms with cuticle striated transversely. Cephalic vesicle weakly developed. Amphidial pores slightly closer to subventral cephalic papillae than to subdorsal ones. Esophagus with a corpus, distinct isthmus and terminating in spherical bulb. Nerve ring at middle of esophageal corpus. Deirid not seen.

*Male (holotype and 10 paratypes)* –Posterior body bent ventrally; length 1.00–1.25 (1.14) mm, maximum width 70–86 (81). Mouth triradiate, surrounded by three lips; distance between amphidial pores 8.2–11.5 (n=2); lateral alae large; total esophagus including pharynx, corpus and bulb 247–277 (254) long: pharynx 9–11 (10) long and 10–13 (11) wide, corpus 170–200 (179) long and 24–29 (26) wide, isthmus 13–15 (13) long and 13–15 (14) wide at narrowest level, bulb 47–56 (52) long by 50–55 (54) wide; nerve ring and excretory pore 100–107 (109) and 376–435 (404) from anterior end, respectively; three mamelons on ventral surface of body provided with many transverse bands, each with central rows of

spinules: anterior mamelon, middle mamelon and posterior mamelon 60–77 (64) long, 35–54 (46) long and 24–38 (32) long; distance from cephalic end to anterior edges of anterior, middle and posterior 592–726 (652), 661–857 (758) and 769–962 (867), respectively; spicule single, thin, unornamented needle-shaped, relatively long, 64–82 (73) long [i.e. 5.5–7.5 (6)% of WL]; gubernaculum 22–28 (25) long; accessory piece of gubernaculum protruded from body 9–12 (10); caudal papillae present in 3 pairs, 2 pairs small pre cloaca and 1pair large post cloacal papillae, protruding posterolaterally; tail 126–157 (149) long including whip-like process [i.e. 10.2–14.3 (13) % of WL].

*Female (allotype and 10 paratypes)* –Length 2.34–2.56 (2.45) mm, width 155–200 (181). Cephalic vesicle present, extending posteriorly to nerve ring. Oral aperture hexagonal. Distance between amphidial pores 16.2–17.8. Lateral alae absent; total esophagus including pharynx, corpus and bulb 273–399 (381) long: pharynx 16–22 (21) long and 18–28 (20) wide, corpus 245–287 (266) long and 44–50 (47) wide, isthmus 18–28 (22) wide at narrowest level, bulb 72–85 (81) long by 83–95 (87) wide; nerve ring 112–148 (141), excretory pore 471–570 (501) from cephalic end; vulva not protruding, 753–853 (811) from cephalic end; vagina and ovejector weakly developed, directed posteriorly; distance between excretory pore and vulva 201–324 (269) [i.e. 8.1–12.8 (10.9) % of WL]. Eggs asymmetrical with one side flattened, having operculum on convex side, closer to equator of egg, shell surface densely pitted, containing embryo with visible esophagus in uterus, 68–74 (71.5) x 24–28 (25.7); uterus occupying in the middle of body, extending from level of excretory pore to near posterior end of middle 1/3 of body; tail long conical with pointed end, relatively long, 469–540 (520) [i.e. 19.4–23.1 (21.1) % of WL].

*Type host –Eropeplus canus* Miller and Hollister, 1921 (Sulawesi soft-furred rat) (Rodentia: Muridae).

*Symbiotype* –The type host was deposited to the American Museum of Natural History with accession number M-267755.

*Site of infection* –Cecum.

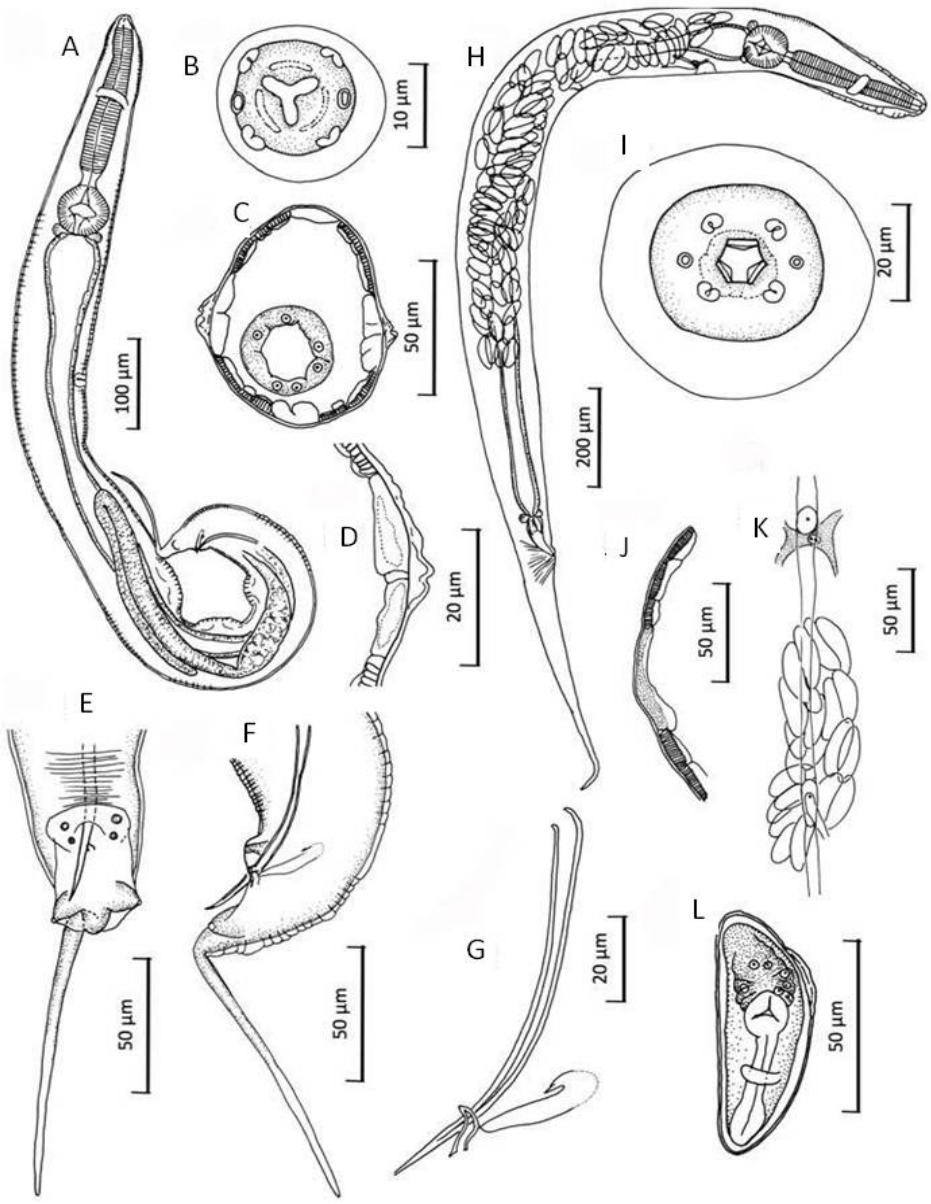
*Type locality* Lambanan, Sulawesi, Indonesia.

*Specimens deposited* –Holotype male and allotype female (MZBNa 624), 10 males and 10 females paratypes (MZBNa 625*),* Lambanan, Sulawesi, Indonesia, coll. H. Hasegawa, 31 July 1992.

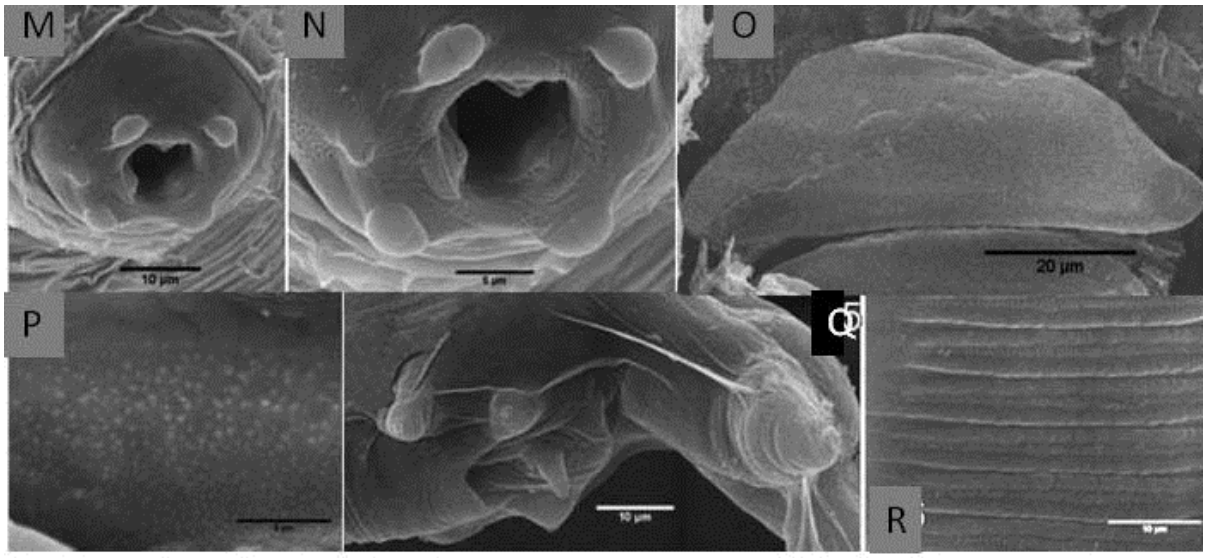
*Etymology* –Subgeneric name was created by combining Indonesian word 'Segienam' meaning hexagonal, symbolizing hexagonal oral shape in female, and *Syphacia*. Species epithet is dedicated to Ms. Yuni Apriyanti, to whom we are greatly indebted on preparation of specimen for SEM observation.

*Remarks* –This is also a typical member of the genus *Syphacia* Seurat, 1914 by having three mamelons in males (Petter and Quentin, 1976; Hugot, 1988). Among the three subgenera recognized, it is close to the subgenus *Syphacia* by lacking cervical alae and developed deirids, and by having an unornamented accessory piece of the gubernaculum and vesicular lateral alae (Hugot, 1988). However, the hexagonal oral shape in the female has not been

known for other members of the subgenus *Syphacia* species and other two subgenera. Hence new subgenus is proposed. Similar oral shape has been known in *Oxyuris*, *Brasilnema* Moravec et al., 1992, *Paraustroxyuris* Mawson, 1964, *Petronema* Hugot, 1983, *Royandersonia* Moravec and Van As, 2004 among the oxyuroids parasitic in vertebrates (Petter and Quentin, 1976; Gibbons, 2010). The egg operculum position is also characteristic because most congeners of *Syphacia* have an egg operculum closer to pole (Quentin, 1971; Petter and Quentin, 1976; Hugot, 1988).




Figs. 2-2a. *Syphacia* (*Segienamsyphacia*) *yuniae*, new species from *Eropeplus canus* in south Sulawesi, Indonesia. (A) male, holotype, lateral view; (B) cephalic end of male, apical view; (C) midbody in cross section of male; (D) midbody in cross section of male, higher magnification; (E) posterior portion of male, ventral view; (F) posterior portion of male; lateral view; (G) spicule and gubernaculum, lateral view; (H) female, lateral view; (I) cephalic end of female, apical view; (J) midbody in cross section of female; (K) excretory pore and vulva, showing poorly developed vagina; (L) egg.




Figs. 2-2b. Scanning electron microscopy of *Syphacia* (*Segienamsyphacia*) *yuniae*, new species from *Eropeplus canus* in south Sulawesi, Indonesia. (M) cephalic end of female, apical view; (N) cephalic end of female, apical view, higher magnification; (O) egg; (P) enlarged view of eggshell surface; (Q) caudal papilla of male, lateral view; (R) mamelon, ventral view.

## *Syphacia* (*Syphacia*) Seurat, 1916

### *Syphacia (Syphacia) rifaii* Dewi and Hasegawa, 2010 (new species)

**(Figs. 2-3a, b)**

*General* –Small worm. Cuticle with transverse striations. Cephalic vesicle. Esophagus of typical oxyuroid form. Cervical alae absent. Deirids not seen. Cephalic plate round; mouth surrounded by 3 weakly elevated lips, 1 dorsal and 2 subventral; 4 cephalic papillae large, arranged almost squarely; amphidial pores with porous patches laterally. Excretory pore posterior to esophago–intestinal junction.

*Male* (holotype and 12 paratypes) –Length 0.60–0.78 (0.67) mm, maximum width 74–109 (89). Distance between amphidial pores 14. Lateral alae large, vesicular, extending from esophageal bulb level to posterior mamelon level. Total esophagus, including pharynx, corpus, and bulb, 167–198 (178) long: pharynx 9–13 (11) long, corpus 122–151 (134) long and 20–31 (24) wide, bulb 34–46 (41) long by 37–52 (44) wide. Nerve ring 80–96 (88), and excretory pore 266–332 (301) from cephalic end, respectively. Mamelons at ventral posterior body, 3 well developed, anterior mamelon 41–53 (46) long, middle mamelon 40–56 (45) long, and posterior mamelon 27–48 (35) long. Distance from cephalic end to anterior edges of anterior, middle, and posterior mamelons 354–423 (386), 396–500 (438), and 467–607 (526), respectively. Spicule thin, needle–shaped, 61–70 (65) long, i.e., 7.9–11.5% (9.8%) of worm length (WL); gubernaculum stout, hook–shaped, 22–27 (25) long; accessory piece of gubernaculum relatively thin, unornamented. Caudal papillae in 3 pairs, 2 pairs near cloaca and 1 posterior pair protruding posterolaterally. Tail including short process 35–60 (44) long, i.e. 5.5–8.1% (6.6%) of WL.

*Female* (allotype and 13 paratypes) –Length 1.40–2.19 (1.82) mm, maximum width 147–244 (182). Distance between amphidial pores 16. Lateral alae absent. Total esophagus, including pharynx, corpus, and bulb, 246–277 (262) long: pharynx 12–16 (15) long, corpus 171–206 (189) long and 30–45 (36) wide, bulb 49–68 (59) long by 58–75 (66) wide. Nerve ring 80–108 (99), excretory pore 322–454 (388) from cephalic end. Vulva not protruding, 449–582 (503), i.e., 22–37% (28%) of WL from cephalic end; vagina and ovejector directed posteriorly. Distance between excretory pore and vulva 95–145 (115), i.e., 4.8–8.4% (6.4%) of WL. Eggs oval, asymmetrical, operculated, concaved side with wrinkled shell, embryonated in uteri, 68–70 (69) x 23–29 (27). Uterus extending anteriorly to the esophageal bulb and ending posteriorly near anus. Tail conical, relatively short, 181–274 (222), i.e., 8.9–15.0% (12.3%) of WL.

*Type host –Bunomys chrysocomus* (Hoffmann, 1887) (Yellow–haired hill rat) (Rodentia: Muridae).

*Other host –Bunomys prolatus* Musser, 1991 (Long–headed hill rat) (Rodentia: Muridae).

*Bunomys penitus* (Miller & Hollister, 1921) (Inland hill rat) (Rodentia: Muridae).

*Site of infection* –Cecum.

*Type locality* –Donggala, Central Sulawesi, Indonesia.

*Other locality* –Lore Lindu, Central Sulawesi, Indonesia.

Masembo Watershed, Mekongga Mountains, south–east Sulawesi, Sulawesi, Indonesia

*Date of collection* –25 June 2008 (host: *B. chrysocomus*), 16 June 2001(host: *B. prolatus*).

*Specimens deposited* –Holotype male and allotype female (MZB Na418), 9 male and 9 female. paratypes (MZB Na 423), 2 male and 4 female, paratypes (NSMT-As 3607) (host: *B. chrysocomus*); 12 females (MZB Na 216) (host: *B. prolatus*).

*Etymology* –Species epithet is dedicated to Prof. Mien A. Rifai, Indonesian Academy of Sciences (AIPI).

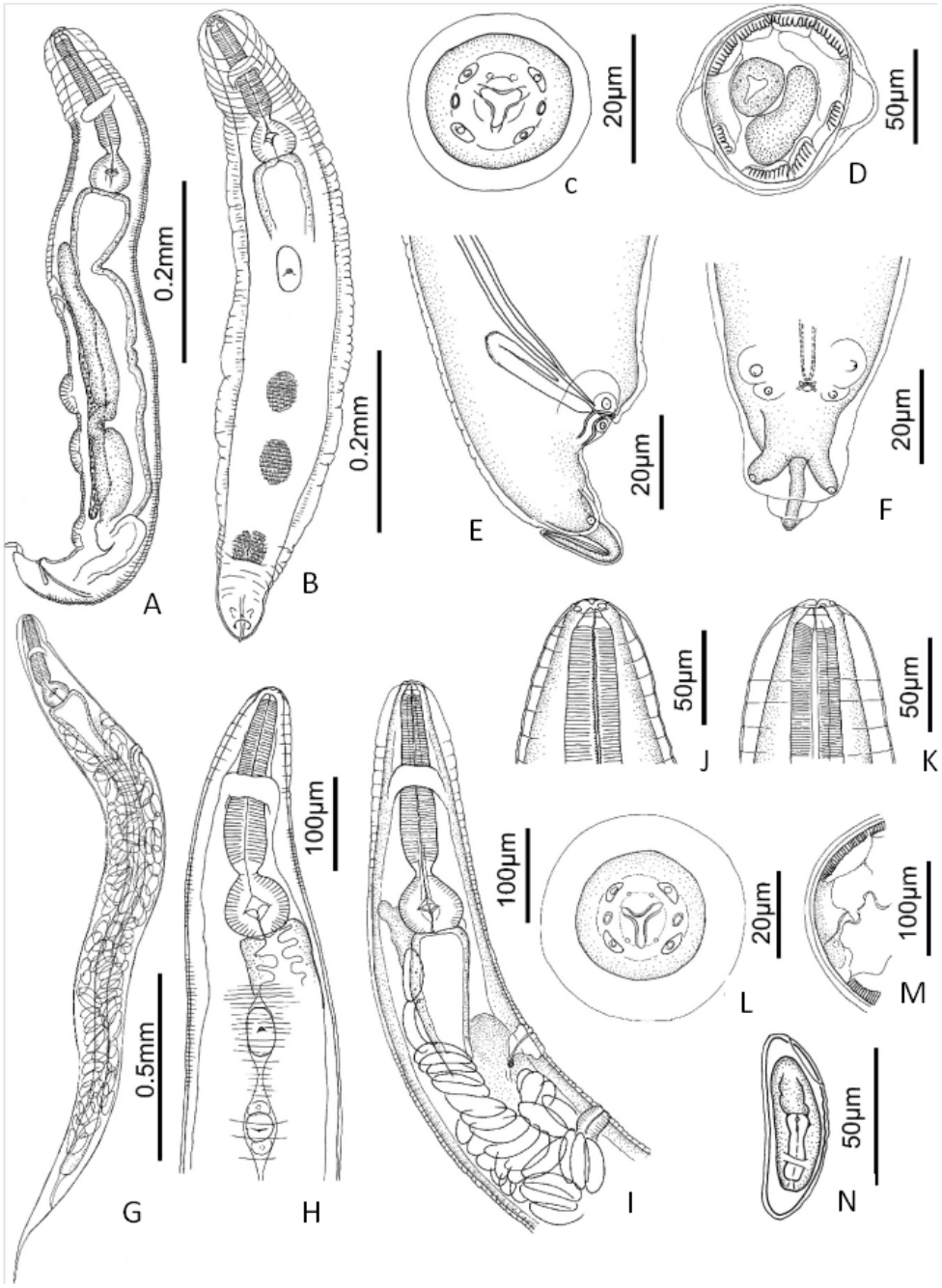



Fig. 2-3a. *Syphacia (Syphacia) rifaii* collected from *Bunomys chrysocomus* in Central Sulawesi, Indonesia. (A) holotype male, left lateral view; (B) paratype male, ventral view; (C) cephalic end of male, apical view; (D) cross section of male midbody; (E) posterior end of paratype male, right lateral view; (F) posterior end of male, ventral view; (G) allotype female, right lateral view; (H) anterior portion of allotype female, ventral view; (I) anterior portion of paratype female, right lateral view; (J) cephalic end of paratype female, ventral view; (K) cephalic end of paratype female, right lateral view; (L) cephalic end of paratype female, apical view; (M) lateral field of female, mid-body in cross section; (N) egg.

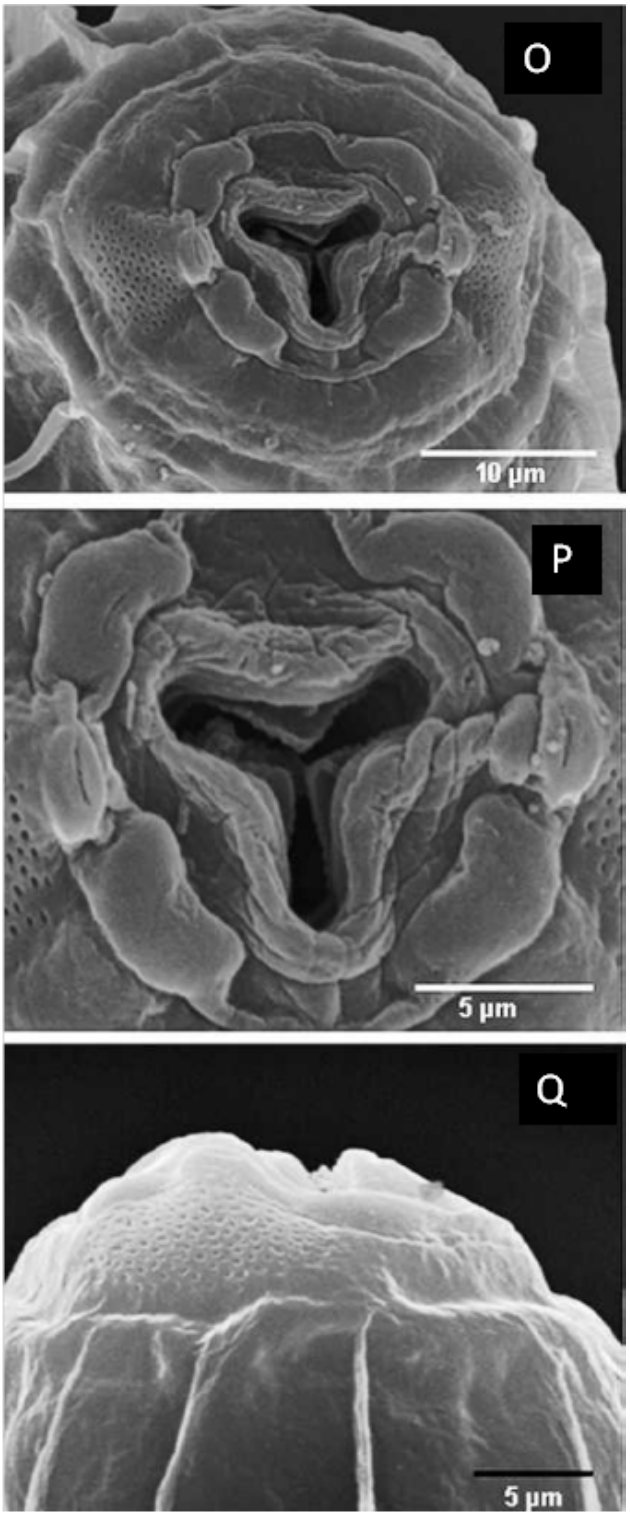



Fig. 2-3b. Scanning electron microscopy of *Syphacia (Syphacia) rifaii* collected from *Bunomys chrysocomus* in Central Sulawesi. (O) cephalic end of female, apical view; (P) enlarged view of cephalic apex of female, apical view; (Q) cephalic end of female, lateral view.

***Syphacia (Syphacia) taeromyos* Dewi and Hasegawa, 2014 (new species)**

**(Figs. 2-4a, b, c)**

*General* –Small nematodes with transverse cuticularstriations; cephalic vesicle developed, continuous to body cuticle posteriorly; cephalic plate round, only slightly extended laterally; mouth opening surrounded by three protruded lips, one dorsal and two subventral. Four cephalic papillae, large, arranged almost square; amphids opening sublaterally, with porous patches laterally; esophagus of typical oxyuroid form with valved bulb; cervical alae absent; deirids not seen.

*Male* (holotype and 6 paratypes) –Posterior body bent ventrally; length 1.95–2.17 (2.09) mm, width 144–165 (153); distance between amphids 23 (n = 1); cephalic vesicle 104–134 (119) wide; lateral alae vesicular, moderately developed; total esophagus including pharynx, corpus and bulb 235–261 (248) long: pharynx 9–13 (12) long and 12–15 (13.5) wide, corpus 163–177 (173) long and 32–41 (36) wide, isthmus 17–21 (19) wide at narrowest level, bulb 59–69 (64) long by 63–72 (66) wide; nerve ring at posterior part of oesophageal corpus, 146–157 (152), and excretory pore far posterior to oesophago–intestinal junction, 821–958 (919) from cephalic end, respectively; three mamelons with prominent transverse furrows present at ventral surface of posterior body: anterior mamelon 119–134 (127) long, middle mamelon 74–96 (82) long and posterior mamelon 61–72 (66) long; distance from cephalic end to anterior edges of anterior, middle and posterior mamelons 1.19–1.36 (1.28), 1.43–1.58 (1.52) and 1.65–1.83 (1.77) mm, respectively; spicule single, thin, needle–shaped, slightly constricted at middle, relatively short, 62–77 (68) long (i.e. 3.0–3.7 (3.3) % of WL); gubernaculum rod–like, 28–34 (31) long; accessory piece of gubernaculum relatively thin, unornamented; caudal papillae present in three pairs, two pairs small, near cloaca and one

posterior pair large, protruding posterolaterally; tail including short terminal process 64–71 (67) long (i.e. 2.95–3.4 (3.2)% of WL).

*Female* (allotype and 4 paratypes) –Body relatively stout; length 4.85–5.85 (5.28) mm, width 390–476 (419); distance between amphidial pores 41–43 (n =2); small flat vesicular lateral alae present; total esophagus including pharynx, corpus and bulb 422–462 (445) long: pharynx 16–22 (19) long and 17–18 wide (n= 2), corpus 302–395 (334) long and 58–70 (65) wide, isthmus 26–32 (30.4) wide at narrowest level, bulb 99–114 (108) long by 96–119 (109) wide; nerve ring at middle of oesophageal corpus, 179–202 (187), excretory pore 1.07–1.15 (1.11) mm from cephalic end; vulva not protruding, 1.19–1.31 (1.27)mm (i.e. 22.4–24.4 (23.8)% of WL) from cephalic end; vagina and ovejector directed posteriorly; distance between excretory pore and vulva 119–133 (155) (i.e. 2–4 (2.9)% of WL); eggs long, elliptical, asymmetrical with one side flattened, operculated, shell surface uneven and densely pitted, containing morulastage embryo in uterus, 57–62 (59) x 21–24 (23); uterus winding, extending anteriorly to oesophageal bulb and ending posteriorly near anus; tail conical with pointed end, relatively long, 693–886 (804) (i.e. 13.5–18.1 (14.7)% of WL).

*Type host –Taeromys celebensis* (Gray, 1867) (long–tailed Taeromys) (Rodentia: Muridae).

*Site of infection* –Cecum.

*Type locality* –Masembo Watershed, Mekongga Mountains, south–east Sulawesi, Sulawesi, Indonesia

*Date of collection* –4 July 2011.

*Specimens deposited* –Holotype male and allotype female (MZB Na 602), five male and three female paratypes (MZB Na 603 and NSMT–As 3904).

*Etymology* –Species epithet is derived from the generic name of the host rodent, *Taeromys*.

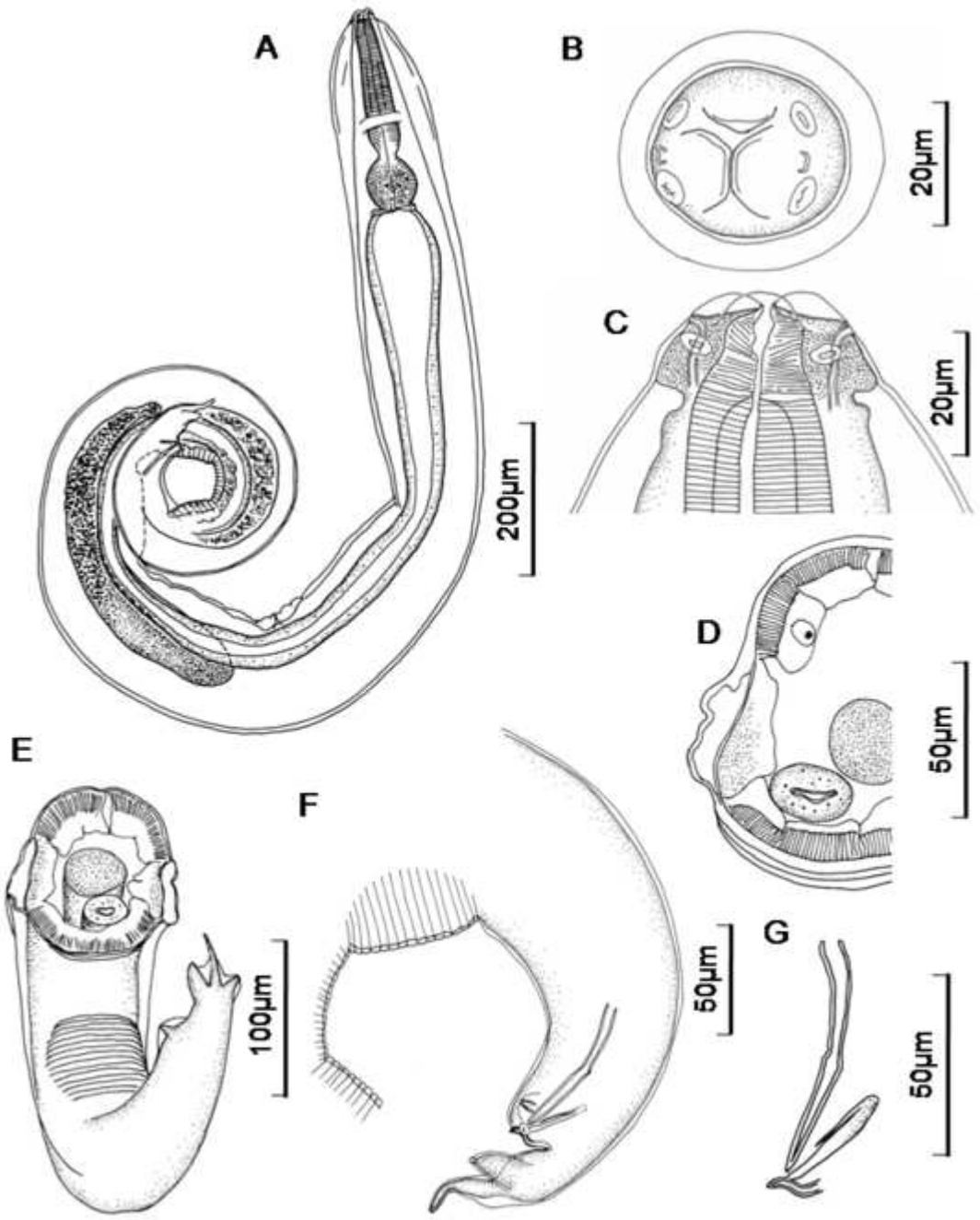



Fig. 2-4a. Male of *Syphacia (Syphacia) taeromyos* from *Taeromys celebensis* in south-east Sulawesi, Indonesia: (A) holotype, lateral view; (B) cephalic end, apical view; (C) cephalic end, ventral view; (D) midbody in cross-section; (E) posterior end, ventral view; (F) posterior end,lateral view; (G) spicule and gubernaculum, lateral view.

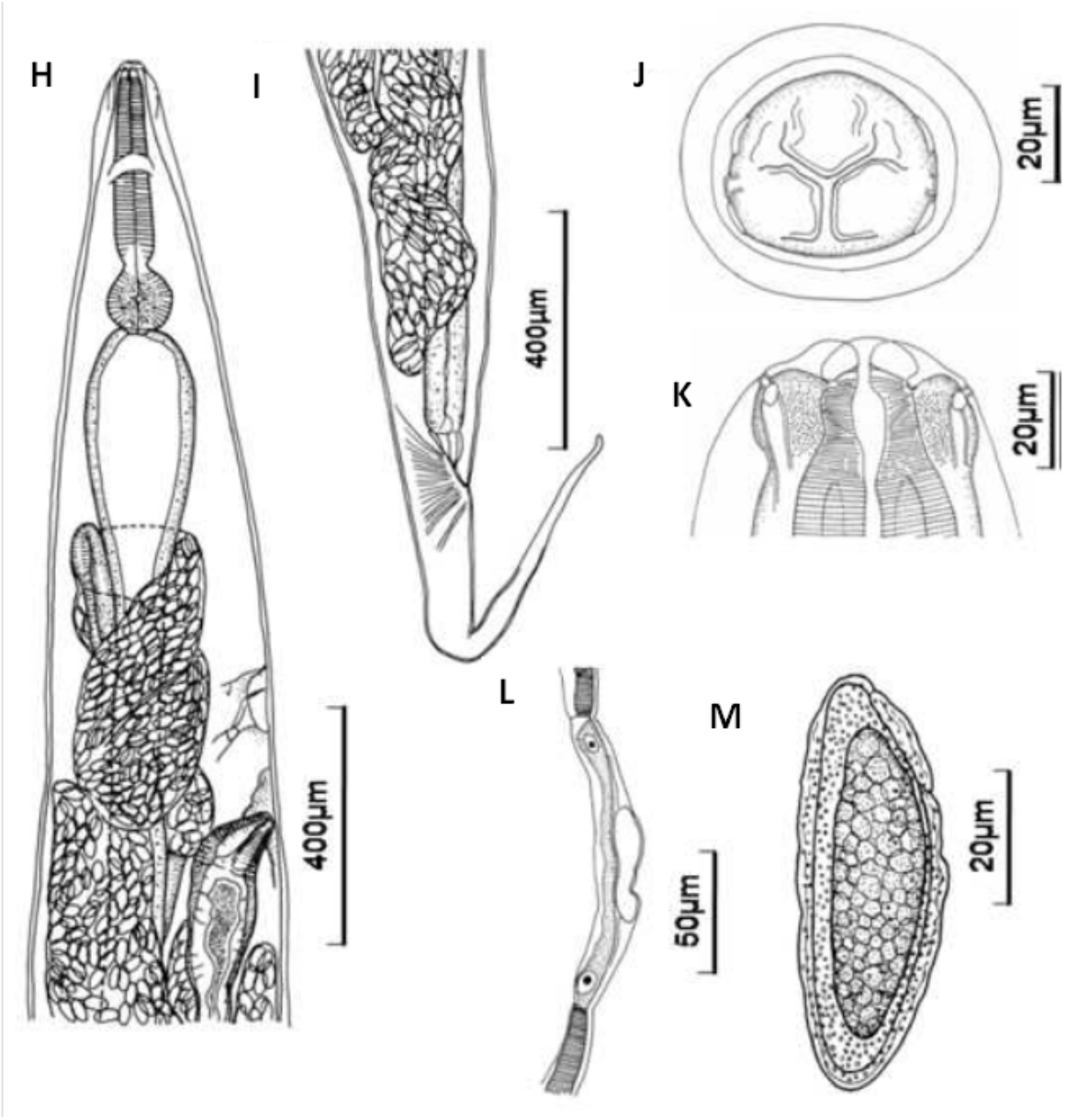



Fig. 2-4b. Female of *Syphacia (Syphacia) taeromyos* from *Taeromys celebensis* in south–east Sulawesi, Indonesia: (H) anterior portion, lateral view; (I) posterior portion, lateral view; (J) cephalic end, apical view; (K) cephalic end, ventral view; (L) lateral field, midbody in cross–section; (M) egg.

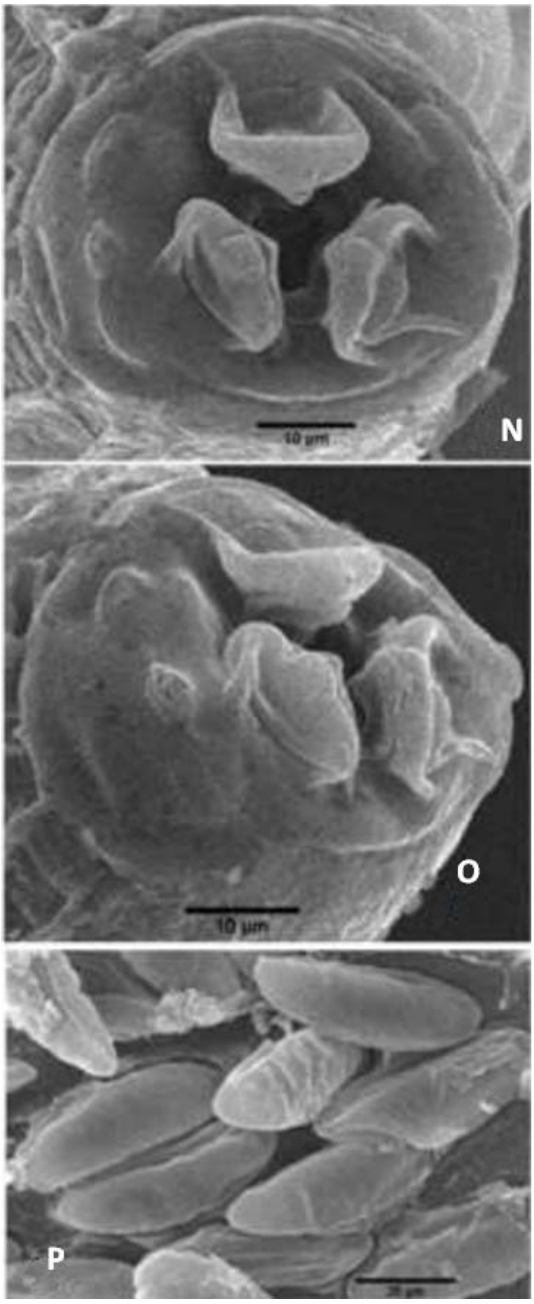



Fig. 2-4c. Scanning electron microscopy of *Syphacia (Syphacia) taeromyos* from *Taeromys celebensis* in south–east Sulawesi, Indonesia: (N) cephalic end, apical view; (O) cephalic end, lateral view; (P) eggs.

***Syphacia (Syphacia) paruromyos* Dewi and Hasegawa, 2014 (new species)**

**(Figs. 2-5a, b, c)**

*General* –Small nematodes, cuticle with faint striations; cephalic portion set–off from body by constriction, especially clearly in female; cephalic plate round, without lateral extension; mouth with three developed lips, one dorsal and two subventral; four large papillae present; two at each lateral side; amphids with porous patches laterally; esophagus of typical oxyuroid form with valved bulb; cephalic vesicle present; cervical alae absent; deirids not seen.

*Male* (holotype and 6 paratypes from *P. dominator* of Mangolo) –Posterior body bent ventrally. Length 1.37–1.65 (1.49) mm, maximum width 114–133 (123); lateral alae large, vesicular; distance between amphids 18 (n =1); cephalic vesicle 67–89 (78) wide; total esophagus 219–245 (229) long: pharynx 13–16 (14) long and 14–16 (15) wide, corpus 157–176 (164) long and 28–33 (30) wide, isthmus 15–18 (17) wide at narrowest level, and bulb 48–56 (51) long by 47–59 (53) wide; nerve ring slightly posterior to midlevel of oesophageal corpus, 104–115 (109), and excretory pore far posterior to oesophago–intestinal junction, 544–618 (568) from cephalic end; three mamelons developed at ventral posterior body; anterior mamelon 66–83 (72) long, middle mamelon 54–64 (58) long and posterior mamelon 45–61 (53) long; distance from cephalic end to anterior edges of anterior, middle and posterior mamelons 0.76–0.88 (0.81) mm, 0.90–1.09 (0.97) mm and 1.06–1.32 (1.15) mm, respectively; spicule single, relatively short, thin, needleshaped, slightly constricted basal to middle, 53–59 (56) long (i.e. 3.5–4.1 (3.8)% of WL); gubernaculum, 27–35 (30) long with thin, unornamented accessory piece of

11–14 (13) long; caudal papillae present in three pairs, two pairs small, near cloaca and one pair, large, protruding posterolaterally; tail 112–134 (124) long (i.e. 6.8–9.3 (8.4)% of WL), with whip–like appendage of 71–102 (82) long.

*Female* (allotype and 9 paratypes from *P. dominator* of Mangolo) –Body relatively stout; length 2.65–2.98 (2.80) mm, width 201–256 (223); distance between amphids 32 (n = 1); lateral alae absent;cephalic vesicle 112–127 (119) wide; total esophagus 299–346 (326) long: pharynx 15–17 (16) long and 17–19 (18) wide, corpus 217–257 (237) long and 45–53 (50) wide, isthmus 24–30 (26) wide at narrowest level, and bulb 67–81 (72) long by 71–90 (83) wide; nerve ring at midlevel of oesophageal corpus, 115–143 (130), excretory pore 396–584 (491), from cephalic end; vulva not protruding, 566–699 (650) from cephalic end (i.e. 21.9–26.4 (23.4) % of WL); vagina and ovejector directed posteriorly; distance between excretory pore and vulva 126–188 (147) (i.e. 4.4–7.1 (5.3) % of WL); eggs elliptical, asymmetrical with one side flattened, operculated, shell surface pitted, embryonated in uteri, 64–72 (68) x 24–29 (26); uterus extending anteriorly to the oesophageal bulb and ending posteriorly near anus; tail relatively long, tapering to pointed end, 384–449 (408) long (i.e. 12.8–17.4 (14.6)% of WL).

*Measurements of worms from P. dominator of Lambanan.*

*Male* (3 worms) –Length 2.04–2.12 (2.07) mm, maximum width 131–138 (134); cephalic vesicle 96–128 (112) wide; total esophagus 237–253 (243) long: pharynx 14–16 (15) long and 14–16 (15) wide, corpus 166–176 (170) long and 30–34 (32) wide, isthmus 15–22 (18) wide at narrowest level, and bulb 51–58 (55) long by 49–61 (54) wide; nerve ring 136–141

(138), and excretory pore 769–825 (797) from cephalic end; anterior, middle and posterior mamelons 74–108 (90), 54–80 (68) and 45–70 (58) long, respectively; distance from cephalic end to anterior, edges of anterior, middle and posterior mamelons 1.12–1.19 (1.16), 1.33–1.45 (1.39) and 1.63–1.71 (1.67) mm, respectively; spicule 56–59 (58) long (i.e. 2.6–2.9 (2.8)% of WL); gubernaculum 26–37 (31) long; accessory piece of gubernaculum relatively thin, 10–13 (11) long; tail 138–158 (150) long (i.e. 6.8–7.7 (7.2)% of WL); whip–like appendage 99–126 (116) long.

*Female* (5 worms) –Length 3.16–3.91 (3.58) mm, width 267–293 (280); cephalic vesicle 131–150 (141) wide; total esophagus 329–352 (338) long: pharynx 19–22 (20) long and 19–21 (21) wide, corpus 224–250 (236) long and 54–61 (57) wide, isthmus 26–32 (30) wide at narrowest level, bulb 74–93 (83) long by 86–102 (95) wide; nerve ring 118–128 (122), and excretory pore 503–650 (587), from cephalic end; vulva 612–871 (783) from cephalic end (i.e. 19.4–23.0 (21.8)% of WL); distance between excretory pore and vulva 109–240 (196) (i.e. 3.5–6.8 (5.4)% of WL); eggs 65–72 (69) x 24–29 (28); tail 541–576 (557) (i.e. 14.4–17.1 (15.6)% of WL).

*Type host*- *Paruromys dominator* (Thomas, 1921) (Rodentia: Muridae).

*Site of infection*- Cecum.

*Type locality* -MasemboWatershed, Mekongga Mountains, south–east Sulawesi, Sulawesi, Indonesia.

*Other locality* -Indonesia: south Sulawesi, Lambanan.

*Date of collection* -June 2011 (Mekongga); July 1992 (Lambanan).

*Specimens deposited* -Holotype male and allotype female (MZB Na 604), six male and nine female paratypes (MZB Na 605); other specimens from Mekongga (MZB Na 612; NSMT–As 3905); three males and five females from Lambanan (NSMT–As 3906).

*Etymology* -Species epithet is derived from the generic name of the host murine, *Paruromys*.

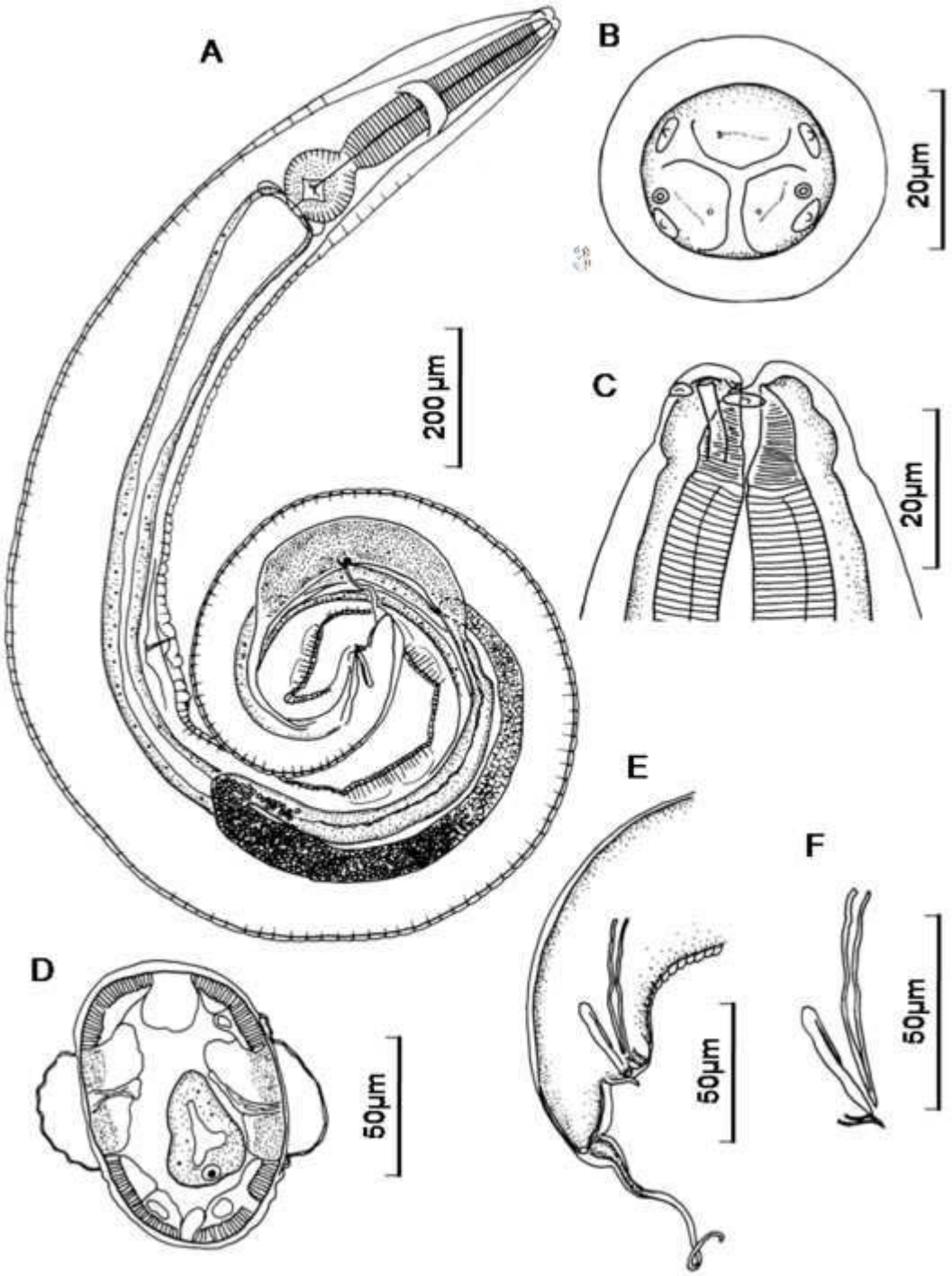



Fig. 2-5a. Male of *Syphacia (Syphacia) paruromyos* from *Paruromys dominator* in south-east Sulawesi, Indonesia: (A) holotype, lateral view; (B) cephalic end, apical view; (C) cephalic end, sublateral view; (D) midbody in cross-section; (E) posterior end, lateral view; (F) spicule and gubernaculum, lateral view.

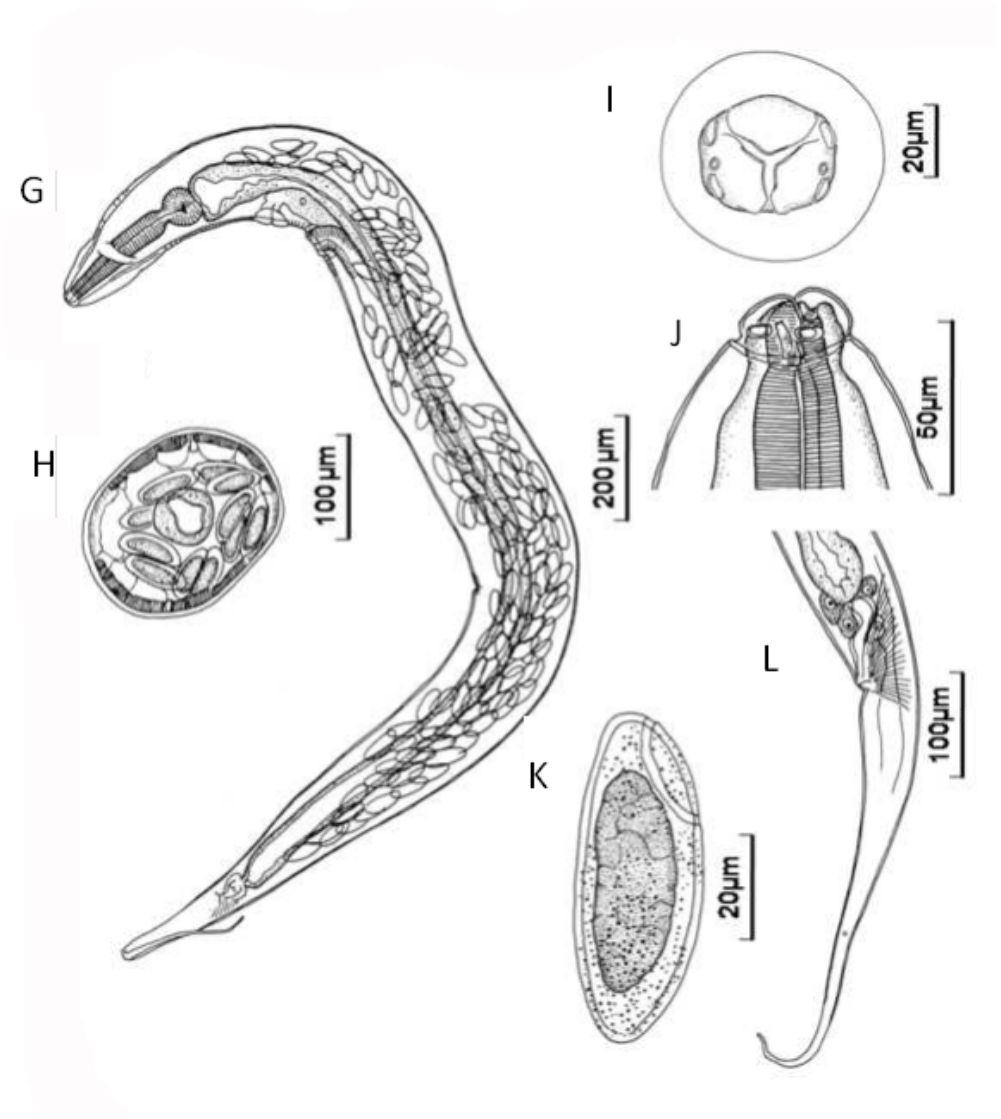



Fig. 2-5b. Female of *Syphacia (Syphacia) paruromyos* from *Paruromys dominator* in south–east Sulawesi, Indonesia: (G) paratype, lateral view; (H) midbody in cross–section; (I) cephalic end, apical view; (J) cephalic end, ventral view; (K) egg; (L) posterior portion, lateral view.

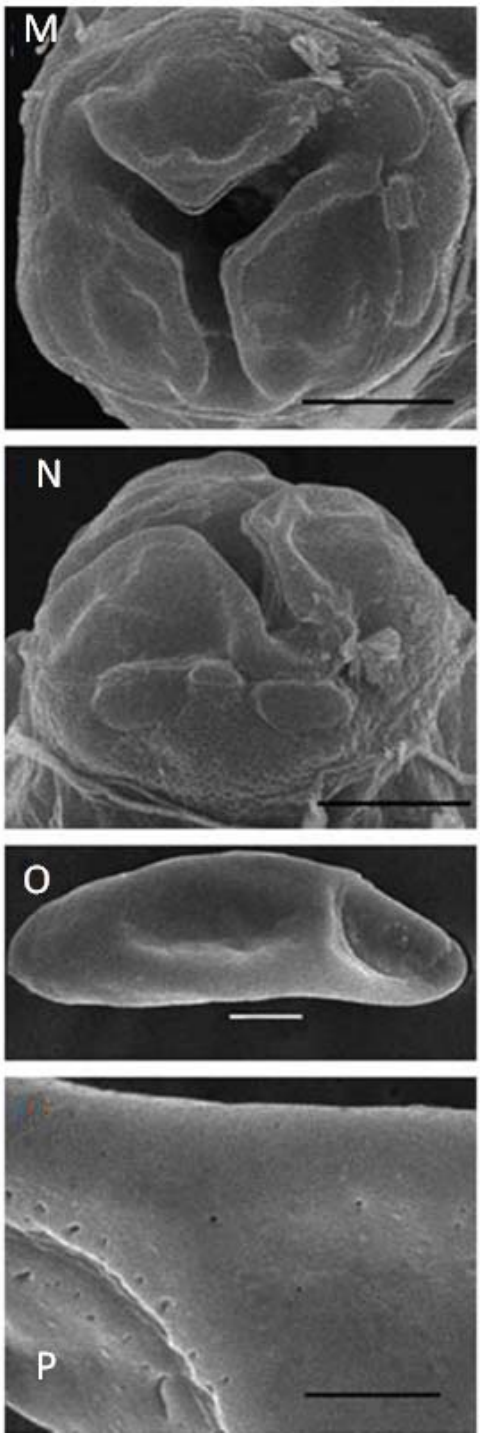



Fig. 2-5c. Scanning electron microscopy of female *Syphacia (Syphacia) paruromyos* from *Paruromys dominator* in south–east Sulawesi, Indonesia: (M) cephalic end, apical view; (N) cephalic end, lateral view; (O) egg, lateral view; (P) enlarged view of eggshell surface. Scale Bar: M, N, O = 20 μm; P = 25 μm.

***Syphacia (Syphacia) semiadii* Dewi, Asakawa and Fitriana, 2014 (new species)**

**(Figs. 2-6a, b)**

*General* –Small worms with transverse cuticular striations. Cuticle forming vesicular widening at head which extends to nerve ring. Mouth leading directly into small pharynx. Esophagus with pharynx, corpus and posterior bulb. Cervical and lateral alae absent in both sexes. Deirids not seen. Cephalic plate round; mouth surrounded by 3 lips with 'teeth'–like structure on apical margin, 1 dorsal and 2 subventral. Four large cephalic papillae; 2 placed at dorsal lip and 1 at each subventral lip, amphidial pores situated between cephalic papillae with porous patches laterally. Excretory pore posterior to oesophago–intestinal junction.

*Male* (holotype and 9 paratypes) –Length 0.88–1.06 (0.93) mm, maximum width 79–95 (89). Total esophagus including pharynx, corpus and bulb 168–221 (203) long: pharynx 13–16 (14) long, corpus 125–153 (144) long and 20–26 (23) wide, bulb 46–53 (49) long by 42–47 (45) wide. Nerve ring 87–100 (93), and excretory pore 341–452 (385) from cephalic end, respectively. Three hemispherical mamelons with transverse striations at ventral posterior body, anterior mamelon 54–62 (57) long, middle mamelon 54–65 (58) long and posterior mamelon 50–56 (53) long. Distance from anterior end to anterior, middle and posterior edges of mamelons 366–488 (390), 488–615 (511), and 604–708 (643), respectively. Posterior extremity bent ventrally. Spicule thin, needle–shaped, anterior proximal portion broad compared to posterior distal portion which is pointed, 61–78 (70) long, i.e. 5.7–6.5 (6.1) % of worm length (WL); gubernaculum stout, hook–shaped, 30–36 (33) long; accessory piece of gubernaculum relatively thin, unornamented. Caudal papillae in 3 pairs, 2 pairs adanal close together and 1 posterior pair protruding posterolaterally. Tail whip–like, 117–134 (126) long, i.e. 11.0–14.6 (13.5) % of WL.

*Female* (10 paratypes) –Length 1.93–2.37 (2.22) mm, maximum width 169–249 (208). Distance between amphidial pores 20. Lateral alae absent. Total esophagus including pharynx, corpus and bulb 271–288 (280) long: pharynx 21–25 (23) long, corpus 171–206 (189) long and 32–40 (35) wide, bulb 66–71 (68) long by 74–79 (77) wide. Nerve ring 114–148 (137), excretory pore 415–485 (452), from cephalic end. Vulva lip salient, 527– 647 (590), i.e. 24.7–29.2 (26.7) % of WL, from cephalic end; vagina and ovejector directed posteriorly. Cephalic vesicle 253–294 (273) long. Distance between excretory pore and vulva 90–145 (139), i.e. 4.0–8.2 (6.26) % of WL. Eggs numerous with a flattened side, operculated, embryonated in uteri, 68–70 (69) x 23–29 (27). Uterus extending anteriorly to the oesophageal bulb and ending posteriorly near anus. Tail long, tapering to a slender point, 440–556 (480) long, i.e. 19.0–25.0 (21.7) % of WL.

*Type host –Halmaheramys bokimekot* Fabre et al., 2013 (Mammalia: Muridae)

*Site of infection* –Cecum.

*Type locality* –Boki Mekot, Central Halmahera, Indonesia (00°36'42.60"N, 128°2'49.00"E.) Type specimen was collected 15 km NW of Sagea village, (central 29 Halmahera, Halmahera Island, North Moluccas, Indonesia), at 723 m elevation.
*Date of collection*-26 January 2010.

*Etymology* –The new species is named after Prof. G. Semiadi (MZB) for his kind help in providing the host specimens.

*Collector*– G. Semiadi, Y. S. Fitriana and N. Supriatna (MZB).

*Specimens deposited* –MZB Na 483 (holotype); MZB Na 484 (paratypes).

*Symbiotypes* –MZB Mamm.33249, MZB Mamm.33251, MZB Mamm.33255.

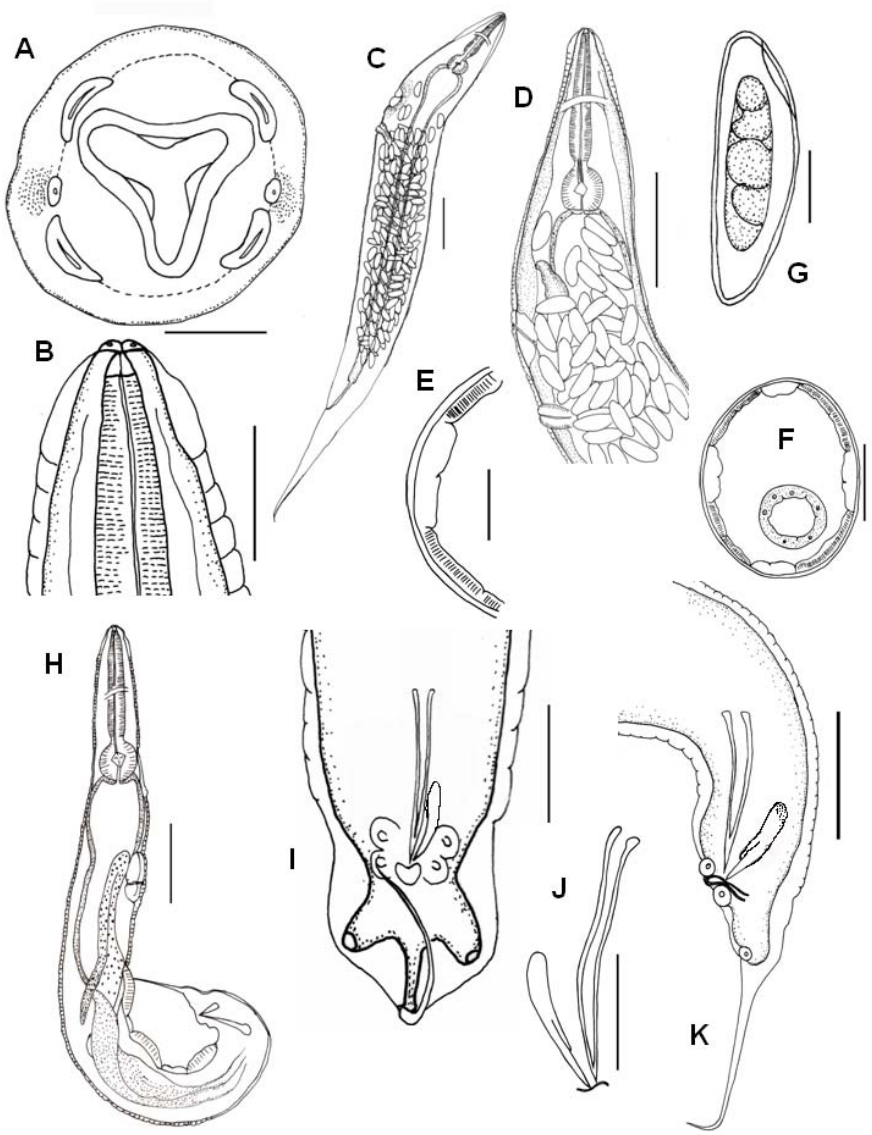



Fig. 2-6a. *Syphacia semiadii* Dewi, Asakawa and Fitriana, 2014 collected from *Halmaheramys bokimekot* on Halmahera Island, Indonesia. (A) cephalic end of female (apical view); (B) cephalic end of female (right lateral view); (C) female (paratype) (left lateral view); (D) anterior portion of female (right lateral view); (E) midbody in cross section of female; (F) midbody in cross section of male; (G) egg; (H) male (holotype) (left lateral view); (I) posterior end of male (ventral view); (J) spicule and gubernaculum (right lateral view); (K) posterior end of male (right lateral view). Scale bars: A: 10µm; B, E, I, K: 50 µm; C, D: 200 µm; F, J: 25 µm , G: 20 µm; H: 100 µm.

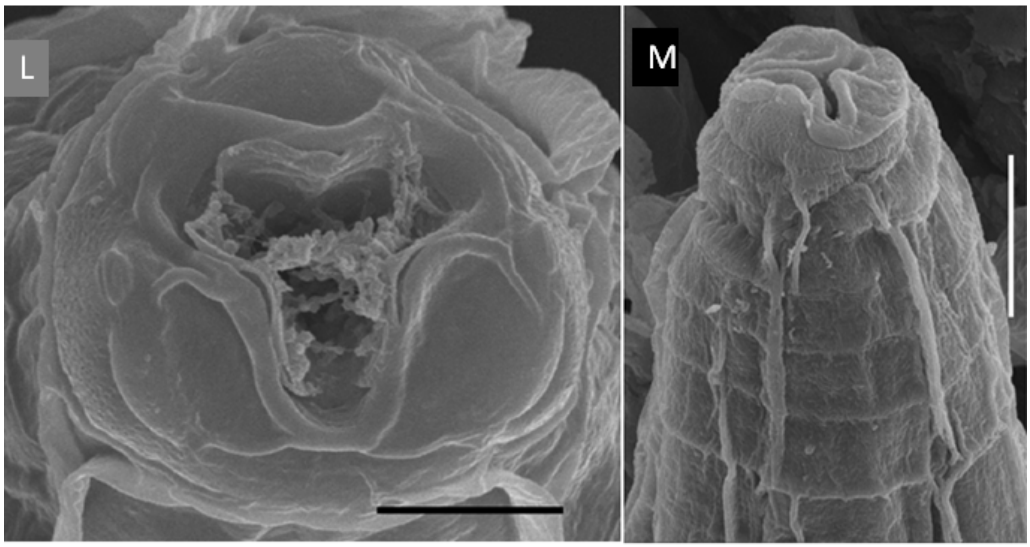



Fig. 2-6b. Scanning electron microscopy of *Syphacia semiadii* Dewi, Asakawa and Fitriana, 2014 collected from *Halmaheramys bokimekot* on Halmahera Island, Indonesia. (L) cephalic end of female (apical view); (M) anterior portion of female (lateral view). Scale bars: L: 10µm; M: 20µm.

***Syphacia (Syphacia) maxomyos* from *Maxomys* spp. (in press)**

**(Fig. 2-7a, b, c)**

*General* –Small nematodes; cuticle with fine transversal striations; cephalic vesicle well developed; soft, making waved contour in apical view cephalic plate elongated laterally with dorsoventral constriction; mouth opening triangular, surrounded by 3 protruded lips, dorsal lip smaller than subventral ones. Two submedian papillae and one amphid, closely set, located at each lateral side of cephalic plate; amphids with porous patches laterally; cephalic vesicle present, soft, making waved contour in apical view; cervical alae absent; deirids not seen; excretory pore posterior to esophago-intestinal junction; esophagus club–shaped with posterior bulb containing a valvular apparatus.

*Male* (holotype and 10 paratypes from *M. musschenbroekii*) –Posterior body bent ventrally. Length 1.29–1.78 (1.63) mm, maximum width 101–138 (122); distance between amphidial pores 29–30 (n=2); lateral alae as slight cuticular theickenings with median furrow; total esophagus 176–230 (209) long; pharynx 14–19 (17) long; corpus 110–152 (133) long, 27–37 (33) wide; isthmus 13–24 (20) wide; bulb 50–64 (58) long by 51–64 (58) wide; nerve ring 86–125 (106), and excretory pore 364–505 (454) from cephalic end: 3 mamelons developed at ventral posterior body; first mamelon 48–75 (63) long, second mamelon 40–69 (60) long and third mamelon 56–83 (73) long; distance from cephalic end to anterior edges of first, second and third mamelons 439–632 (559), 598–830 (757) and 794–1126 (1041), respectively; testis recurrent at level of firts mamelon; spicule single, relatively short, thin, needle-shaped, slightly constricted at 1/3 length from proximal end, sharply pointed distally, 64–78 (72) long [i.e. 3.8–5.6 (4.5) % of WL]; gubernaculum, 27–35 (32) long with relatively large, unornamented accessory piece 21–24 (23) long; caudal papillae 3 pairs: 2

pairs small, near cloaca and 1 pair large, postanal, protruding posterolaterally; tail tapered, forming whip–like process, 213–269 (245) long [i.e. 13.1–17.8 (15.1) % of WL].

*Female* (allotype and 10 paratypes from *M. musschenbroekii*) –Body relatively stout; length 3.44–4.51 (4.08) mm, width 192–260 (212); distance between amphidial pores 38–39 (n=2); lateral alae absent; total esophagus 271–324 (302) long: pharynx 18–24 (20), corpus 177–211 (197) long and 45–51 (47) wide, isthmus 24–32 (29) wide at narrowest level, and bulb 75–102 (90) long by 93–101 (97) wide; nerve ring at midlevel of esophageal corpus and excretory pore 105–160 (127) and 436–711 (558) from cephalic end, respectively; vulva protruding and surrounded by smooth cuticle, 520–813 (676) from cephalic end [i.e. 16.9 % of WL]; vagina and ovejector directed posteriorly; distance between excretory pore and vulva short, 60–161 (118) [i.e. 14.0–18.6 (16.5) % of WL]; eggs elliptical, stumpy, asymmetrical with one side flattened, both poles rounded, operculum reaching polar end, surface not pitted, embryonated in uteri, [57.8 (54–59)] x [24.1 (23–26)] (n=20); tail long, tapering to pointed end, 563–934 (777) long [i.e. 15.2–21.0 (19.0) % of WL].

*Type host –Maxomys musschenbroekii* (Jentink, 1878) (Musschenbroek's spiny rat) (Rodentia: Muridae).

*Other host –Maxomys whiteheadi* (Thomas, 1894) (Whitehead's spiny rat) (Rodentia: Muridae).

*Site of infection* –Cecum.

*Type locality* –Lambanan, West Sulawesi, Indonesia.

*Other locality* –Mambulillin, West Sulawesi; Bukit Batu, Bengkalis, Riau, Sumatra, Indonesia.

*Date of collection* –1 August 1992 (*M. musschenbroekii* in Lambanan); 30 July 1992 (*M. musschenbroekii* in Mambulillin); 6 April 2011 (*M. whiteheadi*).

*Symbiotypes* –AMNH M–267759–267761; MZB Mamm.34132, 34133, 34138, 34143.

*Specimens deposited* –Holotype male and allotype female (host: *M. musschenbroekii*) (MZB Na 675); 10 male and 10 females paratypes (host: *M. musschenbroekii*) (MZB Na 676–678); 2 males and10 females paratypes (host: *M. whiteheadi*) (MZB Na 679–680).

*Etymology* –The species epithet of this taxon is derived from the generic name of the host rodent, *Maxomys*.

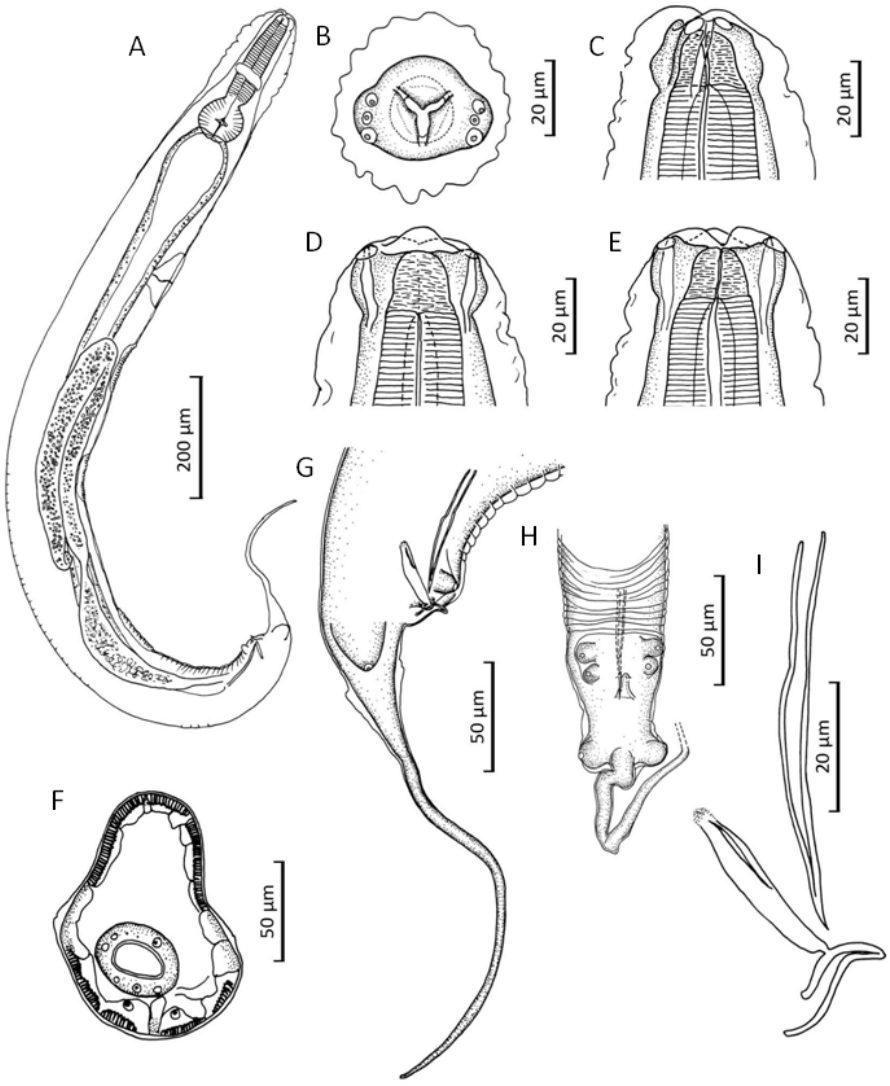



Fig. 2-7a. Male of *Syphacia maxomyos* from *Maxomys musschenbroekii* in Sulawesi, Indonesia. (A) male, holotype, lateral view; (B-E) cephalic portion: (B) apical; (C) lateral; (D) dorsal; (E) ventral view; (F) cross section through midbody; (G-H) posterior extremity: (G) right lateral, (H) ventral view; (I) spicule and gubernaculum, lateral view.

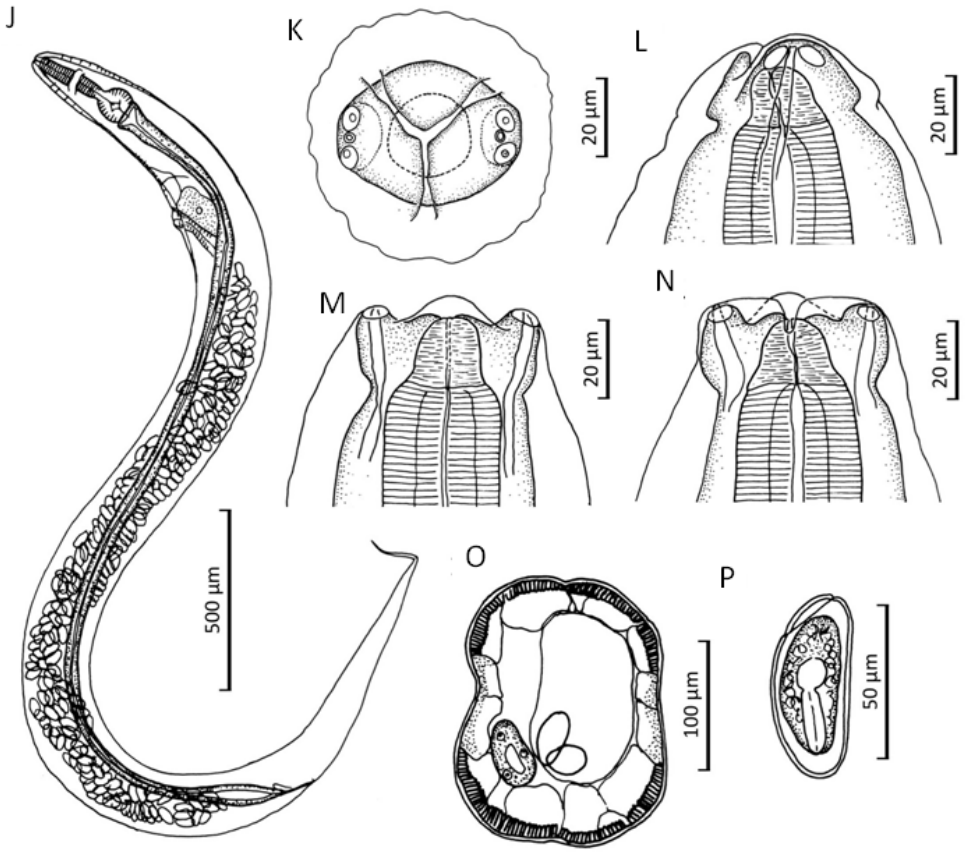



Fig. 2-7b. Female of *Syphacia maxomyos* from *Maxomys musschenbroekii* in Sulawesi, Indonesia. (J) female, allotype, lateral view; (K-N) cephalic portion: (K) apical, (L) lateral, (M) dorsal, (N) ventral view; (O) cross section through midbody; (P) egg.

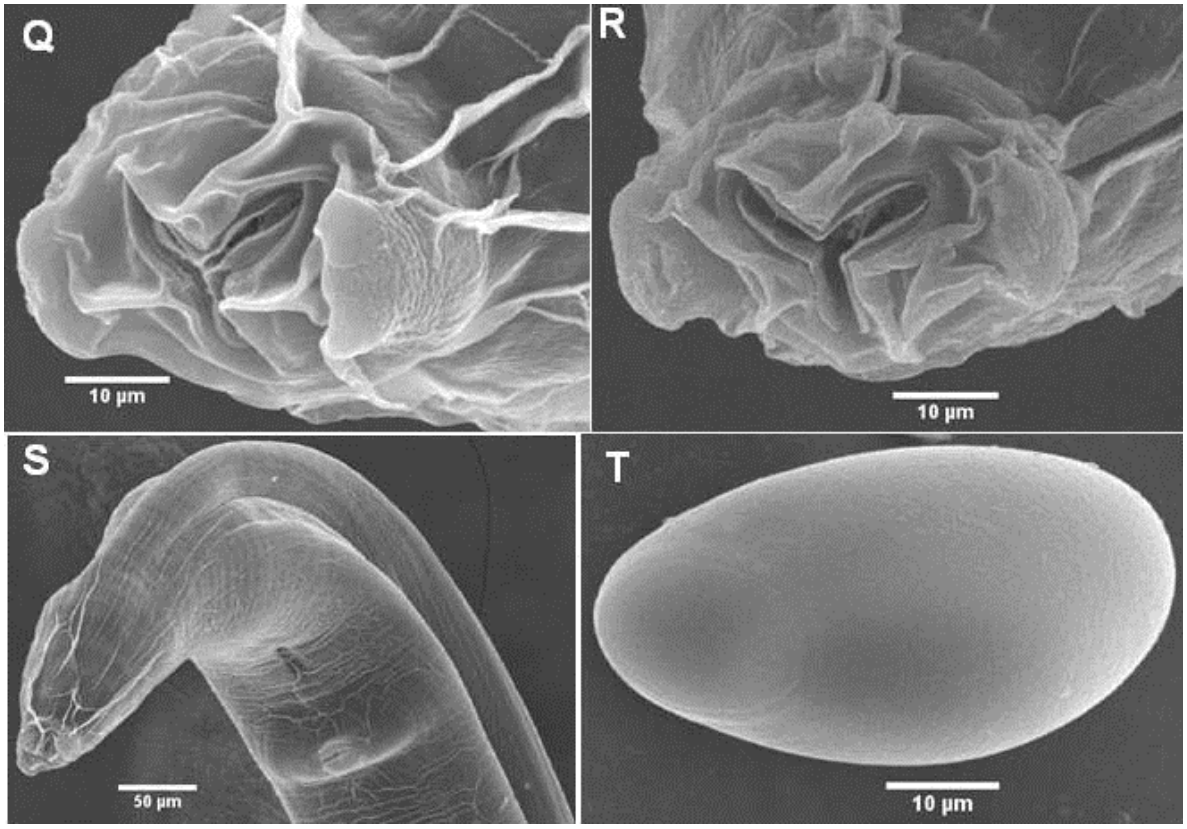



Fig. 2-7c. Scanning electron microscopy of *Syphacia maxomyos* collected from *Maxomys musschenbroekii* in Sulawesi, Indonesia. (Q) cephalic end of female (apical view); (R) cephalic end of female (apical view); (S) anterior portion of female showing cephalic end and vulva (ventro lateral view); (T) egg.

**An overview of the genus *Syphacia* and Indonesian species;** Before the present study, only three subgenera have been recognized in the genus *Syphacia*, i.e. *Syphacia* Seurat, 1916, *Cricetoxyuris* Hugot, 1988 and *Seuratoxyuris* Hugot, 1988 (Hugot, 1988). This study added more two new subgenera, i.e. *Rumbaisyphacia* and *Segienamsyphacia.* Each genus has a new species namely *S.* (*R.*) *kumis* and *S.* (*Se.*) *yuniae*, respectively. Therefore, five subgenera have been hitherto recognized for this genus.

Before the present author's observation, 14 fully described species of the subgenus *Syphacia* had been recorded in Indonesia-Australia bioregion, viz., *S. abertoni* Weaver and Smales, 2006, *S. australasiensis* Smales, 2004, *S. boodjamullaensis* Weaver and Smales, 2010, *S. brevicaudata* Weaver and Smales, 2008, *S. carnarvonensis* Weaver and Smales, 2010, *S. coccymyos* Smales, 2011, *S. darwini* Hugot and Quentin, 1985, *S. helidonensis* Weaver and Smales, 2010, *S. longaecauda* Smales, 2001, *S. lorentzimyos* Smales, 2010, *S. mamelontenuis* Smales, 2010, *S. muris* (Yamaguti, 1935), *S. pseudomyos* Weaver and Smales, 2008, *S. sulawesiensis* Hasegawa and Tarore, 1996 from the area east of the Wallace's line (Hugot and Quentin, 1985; Hasegawa and Tarore, 1996; Smales, 2001, 2004, 2010, 2011; Weaver and Smales, 2006, 2008, 2010). Adding to them, the present author found five more species belonging to this subgenus and all species exhibited considerable diversity in morphology, so they were described as new species as mentioned above, viz., *S. rifaii* Dewi and Hasegawa, 2010, *S. paruromyos* Dewi and Hasegawa, 2014, *S. taeromyos* Dewi and Hasegawa, 2014, *S. semiadii* Dewi, Asakawa and Fitriana, 2014 and *S. maxomyos* from *Maxomys* spp. (in press). Except for the cosmopolitan species *S. muris*, they are endemic species parasitic in endemic murines, suggesting co-speciation with hosts (Hugot and Quentin, 1985; Hasegawa and Tarore, 1996; Smales, 2001, 2004, 2010, 2011; Weaver and Smales, 2006, 2008, 2010; Dewi and Hasegawa, 2010, 2014; Dewi et al., 2014a, b).

Restricting to Indonesia, 10 species of the genus *Syphacia* were hitherto recorded. Eight species belong to the subgenus *Syphacia*: one species from Papua: *S. longaecauda* in *Melomys monktoni* Thomas, 1904, four species from Sulawesi: *S. paruromyos* in *Paruromys dominator* (Thomas, 1921), *S. rifaii* in *Bunomys* spp., *S. sulawesiensi* in *Rattus xanthurus* (Gray, 1867), *S. taeromyos* in *Taeromys celebensis* (Gray, 1867) and one species from Halmahera Island: *S. semiadii* in *Halmaheramys bokimekot* Fabre et al., 2013 (Hasegawa and Tarore, 1996; Dewi and Hasegawa, 2010, 2014; Dewi et al., 2014a). *Syphacia muris*, the cosmopolitan pinworm of *Rattus* spp. and *Niviventer* spp. as mentioned above, has also been recorded in Sulawesi, Halmahera, Ambon, Bawean, Java, Kalimantan, Flores, Obi and Lampung (Hasegawa and Syafruddin 1995; Hasegawa and Tarore, 1996; Dewi and Purwaningsih, 2013; unpublished data); one species of the subgenus *Rumbaisyphacia, S.* (*R.*) *kumis,* and one species of the subgenus *Segienamsyphacia, S.* (*Se.*) *yuniae* were obtained from Sulawesi (Dewi et al., 2014b).

From New Guinea Island, of which western region belongs to Indonesia as Papua (Irian Jaya), six species of *Syphacia* were described i.e. *S. longaecauda* in *Melomys*, *Paramelomys* and *Uromys*, *S. australasiensis* in *Rattus leucopus*, *S. darwini* in *Melomys lutillus* (Smales, 2001, 2009), *S. lorentzimyos* and *S. mamelonitenuis* both in *Lorentzimys nouhuysi*, *S. coccymyos* in *Coccymys ruemmleri* (Smales, 2001, 2009, 2010, 2011, 2012).

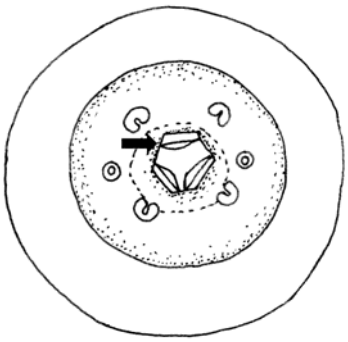
*Lorentzicola wolleyae* Smales, 2010 from *Lorentzimys houhuysi* and *Pogonomicola rugala* Smales, 2013 from *Pogonomys loriae* and *P. sylvestri*, very peculiar syphaciins, were also described from Papua New Guinea (Smales, 2010, 2013).

Weaver and Smales (2010) published a key to 11 species of *Syphacia* in Indonesia to Australian bioregion. Subsequently, Dewi et al. (2014) revised the key by adding seven species and one *Syphacia* sp. of Weaver and Smales, 2010. Herein, an emended key to 22 species in three subgenera of *Syphacia* distributing in Sunda to Sahul is proposed. In this key, the three species of *Syphacia* sp. by Weaver and Smales, 2010 are not included because morphology of males remains unknown.

**Key to species of *Syphacia* in Indo-Australian bioregion (revised after Weaver and Smales, 2010; Dewi et al., 2014)**

A. – Oral aperture hexagonal in female .....*Syphacia* (*Segienamsyphacia*)

One known species *Syphacia* (*Segienamsyphacia*) *yuniae* (Host: *Eropeplus*; Locality: Sulawesi)

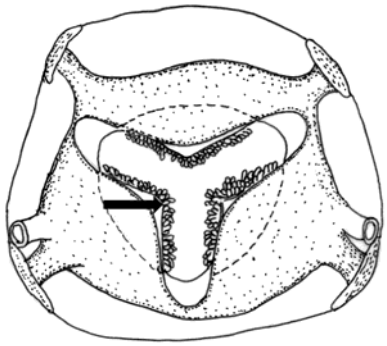


Female cephalic end of *Syphasia yuniae* (after Dewi, Hasegawa and Asakawa, 2014)

- Oral aperture not hexagonal in both sexes..... B

B. – Anterior margin of pharynx setiferous.....*Syphacia* (*Rumbaisyphacia*)

One known species *Syphacia* (*Rumbaisyphacia*) *kumis* (Host: *Eropeplus*; Locality: Sulawesi)



Cephalic end of *Syphacia* (*Rumbaisyphacia*) *kumis* (after Dewi, Hasegawa and Asakawa, 2014)

- Anterior margin of pharynx without setae .....C

C. – Cervical alae developed; deirids apparent; accessory piece of gubernaculum with ornamentations .....*Syphacia (Seuratoxyuris)*

Only one species known from the bioregion..... *Syphacia (Seuratoxyuris) pahangi*

(Host: *Chiropodomys*; Locality: Malay peninsula and Thailand)

– Cervical alae absent or present; deirids not seen; accessory piece of gubernaculum without ornamentations .....*Syphacia (Syphacia)* .....1

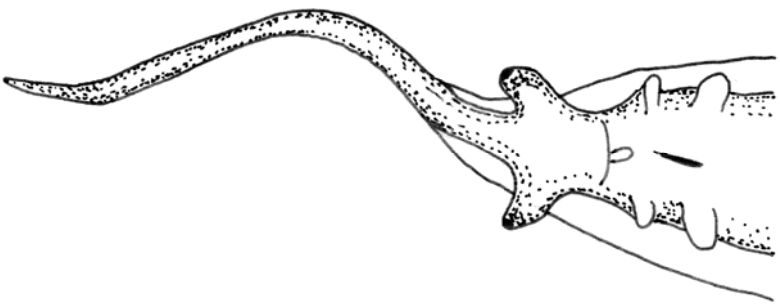
1. - Cephalic plate elongated laterally, often with dorsoventral constriction laterally……2

- Cephalic plate round, oval or square, without dorsoventral constriction laterally.....11

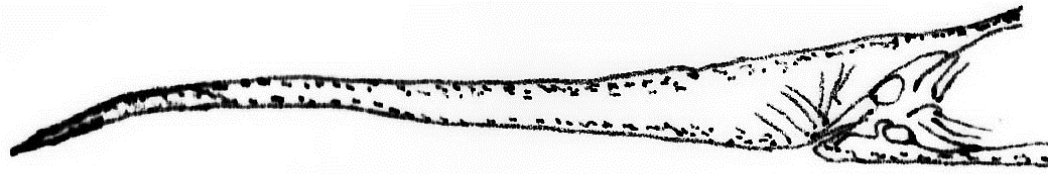
2. - Alae (either lateral and cervical) absent.....3

- Alae present.....6

3. - Female tail length >600, male tail length >350..... *Syphacia longaecauda* (*Melomys*; Australia and Papua New Guinea)



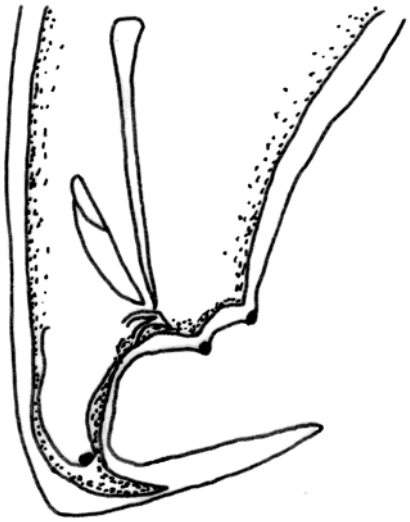
Male tail of *Syphacia longaecauda* (after Smales, 2001)



Female tail of *Syphacia longaecauda* (after Smales, 2001)

- Female tail length <500 , male tail length <150.....4

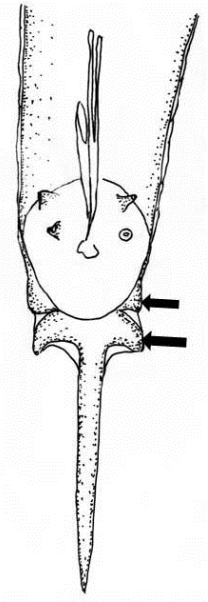
4. - Male spicule length >75; female tail length >580; eggs large, >125 long ..... *Syphacia boodjamullensis* (*Zyzomys;* Australia)



Male tail of *Syphacia boodjamullensis* (after Weaver and Smales, 2010)

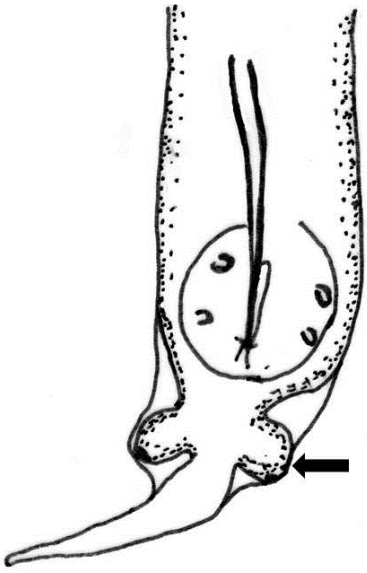
- Male spicule length <70; female tail length <580; eggs ≤125 long .....5

5. - Male with two pairs of postanal papillae; female with excretory pore posterior to oesophageal bulb..... *Syphacia brevicaudata* (*Pseudomys*; Australia)



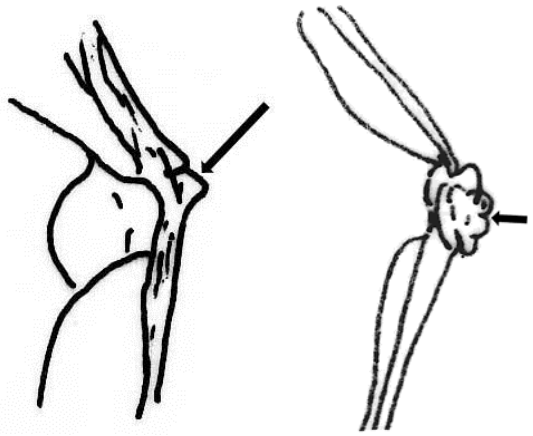
Male tail of *Syphacia brevicaudata* (after Weaver and Smales, 2008)

- Male with one pair of postanal papillae; female with excretory pore close-set to esophago-intestinal junction..... *Syphacia pseudomyos* (*Pseudomys*; Australia)



Male tail of *Syphacia pseudomyos* (after Weaver and Smales, 2008)

6. - Both cervical and lateral alae present..... *Syphacia coccymyos (Coccymys;* Papua New Guinea)



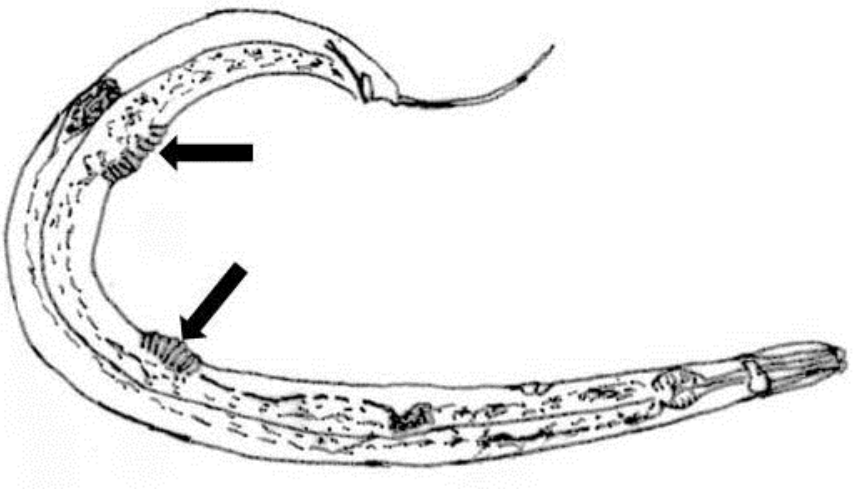
Lateral and cervical alae of *Syphacia coccymyos* (after Smales, 2011)

- Only lateral or cervical alae present.....7

7. - Lateral alae present; cervical alae absent.....8

- Cervical alae present; lateral alae absent.....10

8. - Male with two mamelons..... *Syphacia darwini* (*Melomys*; Australia)



Male of *Syphacia darwini* (after Hugot and Quentin, 1985)

- Male with three mamelons ..... 9

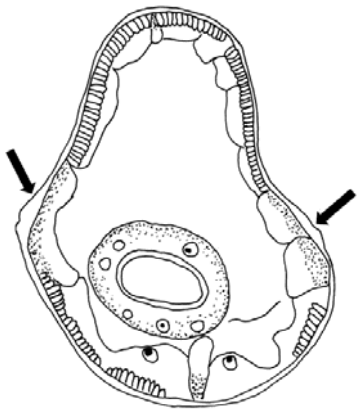
9. - Lateral alae present in both sexes; male tail length <150; eggs >100

long .....*Syphacia helidonensis* (*Pseudomys*; Australia)

Male tail of *Syphacia helidonensis* (after Weaver and Smales, 2010)

- Lateral alae only in male as slight cuticular thickenings; male tail >200; eggs <60

long .....*Syphacia maxomyos* (*Maxomys;* Sumatra, Sulawesi)



Male tail and lateral alae in male of *Syphacia* sp.(cross section)

10. - Cervical alae wide; male tail length >100; spicule length ≤60; egg length <80 ..... .....*Syphacia abertoni* (*Zyzomys;* Australia)

Male tail of *Syphacia abertoni* (after Weaver and Smales, 2006)

- Cervical alae narrow; male tail length <100; spicule length ≥60; egg length >100..... .....*Syphacia carnarvonensis* (*Pseudomys;* Australia)

Male tail of *Syphacia carnarvonensis* (after Weaver and Smales, 2010)

11. - Cephalic plate square……12

- Cephalic plate round……..13

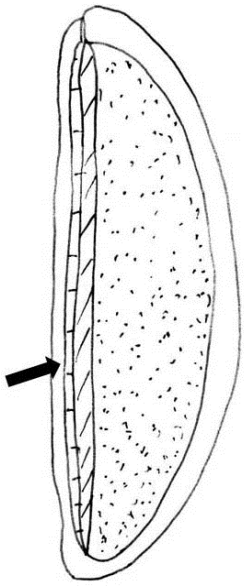
12. - Eggs without longitudinal ridge; spicule length <60**.....** *Syphacia muris*

(*Rattus*; cosmopolitan)

Egg of *Syphacia muris* (after Hugot and Quentin, 1985)

- Eggs with longitudinal ridge; spicule length >60.....*Syphacia australasiensis*

*(Rattus;* Papua New Guinea and Australia)

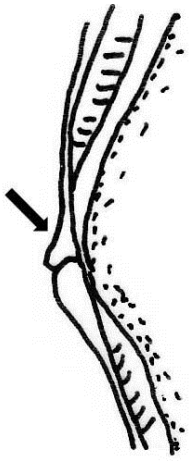


Egg of *Syphacia australasiensis* (after Smales, 2004)

13. - Lateral alae present.....14

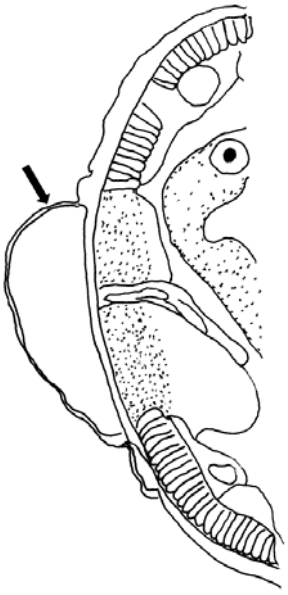
- Lateral alae absent.....18

14. - Lateral alae small.....*Syphacia lorentzymyos* (*Lorentzymys*; Papua New Guinea)



Small lateral alae of *Syphacia lorentzymyos* (after Smales, 2010)

- Lateral alae large.....15



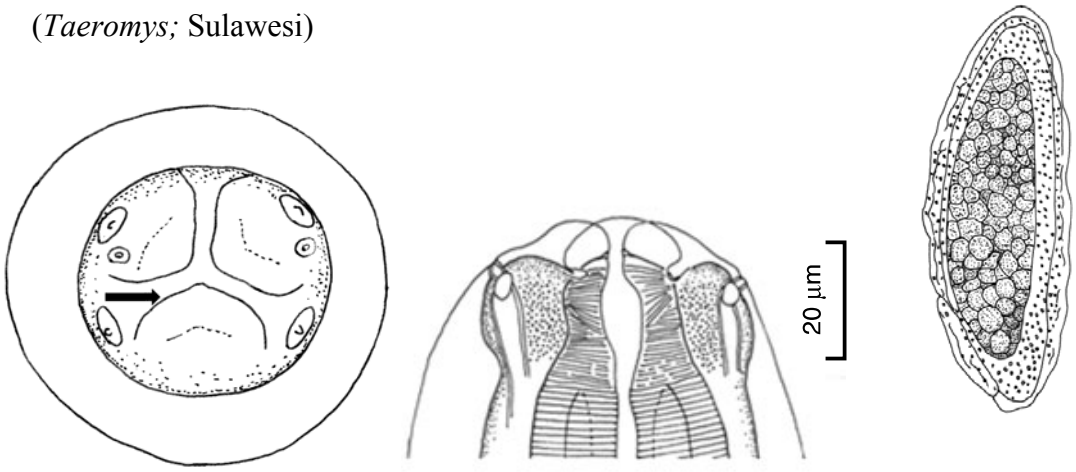
Large lateral alae (in *Syphacia paruromyos*)

15 - Lateral alae present in both sexes .....16

- Lateral alae present only in male .....17

16. - Lips protruded prominently; eggs with uneven shell..... *Syphacia taeromyos*

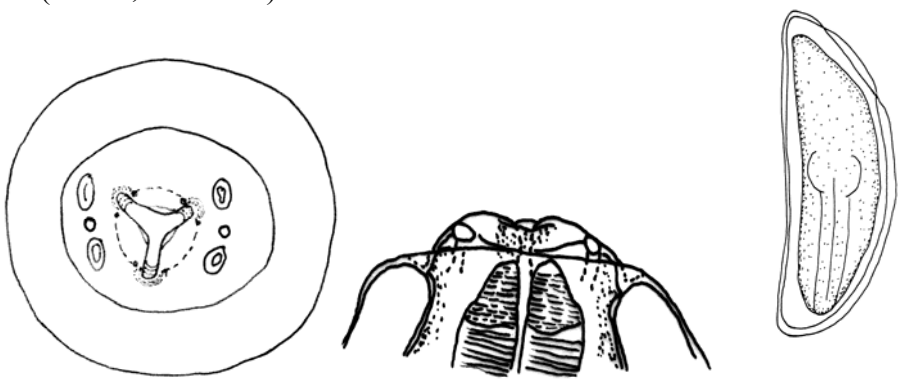
(*Taeromys;* Sulawesi)




Cephalic end and egg of *Syphacia taeromyos* (after Dewi and Hasegawa, 2014)

- Lips not protruded prominently; eggs with even shell.....*Syphacia sulawesiensis*

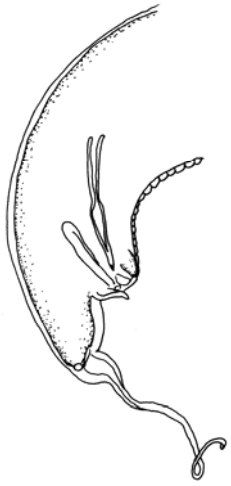
(*Rattus;* Sulawesi)



Cephalic end and egg of *Syphacia sulawesiensis* (after H\asegawa and Tarore, 1996)

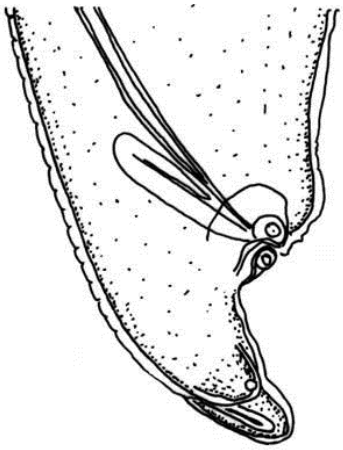
17. - Male tail long with whip like appendages..... *Syphcia paruromyos* (*Paruromys;*

Sulawesi)



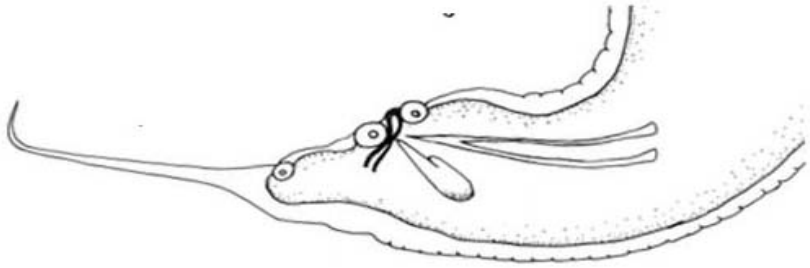
Posterior portion of *Syphacia paruromyos* (after Dewi and Hasegawa, 2014)

- Male tail short without whip like appendages..... *Syphacia rifaii* (*Bunomys*; Sulawesi)



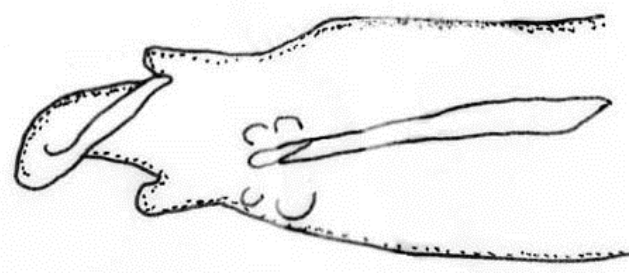
Posterior portion of *Syphacia rifaii* (after Dewi and Hasegawa, 2014)

18. - Male tail thin, >100 long;…..... *Syphacia semiadii* (*Halmaheramys*; Halmahera Island, the Moluccas, Indonesia)



Male tail of *Syphacia semiadii* (after Dewi, Asakawa and Fitriana, 2014)

- Male tail thick, <100 long, ……..*Syphacia mamelonitenuis* (*Lorentzymys*: Papua New Guinea)



Male tail of *Syphacia mamelonitenuis* (after Smales, 2010)

**Summary**

The taxonomical and morphological study on the genus *Syphacia* will not only become a baseline for further faunistic and/or biogeographical study, but also provide useful diagnostic information. Descriptions about the taxa were made and a key to species recorded from Sunda to Sahul bioregion including the newly found taxa from Indonesia was proposed. Before the present study, only three subgenera have been recognized in the genus *Syphacia*, i.e. *Syphacia*, *Cricetoxyuris* and *Seuratoxyuris*. The author added two more new subgenera from Sulawesi, i.e. *Rumbaisyphacia* and *Segienamsyphacia*, each has a new species *S.* (*R.*) *kumis* and *S. (Se.*) *yuniae*, respectively. Furthermore, this study also could find five more new species belonging to the subgenus *Syphacia*, all exhibiting considerable diversity in morphology at both light and scanning electron microscopy studies, viz., *S. paruromyos*, *S. rifaii*, *S. semiadii*, *S. taeromyos*, and *S. maxomyos*. In total, 10 species of the genus *Syphacia* species are distributed in Indonesia with seven new species described by the present author.

# Chapter 3

# Molecular biological analysis and phylogenetic consideration of the genus *Syphacia* from Indonesian murines

## Introduction

As mentioned in the Chapter 2, the species of the genus *Syphacia* are considered to have co-evolved generally with their rodent hosts. However, Okamoto et al. (2007) suggested that such a co-evolutionary relationship might not be so strict and host switching probably occurred during the course of evolution, at least in Japan. In this study, partial sequences of the mitochondrial *Cox1* gene and 28Sr DNA from *Syphacia* species obtained not only from Indonesia, but also from Japan, were determined based on the method of Okamoto et al. (2007) and tried to discuss the relationships between pinworms and their hosts in Indonesia.

**Materials and methods**

Several individuals from three species, viz., *Syphacia rifaii* from *Bunomys* spp. of Sulawesi, *S. muris* from *Rattus tanezumi* of Sumatra and Java (see Chapter 2), and *Syphatineria* sp. from a ground squirrel, *Lariscus hosei* (Sciuridae), of Kalimantan, and some species obtained from Japan and kept in Biological Laboratory, School of Medicine, Oita University, Japan, were used for the present analysis for nucleotides of the mitochondrial *Cox1* gene and 28S r DNA. The DNA sequencing was attempted for pinworms fixed and preserved in 100% ethanol solution. The individual worm was rinsed in phosphate buffer (pH 6.5), and homogenized in a 1.5 mL Eppendorf tube containing 100 µL distilled water using a plastic pestle. Five µL of the homogenized solution was mixed with 50 µL liquid phase Dexpat™ (Takara Bio. Inc., Otsu, Shiga, Japan) in a 200 µl, heated at 196 °C for 30 min, and then cooled on ice. Subsequently, 5 µL of the solution was added to the 50 µL PCR mixture, which contained 0.5 µL of KOD-Neo$^{TM}$ polymerase, 5 µL of 10x PCR buffer, 5 µL of 2mM dNTP, 5 µL of 2 mM $MgSO_4$ (Toyobo Co., Tokyo, Japan) and 0.25µL each of forward and reverse primers. PCR was performed using a thermal cycler, PC-801 (ASTEC Co., Ltd., Fukuoka, Japan). The primer sets for amplification and sequencing of were those used

previously (Gouÿ de Bellocq, 2001; Hu et al., 2002; Okamoto et al., 2009; Hasegawa et al., 2010) or newly designed.

For partial mitochondrial DNA cytochrome *C* oxidase subunit 1 (*Cox1*) gene:

StrCoxAfrF 5'-GTGGTTTTGGTAATTGAATGGTT-3' (forward),

HkCoxMidF 5'-ACTGTTTATCCACCTTTAAGTA-3' (forward),

MH28R 5'-CTAACTACATAAT AAGTATCATG-3'

JB3 5'-TTTTTTGGGCATCCTGAGGTTTAT-3' (forward)

SyphCoxF1 5'-GGTCAGTTGTATAATGTTRT-3' (forward)

SyphCoxF2 5'-TTGRACTTTATATCCTRCTTT-3' (forward)

SyphCoxF3 5'-CWATTTTTAATTTRCGTTCT-3' (forward)

SyphCoxF4 5'-TTTGATCGTAATTTTAATWSTT-3' (forward)

SyphCoxF5 5'-TGAGGTTTATRTTYTDRTTTT-3' (forward)

SyphCoxF6 5'-TAAGTACWCGTTTDTATTTTA-3' (forward)

SyphCoxR1 5'-AAGATTATTTAAACGAGGAAA-3' (reverse)

SyphCoxR2 5'-GCTACATGCAAACCAAAAATAA-3' (reverse)

SyphCoxR3 5'-AAGACACCAACAATAAAAAAGAA-3' (reverse)

SyphCoxR4 5'-ACACCTCCTTTTTACCAGTTAAA-3' (reverse)

SyphCoxR5 5'-CAAAGTTAACAACCAACTAAAAA-3' (reverse)

JB4.5 5’-TAAAGAAAGAACATAATGAAAATG-3’ (reverse).

For partial 28S rDNA:

C1′ 5’-ACCCGCTGAATTTAAGCAT -3’ (forward)

D2 5’-TCCGTGTTTCAAGACGG-3’ (reverse)

The PCR conditions were as follows: initial denaturation at 94 $^{0}$C for 2 min, followed by 30 cycles of 98 $^{0}$C for 10 sec, — 50 $^{0}$C for 1 min, — 68 $^{0}$C for 1 min, 30 cycles of 98 $^{0}$C for 10 sec, — 55 $^{0}$C for 1 min, — 68 $^{0}$C for 1 min, and a post-amplification extension at 68 $^{0}$C for 7 min for *Cox1*.

PCR products were mixed with Ez-Vision$^{TM}$ Three DNA Dye (Amresco, Solon, Ohio, USA), electrophoresed in a 1.5% agarose gel plate and visualized using a UV illuminator. Promising bands, when observed, were dissected and processed using Nucleospin$^{TM}$ column (Machery-Nagel, Germany) according to the instruction provided by the manufacture to purify DNA, and then ethanol precipitated for further purification. Proper amount of the DNA was subjected to direct sequencing using the BigDye$^{TM}$ Terminator Cycle Sequencing Kit Version 3.1 (Applied Biosystems, Foster City, California, United States of America), and purified using CentriSep separation column according to the manifacture’s instruction. Then sequencing was made in a genetic analyzer ABI-PRISM 3130 (Applied Biosystems).

The nucleotide sequences determined in this study were registered in the DNA Database (DDBJ, http://www.ddbj.nig.ac.jp/) with accession numbers LC038086 to LC038099. Sequences were aligned using Clustal W, then phylogenetic analyses were made by neighbor-joining (NJ) and maximum likelihood (ML) methods using MEGA5 (v. 5.2.2) software (Saitou and Nei, 1987; Tamura et al., 2002). Both nucleotide and amino acid sequences translated using invertebrate mitochondrion code were analyzed for *Cox1*. In NJ analysis of nucleotide sequences, the evolutionary distances were computed using the Kimura's two-parameter method (Kimura, 1980). The bootstrap values were calculated by 1,000 replicates (Felsenstein, 1985). *Aspiculuris tetraptera* was used as an outgroup species to root tree of *Cox1*.

**Result and discussion**

Among the Indonesian Syphaciinae materials tested, partial *Cox1* DNA amplification was successful for only three species, viz., *S. rifaii* from *Bunomys penitus* of Southeast Sulawesi, *S. muris* from *R. tanezumi* of Central Java and Lampung, Sumatra (see Appendix 2), and *Syphatineria* sp. from *L. hosei* of Kalimantan, whereas DNA could not be amplified for other seven Indonesian species, in spite of repeated trials. Using primers StrCoxAfrF, JB3,

MH28R and JB4.5, unambiguous sequence of 749bp of *Cox1* was obtained for each one sample of *S. rifaii* [LC038087] and *Syphatineria* sp. [LC038092]. Only shorter sequence [LC038088] corresponding to 106$^{th}$ to 748$^{th}$ positions of LC03087 was obtained from another sample of *S. rifaii*. This shorter sequence had one synonymous substitution from C to T at 147$^{th}$ position in Fig. A-1. Meanwhile, *S. muris* samples responded only to the primer set JB3-JB4.5, giving shorter sequences with 395bp. Because of these differences in length of the sequences obtained and limitation of the sequences in the DNA database, phylogenetic analyses were carried out separately on the two datasets covering 618bp and 249bp, respectively (Appendix Figs. A-1 to A-4). The shorter sequence obtained from *S. rifaii* was not used for phylogenetic analysis.

The striking feature is the peculiarity of *Cox1* of *S. rifaii* in nucleotide and amino acid sequences. By Clustal W alignment, it was found that *S. rifaii* had deletions of three consecutive nucleotides at two sites causing two amino acid deletions (Appendix Figs. A-1, A-2). The genetic distance from other congeners was large (Appendix Tables A-1, A-2), making extraordinarily long branch especially in the tree based on the longer sequences (Fig. 3-1). If outgroup setting was not done, *S. rifaii* diverged at the most basal node in the tree, putting *Aspiculuris* within *Syphacia* spp. When *Aspiculuris* was used as an outgroup, *S. rifaii* and *Syphatineria* sp. formed a clade clearly separated from other species of *Syphacia*. This

peculiarity became less prominent but persisted when the analysis was performed based on the short sequences (Fig. 3-2). *Syphacia rifaii* shared common ancestor with *Syphatineria* sp. In the tree based on the short sequences of *Cox1*, *S. rifaii* and *S. muris* were close each other, and they shared a common ancestor with *Syphatineria* sp. though the bootstrap value was not high.

Phylogenetic reconstruction using ML method was attempted for amino acid sequences translated from the long nucleotide sequences of *Cox1* (Fig. 3-3). Again, *S. rifaii* showed very curious position by having extraordinary long branch.

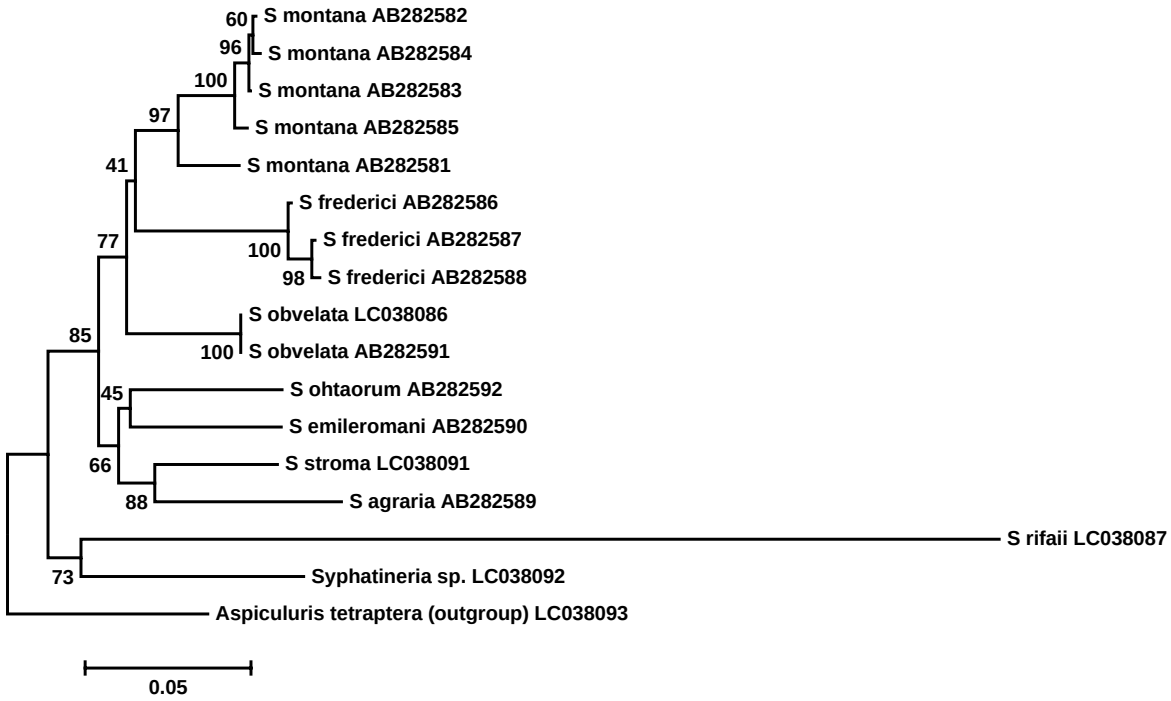



Fig. 3-1. NJ reconstruction of phylogeny of *Syphacia* spp. based on long nucleotide sequences of mtDNA *Cox1*. The optimal tree with the sum of branch length = 0.81201463 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. The evolutionary distances were computed using the Kimura 2-parameter method. The analysis involved 17 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 618 positions in the final dataset.

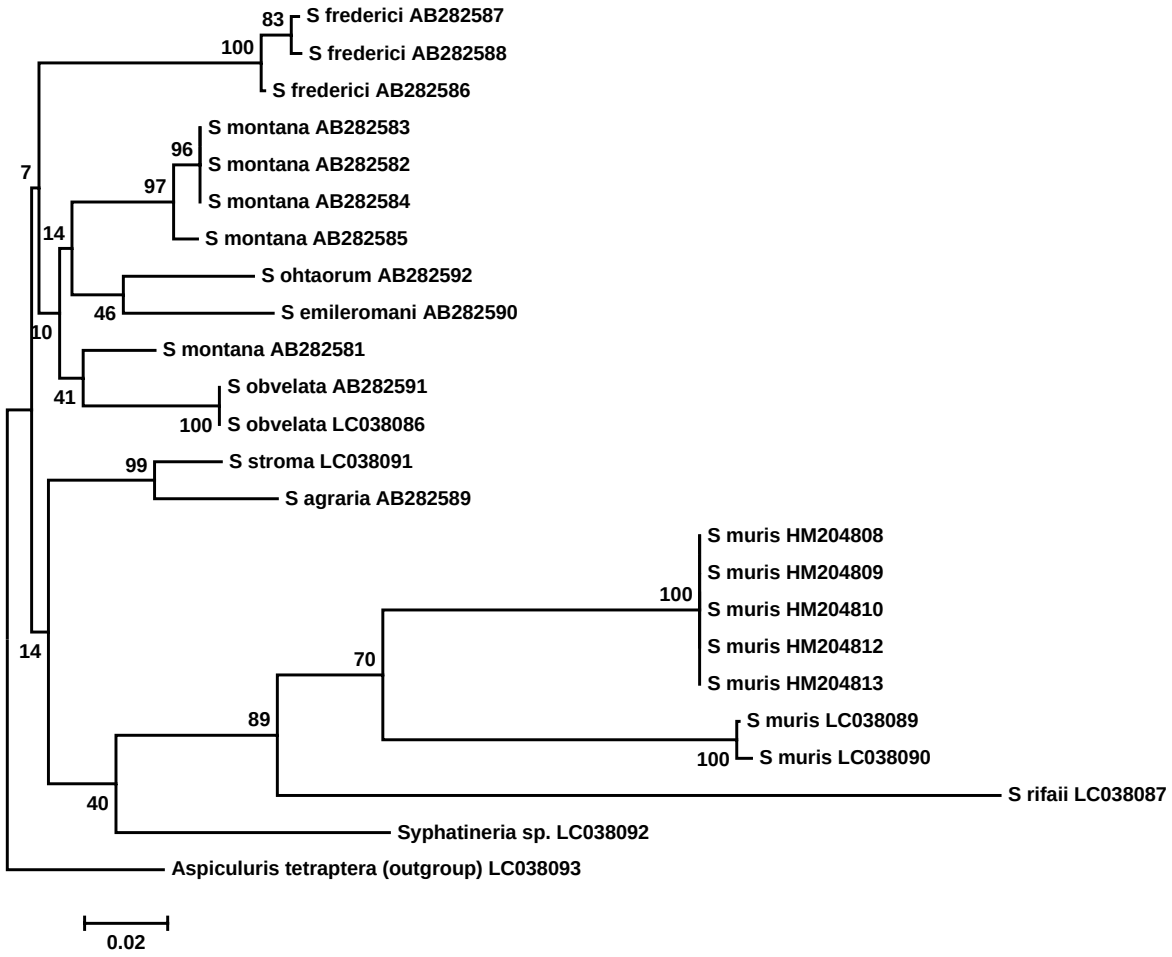



Fig. 3-2. NJ reconstruction of phylogeny of *Syphacia* spp. based on short nucleotide sequences of mtDNA *Cox1*. The optimal tree with the sum of branch length = 0.85148172 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. The evolutionary distances were computed using the Kimura 2-parameter method. The analysis involved 24 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 249 positions in the final dataset.

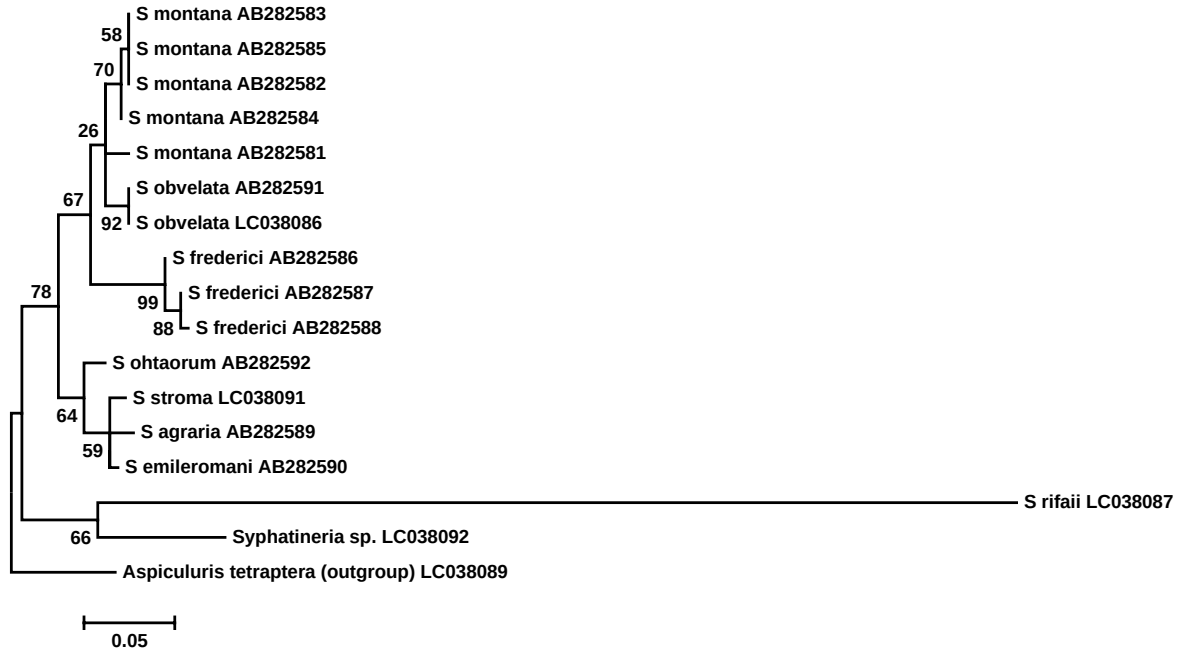



Fig. 3-3. ML reconstruction of phylogeny of *Syphacia* spp. based on amino acids translated from long nucleotide sequences of mtDNA *Cox1* using the General Reverse Transcriptional model. The tree with the highest log likelihood (-1382.5027) is shown. The percentage of trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches. Initial trees for the heuristic search were obtained by applying the Neighbor-Joining method to a matrix of pairwise distances estimated using a JTT model. A discrete Gamma distribution was used to model evolutionary rate differences among sites (2 categories (+*G*, parameter = 0.7383)). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 17 amino acid sequences. All positions containing gaps and missing data were eliminated. There were a total of 206 positions in the final dataset.

Amplification of 28S rDNA was also successful only for *S. rifaii* from *B. penitus* of Sulawesi, *S. muris* from *R. tanezumi* of Lampung, Sumatra and Central Java, and *Syphatineria* sp. from *Lariscus hosei* of Kalimantan (see Appendix 2). DNA could not be amplified for other seven Indonesia species of *Syphacia*. In the NJ tree based on 28S rDNA, bootstrap values were generally high (Fig. 3-4). Even when outgroup setting was not made, *Aspiculuris tetraptera* was located most basal. According to this tree, *Syphacia* (*Seuratoxyuris*) *petrusewiczi* from Japanese *Myodes* (syn. *Clethrionomys*) diverged at the most basal node, and then *Syphatineria* sp. was separated. Among the species of the subgenus *Syphacia*, *S. rifaii* and *S. muris* formed a clade, sharing a long branch, diverging from the common ancestor to the other *Syphacia* species. *Syphacia agraria*, *S. stroma* and *S. emileromani*, all parasitic in *Apodemus* spp., are monophyletic. *Syphacia vandenbrueli*, *S. frederici*, *S. obvelata* and *S. montana* formed another monophyletic group. *Syphacia muris* of *Rattus tanezumi* of Sumatra and Java differed from that of Japan and USA, both were collected from laboratory rats, *Rattus norvegicus*. In ML tree based on 28S rDNA (Fig. 3-5), topology was generally identical with that of NJ tree, but *Syphatineria* sp. diverged earlier than *S.* (*Seu.*) *petrusewiczi*. According to Hugot (1988), Syphaciinae arose with Glires as hosts in Paleocene, and evolved as Syphaciini in Muroidea in early Eocene. Subsequently, Syphaciins were divided into those in murids and sciurids during Eocene, and establishment

of the subgenera of *Syphacia* (i.e., *Syphacia*, *Seuratoxyuris* and *Cricetoxyuris*) and genera of Syphaciins (including *Syphatineria* and *Syphabulea*) of Sciurids occurred in Oligocene. However, the phylogenetic trees based on 28S rDNA may suggest that diversification of murid- and scuirud-parasitic lineages of Syphaciini and diversification of subgenera *Seuratoxyuris* and *Syphacia* occurred in a relatively short geological period.

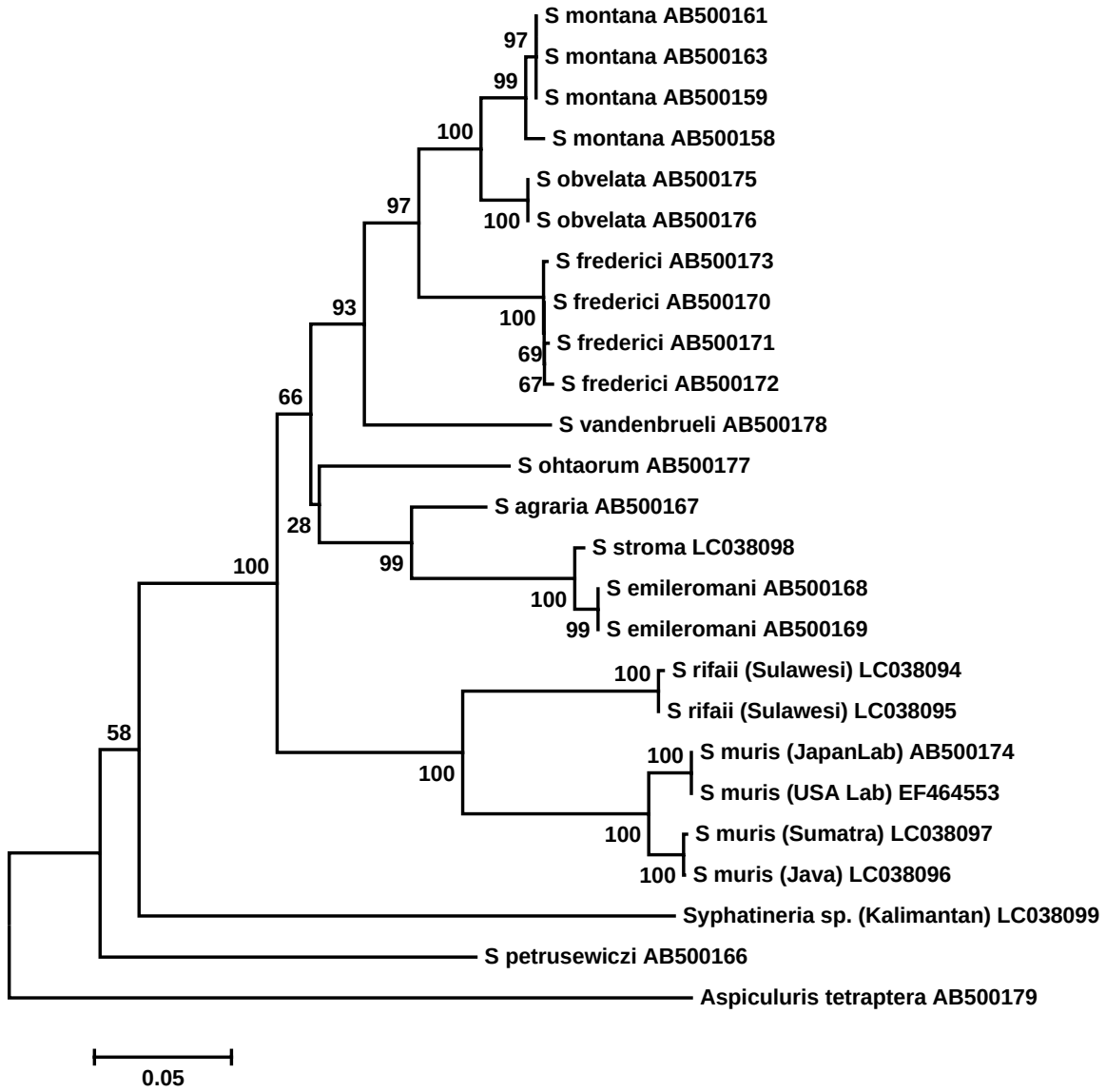



Fig. 3-4. NJ reconstruction of phylogeny of *Syphacia* spp. based on sequences of partial 28S rDNA. The optimal tree with the sum of branch length = 1.35815348 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. The evolutionary distances were computed using the Kimura 2-parameter method. The analysis involved 25 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 689 positions in the final dataset.

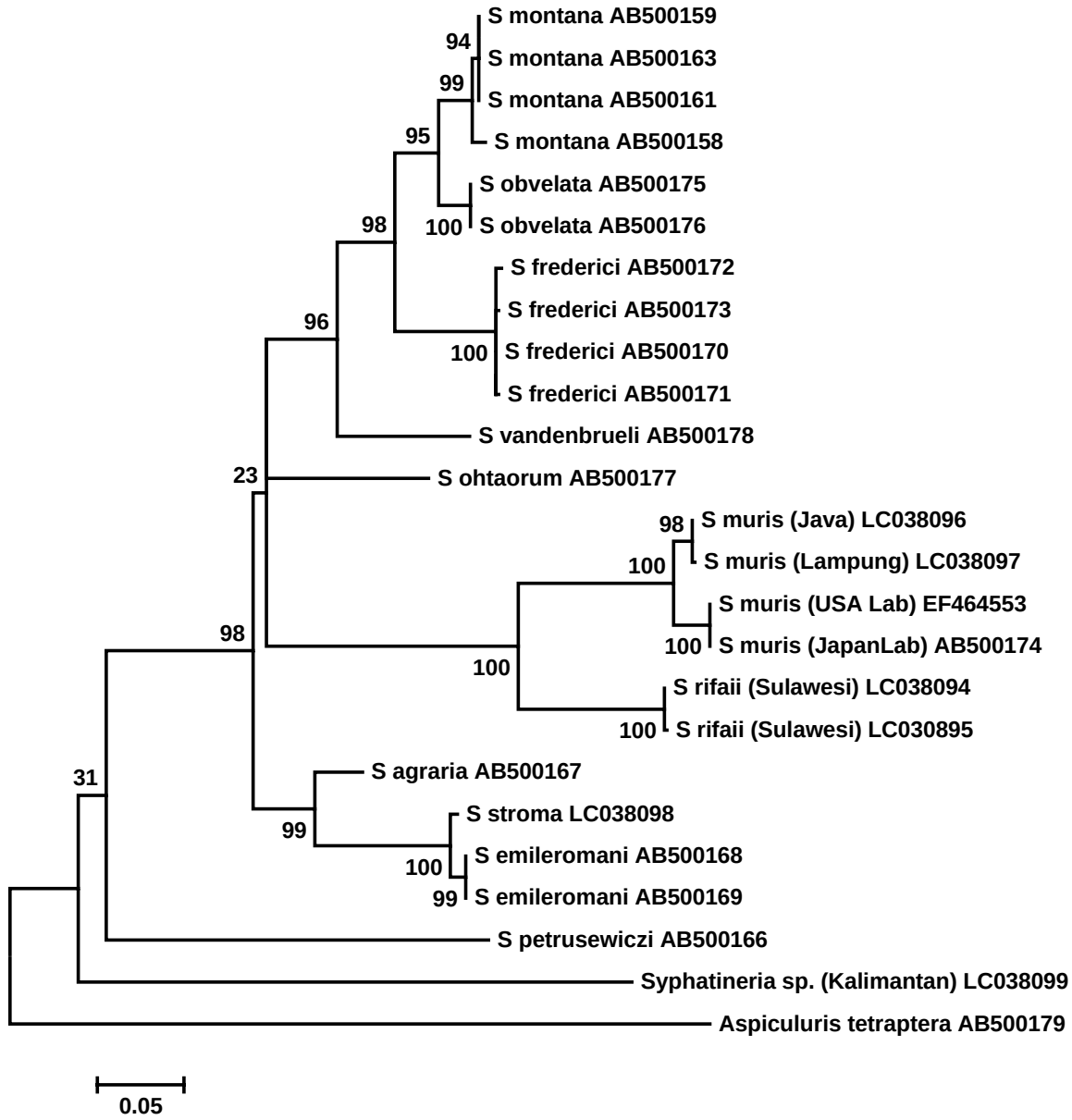



Fig. 3-5. ML reconstruction of phylogeny of *Syphacia* spp. based on sequences of partial 28S rDNA based on the Kimura 2-parameter model. The tree with the highest log likelihood (-4716.7483) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial trees for the heuristic search were obtained by applying the Neighbor-Joining method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach. A discrete Gamma distribution was used to model evolutionary rate differences among sites (2 categories (+*G*, parameter = 0.9215)). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 25 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 689 positions in the final dataset.

As shown above, *S. rifaii* and *S. muris* are located close together both in the phylogenetic trees on *Cox1* and 28S rDNA. This is not unexpected because ancestors of the host genera, *Rattus* and *Bunomys*, are considered to have diverged in early Pliocene while ancestors of *Micromys*, *Mus*, *Apodemus* and Microtines established much earlier, in Miocene (cf. Fabre et al., 2013). The numerous nucleotide and amino acid substitutions in *Cox1* of *S. rifaii* are very curious. Although this pinworm is parasitic in plural *Bunomys* species in Sulawesi, only two worms from two hosts were subjected to analysis. DNA sequence analysis of worms from other *Bunomys* spp. is necessary to elucidate the extent of genomic diversification among *S. rifaii* populations.

It is also noticeable that individuals of *S. muris* of Java and Sumatra were rather diverged from those in the laboratory rats both in *Cox1* and 28S rDNA. Ancestor of *S. muris* might be adapted to ancestral *Rattus* probably in Southeast Asia, and then made dispersal to the surrounding areas. Some *Rattus*, i.e. *R. norvegicus* and *R. rattus*, widened distribution over the world. The laboratory rat was domesticated from feral *R. norvegicus* in Europe or North America in middle of 19th century, and then distributed to various laboratories all over the world. *Syphacia muris* of them also has been maintained in the laboratory conditions. Thus, genetic divergence of *S. muris* in 28S rDNA of U.S. and Japan materials was negligible. Also, *Cox1* in rats in Chinese laboratories lacked variations (Fig. 3-2). However, it is

apparent that feral *Rattus* spp. harbored *S. muris* with genetic diversification as suggested by the present study.

In order to elucidate comprehensive feature of evolution of *Syphacia* in Indonesia, it is essential to analyze more species. In the present study, only nine species were subjected, and DNA analysis was successful only in a few species. The causes of the difficulty might be insufficient fixation/preservation of the worms and unsuitable primers. For best results, worms should be fixed and preserved in pure ethanol. However, in rural field, it is difficult to obtain pure chemicals. Some ethanol sold at local areas had lower concentration and contains impurities, which might affect in DNA. Although various primers were employed to amplify *Cox1*, only a few of them gave positive results. This is apparently due to nucleotide variations as shown in *Cox1* of *S. rifaii*. The primers JB3 and JB4.5 are usually effective for various nematodes, giving about 500bp band. However, in *S. muris*, they gave much shorter sequence. In future studies, it is essential to design more effective or specific primers, or utilize so-called next-generation sequencer.

**Summary**

The species of the genus *Syphacia* are considered to have co-evolved generally with their rodent hosts, in Japan, though host switching is also possible. The present study determined partial sequences of the mitochondrial *Cox1* gene and 28S rDNA from Syphaciinae species, viz., *S. rifaii* from *Bunomys* spp., *S. muris* from *Rattus tanezumi*, and *Syphatineria* sp. from *Lariscus hosei*, obtained from Indonesia, and tried to examine the general aspect of the relationships. In the phylogenetic trees on *Cox1*, the peculiarity of *S. rifaii* was found. Its genetic distance from other congeners was so large, making an extraordinary long branch in the trees based on the long and short length sequences, respectively. *Syphacia rifaii* was positioned close to *S. muris* (bootstrap value 89 in NJ tree). In NJ and ML trees based on 28S rDNA, bootstrap values were generally high. In NJ tree, *S.* (*Seuratoxyuris*) *petrusewiczi* from the Japanese *Myodes* (syn. *Clethrionomys*) diverged at the first node, leaving *Syphatineria* sp. within other *Syphacia* spp., whereas the latter species diverged first in ML tree. In both *Cox1* and 28S rDNA trees, *S. rifaii* and *S. muris* were positioned close together, possibly reflecting their host divergence history. The present samples of *S. muris* derived from Indonesian *R. tanezumi* were much diverged from those from laboratory rats both in *Cox1* and 28S rDNA. Probably, the ancestor of *S. muris* might

be adapted to ancestral *Rattus* in Asia, and then made dispersal to the surrounding areas with commensal rats. It is surmised that only limited strains of *S. muris* were chosen when *Rattus norvegicus* was domesticated for laboratory use, and has been distributed worldwide today. In order to elucidate comprehensive feature of evolution of *Syphacia* in Indonesia, it was essential to analyze more species in future studies.

# CHAPTER 4

# Biogeographical discussion on host–parasite relationship between the Indonesian murines and the genus *Syphacia*

## Introduction

Ten species of the genus *Syphacia* have been recorded from Indonesian murines. They are parasitizing eight genera of murine rodents (see Chapter 2), showing mosaic composition especially within the Wallacea. Some islands have a poor fauna, whereas others have rich fauna with high level of endemism etc. Therefore, the author tried to analyze the mosaic distribution and/or composition biogeographically.

## Geographical history of Indonesian archipelago

The Indo-Pacific Archipelago consists of more than 20,000 islands. Within the area, the Indonesian archipelago includes 17,000 islands spread across the equator in Southeast Asia that includes many countries (Lohman et al., 2011; Fig. 4-1).

For understanding distributions of parasitic nematode faunas in Indonesia, geological history of the archipelagos provides the basis. The Indonesian archipelago was formed by addition of continental fragments, mainly rifted from Australia, to the margins of Sundaland as a result of the subduction event driven by the plate movement. Sundaland was an almost permanent landmass from the beginning of the Mesozoic (Whitmore, 1981). The addition of the continental fragments of Southwest Kalimantan and later East Java–West Sulawesi formed a much larger emerged land by the Late Cretaceous that extended from Indochina to West Sulawesi. Australia began to collide with Southeast Asia about 25 million years ago (MA), effectively closing the deep ocean separating the two continents, and forming the region today known as Wallacea (Hall, 2009). From the Miocene (15 MA before) to the Pleistocene (about 20,000 years before), the islands westward of Borneo and Bali were connected to the Southeast Asian mainland as Sundaland while New Guinea and Australia were connected as Sahul. The remaining lands between these two regions were isolated (Groves et al., 2001; Stelbrink et al., 2012). Finally, the Thai-Malay Peninsula, Sumatra, the Sunda Shelf and Eastern Sundaland (west Borneo and parts of West Java) were joined (Hall, 2009; Stelbrink et al., 2012). The separation of islands due to continental drift or the rising sea levels had influenced on the dispersal of non-volant mammals (Stelbrink et al., 2012), especially the small bodied rodents (Fabre et al., 2013; Fig. 4-2).

Hence, the Indonesian archipelago has been regarded as a good model for the biogeographical field since 19th century (Maryanto and Higashi, 2011; Fig. 4-1). The islands of Indonesia straddle two of the world's seven major biogeographic regions, the Oriental and Australasian, and include Wallacea mentioned above, a unique biotic and geographic area that lies in the broad interface between these two major regions (Stelbrink et al., 2012). These islands have fauna that are not particularly rich in species, but feature a very high level of endemism in many islands. For this, Indonesia is considered one of the most biologically diverse countries by having about 17% of all species and about 12% of mammal species hitherto discovered in the world (Wilson and Reeder, 1993).

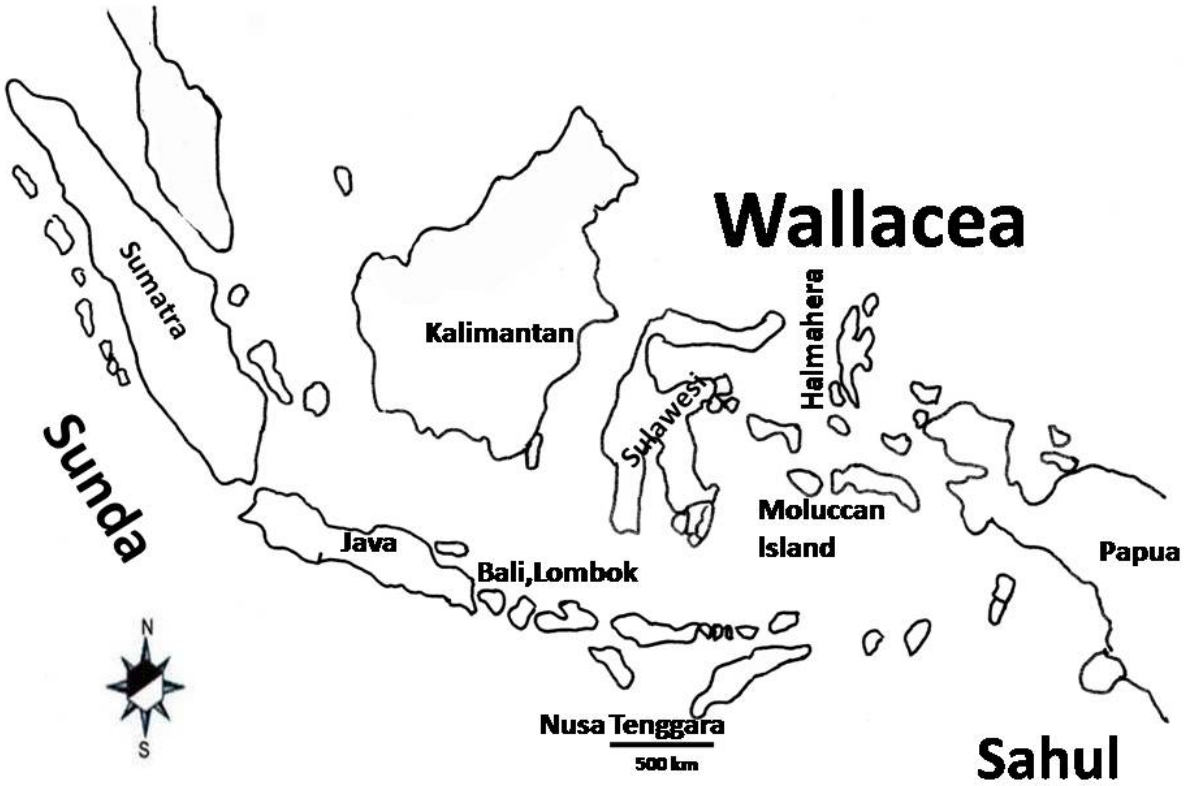



Fig. 4-1. Map of Indonesian archipelago in the present time.

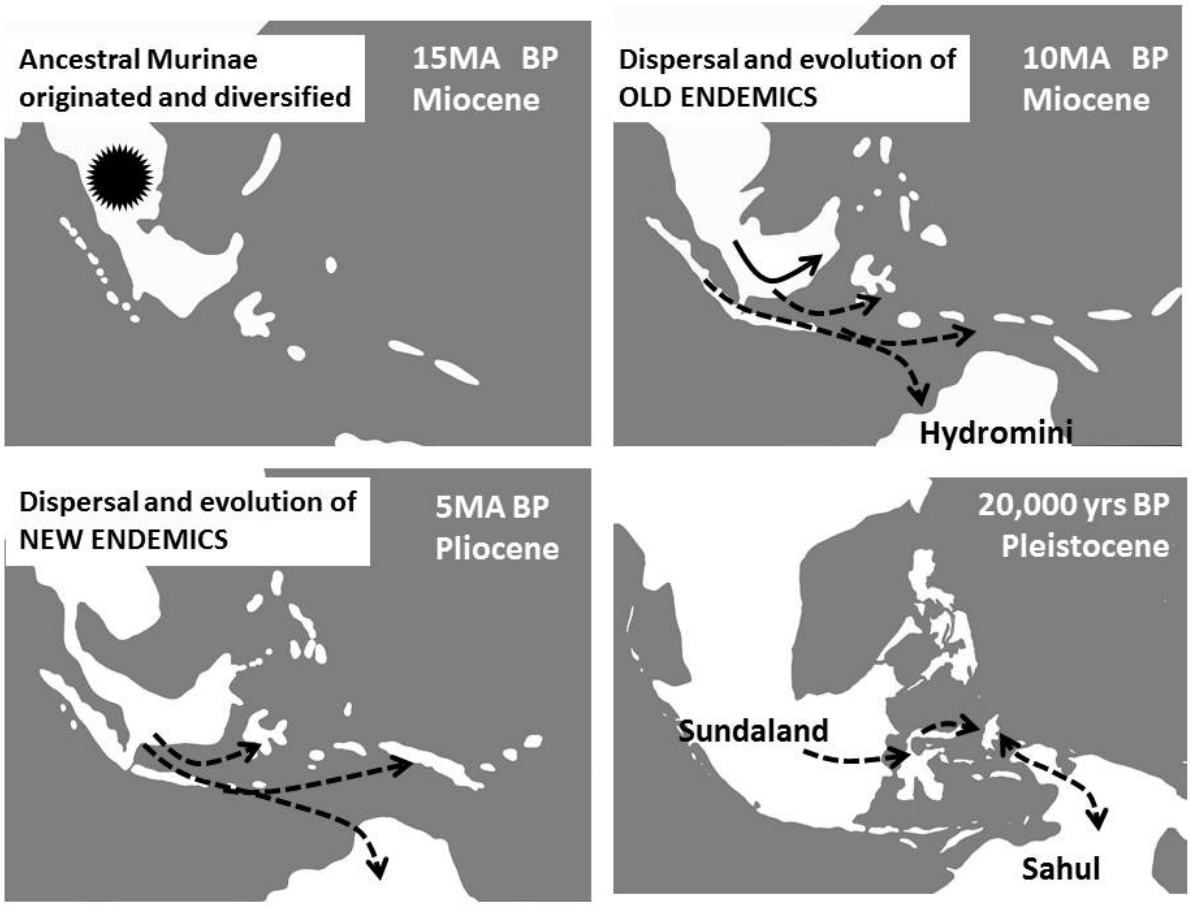



Fig. 4-2. History of the origin of the Murinae based on Stelbrink et al. (2012) and Fabre et al. (2013); ●: Hypothetical ancestor of the Murinae; dotted arrows: dispersal routes; MA: million years ago.

**Host origin and phylogeny**

Ancestor of the subfamily Murinae is suggested to have originated in Asia, and its dispersal from Sundaland to Sulawesi mentioned below occurred between the late Miocene and the Plio-Pleistocene (Fabre et al., 2013; Fig. 4-2). The molecular phylogenetic tree for the genus *Rattus* and its allies in Indo-Pacific area was provided by Fabre et al. (2013) (Fig. 4-3). The rodent taxa from the Indonesian-Australian archipelago used in the present study belong to the tribes Rattini and Hydromyini defined by Fabre et al. (2013). The Rattini includes the genera *Maxomys, Bunomys, Taeromys, Paruromys, Halmaheramys* etc., and the Hydromyini includes *Melomys, Lorentzimys, Pseudomys* etc. The genus *Eropeplus* which is regarded as very important taxon in the present study because two new subgenera of *Syphacia,* viz., *Segienamsyphacia* and *Rumbaisyphacia*, were found (see Chapter 2), was not treated in Fabre et al. (2013).

The two tribes mentioned above are divided by main geographical distribution. The Rattini occurs from Sundaland (Thailand, Malay Peninsula, Sumatra, Java etc) to Sulawesi/ Halmahera, and in Australia as well. However, the Hydromyini are distributed to Sahul and Walacea (Papua Indonesia, Papua New Guinea and Australia). The Hydromyini make only one clade altogether (Fig. 4-3). On the other hand, according to Fabre et al. (2013), the

Rattini contains four main monophyletic lineages: 1) the Southeast Asian *Maxomys* group, 2) the *Melasmothrix* lineage, 3) the *Dacnomys* division clade, and 4) the *Rattus* division clade. Furthermore, the *Rattus* clade was divided by several sub-clades. The genera including *Bunomys, Taeromys, Paruromys* and *Halmaheramys* formed the Sulawesian clade, or they are called as the new endemic as well (Musser, 1987). But the genera of the old endemic including Sulawesian genera *Echiothrix, Melasmothrix* and *Taetomys* may form one clade (see Esselstyn et al., 2012). However, *Maxomys* is nested in *Crunomys* (Achmadi, 2013; Fabre et al., 2013). *Lorentzimys* belongs to Hydromyini and *Coccymys* belongs to Anisomyini (see Esselstyn et al., 2012).

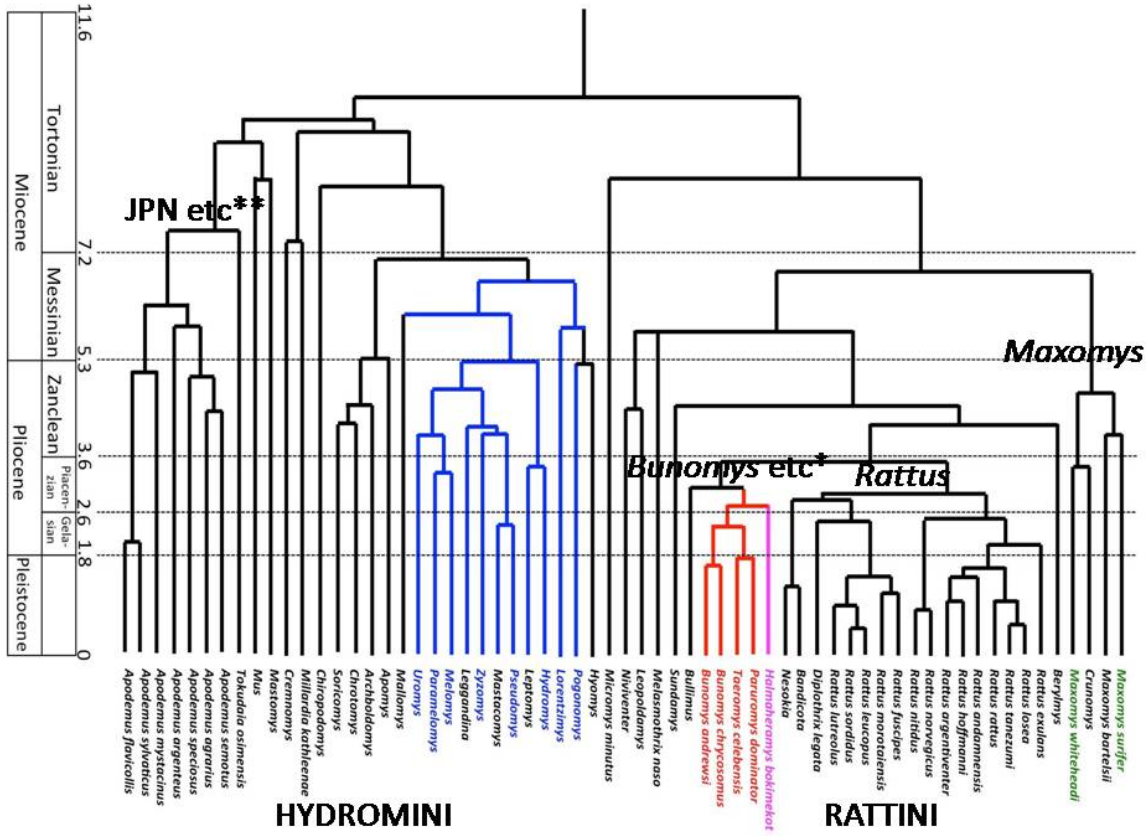



Fig. 4-3. Phylogenetic tree for the subfamily Murinae (modified after Fabre et al., 2013).
*: Showing the genera *Bunomys, Taeromys, Paruromys* and *Halmaheramys* that were used in the present study.

**Host dispersal to Sunda and Sahul**

Because murines migrated mostly through dispersal as mentioned above (Fig. 4-2), the sea level can be the major factor affecting their dispersal and species richness (Fabre et al., 2013). Even if the barrier distance is short, the migration of small mammals such as the murines would be difficult between the islands. In very rare occasions, some murines could manage to make dispersal by drifting across the deep sea surrounding the islands, which were isolated for quite long period (Maryanto and Higashi, 2011). Hence, the murines in Indonesia are divided into two groups, viz., the Sundaic group and the Sahulian group (Musser and Durden, 2002). Adding to two groups, murines of Wallacea (Sulawesi and Halmahera Islands) are located in transition area between the Sunda and Sahul.

**Sundaic group;** There are so many genera (*Maxomys, Niviventer, Sundamys, Leipoldamys, Rattus* etc.) and species recognized in this group, and they have generally broad distributions in the Malay Peninsula, Sumatra, Borneo, Java, the Mentawai Islands, the Palawan group of islands in the Philippines, Thailand, Laos, Vietnam, and China (Achmadi et al., 2013; Fabre et al., 2013). However, ancestor of the subfamily Murinae was originated in Asia (Fabre et al., 2013; Fig. 4-2).

**Sahulian group;** Adding to the dispersal from the Sunda Shelf, Sulawesi also provided the migrating routes from the Sahul region (New Guinea and Australia; Fig. 4-2) with ancestors of the old/new endemic murines accompanied with their parasitic nematodes (Smales, 2012).

**Wallacean group;** The Wallace's line is a boundary separating Oriental and Australian realms (Lomolino et al., 2010). The endemic non-volant eutherian mammals in the region east of this line are considered to have originated in the west region, especially, Sundaland, then dispersed across the line to the east, and diversified (Musser, 1987). The difference of mammalian fauna on each side of the Wallace's line is remarkable. Sulawesi is just east of the Wallace's line, constituting the biogeographical transition area between Oriental and Australian regions (Lomolino et al., 2010). This island has a unique mammalian fauna that is not only species richness, but also with features of very high level of endemism (Musser, 1987). The Sulawesian murines represent approximately 30% of the total mammalian species and approximately 52% of all the endemic species of Sulawesi (Musser and Durden, 2002).

The aboriginal murines of Sulawesi have been assumed to have ancestors on the South–East Asian mainland and on the Sunda Shelf islands (Musser, 1987; Musser and Durden, 2002; Fig. 4-2). They are composed of the new endemics including the genera *Bunomys, Eropeplus, Paruromys, Rattus* and *Taeromys* relatives of which are distributed on

the Sunda Shelf during Pliocene to Pleistocene, and old endemics including 5 genera (*Crunomys*, *Echiotrix, Melasmothrix, Paucidentomys, Tateomys*), of which ancestors were probably derived from the Sunda Shelf in Miocene. Because no oxyurids could be obtained from 19 invididuals belonging to five species of the old endemic murines examined (Hasegawa et al., 2014; Hasegawa, personal communication), the present discussion is focused on the new endemic murines and their pinworms.

There have been arguments on the origin and dispersal of the new endemic murines of Sulawesi. Some researchers believe that the ancestors migrated via a land bridge connecting Sulawesi to the Sunda Shelf in or before the Pleistocene, though there has been no evidence of such a land connection during the Cenozoic era (see Hall, 1998). Meanwhile, mammalogists consider that dispersal by sea level fluctuations as a possible scenario (Musser, 1987; Fabre et al., 2013). In any cases, dispersal to Sulawesi might have exerted a bottleneck effect on the murines, driving them to experience adaptive radiation in the new environment to form many endemic species (Musser, 1987).

Halmahera (North Moluccas) and other Moluccan islands were not connected by a land bridge to the surrounding landmasses during the Pleistocene (Voris, 2000). Hence, dispersal of non-volant mammals to Moluccan islands might have occurred only accidentally, probably by drifting. The endemic murines of the South Moluccas seemed to be allied with

those on New Guinea and small surrounding islands (Musser, 1987). Based on the phylogenetic studies, *Halmaheramys* ancestors probably colonized to Halmahera (North Moluccas) from the west (Sulawesi?) during the Pliocene (Fabre et al., 2013). Based on the molecular reconstruction including most murine genera of Indo-Pacific group within the *Rattus* Division, Fabre et al. (2013) assigned *Halmaheramys* to a new group, which includes *Bullimus, Bunomys*, *Paruromys, Sundamys* and *Taeromys*. *Halmaheramys* differs from other endemic murines of Halmahera Island, *R. morotainensis* and undescribed species of *Melomys*, which probably colonized the North Moluccas in the Pleistocene from the east (Sahul).

**Related studies of Syphaciinae and Heligmonellidae in Indo-Australian archipelago**

The faunistic studies on parasitic nematodes of the related murines from the Indo-Australian archipelago should be reviewed first, because such data will become base for discussion on the origins of the Wallacean nematode fauna. Some studies on the murine nematodes had been done in the subfamily Syphaciinae and the family Helilmonellidae (see Appendixes 3 and 4), and main reliable works of them, including those by the Indonesian researchers (see Chapter 1 and Appendix 1), focused on taxonomy with new locality/host records between the 1990' and 2010's.

The first publication of parasitic nematodes from Malaysian murines was done by Adams (1933). He described *Cyclodonstomum purvisi* and reported *Ancylostoma malayanum* and "*Syphacia obvelata*" from rats (no scientific names, but *Rattus* spp.) collected from both Taiping and Pahang (see Ow-Yang, 1971). Later, Schacher and Chee-Hock (1960) examined 1,117 murine individuals, and found "*Nippostrongylus muris"* and *Syphacia* sp. from *Rattus norvegicus, R. diardi* and/or *R. exulans.* From Thailand, Ohbayashi and Kamiya (1980) described two new species of the genus *Orientostrongylus*, namely *O. siamensis* from "*Rattus surifer"* (now, *Maxomys surifer*) and *O. ratti* from *R. rattus* and *R. norvegicus*. However, Hasegawa et al. (1994) regarded *O. ratti* is a junior synonym of *O. tenorai* Durette-Desset, 1970. Yoshida et al. (1985) studied taxonomy of the genus *Syphacia* from 317 individuals belonging to six murine species in Thailand. They recorded *Syphacia muris* from *Rattus losea, S. pahangi* from *Niviventer confucianus*, *Syphacia* sp. 1 from *Maxomys surifer* and *Syphacia* sp. 2 from *R. tanezumi*. It is presumed that *Syphacia* sp. 1 of Yoshida et al. (1985) is the same species with *S. maxmyos* from *Maxomys* spp. in Sulawesi and Sumatra in the present study (see Chapter 2). On the other hand, *Syphacia* sp. 2 of Yoshida et al. (1985) might be *S. muris*.

Recently, Chaisiri et al. (2012) examined 725 individuals belonging to 17 murines species in various habitats in Thailand, and found "*Syphacia muris"* in 8.6% of them, but without strict taxonomical consideration. Furthermore, the first survey in Lao PDR was made

by Pakdeenarong et al. (2013), who investigated a total of 404 murines belonging to 13 species, and recorded "*S. muris*" from *Berylmys berdmorei, R. exulans, Maxomys surifer* and *Syphacia obvelata* from *Mus caroli* and *M. cookii*. However, so-called "*S. muris*" by Pakdeenarong et al. (2013) might contain plural species because of the host specificity of *Syphacia*. Unfortunately, their report lacked taxonomical and morphological data. Besides this species, "Trichostrongylidae sp." was listed in their study though heligmonellid nematodes were not reported.

In Australia, there are so many *Syphacia* and heligmonellid species reported from murines (Gibbons & Spratt, 1995; Smales, 2008, 2011; Appendixes 3 and 4).

Overall, the reliable faunistic studies on the origin of the Wallacean nematode fauna in the Indo-Australian archipelago are limited. Therefore, for the biogeography of the host-parasite relationships between the murines and their parasitic nematodes, only reliable records of the host specific nematodes should be selected. In general, such nematode groups as preferable candidates are the subfamily Syphaciinae and the families Heligmonellidae and Heligmosomidae in the murinae (Durette-Desset, 1971; Hugot, 1988; Hasegawa, 1999; Hasegawa and Asakawa, 2003; Asakawa, 1991, 1995). However, the species of the Heligmosomidae (see Durette-Desset, 1971; Asakawa, 1991, 1995), especially genus *Heligmosomoides*, were not recorded from the archipelago (see Appendix 1), so this group

was omitted. On the other hand, many species belonging to the family Heligmonellidae have been described and/or reported (see Appendix 4), but Wallacean taxa are now under study, so their analyses will be done in the future. Hence, the most adequate candidate at the present time is the genus *Syphacia.*

**Morpho-phylogenetic relationship in the subgenus *Syphacia***

Phylogenetic analyses of *Syphacia* should be based on the taxonomical (morphological) and/or phylogenetical (molecular biological) data along with host biogeographical/evolutionary evidence (Hugot, 1988; Okamoto et al., 2007). The present morphological and molecular data (see Chapters 2 and 3) are expected to depict a convincing phylogenetical relationship among *Syphacia* spp. recorded not only from the archipelago including Indonesia (Fig. 4-4), but also with those in the other part of the world.

There are distinct tree morphological types in the cephalic end of *Syphacia* spp., especially in the subgenus *Syphacia* shown in Fig. 4-5; namely, round, square and laterally-elongated head, respectively. These cephalic shape types and geographical distributions have relations with each other: square cephalic end is rare, being found in the cosmopolitan *S. muris* and *S. australasiensis* in the new endemic *Rattus* of Sahul; round type is found in most

of representatives of the Wallacean new endemic species and some of Sahul (Papuan) old endemic species; laterally-elongated type is shared by one species in *Maxomys*-parasitic species in Sunda and Wallacea and most species in the old endemic murines of Sahul (Fig. 4-6).

In the evolutionary trend of the morphological characters in *Syphacia* or Oxyuridae, the rounded type has been believed as primitive because such cephalic end is commonly found in pinworms of sciurids and/or ground sciurids (Quentin, 1971; Hugot, 1988). However, this theory should be applicable only for early phase of evolution of Syphaciinae. Among the members of *Syphacia*, laterally-elongated head is predominant, being known in the species of subgenera *Cricetoxyuris*, *Seuratoxyuris* and *Syphacia* from the Indo-Australian archipelago, the Holarctic region, Africa and the New World (Quentin, 1971; Hugot and Quentin, 1985; Hugot, 1988). It is notable that the laterally-elongated head is found in the *Syphacia* (*S.*) spp. of the old endemics murines in Sahul (Fig. 4-6). Therefore, the laterally-elongated type of the head seems to be an ancestral form in the evolution of *Syphacia*, and the round and square heads are thus regarded as derived characteristics.

The above idea of ancestry of cephalic shape is also supported by both of the present molecular relationships on *Cox1* and 28S rDNA (Fig. 4-7). The species with "round" and "square" heads were derived from the ancestor with "laterally-elongated head" species. Each

morpho-species group should be regarded as a phylogenetic lineage; namely, “Round head lineage (abbreviated to R)”, “Square head lineage (abbreviated to S)” and “Laterally-elongated head lineage (abbreviated to LE)”.

When the murines have adapted to and speciated in their new insular environments of Wallacea, some of their host-specific nematodes might become extinct, whereas the others might co-evolve with their hosts or be shifted (switched) to a new hosts (Warner, 1998). In the latter two cases, for example the genus *Syphacia*, each nematode species underwent speciation in Wallacea, finally becoming morphologically distinct from the original species. This could be the beginning of a new evolutionary lineage. Probably, the two new subgenera, *Rumbaisyphacia* and *Segienamsyphacia* found in the present study (see Chapter 2) represent such case: they might have co-evolved with *Eropeplus*, a monotypic murine. Unfortunately, positive molecular data of the new subgenera taxa could not be obtained because of inadequate fixation of the worms in 1990’s. Moreover, the molecular phylogenetic relationship of *Eropeplus* with other murines remains unsolved (cf. Fabre et al., 2013) though close relationship with *Lenothrix*, a member of the earliest group derived from the core murine lineage in Sundaland, was suggested by morphological observation (Musser and Newcomb, 1983; Musser, 1987; Musser & Carleton, 2005).

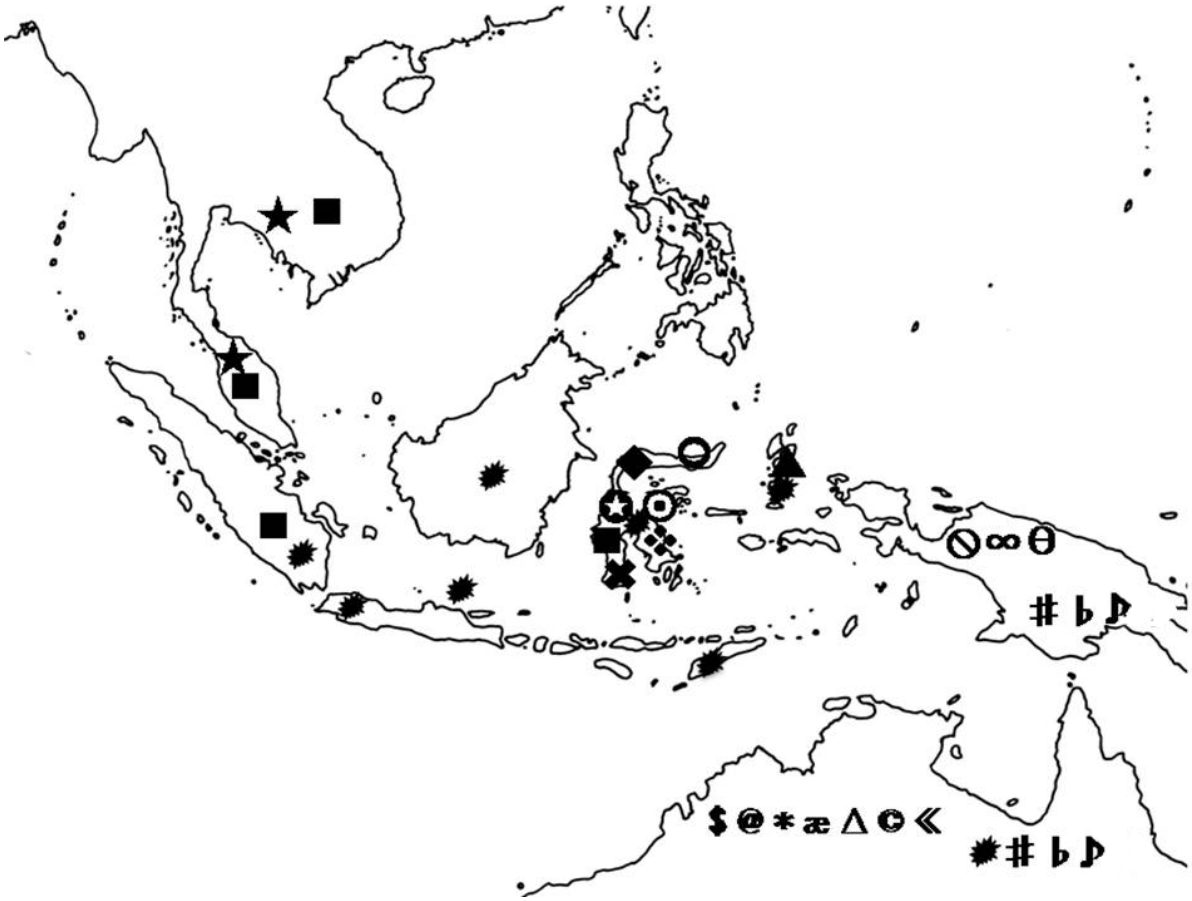


Fig. 4-4. Distribution of *Syphacia* spp. in the areas from Malay Peninsula/ Thailand to Australia. Black marks showing locality of each *Syphacia* in Indonesia. All taxa new species including 2 new subgenera and species derived from long period-isolation and remarkable endemism occurred.

★: *S. (Seu.) pahangi*, ■ : *S.(S.) maxomyos,*⊙: *S. (R.) kumis*, ✪: *S. (S.) yuniae*, ◆: *S. (S.) rifaii,* ✖ : *S. (S.) taeromyos*, ❖ : *S.(S.) paruromyos*, ▲: *S.(S.) semiadii*, ❍: *S.(S.) sulawesiensis,* ⃠**:** *S. (S.) lorentzimyos,* ∞**:** *S. (S.) mamelonitenuis,* **Θ:** *S. (S.) coccymyos*, **$:** *S. (S.) boodjamullensis,* **@:** *S. (S.) brevicaudata*, æ: *S. (S.) pseudomyos*, Δ: *S. (S.) helidonensis*, ©: *S. (S.) abertoni*, « : *S. (S.) carnavonensis,* ♯**:** *S. (S.) longaecauda*, ♭ *: S. (S.) australasiensis,* ♪*: S. (S.) darwini,* ✸: *S. (S.) muris*,

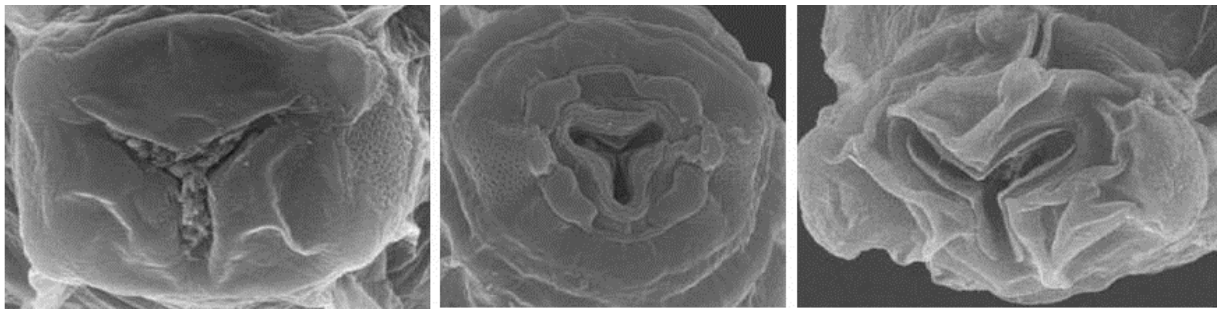


Fig. 4-5. Cephalic shape of *Syphacia* spp. in Indo-Australian Archipelagos. Morphological characters of the cephalic end, namely Square head lineage (abbreviated to S)", "Round head lineage (abbreviated to R)" "and "Laterally-elongated head lineage (abbreviated to LE)".

SEM Photos of upper site, left: *S. muris* from *Niviventer cremoniventer* (Dewi, unpublished); middle: *S. rifaii* from *Bunomys penitus* (see Chapter 2); right: *Syphacia maxomyos* from *Maxomys whiteheadi* (Dewi et al., in press).

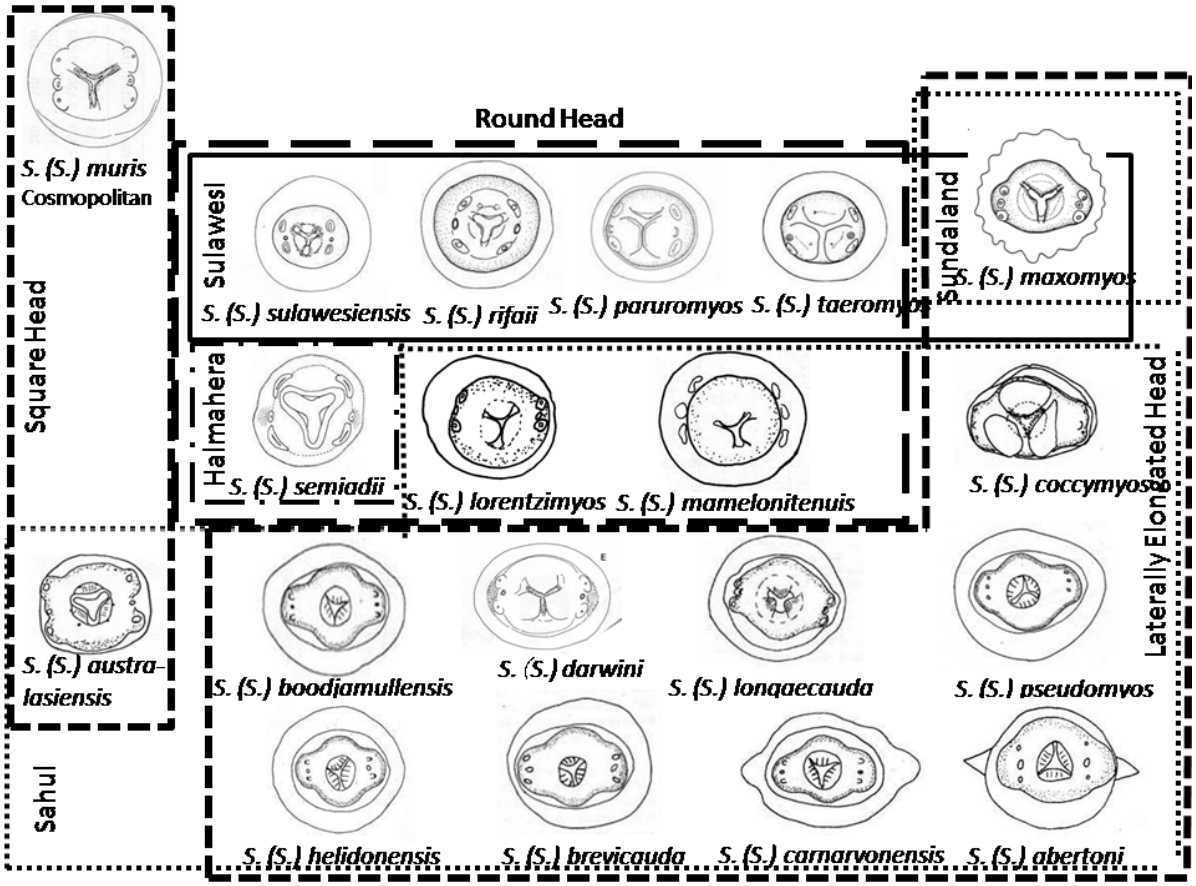



Fig. 4-6. Cephalic shape (en-face view) of *Syphacia (Syphacia)* spp. distributed in Indo-Australian areas. Cephalic plate shape is divided into 3 types, square, round, and laterally-elongated. Thick lines surround each type of the cephalic shape and thin lines surrounds species in the geographical distributions, Sunda, Sulawesi and Sahul.

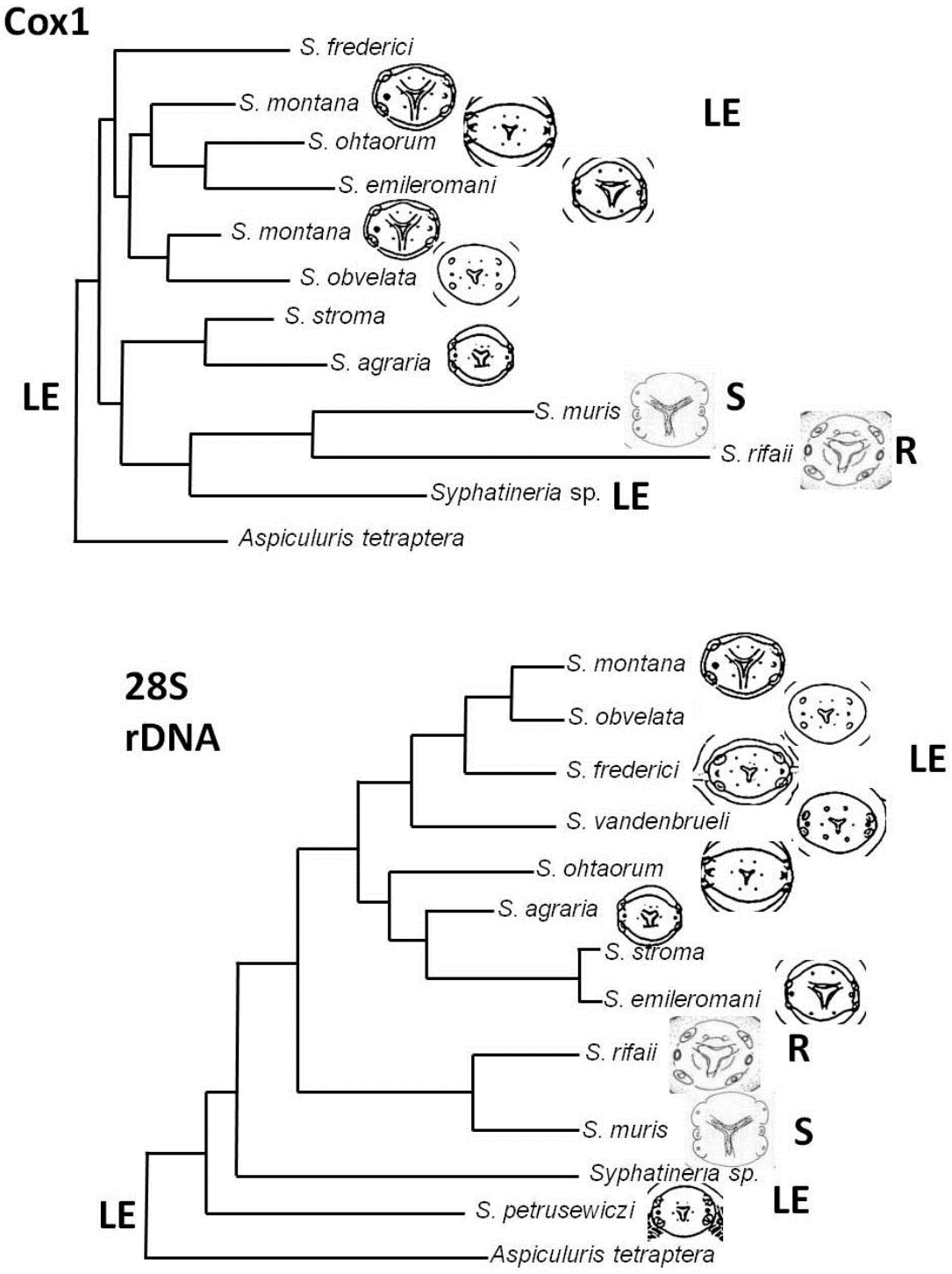



Fig. 4-7. Relationship between the cephalic shapes and molecular phylogenetic trees based on mt DNA *Cox1* and 28S rDNA of the subgenus *Syphacia*. R: Round head, S: Square head, LE: Laterally-elongated head. Phylogenetic trees were simplified based on Figs. 3-2, 3-4. Figures of cephalic ends of Japaneses taxa from Hasegawa et al. (1994).

**Biogeography of host-parasite relationship between murines and subgenus *Syphacia***

**Overview of the world distribution;** The host-parasite relationship between the murines and subgenus *Syphacia* seems to be as follows: at first, an ancestral *Sypacia* LE species parasitized the ancestral murine. The ancestral murine/*Syphacia* LE dispersed from Sundaland to Wallacea, and to Sahul between the late Miocene and the Plio-Pleistocene and coevolved. This process made the *Syphacia* LE species present in the Indo-Australian archipelago with the Rattini and Hydromyini. Almost simultaneously, the species also invaded to north Eurasian Continent including North Africa and its islands with the ancestral murines of the genera *Apodemus, Mus, Micromys* etc. Furthermore, some of the *Syphacia* LE in the Eurasian murines shifted (switched) to the microtines (Microtidae), and the descendant species occur today not only in the Palearctic Subregion with the genera *Myodes, Microtus, Eothenomys* etc., but also in North America with the genera *Myodes* and *Microtus*. *Syphacia obvelata* belonging to the LE group became cosmopolitan with commensal *Mus* spp., and its habitat close to humans might cause zoonotic parasitism (see Chapter 1).

**Indo-Australian Archipelago;** Before the eastward invasion events, the speciation of *Syphacia* species with round head shape (*Syphacia* R) might occur from *Syphacia* LE. The

ancestral *Syphacia* R was introduced with host murine dispersal to Walacea, especially Sulawesi, which is the island with extremely high diversity of fauna. Subsequently, the *Syphacia* R diversified with the evolution of their hosts. Exceptionally, only one species *Syphacia* LE occurs in Sulawesi (*S. maxomyos* from *Maxomys*; Dewi et al., in press). Because this species also occurs in *Maxomys* spp. of Sumatra and Asia continent (see Chapter 2), it could be regarded as an example of dispersal from Sunda to Wallacea with host murines.

**Wallacea;** On the other hand, the LE, R and S lineages of *Syphacia* invaded Sahul, and now many endemic LE, two R and one S species are known in Australia and Papua (see Fig. 4-5). The Sahulian endemic R species, which occur on Papua have a remarkable characteristics of small or absent of lateral alae in both sexes (Smales, 2010). Meanwhile, the R species of Sulawesi have large lateral alae at least in one sex (see Chapter 2). The presence/absence of the alae is regarded as an important key character, and it could be sub-lineage criteria mentioned above. Hence, it is likely that *Syphacia* spp. on Sulawesi belong not only to new two subgenera, but also to plural lineages, namely the R with probably sub-lineages, the LE with one species during colonization of this island.

However, on Halmahera Island an extraordinary event occurred. The R species, *Syphacia semiadii* parasitizes *Halmaheramys* (the new endemic mentioned above) and the

species lacks lateral alae in both sexes. Because the Moluccan islands including Halmahera Island were not connected by a land bridge to the surrounding landmasses as mentioned above, the murine dispersal into the islands is still in controversy (Fabre et al., 2013), but might be by drifting. At least, after *Halmaheramys* ancestors colonized from Sulawesi Island, presumably, ancestral *S. semiadii* invaded from Sahul into Halmahera Island with a Sahul origin murine, and thereafter the pinworm shifted to *Halmaheramys* or ancestral *Halmaheramys* and coevolved on the island, although the ancestral murines brought ancestral *S. semiadii* was unknown. It is expected that the allies of this *Syphacia* will be found from some endemic murines on Halmahera in future, unless the ancestral host became extinct already.

Similar event of the host-shifting/ancestral host died-out is known in the host-parasite relationship between *Apodemus* and *Heligmosomoides* (Asakawa, 1991, 1995). *Heligmosomoides kurilensis* is widely distributed with *A. speciosus* in Japan, but the nematode species of the lineage are typical parasites of the lemmings (Microtinae; Muridae), for example *Dicrostonyx, Lagurus, Lemmus* etc. During the Glacial periods of the Pleistocene, they invaded Japan via land bridge(s), but just after the period, the lemmings were extinct there. Asakawa (1991, 1995) suggested that ancestral *H. kurilensis* shifted to the ancestral *A. speciosus* when both of the old/new hosts shared same habitat.

After the ancestral S diversified from the LE, one endemic species, *S. australasiensis*, in Sahul (Australia) and common species, *S. muris*, occurred there. Since end of the Plesitocene, human commensal rats have continued to invade everywhere with human activities, making *S. muris* as a cosmopolitan species.

Overall, the dispersal to Sulawesi might have exerted a bottleneck effect not only on the new endemic murines, but also on their nematode parasites. Since arrival on Sulawesi, the *Syphacia* species in the new endemic murines of Sulawesi have experienced adaptive radiation and formed 6 endemic taxa including the new subgenera and species.

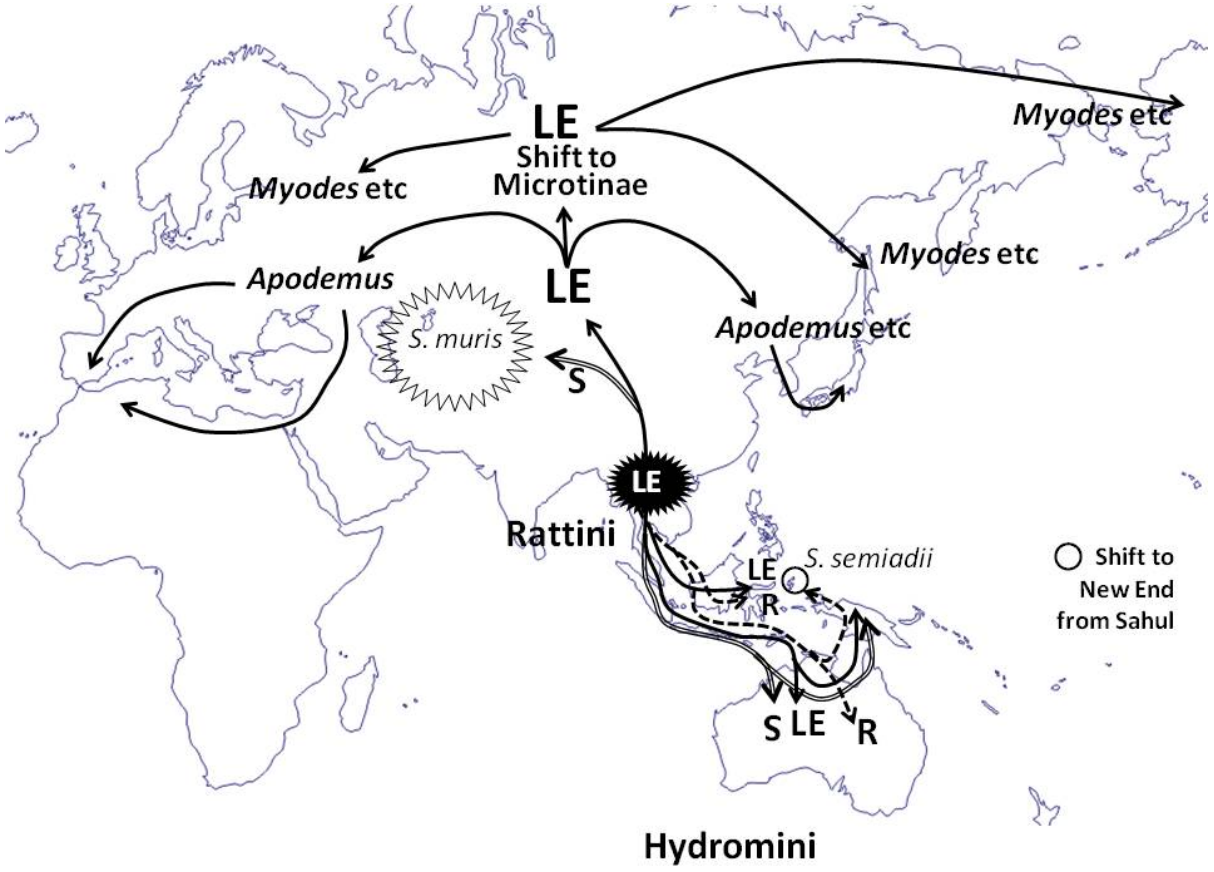



Fig. 4-8. Summarization of hypothetical dispersal and events of the subgenus *Syphacia*. Solid, broken and double lines indicating dispersal routes of LE, R and S cephalic types, respectively.

●: Hypothetical ancestor of the subgenus *Syphacia*, which might belong to LE lineage; *Myodes* etc.: Microtinae occurs in the Holoarctic region, including the genera *Myodes, Microtus, Eothenomys* etc.

*Apodemus* etc.: Murinae occurs in the Palearctic subregion (East and mid-Asia, Japan, Europe, and North Africa), including the genera *Apodemus, Mus* and *Micromys*; Rattini and Hydromyini: see the Fig. 4-3;

O Shift to new end from Sahul: showing the event that ancestral *Syphacia semiadii* invaded into Halmahera Island with an extinct (?) rodent of the Hydromyini and the nematode parasitizes *Halmaheramys*.

Dispersal of *S. muris* with commensal *Rattus* spp. *Syphacia obvelata* belonging to the LE is also cosmopolitan with *Mus* spp., but not included here.

**Conclusion; past, present and future of the host-parasite relationship between murines and their *Syphacia***

Ten species of the genus *Syphacia* have been recorded from Indonesian murines by the present study. Because the species composition shows specific features among the islands of the Wallacea, the *Syphacia* fauna was analyzed in the context of biogeography. Ancestors of the insular murines were suggested to have originated in Asia, and their dispersal from Sundaland to Sahul occurred during the period from the late Miocene to the Plio-Pleistocene. Because the murines migrated generally throughdispersal, the straits separating the lands and islands might be barriers for dispersal even though they became narrower and shallower at glacial age. This geological history has made the Indonesian murines divided into the Sundaic and the Sahulian groups, and Wallacean murines constitute transit but diversified fauna between the two groups. The Wallacean *Syphacia* should be analyzed based not only on their morpho/taxonomy and molecular data, but also on the geological background and host dispersal events. According to the morphological characteristics, the species of the subgenus *Syphacia* were divided into three groups; square (S), round (R) and laterally-elongated (LE) cephalic plate types. By considering the evolutionary trend of the characters, the LE type was regarded to be the primitive character.

A dispersal scenario of the host parasite-relationships between murines and the nematodes was presented. An original dispersal from Southeastern Asia was made with the LE type, spreading not only to Wallacea and Sahul, but also to Europe, North Africa, East-mid Asia and Japan, finally to North America. Before the north-eastward movement, the speciation of the R type occurred, and the ancestral R and LE types invaded Wallacea and colonized. Simultaneously LE, R and S types also invaded Sahul, and many endemic LE, four R and one S species evolved in Australia and Papua. However, the origin of *Syphacia semiadii*, which parasitizes *Halmaheramys* on Halmahera Island seems to be exceptional: the host murine, *Halmaheramys*, is considered to have derived from Sulawesi, its *Syphacia* showed phylogenetic resemblance with Papuan representatives. It remains unknown whether the ancestral murines that introduced ancestral *S. semiadii* to Halmahera became extinct or its descendant is still extant after the pinworm shift to *Halmaheramys*. During such dispersal events, *Syphacia muris* evolved and became the common species of the S type.

The One Health concept is founded on an awareness of the major opportunities that exist to protect public health through policies aimed at preventing and controlling pathogens at the level of animal populations, that is, at the interface between humans, animals and the environment. The Indo-Australia Archipelago is regarded as the biodiversity hotspots, but the archipelago is one of the most suffered areas by the recent climate change as well. The

climate change acts as a threat multiplier that interacts both directly and indirectly with variables such as disease, animal products and conservation of wildlife in the archipelago (Black and Butler, 2014; Romanelli et al., 2014). A better understanding of the links between biodiversity and diseases (or their responsible agents) shows understandable and excellent example of research models in the area. For example, there have been the viral and/or bacteria pathogens such as One Health approach models in South-east Asia and Australia including the archipelago (Pastoret et al., 2014; Godfroid et al., 2014; Peiris and Yen, 2014; de La Rocque and Formenty, 2014; Wang and Crameri, 2014; Michel, 2014). However, a parasitic nematode has not been identifies as a key One Health issue. So, the present study will become an ideal model for the approach, because the agents could infect not only wildlife, but also both human beings and captive animals (e.g., experimental and pet ones).

**Summary**

The *Syphacia* fauna of Indo-Australian regions was analyzed in a context of the biogeography. Ancestors of the host murines were suggested to have originated in Asia continent, and made dispersal from Sundaland to Sahul during the period from the late Miocene and the Plio-Pleistocene by dispersal. By the dispersal and subsequent evolution, the present Indonesian murines are divided into the Sundaic and the Sahulian groups, and Wallacean murines constitute peculiar fauna. According to the morphological characteristics of the cephalic end, members of the subgenus *Syphacia* were divided into the three groups; square (S), round (R) and laterally-elongated (LE) types, and LE type seemed to be the primitive form.

A dispersal scenario was presented to explain the host parasite-relationships between murines and their pinworms. The ancestor of *Syphacia* LE type, which parasitized the ancestor of murines, made dispersal from the original area in continental Asia southward not only to Wallacea and Papua/Australia, but also northward to spread over Northern Hemisphere. Probably before the northward movement, the R type evolved, and the ancestral R and LE types invaded Wallacea and colonized. Simultaneously, the other LE types, R and

S types invaded Sahul, resulting in the presence of many endemic LE, R and S types of *Syphacia* in both Papua and Australia.

During the dispersal of the intimate host-parasite relationship, an extraordinary phenomenon was found in *Syphacia* from Halmahera Island. The ancestor *Halmaheramys* as a host of *S. semiadii* is suggested to be Sundaland origin, whereas *S. semiadii* has similar characters with Sahulian *Syphacia*. Probably, a host-switching was occurred in Halmahera. Furthermore, a cosmopolitan species of the S type, *Syphacia muris*, invade everywhere with human commensal rats. Finally, *Syphacia* could infect to human beings, and to experimental/pet rats, as well, and the issues should be regarded and presented as the One Health model.

## Conclusion

The biogeography is one of the evolutionary biology fields, focusing on a historical process of an animal dispersal. Nowadays, preventive (veterinary) medicine is needed for making preventive measures of an outbreak of infectious diseases including nematodiasis. The preventive (veterinary) medicine related to an ecosystem especially as the One Health context, the preventive measures are based on the past things, viz., from where the nematode came, when and how to invade into the place. Murine rodents (rats and mice) are the principal reservoirs of many important parasitic nematodes of humans beings and livestock because they are commonly live around human. For that reason, it is important to study the nematodes of murines and their biogeography.

One of the interesting nematodes is the pinworms of the genus *Syphacia* because this genus has zoonotic importance in human. Furthermore, *Syphacia* has direct life cycle so it easier to acquired a new host. Therefore, the taxonomical and faunistic study on this genus should be regarded as medical parasitological importance.

Based on this study, 20 species including a new heterakid genus/species, two new subgenera and seven new speciesof *Syphacia* could be newly recorded. Hence, descriptions about the taxa were done, and a key of all *Syphacia* species recorded in Indo-Australia region

including the newly found taxa was given. Adding to the taxonomical study, partial sequences of the mitochondrial *Cox1* gene and 28Sr DNA from Syphaciinae species obtained not only from Indonesia, but also from Japan,were determined. The molecular biology from the Syphaciinae species from Indonesia was succeeded in the extraction of DNA from only three species i.e. *Syphacia rifaii*, *S. muris* and *Syphatineria* sp. Among the species of the subgenus *Syphacia*, *S. rifaii* and *S. muris* formed a clade, sharing a long branch, diverging from the common ancestor to the other *Syphacia* species in both *Cox1* and 28S rDNA trees. The tree lineages of the subgenes *Syphacia* were found based on the morphology of the cephalic end and molecural phylogeny. Finally, the author challenged to analyze the biogeography on the host-parasite relationship between murines and *Syphacia.* If the scenario presented here is correct, the Wallace's line could be applied for almost endemic *Syphacia* spp. as well, and the biogeographical approach could be regarded as one of the One Health model researches.

Up to now, total 35 species and three genera of Indonesian murines have been investigated nematologically. However, there are at least 173 murine species in Indonesia, so over 130 murine species are waited for future faunal studies of parasitic nematodes. Unfortunately, many of the murine species are listed as endangered or extinct. The extinction of hosts means extinction of their parasitic nematodes, especially if they are host-specific or

endemic. Hence, the studies should be kept, and such continuous studies may ultimately provide an intrinsic information of biodiversity of parasites and their coevolution with their hosts in a geographical area that provides the setting for high levels of endemism.

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**References**

Achmadi, A. S., Esselstyn, J. A., Rowe, K. C., Maryanto, I. and Abdullah, M. T. 2013. Phylogeny, diversity, and biogeography of Southeast Asian spiny rats (*Maxomys*). *Journal of Mammalogy* **94**: 1412-1423.

Adams, A. R. D. 1933. Report on a collection of nematodes from the Federal Malay States. *Annals of Tropical Medicine and Parasitology* **27**: 1-13.

Anderson, R. C. 2000. Nematode Parasites of Vertebrates. Their Development and Transmission. 2nd ed. CABI Publishing,Wllingford, Oxfordshire, U.K., 650pp.

Asakawa, M. 1991. Genus *Heligmosomoides* Hall, 1916 (Heligmosomidae: Nematoda) from Japanese islands. *Helminthologia* **28**: 155-163.

Asakawa, M. 1995. A biogeographical study of the parasitic nematodes of Japanese Microtinae and Muridae with systematic and phylogenetic studies of the genera *Heligmosomoides* and *Heligmosomum* (Nematoda: Heligmosomidae). *Journal of Rakuno Gakuen Universty, Natural Science* **19**: 285-379. (in Japanese with English summary)

Asakawa, M. and Tenora, F. 1996. A check list of epidemiology of nematode parasites of the genus *Apodemus* (Murinae: Rodentia) throughout the world excluding Japan. *Journal of Rakuno Gakuen Universty, Natural Science* **20**: 181-213.

Ashford, R. W. and Crewe, W. 2003. The Parasites of *Homo sapiens*. 2nd ed. Taylor Francis, London, UK., 142 pp.

Baker, D. G. 1998. Natural pathogens of laboratory mice, rats, and rabbits and their effects on research. *Clinical Microbiology Reviews* **11**: 231-266.

Beaver, P. C., Jung, R. C. and Cupp, E. W. 1984. Clinical Parasitology. 9th ed. Lea & Febiger, Philadelphia, U.S.A., 825pp.

Bhaibulaya, M. and Indrangarm, S. 1975. Man: an accidental host of *Cyclodontostomum purvisi* (Adam, 1933) and the occurrence in rats in Thailand. *Southeast Asian Journal of Tropical Medicine and Public Health* **6**: 391-394.

Black, P. F. and Butler, C. D. 2014. One Health in a world with climate changes. *Scientific and Technical Review of the World Organization for Animal Health (OIE)* **33**: 465-473.

Brown, R. J., Carney, W. P., Van Peenen, P. F. D., Cross, J. H. and Saroso, J. S. 1975. Capillariasisi in wild rats of Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health* **6**: 219-222.

Chabaud, A. G. 1981. Host range and evolution of nematode parasites of vertebrates. *Parasitology* **82**: 169–170.

Chaisiri, K., Chaeychomsri, W., Siruntawineti, J., Ribas, A., Herbreteau, V. and Morand, S. 2012. Diversity of gastrointesinal helminths in murid rodents from northeastern Thailand. *Southeast Asian Journal of Tropical Medicine and Public Health* **43**: 21-28.

Cross, J. H. (editor). 1979. Studies on angiostrongyliasis in Eastern Asia and Australia. The Special Publication of the U. S. Naval Medical Research Unit No. 2, Taiwan, 164 pp.

Dewi, K. 2008. *Subulura andersoni,* a nematode parasite of rodents. *Fauna Indonesia* **8**: 10-11. (in Indonesian)

Dewi, K. 2010. The taxonomic status of *Pterygodermatites* spp. and the scanning electron microscopy study of *Pterygodermatites whartoni* (Tubangui, 1931) (Nematoda: Rictulariidae) from Indonesian murids. *Zoo Indonesia* **19**: 31-36.

Dewi, K. 2011. Nematode parasite from murid rodents in rural area in Pakuli, Sub district Gumbara, Regency Donggala, Central Sulawesi. *Jurnal Ekologi Kesehatan* **10**: 38-43. (in Indonesian)

Dewi, K., Hasegawa, H. and Asakawa, M. 2013. A preliminary report of trichostrongylid nematodes obtained from *Paruromys dominator* (Muridae; Rodentia) at Mt. Mekkonga, Southeast Sulawesi, Indonesia. Proceeding of the 6th Asian Meeting on Zoo and Wildlife Medicine/Conservation, in Singapore in 2013, Asian Society of Zoo and Willdlife Medicine: 185.

Dewi, K., Asakawa, M. and Fitriana, Y.S. 2014a. *Syphacia (Syphacia) semiadii* n. sp (Nematoda: Oxyuridae) from *Halmaheramys bokimekot* Fabre et al., 2013 (Rodentia: Muridae) on Halmahera Island, Indonesia and a key to the species present in Sulawesi and the Australian bioregion. *Transactions of Royal Society of South Australia* **138**: 98-104.

Dewi, K. and Hasegawa, H. 2010. *Syphacia (Syphacia) rifaii* n. sp. (Nematoda: Oxyuridae) collected from *Bunomys* spp. (Rodentia: Muridae). *Journal of Parasitology* **96**: 125-28.

Dewi, K. and Hasegawa, H. 2014. Two new species of *Syphacia* (Nematoda:Oxyuridae) in endemic murid rodents from Sulawesi, Indonesia. *Journal of Helminthology* **88**: 41-49.

Dewi, K., Hasegawa, H. and Asakawa, M. 2014b. Description of two new species of *Syphacia* (Nematoda: Oxyuridae) collected from *Eropeplus canus* (Rodentia: Muridae), an endemic rat of Sulawesi, Indonesia, with proposal of new subgenera. *Raffles Bulletin of Zoology* **62**: 647-654.

Dewi, K., Hasegawa, H., Fitriana, Y. S. and Asakawa, M. in press. *Syphacia (Syphacia) maxomyos* sp. n. (Nematoda: Oxyuridae) from *Maxomys* spp. (Rodentia: Muridae)

from Sulawesi and Sumatra, Indonesia. *Journal of Veterinary Medical Science.* (in press)

Dewi, K., Hasegawa, H., Sato, A. and Asakawa, M. 2015. Biogeography of *Syphacia* spp. in Indonesia based on morphological and molecular characteristics. Abstracts of the 84th Annual Meeting of the Japanese Society of Parasitology, Kyorin University, Japan, Mar., 2015, 65.

Dewi, K. and Purwaningsih, E. 2013a. A checklist of nematode parasites from Indonesian murids. *Zootaxa* **3608**: 531-546.

Dewi, K. and Purwaningsih, E. 2013b. Helminth parasites of rats from rubber plantations in Bogorejo, Lampung. *Zoo Indonesia* **22**: 1-7. (in Indonesian)

Durette-Desset, M. C. 1969. Les système d'arêtes cuticulaires chez lesNématodes Héligmosomes parasites de Muridés australiens. *Annales de Parasitologie Humaine et Comparée* **44:** 733-747.

Durette-Desset, M. C. 1971. Essai de classification des Nématodes Héligmosomes. Corrélations avec la paléobiogeographie des hôtes. *Mémories du Museum National d'Hitoire Naturelle, Série A. Zoologie* **49:** 1-126.

Durette-Desset, M. C. 1983. No. 10. Keys to genera of the superfamily Trichostrongyloidea. In R. C. Anderson and A. G. Chabaud eds. CIH Keys to the Nematode Parasites of

Vertebrates. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, U.K., 86pp.

Esselstyn, J. A., Achmadi A. and Rowe K. C. 2012. Evolutionary novelty in a rat with no molars. *Biology Letters* **8**: 990-993.

Fabre, P–H., Pagès, M., Musser, G.G., Fitriana, Y.S., Fjeldså, J., Jennings, A., Jønsson, K. A., Kennedy, J, Michaux, J., Semiadi, G., Supriatna, N. and Helgen, K. M. 2013. A new genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini) and its implication for biogeography and Indo–Pacific Rattini systematics. *Biological Journal of the Linnean Society* **169**: 408-447.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* **39**: 783-791.

Gibbons, L. M. 2010. Keys to the Nematode Parasites of Vertebrates. Supplementary volume. CABI publishing, Wallingford, Oxfordshire, U.K., 416pp.

Gibbons, L. M., Crawshaw, M. T. and Rumpus, A. E. 1992. *Molinacuaria indonesiensis* n. sp. (Nematoda: Acuarioidea) from *Rattus argentiventer* in Indonesia. *Systematic Parasitology* **23**: 175-181.

Gibbons, L. M. and Spratt, D. M. 1995. Two new species of *Odilia* (Nematoda; Heligmonellidae) from Australian rodents with comments on *O. bainae* Beveridge & Durette-Desset, 1992. *Systematic Parasitology* **31**: 67-79.

Gouÿ de Bellocq, J., Ferté, H., Depaquit, J., Justine, J. L., Tillier, A., and Durette-Desset, M. C. 2001. Phylogeny of the Trichostrongylina (Nematoda) inferred from 28S rDNA sequences. *Molecular Phylogenetics and Evolution* **19**: 430-442.

Groves, C. 2001. Mammals in Sulawesi: where did they come from and when, and what happened to them when they got there? *In* Metcalfe, I., Smith, J. M. B., Morwood, M. and Davidson, I. eds. Faunal and Floral Migrations and Evolution in SE Asia-Australasia. Swets Zeitlinger Publishers, Lisse, Netherland, pp. 333–342.

Hadi, T. R., Nalim, S., Wasito, S. and Purnomo. 1982. A survey on small mammals and their parasites in Batam Island, Riau, Indonesia. *Bulletin Penelitian Kesehatan* **10** (1): 1-6. (in Indonesian)

Hall, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *In* Biogeography and Geological Evolution of SE Asia. Hall, R. and Holloway. J. D. eds. Backhuys Publishers, Leiden, Netherlands: 99-131.

Hall, R. 2009. Southeast Asia's changing palaeogeography. *Blumea* **54**:148–161.

Hasegawa, H. 1996. Notes on the morphology of three nematode species of the subfamily Nippostrongylinae (Heligmosomoidea: Heligmonellidae) collected from an endemic rat of Halmahera island, Indonesia. *Biological Magazine*, *Okinawa* **34**: 13-21.

Hasegawa, H. 1999. Phylogeny, host–parasite relationship and zoogeography. *Korean Journal of Parasitology* **37** (4): 197–213.

Hasegawa, H. and Asakawa, M. 2003. Parasitic helminth fauna of terrestrial Vertebrates in Japan. *In* Progress of Medical Parasitology in Japan. vol. 7. Otsuru, M., Kamegai, S and Hayashi, S. eds. Meguro Parasitological Museum,Tokyo: 129–145.

Hasegawa, H., Asakawa, M., Yagi, K. and Takao, Y. 1994. Descriptions of three species of the genus *Syphacia* (Nematoda: Oxyuridae) from the murids of Japan. *Biological Magazine, Okinawa* **32:** 7-15.

Hasegawa, H., Dewi, K. and Asakawa, M. 2014. *Musserakis sulawesiensis* gen. et sp. n. (Nematoda: Heterakidae) collected from *Echiothrix centrosa* (Rodentia: Muridae), an old endemic rat of Sulawesi, Indonesia. **2112**: *Zootaxa* 155-164.

Hasegawa, H., Kobayashi, J. and Otsuru, M. 1994. Helminth parasites collected from *Rattus rattus* on Lanyu, Taiwan. *Journal of the Helminthological Society of Washington* **61**: 95-102.

Hasegawa, H. and Mangali, A. 1996. Two new nematode species of *Bunomystrongylus* n. gen. (Trichostrongylina: Heligmonellidae) collected from *Bunomys* spp. (Rodentia: Muridae) of Sulawesi, Indonesia. *Journal of Parasitology* **82**: 998-1004.

Hasegawa, H. and Tarore, D. 1996. *Syphacia* (*Syphacia*) *sulawesiensis* n.sp. and *S.* (*S.*) *muris* (Yamaguti, 1933) (Nematoda: Oxyuridae) collected from *Rattus xanthurus* (Gray 1867) (Rodentia: Muridae) in North Sulawesi, Indonesia. *Tropical Zoology* **9**: 165-175.

Hasegawa, H. and Tarore, D. 1995. *Nippostrongylus sembeli,* new species (Nematoda: Heligmonellidae) collected from *Rattus xanthurus* of North Sulawesi, Indonesia. *Raffles Bulletin of Zoology* **43** (2): 337-342.

Hasegawa, H. and Tarore, D. 1997. *Maxomystrongylus yasumai* gen. and sp. n. (Nematoda: Trichostrongylina: Heligmonellidae) collected from murid rodents in Kalimantan, Indonesia. *Journal of Helminthological Society of Washington* **64**: 263-268.

Hasegawa, H. and Syafrudin. 1994a. *Cyclodonstomum purvisi* (Syn. *Ancistronema coronatom*) (Nematoda: Strongyloidea: Chabertiidae) from rats of Kalimantan and Sulawesi, Indonesia. *Journal of Parasitology* **80** (4): 657-660.

Hasegawa, H. and Syafrudin. 1994b. *Hasanuddinia maxomyos* n. gen., n. sp. and *Heligmonoides musseri* n. sp. (Nematoda: Helligmonellidae) collected from endemic murines of Sulawesi, Indonesia. *Journal of Parasitology* **80:** 781-788.

Hasegawa, H. and Syafrudin. 1994c. *Odilia mallomyos* (Nematoda: Helligmonellidae) from *Malomys rothschildi weylandi* (Rodentia: Muridae) of Irian Jaya, Indonesia. *Journal of Helminthological Society of Washington* **61**: 208-214.

Hasegawa, H. and Syafrudin. 1995a. Nematode fauna of the two sympatric rats, *Rattus rattus* and *R. exulans*, in Kao district, Halmahera Island, Indonesia. *Journal of Helminthological Society of Washington* **62**: 27-31.

Hasegawa, H. and Syafrudin. 1995b. *Nippostrongylus marhaeniae* sp. n. and other nematodes collected from *Rattus* cf. *morotainensis* in North Halmahera, Molucca Islands, Indonesia. *Journal of Helminthological Society of Washington* **62**: 111-116.

Hasegawa, H., Miyata, A. and Syafrudin. 1999. Six new nematodes of Heligmonellidae (Trichostrongylina) collected from endemic murines of Sulawesi, Indonesia. *Journal of Parasitology* **85** (3): 513-524.

Hasegawa, H., Shiraishi, S. and Rochman. 1992. *Tikusnema javaense* n. gen., n. sp. (Nematoda: Acuarioidea) and other nematodes from *Rattus argentiventer* collected in West Java. *Journal of Parasitology* **78**: 800-804.

Hasegawa, H., Kobayashi, J. and Otsuru, M. 1994. Helminth parasites collected from *Rattus rattus* on Lanyu, Taiwan. *Journal of Helminthological Society of Washington* **61**: 95-10.

Hasegawa, H., Sato, H., Fujita, S., Nguema, P. P. M., Nobusue, K., Miyagi, K., Kooriyama, T., Takenoshita, Y., Noda, S., Sato, A., Morimoto, A., Ikeda, Y. and Nishida, T. 2010. Molecular identification of the causative agent of human strongyloidiasis acquired in Tanzania: dispersal and diversity of *Strongyloides* spp. and their hosts. *Parasitology International* **59**: 407-413.

Hildebrand, J., Zalesny, G., Okulewicz, A. and Bazkiewicz, K. 2009. Preliminary studies on the zoonotic importance of rodents as a reservoir of toxocariasis from recreation ground in Wroclaw (Poland). *Helminthologia* **46** (2): 80-84.

Holz, J., 1962. Trichinellosis in the territory of Indonesia. *Wiadomości parazytologiczne* **8**: 29-30. (in German)

Holz, J., 1966. Studies on trichinosis in Java and Sumatra. *Wiadomości parazytologiczne* **12**: 511-518. (in German)

Hu, M., Chilton, N. B., Zhu, X. and Gasser, R. B. 2002. Single-strand conformation polymorphism-based analysis of mitochondrial cytochrome *c* oxidase subunit 1

reveals significant substructuring in hookworm populations. *Electrophoresis* **23**: 27-34.

Hugot, J. P. 1988. Les nématodes Syphaciinae, parasites de rongeurs et de lagomorphes. Memoires du Museum National d'Histoire Naturelle, série A. *Zoologie* **141**: 1-148.

Hugot, J. P. 1990. The Syphaciinae (Oxyuridae, Nematoda) parasitic in rodents and lagomorpha. Numerical taxonomy. Cladistic analysis of evolution. *Annales de Parasitologie Humaine et Comparée* **65** (Suppl. 1): 27-29.

Hugot, J. P. and Quentin, J. C., 1985. Étude morphologique de six espèces nouvelles ou peu connues appartenant au genre *Syphacia* (Oxyuridae, Nématoda), parasites de Rongeurs Cricétidés et Muridés. *Bulletin de la Museum National d'Histoire Naturelle, 4$^{e}$ Série.* **7** *Section A.* no. 2: 383-400.

Kadarsan, S., Purwaningsih, E., Hartini, S. Budiarti, I. and Saim, A. 1986. The pattern of parasitic infection in rodent from Bogor Botanical Garden. *Berita Biologi* **3** (4): 173-177.

Kenney, M., Eveland, L. K., Yermakov, V. & Kassouny, D. Y. 1975. A case of *Rictularia* infection of man in New York. *American Journal of Tropical Medicine and Hygiene* **24**: 596-598.

Kimura, M. 1980. A simple method to estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16**: 111-120.

Kwo, E. H. and Kwo, I. H. 1968. Occurance of *Angiostrongylus cantonensis* in rats in North Sumatra, Indonesia. *Journal of Parasitology* **54**: 537-541.

Lim Boo Liat, Gandahusada, S., Kosin, E., Margono, S. S**.** Sustriayu, N. and Hadi, T. R. 1978. Studies of *Angiostrongylus cantonensis* and *A. malaysiensis* of rodents hosts in two transmigration schemes in South Sumatera. *Bulletin Penelitian Kesehatan* **6**: 9-14

Lim Boo Liat, Sigit, S. and Hadi, T. R., 1986. Status of commensal rodent-borne diseases research on Indonesia. *Buletin Penelitian Kesehatan* **14:** 4-34.

Lohman, D. J., De Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng P. K. L., Shih H. T., Carvalho, G. R. and von Rintelen. T. 2011. Beyond Wallace's Line: genetics and geology inform biogeographic insights in the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics* **42**: 205–226.

Lomolino, M. V., Riddle, B. R., Whittaker, R. J. and Brown, J. H. 2010. Biogeography 4th ed. Sinauer Assoc. Sunderland, MA: 560 pp.

Mahmoud, A. E., Attia, R. A. H., Eldeek, H. E. M., Abdel Baki, L. and Oshaish, H. A. 2009. Oxyurid nematodes detected by colonscopy in patients with unexplained abdominal *Parasitologists United Journal* **2**: 93-102.

Margono, S. S. 1970. *Angiostrongylus contonensis* in Djakarta, Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health* **1**: 158-159.

Margono, S. S. and Ilahude, H. D. 1974. *Angiostrongylus contonensis* in rats and intermediate hosts in Jakarta and its vicinity, Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health* **5**: 236-240.

Maryanto, I. and Higashi, S. 2011. Comparison of zoogeography among rats, fruit bats and insectivorous bats on Indonesian Islands. *Treubia* **38**: 33-52.

Michel, A. L. 2014. Improving specific disease outcomes through a One Health approach-tuberculosis. *Scientific and Technical Review of the World Organization for Animal Health (OIE)* **33**: 583-592.

Miyagi, I. 1994. Medicozoological survey on biogeography and coevolution of vectors, parasites and hosts in Indonesia, 1991-1994. Report of Monbusho International Scientific Research Program, 142 pp.

Musser, G. G. 1987. The mammals of Sulawesi. *In* Biogeographical Evolution of the Malay Archipelago, T. C. Whitmore. ed. Oxford University Press, Oxford, U.K.: 73-93.

Musser, G. G. and Durden, L. A. 2002. Sulawesi rodents: Descriptions of a new genus and species of Murinae (Muridae, Rodentia) and its parasitic new species of sucking louse (Insecta, Anoplura). *American Museum Novitates* **3368**: 1-50.

Musser, G. G. and Newcomb, C. 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History* **174**: 327-598.

Ohbayashi, M. and Kamiya, M. 1980. Studies on the parasite fauna of Thailand. II. Three nematode species of the genus *Orientostrongylus* Durette-Desset, 1970. *Japanese Journal of Veterinary Research* **28**: 7-11.

Okamoto, M., Urushima, H., Iwasa, M. and Hasegawa, H. 2007. Phylogenetic relationships of rodent pinworms (genus *Syphacia*) in Japan inferred from mitochondrial CO1 gene sequences. *Journal of Veterinary Medical Science* **69**: 545-547.

Okamoto, M. and Hasegawa, H. 2009. Phylogenetic relationships of rodent pinworms (genus *Syphacia*) in Japan inferred from 28S rDNA sequences. *Parasitology International* **58**: 330-333.

Ow-Yang, C. K. 1971. Studies on the nematode parasites of Malaysian rodents. I. The Rhabdiasidea, Trichuridea and Oxyuridea. *Journal of Helminthology* **45**: 93-100.

Pakdeenarong, N., Siribat, P., Chaisiri, K., Douangboupha, B., Ribas, A., Chaval, Y., Herbreteau, V. and Morand, S. 2013. Helminth communities in murid rodents from

southern and northern localities in Lao PDR: the role of habitat and season. *Journal of Helminthology*. doi:10.1017/S0022149X13000187 (on line version).

Peiris, M. and Yen, H.-L. 2014. Animal and human influenzas. *Scientific and Technical Review of the World Organization for Animal Health* (*OIE*) **33**: 539-553.

Petter, A. J. and Quentin, J. C. 1976. No. 4. Keys to genera of the Oxyuroidea. In R. C. Anderson, A. G. Chabaud and S. Willmott eds.. CIH Keys to the Nematode Parasites of Vertebrates. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, U.K., 30pp.

Pisanu, B., Jerusalem, C., Huchery, C., Marmet, J. and Chapuis, J. L. 2007. Helminth fauna of the Siberian chipmunk, *Tamias sibiricus* Laxmann (Rodentia, Sciuridae) introduced in suburban French forests. *Parasitology Research* **100**: 1375-1379.

Pozio, E. 2007. World distribution of *Trichinella* spp. infections in animals and humans. *Veterinary Parasitology* **149**: 3-21.

Purnomo and Bangs, M. J. 1996. *Breilia tinjili* sp. n. (Filarioidea: Onchocercidae), from the Malaysian field rat, *Rattus tiomanicus*, on Tinjili Island, West Java, Indonesia. *Journal of Helminthological Society of Washington* **63**: 93-97.

Purwaningsih, E. 2003. Morphological variation and host range of *Subulura andersoni* Cobbold, 1887 from Indonesia and description of *Subulura spiroki* n.sp. *Berita Biologi* **6**: 563-567. (In Indonesian)

Purwaningsih, E. and Saim, A. 1988. Nematode parasitic in rodent in the islands nearby Sunda Strait. *Berita Biologi* **3**: 386-389. (In Indonesian)

Purwaningsih, E. and Dewi, K. 2007. Nematoda in Muridae and the pattern of infection in Lore Lindu National Park, Central Sulawesi. *Berita Biologi* **8**: 509-514. (In Indonesian)

Purwaningsih, E. and Suwito, A. 1996. A note on nematoda from bats and rats from Kayan Mentarang Nature Reserved, East Kalimantan. *Majalah Parasitologi Indonesia* **9**: 6-11. (In Indonesian)

Purwaningsih, E., Hartini, S. and Saim, A. 2000. Nematodes collection from Sulawesi. *Berita Biologi* **5**: 255-257. (In Indonesian)

Quentin, J. C. 1969. Essai de classification des Nématodes Rictulaires. *Mémoires du Museum National d'Histoire Naturelle, Série. A.* **54**: 57-115.

Quentin, J. C. 1971. Morphologie comparée des structures céphaliques et génitales des Oxyures du genre *Syphacia*. *Annlales de Parasitologie Humaine et Comparée* **46**: 15-60.

Riley, W. A. 1919. A mouse oxyurid, *Syphacia obvelata,* as a parasite of man. *Jounal of Parasitology* **6**: 89-93.

Romanelli, C., Cooper, H. D. and de Souza Dias, B. F. 2014. The integration of biodiversity into One Health. *Scientific and Technical Review of the World Organization for Animal Health (OIE)* **33**: 487-496.

Saim, A. and Purwaningsih, E. 1999. The pattern of helminth parasitic in the wild rodent from Siberut Island, West Sumatra. *Majalah Parasitolologi Indonesia* **12**: 49-60.

Saitou, N. and Nei, M. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* **4**: 406-425.

Schacher, J. F. and Chee-Hock, C. 1960. Nematode parasites of three common house rat species in Malaya, with notes on *Rictularia tani* Hoeppli, 1929. *Malaya* **29**: 210-216.

Smit, A. M. 1962. Eosinophilic meningitis at Kisaran (Indonesia) and the problem of its actiology. *Bulletin de la Société de pathologie exotique* **55**: 722-730.

Smales, L. R. 2001. *Syphacia longaecauda* n. sp. (Nematoda: Oxyuridae) Syphacinea from *Melomys* spp. (Muridae: Hydromyinae) from Papua New Guinea and Irian Jaya, Indonesia. *Parasite* **8**: 39-43.

Smales, L. R. 2004. *Syphacia australasiensis* sp. nov. (Nematoda: Oxyuridae) from *Rattus leucopus* (Muridae) from Papua New Guinea and Australia. *Transactions of the Royal Society of South Australia* **128**: 47-51.

Smales, L. R. 2008. Three new species of Heligmonellidae (Nematoda: Trichostrongyloidea) from *Melomys, Paramelomys,* and *Uromys* (Rodentia: Muridae) from Papua, Indonesia and Papua New Guinea. *Comparative Parasitology* **75**: 52-60.

Smales, L. R. 2009. Helminths of *Melomys rufescens* and *Melomys* spp. (Muridae: Hydromyinae) from Papua New Guinea with the description of a new genus and five new species. *Raffles Bulletin of Zoology* **57**: 5-15.

Smales, L. R. 2010. The gastrointestinal helminthes of *Lorentzimys nouhuysi* (Rodentia: Muridae) with descriptions of two new genera and three new species (Nematoda) from Papua New Guinea. *Journal of Parasitology* **96**: 602-613.

Smales, L. R. 2011. Gastrointestinal nematodes of *Coccymys ruemmleri* (rodentia, Muridae) with the description *Montistrongylus giluwensis* sp. nov. (heligmonellidae) and *Syphacia coccymyos* sp. nov. (oxyuridae) from Papua new Guinea. *Acta Parasitologia* **56**: 418–426.

Smales, L. R. 2012. Helminth parasites of hydromyine rodents from the island of New Guinea. *In* Rodents: Habitat, Pathology and Environmental Impact. Triunveri, A. and Scalise, D. eds. Nova Science Publishers, New York: 99-118 pp.

Smales, L. R. 2013. Nematodes from the caecum and colon of *Pogonomys* (Muridae: Anisomyini) from Papua New Guinea with the descriptions of Oxyuridae (Nematoda: Oxyurida) and a new species of Trichuridae (Nematoda: Enoplida). *Zootaxa* 3599: 577-587.

Smit A. M. 1962. Eosinophilic meningitis at Kisaran (Indonesia) and the problem of its aetiology. *Bulletin de la Société de Pathologie Exotique* **55:** 722-730.

Stelbrink, B., Albrecht, C., Hall, R. and von Rintelen, T. 2012. The biogeography of Sulawesi revisited: is there evidence for a vicariant origin of taxa on Wallace's "anomalous island"?. *Evolution* **66**: 2252-2271.

Suyanto, A., Yoneda, M., Maryanto, I. Maharadatunkamsi, and Sugardjito, J. 1998. Checklist of the Mammals of Indonesia. LIPI–JICA Joint Project for Biodiversity Conservation in Indonesia**.** LIPI, Bogor, Indonesia, 34 pp.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. and Kumar, S. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary

distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**: 2731-2739.

Untung, S. and Nalim, S. 1982. [(translated title) Zoonotic aspect of nematode parasites from monkeys and rats in Bengkulu, Sumatra, Indonesia.] *Bulletin Penelitian Kesehatan* **10**: 1-7. (in Indonesian)

Voris, H. K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* **27**: 1153 –1167.

Wang, L.-F. and Crameri, G. 2014. Emerging zoonotic viral diseases. *Scientific and Technical Review of the World Organization for Animal Health (OIE)* **33**: 569-581.

Warner, L. R. 1998. Australian helminthes in Austarlian rodents: an issue of biodiversity. *International Journal for Parasitology* **28**: 839-846.

Weaver, H. J. and Smales, L. R. 2006. *Syphacia (Syphacia) abertoni* n. sp. (Nematoda: Oxyuridae) from *Zyzomys argurus* (Thomas) (Rodentia: Muridae) from northern Australia. *Transactions of the Royal Society of South Australia* **131**: 206-210.

Weaver, H. J. and Smales, L. R.2008, New species of *Syphacia (Syphacia)* Seurat (Nematoda: Oxyuridae) from *Pseudomys* species (Rodentia: Muridae) from central Australia. *Zootaxa* **1775**: 39-50.

Weaver, H. J. and Smales, L. R. 2010. Three new species of *Syphacia (Syphacia)* (Oxyurida: Oxyuridae) from Quennsland, Australia, and a key to the species present in the Australian bioregion. *Comparative Parasitology* **77**: 9-19.

Whitmore, T. C. (eds.) 1981. Wallace's line and plate tectonics. Clarendon Press, Oxford, U.K., 90 pp.

Wilson, D. E. and Reeder, D. M. (eds.) 1993. Mammal Species of the World. Institution Press, Washington, 1206 pp.

Widagdo, Sunardi, Lokollo, D. M. and Margono, S. S. 1977. Ocular angiostrongyliasis in Semarang, Central Java. *American Journal of Tropical Medicine and Hygiene* **26**: 72-74.

Wiroreno, W. 1975. Helminth parasites of *Rattus rattus diardii* in Bogor, West Java, Indonesia. *Southeaset Asian Journal of Tropical Medicine and Public Health* **6**: 136-138.

Wiroreno, W. 1978. Nematode parasites of rats in West Java, Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health* **9**: 520-0525.

Yamaguti, S. 1961. Systema Helminthum. Vol. 3. The Nematodes of Vertebrates. Interscience Publishers, Inc., New York, 679 pp.

Yoshida, F., Asakawa, M. and Ohbayashi, M. 1985. Taxonomical studies on the genus *Syphacia* (Nematoda: Oxyurioidea) from six species of *Rattus* in Thailand. *Japanese Journal of Parasitology* **35**(6, Suppl. 2): 86. (In Japanese)

## Appendix 1
## Checklist of the nematode parasites of Indonesian murids

This checklist was presented in a nematode list by host and also in host list by nematode. The classification mainly follows Anderson (2000). The nematode list by host, families and species are listed in alphabetical order. Data for each species are arranged as follows:

**Family of nematodes** (in bold)
***Scientific name of nematode parasite*** (in bold–faced italic)
*Synonyms occuring in the literature* (if available and the literatures) (in italics)
Site of infection of nematode in the host
LOCATION OF HOST (in capital): *Scientific name of host* (in italic) (author and publication date, if available). [Catalogue number of MZB, if specimen is type].
*Notes*: the formal reported name if any taxonomic changes

In the host list by nematode, data are presented as follows:

***Scientific name of host*** (in bold–faced italic)
*Scientific name of nematode* (in italic)
*; zoonotic agent, or possible one
@; new recorded in Indonesia and/or host species by the present auhor
§; data from MZB catalogue (not published yet)
ɸ; data from the author's observation (not published yet)

**Nematode – host List**

**Acuariidae Railliet, Henry and Sisoff, 1912**
***@Tikusnema javaense* Hasegawa, Shiraishi and Rochman, 1992**
Syn: *Molinacuaria indonesiensis* Gibbons, Crawshaw and Rumpus, 1992 (Gibbons et al., 1992; Smales, 1995)
Site of infection: intestine, stomach
LAMPUNG: *Rattus argentiventer* (Robinson and Kloss) (Purwaningsih, 2000)

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Hasegawa et al., 1992; Gibbons 1992; Purwaningsih 2000), *Rattus tanezumi* Temminck, *Rattus tiomanicus* Miller (Kadarsan et al., 1986)

CENTRAL SULAWESI: *Bunomys prolatus* Musser (Purwaningsih and Dewi, 2007); *Rattus hoffmanni* (Matschie) (Purwaningsih and Dewi, 2007)

*Notes:* Specimens of Kadarsan et al. (1986) were originally identified as *Victorocara* sp.; while Gibbons (1992), Purwaningsih (2000) and Purwaningsih and Dewi (2007) recorded it as *Molinacuaria indonesiensis*

**Angiostrongylidae Bòhm and Gebauer, 1934**

***Angiostrongylus* sp.**

Site of infection**:** lung

§NORTH SUMATRA: *Rattus tanezumi* Temminck

§JAKARTA: *Rattus tanezumi* Temminck

****Angiostrongylus cantonensis* (Chen, 1935)**

§SOUTH SUMATRA: *Rattus exulans* (Peale), *Rattus tiomanicus* Miller

WEST SUMATRA: *Rattus tanezumi* Temminck (Cross, 1979)

NORTH SUMATRA: Rats (Kwo and Kwo, 1968); *Rattus tanezumi* Temminck (Cross 1979), *Rattus tiomanicus* Miller (Cross, 1979)

LAMPUNG: *Rattus argentiventer* (Robinson and Kloss) (Lim Boo Liat, 1978; Cross, 1979); *Rattus tanezumi* Temminck (Cross, 1979); *Rattus exulans* (Peale) (Cross, 1979); *Rattus tiomanicus* Miller (Lim Boo Liat, 1978; Cross, 1979)

JAKARTA: *Bandicota indica* (Bechstein) (Cross, 1979); *Rattus argentiventer* (Robinson and Kloss) (Margono and Ilahude, 1974); *Rattus tanezumi* Temminck (Margono and Ilahude, 1974)

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Cross, 1979); §*Rattus exulans* (Peale), §*Niviventer lepturus* (Jentink); §*Rattus tanezumi* Temminck; §*Rattus tiomanicus* Miller; §*Bandicota indica* (Bechstein), §*Maxomys bartelsii* (Jentink)

§CENTRAL JAVA: *Rattus exulans* (Peale), *Bandicota indica* (Bechstein)

*Notes*: Cross (1979) noted that the host of *A. cantonensis* from West Sumatra was *R. diardii*, but *R. diardii* is synonym of *R. tanezumi* (Anonim, 2012)

****Angiostrongylus malaysiensis* Bhaibulaya and Cross, 1971**

Site of infection**:** lung

§SOUTH SUMATRA: *Rattus* sp.

§WEST SUMATRA: *Rattus lugens* (Miller)

§LAMPUNG: *Rattus exulans* (Peale); *Rattus tiomanicus* Miller

§JAKARTA: *Rattus tanezumi* Temminck

**Capillariidae Moravec, 1982**

***Baruscapillaria traverae (*Ash, 1962)**

Site of infection: intestine

HALMAHERA: *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995)

***Capillaria* sp.**

Site of infection: intestine

WEST SUMATRA: *Maxomys pagensis* (Miller) (Saim and Purwaningsih, 1999)

EAST KALIMANTAN: *Maxomys pagensis* (Miller) (Saim and Purwaningsih, 1999)

CENTRAL SULAWESI: *Maxomys pagensis* (Miller) (Saim and Purwaningsih, 1999)

***Eucoleus bacillatus* (Eberth, 1863)**

Site of infection: intestine

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Hasegawa et al., 1992)

****Calodium hepaticum* (Bancroft, 1893)**

Syn. *Capillaria hepatica* Bancroft, 1893

Site of infection: liver

WEST JAVA: *Rattus* spp. (Wiroreno, 1978)

**Chabertiidae (Popova, 1952)**

****@Cyclodontostomum purvisi* Adams, 1933**

Syn. *Ancistronema coronatum* Smales, 1992

Site of infection**:** caecum

WEST JAVA: *Niviventer lepturus* (Jentink) (Wiroreno, 1978); *Rattus tiomanicus* Miller; *Maxomys whiteheadi* (Thomas) (Wiroreno, 1978)

EAST KALIMANTAN: *Rattus tiomanicus* Miller (Purwaningsih and Suwito, 1996); *Rattus exulans* (Peale) (Purwaningsih and Suwito, 1996); *Maxomys whiteheadi* (Thomas) (Hasegawa and Syafruddin, 1994a); *Lepoldamys sabanus* (Thomas) (Hasegawa and Syafruddin, 1994a); *Niviventer cremoniventer* (Miller) (Hasegawa and Syafruddin, 1994a)

SOUTH SULAWESI: *Eropeplus canus* Miller and Hollister (Hasegawa and Syafruddin, 1994a); *Paruromys dominator* Thomas (Hasegawa and Syafruddin, 1994a); *Rattus hoffmanni* (Matschie) (Hasegawa and Syafruddin, 1994a)

CENTRAL SULAWESI: *Rattus hoffmanni* (Matschie) (Purwaningsih and Dewi, 2007)

**Gongylonematidae (Hall, 1916)**

***Gongylonema* sp.**

Site of infection**:** stomach

ɸCENTRAL SULAWESI: *Bunomys chrysocomus* (Hoffmann)

***@Gongylonema neoplasticum* (Fibiger and Ditlevsen, 1914)**

Syn: *Gongylonema orientale* Yokogawa, 1924 (Yamaguti, 1961)

Site of infection**:** stomach wall

LAMPUNG: **@***Rattus tanezumi* Temminck (Dewi and Purwaningsih, 2013b); §*Niviventer lepturus* (Jentink)

ɸWEST JAVA: *Rattus tanezumi* Temminck

CENTRAL SULAWESI: *Rattus tanezumi* Temminck (Dewi, 2011); *Bunomys chrysocomus* (Hoffmann) (Dewi, 2011)

HALMAHERA: *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995)

**Heligmonellidae (Skrjabin and Schikhobalova, 1952)**

***Bunomystrongylus abadii* Hasegawa and Mangali, 1996**

Site of infection: small intestine

SOUTH SULAWESI: *Bunomys penitus* (Miller and Hollister) (Hasegawa and Mangali, 1996) [Holotype and allotype (MZB Na 282); paratype (MZB Na 283)]

***Bunomystrongylus miyagii* Hasegawa and Mangali, 1996**

Site of infection: small intestine

SOUTH SULAWESI: *Bunomys andrewsi* (Allen) (Hasegawa and Mangali, 1996) [Holotype and allotype (MZB Na 282); paratype (MZB Na 283)]

***Hasanuddinia maxomyos* Hasegawa and Syafruddin, 1994**

Site of infection: small intestine

SOUTH SULAWESI: *Eropeplus canus* Miller and Hollister (Hasegawa and Syafruddin 1994b); *Maxomys musschenbroekii* (Jentink) (Hasegawa and Syafruddin, 1994b)

***Heligmonoides musseri* Hasegawa and Tarore, 1994**

Site of infection: small intestine

SOUTH SULAWESI: *Maxomys musschenbroekii* (Jentink) (Hasegawa and Syafruddin, 1994b). [Holotype and allotype (MZB Na 235), paratype (MZB Na 278)]; *Margaretamys elegans* Musser (Hasegawa and Syafruddin, 1994b); *Eropeplus canus* Miller and Hollister (Hasegawa and Syafruddin, 1994b)

***Maxomystrongylus yasumai* Hasegawa and Syafruddin, 1997**

Site of infection: small intestine

EAST KALIMANTAN: *Maxomys whiteheadi* (Thomas) (Hasegawa and Syafruddin, 1997) [Holotype and allotype (MZB Na 286); paratype (MZB Na 287)]; *Niviventer*

*cremoniventer* (Miller) (Hasegawa and Syafruddin, 1997); *Rattus tanezumi* Temminck (Hasegawa and Syafruddin, 1997)

***@Nippostrongylus brasiliensis* (Travassos, 1914)**

Site of infection: small intestine

Syn: *Heligmosomum muris* Yokogawa, 1920, *Nippostrongylus muris* (Yokogawa, 1920) (Yamaguti, 1961; Anderson, 2000)

LAMPUNG: *Rattus tanezumi* Temminck (Dewi and Purwaningsih, 2013b); *Rattus exulans* (Peale) (Dewi and Purwaningsih, 2013b); *Rattus tiomanicus* Miller (Dewi and Purwaningsih, 2013b)

§JAKARTA: *Rattus tanezumi* Temminck

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Hasegawa et al., 1992); §*Rattus sabanus* (Thomas)

§CENTRAL JAVA: *Rattus tanezumi* Temminck

§CENTRAL SULAWESI: *Taeromys* sp.

HALMAHERA: *Rattus tanezumi* Temminck (Hasegawa and Syafruddin, 1995a)

***Nippostrongylus marhaeniae* Hasegawa and Syafruddin, 1995**

Site of infection: small intestine

HALMAHERA: *Rattus* cf. *morotainensis* Kellogg (Hasegawa and Syafruddin, 1995b)

***Nippostrongylus sembeli* Hasegawa and Tarore, 1995**

Site of infection: small intestine

NORTH SULAWESI: *Rattus xanthurus* (Gray) (Hasegawa and Tarore, 1995) [Holotype and allotype MZB Na 261; paratype MZB Na 262]

***Odilia* sp.**

Site of infection: small intestine

HALMAHERA: *Rattus* cf. *morotainensis* Kellogg (Hasegawa and Syafruddin, 1995b)

***Odila moatensis* Hasegawa, Miyata and Syafruddin, 1999**

Site of infection: small intestine

NORTH SULAWESI: *Rattus xanthurus* (Gray) (Hasegawa, Miyata and Syafruddin, 1999) [Holotype and allotype (MZB Na 259); paratype (MZB Na 260)]

***Odilia mallomyos* Hasegawa and Syafruddin, 1994**

Site of infection: small intestine

PAPUA: *Mallomys rothschildi* Thomas (Hasegawa and Syafruddin 1994c) [Holotype and allotype (MZB Na 274), paratype (MZB Na 275)]

***Odilia mamasaensis*, Hasegawa, Miyata and Syafruddin, 1999**

Site of infection: small intestine

NORTH SULAWESI: *Maxomys musschenbroekii* (Jentink) (Hasegawa et al., 1999) [Holotype and allotype (MZB Na 355); paratype (MZB Na 356)]

***Odilia maxomyos* Hasegawa, Miyata and Syafruddin, 1999**

Site of infection: small intestine

NORTH SULAWESI: *Maxomys musschenbroekii* (Jentink) (Hasegawa et al., 1999) [Holotype and allotype (MZB Na 357); paratype (MZB Na 358)]

***Odilia sulawesiensis* Hasegawa, Miyata and Syafruddin, 1999**

Site of infection: small intestine

SOUTH SULAWESI: *Rattus xanthurus* (Gray) (Hasegawa et al., 1999)

***Orientostrongylus* sp.**

Site of infection: small intestine

NORTH SULAWESI: *Rattus xanthurus* (Gray) (Hasegawa et al., 1999)

HALMAHERA: *Rattus* cf. *morotaiensis* Kellogg (Hasegawa and Syafruddin, 1995b)

***Orientostrongylus tenorai* Durette–Desset, 1970**

Site of infection: small intestine

HALMAHERA: *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995a)

***Paraheligmonelloides eropeplios* Hasegawa, Miyata and Syafruddin, 1999**

Site of infection: small intestine

SOUTH SULAWESI: *Eropeplus canus* Miller and Hollister (Hasegawa et al., 1999) [Holotype and allotype (MZB Na 359), paratype (MZB Na 360)]

***Paraheligmonelloides paruromys* Hasegawa, Miyata and Syafruddin, 1999**

Site of infection: small intestine

SOUTH SULAWESI: *Paruromys dominator* Thomas (Hasegawa et al., 1999) [Holotype and allotype (MZB Na 361), paratype (MZB Na 362)]

**Heterakidae Railliet and Henry, 1912**

***Heterakis* sp.**

Site of infection: intestine, stomach

§WEST SUMATRA: *Rattus lugens* (Miller)

***@Heterakis spumosa* Scneider, 1866**

Syn. *Ganguleterakis gangula* Lane, 1914; *Heterakis dahomensis* Gendre, 1911 (Yamaguti, 1961)

Site of infection: intestine, stomach, caecum

LAMPUNG: *Rattus tanezumi* Temminck (Dewi and Purwaningsih, 2013b); *Rattus tiomanicus* Miller (Dewi and Purwaningsih, 2013b)

CENTRAL SULAWESI: *Bunomys andrewsi* Allen (Hasegawa et al., 2014); *Bunomys chrysocomus* (Hoffmann) (Purwaningsih and Dewi, 2007; Hasegawa et al., 2014); *Bunomys prolatus* Musser (Purwaningsih and Dewi, 2007); *Crunomys celebensis* Musser (Hasegawa et al., 2014); *Rattus hoffmanni* (Matschie) (Purwaningsih and Dewi, 2007); *Rattus marmosurus* Thomas (Purwaningsih and Dewi, 2007); *Rattus xanthurus* (Gray) (Purwaningsih and Dewi, 2007); *Tateomys macrocercus* Musser (Hasegawa et al., 2014); *Tateomys rhinogradoides* Musser (Hasegawa et al., 2014)

WEST SULAWESI: *Bunomys penitus* (Miller and Hollister) (Hasegawa et al., 2014); *Eropeplus canus* Miller and Hollister (Hasegawa et al., 2014); *Margaretamys elegans* Musser) (Hasegawa et al., 2014); *Paruromys dominator* Thomas (Hasegawa et al., 2014); qpFLORES: *Rattus hainaldi* Kitchener, How and Maharadatunkamsi

***@Musserakis sulawesiensis* Hasegawa, Dewi and Asakawa, 2014**

Site of infection: caecum

CENTRAL SULAWESI: *Echiothrix centrosa* Miller & Hollister (Hasegawa, Dewi and Asakawa, 2014) [Paratype (MZB Na 646)]

**Heteroxynematidae (Skrjabin and Schikhobalova, 1948)**

***@Aspiculuris* sp.**

Site of infection: caecum

LAMPUNG: *Rattus tanezumi* Temminck (Dewi and Purwaningsih, 2013b; *Maxomys surifer* (Miller) (Dewi and Purwaningsih, 2013b)

**Molineidae Skrjabin and Schulz, 1937**

***Molineus* sp.**

Site of infection: bile duct

RAKATA ISLAND: *Rattus tanezumi* Temminck (Purwaningsih and Saim, 1988), *Maxomys surifer* (Miller) (Purwaningsih and Saim, 1988)

***Hepatojarakus* sp**.

Site of infection: liver, ductus choledochus, lung

§NORTH SUMATRA: *Lepoldamys sabanus* (Thomas)

§WEST SUMATRA: *Maxomys pagensis* (Miller); *Rattus lugens* (Miller)

§LAMPUNG: *Rattus exulans* (Peale); *Rattus tiomanicus* Miller

§UJUNG KULON: *Rattus tiomanicus* Miller

§PEUCANG ISLAND: *Rattus tanezumi* Temminck

§WEST JAVA: *Rattus* sp.

§NORTH SULAWESI: *Rattus tanezumi* Temminck

§SOUTH EAST SULAWESI: *Rattus tanezumi* Temminck

§CENTRAL SULAWESI: *Lenothrix* sp.

***Hepatojarakus malayae* Yeh, 1955**

Site of infection: liver, bile duct

§LAMPUNG: *Rattus argentiventer* (Robinson and Kloss); *Rattus tanezumi* Temminck; *Rattus tiomanicus* Miller

§PEUCANG ISLAND: *Rattus tiomanicus* Miller

WEST JAVA: §*Rattus argentiventer* (Robinson and Kloss); *Rattus tiomanicus* Miller (Purwaningsih and Saim, 1988)

CENTRAL SULAWESI: *Margaretamys elegans* Musser (Purwaningsih and Dewi, 2007); *Rattus hoffmanni* (Matschie) (Purwaningsih and Dewi 2007); *Rattus marmosurus* Thomas (Purwaningsih and Dewi, 2007)

**Molineidae gen. sp.**

Site of infection: intestine

SOUTH EAST SULAWESI: *Paruromys dominator* (Thomas, 1921) (Dewi et al., 2013)

**Onchocercidae** Chabaud and Anderson, 1959

***Onchocerca* sp.**

Site of infection: intestine

§LAMPUNG: *Rattus tiomanicus* Miller

***Breinlia tinjili* Purnomo and Bangs, 1996**

Site of infection: intestine

WEST JAVA: *Rattus tiomanicus* Miller (*Rattus tiomanicus*) (Purnomo and Bangs, 1996)

**Oxyuridae Cobbold, 1864**

***Syphacia longaecauda* Smales, 2001**

Site infection: caecum and colon

PAPUA: *Melomys monktoni* Thomas, 1904 (Smales, 2001)

***@Syphacia maxomyos* Dewi et al., xxxx**

Site infection: caecum

WEST SULAWESI: *M. musschenbroekii* (Jentink, 1878) (Dewi et al., in press)

RIAU: *Maxomys whitheadi* (Thomas, 1894) (Dewi et al., in press)

***@Syphacia muris* Yamaguti, 1941**

Site of infection: intestine, caecum

LAMPUNG: *Rattus tanezumi* Temminck (Dewi and Purwaningsih, 2013b)

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Hasegawa et al., 1992)

CENTRAL JAVA: *Rattus tanezumi* Temminck; *Rattus tiomanicus* Miller

EAST KALIMANTAN: *Rattus tanezumi* Temminck

NORTH SULAWESI: *Rattus xanthurus* (Gray) (Hasegawa and Tarore, 1996)

HALMAHERA: *Rattus exulans* (Peale) (Hasegawa and Syafruddin, 1995); *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995)

φFLORES: *Rattus hainaldi* Kitchener, How and Maharadatunkamsi

φBAWEAN ISLAND: *Rattus* sp.

***@Syphacia paruromyos* Dewi and Hasegawa, 2014**

SOUTH EAST SULAWESI: *Paruromys dominator* (Thomas, 1921) Dewi and Hasegawa, 2014. [Holotype and allotype (MZBNa 604), paratype (MZB Na 605)]

***@Syphacia rifaii* Dewi** and **Hasegawa, 2010**

Site of infection: intestine, caecum

CENTRAL SULAWESI: *Bunomys chrysocomus* (Hoffmann) (Dewi and Hasegawa, 2010) [Holotype and allotype (MZB Na 418), paratypes (MZB Na 423)]; *Bunomys prolatus* Musser (Dewi and Hasegawa, 2010; Purwaningsih and Dewi, 2007) [Paratypes (MZB Na 216)]

*Notes:* Specimens of Purwaningsih and Dewi, 2007 were oiginally identified as *S. muris.*

***@Syphacia semiadii* Dewi, Asakawa and Fitriana, 2014**

Site of infection: intestine, caecum

HALMAHERA: *Halmaheramys bokimekot* Fabre et al., 2013 (Dewi, Asakawa and Fitriana, 2014) [Holotype and allotype (MZB Na 483), paratypes (MZB Na 484)]

***Syphacia sulawesiensis* Hasegawa** and **Tarore, 1996**

Site of infection: intestine, caecum

NORTH SULAWESI: *Rattus xanthurus* (Gray) (Hasegawa and Tarore, 1996) [Holotype and allotype (MZB Na 254), paratype (MZB Na 255)]

***@Syphacia taeromyos* Dewi and Hasegawa, 2014**

Site of infection: intestine, caecum

SOUTH EAST SULAWESI: *Taeromys celebensis* (Gray, 1867) (Dewi and Hasegawa, 2014) [Holotype and allotype (MZB Na 602), paratype (MZB Na 603)]

***@Syphacia kumis* Dewi, Hasegawa and Asakawa, 2014**

Site of infection: intestine, caecum

CENTRAL SULAWESI: *Eroplepus canus* Miller and Hollister, 1921 (Dewi et al., 2014) [Holotype and allotype (MZB Na 624), paratype (MZB Na 625)]

***@Syphacia yuniae* Dewi, Hasegawa and Asakawa, 2014**

Site of infection: intestine, caecum

CENTRAL SULAWESI: *Eroplepus canus* Miller and Hollister, 1921 (Dewi et al., 2014) [Holotype and allotype (MZB Na 624), paratype (MZB Na 625)]

**Physalopteridae (Railliet, 1893)**

***Physaloptera* sp.**

Site of infection: intestine, stomach

§WEST SUMATRA: *Rattus lugens* (Miller)

§LAMPUNG: *Rattus tiomanicus* Miller

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Hasegawa et al., 1992); §*Maxomys bartelsii* (Jentink); §*Niviventer fulvescens* Gray

§EAST JAVA: *Rattus tiomanicus* Miller

§EAST KALIMANTAN: *Maxomys whiteheadi* (Thomas)

§WEST NUSA TENGGARA: *Rattus tanezumi* (Jentink)

**Rictulariidae (Hall, 1915)**

****@Pterygodermatites* sp.**

Site of infection: intestine, stomach

NORTH SUMATRA: *Lepoldamys sabanus* (Thomas) (Dewi, 2010); §*Rattus tanezumi* (Jentink); §*Sundamys muelleri* (Jentink)

LAMPUNG: *Rattus tanezumi* Temminck (Dewi and Purwaningsih, 2013b)

KRAKATAU ISLAND: *Rattus tanezumi* (Jentink) (Dewi, 2010)

SOUTH SULAWESI: *Rattus* sp. (Dewi, 2010)

FLORES: *Rattus hainaldi* Kitchener, How and Maharadatunkamsi (Dewi, 2010)

***@Pterygodermatites tani* (Hoeppli, 1929)**

Syn: *Rictularia tani* Hoeppli, 1929 (Hasegawa et al., 1993)

Site of infection: intestine, stomach

KRAKATAU ISLAND: *Rattus tanezumi* Temminck (Purwaningsih and Saim, 1988)

WEST JAVA: *Maxomys bartelsii* (Jentink) (Wiroreno, 1978); *Rattus tanezumi* Temminck (Wiroreno, 1978)

CENTRAL SULAWESI: *Rattus xanthurus* (Gray) (Purwaningsih and Dewi, 2007)

*Notes:* Wiroreno (1978) noted the host of *P. tani* from West Java as *R. diardii* whereas *R. diardii* is synonym of *R. tanezumi* (Anonim, 2012)

***@Pterygodermatites whartoni* (Tubangui, 1931)**

Site of infection: intestine, stomach

§WEST JAVA: *Rattus xanturus* (Gray)

CENTRAL SULAWESI: *Rattus tanezumi* Temminck (Dewi 2010~~; Dewi~~, 2011); *Rattus xanturus* (Gray), *Bunomys chrysocomus* (Hoffmann) (Dewi, 2011)

HALMAHERA: *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995); *Rattus exulans* (Gray) (Hasegawa and Syafruddin, 1995)

**Seuratidae (Hall, 1916)**

***Seuratum* sp.**

Site of infection: unspecified habitat

EAST KALIMANTAN: *Maxomys whiteheadi* (Thomas) (Purwaningsih and Suwito, 1996)

**Spiruridae Oerley, 1885**

***@Masthoporus muris* (Gmelin, 1790)**

Syn: *Protospirura muris* Gmelin, 1790; *Spiroptera obtusa* Rud., 1809; *Mastophorus echiurus* Dies., 1853; *Protospirura ascaroidea* Hall, 1916; *P. gracilis* Cram. 1924; *P. columbiana* Cram, 1926; *P. marsupialis* Baylis, 1934*; P. glareoli* Soltys, 1949; *P. bestiarum* Kreis, 1953 (Yamaguti, 1961; Anderson, 2000)

Site of infection: intestine, stomach

§LAMPUNG: *Sundamys muelleri* (Jentink)

§PANGGANG ISLAND: *Sundamys muelleri* (Jentink)

§WEST JAVA: *Niviventer lepturus* (Jentink); *Sundamys muelleri* (Jentink); *Niviventer lepturus* (Jentink)

qpCENTRAL JAVA: *Rattus tiomanicus* Miller

CENTRAL SULAWESI: *Bunomys chrysocomus* Hoffmann (Purwaningsih and Dewi, 2007); *Rattus xanthurus* (Gray) (Purwaningsih and Dewi, 2007); *R. tanezumi* (Dewi, 2011)

HALMAHERA: *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995)

***Physocephalus sexalatus* (Molin, 1860)**

Syn: *Spiroptera strongylina suis labiata* Molin, 1860

Site of infection: intestine

qpCENTRAL JAVA: *Leopoldamys sabanus* (Thomas)

**Strongyloididae Chitwood and McIntosh, 1934**

***Strongyloides ratti* Sandground, 1925**

Site of infection: intestine

WEST JAVA: *Rattus argentiventer* (Robinson and Kloss) (Hasegawa et al., 1992)

HALMAHERA: *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995)

***Strongyloides venezuelensis* Brumpt, 1934**

Site of infection: intestine

HALMAHERA: *Rattus exulans* (Peale) (Hasegawa and Syafruddin, 1995); *Rattus rattus* (Linnaeus) (Hasegawa and Syafruddin, 1995)

**Subuluridae (Travassos, 1914)**

***@Subulura andersoni* Cobbold, 1887**

Syn. *Latibuccana funambulensis* Patwardhan, 1935; *Subulura hindi* Mirza, 1936 (Yamaguti 1961)

Site of infection: intestine, caecum, stomach

WEST SUMATRA: *Rattus lugens* (Miller) (Saim and Purwaningsih, 1999)

KRAKATAU ISLAND: *Rattus tanezumi* Temminck (Purwaningsih and Saim, 1988; Purwaningsih, 2003)

WEST JAVA: *Maxomys bartelsii* (Jentink); *Rattus tiomanicus* Miller

NORTH SULAWESI: *Bunomys chrysocomus* (Hoffmann) (Purwaningsih et al*.,* 2000); *Rattus hoffmanni* Thomas (Purwaningsih et al., 2000)

CENTRAL SULAWESI: *Bunomys chrysocomus* (Hoffmann) (Purwaningsih and Dewi, 2007); *Margaretamys elegans* Musser (Purwaningsih and Dewi, 2007); *Maxomys bartelsii* (Jentink) (Purwaningsih and Dewi 2007); *Rattus hoffmanni* Thomas (Purwaningsih and Dewi, 2007); *Rattus marmosurus* Thomas (Purwaningsih and Dewi 2007); *Bunomys prolatus* Musser (Dewi, 2008); *Rattus xanthurus* (Gray ) (Purwaningsih and Dewi, 2007)

SOUTH EAST SULAWESI: *Bunomys penitus* (Miller and Hollister) (Purwaningsih et al*.*, 2000); §*Rattus* sp.

*Notes:* Specimens of Purwaningsih and Saim, 1988 were oiginally identified as *Cruzia* sp.

***Subulura spiroki* Purwaningsih, 2003**

Site of infection: intestine, caecum

NORTH SUMATRA: *Lepoldamys sabanus* (Thomas) (Purwaningsih, 2003) [Holotype and allotype (MZB Na 306), paratype (MZB Na 312)]

**Trichuridae Ransom, 1911**

***@Trichuris muris* Schrank, 1788**

Syn: *Trichocephalus nodosus* Rud., 1809 (Yamaguti, 1961)

Site of infection: intestine

CENTRAL SULAWESI: *Bunomys chrysocomus* (Hoffmann) (Purwaningsih and Dewi, 2007)

**Host– nematode List**

***Bandicota indica* (Bechstein)**
*Angiostrongylus cantonensis* (Chen, 1935)

***Bunomys andrewsi* (Allen)**
*Bunomystrongylus miyagii* Hasegawa and Mangali, 1996
*Heterakis spumosa* Scneider, 1866
***Bunomys chrysocomus* (Hoffmann)**
*Gongylonema* sp.
*Heterakis spumosa* Scneider, 1866
*Masthoporus muris* (Gmelin, 1790)
*Pterygodermatities whartoni* (Tubangui, 1931)
*Subulura andersoni* Cobbold, 1887
*Syphacia rifaii* Dewi and Hasegawa, 2010
*Trichuris muris* Schrank, 1788

***Bunomys penitus* (Miller and Hollister)**
*Bunomystrongylus abadii* Hasegawa and Mangali, 1996
*Heterakis spumosa* Scneider, 1866
*Subulura andersoni* Cobbold, 1887

***Bunomys prolatus* Musser**
*Heterakis spumosa* Scneider, 1866
*Subulura andersoni* Cobbold, 1887
*Syphacia rifaii* Dewi and Hasegawa, 2010
*Tikusnema javaense* Hasegawa, Shiraishi and Rochman, 1992

***Crunomys celebensis* Musser**
*Heterakis spumosa* Scneider, 1866

***Echiothrix centrosa* Miller & Hollister**
*Musserakis sulawesiensis* Hasegawa, Dewi and Asakawa, 2014

***Eropeplus canus* Miller and Hollister**
*Cyclodontostomum purvisi* Adams, 1933
*Hasanuddinia maxomyos* Hasegawa and Syafruddin, 1994
*Heligmonoides musseri* Hasegawa and Tarore, 1994
*Heterakis spumosa* Scneider, 1866
*Paraheligmonelloides eropeplios* Hasegawa, Miyata and Syafruddin, 1999

***Lenothrix* sp.**
*Hepatojarakus* sp.

***Lepoldamys sabanus* (Thomas)**
*Cyclodontostomum purvisi* Adams, 1933
*Hepatojarakus* sp.
*Physocephalus sexalatus* (Molin, 1860)
*Pterygodermatities* sp.
*Subulura spiroki* Purwaningsih, 2003

***Mallomys rothschildi* Thomas**
*Odilia mallomyos* Hasegawa and Syafruddin, 1994

***Margaretamys elegans* Musser**
*Hepatojarakus malayae* Yeh, 1955
*Heterakis spumosa* Scneider, 1866
*Subulura andersoni* Cobbold, 1887

***Maxomys bartelsii* (Jentink)**
*Angiostrongylus cantonensis* (Chen, 1935)
*Physaloptera* sp.
*Pterygodermatities tani* (Hoeppli, 1929)
*Subulura andersoni* Cobbold, 1887

***Maxomys pagensis* (Miller)**
*Capillaria* sp.
*Hepatojarakus* sp.

***Maxomys musschenbroekii* (Jentink)**

*Hasanuddinia maxomyos* Hasegawa and Syafruddin, 1994

*Heligmonoides musseri* Hasegawa and Tarore, 1994

*Odilia mamasaensis*, Hasegawa, Miyata and Syafruddin, 1999

*Odilia maxomyos* Hasegawa, Miyata and Syafruddin, 1999

*Syphacia maxomyos* Dewi et al., xxxx

***Maxomys surifer* (Miller)**

*Aspiculuris* p.

*Molineus* sp.

***Maxomys whiteheadi* (Thomas)**

*Cyclodontostomum purvisi* Adams, 1933

*Maxomystrongylus yasumai* Hasegawa and Syafruddin, 1997

*Physaloptera* sp.

*Seuratum* sp.

*Syphacia maxomyos* Dewi et al., xxxx

***Niviventer cremoniventer* (Miller)**

*Cyclodontostomum purvisi* Adams, 1933

*Maxomystrongylus yasumai* Hasegawa and Syafruddin, 1997

***Niviventer fulvescens* Gray**

*Physaloptera* sp.

***Niviventer lepturus* (Jentink)**

*Angiostrongylus cantonensis* (Chen, 1935)

*Gongylonema neoplasticum* (Fibiger and Ditlevsen, 1914)

*Masthoporus muris* (Gmelin, 1790)

***Paruromys dominator* Thomas**

*Cyclodontostomum purvisi* Adams, 1933

*Heterakis spumosa* Scneider, 1866

*Paraheligmonelloides paruromys* Hasegawa, Miyata and Syafruddin, 1999

*Syphacia paruromyos*

***Rattus* sp.**

*Angiostrongylus malaysiensis* Bhaibulaya and Cross, 1971

*Hepatojarakus* sp.

***Rattus argentiventer* (Robinson and Kloss)**

*Angiostrongylus cantonensis* (Chen, 1935)

*Eucoleus bacillatus* (Eberth, 1863)

*Hepatojarakus malayae* Yeh, 1955

*Nippostrongylus brasiliensis* (Travassos,1914)

*Physaloptera* sp.

*Strongyloides ratti* Sandground, 1925

*Syphacia muris* Yamaguti, 1941

*Tikusnema javaense* Hasegawa, Shiraishi and Rochman, 1992

***Rattus exulans* (Peale)**

*Angiostrongylus cantonensis* (Chen, 1935)

*Angiostrongylus malaysiensis* Bhaibulaya and Cross, 1971

*Cyclodontostomum purvisi* Adams, 1933

*Hepatojarakus* sp.

*Nippostrongylus brasiliensis* (Travassos,1914)

*Strongyloides venezuelensis* Brumpt, 1934

*Syphacia muris* Yamaguti, 1941

***Rattus hainaldi* Kitchener, How and Maharadatunkamsi**

*Heterakis spumosa* Scneider, 1866

*Pterygodermatities* sp.

*Subulura andersoni* Cobbold, 1887

*Syphacia muris* Yamaguti, 1941

***Rattus hoffmanni* (Matschie)**

*Cyclodontostomum purvisi* Adams, 1933

*Hepatojarakus malayae* Yeh, 1955

*Heterakis spumosa* Scneider, 1866

*Subulura andersoni* Cobbold, 1887

*Tikusnema javaense* Hasegawa, Shiraishi and Rochman, 1992

***Rattus lugens* (Miller)**

*Angiostrongylus malaysiensis* Bhaibulaya and Cross, 1971

*Hepatojarakus* sp.

*Heterakis* sp.

*Physaloptera* sp.

*Subulura andersoni* Cobbold, 1887

***Rattus marmosurus* Thomas**

*Hepatojarakus malayae* Yeh, 1955

*Heterakis spumosa* Scneider, 1866

*Subulura andersoni* Cobbold, 1887

***Rattus* cf. *morotainensis* Kellogg**

*Nippostrongylus marhaeniae* Hasegawa and Syafruddin, 1995

*Odilia* sp.

*Orientostrongylus* sp.

***Rattus xanthurus* (Gray)**

*Heterakis spumosa* Scneider, 1866

*Masthoporus muris* (Gmelin, 1790)

*Nippostrongylus sembeli* Hasegawa and Tarore, 1995

*Odila moatensis* Hasegawa, Miyata and Syafruddin, 1999

*Odilia sulawesiensis* Hasegawa, Miyata and Syafruddin, 1999

*Orientostrongylus* sp.

*Pterygodermatities tani* (Hoeppli, 1929)

*Syphacia muris* Yamaguti, 1941

*Syphacia sulawesiensis* Hasegawa and Tarore, 1996

***Rattus rattus* (Linnaeus)**

*Capillaria traverae* Ash, 1962

*Gongylonema neoplasticum* (Fibiger and Ditlevsen, 1914)

*Nippostrongylus brasiliensis* (Travassos, 1914)

*Orientostrongylus tenorai* Durette–Desset, 1970

*Pterygodermatities whartoni* (Tubangui, 1931)

*Strongyloides ratti* Sandground, 1925

*Strongyloides venezuelensis* Brumpt, 1934

*Syphacia muris* Yamaguti, 1941

***Rattus tanezumi* Temminck**

*Angiostrongylus* sp.
*Angiostrongylus cantonensis* (Chen, 1935)
*Angiostrongylus malaysiensis* Bhaibulaya and Cross, 1971
*Aspiculuris* sp.
*Gongylonema neoplasticum* (Fibiger and Ditlevsen, 1914)
*Hepatojarakus* sp.
*Hepatojarakus malayae* Yeh, 1955
*Heterakis spumosa* Scneider, 1866
*Maxomystrongylus yasumai* Hasegawa and Syafruddin, 1997
*Masthoporus muris* (Gmelin, 1790)
*Molineus* sp.
*Nippostrongylus brasiliensis* (Travassos, 1914)
*Physaloptera* sp.
*Pterygodermatities* sp.
*Pterygodermatities tani* (Hoeppli, 1929)
*Pterygodermatities whartoni* (Tubangui, 1931)
*Subulura andersoni* Cobbold, 1887
*Syphacia muris* Yamaguti, 1941
*Tikusnema javaense* Hasegawa, Shiraishi and Rochman, 1992

***Rattus tiomanicus* Miller**

*Angiostrongylus cantonensis* (Chen, 1935)
*Angiostrongylus malaysiensis* Bhaibulaya and Cross, 1971
*Breinlia tinjili* Purnomo and Bangs, 1996
*Cyclodontostomum purvisi* Adams, 1933
*Hepatojarakus* sp.
*Hepatojarakus malayae* Yeh, 1955
*Heterakis spumosa* Scneider, 1866
*Masthoporus muris* (Gmelin, 1790)
*Nippostrongylus brasiliensis* (Travassos,1914)
*Onchocerca* sp.
*Physaloptera* sp.
*Subulura andersoni* Cobbold, 1887

*Syphacia muris* Yamaguti, 1941
*Tikusnema javaense* Hasegawa, Shiraishi and Rochman, 1992

***Sundamys muelleri* (Jentink)**
*Masthoporus muris* (Gmelin, 1790)
*Pterygodermatities* sp.

***Taeromys* sp.**
*Nippostrongylus brasiliensis* (Travassos,1914)

***Taeromys celebensis* (Gray, 1867)**
*Heterakis spumosa* Scneider, 1866
*Syphacia taeromyos* Dewi and Hasegawa, 2014

***Tateomys macrocercus* Musser**
*Heterakis spumosa* Scneider, 1866

***Tateomys rhinogradoides* Musser**
*Heterakis spumosa* Scneider, 1866

# Appendix 2. DNA Sequence of *Syphacia* spp.

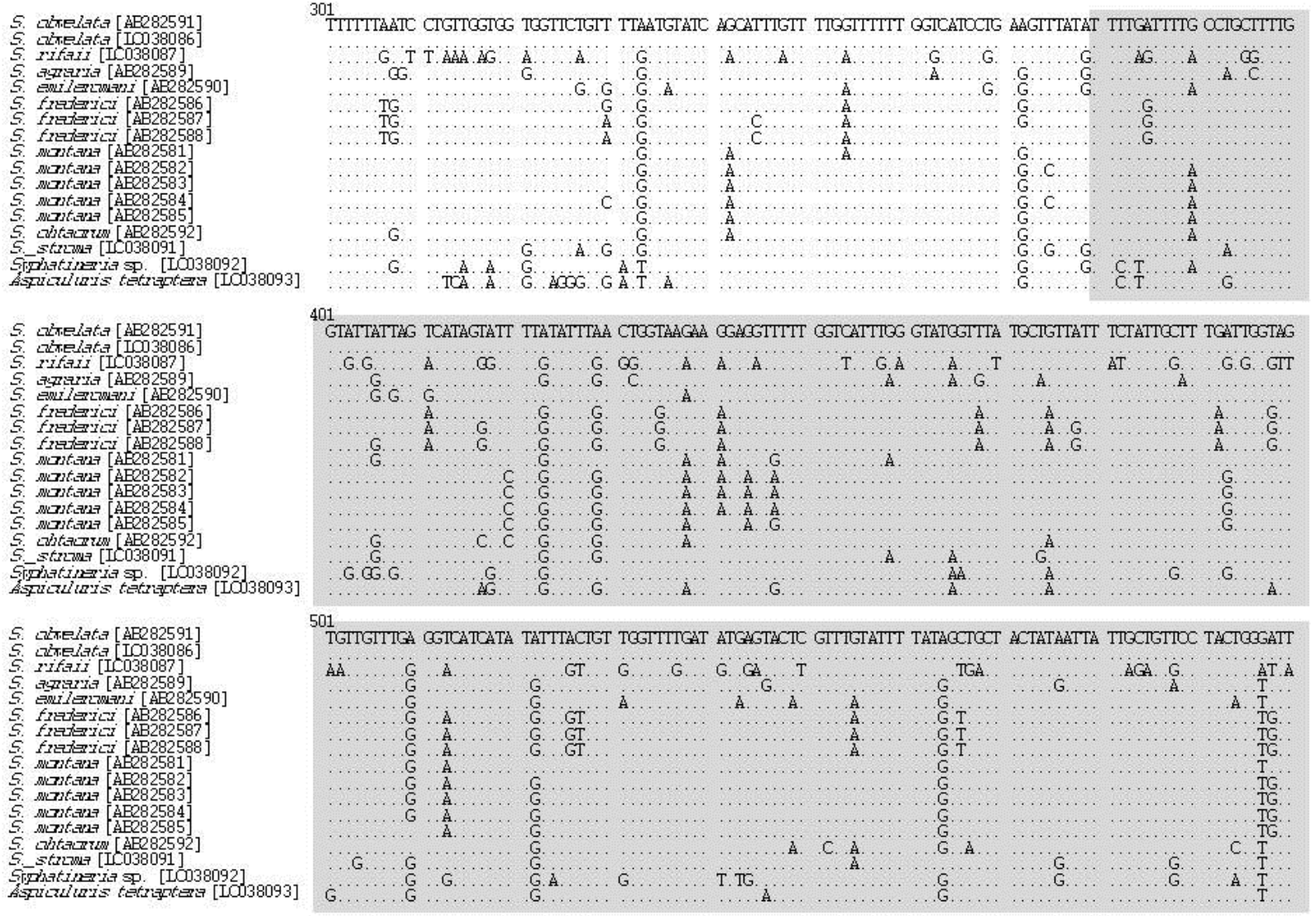
Fig. A-1. Nucleotide sequences of partial mitochondrial DNA *Cox1* gene aligned by Clustal W (long sequences)*.



*Dots indicate homologous nucleotides with *Syphacia obvelata* [AB282591]; dash indicates absence of nucleotide.

[To be continued.]

Fig. A-1. [continued]




Shaded portion is used for short sequences (Fig. A- 3).

[To be continued.]

Fig. A-1. [continued]

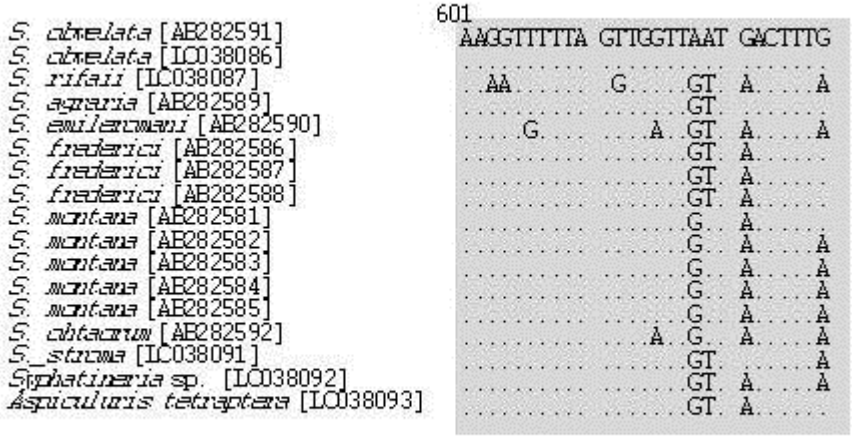
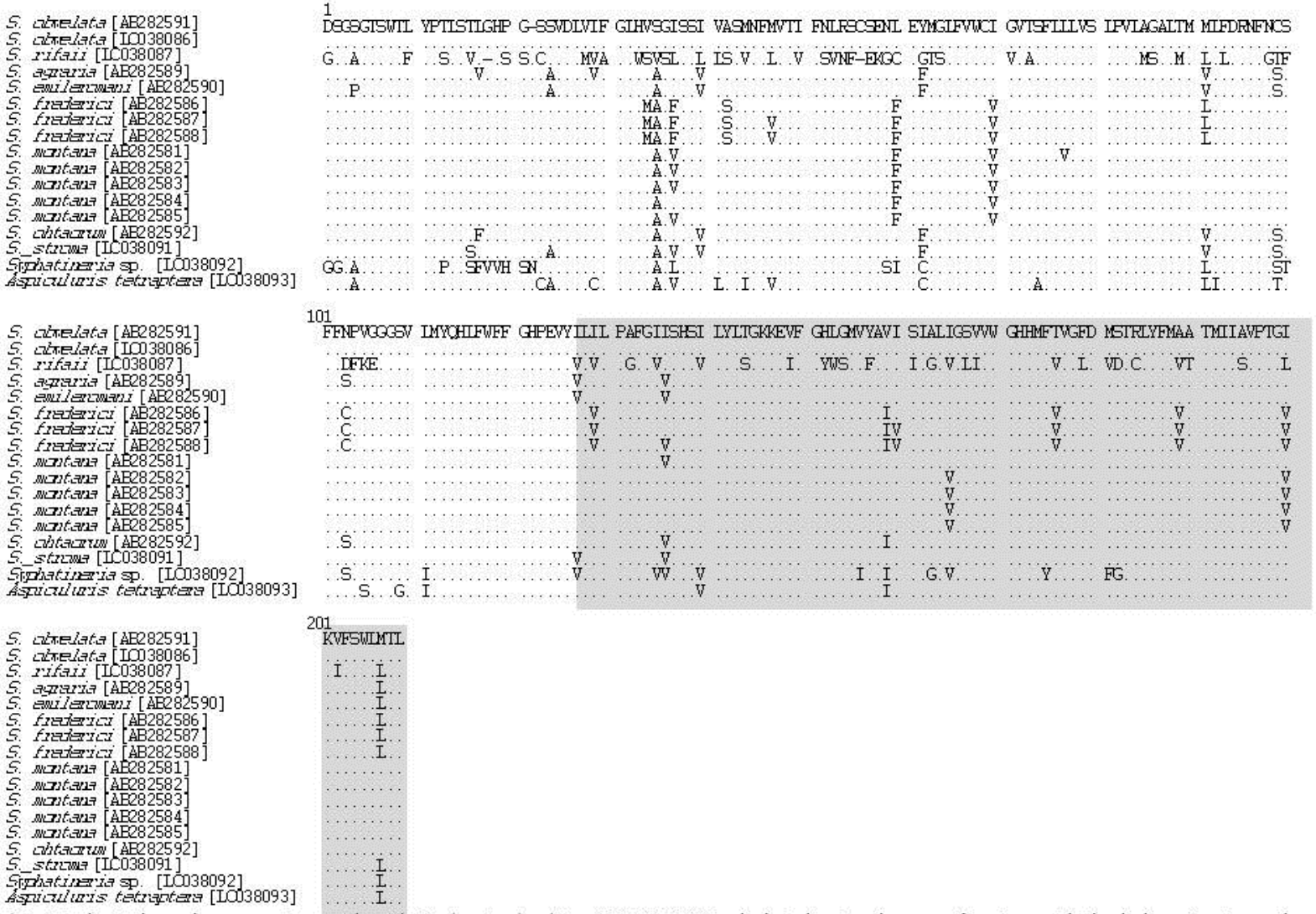
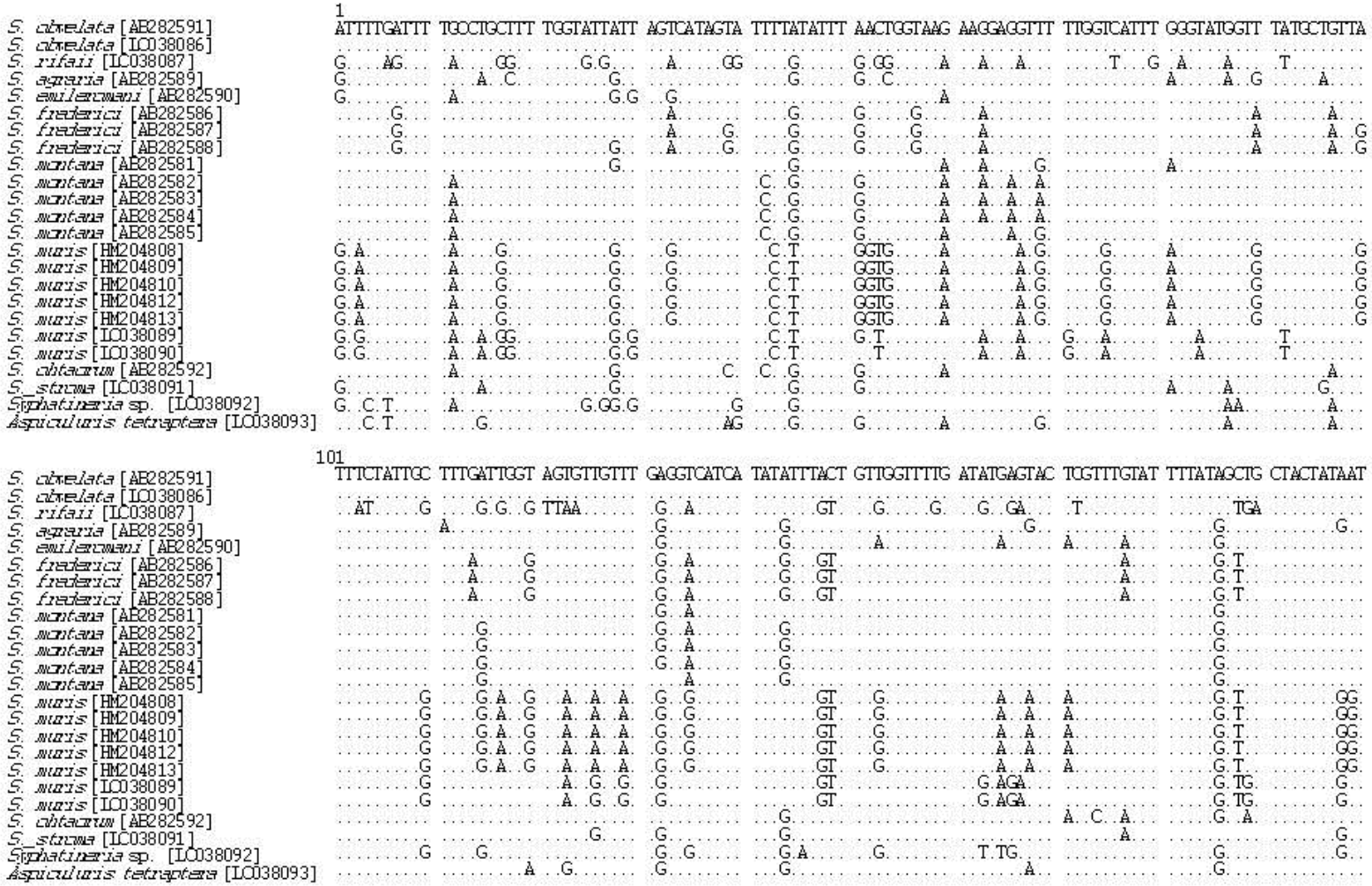


Fig. A-2. Translated amino acid sequences of partial mitochondrial DNA *Cox1* gene aligned by Clustal W (long sequences).




*Dots indicate homologous amino acids with *Syphacia obvelata* [AB282591]; dash indicates absence of amino acid. Shaded portion is used for short sequences (Fig. A-4).

Fig. A-3. Nucleotide sequences of partial mitochondrial DNA *Cox1* gene aligned by Clustal W (short sequences)*.




*Dots indicate homologous nucleotides with *Syphacia obvelata* [AB282591]; dash indicates absence of nucleotide. [To be continued.]

Fig. A-3. [continued]

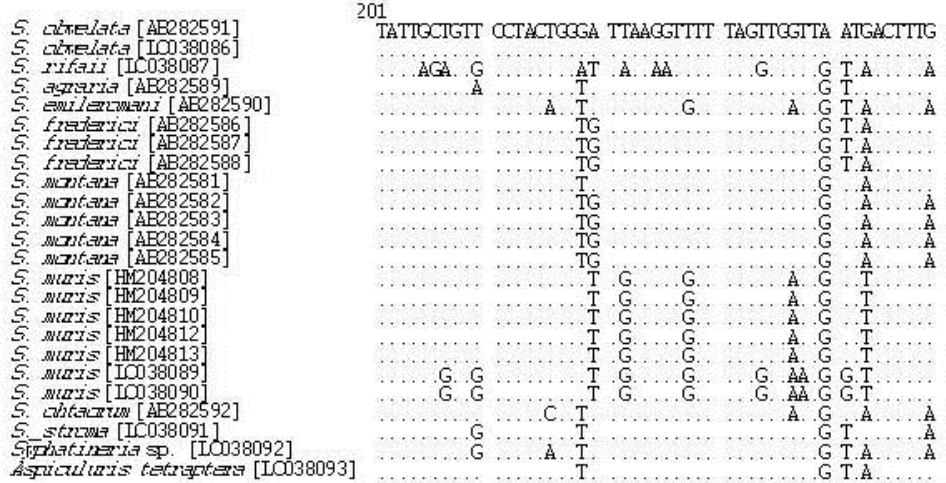
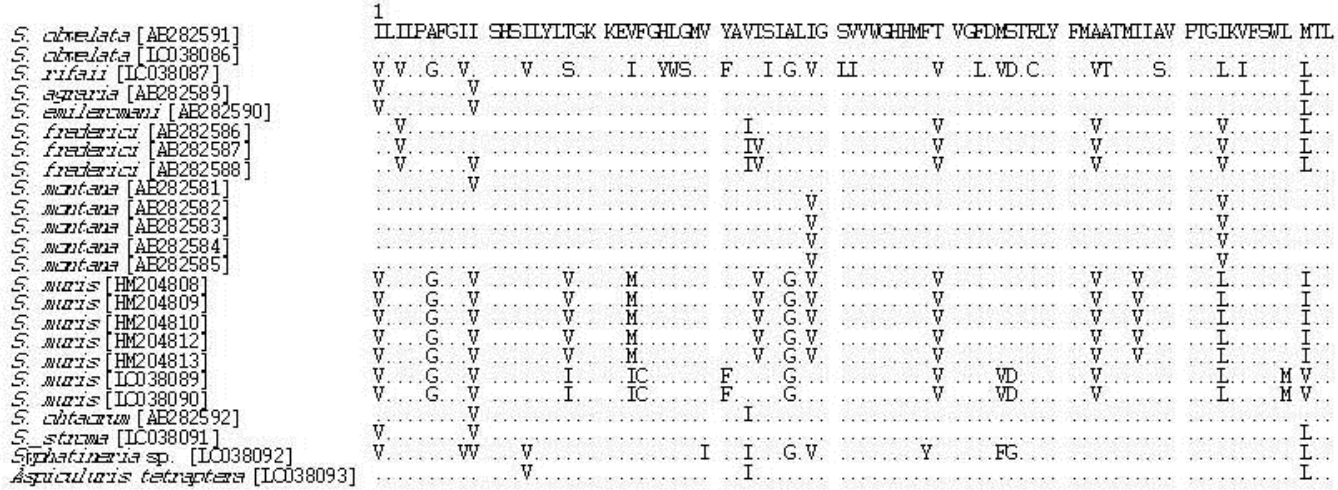


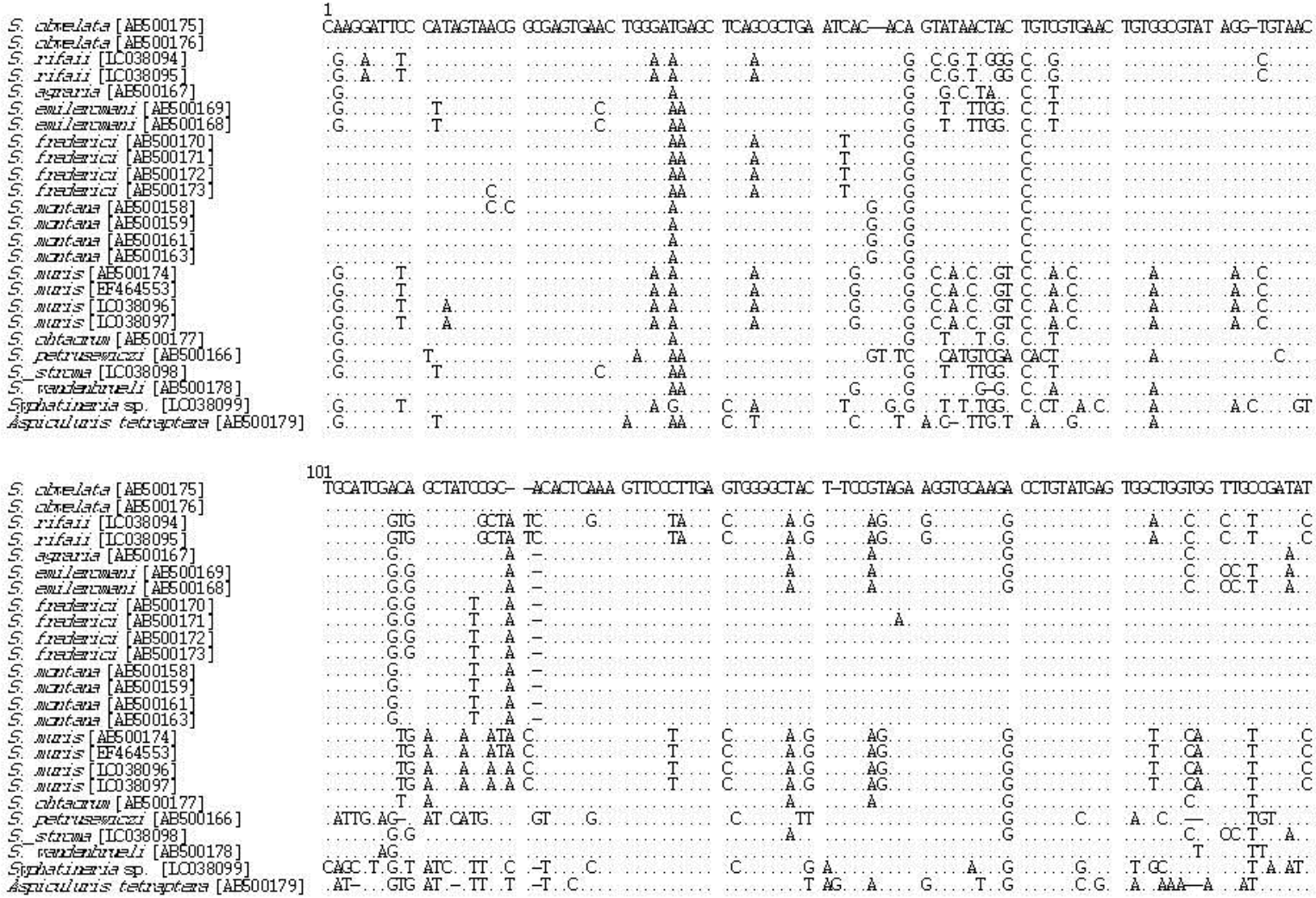



Fig. A-4. Translated amino acid sequences of partial mitochondrial DNA *Cox1* gene aligned by Clustal W (short sequences)*.



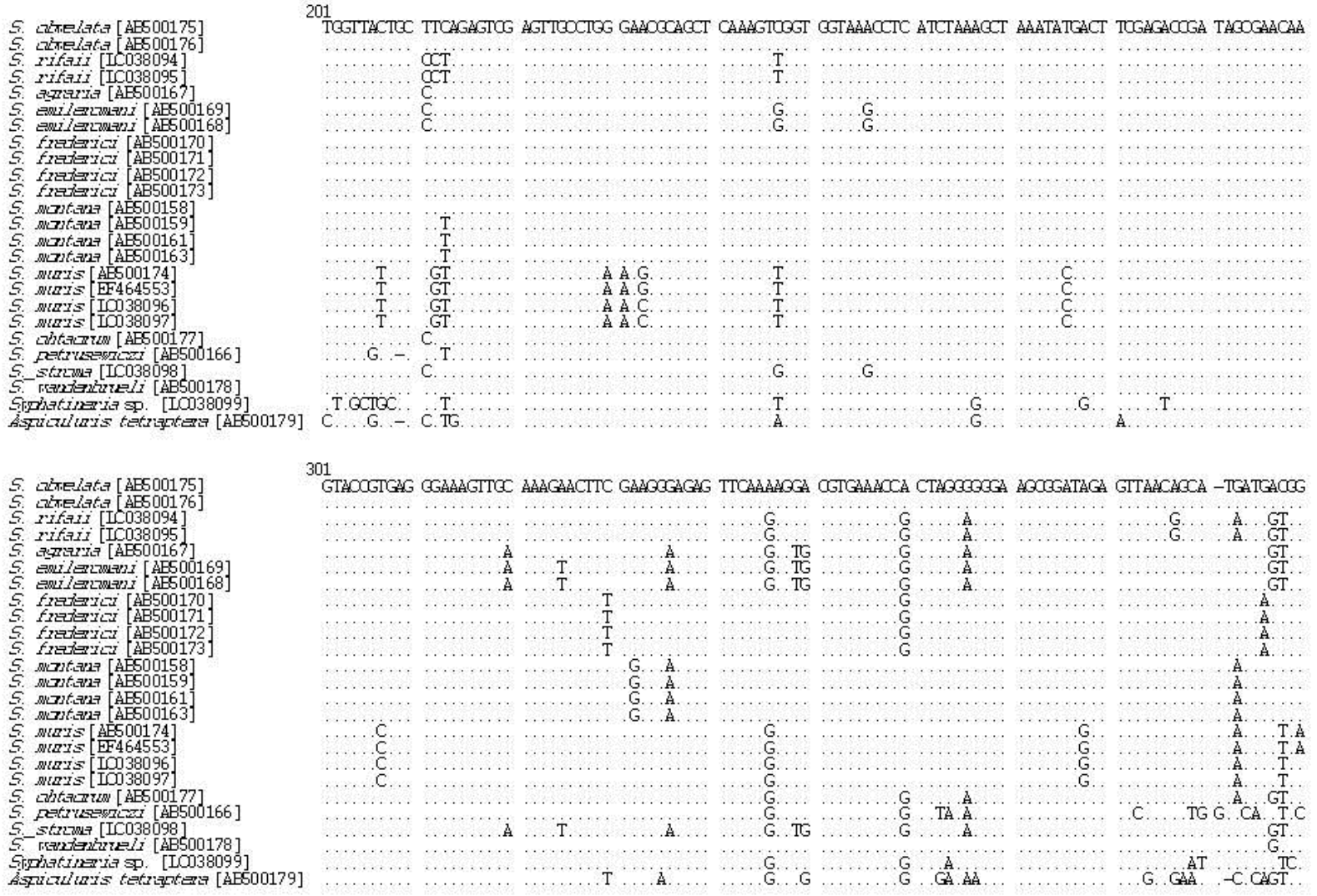

*Dots indicate homologous amino acids with *Syphacia obvelata* [AB282591].

Fig. A-5. Nucleotide sequences of partial 28S rDNA aligned by Clustal W (long sequences)*.



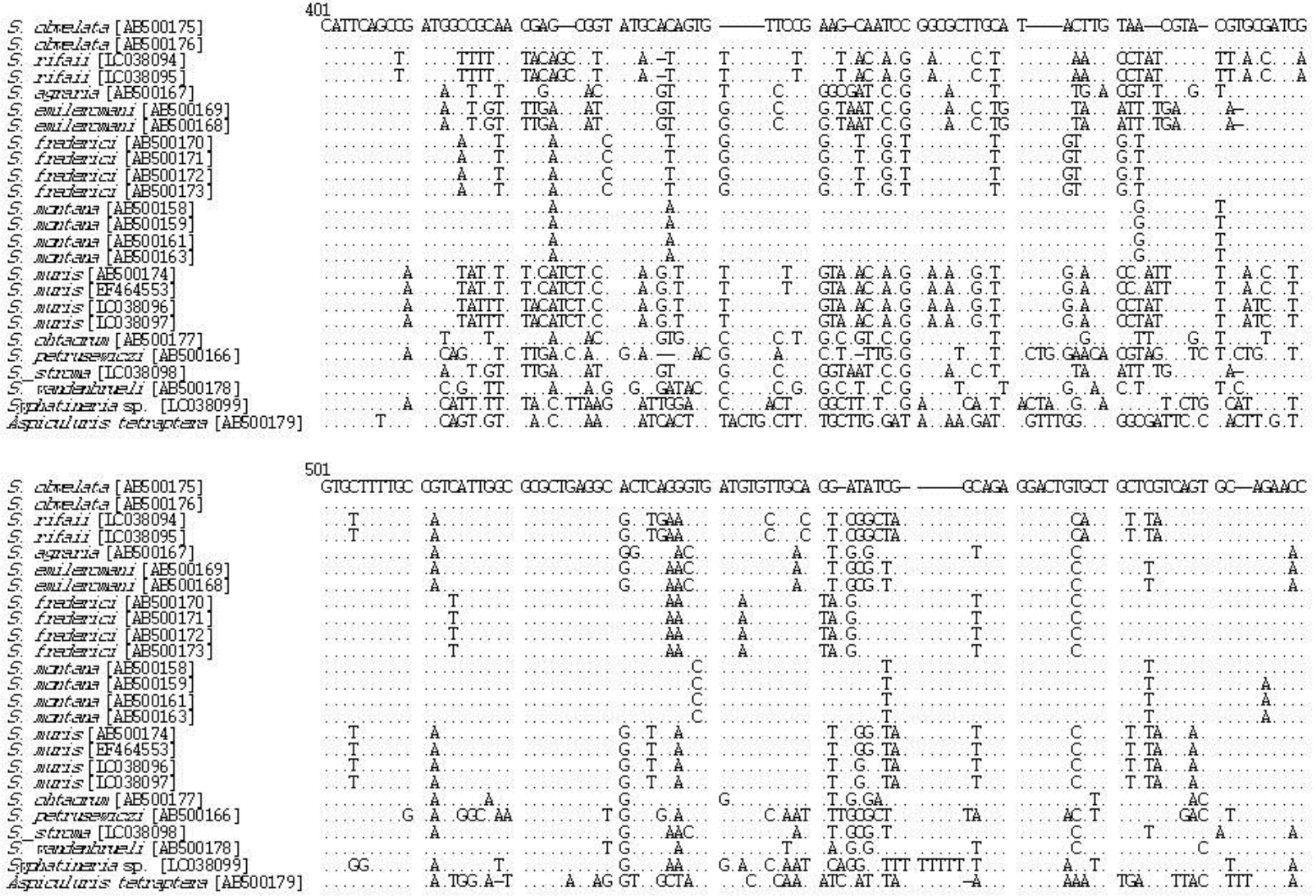

*Dots indicate homologous nucleotides with *Syphacia obvelata* [AB500175]; dash indicates absence of nucleotide. [To be continued.]

Fig. A-6. [continued]




[To be continued.]

Fig. A-6. [continued]




[To be continued.]

Fig. A-6. [continued]

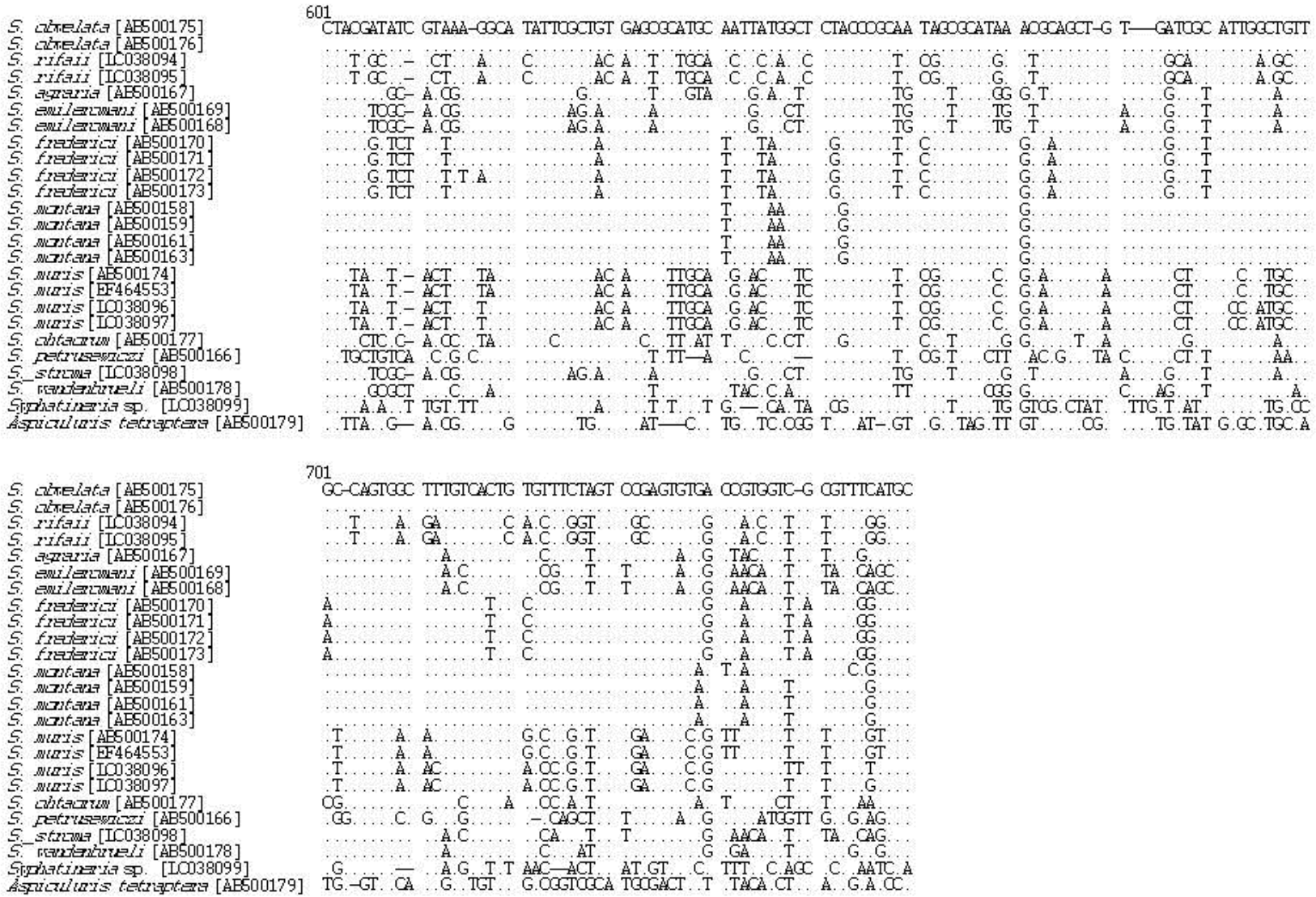


Table A-1. Estimates of evolutionary divergence between nucleotide sequences (lower-left diagonal) and amino acid sequences (upper-right diagonal) of partial mitochondrial *Cox1* gene (long sequences)*.

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *S. obvelata* [AB282591] | | 0.00 | 0.36 | 0.06 | 0.05 | 0.07 | 0.08 | 0.08 | 0.03 | 0.03 | 0.03 | 0.02 | 0.03 | 0.04 | 0.05 | 0.15 | 0.10 |
| 2 | *S. obvelata* [LC038086] | 0.00 | | 0.36 | 0.06 | 0.05 | 0.07 | 0.08 | 0.08 | 0.03 | 0.03 | 0.03 | 0.02 | 0.03 | 0.04 | 0.05 | 0.15 | 0.10 |
| 3 | *S. rifaii* [LC038087] | 0.28 | 0.28 | | 0.36 | 0.36 | 0.34 | 0.34 | 0.35 | 0.37 | 0.36 | 0.36 | 0.36 | 0.36 | 0.37 | 0.36 | 0.34 | 0.35 |
| 4 | *S. agraria* [AB282589] | 0.11 | 0.11 | 0.29 | | 0.02 | 0.10 | 0.11 | 0.10 | 0.07 | 0.08 | 0.08 | 0.07 | 0.08 | 0.03 | 0.02 | 0.14 | 0.11 |
| 5 | *S. emiliromani* [AB282590] | 0.09 | 0.09 | 0.28 | 0.11 | | 0.09 | 0.10 | 0.10 | 0.06 | 0.07 | 0.07 | 0.06 | 0.07 | 0.03 | 0.01 | 0.14 | 0.10 |
| 6 | *S. frederici* [AB282586] | 0.08 | 0.08 | 0.27 | 0.12 | 0.11 | | 0.01 | 0.01 | 0.06 | 0.05 | 0.05 | 0.05 | 0.05 | 0.08 | 0.09 | 0.17 | 0.12 |
| 7 | *S. frederici* [AB282587] | 0.09 | 0.09 | 0.27 | 0.13 | 0.12 | 0.01 | | 0.00 | 0.07 | 0.06 | 0.06 | 0.06 | 0.06 | 0.09 | 0.10 | 0.17 | 0.12 |
| 8 | *S. frederici* [AB282588] | 0.09 | 0.09 | 0.27 | 0.13 | 0.12 | 0.01 | 0.00 | | 0.07 | 0.07 | 0.07 | 0.07 | 0.07 | 0.09 | 0.10 | 0.17 | 0.13 |
| 9 | *S. montana* [AB282581] | 0.06 | 0.06 | 0.27 | 0.11 | 0.09 | 0.08 | 0.08 | 0.08 | | 0.02 | 0.02 | 0.02 | 0.02 | 0.05 | 0.05 | 0.15 | 0.11 |
| 10 | *S. montana* [AB282582] | 0.07 | 0.07 | 0.28 | 0.12 | 0.10 | 0.08 | 0.08 | 0.09 | 0.04 | | 0.00 | 0.00 | 0.00 | 0.06 | 0.06 | 0.15 | 0.11 |
| 11 | *S. montana* [AB282583] | 0.07 | 0.07 | 0.28 | 0.12 | 0.10 | 0.07 | 0.08 | 0.08 | 0.04 | 0.00 | | 0.00 | 0.00 | 0.06 | 0.06 | 0.15 | 0.11 |
| 12 | *S. montana* [AB282584] | 0.07 | 0.07 | 0.28 | 0.12 | 0.10 | 0.08 | 0.08 | 0.09 | 0.04 | 0.00 | 0.00 | | 0.00 | 0.06 | 0.07 | 0.15 | 0.11 |
| 13 | *S. montana* [AB282585] | 0.06 | 0.06 | 0.28 | 0.12 | 0.10 | 0.07 | 0.08 | 0.08 | 0.04 | 0.01 | 0.01 | 0.01 | | 0.06 | 0.06 | 0.15 | 0.11 |
| 14 | *S. ohtaorum* [AB282592] | 0.09 | 0.09 | 0.28 | 0.10 | 0.09 | 0.10 | 0.11 | 0.11 | 0.09 | 0.09 | 0.09 | 0.09 | 0.08 | | 0.04 | 0.13 | 0.11 |
| 15 | *S. stroma* [LC038091] | 0.09 | 0.09 | 0.28 | 0.09 | 0.09 | 0.11 | 0.12 | 0.12 | 0.09 | 0.10 | 0.10 | 0.10 | 0.10 | 0.09 | | 0.13 | 0.10 |
| 16 | *Syphatineria* sp. [LC038092] | 0.13 | 0.13 | 0.27 | 0.14 | 0.13 | 0.14 | 0.14 | 0.14 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | | 0.16 |
| 17 | *Aspiculuris tetraptera* [LC038093] | 0.12 | 0.12 | 0.28 | 0.14 | 0.13 | 0.13 | 0.13 | 0.13 | 0.12 | 0.13 | 0.13 | 0.13 | 0.12 | 0.14 | 0.12 | 0.14 | |

* The number of base and amino acid differences per site between sequences are shown. The analysis involved 17 sequences. Codon positions included were 1st+2nd+3rd. All positions containing gaps and missing data were eliminated. There were a total of 618 nucleotide and 209 amino acid positions in the final dataset.

Table A-2. Estimates of evolutionary divergence between nucleotide sequences (lower-left diagonal) and amino acid sequences (upper-right diagonal) of partial mitochondrial *Cox1* gene (short sequences)*.

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *S. obvelata* [AB282591] | | 0.00 | 0.33 | 0.04 | 0.04 | 0.07 | 0.08 | 0.10 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.16 | 0.16 | 0.16 | 0.16 | 0.16 | 0.18 | 0.18 | 0.02 | 0.04 | 0.14 | 0.04 |
| 2 | *S. obvelata* [LC038086] | 0.00 | | 0.33 | 0.04 | 0.04 | 0.07 | 0.08 | 0.10 | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | 0.16 | 0.16 | 0.16 | 0.16 | 0.16 | 0.18 | 0.18 | 0.02 | 0.04 | 0.14 | 0.04 |
| 3 | *S. rifaii* [LC038087] | 0.24 | 0.24 | | 0.31 | 0.31 | 0.29 | 0.30 | 0.31 | 0.34 | 0.31 | 0.31 | 0.31 | 0.31 | 0.28 | 0.28 | 0.28 | 0.28 | 0.28 | 0.24 | 0.24 | 0.35 | 0.31 | 0.30 | 0.31 |
| 4 | *S. agraria* [AB282589] | 0.08 | 0.08 | 0.25 | | 0.00 | 0.08 | 0.10 | 0.08 | 0.02 | 0.06 | 0.06 | 0.06 | 0.06 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.16 | 0.16 | 0.04 | 0.00 | 0.11 | 0.05 |
| 5 | *S. emileromani* [AB282590] | 0.08 | 0.08 | 0.25 | 0.10 | | 0.08 | 0.10 | 0.08 | 0.02 | 0.06 | 0.06 | 0.06 | 0.06 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.16 | 0.16 | 0.04 | 0.00 | 0.11 | 0.05 |
| 6 | *S. frederici* [AB282586] | 0.09 | 0.09 | 0.21 | 0.11 | 0.11 | | 0.01 | 0.02 | 0.08 | 0.07 | 0.07 | 0.07 | 0.07 | 0.16 | 0.16 | 0.16 | 0.16 | 0.16 | 0.18 | 0.18 | 0.07 | 0.08 | 0.17 | 0.06 |
| 7 | *S. frederici* [AB282587] | 0.10 | 0.10 | 0.21 | 0.12 | 0.12 | 0.01 | | 0.01 | 0.10 | 0.08 | 0.08 | 0.08 | 0.08 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.19 | 0.19 | 0.08 | 0.10 | 0.18 | 0.07 |
| 8 | *S. frederici* [AB282588] | 0.10 | 0.10 | 0.22 | 0.11 | 0.11 | 0.01 | 0.00 | | 0.08 | 0.10 | 0.10 | 0.10 | 0.10 | 0.13 | 0.13 | 0.13 | 0.13 | 0.13 | 0.18 | 0.18 | 0.07 | 0.08 | 0.17 | 0.08 |
| 9 | *S. montana* [AB282581] | 0.05 | 0.05 | 0.23 | 0.08 | 0.08 | 0.08 | 0.08 | 0.08 | | 0.04 | 0.04 | 0.04 | 0.04 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.17 | 0.17 | 0.01 | 0.02 | 0.13 | 0.05 |
| 10 | *S. montana* [AB282582] | 0.07 | 0.07 | 0.22 | 0.10 | 0.08 | 0.08 | 0.08 | 0.09 | 0.04 | | 0.00 | 0.00 | 0.00 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.19 | 0.19 | 0.05 | 0.06 | 0.14 | 0.06 |
| 11 | *S. montana* [AB282583] | 0.07 | 0.07 | 0.22 | 0.10 | 0.08 | 0.08 | 0.08 | 0.09 | 0.04 | 0.00 | | 0.00 | 0.00 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.19 | 0.19 | 0.05 | 0.06 | 0.14 | 0.06 |
| 12 | *S. montana* [AB282584] | 0.07 | 0.07 | 0.22 | 0.10 | 0.08 | 0.08 | 0.08 | 0.09 | 0.04 | 0.00 | 0.00 | | 0.00 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.19 | 0.19 | 0.05 | 0.06 | 0.14 | 0.06 |
| 13 | *S. montana* [AB282585] | 0.06 | 0.06 | 0.22 | 0.10 | 0.08 | 0.08 | 0.09 | 0.10 | 0.05 | 0.01 | 0.01 | 0.01 | | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.19 | 0.19 | 0.05 | 0.06 | 0.14 | 0.06 |
| 14 | *S. muris* [HM204808] | 0.18 | 0.18 | 0.24 | 0.18 | 0.16 | 0.18 | 0.18 | 0.18 | 0.16 | 0.17 | 0.17 | 0.17 | 0.17 | | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 0.13 | 0.16 | 0.13 | 0.19 | 0.18 |
| 15 | *S. muris* [HM204809] | 0.18 | 0.18 | 0.24 | 0.18 | 0.16 | 0.18 | 0.18 | 0.18 | 0.16 | 0.17 | 0.17 | 0.17 | 0.17 | 0.00 | | 0.00 | 0.00 | 0.00 | 0.13 | 0.13 | 0.16 | 0.13 | 0.19 | 0.18 |
| 16 | *S. muris* [HM204810] | 0.18 | 0.18 | 0.24 | 0.18 | 0.16 | 0.18 | 0.18 | 0.18 | 0.16 | 0.17 | 0.17 | 0.17 | 0.17 | 0.00 | 0.00 | | 0.00 | 0.00 | 0.13 | 0.13 | 0.16 | 0.13 | 0.19 | 0.18 |
| 17 | *S. muris* [HM204812] | 0.18 | 0.18 | 0.24 | 0.18 | 0.16 | 0.18 | 0.18 | 0.18 | 0.16 | 0.17 | 0.17 | 0.17 | 0.17 | 0.00 | 0.00 | 0.00 | | 0.00 | 0.13 | 0.13 | 0.16 | 0.13 | 0.19 | 0.18 |
| 18 | *S. muris* [HM204813] | 0.18 | 0.18 | 0.24 | 0.18 | 0.16 | 0.18 | 0.18 | 0.18 | 0.16 | 0.17 | 0.17 | 0.17 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | | 0.13 | 0.13 | 0.16 | 0.13 | 0.19 | 0.18 |
| 19 | *S. muris* [LC038089] | 0.17 | 0.17 | 0.22 | 0.18 | 0.17 | 0.19 | 0.20 | 0.20 | 0.17 | 0.19 | 0.19 | 0.19 | 0.20 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | | 0.00 | 0.18 | 0.16 | 0.22 | 0.20 |
| 20 | *S. muris* [LC038090] | 0.18 | 0.18 | 0.22 | 0.18 | 0.17 | 0.19 | 0.20 | 0.19 | 0.18 | 0.19 | 0.19 | 0.19 | 0.20 | 0.14 | 0.14 | 0.14 | 0.14 | 0.14 | 0.00 | | 0.18 | 0.16 | 0.22 | 0.20 |
| 21 | *S. ohtaorum* [AB282592] | 0.08 | 0.08 | 0.25 | 0.11 | 0.06 | 0.10 | 0.10 | 0.10 | 0.07 | 0.06 | 0.06 | 0.06 | 0.06 | 0.18 | 0.18 | 0.18 | 0.18 | 0.18 | 0.20 | 0.20 | | 0.04 | 0.12 | 0.04 |
| 22 | *S. stroma* [LC038091] | 0.07 | 0.07 | 0.24 | 0.04 | 0.08 | 0.10 | 0.11 | 0.10 | 0.07 | 0.09 | 0.09 | 0.09 | 0.09 | 0.18 | 0.18 | 0.18 | 0.18 | 0.18 | 0.17 | 0.17 | 0.09 | | 0.11 | 0.05 |
| 23 | *Syphatineria* sp. [LC038092] | 0.13 | 0.13 | 0.22 | 0.12 | 0.10 | 0.14 | 0.15 | 0.15 | 0.12 | 0.12 | 0.12 | 0.12 | 0.12 | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 | 0.19 | 0.20 | 0.12 | 0.10 | | 0.11 |
| 24 | *Aspiculuris tetraptera* [LC038093] | 0.08 | 0.08 | 0.23 | 0.09 | 0.10 | 0.09 | 0.10 | 0.10 | 0.07 | 0.08 | 0.08 | 0.08 | 0.08 | 0.19 | 0.19 | 0.19 | 0.19 | 0.19 | 0.21 | 0.21 | 0.09 | 0.09 | 0.11 | |

* The number of base and amino acid differences per site between sequences are shown. The analysis involved 24 sequences. Codon positions included were 1st+2nd+3rd. All positions containing gaps and missing data were eliminated. There were a total of 249 nucleotide and 83 amino acid positions in the final dataset.

Table A-3. Estimates of evolutionary divergence between nucleotide of partial 28S rDNA*.

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *S. obvelata* [AB500175] | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | *S. obvelata* [AB500176] | 0.00 | | | | | | | | | | | | | | | | | | | | | | | |
| 3 | *S. rifaii* [LC038094] | 0.20 | 0.20 | | | | | | | | | | | | | | | | | | | | | | |
| 4 | *S. rifaii* [LC038095] | 0.20 | 0.20 | 0.00 | | | | | | | | | | | | | | | | | | | | | |
| 5 | *S. agraria* [AB500167] | 0.13 | 0.13 | 0.20 | 0.20 | | | | | | | | | | | | | | | | | | | | |
| 6 | *S. emileromani* [AB500168] | 0.17 | 0.17 | 0.19 | 0.19 | 0.09 | | | | | | | | | | | | | | | | | | | |
| 7 | *S. emileromani* [AB500169] | 0.17 | 0.17 | 0.19 | 0.19 | 0.09 | 0.00 | | | | | | | | | | | | | | | | | | |
| 8 | *S. frederici* [AB500170] | 0.08 | 0.08 | 0.20 | 0.20 | 0.13 | 0.17 | 0.17 | | | | | | | | | | | | | | | | | |
| 9 | *S. frederici* [AB500171] | 0.08 | 0.08 | 0.20 | 0.20 | 0.13 | 0.17 | 0.17 | 0.00 | | | | | | | | | | | | | | | | |
| 10 | *S. frederici* [AB500172] | 0.08 | 0.08 | 0.20 | 0.20 | 0.13 | 0.17 | 0.17 | 0.00 | 0.00 | | | | | | | | | | | | | | | |
| 11 | *S. frederici* [AB500173] | 0.08 | 0.08 | 0.20 | 0.20 | 0.13 | 0.17 | 0.17 | 0.00 | 0.00 | 0.00 | | | | | | | | | | | | | | |
| 12 | *S. montana* [AB500158] | 0.04 | 0.04 | 0.20 | 0.20 | 0.14 | 0.18 | 0.18 | 0.09 | 0.09 | 0.09 | 0.08 | | | | | | | | | | | | | |
| 13 | *S. montana* [AB500159] | 0.04 | 0.04 | 0.19 | 0.19 | 0.13 | 0.17 | 0.17 | 0.08 | 0.08 | 0.08 | 0.08 | 0.01 | | | | | | | | | | | | |
| 14 | *S. montana* [AB500161] | 0.04 | 0.04 | 0.19 | 0.19 | 0.13 | 0.17 | 0.17 | 0.08 | 0.08 | 0.08 | 0.08 | 0.01 | 0.00 | | | | | | | | | | | |
| 15 | *S. montana* [AB500163] | 0.04 | 0.04 | 0.19 | 0.19 | 0.13 | 0.17 | 0.17 | 0.08 | 0.08 | 0.08 | 0.08 | 0.01 | 0.00 | 0.00 | | | | | | | | | | |
| 16 | *S. muris* [AB500174] | 0.20 | 0.20 | 0.14 | 0.14 | 0.21 | 0.23 | 0.23 | 0.21 | 0.21 | 0.21 | 0.21 | 0.20 | 0.20 | 0.20 | 0.20 | | | | | | | | | |
| 17 | *S. muris* [EF464553] | 0.20 | 0.20 | 0.14 | 0.14 | 0.21 | 0.23 | 0.23 | 0.21 | 0.21 | 0.21 | 0.21 | 0.20 | 0.20 | 0.20 | 0.20 | 0.00 | | | | | | | | |
| 18 | *S. muris* [LC038096] | 0.20 | 0.20 | 0.13 | 0.13 | 0.21 | 0.23 | 0.23 | 0.20 | 0.20 | 0.20 | 0.20 | 0.21 | 0.20 | 0.20 | 0.20 | 0.03 | 0.03 | | | | | | | |
| 19 | *S. muris* [LC038097] | 0.20 | 0.20 | 0.13 | 0.13 | 0.21 | 0.23 | 0.23 | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 | 0.03 | 0.03 | 0.00 | | | | | | |
| 20 | *S. ohtaorum* [AB500177] | 0.13 | 0.13 | 0.20 | 0.20 | 0.12 | 0.15 | 0.15 | 0.16 | 0.16 | 0.16 | 0.16 | 0.13 | 0.13 | 0.13 | 0.13 | 0.20 | 0.20 | 0.20 | 0.20 | | | | | |
| 21 | *S. petrusewiczi* [AB500166] | 0.24 | 0.24 | 0.26 | 0.26 | 0.22 | 0.23 | 0.23 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.25 | 0.27 | 0.27 | 0.27 | 0.27 | 0.23 | | | | |
| 22 | *S. stroma* [LC038098] | 0.16 | 0.16 | 0.19 | 0.19 | 0.09 | 0.01 | 0.01 | 0.16 | 0.16 | 0.16 | 0.16 | 0.17 | 0.17 | 0.17 | 0.17 | 0.23 | 0.23 | 0.23 | 0.23 | 0.15 | 0.23 | | | |
| 23 | *S. vandenbrueli* [AB500178] | 0.11 | 0.11 | 0.21 | 0.21 | 0.13 | 0.16 | 0.16 | 0.12 | 0.12 | 0.12 | 0.12 | 0.12 | 0.12 | 0.12 | 0.12 | 0.22 | 0.22 | 0.22 | 0.22 | 0.14 | 0.22 | 0.16 | | |
| 24 | *Syphatineria* sp. [LC038099] | 0.27 | 0.27 | 0.30 | 0.30 | 0.26 | 0.28 | 0.28 | 0.27 | 0.27 | 0.27 | 0.27 | 0.27 | 0.27 | 0.27 | 0.27 | 0.29 | 0.29 | 0.30 | 0.30 | 0.26 | 0.29 | 0.28 | 0.28 | |
| 25 | *Aspiculuris tetraptera* [AB500179] | 0.33 | 0.33 | 0.35 | 0.35 | 0.30 | 0.30 | 0.30 | 0.32 | 0.32 | 0.32 | 0.32 | 0.34 | 0.33 | 0.33 | 0.33 | 0.35 | 0.35 | 0.35 | 0.35 | 0.32 | 0.32 | 0.31 | 0.32 | 0.35 |

* The number of base differences per site from between sequences are shown. The analysis involved 25 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 689 positions in the final dataset.

# Appendix 3. Geographical distribution of Syphaciinae

Geographical distribution of Syphaciinae (Oxyuridae) in the area from Malay Peninsula to Australia and their host genera.

| Syphaciinae species | Malay Peninsula | Kalimantan/ Borneo | Sumatra/ Java | Sulawesi | Maluku (Halmahera, Ambon) | Papua Indonesia/ Papua New Guinea |
|---|---|---|---|---|---|---|
| *Syphcia muris* | *Rattus, Sundamys, Leopoldamys* | *Niviventer* (?) | *Rattus* | *Rattus* | *Rattus* | |
| *S. pahangi* | *Chiropodomys* | | | | | |
| *S.* sp. 'Maxomys' | *Maxomys* (?) | | *Maxomys* | *Maxomys* | | |
| *S. sulawesiensis* | | | | *Rattus* | | |
| *S. rifaii* | | | | *Bunomys* | | |
| *S. taeromyos* | | | | *Taeromys* | | |
| *S. paruromyos* | | | | *Paruromys* | | |
| *S. kumis* | | | | *Eropeplus* | | |
| *S. yuniae* | | | | *Eropeplus* | | |
| *S. semiadii* | | | | | *Halmaheramys* | |
| *S. lorentzimyos* | | | | | | *Lorentzimys* |
| *S. malelonitenuis* | | | | | | *Lorentzimys* |
| *S. coccymyos* | | | | | | *Coccymys* |
| *S. longaecauda* | | | | | | *Melomys, Paramelomys* |
| | | | | | | *Uromys* |
| *S. australasiensis* | | | | | | *Rattus* |
| *S. darwini* | | | | | | *Melomys* |
| *S. boodjamullensis* | | | | | | |
| *S. brevicaudata* | | | | | | |
| *S. pseudomyos* | | | | | | |
| *S. helidonensis* | | | | | | |
| *S. abertoni* | | | | | | |
| *S. carnavorensis* | | | | | | |
| *S.* sp. 1 of W. & S. | | | | | | |
| *S.* sp. 2 of W. & S. | | | | | | |
| *S.* sp. 3 of W. & S. | | | | | | |
| *Pogonomicola rugala* | | | | | | *Pogonomys* |
| *Lorentzicola woolleyae* | | | | | | *Lorentzimys* |

# Appendix 4. Geographical distribution of Heligmonellidae

Geographical distribution of Heligmonellidae (Trichostrongyloidea) in the area from Malay Peninsula to Australia and their host genera.

| Heligmonellid species | Malay Peninsula | Kalimantan/ Borneo | Sumatra/ Java | Sulawesi | Maluku (Halmahera, Ambon) | Papua Indonesia/ Papua New Guinea |
|---|---|---|---|---|---|---|
| *Nippostrongylus brasiliensis* | *Rattus, Maxomys, Niviventer* | *Rattus* | *Rattus, Niviventer* | *Rattus* | *Rattus* | *Melomys* |
| *Nippostrongylus sembeli* | | | | *Rattus* | | *Melomys, Uromys* |
| *Nippostrongylus markaeniae* | | | | | *Rattus* | |
| *Nippostrongylus magnus* | | | | | | *Rattus* |
| *Nippostrongylus typicus* | | | | | | |
| *Nippostrongylus* sp. | | *Maxomys* | | | | |
| *Heligmonoides bulbosus* | *Maxomys* | | | | | |
| *Heligmonoides lanceolatus* | *Maxomys* | | | | | |
| *Heligmonoides mirzai* | | | | | | *Melomys* |
| *Malaistrongylys odontospicularis* | *Rattus, Maxomys Chiropodomys* | | | | | |
| *Paraheligmonelloides annandalei* | *Rattus, Sundamys* | | | | | |
| *Paraheligmonelloides triangulus* | *Leopoldamys , Maxomys, Chiropodomys* | | | | | |
| *Paraheligmonelloides rajah* | *Maxomys* | | | | | |
| *Paraheligmonelloides eropeplios* | | | | *Eropeplus* | | |
| *Paraheligmonelloides paruromyos* | | | | *Paruromys* | | |
| *Paraheligmonelloides amplicaudae* | | | | | | *Paramelomys* |
| *Paraheligmonelloides emisae* | | | | | | *Paramelomys* |
| *Paraheligmonelloides singawaensis* | | | | | | *Melomys, Paramelomys* |
| *Paraheligmonelloides* sp. | | | | | | *Chiruromys* |
| *Macrostrongylus ratti* | *Rattus, Maxomys, Leopoldomys* | | | | | |
| *Macrostrongylus ingens* | | | | | | *Melomys, Paramelomys, Uromys* |
| *Melomystrongylus sepikensis* | | | | | | *Melomys* |
| *Melomystrongylus somoroensis* | | | | | | *Paramelomys* |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Rattustrongylus odontoconus* | *Leopoldamys, Maxomy* | | | | | | | | |
| *Rattustrongylus rotundoconus* | *Leopoldamys, Maxomys* | | | | | | | | |
| *Sabanema sabana* | *Leopoldamys Rattus, Maxomys, Chiropodomys* | | | | | | | | |
| *Sabanema kepongi* | *Rattus, Leopoldamys, Chiropodomys* | | | | | | | | |
| *Sabanema montana* | *Maxomys* | | | | | | | | |
| *Sabanema longispicularis* | *Leopoldamys, Maxomys* | | | | | | | | |
| *Sabanema macrovulva* | *Leopoldamys* | | | | | | | | *Uromys* |
| *Calypsostrongylus malayensis* | *Rattus, Maxomys, Leopoldomys* | | | | | | | | |
| *Fissicauda callosciuri* | *Rattus, Sundamys, Maxomys, Callosciurus* | | | | | | | | |
| *Fissicauda brevispicula* | *Rattus, Sundamys, Maxomys, Callosciurus* | | | | | | | | |
| *Orientostrongylus tenorai* | *Rattus, Leopoldamys, Sundamys, Bandicota, Maxomys* | *Maxomys* (?) | *Rattus* | *Rattus, Maxomys, Eropeplus,* | *Rattus* (?) | | | | |
| *Orientostrongylus krishnansamy* | *Rattus, Maxomys, Iomys* | | | | | | | | |
| *Orientostrongylus siamensis* | *Rattus* | | | | | | | | |
| *Maxomystrongylus yasumai* | | *Maxomys, Rattus, Niviventer* | | | | | | | |
| *Maxomystrongylus musseri* | | | | *Maxomys, Eropeplus, Margaretamys* | | | | | |
| *Bunomystrongylus abadi* | | | | *Bunomys* | | | | | |
| *Bunomystrongylus miyagii* | | | | *Bunomys* | | | | | |

| | | | |
|---|---|---|---|
| *Odilia mamasaensis* | *Maxomys* | | |
| *Odilia maxomyos* | *Maxomys* | | |
| *Odilia moatensis* | *Rattus* | | |
| *Odilia sulawesiensis* | *Rattus* | | |
| *Odilia mackerasae* | | *Rattus* (?) | *Uromys, Abeoomelomys, Chiruromys Paramelomys, Parayhydromys, Melomys, Coccymys* |
| *Odilia mallomyos* | | | *Mallomys* |
| *Odilia similis* | | | *Melomys* |
| *Odilia uromyos* | | | *Uromys* |
| *Odilia carinatae* | | | *Uromys* |
| *Odilia imprexa* | | | *Uromys* |
| *Odilia wauensis* | | | *Lorentzimys* |
| *Odilia emanuelae* | | | *Hyomys, Pseudohydromys, Parahydromys, Mayermys, Rattus* |
| *Odilia mawsonae* | | | *Melomys* |
| *Odilia melomyos* | | | *Uromys, Melomys* |
| *Odilia bainae* | | | |
| *Odilia brachybursa* | | | |
| *Odilia polyrhabdonte* | | | |
| *Odilia praeputialis* | | | |
| *Odilia tasmaniensis* | | | |
| *Odilia dividua* | | | *Pagonomys* |
| *Hassanuddinia maxomyos* | *Maxomys, Eropeplus* | | |
| *Hassanuddinia chiruromyos* | | | *Chiruromys* |
| *Hasanuddinia pogonomyos* | | | *Pagonomys* |
| *Hassanuddinia* sp. | | | *Lorentzimys* |
| *Parasabanema szalayi* | | | *Paramelomys* |
| *Mawsonema mokwaensis* | | | *Paramelomys* |

| | |
|---|---|
| *Montistrongylys giluwensis* | *Coccymys* |
| *Montistrongylys ingati* | *Paramelomys* |
| *Montistrongylys karungi* | *Abeomelomys* |
| *Mammanidula melomyos* | |
| *Pogonomystrongylus domainses* | *Pogonomys* |

## Abstract

1) Murine rodents are of special interest due to the role as reservoir of many important parasitic nematodes for humans and livestock. For this reason, the study on parasitic nematodes of murines was carried out to prevent outbreak of infectious diseases especially nematodiasis. About 800 murines deposited in MZB were examined and published papers on nematodes in Indonesia were overviewed as baseline data for the present study. In total, 20 nematode species including a new genus and two new subgenera are newly recorded in the present study. The new taxa consist of *Musserakis sulawesiensis* from *Echiothrix centrosa* (Sulawesi) and seven new species of the genus *Syphacia* including two new subgenera, *Rumbaisyphacia* and *Segienamsyphacia*. A nematode species of Molineidae from *Paruromys dominator* (Sulawesi) is possibly represent a new genus and a new species. It was also discussed the role of *Syphacia* spp. as zoonotic agents. Furthermore, *Angiostrongylus cantonensis, A. malaysiensis, Cyclodonstomum purvisi* and *Pterygodermatities* sp. are also possible zoonotic agents. In total, 61 nematode taxa (46 known species and 15 other unknown species identified up to the generic level) including zoonotic agents were recorded. All nematodes studied were recorded from 38 Indonesian murine species including three species that were identified only to the generic level

2) The taxonomical and morphological studies on the genus *Syphacia* will become a baseline for further faunistic and/or biogeographical study, and also provide a quick diagnosis method. The descriptions of the studied *Syphacia* and a key to *Syphacia* species recorded in Indonesia and Australia are provided. Three subgenera have been hitherto recognized in the genus *Syphacia*, i.e., *Syphacia*, *Cricetoxyuris* and *Seuratoxyuris*. In this present study, two new subgenera from Sulawesi, i.e., *Rumbaisyphacia* and *Segienamsyphacia*, are added with a new species in each genus, i.e., *S.* (*R.*) *kumis* and *S.* (*Se.*) *yuniae*, respectively. Furthermore, this study also described five new species belonging to the subgenus *Syphacia*, viz., *S. rifaii*, *S. paruromyos*, *S. taeromyos, S. semiadii* and *S. maxomyos*. All of these species exhibited considerable diversity in morphology as confirmed by both light and scanning electron microscope studies. Hence, restricting to Indonesia, 10 species of *Syphacia* species have been recorded in total.

3) The species of the genus *Syphacia* are considered to have generally co-evolved with their rodent hosts. However, in Japan such an intimate relationship might be not so strict. Hence,

the present study determines a general trend of the relationships among Syphaciinae species, viz., *S. rifaii* from *Bunomys* spp., *S. muris* from *Rattus tanezumi*, and *Syphatineria* sp. from *Lariscus hosei*, obtained from Indonesia through partial sequences of the mitochondrial *Cox1* gene and 28S rDNA. The *Cox1* phylogram shows that *S. rifaii* is quite peculiar by having long genetic distance compared to the other studied species. It has an extraordinary long branch from the base of the tree in both long and short sequences analyzed with NJ and ML. The *Cox1* bootstrap values are generally high. In the NJ tree of 28S rDNA, *Syphacia* (*Seuratoxyuris*) *petrusewiczi* from the Japanese *Myodes* (syn. *Clethrionomys*) diverge from the subgenus *Syphacia* at the first node. However, in ML tree, *Syphatineria* sp. diverge at the first node, and make *S. petrusewiczi* in one clade with other *Syphacia* spp. *Syphacia rifaii* and *S. muris* are closed to each other in both NJ and ML trees. The results may reflect their host divergence history. Even in *S. muris*, the present isolates from Indonesia are much diverged from those in laboratory rats, both in *Cox1* and 28S rDNA. The ancestor of *S. muris* might be adapted to the ancestral *Rattus* in Asia, and then made dispersal to the surrounding areas, after then some of them were domesticated for laboratory use up to the present days. Probably, this history of *Rattus* is reflected in the divergence found in *S. muris*.

4) The species composition of *Syphacia* seems to be mosaic among the islands, especially in Wallacea. Based on the morphological characteristics of the cephalic ends, the species of the subgenus *Syphacia* are divided into three lineages with square (S), round (R) and laterally-elongated (LE) cephalic shapes. The LE type is considered primitive, and the S and R types are derived from the LE type. Based on the types of the cephalic shape, a dispersal scenario of the host-parasite relationships between murines and *Syphacia* is presented. The original dispersal was made from southeastern Asia not only to Wallacea and Papua/Australia, but also to Europe, North Africa, East-mid Asia and Japan, and finally North America by the LE type. Before the north-eastward movement, the R type diverged from the LE type, and the ancestral R and LE types invaded and colonized Wallacea. On the other hand, the LE, R and S types invaded Sahul. The origin of *S. semiadii*, parasitic in *Halmaheramys bokimekot* on Halmahera Island, seems to be extraordinary. The ancestor of *Halmaheramys* is suggested to have originated from Sundaland. However, *S. semiadii* has similar characters with some Sahulian *Syphacia*. Probably, a host-switching was occurred in Halmahera. Furthermore, a cosmopolitan species of the S type, *Syphacia muris*, invade everywhere with human commensal rats. Human commensal *Syphacia*, especially *S. obvelata* sometimes could infect human being, and experimental/pet murines. If the scenario presented here is correct, the

Wallace's line could be applied for endoparasites like *Syphacia* spp. as well, and the biogeographical approach could be regarded as one of the One Health model researches.