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Musserakis sulawesiensis gen. et sp. n. (Nematoda: Heterakidae) collected from *Echiothrix centrosa* (Rodentia: Muridae), an old endemic rat of Sulawesi, Indonesia

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Abstract

Musserakis sulawesiensis **gen. et sp. n.** (Nematoda: Heterakidae) is described from the large-bodied shrew rat, *Echiothrix centrosa*, one of the old endemic rats of Sulawesi, Indonesia. *Musserakis* is readily distinguished from other heterakid genera by having non-recurrent and non-anastomosing cephalic cordons, by lacking papillae between papillae groups around precloacal sucker and cloacal aperture and by lacking teeth in the pharyngeal portion. The spicules are equal but with marked dimorphism among individuals. Heterakids collected from other old endemic murids examined, i.e., *Crunomys celebensis*, *Tateomys macrocercus* and *Tateomys rhinogradoides*, and the new endemic rats of Sulawesi, were *Heterakis spumosa* Schneider, 1866, a cosmopolitan nematode of various murids. It is suggested that *M. sulawesiensis* is specific to *Echiothrix*.

Key words: *Musserakis* **gen. et sp. nov.**, Heterakidae, Nematoda, *Echiothrix*, old endemic murids, Sulawesi, Indonesia, zoogeography

Introduction

Sulawesi Island, Indonesia, is in a famous transitional area from Oriental to Australian bioregions. Numerous species of endemic murines reside on this island. They have been classified as new endemic and old endemic groups. Some helminthological studies have been done on the new endemic murines, while no study has been made for the old endemic species. Recently, we had an opportunity to examine carcasses of five species of old endemic rats belonging to four genera borrowed from the American Museum of Natural History (AMNH), New York, U.S.A. Nematodes belonging to Heterakidae were found from all of the species examined. Among them, the heterakid from one murine species was revealed to represent a new species of an unknown genus as described herein. A biogeographical discussion is made on this species and *Heterakis spumosa* Schneider, 1866, which was found from the other old endemic rats and new endemic rats of Sulawesi.

Material and methods

The old endemic rats of Sulawesi were collected by Dr. Guy G. Musser, and the carcasses were fixed in 10% formalin and preserved in 95% ethanol at AMNH. The cecum and large intestine were cut open and washed with running tap water on a fine sieve. The residues left on the sieve were transferred to petri dish and examined under stereomicroscope with transillumination. Nematodes found were stored in 70% ethanol, cleared in glycerol-ethanol solution by evaporation of ethanol, and mounted on glass slide with 50% glycerol aqueous solution. They were

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observed under a Nikon microscope equipped with interference contrast. Drawings were made with the aid of a Nikon drawing tube. Measurements, given in micrometers unless otherwise stated, are those of holotype male and allotype female, followed by the range of paratypes in parentheses and average in brackets. For scanning electron microscope (SEM) observation, the worms were re-fixed with glutaraldehyde, dehydrated through an ethanol series and vacuum dried using TAITEC VC-96N spin vacuum for at least 30 minute to make them sufficiently dried. Then they were coated with gold at 5–8 mÅ for 5 min, and observed using JEOL JSM5310LV at an accelerating voltage of 20 kV. For comparative purpose, heterakids collected from the new endemic rats captured in the medicozoological survey of Indonesia during 1991–1993 (Hasegawa *et al.*, 1999) and those newly collected by the junior author (K. D.) were also observed. Type and voucher specimens are deposited in the National Museum of Natural History (USNM), Washington, D.C., U.S.A., and Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia (Table 1).

Results

Heterakid nematodes were found from all of the five species of the old endemic rats. Close examination revealed that those from one rat species, *Echiothrix centrosa*, captured in Kuala Navusu, Malakasa, represented a new genus (Table 1). Meanwhile, heterakids from other old endemic rats, i.e., *Crunomys celebensis*, *Tateomys macrocercus* and *Tateomys rhinogradoides*, trapped in different localities were *Heterakis spumosa*, and *Melasmothrix naso* harbored only one larval form (Table 1). Among 11 species of new endemic rats examined, eight species in five genera, i.e., *Bunomys andrewsi*, *B. penitus*, *B. chrysocomus*, *Eropeplus canus*, *Paruromys dominator*, *Rattus hoffmanni*, *R. xanthurus* and *Taeromys celebensis* were found to harbor *H. spumosa* (Table 1).

Description

Musserakis gen. n.

Diagnosis. Heterakoidea: Heterakidae: Heterakinae. Cephalic end with 3 round lips not connected by lateral lobes: dorsal lip with 2 cephalic papillae; subventral lips each with 1 cephalic papilla and amphidial pore. Interlabia forming slightly curved, non-recurrent, non-anastomosing cordons. Lateral alae widest at esophageal region, becoming smaller posteriorly. Esophagus relatively long, with posterior bulb with valve. Caudal alae wide, supported by 3 pairs of stout papillae. Few sessile papillae on tail. Sucker with clear rim present anterior to cloaca. Spicules similar, non-alate. Parasitic in mammals.

Type and only species: *Musserakis sulawesiensis* **sp. n.**

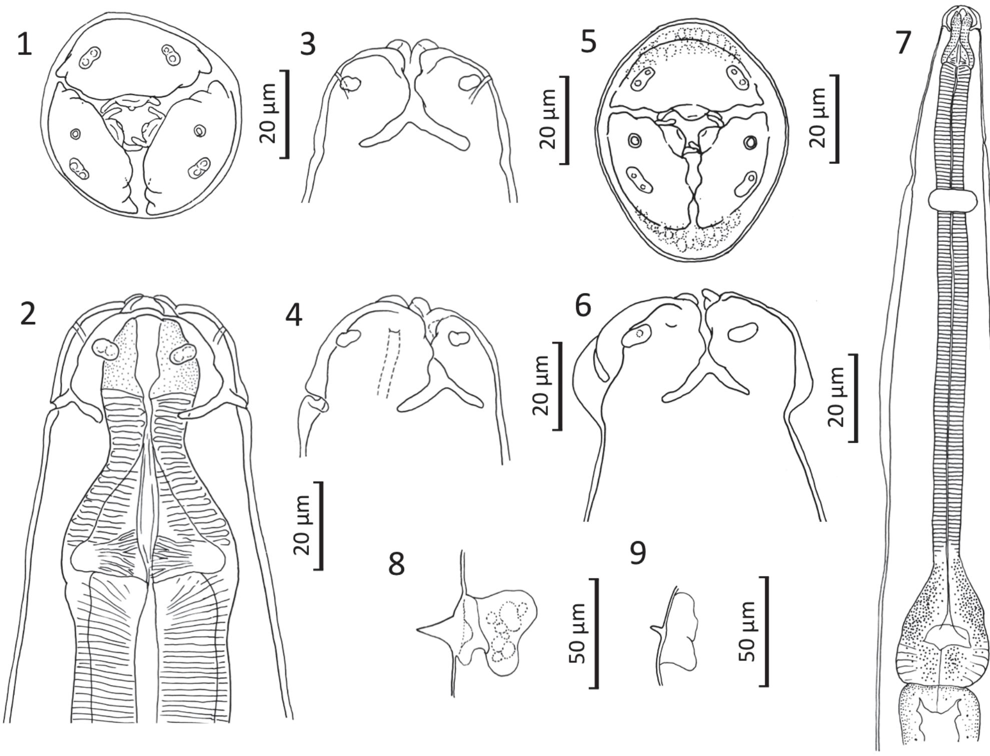
Musserakis sulawesiensis sp. n.

(Figs. 1–22)

General. Small nematodes. Cephalic extremity with characteristics defined above (Figs. 1–4, 19–21). Some worms with cephalic end dorso-ventrally elongated, giving inflated appearance in lateral view (Figs. 5, 6, 22). Anterior body usually bent dorsally (Figs. 10, 15). Lips with weak lateral projections (Figs. 1–6, 19–22). Each proximal lobe of pharyngostome forming onchium with side projections (Figs. 1, 5, 19–22). Esophagus long and slender (Figs. 7, 10, 15). Isthmus not clearly defined. Esophageal bulb divided into anterior and posterior portions (Fig. 7). Cervical alae triangular, strongly pointed, commencing anterior to nerve ring, continuing to small, thin lateral alae (Figs. 7–9). Deirids not discernible. Somatic papillae absent.

Male *(holotype and 10 paratypes):* Worm length 2.91 (2.61–3.47) [3.02] mm, width in midbody 131 (115–131) [125]. Total esophagus including pharynx 712 (632–755) [722] long, i.e., 24.5 (21.5–26.2) [24.0] % of worm length (WL); pharynx 64 (56–70) [63] long, combined length of corpus and isthmus 520 (452–569) [530] long by 32 (30–38) [35] wide, bulb 128 (122–138) [128] long by 96 (83–96) [89] wide. Nerve ring 205 (202–234) [221] and excretory pore 320 (275–346) [312] from cephalic apex. Sucker, 32 (30–43) [35] in diameter, 85 (56–96)

[86] in front of cloaca. Spicules equal, longitudinally striated faintly, variable in width and length, 227 (167–263) [218] long, i.e., 7.8 (5.2–9.3) [7.3] % of WL. In holotype and 5 paratypes, spicules stout, bent ventrally, flattened distally, often protruded from cloacal aperture (Figs. 11–13). In 5 paratypes spicules thin, tapered and winding distally, not projecting from cloacal aperture (Fig. 14). Ten pairs of caudal papillae present: 2 pairs slender, aside of sucker; 2 sessile large papillae lateral to cloacal aperture and 3 stout long papillae, forming cloacal group, supporting caudal alae; 3 small sessile pairs in middle of tail (Figs. 11, 12). Tail slender, ending in pointed tip, 237 (212–247) [228] long (Figs. 11, 12).



FIGURES 1–6. Cephalic portions of *Musserakis sulawesiensis* **gen. et sp. n.** 1–4. Apical (1), dorsal (2), ventral (3) and lateral (4) views in females. 5, 6. Apical (5) and lateral (6) views in female with inflated cephalic portion. 7. Esophageal portion of male, dorsal view. 8. Cervical ala in cross section of male. 9. Lateral ala in cross section at midbody of male.

Female *(Allotype and 10 paratypes):* Worm length 3.3 (3.2–3.5) [3.4] mm, width in midbody 138 (128–147) [133]. Total esophagus including pharynx 731 (712–811) [759] long, i.e., 22.2 (21.4–24.1) [22.7] % of WL; pharynx 59 (58–67) [62] long, corpus 550 (517–628) [571] long by 40 (32–43) [37] wide, bulb 122 (122–134) [127] long by 88 (83–102) [96] wide. Nerve ring 218 (208–249) [222] and excretory pore 330 (282–335) [307] from cephalic apex. Vulva 1.92 (1.87–2.09) [2.00] mm from cephalic apex, i.e., 58.2 (57.5–62.2) [59.4] % of WL; opening in depression with small diverticulum; perivulval cuticle swollen, one low tubercle present at ca. 100 posterior to vulva (Figs. 15, 16). Vagina thick, muscular, strongly anteriorly curved, then abruptly recurved as ovejector, running posteriorly far beyond vulval level to join uteri (Fig. 16). Anterior and posterior ovaries ending at posterior to esophago-intestinal junction and anal level, respectively (Figs. 15, 17). Tail slender, ending in pointed tip, 448 (363–476) [429] long, i.e., 13.6 (10.9–14.1) [12.8] % of WL (Fig. 17). Eggs ellipsoidal, thick shelled, with round concave ornamentations on surface, unembryonated at deposition, 59–72 [68] by 40–48 [45] (Fig. 18).

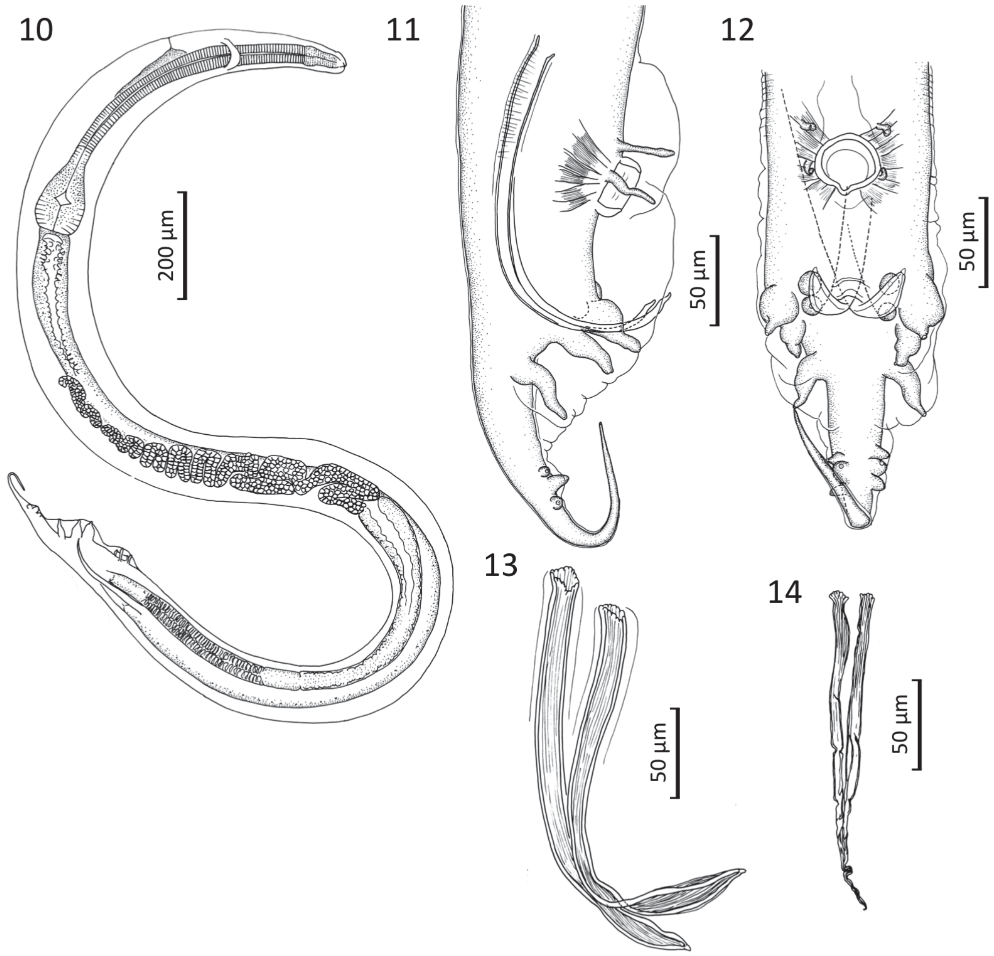
Taxonomic summary.

Type host: *Echiothrix centrosa* Miller & Hollister, 1921 (large-bodied shrew rat)

Type locality: Kuala Navusu, Malakasa, Central Sulawesi, Indonesia.

Prevalence and intensity: All of 5 *E. centrosa* harbored numerous individuals.

Specimens deposited: USNM 1251671 (holotype male and allotype female), 1251672 (10 male and 10 female paratypes); Voucher specimens USNM 1251673–1251676, MZB Na 646.



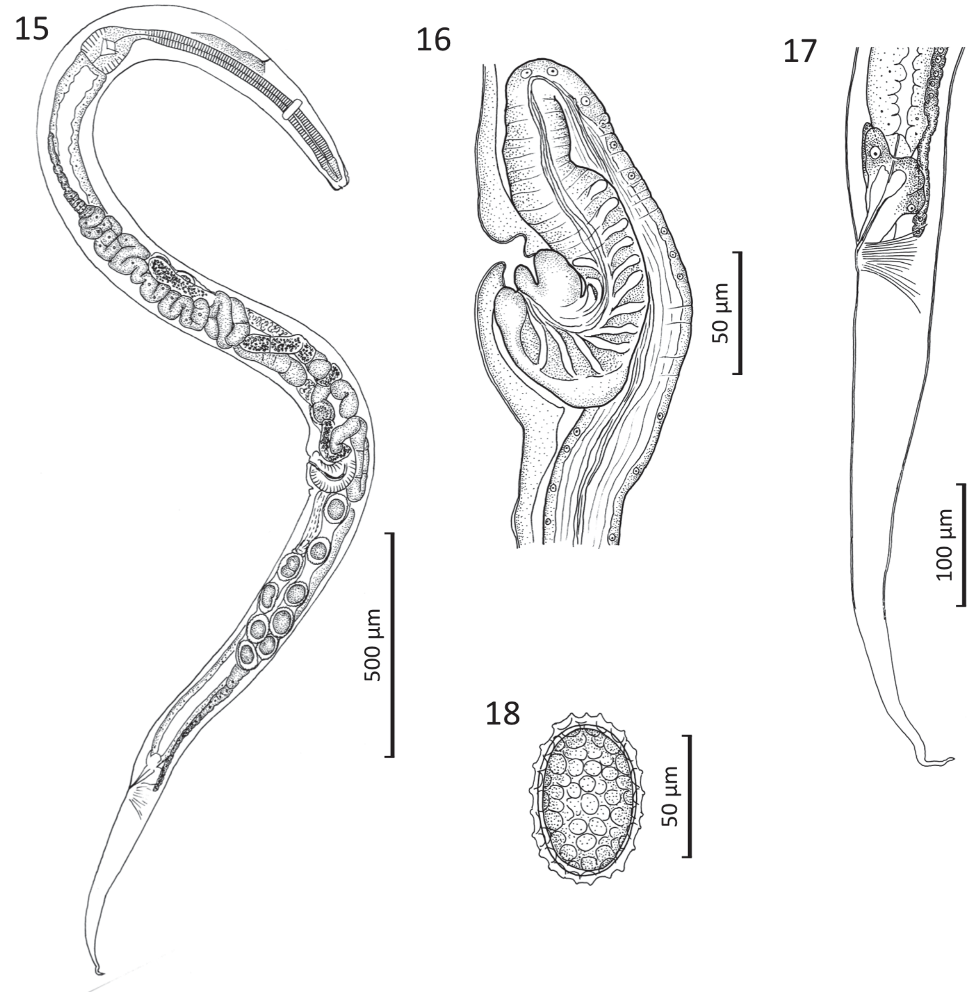
FIGURES 10–14. Male of *Musserakis sulawesiensis* **gen. et sp. n.** 10. Holotype, left lateral view. 11, 12 Caudal end in right lateral (11) and ventral (12) views. 13, 14. Spicules of thick (13) and thin (14) types.

Coparasites: *Trichuris* sp. (Site cecum; prevalence 4/5; intensity 1-5), Heligmonellidae gen. sp. (small intestine; 1/5; 1), Ascarididae gen. sp. (larva) (abdominal cavity; 1/5; 1) and Rhigonematidae gen. sp. (cecum; 1/5; 1).

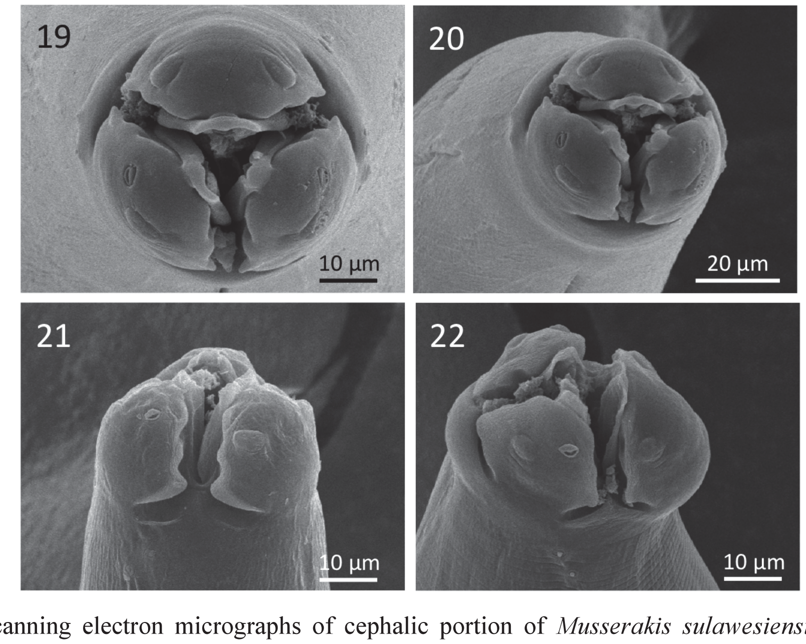
Symbiotypes: AMNH 225678–225681, 225685.

Etymology. Generic name is dedicated to Dr. G. G. Musser, an outstanding mammalogist, who has made invaluable contributions on the murid rodents of Sulawesi for many years. The species epithet is named after the locality.

Remarks. By having 3 well defined lips, an esophagus with valved bulb, thick shelled eggs, a preanal sucker in male, *Musserakis* belongs to the superfamily Heterakoidea (Chabaud, 1974). Because the lips are round and not connected by lateral lobes, it is assigned to the family Heterakidae (Chabaud, 1978). By having interlabia and only limited number of sessile papillae on male tail, it is included in the subfamily Heterakinae (Chabaud, 1978). Five genera are currently recognized in this subfamily: *Heterakis* Dujardin, 1945, *Haroldakis* Inglis, 1991, *Neoheterakis* Kumar & Thienpoint, 1974, *Pseudoaspidodera* Baylis & Daubney, 1922, *Odontoterakis* Skrjabin & Schikhobalova, 1947 (Chabaud, 1978; Inglis, 1991a; Gibbons, 2010). *Musserakis* resembles *Haroldakis* and *Odontoterakis* by having non-recurrent and non-anastomosing cephalic cordons, whereas it differs clearly from *Heterakis*, which lacks cordons, and *Neoheterakis* and *Pseudoaspidodera*, which possess recurrent cephalic cordons (Chabaud, 1978; Inglis, 1991a; Gibbons, 2010). *Musserakis* is readily distinguished from *Haroldakis*, which has 5 teeth on each proximal end of pharyngostome, transverse cushion with 2 sessile papillae between sucker and cloaca, and 2 sessile papillae on posterior cloacal lip in male (Inglis, 1991a). It also differs from *Odontoterakis*, which has 1 pair of additional thin pedunculate papillae between papillae groups around sucker and cloaca (Inglis, 1991a).



FIGURES 15–18. Female of *Musserakis sulawesiensis* **gen. et sp. n.** 15. Allotype, left lateral view. 16. Vulval portion, left lateral view. 17. Tail, left lateral view. 18. Uterine egg.



FIGURES 19–22. Scanning electron micrographs of cephalic portion of *Musserakis sulawesiensis* **gen. et sp. n.** 19–21. Female with usual cephalic portion, in apical (19), subapical (20), and apico-lateral (21) views. 22. Female with inflated cephalic portion, apico-lateral view.

TABLE 1. Prevalence of heterakids in Sulawesi rats.

Rat species examined	Locality[*]	Heterakids found	Prevalence[**]	Museum Accession No.
Old endemics				
Echiothrix centrosa	Kuala Navusu, Malakasa, CS	*Musserakis sulawesiensis*	5/5	USNM 1251671 —1251676, MZB Na 646
Crunomys celebensis	Sungai Sadaunta, CS	*Heterakis spumosa*	1/1	USNM 1251677
Melasmothrix naso	Gunung Nokilalaki, CS	Heterakidae sp.[§]	1/5	USNM 1251680
Tateomys macrocercus	Gunung Nokilalaki, CS	*Heterakis spumosa*	3/5	USNM 1251678
Tateomys rhinogradoides	Gunung Nokilalaki, CS	*Heterakis spumosa*	3/3	USNM 1251679
New endemics				
Bunomys andrewsi	Lambanan, WS	*Heterakis spumosa*	1/1	MZB Na 655
	Sumarorong, WS		0/7	
	Mambulillin, WS	*Heterakis spumosa*	1/3	MZB Na 660
	Mekongga Mountain, SES		0/2	
Bunomys chrysocomus	Tomado, CS	*Heterakis spumosa*	1/1	MZB Na 656
	Lore Lindu, CS	*Heterakis spumosa*	7/12	MZB Na 661
	Mekongga Mountain, SES	*Heterakis spumosa*	2/3	MZB Na 662
Bunomys penitus	Lambanan, WS	*Heterakis spumosa*	4/4	MZB Na 657
	Sumarorong, WS		0/1	
	Mekongga Mountain, SES	*Heterakis spumosa*	2/4	MZB Na 659
Eropeplus canus	Lambanan, WS	*Heterakis spumosa*	1/4	—[†]
Margaretamys elegans	Lambanan, WS		0/1	

……*continued on the next page*

TABLE 1. (Continued)

Rat species examined	Locality*	Heterakids found	Prevalence**	Museum Accession No.
Maxomys musschenbroekii	Mambulillin, WS		0/2	
	Lambanan, WS		0/1	
	Tomado, CS		0/1	
Paruromys dominator	Sumarorong, WS		0/2	
	Mambulillin, WS	*Heterakis spumosa*	1/1	MZB Na 648
	Lambanan, WS	*Heterakis spumosa*	3/5	MZB Na 649
	Mekongga Mountain, SES	*Heterakis spumosa*	1/6	MZB Na 650
Rattus hoffmanni	Tomado, CS		0/4	
	Mekongga Mountain, SES	*Heterakis spumosa*	1/3	MZB Na 652
Rattus xanthurus	Moat, NS	*Heterakis spumosa*	1/11	MZB Na 653
	Lambanan, WS		0/2	
Taeromys celebensis	Mekongga Mountain, SES	*Heterakis spumosa*	1/4	MZB Na 651
Recent arrivals				
Rattus norvegicus	Manado, NS		0/1	
Rattus tanezumi	Likupang, NS		0/11	
	Lore Lindu, CS		0/23	

* CS: Central Sulawesi, NS: North Sulawesi, SES: South West Sulawesi, SS: South Sulawesi, WS: West Sulawesi.

** No. hosts infected/No. hosts examined. §Larval stage. † Specimens were lost.

Discussion

The superfamily Heterakoidea is currently composed of four families, Heterakidae, Ascaridiidae, Aspidoderidae and Kiwinematidae (Gibbons, 2010). Among them, the ascaridiids are parasitic in birds; the aspidoderids are mostly parasites of edentates and rodents of South America except *Narsingiella* Rao, 1978, which is parasitic in Indian toads; members of the Kiwinematidae are harbored by birds and reptiles of New Zealand and mole rats of the old world; the heterakids are mostly parasitic in birds, and only 3 genera, *Gireterakis* Lane, 1917, *Heterakis* and *Musserakis*, include mammal-parasitic species (cf. Chabaud, 1978; Gibbons, 2010; Inglis, 1991b). This sporadic utilization of mammalian hosts by the heterakids suggests that adaptation to the mammals had occurred separately. The host range of heterakid nematodes of mammals provides an interesting feature. For example, *H. spumosa* is not only common in *Rattus* spp. but also has been recorded from various murids belonging to the genera *Apodemus*, *Arvicanthis*, *Clethrionomys*, *Cricetomys*, *Eothenomys*, *Lemniscomys*, *Mastomys*, *Microtus, Mus*, *Proechimys* and *Tatera*, indicating low host-specificity (Natural History Museum, 2014). In Indonesia, this nematode has been also recorded from *Bunomys* spp. (cf. Dewi & Purwaningsih, 2013). *Heterakis spumosa* was also recorded from old endemic rats, *Hydromys chrysogaster* and *Melomys rufescens* of Australia and New Guinea, respectively (Fielding, 1928 cited by Smales & Cribb, 1997; Smales, 2009). Presence of *H. spumosa* in the old endemic rats was considered as host switching from new endemic murids (Smales, 2012). The present study adds the old endemic genera, *Crunomys* and *Tateomys*, along with the new endemic genera, *Eropeplus*, *Paruromys* and *Taeromys*, to the host genera list of *H. spumosa*. This cosmopolitan heterakid was also reported from an insectivore, *Mogera kobeae*, and a marsupial, *Isoodon macrourus* (Yokohata *et al.*, 1989; Beveridge & Spratt, 1996). The former case was considered as pseudoparasitism due to eating prey rats (Yokohata *et al.*, 1989), while the latter case was interpreted as acquisition of the nematode from *Rattus* (Beveridge & Spratt, 1996).

In contrast to *H. spumosa*, other heterakid species of murids have been known from only limited hosts. *Heterakis fieldingi* Smales, 1996 was found only in the old endemic rats of Australia and Papua New Guinea, namely *H. chrysogaster, H. shawmayeri*, *Leptomys elegans, L. paulus*, *Parahydromys asper*, *Paraleptomys wilhelmina* and *Pseudohydromys murinus*, while new endemic rats of Australia, namely *Rattus fuscipes*, *R. lutreolus* and *R. sordidus*, harbor only *H. spumosa* (Smales, 1996, 1997, 2001, 2006a, b). Phylogenetically, *Echiothrix* is surmised to form a clade with *Melasmothrix*, *Tateomys* and *Paucidentomys* (Esselstyn *et al.*, 2012; Musser & Durden, 2014). In the present study, however, *Tateomys* spp. harbored *H. spumosa* and the only heterakid found from *M. naso* was larva, of which species identification was not possible (Table 1). Because the number of murines examined in the present study was limited, it is inappropriate to draw a conclusion on the host specificity of *M. sulawesiensis*. However, high prevalence and intensity suggest host-specificity of this nematode to *Echiothrix*. Presumably, *M. sulawesiensis* also parasitizes *Echiothrix leucura*, the only congener inhabiting North Sulawesi (Musser & Durden, 2014), and *Paucidentomys*, a recently described shrew rat of Sulawesi, that is considered to be a sister taxon of *Echiothrix* (Esselstyn *et al.*, 2012).

Among the coparasites observed in the present study, *Trichuris* sp. seems to be a specific parasite of *E. centrosa* because its prevalence was high though intensity was low. This whipworm has a smaller body, less than 10 mm long in both sexes but a spicule of about 1 mm long, differing from *Trichuris muris* (Schrank, 1788), a cosmopolitan species parasitic in various murids, of which body length is 14.6 to 28.6 mm and spicule length is 571 to 732 µm (cf. Skrjabin *et al.*, 1957). Detail accounts of this whipworm will be reported elsewhere. As only one individual of Heligmonellidae gen. sp. was recovered, it is questionable that *E. centrosa* is the principal host of this nematode. Ascarididae gen. sp. (larva) in the abdominal cavity is surmised to be parasitic in other vertebrate, presumably a snake, at adult stage, and the murine serves as an intermediate host (cf. Anderson, 2000). Rhigonematidae gen. sp. is apparently a pseudoparasite acquired with diet because rhigonematids are exclusively parasitic in arthropods (Poinar, 1977).

Ectoparasites of *E. centrosa* are also composed of host-specific and less host-specific species. The fur-mite, *Listrophoroides* (*Marquesania*) *echiothrix* Bochkov *et al.*, 2004 and the sucking louse, *Polyplax beaucournui* Musser & Durden, 2014 have been considered to be specific to *Echiothrix* (Bochkov *et al.*, 2004; Musser & Durden, 2014). Meanwhile, the flea, *Farhangia quattuordecimdentata* Mardon & Durden, 2003, found from *E. centrosa*, had been already reported from *Margaretamys beccarii* and *Prosciurillus murinus*, Sulawesi-endemic murine and dwarf squirrel, respectively (Mardon & Durden, 2003; Musser & Durden, 2014).

Heterakids require no intermediate host, but it has been demonstrated that earthworms play a role as paratenic host for *Heterakis gallinarum* (Schrank, 1788) and *H. spumosa* (cf. Anderson, 2000). Saitoh *et al.* (1993) found natural infection of earthworms, *Pheretima hilgendorfi*, with heterakid larvae, which developed to adults to be identified as *H. spumosa* when given to Wister strain brown rats, *Rattus norvegicus*. They also fed earthworms, *Eisenia foetida*, with larvated eggs of *H. spumosa* and demonstrated that the larvae invaded the epithelium of digestive tract. Moreover, they observed higher infectivity of the larvae from the earthworms than the larvated eggs (Saitoh *et al.*, 1993). It is interesting that *E. centrosa* is an aggressive earthworm predator (Musser & Durden, 2014). If *M. sulawesiensis* also utilizes earthworms as paratenic host, this feeding habit of *E. centrosa* may be advantageous for transmission of the nematode. Although *T. macrocercus* and *T. rhinogradoides* also prey on small earthworms exclusively (Musser, 1982), their heterakids found in this study differed from *M. sulawesiensis*. Further study is necessary to determine the source of infection of the heterakids in Sulawesi forests.

The variations in the spicule shape found in *M. sulawesiensis* are of special interest. The spicules of thick type are presumed to function in copulation because protrusion was often observed. Meanwhile, the role of the thin type spicules in mating remains unknown because protrusion was not observed. It is noteworthy that the longitudinally-striated and distally winding nature of the thin type spicules resembles the feature of the spicules of *H. spumosa* (Hall, 1916, cited in Skrjabin *et al.*, 1961). Although the spicules are more or less stout in most of the heterakids, a few species have been known to possess whip-like or thin spicules, e.g. *Heterakis skrjabini* Cram, 1927, *Haroldakis multidentata* (Baylis, 1944), and *Meteterakis varani* (Maplestone, 1931) besides *H. spumosa* (Skrjabin *et al.*, 1961; Inglis, 1991a). However, no report is found on dimorphism/polymorphism in the spicule morphology of heterakids.

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