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New species of *Neoapenesia* (Hymenoptera: Bethylidae) from Japan, with special remarks on female morphology and bionomics

Hikaru SAWADA¹, Mamoru TERAYAMA² and Toshiharu MITA¹

¹Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Atsugi, Japan and ²Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan

Abstract

A bethylid wasp is described as Neoapenesia makiharai n. sp. based on adults obtained from dead wood collected from the Ryukyus, Japan. The male is distinguishable from N. leytensis Terayama, the monotypic species of the genus, on the basis of the following characteristics: presence of short 2Rs vein, rounded propodeum, absence of sculpture on propodeum, widened subgenital plate, and apically rounded aedeagus. The female of *Neoapenesia* is described for the first time. Its morphological characteristics closely resemble those of Apenesia, but sex association was confirmed by the following facts: partial mitochondrial COI gene sequences (582 bp) of males and females were identical, and mating behavior was often observed. The female is easily distinguishable from females of Apenesia on the basis of the following characteristics: distinctly short antenna (not reaching posterior margin of head) and a disproportionately large head (head width about twice the dorsal pronotal width). Although females were active at night, males were active in the daytime and copulation was observed during this period. Since the female is larger than the male, phoretic copulation may not occur. Dead wood was collected and kept in plastic bags, from which a total of 16 species of coleopteran wood-borers and two predators were obtained together with N. makiharai n. sp. Many individuals of N. makiharai n. sp. were reared from dead wood severely affected by Cerecium longicorne and it was the most common species obtained from our wood samples. Therefore, the cerambycid species is considered a potential host species.

Key words: Cerambycidae, host, mating behavior, mtDNA.

INTRODUCTION

Neoapenesia Terayama, 1995 is a monotypic bethylid genus based on *N. leytensis* Terayama, 1995 from the Philippines. Although the female is unrecorded, the male is easily distinguished from other related genera of Pristocerinae by the short antenna, absence of notaulus, and three stalks on the subgenital plate. Dozens of bethylid wasps are sometimes found in dead wood on the forest floor. They are parasitoids of wood-boring

Correspondence: Toshiharu Mita, Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, 1737 Funako, Atsugi, Kanagawa 243-0034, Japan.

Email: tkp_ex@hotmail.com

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coleopteran larvae. We obtained females and males of Pristocerinae from dead wood collected from the Ryukyus, southwestern Japan. The males are considered Neoapenesia, but the females appear to be Apenesia, according to the keys to genera of world Bethylidae (Terayama 2003; Lanes & Azevedo 2007). Although the classification of males and females based on morphology is incongruent, they should be the same species because copulation was frequently observed. Members of Pristocerinae show great sexual dimorphism and females have been rarely collected. Therefore, the association between genders is not understood well, and many species, even genera, are known only by the males (Gordh & Moczar 1990; Terayama 1996). Finnamore and Gauld (1995) regarded Apenesia as a junior synonym of Pristocera Klug, 1808. On the other hand, Terayama (1996) demonstrated their generic differences following cladistic analysis. However, the analysis was only based on male morphology because of the lack of information concerning females. Further understanding of the sexual dimorphism and morphology of the female will result in a better classification of *Apenesia* and related genera.

In the present study, we clarify their identity based on observations of morphological characteristics in comparison to *N. leytensis*, mating behavior, and partial mitochondrial cytochrome oxidase subunit I (*COI*) gene sequences, and describe them as a new species of *Neoapenesia*. We also report and discuss the bionomics and potential host of this species.

MATERIALS AND METHODS

Collection and observation

Dead wood was collected in 2011 and 2012 from the Ryukyus, southern Japan. It was packed in five large plastic bags and kept in the laboratory at around 25°C under a natural photoperiod. Wood-boring beetles and newly emerged bethylid wasps were collected (Table 2) once or twice a week. The behavior of adult wasps observed (daytime 07.00-18.00 h; nighttime 21.00-02.00 h). Observations were conducted under room light. Some specimens collected by Mr Hiroshi Makihara (Forestry and Forest Products Research Institute, Tsukuba, Japan) were also examined. All specimens examined are deposited in the Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Atsugi, Japan (TUA), but specimens referenced as "NIAES" were deposited in the National Institute for Agro-Environmental Sciences, Tsukuba, Japan.

Molecular experiments

To confirm the couplet of the species, partial mitochondrial COI sequences of males and females that emerged from a single piece of dead wood were compared. Fresh specimens kept in 99% ethanol were used for molecular experiments. Sclerodermus harmandi (Buysson) obtained from the same wood was used as an outgroup. DNA samples were extracted from legs obtained from one side (fore, middle and hind legs) using the DNeasy Tissue Kit (Qiagen, Tokyo, Japan). The DNA barcode region of mitochondrial COI gene was amplified using the universal primers 5'- GGTCAACAAATCATAAAGA TATTGG- 3' (HCO1490) and 5'- TAAACTTCAGGG TGACCAAAAATCA-3' (LCO2198) designed by Folmer et al. (1994) (Jinbo et al. 2011). The polymerase chain reaction (PCR) program in a DNA thermal cycler was as follows: pre-heated to 94°C followed by 35 cycles at 94°C for 30 s, 50°C for 1 min, 72°C for 1 min,

Table 1 Specimens of *Sclerodermus harmandi* and *Neoapenesia makiharai* n. sp. used for DNA extraction[†]

Species	ID	Sex	Accession #		
Sclerodermus harmandi	HS08	F	AB795306		
Neoapenesia makiharai	HS05	M	AB795307		
N. makiharai	HS06	F	AB795308		
N. makiharai	HS09	M	AB795309		
N. makiharai	121024G	M	AB795311		
N. makiharai	121024N	F	AB795312		
N. makiharai	121024O	F	AB795313		
N. makiharai	121024P	F	AB795310		

[†]All specimens collected from Ishigaki-jima Island, Ryukyus, 23.x.2011.

and 72°C for 5 min as a final extension. Each sample was sequenced twice for both strands. Sequences are available from DDBJ/EMBL/GenBank. Accession numbers are indicated with collection data for each specimen (Table 1).

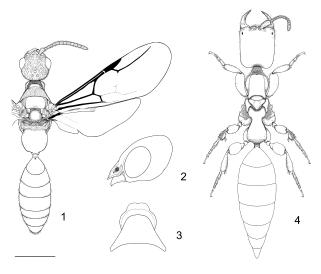
Description

Special terms used in this paper follow those of Terayama (2006), but those regarding male genitalia follow Evans (1963). The following abbreviations are used in descriptions: LH, length of head excluding mandibles; WH, width of head; WF, width of frons; LE, maximum diameter of compound eye in lateral view; DAO, diameter of anterior ocellus; WOT, width of ocellar triangle including ocelli; POL, posterior ocellar line excluding ocelli; AOL, antero-posterior ocellar line excluding ocelli; OOL, ocello-ocular line; WP, width of pronotum; LP, length of pronotum; WPD, width of propodeal disc; LM, length of mesosoma; LFW, length of forewing; TL, total body length. The following abbreviations are used regarding collection data: Coll., collection date of dead wood; Emr., date concerning emergence of adult wasp.

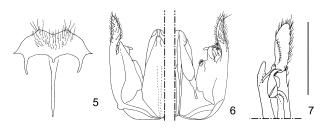
RESULTS

Taxonomy

Compared to *Neoapenesia leytensis*, the male is easily distinguished by the presence of a short 2Rs vein (Fig. 1), rounded propodeum, absence of sculpture on propodeum (Fig. 1), widened subgenital plate (Fig. 5), and apically rounded aedeagus. The male was therefore regarded as a different species as described below. Partial *COI* sequences of unambiguous 582 bp were determined for each sample. All sequences of both genders were identical, but differed by 16% from those of *Sclerodermus harmandi*. Therefore, males and



Figures 1–4 *Neoapenesia makiharai* n. sp. 1–3 Male (holotype): 1 general habitus; 2 head in lateral view; 3 pronotum in dorsal view. 4 Female (paratype) from Ishigaki-jima Island, general habitus. Scale: 1.0 mm (1, 4), 0.5 mm (2, 3).



Figures 5–7 *Neoapenesia makiharai* n. sp., paratype male from Ishigaki-jima Island. 5 Eighth sternite and subgenital plate. 6 Genitalia in ventral view (left) and dorsal view (right). 7 Inner aspect of genitalia. Scale: 0.5 mm (5, 6), 0.7 mm (7).

females that emerged from dead wood collected from the Ryukyus are considered to be the same species of *Neoapenesia*. Among the 10 genera, which are known by females in Pristocerinae (Lanes & Azevedo 2007), the female closely resembles females of *Apenesia* Westwood by the moderately constricted propodeum (weakly to moderately constricted in *Apenesia*), developed mesopleuron, and palpal formula of 4/3 (4, 3/3, 2 in *Apenesia*). However, it is easily separated from the latter by the distinctly short antenna (not reaching posterior margin of head), and disproportionately large head (head width about twice dorsal pronotal width). Detailed diagnostic characters are described below.

Genus Neoapenesia Terayama, 1995

Type species: *Neoapenesia leytensis* Terayama, 1995. *Diagnosis*. **Male:** Head rounded (Figs 1,2); palpal formula 4/3 (MP/LP); pronotum short (Figs 1,3), shorter

than 0.5 times width of mesoscutum; notaulus absent (Fig. 1); subgenital plate bearing three stalks, with concave sides, forming distinct corner (Fig. 5). Details of generic characters of the male are found in Terayama (1995). Female: Head large, flat, and rectangular (Fig. 4), head width about 2.0 times dorsal pronotal width; anterior margin of clypeus concave medially; palpal formula 4/3; antenna short, not reaching posterior margin of head; eye small; pronotum flat and short (Fig. 4), less than 0.7 times width of mesoscutum, rectangular; mesonotum triangular in dorsal view; mesopleuron large in dorsal view; propodeum moderately constricted near the spiracles (Fig. 4); middle tibiae spinose; abdomen sessile.

Neoapenesia makiharai Sawada, Terayama & Mita, new species (Figs 1-7)

Description of male (n = 10). Head rounded, as long as wide, hairy, microreticulate; FW 1.36–1.55 times LE; eye covered with minute setae, convex in dorsal view; anterior margin of eye almost touching mandible in lateral view (Fig. 2). Mandible bearing apical acute tooth, two minute median teeth and basal rounded tooth. Antenna short, 1.27–1.61 times as long as HW; ratio of first 5 antennomeres as follows: 10:2.9–4.5:2.3–3.8:2.2–3.5:2.4–3.6; scape 1.66–2.68 times as long as wide; pedicel 1.12–1.53 times as long as wide; FI 1.0–1.42 times as long as wide; FII–FIII as long as wide; following flagellomeres longer than wide. Ocelli forming regular triangle; OOL 1.01–1.34 times WOT; DAO 0.06–0.08 mm.

Pronotum rounded in lateral view, hairy, faintly microreticulate; anterior margin of collar excavated (Figs 1,3); length of disc 0.28–0.38 times width of thorax, longer in larger specimen; mesoscutum slightly longer than pronotal disc, hairy, smooth; scutellum as long as mesoscutum, almost hairless, smooth; anterior transverse groove deep and narrow (Fig. 1); metanotum hairless, smooth; mesopleuron smooth, except anterior part narrowly microsculptured; propodeum 1.14–1.56 times as long as wide, hairless on dorsal surface, smooth.

Forewing with radial vein basally curved, nearly reaching anterior margin of wing; post marginal vein absent; short track of 2Rs tubular and pigmented from intersection with radial vein; transverse median vein forming obtuse corner; discoidal vein tubular, weakly pigmented; first recurrent vein tubular, weakly pigmented. Hindwing with five humuli.

Metasoma oval, smooth. Subgenital plate (Fig. 5) about 1.1–1.2 times as long as wide, with short median stalk; genitalia (Figs 6,7): paramere 0.7 times longer than basiparamere, outer surface setose; dorsal margin more developed, rounded; basivolsella distally

triangular; inner margin partly setose, folded; ventral surface fusing with basiparamere; digitus with dorsal surface denticulate (Fig. 7); cuspis developed dorsad; dorsal arm with distal lobe bearing setae (Fig. 7); ventral arm curving mesad, setose (Fig. 6); aedeagus conical with apical margin rounded.

Measurements (mm): LH 0.66–0.92 (mean = 0.80); WH 0.68–0.96 (0.81); WF 0.43–0.62 (0.53); LE 0.31–0.43 (0.36); DAO 0.06–0.09 (0.08); WOT 0.20–0.25 (0.23); POL 0.07–0.12 (0.09); AOL 0.05–0.09 (0.06); OOL 0.22–0.33 (0.28); WP 0.70–1.06 (0.90); LP 0.53–0.78 (0.66); WPD 0.51–0.79 (0.64); LM 1.44–2.07 (1.75); LFW 2.82–4.09 (3.48); TL 3.54–5.55 (4.62).

Color: Body black to brownish black, rarely reddish dark brown; mandible testaceous with reddish black teeth; legs testaceous; wings weakly tinged with brown. Female (n = 10). Head rectangular, 1.12–1.25 times as long as wide, smooth with sparsely located small punctures; posterior margin of head weakly concave and posterolateral corner convex, not forming angle; head width 2.05-2.15 times dorsal pronotal width; in lateral view, head 1.46-1.91 times as long as high; anterior margin of clypeus with median notch. Mandible bidentate. Antenna short, 1.05-1.25 times as long as HW, not reaching posterior margin of head; ratio of first 5 antennomeres as follows: 10:1.9-3.3:1.5-2.9: 1.4-2.1:1.4-2.1; scape 1.88-1.03 times as long as wide; pedicel 1.02-1.48 times as long as wide; FI 0.78-1.26 times as long as wide; FII-FIII as long as wide; following flagellomeres longer than wide. Eye small and oval, 0.07-0.13 mm in maximum diameters, ommatidia indistinct.

Pronotum flat in lateral view, smooth on disc, shagreened on collar; anterior part of disc bearing track of median groove; pronotal disc 1.03–1.28 times as long as wide; mesonotal disc flat, smooth, wider than long; mesopleuron, in dorsal view, developed, with straight and carinate dorsal margin; lateral face widely concave; ventral margin with an obtuse tooth at anterior portion, large broad lobe at near middle and small lobe at posterior portions; propodeum flat, weakly microreticulate; maximum width 1.48-1.82 times minimum width (Fig. 4); lateral margin behind the constriction weakly convex. Foretibia with distal apex bearing two spines and single spur; mid-tibia spinose on outer margin (Fig. 4), bearing two spurs; spurs serrate, same in length; hind-tibia bearing single spine and two serrate spurs; one spur distinctly shorter than the other.

Metasoma sessile, faintly microreticulate, weakly compressed dorso-ventrally.

Measurements (mm): LH 0.89–1.28 (1.10); WH 0.76–1.09 (0.92); WF 0.63–0.87 (0.75); LE 0.07–0.11 (0.10); WP 0.52–0.67 (0.60); LP 0.63–1.01 (0.83); WPD

0.34-0.46 (0.40); LM 1.49-2.05 (1.78); TL 5.20-6.60 (6.02).

Color: Body testaceous to reddish brown with teeth reddish black.

Type series. Holotype: O, JAPAN "Mt. Omoto-dake, Ishigaki-jima I., Ryukyus, from Castanopsis sieboldii (Fagaceae) collected at 23. X .2011, adult emerged at 18. II. 2012, H. Sawada leg.". Paratypes: JAPAN, Ryukyus: 3♂ 34♀, Mt. Yui-dake, Amami-oshima I., dead wood of Morus australis (Moraceae) Coll. 24.vii. 2004, Emr. 10.vi.2005, H. Makihara leg.; 19, same as above, but Mt. Yuwan-dake, from Cinnamomum tenuifolium (Lauraceae), Coll. 9.iii.2012, H. Sawada leg.; 32, Okinoerabu-jima I., from Symplocos nakaharae (Symplocaceae), Coll. 12.x.2003, Emr. 16.i.2004, H. Makihara leg.; 29, Oshikawa, Okinawa-jima I., from Acacia confusa (Leguminosae), Coll. 15.iii.2012, Emr. 12.vii.2012, H. Sawada leg.; 3♀, Mt. Nago-dake, Okinawa-jima I., from Diospyros morrisiana (Ebenaceae), Coll. 15.x.2003, Emr. 9.i.2004, H. Makihara leg.; 20, Tamagusuku, Okinawa-jima I., from Ficus superba (Moraceae), Coll. 1.iii.2003, Emr. 4-13.vi.2003, H. Makihara leg.; 29, Tarama-jima I., from Melia azedarach (Meliaceae), Coll. 23.x.2003, Emr. 16.i.2004, H. Makihara leg.; 30679, Mt. Omoto-dake, Ishigakijima I., plant species unknown, Coll. 5.iii.2003, Emr. 4.vi.2003, H. Makihara leg.; $1 \circlearrowleft 36 \circ Q$, same data as above, but from Machilus japonica (Lauraceae), Coll. 5.iii.2003, Emr. 3.x.2003; 10, same data as above, but Emr. 30.iv-6.v.2003; 7, same data as above, but Coll. 21.x.2003, Emr. 16.i-27.ii.2004; 12, same data as above, but Emr. 9.i.2004; 1♀, same data as above, but 27.ii–11.iii.2004; 21♂21♀, same data as above, but from Castanopsis sieboldii (Fagaceae), Coll. 23.x.2011, Emr. 18.ii.2012, H. Sawada leg.; $30^{\circ}4$, same data as above, but bearing DNA sample ID: HS05, HS06, HS09, 121024G, 121024N, 121024O and 121024P, respectively; $100^{7}54$ \, same data as above, but Emr. 11.xii.2011; 2029, same data as above, but deposit in NIAES; 2072, same as above, but Takeda-rindô, plant species unknown, Coll. 21.x.2011, Emr. unknown; $10^{3}2^{\circ}$, same data as above, but Coll. 23.x.2011; 3\,\frac{1}{2}\,\text{q}, same data as above, but Coll. 20-24.x.2011, Emr. 17.xi.2011; 19, same data as above, but Mt. Yarabu-dake, Coll., 23-31.iii.2010, Emr. unknown; 1, same data as above, but Coll. 27.iii.2012; 1♂5♀, Komi, Iriomote-jima I., from *Machilus thunbergii* (Lauraceae) Coll. 30.iv.2012, Emr. 9.vi.2012, Y. Fujisawa leg.; 29, Hateruma-jima I., from Leucaena leucocephala (Leguminosae), Coll. 20.x.2003, Emr. 16.i.2004, H. Makihara leg.

Distribution. JAPAN: Ryukyus (Amami-oshima I., Okinoerabu-jima I., Okinawa-jima I., Tarama-jima I., Ishigaki-jima I., Iriomote-jima I., Hateruma-jima I.).

Etymology. The species name is dedicated to a coleopterist, Mr Hiroshi Makihara, who provided many materials reared from dead wood used in this study. Remarks. The male of Neoapenesia makiharai is easily distinguished from that of N. leytensis by the presence of a short 2Rs vein (Fig. 1), rounded propodeum, absence of sculpture on propodeum (Fig. 1), widened subgenital plate (Fig. 5), and apically rounded aedeagus. The female is easily distinguished from the known females of Apenesia, the most closely related genus according to female morphology, by the short antenna, disproportionately large head, and distinctly constricted propodeum (Fig. 4). The median stalk of the subgenital plate in N. leytensis appears to be very long (fig. 14 in Terayama 1995), but is actually a sclerite of the adjacent sternum (Fig. 5).

Bethylid wasps and beetles reared from dead wood

Adults of Neoapenesia makiharai emerged from nine plant species belonging to seven families (see type series). All bethylid wasps and beetles obtained from five plastic bags are listed in Table 2. Four species of other bethylid wasps, Paraschreloderma ishana Terayama, Allobethylus tomoae Terayama, Sclerodermus harmandi (Buysson) and Sclerodermus yakushimensis Terayama, were also obtained from the same wood samples. Most of these species were collected around the wood or on the surface of the plastic bags; however, a few individuals of N. makiharai and S. harmandi were found in the tunnels of borers, and two males of P. ishana were found under bark. Beetles included 14 species of Cerambycidae, one species of Buprestidae, two species of Cleridae and one species of Curculionidae that emerged from the collected dead wood together with bethylid wasps. All species of beetles were obtained from one plant species, excluding Cerecium longicorne Pic.

Behavior

Female *Neoapenesia makiharai* invaded the gallery of wood-boring coleopteran larvae from a tunnel entrance. The female dug a small tunnel in the powder stuffed in the gallery using mandibles and forelegs. Tough spines on the middle tibia prevented slipping in the tunnel. Host feeding was observed in the female but the male did not attack host larva. Females were active at night, and stayed inside narrow pits or slits located under bark or at the tunnel entrance of borers during the daytime. In contrast, males rested at these locations at nighttime. Although females were active at night, copulation was observed in the daytime. Males flew and walked around

Table 2 Number of bethylid wasps and beetles emerged from dead wood

Insect species	Plant species and locality					
	CT	AC	CS1	CS2	MJ	
Hymenoptera						
Bethylidae						
Paraschreloderma ishana		7				
Allobethylus tomoae		5				
Neoapenesia makiharai n. sp.	1	2	77	32	3	
Sclerodermus harmandi	3					
S. yakushimensis			13			
Coleoptera						
Cerambycidae						
Ceresium unicolor			5			
pseudounicolor						
C. fuscum fuscum		9				
C. elongatum			4			
C. longicorne		16	>100	21	9	
Obrium hattai			5			
Pseudiphra elegans					12	
Longipalpus dilatipennis			3			
Merionoeda formosana	8					
rubriventris						
M. f. iriomotensis					7	
Xylotrechus atronotatus		7				
angulithorax						
Ropica loochooana loochooana		7				
Pterolophia annulata		1				
Xenolea asiatica			35	9		
Exocentrus nobuoi okinawensis		9				
Sciades sakishimanus deguchii		3				
Buprestidae						
Aglius aritai			5			
Cleridae						
Opilo formosanus			4			
Tenerus hilleri		3				
Curculionidae						
Psepholacini gen. sp.			1			

AC, Acacia confusa from Okinawa-jima Island; CS1 and CS2, Castanopsis sieboldii from Ishigaki-jima Island; CT, Cinnamomum tenuiforium from Amami-oshima Island; MJ, Machilus japonica from Iriomote-jima Island.

dead wood seeking females. Females hid in gaps, but the distal apices of their metasoma remained outside. A male who found a female approached her exposed body using antennae. The female then came out and mated with the male on the piece of wood. A female that had finished mating hid inside the wood, but did not leave her metasoma outside again.

DISCUSSION

The bionomics of Pristocerinae is poorly understood. However, those of *Pristocera rufa* Kiffer parasitizing

Pantorhytes szentivanyi Marshall (Curculionidae) (Baker 1976), and Apenesia sahyadrica Azevedo & Waichert parasitizing Xylotrechus quadripes Chevrolat (Cerambycidae) (Seetharama et al. 2002, 2007; Azevedo & Waichart 2006), are relatively well investigated. Both species show similar traits: females invade the gallery of host larvae from a tunnel entrance; the female lays several eggs on a single host and attends her progeny; and females feed host larvae. Invasion from the tunnel entrance and host feeding were also observed for Neoapenesia makiharai. Although we have not observed it, maternal care is highly probable because it is a distinctive characteristic of Bethylidae (Quicke 1997).

Phoretic copulation has been reported in *Apenesia* (Evans 1963, 1969; Gordh 1990). In fact, the body size of females in *Apenesia* is very much smaller than that of males. However, this behavior may not occur because the body size of the female is larger than that of the male in *N. makiharai*. Thus, the dispersal should depend on female activity.

Beetles that emerged together with *N. makiharai* (Table 2) were mostly polyphagous borers and a few were predators. They are at least as large as *N. makiharai* (data not shown), except for *Obrium hattai* and an unidentified species of Psepholacini (Curuclionidae) (<4.0 mm). Adults of *Cerecium longicorne* were often collected together with *N. makiharai*. Most samples of *N. makiharai* were obtained from two wood samples of *Castanopsis seiboldii* that was severely affected by *C. longicorne*. Although the number of dominant host species may have been lowered by parasitization and consumption, *C. longicorne* is considered a potential host species.

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