



## Two new species of *Trichuris* (Nematoda: Trichuridae) collected from endemic murines of Indonesia

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### Abstract

Two new species of the genus *Trichuris* (Nematoda: Trichuridae) parasitic in the old endemic murids of Indonesia are described: *T. musseri* **sp. nov.** from *Echiothrix centrosa* (Murinae: Rattini) in Sulawesi and *T. mallomyos* **sp. nov.** from *Mallomys rothschildi* (Murinae: Hydromyini) in Papua Indonesia. Both species are characterized by having a gradually tapered and sharply pointed distal end of the spicule, being readily distinguished from most of the congeners known from murid rodents. *Trichuris musseri* is readily distinguished from *T. mallomyos* by having a much smaller body and large number of nuclei per subdivision of stichosome. The resemblance in spicule morphology between the two new species is of special interest because both hosts belong to different tribes and have different habitats and habits. It remains to be elucidated whether the resemblance is merely homoplasy or actually reflects close phylogenetic relationship of the parasites.

**Key words:** *Trichuris musseri* **sp. nov.**, *Trichuris mallomyos* **sp. nov.**, *Echiothrix*, *Mallomys*, old endemic murids, Sulawesi, Papua, Indonesia, zoogeography

### Introduction

Nematodes of the genus *Trichuris* (Trichuridae) are parasitic in the large intestine of various mammals including murine rodents (Anderson & Bain, 1982). Indonesia is known as an area with very high diversity of murines with more than 170 species, especially many endemic species in Sulawesi and Papua Indonesia (=West New Guinea) (Suyanto *et al.*, 1998; Musser & Carleton, 2005; Fabre *et al.*, 2013). These endemic species are classified into old endemics and new endemics. The old endemic murines have many archaic features and exhibit unique combinations of specializations, and have no close living relatives in continental Asia and islands on Sunda Shelf (see Musser, 1981, 1987). It has been considered that ancestors of the old endemics arrived in the Miocene and early Pliocene, whereas the new endemics colonized later (see Rowe *et al.*, 2016 and literature cited therein). Because a new whipworm, *T. germani* Smales, 2013, was recently described from *Pogonomys* spp., old endemic murines, in Papua New Guinea (=East New Guinea) (Smales, 2013), it is expected that more *Trichuris* species may be present in the endemic murines in these areas. On examination of nematode material collected from old endemic rats of Indonesia, two new species of *Trichuris* were recovered. Their morphology is described herein with a zoogeographical discussion.

### Materials and methods

Two individuals of *Mallomys rothschildi* were purchased at a local market in Wamena, Papua, and their alimentary canals were fixed in 10% formalin (Hasegawa & Syafruddin, 1994). Individuals of *Echiothrix centrosa* were captured in Malakosa, Kuala Navusu, Sulawesi, by Dr. Guy G. Musser, and their carcasses were fixed in 10% formalin and preserved in 95% ethanol at the American Museum of Natural History (AMNH), New York, (Musser

& Durden, 2014). The contents of the cecum and large intestine were removed and washed with running tap water on a fine sieve. The residues left on the sieve were transferred to a petri dish and examined under a stereomicroscope. Nematodes found were stored in 70% ethanol, cleared in glycerol-ethanol solution by evaporation of ethanol, and mounted on glass slides with a 50% glycerol solution. Measurements, given in micrometers unless otherwise stated, are averages followed by the ranges in parentheses. Type specimens were deposited in the National Museum of Natural History (USNM), Washington, D.C., U.S.A., and Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia.

## Description

### *Trichuris musseri* sp. nov.

(Figs. 1–12)

**General.** Small sized as a *Trichuris* in murids. Cuticle with fine transversal striation. Anterior part of body narrow, thread-like, tapering to cephalic end; gradually increasing to widest portion in posterior body and again slightly tapered to posterior end (Figs. 1, 2, 9). Minute cephalic stylet present. Stichosome with 1 row of stichocytes, and 1 pair of conspicuous cells at esophago-intestinal junction level (Figs. 2–5, 10). Nuclei of stichosome numerous, almost 1 nucleus per 1 to 2 subdivisions, in middle to posterior portions (Figs. 3–5). Bacillary band commencing just after cephalic end, well developed in middle portion of anterior body (Figs. 2–5), becoming narrower and invisible anterior to esophago-intestinal junction. Round cuticular inflations of various size bordering bacillary band present in anterior portion of body (Fig. 2).

**Male** (9 specimens): Length 8.79 (7.89–9.24) mm. Anterior portion of body 5.32 (4.93–5.65) mm long, corresponding to 61 (58–63) % of body length. Width at middle of anterior body 57 (44–69), esophago-intestinal junction 129 (99–162) and thick portion of posterior body 182 (162–210). Round cuticular inflations present in area from 192–258 to 618–860 from anterior end. Stichosome with ca. 160 nuclei. Testis recurved posterior to esophago-intestinal junction, directed posteriorly forming convolutions, ending near anterior end of proximal cloacal tube (Fig. 1). Proximal cloacal tube stout, 0.66 (0.45–0.91) mm long, united laterally to distal cloacal tube of 0.53 (0.35–0.71) mm long (Fig. 1). Spicular pouch 0.18 (0.09–0.28) mm long (Fig. 1). Spicule slender, 1.11 (0.90–1.28) mm long, corresponding to 12.7 (10.0–14.1) % of body length, sharply pointed distally (Figs. 6–7). Distal portion of spicule with pit-like structures on one side (Fig. 7). Spicular sheath densely spinose (Figs. 6–7). Distal end of fully extended spicular sheath devoid of spines, with faint reticulate markings (Fig. 8). Cloaca subterminal with 1 pair of simple papillae (Fig. 6).

**Female** (10 specimens): Length 10.9 (9.3–12.4) mm. Anterior body 6.20 (5.55–7.22) mm long, corresponding to 57.0 (54.6–59.6) % of body length. Width at middle of anterior body 58 (51–67), esophago-intestinal junction 135 (121–158) and thick portion of posterior body 202 (184–218). Round cuticular inflations present in area from 162–300 to 684–1039 from anterior end. Stichosome with ca. 160–170 nuclei. Vulva 40 (10–71) posterior to esophago-intestinal junction, with anterior lip of varying degree of development and minute posterior lip (Figs. 9, 10). Vagina muscular, winding posteriorly, 0.67 (0.56–0.78) mm long (Figs. 11, 12). Ovary extending to preanal level (Figs. 9, 11). Anus subterminal (Fig. 11). Eggs lemon-shaped, thick shelled, brownish, with polar plugs,  $73.6 \pm \text{SD } 1.7$  (71–77) by  $33.0 \pm \text{SD } 1.4$  (30–35) (n=25), with exception of one egg sized 91 by 38 (Fig. 12).

### Taxonomic summary

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

Site in host: Cecum.

Type locality: Kuala Navusu (00°58'S, 120°27'E; 38–155 m elevation), Malakosa, Central Sulawesi, Indonesia.

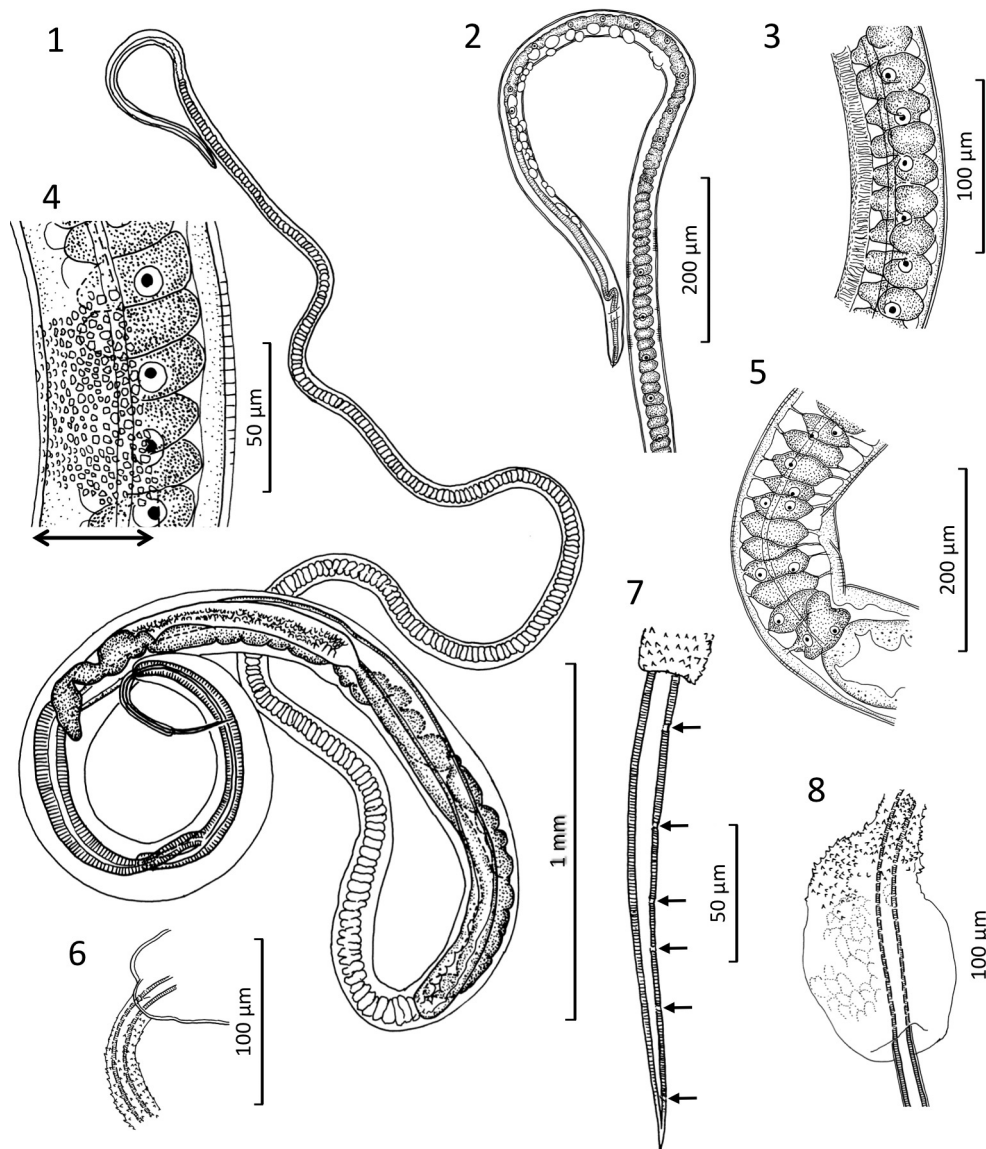
Date of collection: October 1975.

Type specimens: USNM 1422103 (holotype male and allotype female), USNM 1422104 (5 male and 6 female paratypes), MZB Na 720 (3 male and 3 female paratypes).

Coparasites: *Musserakis sulawesiensis* Hasegawa, Dewi & Asakawa, 2014 (Nematoda: Heterakidae) (Hasegawa *et al.*, 2014).

Symbiotypes: AMNH M-225678 – M-225681.

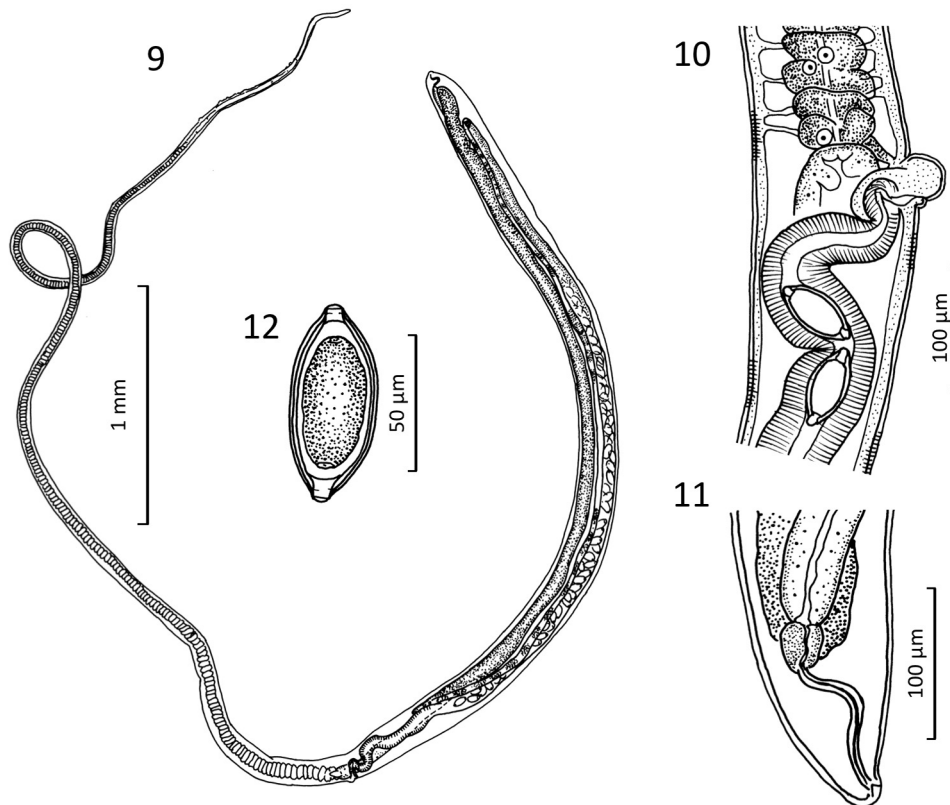
**Etymology.** The species epithet is dedicated to Dr. G. G. Musser, an outstanding mammalogist, who has made invaluable contributions on the systematics of murid rodents of Indonesia.



**FIGURES 1–8.** Male of *Trichuris musseri* sp. nov. collected from *Echiothrix centrosa* in Sulawesi, Indonesia. 1. Holotype. 2. Anterior end of holotype. 3. Middle portion of stichosome showing bacillary band at left side. 4. Enlarged view at posterior one-third of stichosome, showing surface of bacillary band partially; two-way arrow indicating width of bacillary band at this level. 5. Esophago-intestinal junction. 6. Caudal end. 7. Distal end of spicule; arrows showing pit-like structures. 8. Distal end of spicular sheath fully extended.

**Remarks.** By having a stichosome, tubular intestine, vulva positioned near esophago-intestinal junction, monodelphic reproductive system and eggs with polar plugs but without membranous envelope or polar filaments, the present species belongs to the family Trichuridae in the superfamily Trichinelloidea (Chabaud, 1974; Anderson & Bain, 1982). By possessing much thicker posterior portion of body, a bacillary band at esophageal portion, stichocytes similar in form and arranged in a single row and unembryonated eggs in the uterus, it belongs to the subfamily Trichurinae which includes only the genus *Trichuris* Roederer, 1761 (Anderson & Bain, 1982). By having a small body, the present species is readily distinguished from all congeners known from murids because all have average body length over 10 mm in males and 15 mm in females (cf. Skrjabin *et al.*, 1957; Quentin, 1966; Bernard, 1969; Tenora, 1969; Johnson, 1973; Sadighian *et al.*, 1974; Feliu *et al.*, 2000; Robles, 2011; Ribas *et al.*, 2013; Smales, 2013; Robles *et al.* 2014). The present species is characteristic by having a gradually-tapered and sharply pointed distal end of the spicule, being readily distinguished from most congeners parasitic in murids, which have dull or round distal end or suddenly narrowed near distal end of the spicule (cf. Quentin, 1966; Robles, 2011; Robles *et al.*, 2014; Smales, 2013; Feliu *et al.*, 2000; Ribas *et al.*, 2013). Among the congeners parasitic in

murids, only *T. petrowi* in *Arvicola terrestris* of Tatarstan, Russia, and *T. spalacis* in the mole rat, *Spalacis microphthalmus*, of Ukraine, have been known to have gradually tapered and pointed spicule (Petrov & Potekhina, 1953; Skrjabin *et al.*, 1957). However, the former species has a cephalic expansion in the male and much longer distance (>1 mm) between the anus and posterior end of body in female, and the latter species has a smaller ratio (<58 %) of anterior body to worm length in males and smaller eggs (62–65 by 29  $\mu\text{m}$ ), differing from the present species (Petrov & Potekhina, 1953; Skrjabin *et al.*, 1957).



**FIGURES 9–12** Female of *Trichuris musseri* sp. nov. collected from *Echiothrix centrosa* in Sulawesi, Indonesia. 9. Allotype. 10. Esophago-intestinal junction. 11. Caudal end. 12. Egg.

***Trichuris mallomyos* sp. nov.**

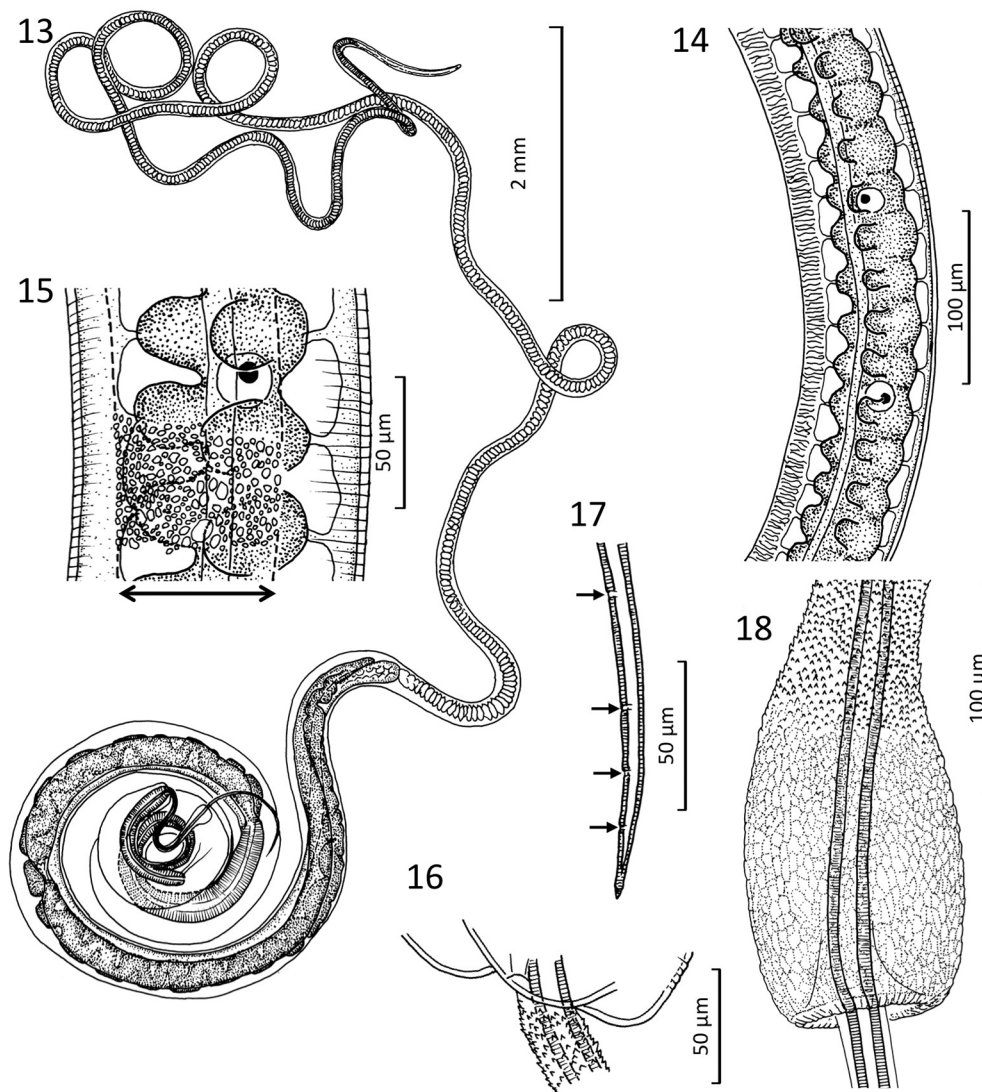
(Figs. 13–22)

**General.** Usual size as a *Trichuris* in murids. Cuticle with fine transversal striation. Anterior part of body narrow, thread-like, tapering to cephalic end; posterior part of body stout (Figs. 13, 19). Minute cephalic stylet present. Stichosome with 1 row of stichocytes, and 1 pair of conspicuous cells at esophago-intestinal junction level (Figs. 13, 19). Nucleus of stichosome present per 4 to 5 subdivisions, in middle portion (Fig. 14). Bacillary band commencing just after cephalic end, well developed in middle portion of anterior body (Figs. 14, 15), becoming narrower and invisible anterior to esophago-intestinal junction. Round cuticular inflations of various sizes bordering bacillary band present in anterior portion of body.

**Male** (10 specimens): Length 28.8 (24.6–32.4) mm. Anterior portion of body 18.7 (15.3–21.0) mm long, corresponding to 65 (62–68) % of body length. Width at middle of anterior body 101 (95–111), esophago-intestinal junction 227 (202–259) and thick portion of posterior body 359 (331–397). Round cuticular inflations present in area from 258–370 to 1287–1990 from anterior end. Stichosome with ca. 180–200 nuclei. Testis recurved posterior to esophago-intestinal junction, directed posteriorly forming convolutions, ending near anterior end of proximal cloacal tube (Fig. 13). Proximal cloacal tube stout, 2.53 (2.25–2.77) mm long, united laterally to distal cloacal tube of 0.92 (0.75–1.37) mm long (Fig. 13). Spicular pouch 0.28 (0.09–0.73) mm long (Fig. 13). Spicule length 2.89 (2.75–3.13) mm long, corresponding to 10.1 (8.5–11.9) % of body length, sharply pointed distally (Figs. 16–18).

Distal portion of spicule with pit-like structures on one side (Fig. 17). Spicular sheath densely spinose; distal end of fully extended spicular sheath devoid of spines, with reticulate markings (Fig. 18). Cloaca subterminal with 1 pair of simple papillae (Fig. 16).

**Female** (10 specimens): Length 35.1 (28.1–41.4) mm. Anterior body 22.0 (17.2–27.1) mm long, corresponding to 62.6 (59.6–66.9) % of body length. Width at middle of anterior body 100 (86–109), esophago-intestinal junction 243 (202–274) and thick portion of posterior body 420 (372–486). Round cuticular inflations present in area from 198–455 to 1505–2109 from anterior end. Stichosome with ca. 190–210 nuclei. Vulva slightly elevated, 81 (0–137) posterior to esophago-intestinal junction (Fig. 20). Vagina muscular, winding posteriorly, 1.37 (1.01–1.65) mm long (Fig. 21). Ovary extending to preanal level (Figs. 19, 21). Anus subterminal (Fig. 20). Eggs lemon-shaped, thick shelled, brownish, with polar plugs,  $90.1 \pm \text{SD } 2.9$  (83–95) by  $39.2 \pm \text{SD } 1.2$  (36–41) (n=50) (Fig. 22).



**FIGURES 13–18.** Male of *Trichuris mallomyos* sp. nov. collected from *Mallomys rothschildi* in Papua, Indonesia. 13. Holotype. 14. Middle portion of stichosome showing bacillary band at left side. 15. Enlarged view at middle showing surface of bacillary band partially; two-way arrow indicating width of bacillary band at this level. 16. Caudal end. 17. Distal end of spicule; arrows showing pit-like structures. 18. Distal end of spicular sheath fully extended.

#### Taxonomic summary.

Type host: *Mallomys rothschildi* Thomas, 1898 (Rothschild's woolly rat) (Hydromini: Murinae: Muridae).

Site in host: Cecum.

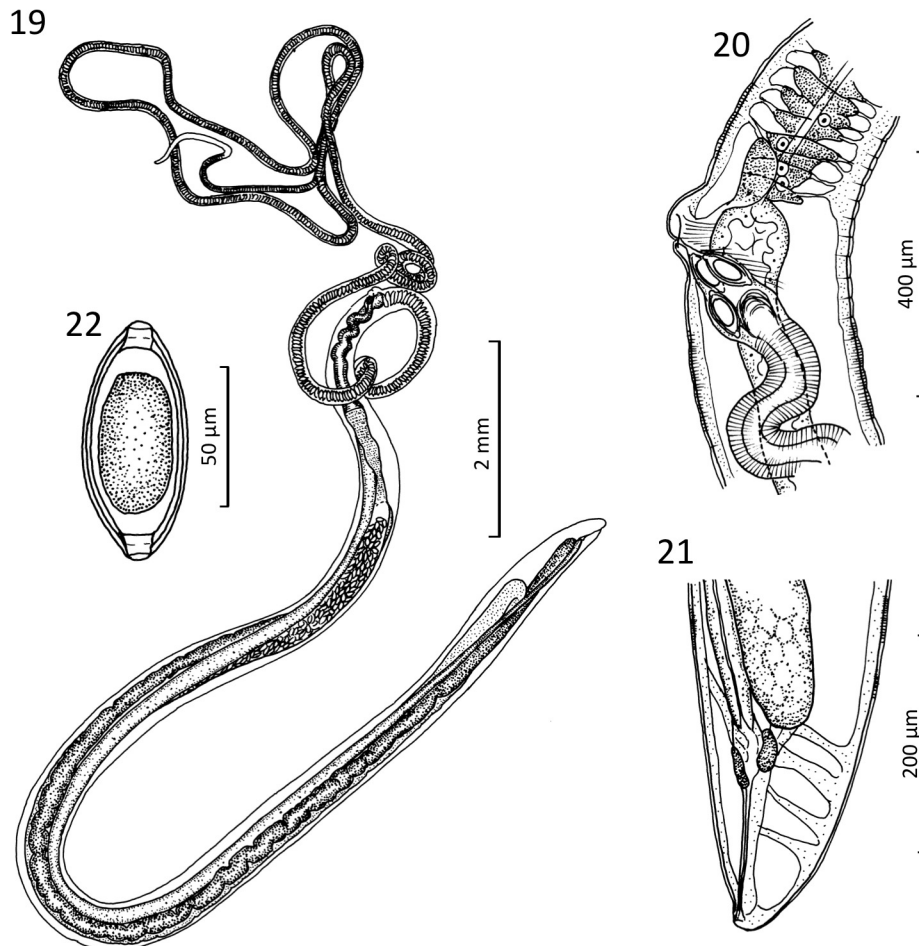
Type locality: Highland forest near Wamena (4°11'S, 138°58'E; 1500 m elevation), Papua Indonesia, Indonesia.

Date of collection: 4 August 1993.

Type specimens: USNM 1422105 (holotype male and allotype female), USNM 1422106 (6 male and 6 female paratypes), MZB Na 721 (3 male and 3 female paratypes).

Coparasites: *Odilia mallomyos* Hasegawa & Syafruddin, 1994 (Nematoda: Heligmonellidae) (Hasegawa & Syafruddin, 1994).

Symbiotypes: AMNH M-267742, M-267743.



**FIGURES 19–22.** Female of *Trichuris musseri* **sp. nov.** collected from *Mallomys rothschildi* in Papua Indonesia. 19. Allotype. 20. Esophago-intestinal junction. 21. Caudal end. 22. Egg.

**Etymology.** Species epithet is derived from the generic name of the type host.

**Remarks.** This species is also assigned to *Trichuris* for the same reasons as for the preceding species. By having a gradually tapered and sharply pointed spicule, it resembles *T. musseri*, *T. petrowi* and *T. spalacis* among those parasitic in murids (Petrov & Potekhina, 1953; Skrjabin *et al.*, 1957). It is easily distinguished from *T. musseri* in that the body is much larger and the number of nuclei per divisions of stichosome is fewer. It also differs from the latter two species by the following features: *T. petrowi* has a cephalic expansion and a larger ratio of anterior body to worm length (>70 %) in male, and much longer distance (>1 mm) between the anus and posterior end of body in female; *T. spalacis* has a smaller ratio of anterior body to worm length (<60 %) in both sexes and much smaller eggs (62–65 by 29 µm) (Petrov & Potekhina, 1953; Skrjabin *et al.*, 1957). Morphology of the distal end of the spicule has not been described or figured in some *Trichuris* species in murids, namely, *T. neotomae* Chandler, 1945 and *T. peromysci* Chandler, 1946. Although their males have body length comparable to the present males (22–23 mm in *T. neotomae* and 14.7–31.8 mm in *T. peromysci*), they possess a much shorter spicule (1.15–1.23 mm and 0.86–1.4 mm long, respectively), being readily distinguished from *T. mallomyos* **sp. nov.** (Chandler, 1945, 1946). *Trichuris germani*, an endemic congener parasitic in the endemic murids of Papua New Guinea, differs from the present species by having smaller eggs (42.5–63 by 25.5–27.7 µm) in addition to the rounded distal end of the spicule (Smales, 2013).

## Discussion

*Trichuris* spp. are widely distributed among mammals regardless of their dietary habits and habitat preference. *Echiothrix centrosa* is a ground dweller, feeding mainly on earthworms (Musser & Durden, 2014) while *M. rothschildi* is of arboreal nature principally, consuming a mainly abrasive vegetable diet (Flannery *et al.*, 1989). *Trichuris* eggs are unembryonated when passed in the host feces and take several weeks to one month in a humid environment to become infective, but require no intermediate host (Anderson, 2000). The hosts acquire the infection by eating diets or drinking water contaminated with embryonated eggs. This life history pattern may facilitate host-shifts. Actually, occurrence of such host-shift events in *Trichuris* evolution has been suggested by molecular phylogenetic studies (cf. Callejón *et al.*, 2015; Doležalová *et al.*, 2015).

The present two new species resemble each other by having a sharply pointed spicule with lined pit-like structures on one side near distal end. The pit-like structures are surmised to be of sensory nature as are those observed at the dull distal end of the spicule of *T. muris* (see Wright, 1978). The morphological resemblance in the spicule morphology between the present two new species suggests their close phylogenetic relationship. Although *Echiothrix* and *Mallomys* are old-endemic murine genera of the area, they belong to different tribes, Rattini and Hydromini, and were considered to have diverged in the Tortonian era of the Miocene about 12.5 million years ago (Fabre *et al.*, 2013; Rowe *et al.*, 2016). It remains to be elucidated whether the morphological resemblance between the two new species of *Trichuris* described herein is only homoplasy or actually reflects a close phylogenetic relationship of the parasites.

Identification of *Trichuris* species is generally difficult because their cephalic end is very minute for observation by light microscopy and the caudal region of the male lacks multiple caudal papillae or bursal rays that provide distinguishing characteristics in other groups of parasitic nematodes. Presence or absence of a cephalic stylet and protuberance at the vulval portion are often used as key characters. The taxonomic significance of these features remains unsure, however, because the former was often difficult to be observed and the latter may vary depending on the maturation and physiological condition of worms (cf. Skrjabin *et al.*, 1957). The number of stichocytes has been also regarded as a key feature. However, the number of stichocytes is difficult to count because a stichocyte is usually subdivided, these subdivisions often being indistinguishable from the actual divisions between stichocytes. Instead, the number of nuclei of stichosomes is rather easy to be counted. The number of nuclei does not coincide with the number of stichocytes because plural nuclei are often present in a stichocyte. The number of subdivisions per nucleus differed between the present two species. Taxonomical significance of the nuclei number should be further investigated in other congeners.

Published records of *Trichuris* in murids of Indonesia are very limited even in commensal rats. Wireno (1978) examined many rats including 66 *Rattus tanezumi* (recorded as *Rattus rattus*) and 10 *Rattus exulans*, but did not find species of *Trichuris*. Hasegawa & Syafruddin (1995) examined 29 *R. tanezumi* (recorded as *R. rattus*) and 20 *R. exulans* on Halmahera Island, but could not collect species of *Trichuris*. In the checklist of murine helminths of Indonesia by Dewi & Purwaningsih (2013), only one record of *T. muris* from *Bunomys chrysocomus*, an endemic rat in Sulawesi, was cited. Meanwhile, *T. muris* has been recorded from commensal murines, i.e., *Rattus norvegicus*, *R. rattus* and *Mus musculus* in Australia (cf. Mackerras, 1958), as well as old endemic rats, *Hydromys chrysogaster*, *Melomys cervinipes* and *Uromys caudimaculatus* (Smales & Cribb, 1997; Smales, 2005; Smales & Spratt, 2008) in Australia and a new endemic rat, *Rattus leucopus*, of New Guinea (Smales, 1997; Smales & Cribb, 1997; Smales & Spratt, 2004). The presence of *T. muris* in the Australian endemic rats has been surmised to be a secondary adaptation which occurred after introduction by commensal murines (Smales, 2012). However, it is also possible that so-called *T. muris* in these endemic rats represent cryptic species. DNA sequence analysis of *Trichuris* species parasitic in murids in the Indonesia-Australian region is essential to understand their phylogeny and biogeographical relationship with their hosts.

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## References

- Anderson, R.C. (2000) *Nematode Parasites of Vertebrates. Their Development and Transmission*. 2nd ed. CABI Publishing, Wallingford, Oxfordshire, 650 pp.  
<https://doi.org/10.1079/9780851994215.0000>
- Anderson, R.C. & Bain, O. (1982) No. 9. Keys to genera of the superfamilies Rhabditoidea, Dioctophymatoidea, Trichinelloidea and Muspiceoidea. In: Anderson, R.C., Chabaud, A.G. & Willmott, S. (Eds.), *CIH Keys to the Nematode Parasites of Vertebrates*. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, pp. 1–26.
- Bernard, J. (1969) Quelques nématodes parasites nouveaux ou non encore signalés en Tunisie. *Archives de l'Institut Pasteur de Tunis*, 46, 397–400.
- Callejón, R., Cutillas, C. & Nadler, S.A. (2015) Nuclear and mitochondrial genes for inferring *Trichuris* phylogeny. *Parasitology Research*, 114 (12), 4591–4599.  
<https://doi.org/10.1007/s00436-015-4705-7>
- Chabaud, A.G. (1974) No. 1. Keys to subclass, orders and superfamilies. In: Anderson, R.C., Chabaud, A.G. & Willmott, S. (Eds.), *CIH Keys to the Nematode Parasites of Vertebrates*. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, pp. 6–17.
- Chandler, A.C. (1945) *Trichuris* species from California rodents. *Journal of Parasitology*, 31 (4), 248–286.  
<https://doi.org/10.2307/3273006>
- Chandler, A.C. (1946) *Trichuris peromysci* n. sp. from *Peromyscus californicus*, and further notes on *T. perognathi* Chandler, 1945. *Journal of Parasitology*, 32 (2), 208.  
<https://doi.org/10.2307/3272598>
- Dewi, K. & Purwaningsih, E. (2013) A checklist of nematode parasites from Indonesian murids. *Zootaxa*, 3608 (7), 531–546.  
<https://doi.org/10.11646/zootaxa.3608.7.1>
- Doležalová, J., Oborník, M., Hajdusková, E., Jirku, M., Petrzelková, K.J., Bolechová, P., Cutillas, C., Callejón, R., Jaros, J., Beránková, Z. & Modry, D. (2015) How many species of whipworms do we share? Whipworms from man and other primates form two phylogenetic lineages. *Folia Parasitologica*, 62, 63.  
<https://doi.org/10.14411/fp.2015.063>
- Fabre, P.H., Pagés, M., Musser, G.G., Fitriana, Y.S., Fjeldså, J., Jennings, A., Jönssoni, K.A., Kennedy, J., Michaux, J., Semiadi, G. & Supriatna, N. (2013) A new genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini), and its implication for biogeography and Indo-Pacific Rattini systematics. *Zoological Journal of the Linnean Society*, 169 (2), 408–447.  
<https://doi.org/10.1111/zoj.12061>
- Feliu, C., Spakulová, M., Casanova, J.C., Renaud, F., Morand, S., Hugot, J.P., Santalla, F. & Durand, P. (2000) Genetic and morphological heterogeneity in small rodent whipworm in southwestern Europe: Characterization of *Trichuris muris* and description of *Trichuris arvicolae* n. sp. (Nematoda: Trichuridae). *Journal of Parasitology*, 86 (3), 442–449.  
<https://doi.org/10.2307/3284855>
- Flannery, T.F., Aplin, K., Groves, C.P. & Adams, M. (1989) Revision of the New Guinean genus *Mallomys* (Muridae: Rodentia), with descriptions of two new species from subalpine habitats. *Records of the Australian Museum*, 41 (1), 83–105.  
<https://doi.org/10.3853/j.0067-1975.41.1989.137>
- Hasegawa, H., Dewi, K. & Asakawa, M. (2014) *Musserakis sulawesiensis* gen. et sp. n. (Nematoda: Heterakidae) collected from *Echiothrix centrosa* (Rodentia: Muridae), an old endemic rat of Sulawesi, Indonesia. *Zootaxa*, 3881 (2), 155–164.  
<https://doi.org/10.11646/zootaxa.3881.2.4>
- Hasegawa, H. & Syafruddin (1994) *Odilia mallomyos* sp. n. (Nematoda: Heligmonellidae) from *Mallomys rothschildi weylandi* (Rodentia: Muridae) of Irian Jaya, Indonesia. *Journal of the Helminthological Society of Washington*, 61 (2), 208–214.
- Hasegawa, H. & Syafruddin (1995) Nematode fauna of the two sympatric rats, *Rattus rattus* and *R. exulans*, in Kao District, Halmahera Island, Indonesia. *Journal of the Helminthological Society of Washington*, 62 (1), 27–31.
- Johnson, S. (1973) A new trichurid nematode from the Indian gerbil, *Tatera indica indica*. *Folia Parasitologica*, 20 (3), 275–277.
- Mackerras, M.J. (1958) Catalogue of Australian mammals and their recorded internal parasites. I-IV. *Proceedings of the Linnean Society of New South Wales*, 83 (2), 101–160.
- Musser, G.G. (1981) The giant rat of Flores and its relatives east of Borneo and Bali. *Bulletin of the American Museum of Natural History*, 169 (2), 67–176.
- Musser, G.G. (1987) The mammals of Sulawesi. In: Whitmore, T.C. (Ed.), *Biogeographical Evolution of the Malay Archipelago*. Clarendon Press, Oxford, pp. 73–93.
- Musser, G.G. & Carleton, M.D. (2005) Order Rodentia. In: Wilson, E.D. & Reeder, D.M. (Eds.), *Mammal Species of the World*:



- A Taxonomic and Geographic Reference. Vol. 2. 3<sup>rd</sup> Edition.* Johns Hopkins University Press, Baltimore, pp. 895–1531.
- Musser, G.G. & Durden, L. (2014) Morphological and geographic definitions of the Sulawesi shrew rats *Echiothrix leucura* and *E. centrosa* (Muridae, Murinae), and description of a new species of sucking louse (Phthiraptera: Anoplura). *Bulletin of the American Museum of Natural History*, 391, 1–87.  
<https://doi.org/10.1206/871.1>
- Petrov, A.M. & Potekhina, L.F. (1953) A new species *Trichocephalus spalacis* nov. sp. from a mole rat. *Trudy Instituta Gel'mintologii*, 5, 95–98. [in Russian]
- Quentin, J.C. (1966) Trichuroidea de rongeurs de République Centralafricaine. *Cahiers de la Maboké*, 4, 141–150.
- Ribas, A., López, S., Makundi, R.H., Leirs, H. & Bellocq, J.G. (2013) *Trichuris* spp. (Nematoda: Trichuridae) from two rodents, *Mastomys natalensis* and *Gerbilliscus vicinus* in Tanzania. *Journal of Parasitology*, 99 (5), 868–875.  
<https://doi.org/10.1645/12-151.1>
- Robles, M.R. (2011) New species of *Trichuris* (Nematoda: Trichuridae) from *Akodon montensis* Thomas, 1913, of the Paranaense forest in Argentina. *Journal of Parasitology*, 97 (2), 319–327.  
<https://doi.org/10.1645/ge-2434.1>
- Robles, M.R., Cutillas, C., Panei, C.J. & Callejón, R. (2014) Morphological and molecular characterization of a new *Trichuris* species (Nematoda- Trichuridae), and phylogenetic relationships of *Trichuris* species of cricetid rodents from Argentina. *PLoS ONE*, 9, e112069.  
<https://doi.org/10.1371/journal.pone.0112069>
- Rowe, K.C., Achmadi, A.S. & Esselstyn, J.A. (2016) Repeated evolution of carnivory among Indo-Australian rodents. *Evolution*, 70 (3), 653–665.  
<https://doi.org/10.1111/evo.12871>
- Sadighian, A., Ghadirian, E. & Sadjadpour, E. (1974) Two new species of nematodes of lagomorphs and rodents from Iran. *Journal of Helminthology*, 48 (4), 241–245.  
<https://doi.org/10.1017/S0022149X00022926>
- Skrjabin, K.I., Shikhobalova, N.P. & Orlov, I.V. (1957) *Essentials of Nematodology. 6. Trichocephalidae and Capillariidae of Animals and Man and the Diseases Caused by Them.* Israel Program for Scientific Translations, Jerusalem, 1970, 599 pp. [translated from Russian]
- Smales, L.R. (1997) A review of the helminth parasites of Australian rodents. *Australian Journal of Zoology*, 45 (5), 505–521.  
<https://doi.org/10.1071/zo97013>
- Smales, L.R. (2005) Helminth parasites of the grassland melomys (Muridae: Hydromyinae) from Australia and Papua New Guinea. *Australian Journal of Zoology*, 53 (6), 369–374.  
<https://doi.org/10.1071/zo05039>
- Smales, L.R. (2012) Chapter 6. Helminth parasites of hydromyine rodents from the Island of New Guinea. In: Triunverri, A. & Scalise, D. (Eds.), *Rodents*. Nova Science Publisher, New York, 99–117.
- Smales, L.R. (2013) Nematodes from the caecum and colon of *Pogonomys* (Muridae: Anisomyini) from Papua New Guinea with the description of a new genus of Oxyuridae (Nematoda: Oxyurida) and a new species of Trichuridae (Nematoda: Enoplida). *Zootaxa*, 3599 (6), 577–587.  
<https://doi.org/10.11646/zootaxa.3599.6.6>
- Smales, L.R. & Cribb, T.H. (1997) Helminth parasite communities of the water rat, *Hydromys chrysogaster*, from Queensland. *Wildlife Research*, 24 (4), 445–457.  
<https://doi.org/10.1071/WR96074>
- Smales, L.R. & Spratt, D.M. (2004) Helminth community structure in *Rattus leucopus* (Gray) (Muridae) from Australia, Papua New Guinea and Papua. *Australian Journal of Zoology*, 52 (3), 283–291.  
<https://doi.org/10.1071/ZO03051>
- Smales, L.R. & Spratt, D.M. (2008) Helminth assemblages of *Uromys* spp. (Muridae: Hydromyinae) from Australia, Papua New Guinea and Papua Indonesia and comparison with assemblages in *Melomys* spp. *Australian Journal of Zoology*, 56 (2), 85–94.  
<https://doi.org/10.1071/ZO08011>
- Suyanto, A., Yoneda, M., Maryanto, I., Maharadatunkamsi & Sugardjito, J. (1998) *Checklist of the Mammals of Indonesia. LIPI–JICA Joint Project for Biodiversity Conservation in Indonesia.* LIPI, Bogor, 34 pp.
- Tenora, F. (1969) Parasitic nematodes of certain rodents from Afghanistan. *Věstník Československé Společnosti Zoologické*, 33 (2), 174–192.
- Wiroreno, W. (1978) Nematode parasites of rats in West Java, Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health*, 9 (4), 520–525.
- Wright, K.A. (1978) Structure and function of the male copulatory apparatus of the nematodes *Capillaria hepatica* and *Trichuris muris*. *Canadian Journal of Zoology*, 56 (4), 651–662.  
<https://doi.org/10.1139/z78-093>