

A REVIEW OF THE GENUS *SYPHACIA* (NEMATODA: OXYURIDAE) FROM MURINE RODENTS IN SOUTHEAST ASIA TO AUSTRALIA WITH SPECIAL REFERENCES TO INDONESIA

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ABSTRACT

The pinworms of the genus *Syphacia* are of special interest because they have coevolutionary relationships with their murine rodent hosts. From Southeast Asia to Australia, 21 species in four subgenera have been recorded, two species of these are endemic to Sulawesi. Their biogeographical distribution and dispersal processes are discussed herein. 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 assumed to be primitive and the S and R types are derived from the LE type as shown by a molecular phylogeny based on 28S rDNA previously. This assumption was supported by the fact that the old endemics murines in the regions studied mostly harboured *Syphacia* with LE type. A hypothesis on the formation of the host-parasite relationships between murines and subgenus *Syphacia* in the areas is presented. A key to *Syphacia* species recorded is also provided.

Key words: Indonesia, murine rodents, Southeast Asia to Australia, *Syphacia*

INTRODUCTION

Nematodes of the genus *Syphacia* Seurat, 1916 (family Oxyuridae) are parasitic pinworms found in various muroid rodents (Hugot 1988). Their life cycle is typical of the oxyurids in that it lacks any period of exposure to environments outside the host. The simplicity of the life cycle is likely to provide less opportunity to acquire a new host compared to other parasites that require a long period in the external environment or in an intermediate host to become infective. Therefore, *Syphacia* nematodes are considered to have co-evolved with their hosts (Hugot 1988, 1990), although host switching events are also known (Dewi *et al.* 2014a, Weaver 2016). This study is a review for genus *Syphacia* in the area of Southeast Asia to Australia, with special references to Indonesia. Southeast Asia consists of two geographic regions: (a) mainland Southeast Asia (Indochina) comprising Vietnam, Laos, Cambodia, Thailand, Myanmar (Burma) and West Malaysia, and (b) maritime Southeast Asia comprising Indonesia East Malaysia, Singapore, Philippines, East Timor, Brunei, Cocos (Keeling) Islands, and Christmas Island. Except for the cosmopolitan species *S. muris*, which is known to infect several species of murines, *Syphacia* spp. in the areas from Southeast Asia to Australia are endemic species parasitic in endemic murines, suggesting co-speciation with hosts (Hugot & Quentin 1985, Hasegawa & Tarore 1996, Smales

2001, 2004, 2010, 2011, Weaver & Smales 2006, 2008, 2010, Dewi & Hasegawa 2010, 2014, Dewi *et al.* 2014a, b). Actually, the *Syphacia* spp. found in Indonesia seem to be specific to host species or genus (Hasegawa & Tarore, 1996, Dewi *et al.* 2010, 2014a, b, 2015a). This means that *Syphacia* nematodes could provide interesting clues to understand biogeographical formation of the area.

The genus *Syphacia* also could be zoonotic because a human case infested with *Syphacia obvelata* was reported in the Philippines (Riley 1919). More recently, Mahmoud *et al.* (2009) reported 25 human cases of *Syphacia* infection in Egypt. They found *S. muris*, *Syphacia* spp. and *Enterobius vermicularis*. Very curiously, only females were found among the worms identified as *Syphacia*, whereas all males observed were *E. vermicularis*. Judging from the photomicrographs presented, the identification may need further confirmation. *Syphacia* species are minute and resemble each other, strict taxonomical and morphological study on this nematode genus will become a baseline of an accurate diagnosis method.

In this paper, species of the genus *Syphacia* in the murines in the region ranging from Southeast Asian continent to Australia is reviewed from the biogeographical viewpoint. A hypothesis on the formation of the *Syphacia*-host murine relationships in this region is proposed based on the cephalic morphology and previous reports of molecular analysis of *Syphacia* and phylogeny of host murines. A key to subgenera and species of *Syphacia* in this region is also provided.

***Syphacia* spp. in Southeast Asia to Australia**

Based on the literature study, more than fifteen studies on murine nematodes of the genus *Syphacia* from Southeast Asia to Australia had been done, focusing on taxonomy with new species. Among the five subgenera hitherto recognised for this genus (Hugot 1988, Dewi *et al.* 2014), four subgenera have been reported from murines in the area *i.e.* *Syphacia (Seuratoxyuris)*, *Syphacia (Syphacia)*, *S. (Rumbaisyphacia)* and *S. (Segienamsyphacia)*. Occurrence records of *Syphacia* spp. from Southeast Asia to Australia are shown in Fig. 1. Indonesia is stretching between the Australian and Asian continental lands. It spans three major regions *i.e.* Sunda, Wallacea and Sahul. In the west, Sunda region includes Sumatra, Java, Kalimantan and the smaller surrounding islands, while Sahul region is part of the continental shelf of the Australian continent. Wallacea represents the biogeographical transitional zone between Sunda and Sahul. This zone covers multiple small islands between Wallace's line and Lydekker's line *i.e.* Sulawesi, North Maluku, Buru and Seram in Maluku, the Lesser Sunda Islands (with Sumba, Timor) and the islands in the Banda Sea.

Six endemic species of the subgenus *Syphacia* have been recorded from Indonesia: one species, *S. maxomyos*, from both Sunda (on Sumatra Island) and Wallacea (on Sulawesi island) regions; five species from Wallacea that comprised four species from Sulawesi: *S. paruromyos*,

S. rifaii, *S. sulawesiensis*, *S. taeromyos*; and one species from Halmahera Island: *S. semiadii* (Table 1) (Hasegawa & Tarore 1996, Dewi & Hasegawa 2010, 2014, Dewi *et al.* 2014a, 2015a, Smales, 2001). *Syphacia muris*, the cosmopolitan pinworm of *Rattus* spp. and *Niviventer* spp. also has been recorded from the islands Sumatra, Kalimantan, Java, Bawean, Sulawesi, Halmahera, Obi, Ambon and Flores (Hasegawa *et al.* 1992, Hasegawa & Syafruddin 1995, Hasegawa & Tarore 1996, Dewi & Purwaningsih 2013a,b, unpublished data). One species of the subgenus *Rumbaisyphacia*, *S. (R.) kumis*, and one species of the subgenus *Segienamsyphacia*, *S. (Se.) yuniae* were described from Sulawesi (Dewi *et al.* 2014b). Both subgenera are known only from Sulawesi. All of the hitherto known hosts of *Syphacia* in Indonesia were new endemics and recent arrivals.

From Sahul region (Australia and New Guinea) 12 *Syphacia* species, all belonging to the subgenus *Syphacia*, have been reported namely: *S. abertoni*, *S. australasiensis*, *S. boodjamullensis*, *S. brevicaudata*, *S. carnarvonensis*, *S. coccymyos*, *S. darwini*, *S. helidonensis*, *S. lorentzimyos*, *S. mamelontenuis*, *S. longaecauda* and *S. pseudomyos* (Table 1) (Hugot & Quentin 1985, Smales 2004, 2009, 2010, 2011, 2012, Weaver & Smales 2006, 2008, 2010). These species except *S. australasiensis* were parasitic in the old endemic murines (Weaver *et al.* 2016).

Adams (1933) reported “*Syphacia obvelata*“ from rats (no scientific names) collected from Taiping and Pahang, Malaysia. Later, Schacher & Chee-Hock (1960) examined 1,117 murine individuals and found *Syphacia* sp. from *Rattus norvegicus*, *R. diardi* (= *R. tanezumi*) and *R. exulans*. Furthermore, Ow-Yang (1971) examined about 2,500 individual rodents representing 15 species from various habitats in Malaysia. He described a new species *S. (Se.) pahangi* from *Chiropodomys gliroides* and found *S. muris* from *Rattus* spp. From the Philippines, “*S. obvelata*” was recorded from *Rattus norvegicus* of Manila and *R. rattus* of Leyte (Tubangui 1931, Fedoko 1999). However, the identification seems to be questionable because *S. obvelata* is a mouse pinworm. No endemic species of *Syphacia* has been known from the Philippines. From the Indochina, Yoshida *et al.* (1985) studied taxonomy of the genus *Syphacia* from 317 individuals belonging to six murine species in Thailand. They recorded *S. 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. maxomyos* from *Maxomys* spp. in Sulawesi and Sumatra (Dewi *et al.* 2015a). 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 they found “*Syphacia muris*” in 8.6% of murines, but without strict taxonomical consideration. 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, the so-called

“*S. muris*” by Pakdeenarong *et al.* (2013) might contain multiple species because of the host specificity of *Syphacia*. Moreover, their “*S. obvelata*” is also questionable because *Syphacia ohtaorum* Hasegawa, 1991 was known from *M. caroli* (Hasegawa 1991). Unfortunately, their report lacked taxonomical and morphological data.

Table 1. Host-*Syphacia* associations from Southeast Asia to Australia, except *S. muris* as cosmopolitan species

<i>Syphacia</i> species	Host rodent	References
Malay Peninsula		
<i>S. (Se.) pahangi</i>	<i>Chiropodomys gliroides</i>	Ow-Yang 1971
<i>S. (S.) obvelata</i> ?	Rats (no scientific name), <i>Rattus</i> spp.	Adams 1933, Tubangui, 1931, Fedoko, 1999
<i>Syphacia</i> sp.	<i>Rattus</i> spp.	Schacher & Chee-Hock 1960, Ow-Yang 1971
	<i>Maxomys surifer</i>	Yoshida <i>et al.</i> 1985
Sunda		
<i>S. (S.) maxomyos</i>	<i>Maxomys whiteheadi</i>	Dewi <i>et al.</i> 2015
Wallacea (Sulawesi)		
<i>S. (S.) maxomyos</i>	<i>Maxomys musschenbroekii</i>	Dewi <i>et al.</i> 2015
<i>S. (S.) paruromyos</i>	<i>Paruromys dominator</i>	Dewi & Hasegawa 2014
<i>S. (S.) rifaii</i>	<i>Bunomys</i> spp.	Dewi & Hasegawa 2010
<i>S. (S.) sulawesiensis</i>	<i>Rattus xanthurus</i>	Hasegawa & Tarore 1996
<i>S. (S.) taeromyos</i>	<i>Taeromys celebensis</i>	Dewi & Hasegawa 2014
<i>S. (R.) kumis</i>	<i>Eropeplus canus</i>	
<i>S. (Se.) yuniae</i>	<i>Eropeplus canus</i>	Dewi <i>et al.</i> 2014b
(Halmahera)		
<i>S. (S.) semiadii</i>	<i>Halmaheramys bokimekot</i>	Dewi <i>et al.</i> 2014a
Sahul		
<i>S. (S.) abertoni</i>	<i>Zyomys argurus</i>	Weaver & Smales 2006
<i>S. (S.) australasiensis</i>	<i>Rattus leucopus</i>	Smales 2004
<i>S. (S.) boodjamullensis</i>	<i>Zyomys argurus</i>	Weaver & Smales 2010
<i>S. (S.) brevicaudata</i>	<i>Pseudomys desertor</i>	Weaver & Smales 2008
<i>S. (S.) carnarvonensis</i>	<i>Pseudomys delicatus</i>	Weaver & Smales 2010
<i>S. (S.) coccymyos</i>	<i>Coccymys ruemmleri</i>	Smales 2011
<i>S. (S.) darwini</i>	<i>Melomys lutillus</i>	Hugot & Quentin 1985
<i>S. (S.) helidonensis</i>	<i>Pseudomys gracilicaudatus</i>	Weaver & Smales 2010
<i>S. (S.) lorentzimyos</i>	<i>Lorentzimys nouhuysi</i>	Smales 2010
<i>S. (S.) mamelontenuis</i>	<i>Lorentzimys nouhuysi</i>	Smales 2010
<i>S. (S.) pseudomyos</i>	<i>Pseudomys hermannsburgensis</i>	Weaver & Smales 2008
<i>S. (S.) longaecauda</i>	<i>Melomys monktoni</i>	Smales 2001

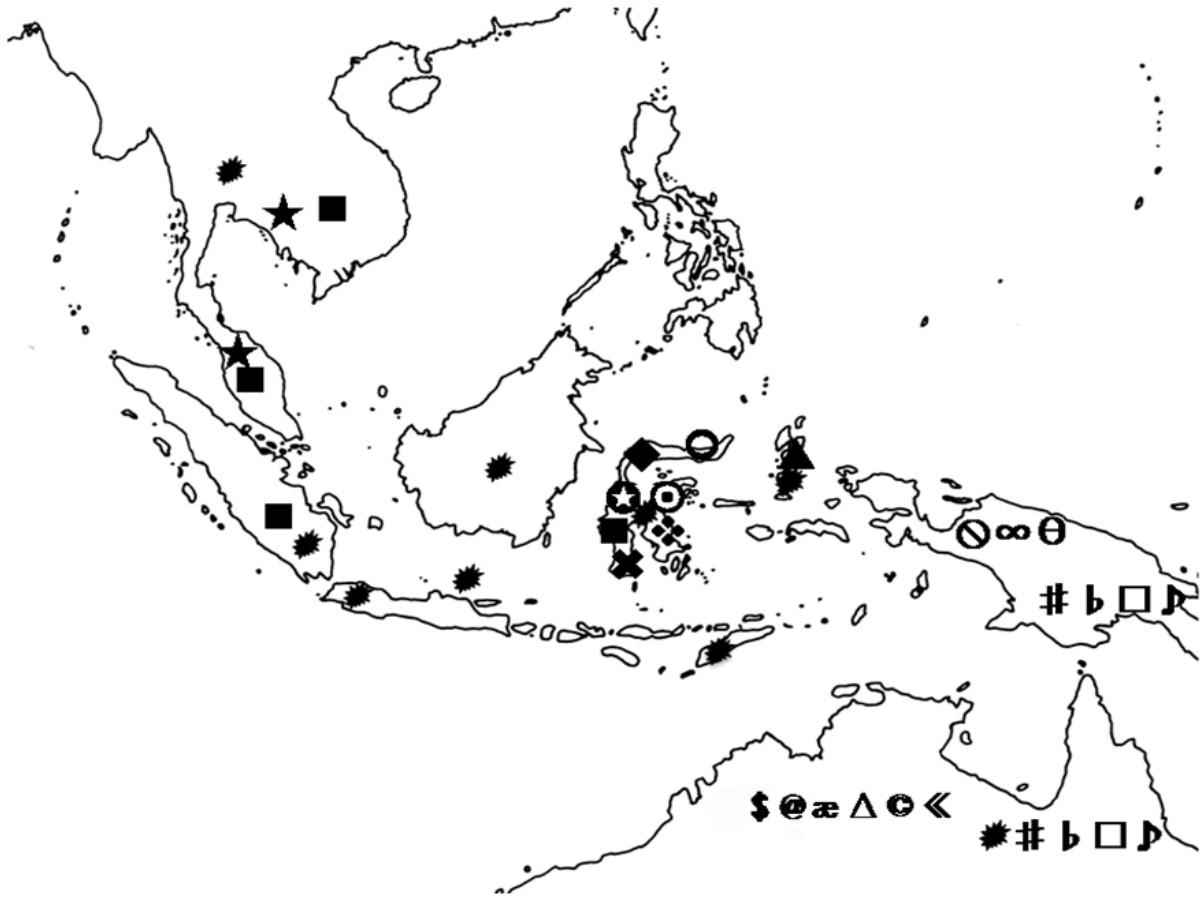


Figure 1. Occurrence records of *Syphacia* spp. from Southeast Asia to Australia. Black marks showing locality of each *Syphacia*.

★ : *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*, x : *S. (S.) lorentzimyos*, ∞ : *S. (S.) mamelonitenuis*, ⊙ : *S. (S.) coccymyos*, \$: *S. (S.) boodjamullensis*, @ : *S. (S.) brevicaudata*, æ : *S. (S.) pseudomyos*, Δ : *S. (S.) helidonensis*, © : *S. (S.) abertoni*, « : *S. (S.) carnayonensis*, ‡ : *S. (S.) longaecauda*, † : *S. (S.) australasiensis*, ♪ : *S. (S.) darwini*, * : *S. (S.) muris*.

Morpho-phylogenetic relationship in the subgenus *Syphacia* and their evolution

The systematic value of the cephalic structures was demonstrated by Quentin (1971). Among the members of the genus *Syphacia*, three distinct morphological types of the cephalic end are recognised, especially in the subgenus *Syphacia* as shown in Fig. 2; namely, round (R), square (S) and laterally-elongated (LE) types. These cephalic shape types and geographical distributions have interesting relationships: S type cephalic end is rare, being found only in the cosmopolitan *S. muris* of *Rattus* and in *S. australasiensis* from the new endemic *Rattus* of Sahul; R type is found in most of representatives of the Wallacean new endemic species and some of Sahul old endemic species; LE type is shared by one species in *Maxomys*-parasitic species in Sunda and Wallacea and most species in the old endemic murines of Sahul (Hugot & Quentin 1985, Smales 2001, 2004, 2009, 2010, 2011, 2012, Hasegawa & Tarore 1996, Weaver & Smales 2006, 2008, 2010, Dewi & Hasegawa 2010, 2014, Dewi *et al.* 2015a, Dewi *et al.* 2014a, 2015a).

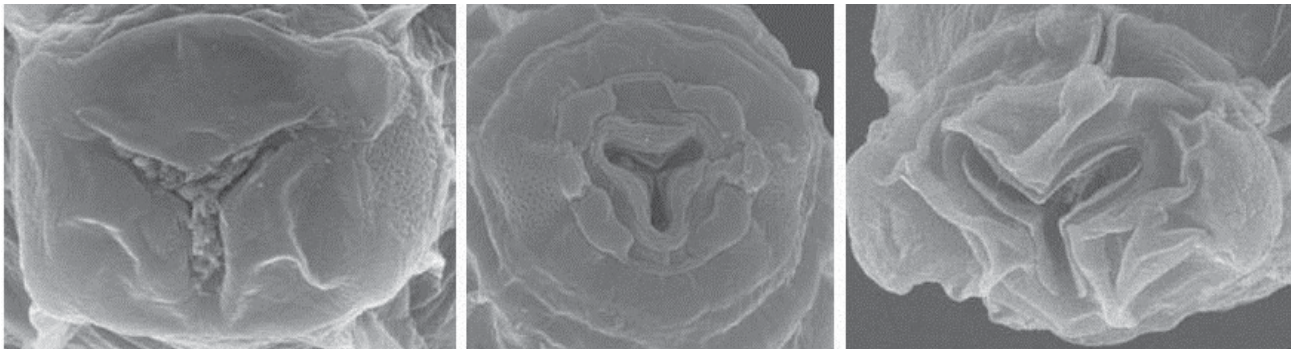


Figure 2. SEM photos of the cephalic ends of *Syphacia* spp. showing square (S), round (R) and laterally-elongated (LE) types (from left to right). Left: *S. muris* from *Niviventer cremoniventer* (Dewi, unpublished); middle: *S. rifaii* from *Bunomys penitus* (Dewi & Hasegawa 2010); right: *Syphacia maxomyos* from *Maxomys whiteheadi* (Dewi *et al.* 2015a).

In the evolutionary trend of the morphological characters in *Syphacia* or Oxyuridae, R type has been believed to be primitive because it is the common morphology of more distantly related pinworms found in squirrels (Rodentia: Sciuridae) (Quentin 1971, Hugot 1988). However, this idea should be applicable only for early phase of evolution of Syphaciinae. Among the members of *Syphacia*, LE type head is predominant, being known in the species of subgenera *Cricetoxyrus*, *Seuratoxyrus* and *Syphacia* from the Indo-Australian archipelago, the Holarctic region, Africa and the New World (Quentin 1971, Hugot & Quentin 1985, Hugot 1988). It is notable that LE type head is found in the *Syphacia* (*S.*) spp. of the old endemics murines of Sahul (Fig. 3). Therefore, LE type seems to be an ancestral form in the evolution of *Syphacia*, and R and S type heads are thus regarded as derived character. This assumption was supported by molecular phylogeny of *Syphacia* spp. based on partial 28S rDNA (Dewi *et al.* 2015b).

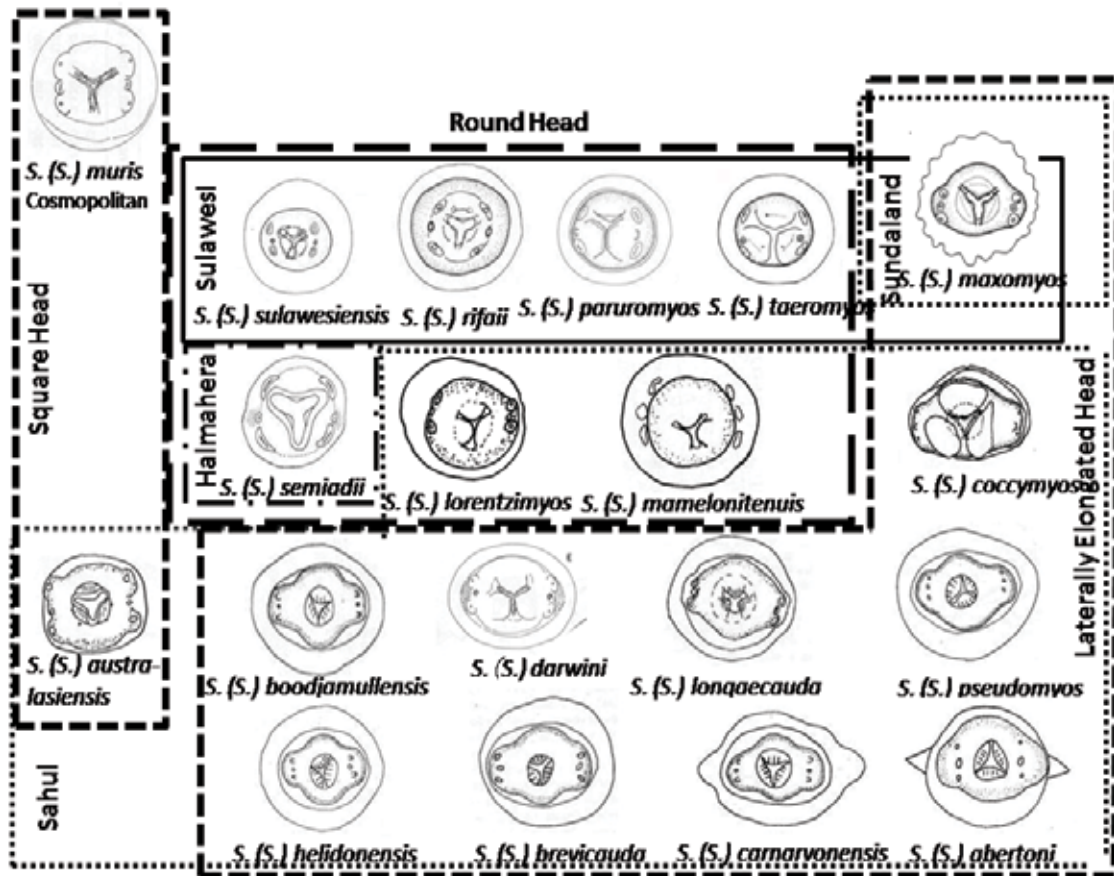


Figure 3. Cephalic shape (en-face view) of *Syphacia* (*Syphacia*) spp. distributed in the area Malay Peninsula/ Thailand to Australia. Cephalic plate shape is divided into 3 types, square, round, and laterally-elongated. Thick lines surround each type of the cephalic shape and thin lines surrounds species in the geographical distributions, Sunda, Sulawesi and Sahul.

When the murines adapted to and speciated in their new insular environments, some of their host-specific nematodes might have become extinct, whereas the others might co-evolve with their hosts or be shifted (switched) to a new host (Warner 1998). In the latter two cases, for example in the genus *Syphacia*, each nematode species underwent speciation in new environment, finally becoming morphologically distinct from the original species. This could be the beginning of a new evolutionary lineage. It is unknown how frequently host-switching occurred in the formation of the parasite-host relationships during the evolution of *Syphacia*. Based on molecular phylogeny of mtDNA *Cox1* and 28S rDNA sequences, Okamoto *et al.* (2007, 2009) suggested that co-evolutionary relationship of *Syphacia* is not so strict but host switching occurred frequently. They found that *Apodemus*-parasitic species did not form their own clade but scattered in different clades. However, they did not pay enough attention to the substantial morphological difference of one species, *S. frederici*, from other two species, *S. agraria* and *S. emileromani*. Later, Dewi *et al.* (2015b), based on mtDNA *Cox1* and 28S rDNA sequence analyses, demonstrated co-evolutionary relationship among *S. agraria*, *S. emileromani* and *S. stroma*, all parasitic in *Apodemus*.

Recently, Weaver *et al.* (2016) made phylogenetic analysis on *Syphacia* species in the region from Indonesia to Australia. They used cladistic analysis using TNT program based on

morphological characters, and found that species of *Syphacia* had close host–parasite relationships but also pointed out evidence for ecological fitting/host switching events. They suggested that murines migrated with *Syphacia* between Sulawesi-Australia at least three times during the course of evolution. However, Sulawesi murine fauna has no Australian-Papua New Guinean element (see Fabre *et al.* 2013). Only one Moluccan endemic rat, *Rattus morotaiensis*, has close relationship with those in Sahul (Fabre *et al.* 2013). It is therefore considered that migration of murines with pinworms between Sulawesi and Sahul was actually impossible. Weaver *et al.* (2016) used *S. muris* as an outgroup in their analysis. This assignment is also questionable because the hosts of *S. muris* seem to be of rather recent origin than the old endemic hosts of *Syphacia* in Sahul, and this nematode gained worldwide distribution by artificial dispersal of the commensal rats. According to the phylogenetic analysis based on mtDNA *CoxI* and 28S rDNA nucleotide sequences, *S. muris* and *S. rifaii* form a clade (Dewi *et al.* 2015b).

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

Based on the above hypothesis of the phylogeny of the cephalic morphology of *Syphacia* spp., the formation of their host-parasite relationships in the area from Southeast Asia to Australia could be discussed as follows.

Host origin; Ancestor of the subfamily Murinae is suggested to have originated in Asia, and dispersal from Sundaland to Sulawesi and Sahul occurred multiple times between the late Miocene and the Plio-Pleistocene (Fabre *et al.* 2013) (Fig. 4). For murines, the sea level is a major factor affecting their dispersal (Fabre *et al.* 2013). Certainly, their dispersal was accompanied by their parasitic nematodes.

Overview of the world distribution; The host-parasite relationship between the murines and subgenus *Syphacia* seems to be as follows: at first, an ancestral species of *Syphacia* with LE type head (*Syphacia* LE) parasitizes the ancestral murine. The ancestral murine/*Syphacia* dispersed from Sundaland to Wallacea, and 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 murines of Rattini and Hydromyini. Almost simultaneously, the species also invaded 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 species 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* (Fig. 5). *Syphacia obvelata* belonging to the LE type head group became cosmopolitan with commensal *Mus* spp., and its habitat close to humans might cause zoonotic parasitism.

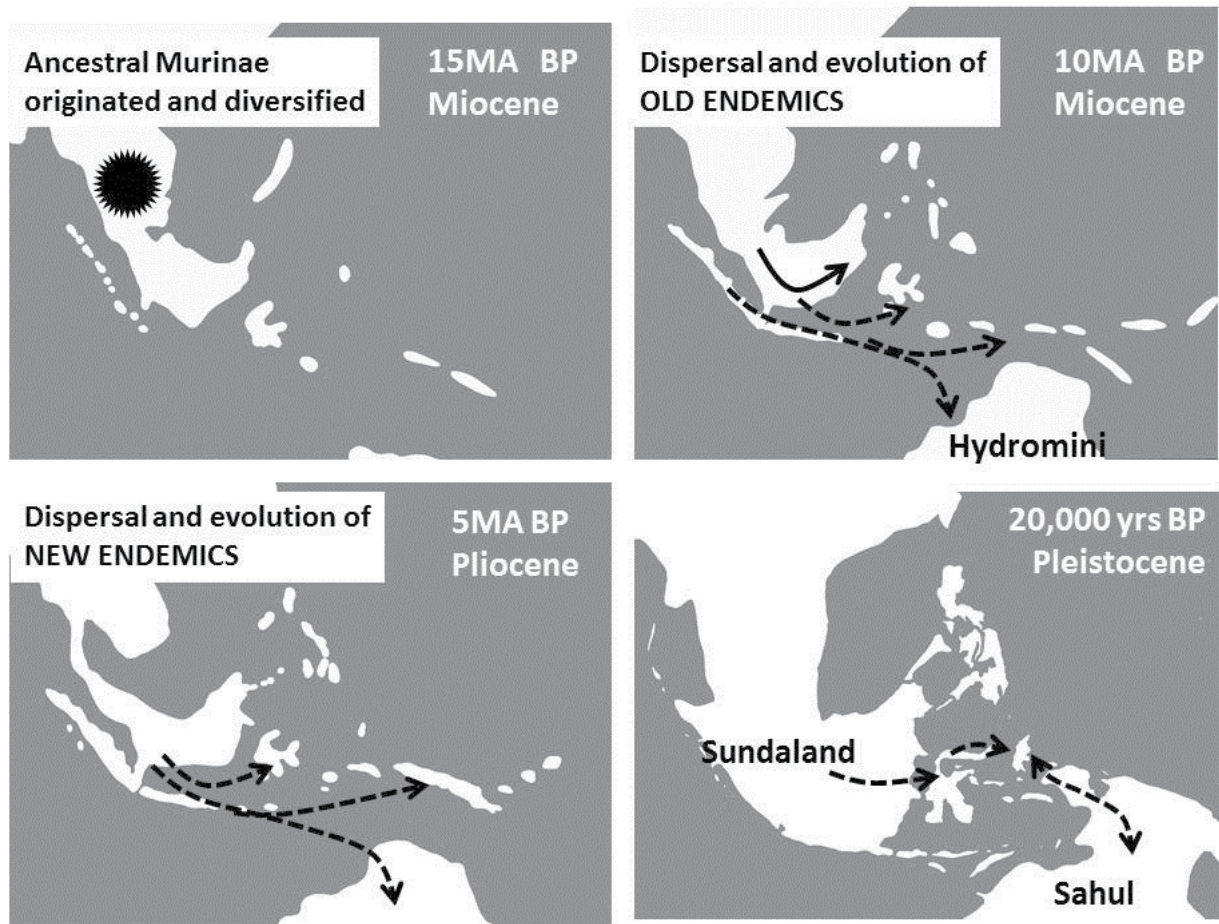



Figure 4. History of the origin of the Murinae based on Stelbrink *et al.* (2012) and Fabre *et al.* (2013);  : Hypothetical ancestor of the Murinae; dotted arrows: dispersal routes; MA: million years ago.

Indo-Australian Archipelago; Before the eastward invasion events, the speciation of *Syphacia* with R type head (*Syphacia* R) might have occurred from *Syphacia* LE. The ancestral *Syphacia* R was introduced with host murine dispersal to Wallacea, especially Sulawesi, which is the island with extremely high degree of endemism. Subsequently, the *Syphacia* R diversified with the evolution of their hosts. However, only one species *Syphacia* LE occurs in Sulawesi (*S. maxomys* from *Maxomys*). Because this species also occurs in *Maxomys* spp. of Sumatra and Asia continent, it could be regarded as an example of dispersal from Sunda to Wallacea with host murines.

On the other hand, the LE, R and S lineages of *Syphacia* invaded Sahul, and now many endemic *Syphacia* LE, two R and one S species are known in Australia and New Guinea (see Fig. 3). The Sahulian endemic *Syphacia* R species, which occur on New Guinea, have remarkable characteristics of small or absent of lateral alae in both sexes (Smales 2010). Meanwhile, *Syphacia* R species of Sulawesi have large lateral alae at least in one sex (Hasegawa & Tarore 1997, Dewi & Hasegawa 2010, 2014, Dewi *et al.* 2014, a,b). 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 two lineages, but also to additional lineages, that were formed during colonisation on this island.

However, on Halmahera Island an extraordinary event seemed to have occurred. The *Syphacia* R species, *S. semiadii* parasitises *Halmaheramys* and the species lacks lateral alae in both sexes (the character that is similar to *Syphacia* from Sahul) (Dewi *et al.* 2014a). 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, ancestral *S. semiadii* presumably invaded from Sahul into Halmahera Island with a Sahul origin murine, and thereafter the pinworm shifted to (ancestral) *Halmaheramys* and coevolved on the island, though the ancestral murines that 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.

A similar event of 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 species of *Syphacia* with type S head (*Syphacia* S) diversified from *Syphacia* LE, one endemic species, *S. australasiensis*, in Sahul (Australia) and common species, *S. muris*, occurred there. Since end of the Pleistocene, human commensal rats have continued to invade everywhere with human activities, making *S. muris* as a cosmopolitan species.

The above hypothesis on the evolutionary process of *Syphacia* was presented based on morphological consideration of the cephalic shape. Such a hypothesis should be tested by molecular evidence. Our preliminary trial of DNA sequence analysis of 28S rDNA and mtDNA *CoxI* has suggested that *S. rifaii* (R type) and *S. muris* (S type) form a clade, differing from those of LE type species (Dewi *et al.* 2015b). Unfortunately, only a few species from the subjected areas have been analyzed yet. Further sequencing of other representatives of *Syphacia* is necessary to prove the evolutionary history of this genus in Indonesia and the neighbouring regions.

Besides the subgenus *Syphacia*, two subgenera have been described from Wallacea: *Rumbaisyphacia* and *Segienamsyphacia* (Dewi *et al.* 2014). They have been found only from *Eropeplus canus*, a monotypic endemic rat of Sulawesi, and supposed to have co-evolved

with *Eropeplus*. Unfortunately, positive molecular data of the new subgenera could not be obtained because of inadequate fixation of the worms in the 1990's. Moreover, the molecular phylogenetic relationship of host *Eropeplus* with other murines also remains unresolved (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 & Newcomb 1983, Musser 1987).

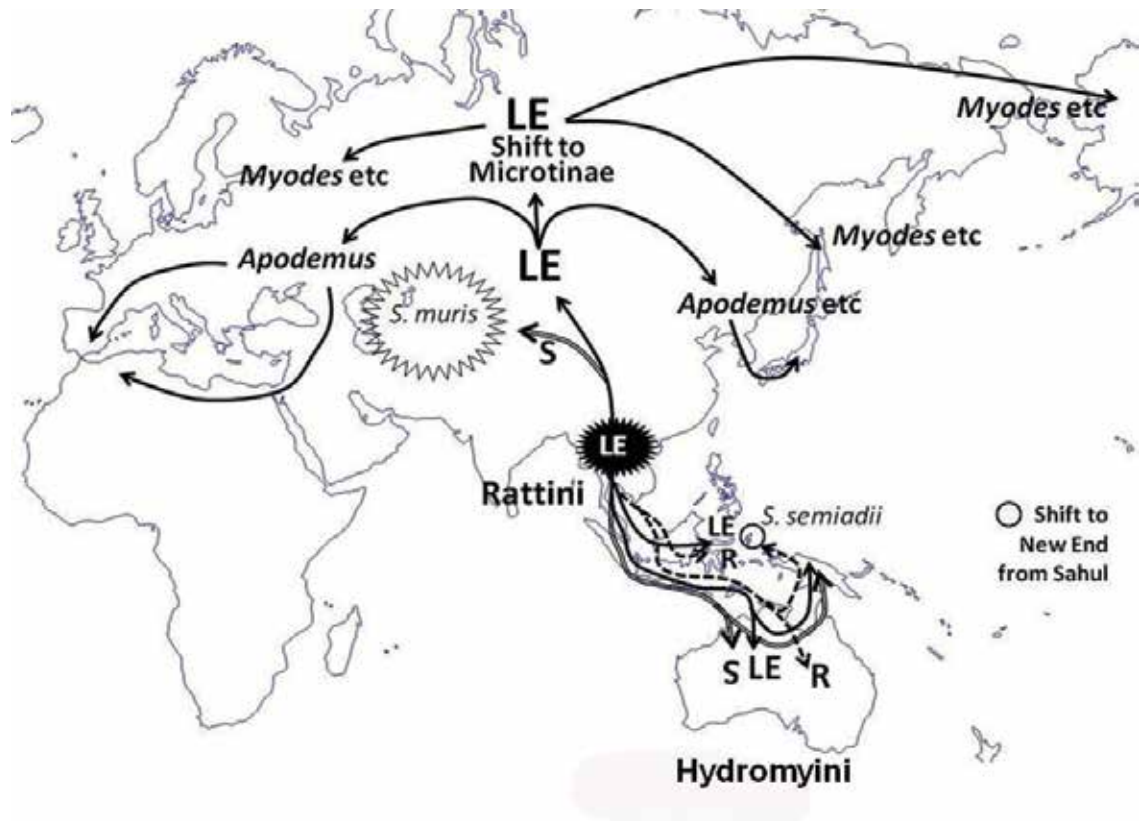


Figure 5. Summary of hypothetical dispersal events of the subgenus *Syphacia*. Solid, broken and double lines indicating dispersal routes of LE, R and S cephalic types, respectively.



: Hypothetical ancestor of the subgenus *Syphacia*, which might belong to LE lineage;

Myodes etc.: Microtinae occurs in the Holarctic 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.

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



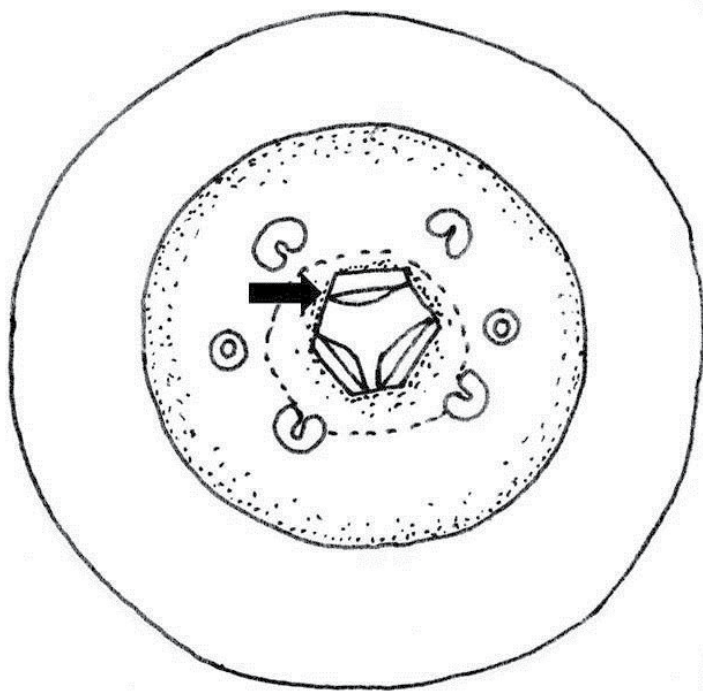
: Dispersal of *S. muris* with commensal *Rattus* spp. and *Niviventer* spp. *Syphacia obvelata* belonging to the LE is also cosmopolitan with *Mus* spp., but not included here.

Key to species of *Syphacia* in Malay Peninsula/ Thailand to Australia (revised after Weaver & Smales 2010; Dewi *et al.* 2014)

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 & Smales 2010. Herein, an emended key to 22 species in three subgenera of *Syphacia* distributed from the Malay Peninsula/ Thailand to Australia is proposed. In this key, the three undetermined species of *Syphacia* by Weaver & Smales 2010 are not included because morphology of males remains unknown.

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

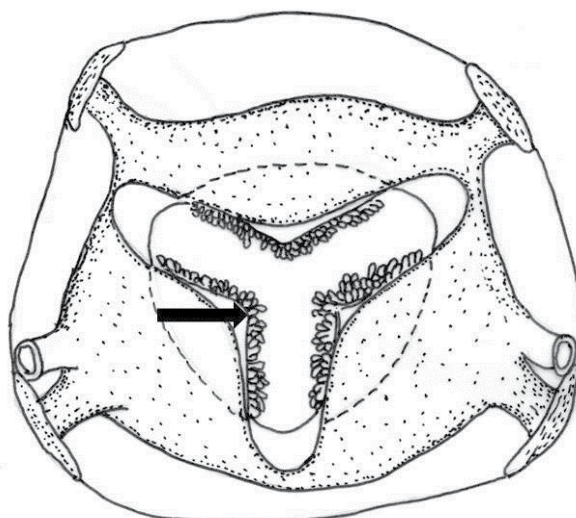
One known species *Syphacia* (*Segienamsyphacia*) *yuniae* (Host: *Eropeplus*; Locality: Sulawesi)



Female cephalic end of *Syphacia yuniae*
(Redrawn after Dewi, Hasegawa & Asakawa, 2014)

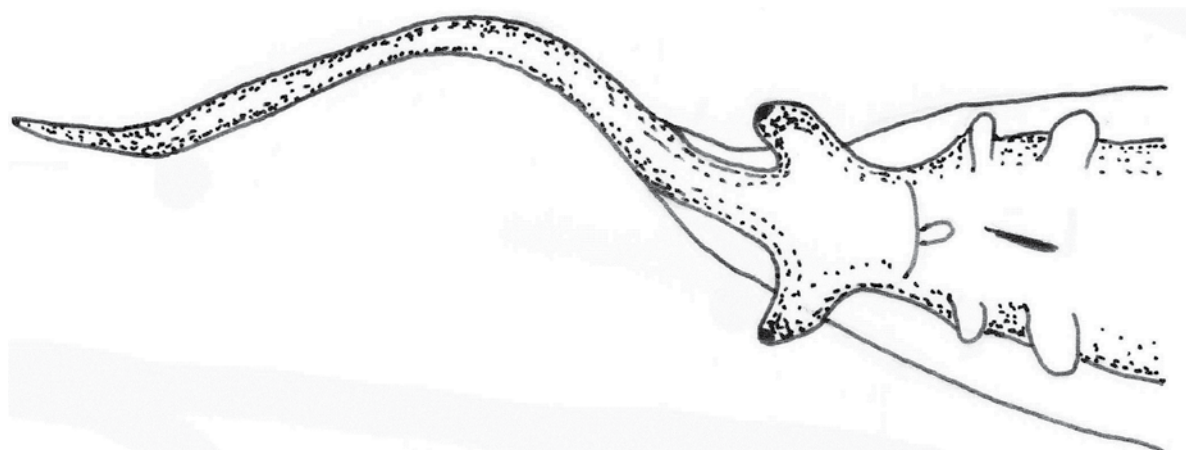
- Oral aperture not hexagonal in both sexes B

- B. – Anterior margin of pharynx setiferous.....*Syphacia* (*Rumbaisyphacia*)
 One known species *Syphacia* (*Rumbaisyphacia*) *kumis* (Host: *Eropeplus*; Locality: Sulawesi)

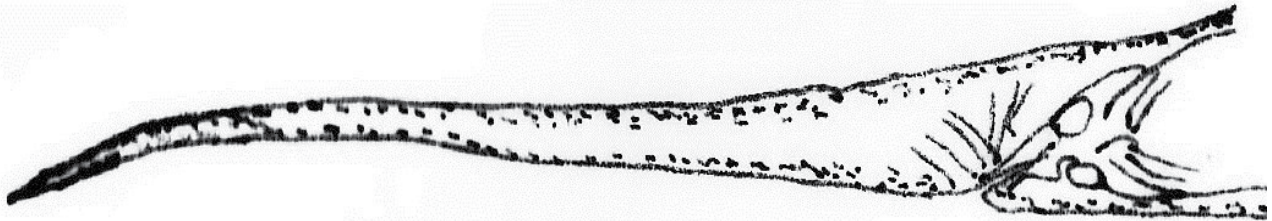


Cephalic end of *Syphacia* (*Rumbaisyphacia*) *kumis*
 (Redrawn after Dewi, Hasegawa & Asakawa 2014)

- Anterior margin of pharynx without setaeC
- 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)



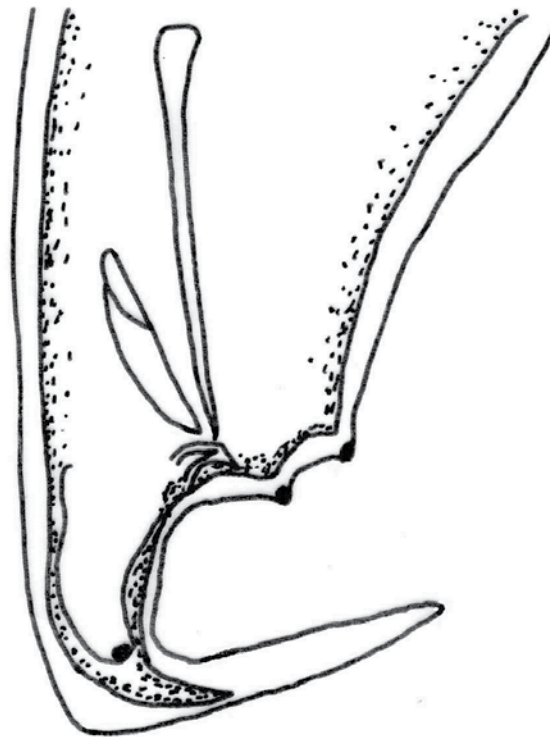
Male tail of *Syphacia longaecauda*
 (Redrawn after Smales 2001)



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

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

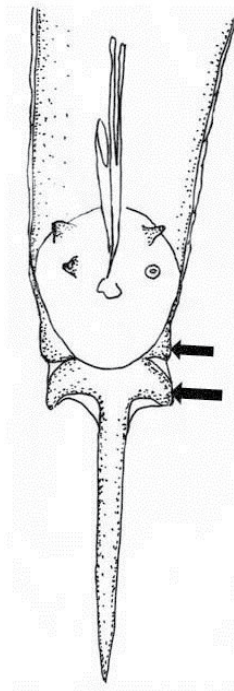
4. - Male spicule length >75; female tail length >580; eggs large, >125 long
.....*Syphacia boodjamullensis* (*Zyzomys*; Australia)



Male tail of *Syphacia boodjamullensis*.
(Redrawn after Weaver & Smales 2010)

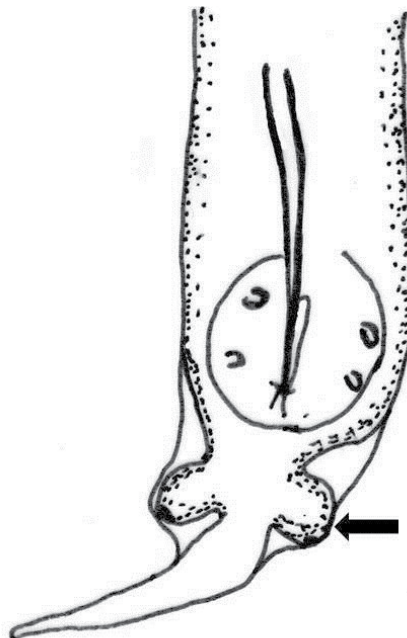
- Male spicule length <70; female tail length <580; eggs \leq 125 long5

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



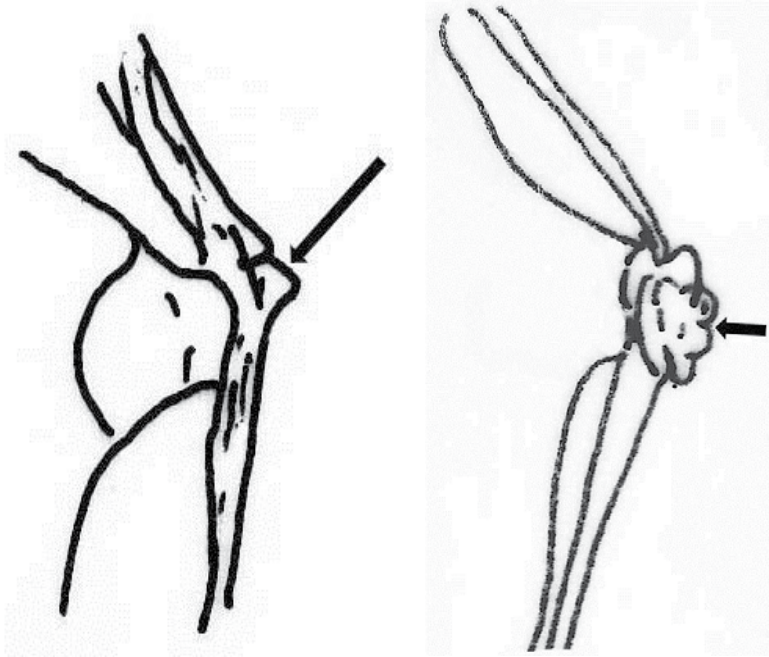
Male tail of *Syphacia brevicaudata*
(Redrawn after Weaver & Smales 2008)

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



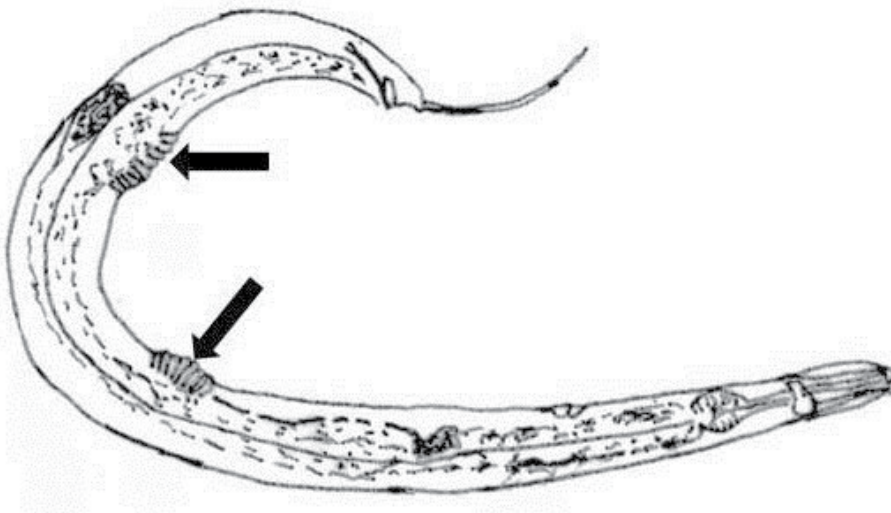
Male tail of *Syphacia pseudomyos*
(Redrawn after Weaver & Smales 2008)

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



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

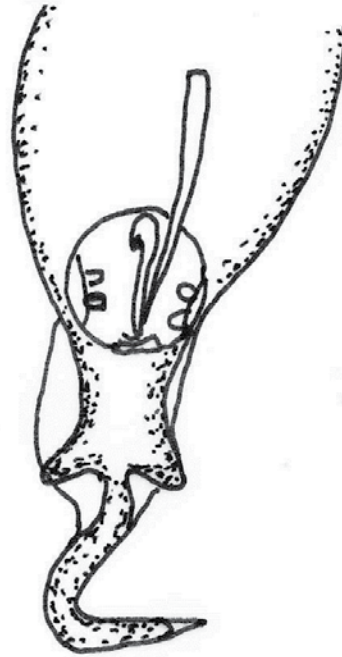
- Only lateral or cervical alae present.....7
- 7. - Lateral alae present; cervical alae absent.....8
- Cervical alae present; lateral alae absent.....10
- 8. - Male with two mamelons..... *Syphacia darwini* (*Melomys*; Australia)



Male of *Syphacia darwini*
(Redrawn after Hugot & Quentin 1985)

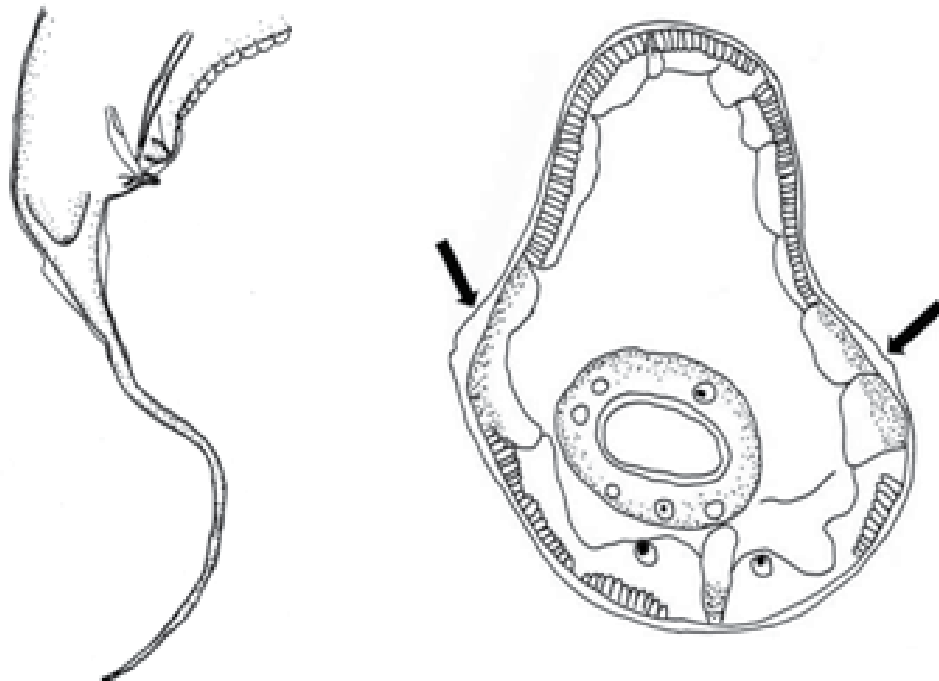
- Male with three mamelons 9

9. - Lateral alae present in both sexes; male tail length <150; eggs >100 long*Syphacia helidonensis* (*Pseudomys*; Australia)



Male tail of *Syphacia helidonensis*
(Redrawn after Weaver & 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 (cross section) in male of *Syphacia maxomyos*
(Redrawn after Dewi *et al.* 2015a)

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



Male tail of *Syphacia abertoni*
(Redrawn after Weaver & Smales 2006)

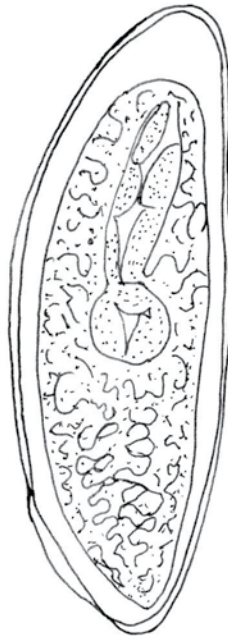
- Cervical alae narrow; male tail length <100 ; spicule length ≥ 60 ; egg length >100
.....*Syphacia carnarvonensis* (*Pseudomys*; Australia)



Male tail of *Syphacia carnarvonensis*
(Redrawn after Weaver & Smales 2010)

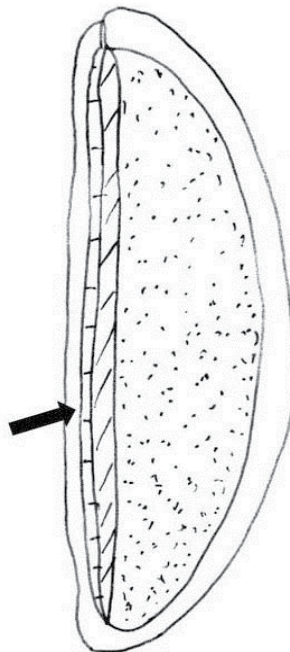
- 11. - Cephalic plate square.....12
- Cephalic plate round.....13

- 12. - Eggs without longitudinal ridge; spicule length <60.....
 *Syphacia muris* (*Rattus*, *Niviventer*; cosmopolitan)



Egg of *Syphacia muris*
(Redrawn after Hugot & Quentin 1985)

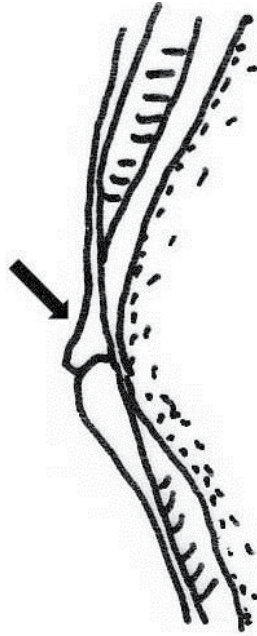
- Eggs with longitudinal ridge; spicule length >60.....
 *Syphacia australasiensis* (*Rattus*; Papua New Guinea and Australia)



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

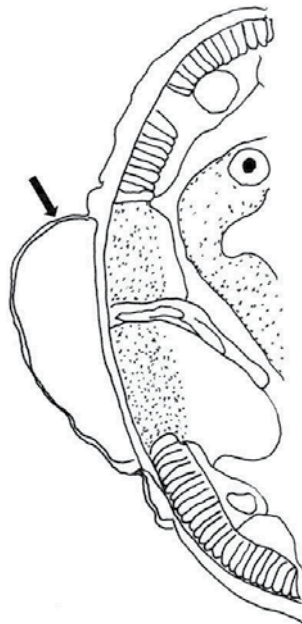
- 13. - Lateral alae present.....14
- Lateral alae absent.....18

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



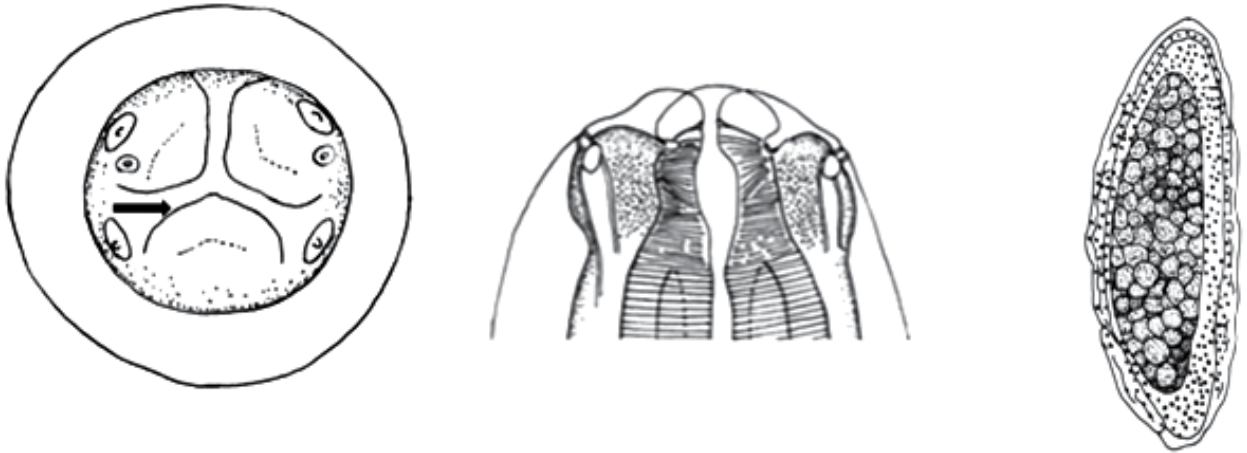
Small lateral alae of *Syphacia lorentzymys*
(Redrawn after Smales 2010)

- Lateral alae large.....15



Large lateral alae (in *Syphacia paruromyos*)
(Redrawn after Dewi & Hasegawa 2014)

- 15 - Lateral alae present in both sexes16
 - Lateral alae present only in male17
16. - Lips protruded prominently; eggs with uneven shell.....
*Syphacia taeromyos* (*Taeromys*; Sulawesi)



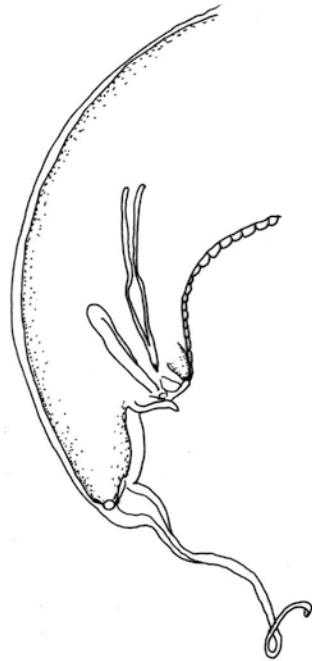
Cephalic end and egg of *Syphacia taeromyos*
 (after Dewi & Hasegawa 2014)

- Lips not protruded prominently; eggs with even shell.....
*Syphacia sulawesiensis* (*Rattus*; Sulawesi)



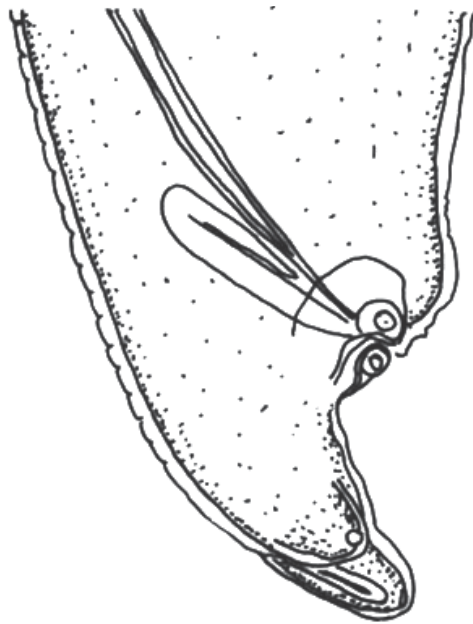
Cephalic end and egg of *Syphacia sulawesiensis*.
 (Redrawn after Hasegawa & Tarore 1996)

17. - Male tail long with whip like appendages.....
.....*Syphacia paruomyos* (*Paruromys*; Sulawesi)



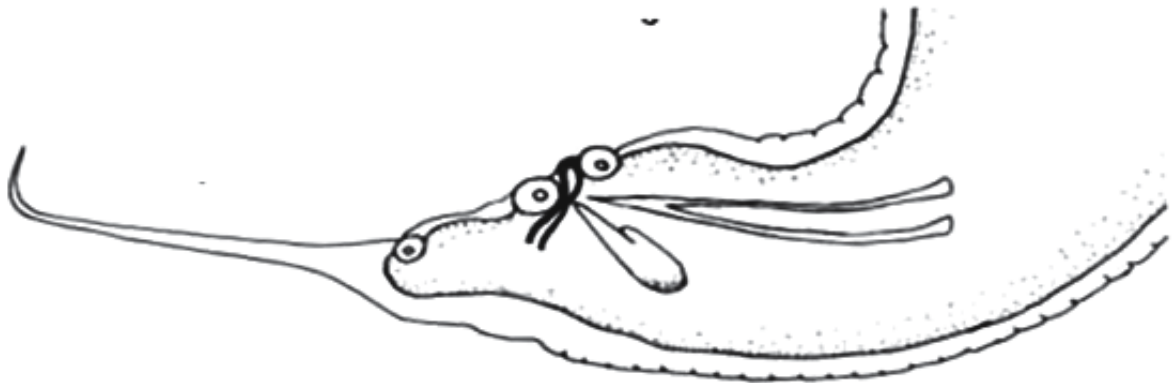
Posterior portion of *Syphacia paruomyos*
(Redrawn after Dewi & Hasegawa 2014)

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



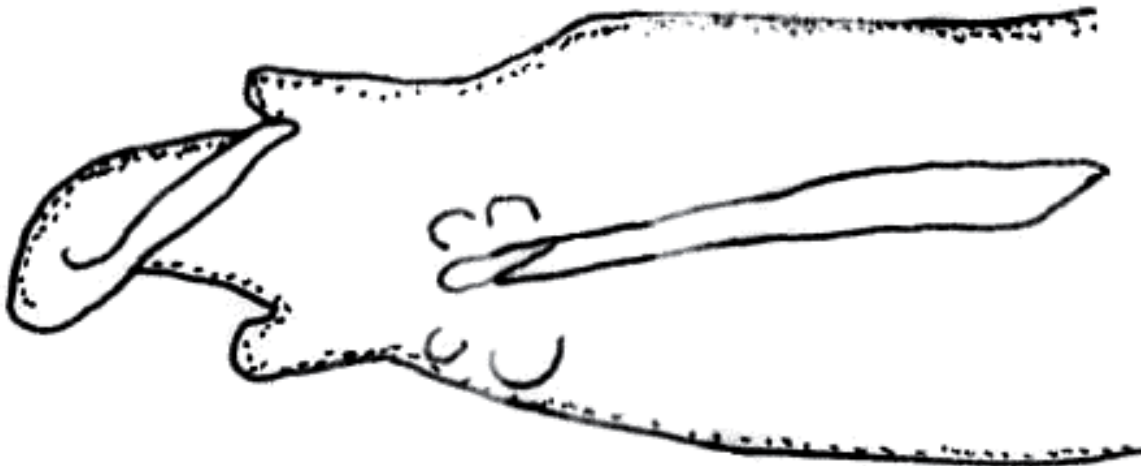
Posterior portion of *Syphacia rifaii*
(Redrawn after Dewi & Hasegawa 2014)

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



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

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



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

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