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Morphological Observation on *Physaloptera* Species (Nematoda: Spirurida: Physalopteridae) in Murine Rodents of Indonesia and East Asian Islands with Special Reference to Their Zoogeographical Features

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ABSTRACT. – Morphological observations of specimens from the genus *Physaloptera* spp. (Spirurida: Physalopteridae) collected from murine species in Indonesia and some islands of East Asia were made. The physalopterid worms found from *Maxomys whiteheadi* and *Maxomys bartelsii* of Kalimantan and West Java, Indonesia, respectively, *Apodemus speciosus* of the Izu Islands, Japan, *Apodemus agrarius* of Jeju Island, Korea, and *Rattus tanezumi* of Uotsuri Island, in the Senkaku Islands, Japan, were identified as *P. apodemi* Wang & Zhang, 2020, previously only reported from Tianjin, China. On the other hand, those in *Rattus argentiventer* of West Java were identified with *P. ngoci* Le-Van-Hoa, 1961 as the first geographical record outside of the continental portion of Southeast Asia. Supplemental morphological remarks were made for *P. apodemi* with special attention to the differentiation from other congeners. The distribution of *P. apodemi* on these small remote islands suggests that dispersal occurred accidentally via synanthropic rats and/or intermediate host insects that possibly escaped from shipwrecks onto these islands.

KEYWORDS: *Physaloptera, Maxomys, Apodemus, Rattus*, insular distribution, morphology, dispersal

INTRODUCTION

Nematodes of the genus *Physaloptera* Rudolphi, 1819 (Spirurida: Physalopteridae) are parasitic in the alimentary canal, mainly the stomach, of amphibians, reptiles, birds and mammals (Chabaud, 1975; Pereira et al., 2012). About one hundred species are currently recognized in the genus, but 46 of them were proposed more than 100 years ago (see Pereira et al., 2012). Many of these species proposed during the early days of research were only briefly described in the original articles, often without detailed figures, making it quite difficult to accurately identify a *Physaloptera* species at the present time. Murine rodents over the world are often known to harbor *Physaloptera* species (Morgan, 1943; Le-Van-Hoa, 1961; Wang and Zhang, 2020). In the continental portion of Southeast Asia, *Physaloptera ngoci* Le-Van-Hoa, 1961 has been reported from various murine species (Veciana et al., 2013). When we started to examine the specimens of *Physaloptera* collected from *Maxomys* spp. of Kalimantan and Java, Indonesia, we supposed that they might be *P. ngoci* because of the geographical proximity of these areas, previously connected with the continent forming Sundaland during the Pleistocene (Bird et al., 2005). Unexpectedly, however, we found that they actually represent another species, *Physaloptera apodemi* Wang & Zhang, 2020, which was recently described from a field mouse in Tianjin, China (Wang and Zhang, 2020). Moreover, it was found that the physalopterids recorded from some islands of East Asia (Hasegawa et al., 1993; Sakata et al., 2006) are conspecific with this species. In order to supplement the original description, a morphological description of this species is given herein based on light microscopy and scanning electron microscopy (SEM), enhanced with a biogeographical discussion.

MATERIALS AND METHODS

The following specimens of *Physaloptera* collected from the stomach of murines were utilized for the present study. They were deposited in the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB), National Museum of Nature and Science, Tsukuba, Japan (NSMT) and United States National Museum of Natural History (USNM). The localities are shown in Fig. 1 along with some localities referred to in the text.

1. Fifteen males and 7 females from *Maxomys whiteheadi* captured in Bukit Soeharto, Kalimantan, July 1993 (MZB Na 837, 838, NSMT-As 4628).

2. One male and 2 females from *Maxomys bartelsii* captured in Cibodas, West Java, 1975 (Wiroreno, 1978) (MZB Na 53).

3. Six males and 9 females from *Apodemus speciosus* captured on Izu-oshima Is., Miyakejima Is. and Kozushima Is. of the Izu Islands, Japan, during the period from 1984 to 1998 (Sakata et al., 2006) (NSMT-As 4629, 4630, 4631).

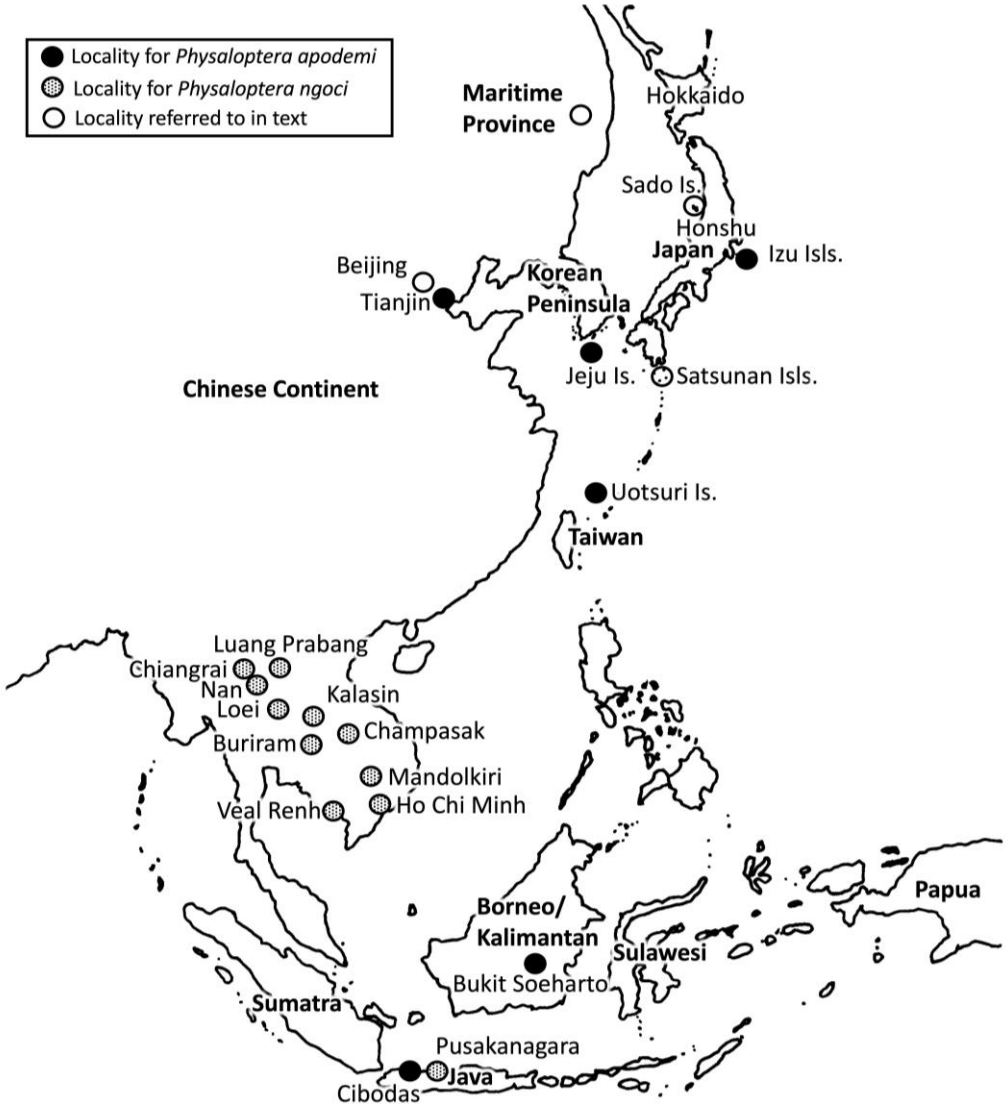

FIGURE 1. A map of Asia showing the localities where the described worms were collected and the localities where *Physaloptera apodemi* and *Physaloptera ngoci* have been recorded previously. Some additional localities referred to in the text are also shown.

4. Nine males and 5 females from *Apodemus agrarius* captured on Jeju Island, Korea, 16 December 1982 (NSMT-As 4632).

5. Six males and 6 females from *Rattus tanezumi* (originally recorded as *R. rattus*) captured on Uotsuri Island, Senkaku Island chain, Japan, in 1979 (Hasegawa et al., 1993) (NSMT-As 4633).

6. Three males and 3 females from *Rattus argentiventer* in Pusakanagara, West Java, Indonesia, February 1981 (Hasegawa et al., 1992) (MZB Na 234, USNM 1377523).

Methods of collection of the host murines were given in Hasegawa et al. (1993), Sakata et al. (2006), and Asakawa and Hasegawa (2018). The nematodes were isolated from the viscera resected and preserved in 10% formalin. They were cleared in lactophenol solution or chloral gum and temporarily mounted on glass slides for morphological observation under a BX50 microscope equipped with an interference contrast apparatus (Olympus Corporation, Tokyo, Japan). Uterine branching pattern and accurate spicule length were confirmed by dissection. Figures were made using an Olympus U-DA drawing tube. For SEM observation, nematodes were re-fixed in glutaraldehyde and cacodylate buffer, dehydrated in ethanol concentration series beginning from 50% to absolute, vacuum-dried at least for 30 minutes using TAITEC VC-96N, mounted in a specimen stub, and then coated with gold at 5–8 mÅ for 5 min. They were examined using a JEOL JSM-IT 200 scanning electron microscope at an accelerating voltage of 5 kV. Number assignment to the male caudal papillae follows Chabaud (1956).

RESULTS

Because all of the worms were collected more than 20 years ago, it was difficult to make them transparent enough for microscopical examination. Those from Kalimantan had more or less shrunk, while worms from Izu Islands were fixed in a relaxed condition. Those from Jeju Island had distended and wrinkled cuticles due to inadequate penetration of the fixative. Moreover, the specimens (6 males and 3 females) from Uotsuri Island deposited in the museum were found to have deteriorated during preservation, and only 3 separately preserved females could be observed. Also, the specimens from *Rattus argentiventer* of West Java were found to be unsuitable for detailed re-observation. For these worms, morphological and morphometrical data were based on unpublished observation made by the senior author (H.H.) in the 1990's.

The physalopterids shared common morphological features as described below except those from *R. argentiventer* of West Java, which differed in the number of uterine branches.

REDESCRIPTION

Physaloptera apodemi Wang & Zhang, 2020

(Figs. 2, 3)

General: Medium-sized stout worm tapering to anterior end (Fig. 2A). Cuticle finely striated transversely. Cephalic collarette present (Figs. 2A – 2C, 3A, 3D). Mouth dorsoventrally elongated, surrounded by two developed lateral pseudolabia (Figs. 2B, 2C, 3A, 3D). Each pseudolabium with one large externolateral tooth and three small internolateral teeth of similar sizes apically; submedian teeth absent (Figs. 2B, 2C, 3A, 3D). Esophagus divided into anterior short muscular portion and posterior long glandular portion (Fig. 2A). Maximum width of muscular portion of esophagus near anterior end. Nerve ring surrounding posterior portion of muscular esophagus; excretory pore with canal directing anteriorly (Fig. 2A). Deirids minute, pointed, symmetrical or subsymmetrical, usually slightly anterior to, but sometimes at same level with excretory pore (Figs. 2A, 2D).

Male: Caudal alae well developed, vesicular, united on ventral surface anterior to anus (Figs. 2F, 3B, 3E). Area rugosa prominent, extending posterolaterally to level of posterior-most pair of caudal papillae (Figs. 2F, 3B, 3E). Four pairs of pedunculate papillae (I – IV) and six pairs of sessile papillae (V – VII, IX –XI) and one unpaired sessile papilla (VIII) present in typical arrangement: first pair (I) of pedunculate papillae inside of area rugosa; other pedunculate papillae situated at peripheral border of area rugosa (Figs. 2F, 3B, 3E). One pair of sessile papillae (IX) and one unpaired median sessile papilla (VIII) just anterior to anus; two pairs of sessile papillae (X, XI), closely set, on posterior rim of anus; two pairs of sessile papillae (V, VI) in anterior half of tail; one pair of sessile papillae (VII) situated in posterior half of tail (Figs. 2F, 3B). Considerable variations, including excess, absence, translocation and/or fusion of papillae also observed (Fig. 3E). Phasmidial pores slightly anterior to posterior-most sessile papillae (VII) (Figs. 2F, 3B, 3E). Round elevation of caudal gland present between posterior-most sessile papillae (Figs. 2F, 3B, 3C, 3E). Spicules dissimilar, right spicule shorter than but almost same width with left spicule, both with pointed tips, often with wrinkled sheath (Fig. 2E).

Female: Vulva slightly posterior to esophago-intestinal junction, not prominently protruded (Fig. 2G). Vagina long, muscular, running posteriorly; vagina uterina relatively short, divided into two uterine branches (Fig. 2H). Tail round, often with greatly distended cuticle (Fig. 2I). Eggs ellipsoidal, thick-shelled, containing developed larva (Fig. 2J).

Measurements: Given in Tables 1 and 2.

Taxonomic summary

Hosts: Maxomys whiteheadi, *Maxomys bartelsii*, *Apodemus speciosus*, *Apodemus agrarius*, *Rattus tanezumi* (Rodentia: Muridae: Murinae).

Site of infection: Stomach.

Localities: Bukit Soeharto, Kalimantan and Cibodas, West Java, Indonesia, Izu Islands and Uotsuri Island, Senkaku Islands, Japan and Jeju Island, Korea.

Remarks

The present worms are morphologically identical with *P. apodemi* though the internolateral teeth are almost equal and the eggs are somewhat larger (Tables 1, 2). In the original description, Wang and Zhang (2020) distinguished *P. apodemi* from 14 congeners known from rodents. However, the 14 species included *Physaloptera troughtoni* Johnston & Mawson, 1941, which was synonymized with *Physaloptera banfieldi* Johnston & Mawson, 1941 (see Smales 2005), and *Physaloptera funambuli* Parihar & Nama, 1978, which was transferred to *Abbreviata* Travassos, 1920 (see Pereira, 2012). Meanwhile, they seemed to have overlooked 7 more species recorded from rodents, namely *P. circularis* Linstow, 1897 (Type host: *Rattus rattus*; Type locality: Madagascar), *P. getula* Seurat, 1917 (*R. rattus*; Morocco), *P. inermis* Linstow, 1906 (*Sciurus pervosti*; Germany), *P. ruwenzorii* Parona, 1907 (*Arvicanthis abyssinus*; Uganda), *P. sciuri* Parona, 1898 (*Sciurus melanogaster*; Indonesia), *P. spinicauda* McLeod, 1933 (*Citellus* spp.; Canada) and *P. torresi* (Travassos, 1920) (*Agouti paca*, *Dasyprocta aguti*;

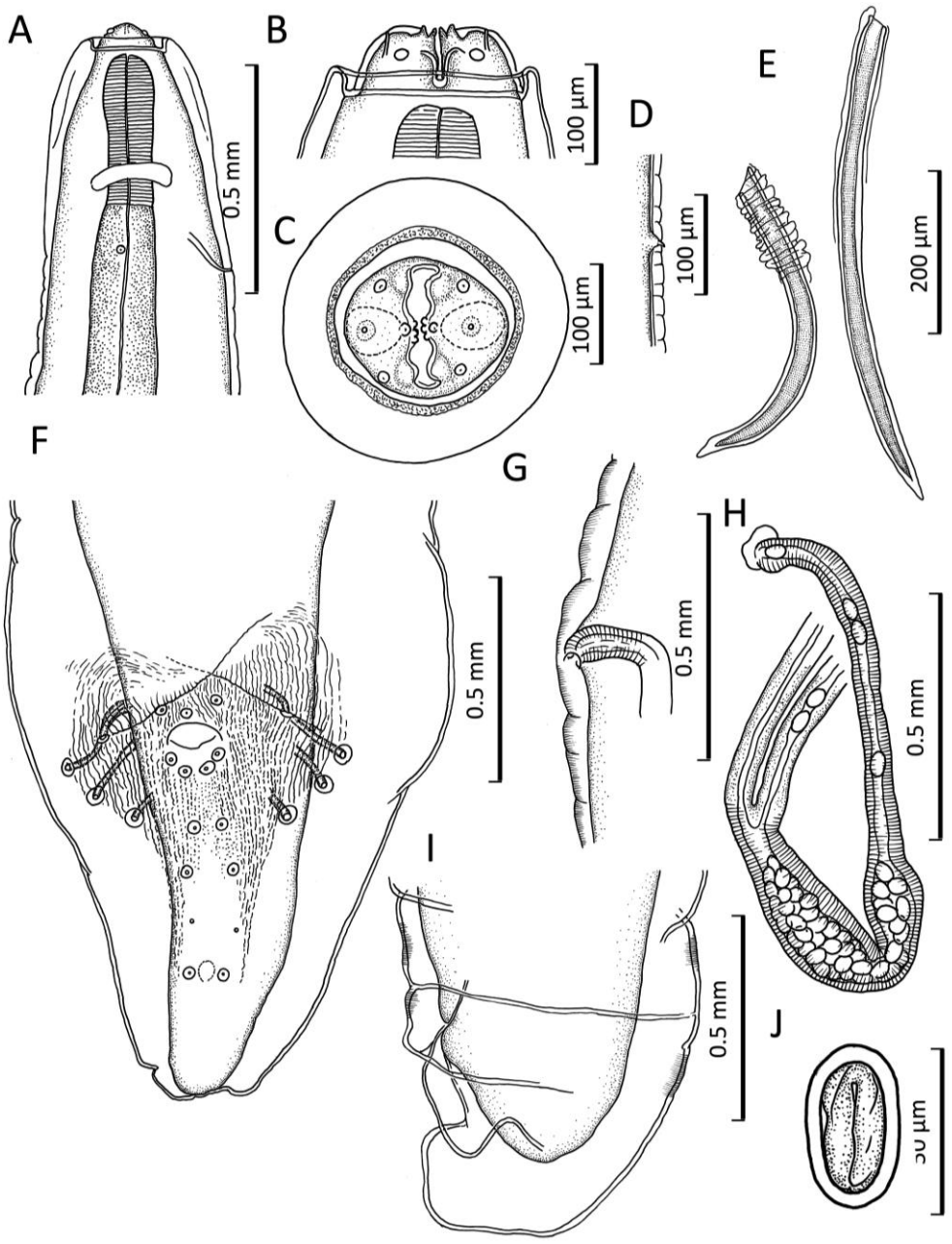

FIGURE 2. *Physaloptera apodemi* collected from *Maxomys whiteheadi* of Kalimantan, Indonesia. **A–C.** Anterior extremity of male, right lateral (A), ventral (B) and apical (C) views. **D.** Deirid, ventral view. **E.** Spicules dissected out. **F.** Posterior end of male, ventral view showing area rugosa and typical arrangement of caudal papillae. **G.** Vulval region, left lateral view. **H.** Vagina and ovejector, dorsal view. **I.** Tail of female, left lateral view. **J.** Egg.

Brazil). Wang and Zhang (2020) considered that *P. apodemi* is differentiated from the known congeners by having 22 caudal papillae, striated sheaths of spicules, a vulva located in the anterior fifth of body, and egg size. However, the structure called as 'post-cloacal single sessile papilla' by them was presumably the elevation of the caudal gland (see Seurat, 1917), which has been often confused with a sessile papilla (e. g. Pereira et al., 2012; São Luiz et al., 2015). The transverse striae of the spicular sheath have been described and/or figured in some physalopterids (e.g., Quentin, 1968; Ederli et al., 2018; Pereira et al., 2012). Because such striae could be formed by contraction from the movement of the spicule, their taxonomical significance remains unsettled.

The vulval position in the anterior fifth of the body is also observed in *P. banfieldi* and *P. getula* (Johnston and Mawson, 1941; Seurat, 1917). Hence, the validity of *P. apodemi* should be further proved based on other characteristics.

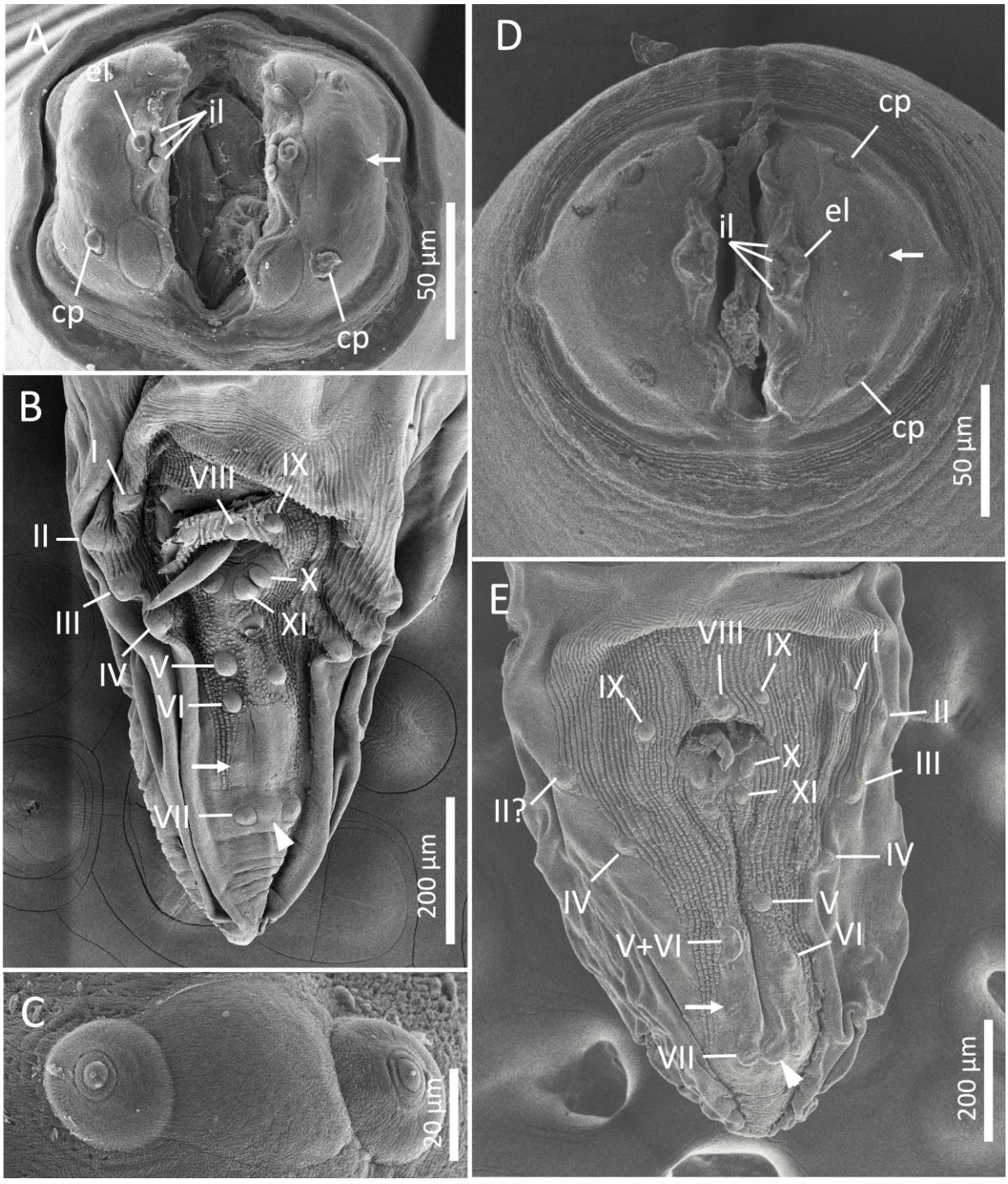

FIGURE 3. Scanning electron micrographs of *Physaloptera apodemi*. **A – C.** Male collected from *Maxomys whiteheadi* of Kalimantan, Indonesia, anterior extremity, apical view (A), posterior extremity, ventral view (B) and magnified view of posterior most pair of caudal papillae (C). **D – E.** Male collected from *Apodemus speciosus* of Izu Islands, Japan. Anterior extremity, apical view (D) and posterior extremity, ventral view (E). Abbreviations: cp. cephalic papilla; el. externolateral tooth; il. internolateral teeth; I – XI. caudal papilla number according to Chabaud (1956); Arrow and arrowhead showing phasmidial pore and elevation of caudal gland, respectively.

Seven species, namely, *P. banfieldi*, *P. bispiculata* Vaz & Pereira, 1935, *P. getula*, *P. hispida* Schell, 1950, *P. massino* Schulz, 1928, *P. murisbrasiliensis* Diesing, 1861 and *P. spinicauda*, have two uterine branches, as in *P. apodemi* females. However, *P. banfieldi* has 6 pairs of pedunculate papillae (Johnston and Mawson, 1941), *P. bispiculata* has lateral alae in the cervical portion and a hook-like process near the distal end of the shorter spicule (Vaz and Pereira, 1935), *P. getula* has five pairs of ‘outer’ (pedunculate?) papillae and

TABLE 1. Measurements of *Physaloptera* spp. males collected from murids of Indonesia and some islands of the Far East in comparison with type material of *P. apodemi* (range followed by mean in parenthesis; in mm unless otherwise stated).

Species	***Physaloptera apodemi***						***Physaloptera ngoci***
Host	***Maxomys whiteheadi***	***Maxomys bartelsi***	***Apodemus speciosus***	***Apodemus agrarius***	***Rattus tanezumi***	***Apodemus sylvaticus***	***Rattus argentiventer***
Locality	**Kalimantan, Indonesia**	**Java, Indonesia**	**Izu Islands, Japan**	**Jeju Island, Korea**	**Uotsuri Island, Japan**	**Tianjin, China*1**	**Java, Indonesia**
[No. worms measured]	[15]	[1]	[8]	[9]	[6]	[10]	[4]
Length	11.6 – 16.1 (14.3)	16.6	10.0 – 21.2 (15.0)	9.3 – 15.2 (12.1)	9.3 – 20.2 (12.9)	13. 7 – 18.3 (15.9)	10.6 – 14.0 (12.3) [n=2]
Width in midbody	0.80 – 1.02 (0.91)	0.86	0.37 – 1.08 (0.81)	0.48 – 0.80 (0.66)	0.38 – 0.96 (0.66)	0.79 – 1.14 (0.94)	0.65 – 0.81 (0.73) [n=3]
Cephalic diameter	0.13 – 0.16 (0.14)	0.15	0.09 – 0.16 (0.14)	0.12 – 0.15 (0.13)			
Muscular esophagus length	0.27 – 0.58 (0.41)	0.55	0.31 – 0.50 (0.40)	0.27 – 0.33 (0.29) [n=5]	0.28 – 0.51 (0.37)	0.43 – 0.56 (0.48)	0.40 [n=1]
Muscular esophagus width	0.10 – 0.17 (0.13)	0.11	0.08 – 0.15 (0.13)	0.10 – 0.13 (0.11) [n=5]	0.07 – 0.14 (0.10)		0.11 [n=1]
Glandular esophagus length	1.96 – 2.87 (2.50)	2.79	1.41 – 3.11 (2.50)	1.75 – 2.41 (2.08) [n=7]	1.70 – 2.88 (2.06)	2.21 – 2.91 (2.54)	2.57 – 3.19 (2.88) [n=2]
Glandular esophagus width	0.25 – 0.33 (0.30)	0.26	0.14 – 0.32 (0.28)	0.18 – 0.31 (0.23) [n=7]	0.15 – 0.28 (0.21)		0.23 – 0.28 (0.26) [n=2]
Nerve ring*2	0.26 – 0.45 (0.35)	0.44	0.32 – 0.45 (0.41)	0.25 – 0.33 (0.29) [n=4]	0.27 – 0.48 (0.35)	0.39 – 0.47 (0.44)	
Excretory pore*2	0.30 – 0.85 (0.53)	0.79	0.55 – 0.97 (0.77)	0.37 – 0.51 (0.44) [n=2]	0.51 – 0.86 (0.69) [n=4]		
Deirids*2	0.35 – 0.73 (0.49)	-	0.54 – 0.84 (0.71)		0.51 – 0.78 (0.64) [n=4]	0.69 – 0.85 (0.78)	
Right spicule length	0.21 – 0.39 (0.31) [n=4]	0.39			0.16 – 0.25 (0.21) [n=4]	0.35 – 0.40 (0.38)	0.25 – 0.28 (0.27)
	0.41 – 0.44 (0.43)*3 [n=2]		0.40 – 0.44 (0.42)*3 [n=2]	0.27 – 0.34 (0.31)*3 [n=3]			
Left spicule length	0.54 – 0.58 (0.56) [n=4]	0.57			0.26 – 0.42 (0.34) [n=4]	0.45 – 0.53 (0.48)	0.35 – 0.53 (0.44)
	0.59 (0.59)*3 [n=2]		0.54 – 0.55 (0.55)*3 [n=2]	0.39 – 0.46 (0.42)*3 [n=3]			
Tail length	0.75 – 1.09 (0.89)	1.09	0.39 – 0.97 (0.75)	0.82 – 1.14 (0.95)	0.36 – 0.98 (0.61)	0.62 – 0.99 (0.80)	0.57 – 0.68 (0.61)

*1 Data by Wang and Zhang (2020). *2 Distance from cephalic apex. *3 Based on spicules dissected out.

TABLE 2. Measurements of *Physaloptera* spp. females collected from murids of Indonesia and some islands of the Far East in comparison with type material of *P. apodemi* (range followed by mean in parenthesis; in mm unless otherwise stated).

Species	***Physaloptera apodemi***						***Physaloptera ngoci***
Host	***Maxomys whiteheadi***	***Maxomys bartelsi***	***Apodemus speciosus***	***Apodemus agrarius***	***Rattus tanezumi***	***Apodemus sylvaticus***	***Rattus argentiventer***
Locality	**Kalimantan, Indonesia**	**Java, Indonesia**	**Izu Islands, Japan**	**Jeju Island, Korea**	**Uotsuri Island, Japan**	**Tianjin, China*[1]**	**Java, Indonesia**
[No. worms measured]	[7]	[1]	[10]	[5]	[6]	[10]	[4]
Length	18.7 – 22.5 (21.0)	23.7	15.1 – 27.8 (23.6)	17.6 – 27.1 (22.0)	18.2 – 38.8 (31.0)	24.5 – 32.6 (29.4)	21.3 – 29.4 (25.1) [n=3]
Width in midbody	1.16 – 1.44 (1.34)	1.09	0.59 – 1.28 (1.00)	0.96 – 1.36 (1.11)	1.02 – 1.58 (1.32)	1.19 – 1.71 (1.42)	0.83 – 1.01 (0.90)
Cephalic diameter	0.15 – 0.23 (0.20)	0.19	0.13 – 0.22 (0.18)	0.16 – 0.19 (0.17)	0.17 – 0.23 (0.21) [n=3]		
Muscular esophagus length	0.31 – 0.53 (0.44) [n=5]	0.52	0.34 – 0.53 (0.47)	0.35 – 0.51 (0.42)	0.40 – 0.59 (0.50)	0.49 – 0.62 (0.57)	0.51 – 0.52 (0.52)
Muscular esophagus width	0.13 – 0.18 (0.15) [n=4]	0.12	0.10 – 0.20 (0.17)	0.12 – 0.16 (0.14)	0.13 – 0.20 (0.17)		0.11 – 0.15 (0.13)
Glandular esophagus length	2.90 – 4.86 (3.00) [n=5]	3.58	2.15 – 3.54 (3.00)	2.33 – 3.66 (2.81)	2.84 – 4.16 (3.61)	3.22 – 4.08 (3.59)	2.95 – 3.41 (3.17)
Glandular esophagus width	0.30 – 0.38 (0.35) [n=6]	0.33	0.24 – 0.37 (0.32)	0.25 – 0.35 (0.28)	0.26 – 0.45 (0.37)		0.21 – 0.28 (0.24)
Nerve ring*[2]	0.28 – 0.50 (0.39) [n=6]	0.42	0.34 – 0.53 (0.47)	0.30 – 0.47 (0.38)	0.37 – 0.61 (0.49)	0.47 – 0.55 (0.50)	0.44 – 0.55 (0.49)
Excretory pore*[2]	0.45 – 0.97 (0.72) [n=6]	0.72	0.65 – 0.98 (0.90) [n=9]	0.52 – 0.83 (0.65)	0.65 – 1.28 (1.04)		0.60 – 0.94 (0.76)
Deirids*[2]	0.52 – 0.65 (0.59) [n=2]	-	0.58 – 0.96 (0.80)		0.57 – 1.08 (0.87)	0.79 – 1.21 (0.94)	0.56 – 0.91 (0.71)
Vulva*[2]	2.43 – 4.16 (3.18)	4.74	3.90 – 7.58 (5.70)	2.34 – 3.34 (2.90)	5.43 – 8.70 (6.47)	4.52 – 7.71 (5.68)	2.21 – 5.33 (3.11)
% to worm length	11.5 – 18.9 (15.2)	20.0	20.2 – 27.7 (24.1)	11.9 – 14.6 (13.2)	14.8 – 29.8 (22.3)	16.8 – 24.1 (19.7)	10.6 – 18.1 (13.2) [n=3]
No. of uteri	2	2	2	2	2	2	4
Tail length	0.30 – 0.58 (0.47) [n=6]	0.48	0.21 – 0.60 (0.50)	0.45 – 0.62 (0.53)	0.35 – 0.90 (0.61) [n=4]	0.51 – 0.63 (0.56)	0.50 – 0.59 (0.54) [n=3]
Eggs (µm)	43 – 49 (46)	44 – 48 (46)	45 – 50 (48)	40 – 50 (46)	44 – 49 (46)	39 – 44 (42)	46 – 50 (49)
	x 27 – 30 (29) [n=25]	x 25 – 30 (28) [n=25]	x 26 – 28 (27) [n=25]	x 24 – 26 (25) [n=25]	x 24 – 30 (26) [n=25]	x 21 – 27 (24)	x 34 – 36 (35) [n=6]

*[1] Data by Wang and Zhang (2020). *[2] Distance from cephalic apex.

spinous cuticular ornamentation in the area rugosa and thicker right spicule in males (Seurat, 1917, 1937), *P. hispida* has a right spicule longer than the left one (Schell, 1950), *P. massino* has the posterior-most caudal papillae at the middle of the tail (Skrjabin and Sobolev, 1964), *P. murisbrasiliensis* has a large unpaired sessile papilla between the second and third postanal papillae and equal spicules (Ortlepp, 1922), all being readily distinguished from *P. apodemi*. The original description of *P. spinicauda* was rather vague, but Morgan (1943) synonymized it with *P. massino* after examining the type material.

A uterine branching pattern was not previously described in *P. calnuensis* Sutton, 1989, *P. circularis*, *P. inermis*, *P. longispicula* Quentin 1968, *P. ruwenzorii*, and *P. sciuri*. However, they could be distinguished from *P. apodemi* by the following characteristics: *P. calnuensis* has a vulva posterior to the middle of the body (Sutton, 1989); *P. inermis* has a much longer spicule, 2.37 mm long in a male of 21.5 mm long and four pairs of equidistant ventral papillae, of which the anterior-most pair situated at about the middle of the tail (Ortlepp, 1922); *P. longispicula* has a much larger body (male of 34.4 mm long) and longer spicules (right 0.71 mm, left 0.85 mm), and posterior-most papillae positioned in the middle of the tail (Quentin, 1968); *P. ruwenzorii* and *P. sciuri* have a large unpaired median papilla posterior to the anus (Ortlepp, 1922). In the original description of *P. circularis*, some papillae might have been overlooked, and this species was suggested to be the same or a closely allied species of *P. murisbrasiliensis* (Ortlepp, 1922).

All of the present hosts and localities are new records for *P. apodemi*. However, it is questionable that the type host in China was *A. sylvaticus* because this species is distributed only in Europe and Northwestern Africa (Alcántara, 1991). The actual type host may be *A. agrarius*, of which infection with *P. apodemi* was proved herein, or *A. peninsulae*. From *A. agrarius* and *Niviventer confucianus* at Zhoukoudian, Beijing, Zhang (1985) recorded adults of *Pentadentoptera mustelae* (Zhang & Yin, 1980) (=*Physalopteriata mustelae*), which was described from a weasel (Zhang and Yin, 1980). Nevertheless, it is questionable that a physalopterid species has such a wide host range covering carnivores and rodents. In Far East Russia, an immature *Physaloptera* sp. was recorded from '*Apodemus speciosus*' (?*A. peninsulae*) at the left bank of the River Amur in Maritime Province by Kontrimavichus and Chochlowa (1964), who surmised that the mouse as a paratenic host. Careful re-examination of these physalopterids from *Apodemus* may be necessary to determine their association with *P. apodemi*.

***Physaloptera ngoci* Le-Van-Hoa, 1961**

Morphology: Similar to *P. apodemi* redescribed above but female with four uterine branches. Measurements are given in Tables 1and 2.

Taxonomic summary

Host: Rattus argentiventer.
Site in host: Stomach.
Locality: Pusakanagara, West Java, Indonesia.

Remarks

Physaloptera ngoci was originally described from *Rattus norvegicus* of Saigon (Ho-Chi-Minh), Vietnam (Le-Van-Hoa, 1961), and has been known from various murines of the continental portion of Southeast Asia including *R. argentiventer* of Veal Renh, Cambodia (Veciana et al., 2013). This is the first record of *P. ngoci* outside of the continental portion of Southeast Asia.

DISCUSSION

In the systematics of *Physaloptera*, the uterine branching pattern has been regarded as one of the key characteristics (Seurat, 1917; Travassos, 1920; Ortlepp, 1922; Chabaud, 1956, 1975). The presence of two *Physaloptera* species with different numbers of uterine branches in murines of Southeast Asia is of special interest. Because *P. apodemi* and *P. ngoci* closely resemble each other, it is difficult to distinguish them by observing only the external morphology. Host specificity seems to not be very strict as they were found from murines of various genera (Veciana et al., 2013; this study). Hence, it is surmised that both species are distributed widely in Southeast Asian murines.

It should be noticed that *Apodemus* spp. are naturally distributed in insular localities, which were found positive for *P. apodemi* in the present study (see Musser and Carleton, 2005; Ohdachi et al., 2015). For *A. agrarius* on Uotsuri Is. and Jeju Is., dispersal from the neighboring continent/mainland through land bridges formed in the Pleistocene is plausible. Interestingly, genetic analyses revealed that the *A. agrarius* population on Jeju Is. forms a distinct lineage from those in the Korean Peninsula and the Chinese Continent (Koh et al., 2014; Latinne et al., 2020). Meanwhile, rafting dispersal has been suggested for *A. speciosus* on the Izu Islands (cf. Takada et al., 2006). Curiously, the *A. speciosus* populations on Kozushima Is. and Miyakejima Is. belong to clade II of mitochondrial cytochrome *b* gene, which is found in peripheral areas of Japan, namely Hokkaido, Sado Is. and Satsunan Islands. Meanwhile, the population on Izu-oshima Is. belongs to clade I in the neighboring Honshu mainland (Suzuki et al., 2004). However, it is

questionable that the dispersal of *P. apodemi* was made with the host *Apodemus* because *Physaloptera* has not been observed from any murid species of the neighboring mainlands of Japan and Korea (see Asakawa 1997; Seo et al., 1968; Lee et al., 2013; Sohn et al., 2014). Instead, it is more plausible that *P. apodemi* was introduced by synanthropic rats and/or intermediate host insects that escaped from ships. Such a dispersal pattern was previously surmised for *Subulura* (*Murisubulura*) *suzukii* Yagi & Kamiya, 1981 (Nematoda: Subuluridae), which is also known only on remote islands of Japan and a few limited localities in the main islands of Japan (Dewi et al., 2018).

The distribution of *Physaloptera* spp. on the islands in the Pacific shows complicated various features. *Physaloptera murisbrasiliensis* was reported from *R. rattus* and *R. norvegicus* on the Hawaii Islands (Swanson 1939; Ash, 1962) and from *Rattus exulans* in the Tokelau Islands (Mosby and Wodzicki, 1972); *P. getula* was highly prevalent among *R. rattus* in Manawatu District, North Island, New Zealand (Charleston and Innes, 1980). Because these islands had no endemic rodents, the host rats and their *Physaloptera* were apparently introduced by human activities (Roberts, 1991; Harper and Bunbury, 2015). Unfortunately, the morphological bases of identification of *P. murisbrasiliensis* and *P. getula* on these Pacific islands have not been described in detail. Therefore, close re-examination of *Physaloptera* spp. worms from the Pacific region is necessary to understand their species composition.

Because *Physaloptera* worms are generally stout and resistant to clearing procedure, the uterine branching pattern can often be confirmed only by a destructive examination. Besides the uterine branching pattern, the shape of the spicules and caudal papillae arrangement of males have been used as useful distinguishing features. However, the spicules are usually positioned obliquely in the thick body, preventing accurate *in situ* measurement. Moreover, the similarity/dissimilarity of the left and right spicules can vary in some species (see descriptions of *P. getula* by Seurat, 1917 and 1937). The caudal papillae arrangement in males of *Physaloptera* may also have intraspecific variations (see Norman and Beveridge, 1999). Employment of DNA sequencing technology such as that used by Maldonado et al. (2019) is needed for strict species identification and also for a better understanding of the dispersal history of *Physaloptera* in murine hosts.

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