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Review of the genus *Vespina* (Lepidoptera, Incurvariidae) with two new species from China and Japan

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Abstract

Asian species of the genus *Vespina* Davis, 1972 (Lepidoptera, Incurvariidae) are mainly reviewed. *Vespina meridiana* Hirowatari & Yagi **sp. nov.** from the Ryukyu Islands, Japan, and *Vespina sichuana* Hirowatari, Huang & Wang **sp. nov.** from Sichuan, China, are described. The previously known *Vespina* species are associated with plants from the Fagaceae family on the western coast of the USA and East Asia and with Sapindaceae (Aceraceae) in eastern Europe. The two new species described here are associated with Fagaceae and Myricaceae, respectively, in warm temperate areas in Asia. *Vespina nielseni* Kozlov, 1987, which was only known from East Asia, is newly recorded from South China. A checklist for the genus is provided herein. Morphological information of the immature stages of the two new species is partially provided. The absence or reduction of a female frenulum and presence of approximately 20 thin pseudofrenular bristles, the dorsoventrally flattened pupa, and the minute tergal spines scattered on abdominal segments 3–8 are considered as possible autapomorphies of *Vespina*.

Key words: frenular bristles, immature stages, morphology, taxonomy, tergal spines

Introduction

The superfamily Adeloidea Bruand, 1850 (formerly Incurvarioidea), is made up of five families: Cecidosidae Bréthes, Prodoxidae Riley, Tridentaformidae Davis, Incurvariidae Spuler, Heliozelidae Heinemann & Wocke, and Adelidae Bruand, with 43 genera and 582 species having been described globally (Regier *et al*. 2015). Among them, approximately 30 species of Adelidae (T. Hirowatari unpublished data) and five species of Heliozelidae (Wang *et al*. 2018; Liao *et al*. 2019) have been recognized from mainland China. On the other hand, many more species of Adeloidea are known from Japan: Prodoxidae (two genera, 5 spp.), Incurvariidae (seven genera,15 spp.), Heliozelidae (four genera, 23 spp.), and Adelidae (three genera, 34 spp.) (Okamoto & Hirowatari 2004; Hirowatari 2013). This indicates that there is a lack of taxonomic studies on Adeloidea in China.

The family Incurvariidae has 12 genera and 51 species worldwide (Regier *et al*. 2015). In Japan, seven genera and 15 species from Incurvariidae are known to be present (Okamoto & Hirowatari 2004; Hirowatari 2013). In China, some *Nemophora* species were recorded under Incurvariidae (e.g., Hua 2005), but are currently placed in Adelidae. As of now, no reliable data on Incurvariidae have been recorded from China.

In 1972, Davis established the monotypic incurvariid genus *Careospina* for a North American species, *C. quercivora* (Davis 1972a), based on the large compound eyes, narrow wing, and absence of epiphysis on the foreleg. Subsequently, Davis (1972b) proposed a replacement name, *Vespina*, for *Careospina*, because the latter was at the time preoccupied by *Careospina* Peters, 1971 (Ephemeroptera). Subsequently, *Vespina nielseni* was described by

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Kozlov (1987) from the Russian Far East based on adults collected at light. In 2000, Okamato & Hirowatari recorded *V. nielseni* on a few *Quercus* spp. (as host plants) in Japan and provided the morphology of their immature stages. Later, Lee *et al*. (2007) recorded this species in Korea. In 1990, *Lampronia slovaciella* Zagulajev & Tokar was described from eastern Europe, Slovakia (Zagulajev 1990). Szabóky (2005) subsequently recorded it from Hungary and reported that the larvae fed on *Acer campestre* L. (Sapindaceae). This species is currently placed in the genus *Vespina* (e.g., Szabóky 2005; Karsholt & Nieukerken 2013). Thus, the genus *Vespina* contains three species and shows disjunct distribution in North America, Europe, and East Asia.

In June 2016, many portable larval cases of an unknown incurvariid species feeding on *Castanopsis fargesii* Franch. (Fagaceae) were collected at Longcangou, Yingjing, Sichuan, China. Moreover, in March 1996 and 2017 and thereafter, larvae of another incurvariid, feeding on *Morella rubra* Lour. (Myricaceae), were also found in the Ryukyu Islands, Japan. Examination of the immature stages and adult morphology revealed that they were undescribed species of the genus *Vespina.*

In the present study, we describe these two new species and provide a checklist of the genus *Vespina*. The immature stages of the new species are partially described, and the autapomorphies of the genus *Vespina* are briefly discussed.

Materials and methods

Specimens of the new Chinese species used in this study were obtained from field surveys conducted around Moxi (1,600 m a.s.l.) and Longcangou National Nature Reserve (1,500 m a.s.l.), Sichuan Province, in June 2016 and July 2017. Materials of the new Japanese species were collected in Amami-Oshima Island (400 m a.s.l.) in April 1996 and north of Okinawa Island (200–400 m a.s.l.) in April 2004, March 2017, and March 2020.

Wing venations were examined after scale removal, and wings were stained with acetocarmine and embedded in Euparal on a slide. Male and female genitalia were preserved in glycerin after the abdomen was macerated for approximately 5 min in 10% KOH heated in a boiling water bath.

Examined specimens were deposited in the collection of Hunan Agricultural University, Changsha, China (HUNAU), Entomological Laboratory, Osaka Prefecture University, Sakai, Japan (OPU), and the Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (ELKU).

The terminology for morphological characters follows Davis (1972a) and Davis (1999) except for the term “pseudofrenular bristles”. Although many terms were used for the subcostal bristles on the hindwing (e.g. costal bristles, subcostal setae, and so on), we adopt “pseudofrenular bristles” following Nielsen & Common (1991) because they used it as a key character for separating superfamilies of non-Ditrysian Glossata in Australia and clearly indicated those of incurvariid moths (fig. 41.24).

DNA analysis. Some collected specimens (Table 1) were used for DNA extraction. DNA was extracted from the abdomen of each specimen using the DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer’s protocol. We amplified a barcoding region of the mitochondrial COI gene (658 bp) using the primer set LCO1490+HCO2198 (Folmer *et al*. 1994) or LepF1+LepR1 (Herbert *et al*. 2003). The DNA material of two specimens (SaY89 and SaY91) was degraded, and thus newly designed internal primers were used (Table 2).

Subsequent PCR, purification, and sequencing procedures were performed as described in Ohshima *et al*. (2018), except for the use of LA *Taq* for the degraded materials. The obtained sequences were aligned manually without ambiguity or indels using Mesquite (Maddison & Maddison 2016). Then, the sequences of the outgroups were obtained from GenBank and added to our data. The alignment of the sequences was carried out with MAFFT v7.222 (Katoh & Sandley 2013) using the accurate alignment method L-INS-i. Pairwise sequence distances were calculated using MEGA 7.0.26 (Kumar *et al*. 2016) with the Kimura 2-parameter model (K2P).

For phylogenetic analyses, maximum parsimony (MP) analysis was conducted using MEGA 10.1.8 (Stecher *et al*. 2020). All characters were equally weighted, and MP trees were searched by 100 random addition replications with tree bisection reconnection (TBR) branch swapping. To assess confidence in clades, bootstrap tests (Felsenstein 1985) were performed using 1,000 replicates with TBR branch swapping. We also carried out a maximum likelihood (ML) analysis, and model selection was conducted based on the Akaike Information Criterion (AIC) (Akaike 1974) using Kakusan 4 (Tanabe 2011). Maximum likelihood trees were created using RAxML 8.2.9 (Stamatakis 2014), and bootstrap values were calculated with 1,000 replicates.

TABLE 1. Sample IDs for specimens used in the molecular phylogenetic analysis.

Species name	Sample ID	Process ID	Genbank accession number	References
Vespina meridiana **sp. nov.** (holotype)	SaY89	INCJP001-20	MW378311	This study
Vespina meridiana **sp. nov.**	SaY90	INCJP002-20	MW378312	This study
Vespina meridiana **sp. nov.**	SaY91	INCJP003-20	MW378319	This study
Vespina meridiana **sp. nov.**	SaY448	INCJP011-20	MW378320	This study
Vespina sichuana **sp. nov.**	SaY92	INCJP004-20	MW378318	This study
Vespina sichuana **sp. nov.**	SaY93	INCJP005-20	MW378313	This study
Vespina sichuana **sp. nov.**	SaY94	INCJP006-20	MW378317	This study
Vespina nielseni	SaY95	INCJP007-20	MW378311	This study
Vespina nielseni	SaY96	INCJP008-20	MW378321	This study
Vespina nielseni	SaY97	INCJP009-20	MW378315	This study
Vespina nielseni	SaY98	INCJP010-20	MW378314	This study
Vespina quercivora	AF150925	GBGL0158-06	AF150925	Pellmyr & Leebens-Mack (1999)
Incurvaria pectinea	MK978243	GBMNB43294-20	MK978243	Milla *et al*. (2020)
Paraclemensia acerifoliella	AF150927	GBGL0160-06	AF150927	Pellmyr & Leebens-Mack (1999)
Alloclemensia mesospilella	MM17932	LEFIK357-10	JF853993	Mutanen *et al*. (2012)
Crinopteryx familiella	JCR-95-112	LEFIA1071-10	GU828561	Mutanen *et al*. (2010)
Lampronia flavimitrella	MM03828	LEFIC324-10	HM872168	Mutanen *et al*. (2016)

TABLE 2. Primer sets used for the amplification of degraded DNA samples.

Primer name	Forward/Reverse	Primer sequence (5' to 3')	Length of amplicon
LCO1490/LepF1	Forward	GGTCAACAAATCATAAAGATATTGG/ ATTCAACCAATCATAAAGATATTGG	
GraR2	Reverse	GGDAYWARTCARTTWCCRAATCC	181 bp
GraF1	Forward	YTAGGDAMYCCNGGDTCWYTAATYGG	
GraR4	Reverse	GTTCADCCWGTWCCWRCYCCDKWTTC	208 bp
GraF3	Forward	ATAAGWTTYTGAYTWYTHCCHCC	
GraR5	Reverse	GCYCCYARRATWGADGARATWCC	139 bp
GraF4	Forward	GAAWMHGGRGYWGGWACWGGHTGAAC	
GraR6	Reverse	GTRATWGCWCCHGCTAAWACWGG	217 bp
GraF5	Forward	GGWATYTCHTCWATYYTRGGRGC	
HCO2198/LepR1	Reverse	TAAACTTCAGGGTGACCAAAAAATCA/ TAAACTTCTGGATGTCCAAAAAATCA	223 bp
VesF1	Forward	CAATTGTTACRGCWCAYGCT	
VesR1	Reverse	GCRTGRGCAATATTDGAAGA	210 bp
VesF2	Forward	AATTGGTGGATTYGGAAAYTG	
VesR2	Reverse	GCYCCATTTTCAACAAATCTT	102 bp

GraF1–R6 were newly designed on the basis of internal primers used in Lees *et al*. (2011) with the information of several gracillariid COI sequences. VesF1–R2 were newly designed based on COI barcoding sequences obtained from fresh *Vespina* materials used in the present study (amplified by LCO1490/LepF1 and HCO2198/LepR1).

Results

Taxonomy

Vespina Davis, 1972

Careospina Davis, 1972: Davis 1972a: 121; preocc. Peters, 1971.
Type species: *Careospina quercivora* Davis, 1972a: 123.
Vespina Davis: Davis 1972b: 472.

Among the generic characteristics of *Careospina* (=*Vespina*) proposed by Davis (1972a), the following were seen as being important: head densely hairy, entirely rough; compound eyes large; galea short, approximately equal to the length of the labial palpi; wings relatively narrow, with subacute apices; forewings 12-veined, all veins arising separately from the discal cell; prothoracic tibia without an epiphysis; valvae relatively slender; ventral margin with a single pecten present; phallus (as aedeagus) relatively short and stocky; cornuti present; apex of ovipositor depressed, broad and stout, acuminate; apophyses relatively stout.

Remarks. Generic characteristics of *Vespina* (=*Careospina*) proposed by Davis (1972a) were checked based on the two new species described in this paper and it was found that most of the characteristics were applicable. However, in the 12-veined forewings, veins 7 and 8 (R4 and R5) are stalked in *V. quercivora* (Davis 1972a) but not stalked in *V. nielseni* (Kozlov 1987) and *V. sichuana* **sp. nov.**

Davis (1972a) described that accessory and intercalary cells are faintly present in *Careospina* (=*Vespina*), but these cells are indistinct in both wings of *Vespina sichuana*. In the female genitalia, the signum is absent in *V. quercivora* (Davis 1972a) and in the two new species described herein, but present in *V. nielseni* (Okamoto & Hirowatari 2000). These characteristics may vary at the species level. In addition to the above characteristics, the absence or reduction of a female frenulum and presence of pseudofrenular bristles, the dorsoventrally flattened pupa, and the minute spines scattered on the dorsal surface of abdominal segments 3–8 of the pupa may be characteristic of the genus *Vespina* (see Discussion).

Biology. The first-instar larva of Incurvariidae is known to be a leaf miner. Referring to Brown & Eads (1965), Davis (1972a) detailed the feeding habit of *Vespina quercivora* on *Quercus agrifolia*. At the final stage of mining, the larva constructs a flat case by cutting an oval patch out of both the upper and lower epidermal layers of the mine and then sewing them together around the edge with silk. The later-instar larvae of the two new species described here also construct a case as in the other members of *Vespina*, but we could not observe the mining behavior of the first instar.

Vespina nielseni Kozlov, 1987

(Figs 1A–C, 2A–C, 3A–C, 13E, F)

Vespina nielseni Kozlov, 1987: 16; Kozlov, 1996: 56; Okamoto & Hirowatari, 2000: 511; Okamoto & Hirowatari, 2004: 175; Lee *et al*., 2007: 113; Niimi & Murase, 2012: 102; Hirowatari, 2013: 112.
Vespina sp.: Oku 2003: 5.

Material examined: (Additional material to Okamoto & Hirowatari, 2000). Japan: [Honshu] 1 ♂, Mt. Goyo, Hikoroishi, Iwate Pref., larvae 15.x.2016, emerged 11.i.2017, S. Yagi. Host plant: *Quercus serrata*, genitalia slide no. SY482, Sample ID SaY96 (ELKU); 1 ♀, Chokai, Toshi, Nikaho, Akita Pref., larva 23.ix.2017, emerged 14.iii.2018, S. Yagi. Host plant: *Quercus crispula* (ELKU); 1 ♀, same data, emerged 19.iii.2018 (ELKU); 1 ♀, Mizuho, Hakuba, Kita-azumi, larva 2.x.2018, emerged 26. xii. 2018, S. Yagi. Host plant: *Quercus dentata* (ELKU); 1 ♂, Aoyagi, Chino, Nagano Pref., larva 14.x.1999, emerged 23. iv. 2000, N. Hirai. Host plant: *Castanea crenata* (OPU); 2 ♂, Kitayama, Chino, Nagano Pref., larvae 15.ix.2017, emerged 1.i.2018, S. Yagi. Host plant: *Quercus crispula* (ELKU); 1 ♀, same data, emerged 12.i.2018 (ELKU); 1 ♂, 1 ♀, same locality & collector, emerged 27.xii.2017. Host plant: *Castanea crenata*, genitalia slide no. SY481, Sample ID SaY95 (♂) (ELKU); 1 ♂, Hirano, Yamanakako, larva on *Fagus crenata* 24.x.2016, emerged 3.i.2017, S. Yagi (ELKU); 1 ♀, Misawa, Toyone, Aichi Pref., larva 21.x.2007, emerged 25.v.2008, N. Hirano. Host plant: *Quercus serrata* (ELKU); 1 ♂, Misawa, Toyone, Kita-shitara, Aichi

Pref., larva 18.ix.2017, emerged 14.iii.2018, S. Yagi. Host plant: *Quercus serrata* (ELKU); 1 ♂, same data, emerged 19.iii.2018 (ELKU); 1 ♀, Ikuma (Kamitonda), Wakayama Pref., 22.v.2004, T. Saito. (OPU). [Shikoku] 1 ♀, Kinsha-Lake, Iyomishima, Ehime Pref., larva 23.ix.1999, emerged 24.iii.2000, H. Okamoto. Host plant: *Quercus* sp. (OPU); 1 ♂, 2 ♀, same label, emerged 20.iv.2000 (OPU) [Tsushima Is.] 1 ♀, Mt. Asaji, Mitsushima, Tsushima Is., Nagasaki Pref., larva 2.x.2018, emerged 26. xii.2018, S. Yagi. Host plant: *Quercus variabilis* (ELKU). [Kyushu] 1 ♂, Hikosan, Soeda, Tagawa, larva 8.x.2016, emerged 30.vii.2017, T. Hirowatari. Host plant: *Quercus crispula*, genitalia slide no. SY481, Sample ID SaY95 (ELKU); 2 ♂, 1 ♀, Meisuinitaki, Mt. Kuro, Yufu, Oita Pref., 13.vi.2015 (L.T.), S. Yagi (ELKU); 1 ♀, Tano, Kokonoe, Kusu, Oita Pref., larva 2.x.2017, emerged 27.xii.2017, S. Yagi. Host plant: *Quercus dentata* (ELKU); 1 ♀, Chojyabaru, Kusu, Oita Pref., larva x.2015, emerged 18.xi.2015, T. Kawano. Host plant: *Quercus serrata* (ELKU); China: 1 ♀, Moxi, Sichuan, 22.vi.2016 (L.T.), M. Wang, genitalia slide no. SY484, Sample ID SaY98 (HUNAU).

FIGURE 1. Adults of *Vespina* spp. in South and East Asia. A, *V. nielseni*, male from Japan; B, *V. nielseni*, female from Japan; C, *V. nielseni*, female from China; D, *V. meridiana* **sp. nov.**, female, holotype; E, *V. sichuana* **sp. nov.**, male, holotype; F, *V. sichuana* **sp. nov.**, female, paratype. Scale bars: 4.0 mm.

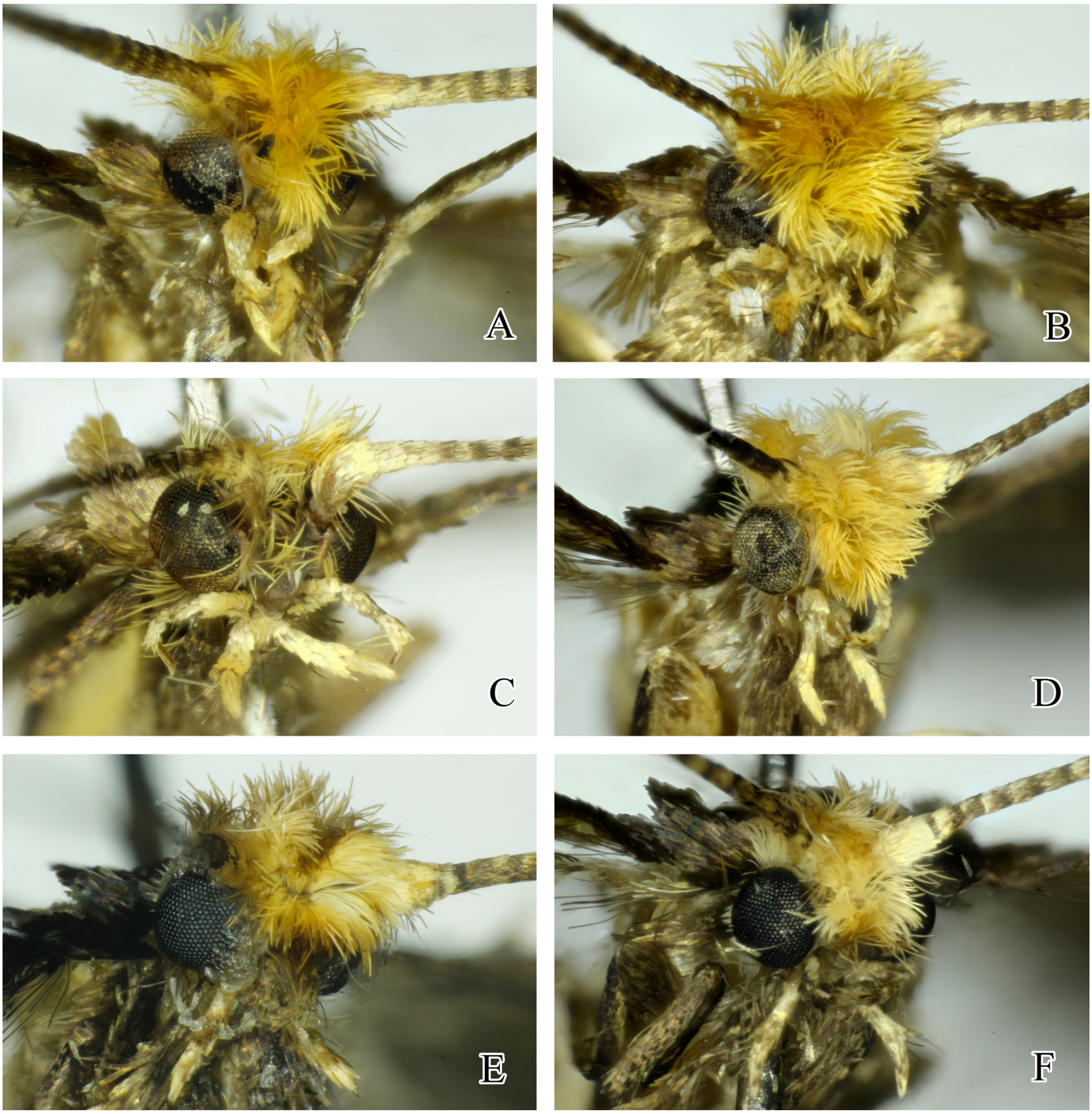

FIGURE 2. Head of *Vespina* spp. in South and East Asia. A, *V. nielseni*, male from Japan; B, *V. nielseni*, female from Japan; C, *V. nielseni* female from China; D, *V. meridiana* **sp. nov.**, female, holotype; E, *V. sichuana* **sp. nov.**, male, holotype; F, *V. sichuana* **sp. nov.**, female, paratype.

Diagnosis. Distinguished from the other species by a small triangular creamy-white tornal spot on the forewing. In the male genitalia, the apical half of the valva is slender and the sacculus is slightly expanded. The phallus is short and stout, 1.2 × as long as valva, with a large spine-like subapical carina penis. In the female genitalia, the corpus bursae is elongate and ellipsoidal; the signum is present, nearly heart-shaped with the anterior portion pointed.

Description. See Okamoto & Hirowatari (2000) for detailed description.

Barcode data. DNA barcodes of the four specimens were generated (Table 1). The intraspecific pairwise distances between the Japanese *V. nielseni* specimens (SaY95, SaY96, SaY97) were small (0.15–0.30%); additionally, a single female specimen (SaY98) from China also showed small pairwise distances from the Japanese specimens (1.07–1.38%). Therefore, they were concluded to be the same species, supported by observation of morphological characteristics such as the shape of the signa in the genitalia, even though these specimens show paraphyly with low support in the ML tree.

Host plants. Fagaceae: *Quercus acutissima* Carruth, *Q. aliena* Blume, *Q. crispula* Blume, *Q. dentata* Thunb. (new record), *Q. serrata* Murray, *Q. variabilis* Blume (new record), and *Castanea crenata* Siebold & Zucc..

Biology. Okamoto & Hirowatari (2000) reported that the larvae of this species fed on *Quercus aliena*, *Q. serrata*, and occasionally on *Q. acutissima*. Niimi & Murase (2012) added *Castanea crenata* (Fagaceae) as a host plant. This species is univoltine in Japan. Adults appear in Honshu and Kyushu during the month of June and are attracted to light. In June 2016 in Jiaozinping (ca. 2,000 m a.s.l.), Luding County, Sichuan, China, we found some circular skeletonized patches on the leaf of a chestnut tree, *Castanea crenata*, which were considered to be feeding traces made by *V. nielseni* (Fig. 13F).

Distribution. Russia (Far East), Korea, Japan (Hokkaido, Honshu, Shikoku, and Kyushu [Tsushima Islands: new record]), China (Sichuan) (new record).

Remarks. In June 2016, we collected a female of this species at Moxi (ca. 1,600 m a.s.l.), Luding County, Sichuan, China, using a light trap (Fig. 1C). We identified it as *Vespina nielseni* by examining the genitalia and via DNA barcoding, as described above. This is the first record of *V. nielseni* in China.

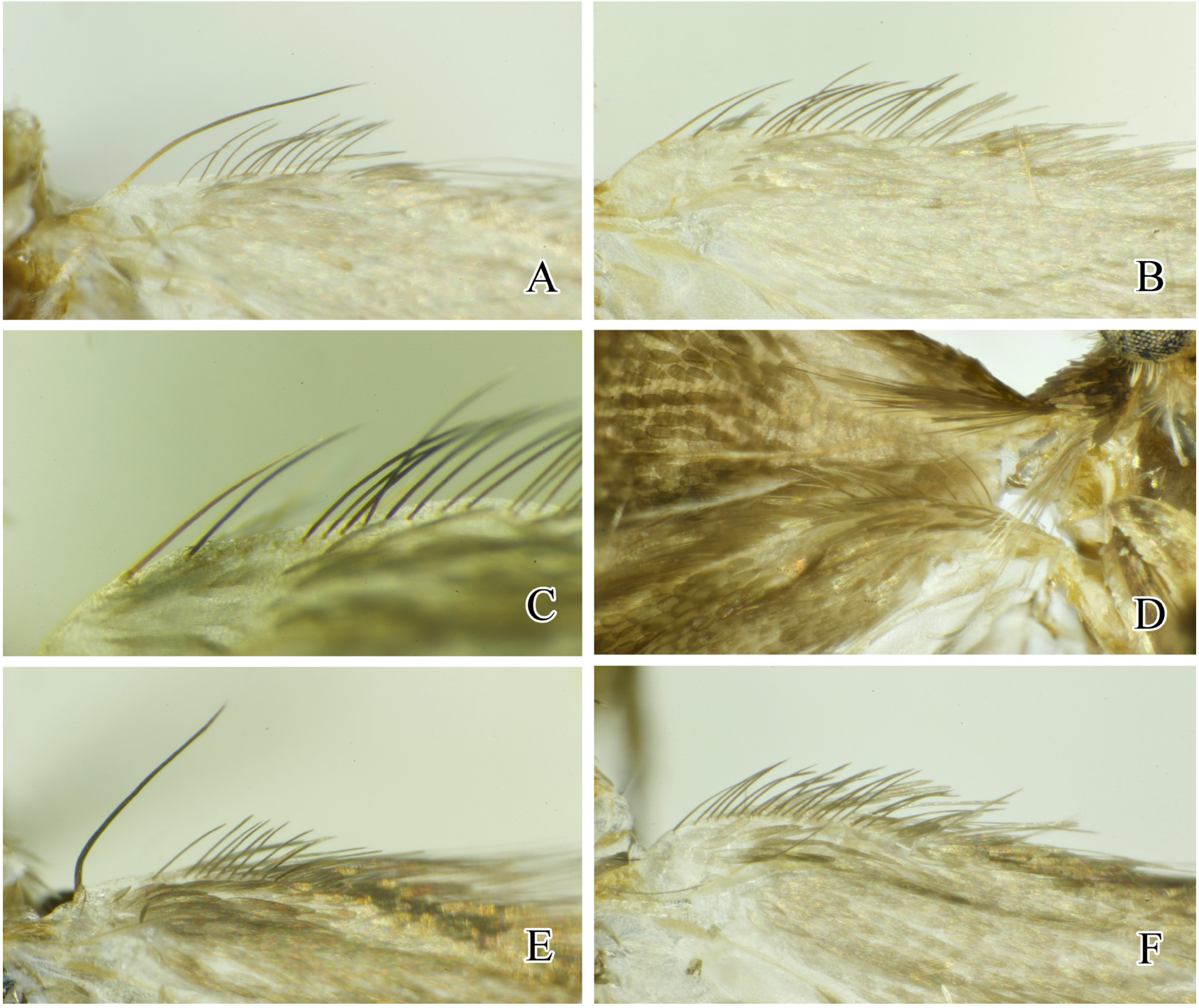

FIGURE 3. Frenular and pseudofrenular bristles of *Vespina* spp. A, *V. nielseni*, male, dorsal view; B, C, *V. nielseni*, female, dorsal view; D, *V. meridiana* **sp. nov.**, female, holotype, ventral view; E, *V. sichuana* **sp. nov.**, male, paratype, dorsal view; F, *V. sichuana* **sp. nov.**, female, paratype, dorsal view.

Vespina meridiana Hirowatari & Yagi, sp. nov.

(Figs 1D, 2D, 3D, 4–6, 13C, D)

Type material: holotype ♀, "Japan [Ryukyu]/ Yonahadake/ Kunigami-son/ Okinawa Pref./ 21.iv.2004/ T. Ueda", "Host: / em. 28.VI. 2004" Sample ID SaY89 in OPU.

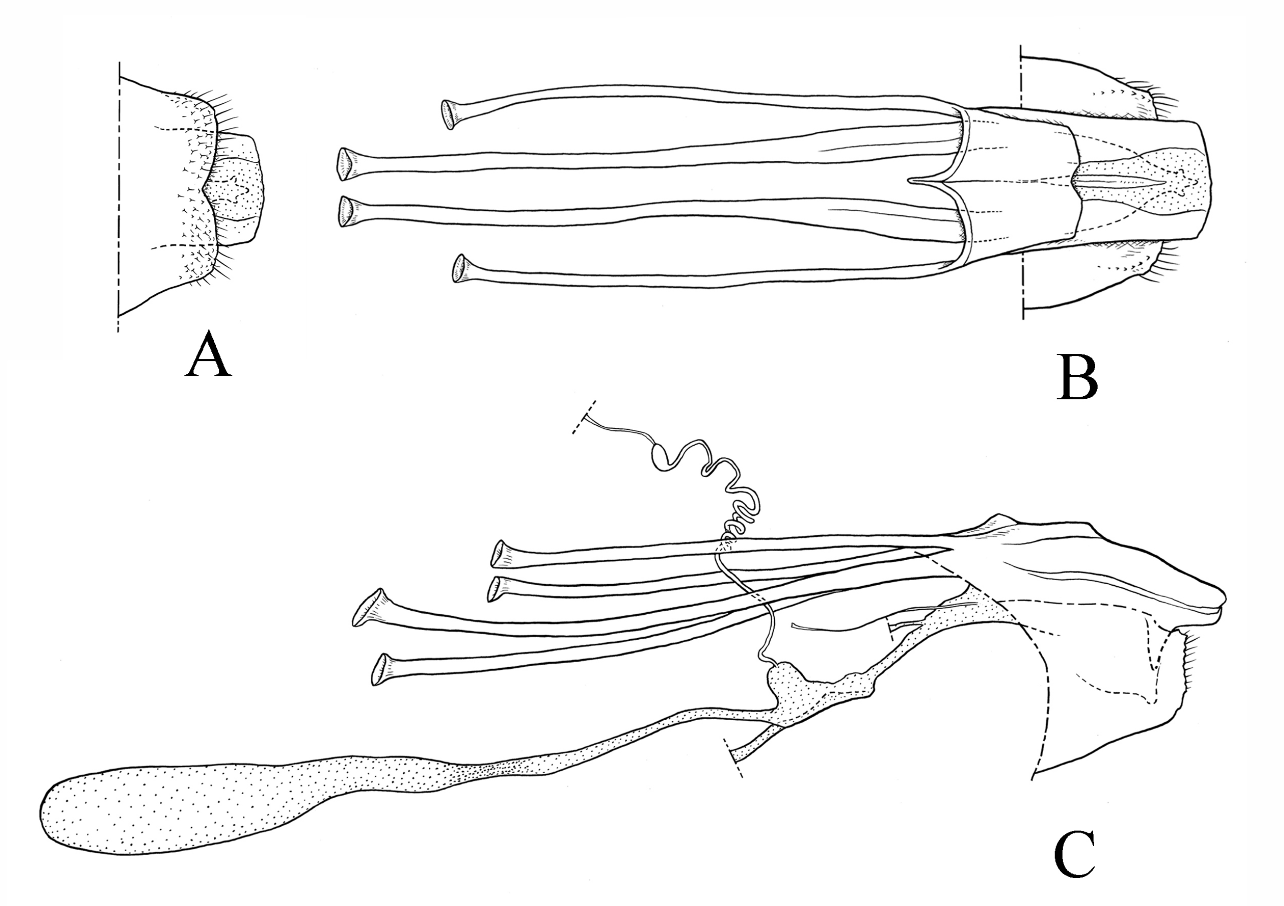

FIGURE 4. Female genitalia of *Vespina meridiana* **sp. nov.**, holotype. A, terminalia (part), ventral view; B, terminalia, dorsal view; C, terminalia, lateral view.

Other material. Larvae: 6 exs 4–6.iv.1996, Hatsuno, Amami-Oshima, Kagoshima Pref.; 10 exs 22–24.iii.2002, Kunigami-son, Okinawa Pref., T. Hirowatari (OPU); 20 exs 15–18.iii.2017, Hentona–Okuni-rindo, T. Hirowatari & S. Yagi, Sample ID SaY90, 91 (ELKU); 2 exs Benoki, 19.iii.2020, S. Yagi, DNA extraction number No. SaY448 (ELKU) (some of them were preserved in ca. 80 or 100% ethanol; all collected on *Morella rubra*, Myricaceae).

Diagnosis. Difficult to distinguish from other Asian *Vespina* species externally, but may be distinguishable by the entirely pale yellow hairs of the head (Fig. 2D); in *V. nielseni*, the yellow hairs are mixed with orange hairs on the vertex (Fig. 2A, B), whereas in *V. sichuana*, they are mixed with light-brown hairs on the posterior side of the head (Fig. 2E, F). The triangular creamy-white tornal spot on the forewing is absent (well-developed in *V. nielseni* and indistinct in *V. sichuana*). In the female genitalia, the anterior end of the apophysis posterioris is rather small, 2–2.5 × as wide as the base, and the ductus bursae is relatively long, as long as the corpus bursae.

Description.

Male unknown.

Female (Figs 1D, 2D, 3D). Wingspan 10.0 mm in holotype. Forewing length 4.7 mm in holotype.

Head: Vertex and frons with pale yellow hairs, entirely rough; antenna 2/3 the length of the forewing. Ocellus absent. Compound eye large. Maxillary palpus short (slightly shorter than the labial palpus), pale yellow mixed with pale brown. Labial palpus porrect, short and slender, pale yellow, second segment with several distal brown bristles.

Thorax: Tegula, prothorax and mesothorax dorsally dark brown with a weak purple gloss. Metathorax with dark brown scales on the posterior. Foreleg dark brown, mixed with pale yellow on the femur; midleg dark brown, mixed with pale yellow on the femur, with blackish brown tibial spurs; hindleg dorsally dark brown and partly mixed with pale yellow, with pale yellow hairs ventrally on the tibia, and pale yellow tibial spurs. Wings narrow. Forewing brown. Hindwing brown. Frenulum absent or reduced with approximately 15 thin pseudofrenular bristles at the costal margin.

Abdomen: Brown with golden luster.

Female genitalia (Fig. 4): Apophyses stout, each anterior end swollen, trumpet-shaped; apophysis posterioris slightly longer than the apophysis anterioris, with the anterior end rather small and the posterior half depressed and expanded laterally. Apex of ovipositor dorsoventrally flattened with one median semicircular projection. Spermathecal vesicle small and oval. Corpus bursae elongate, ellipsoidal; signa absent. Ductus bursae relatively long, as long as corpus bursae, weakly sclerotized near the caudal portion of the corpus bursae.

Immature stages (Figs 5, 6).

Pre-mature larva (Figs 5H, 6A–D). Color: Yellowish-white.

Length: 5.2 –5.7 mm (n = 5). Head: Prognathous with six pairs of stemmata. Head capsule dark brown. Antennae with three sclerotized segments. Thorax: Prothoracic tergite well sclerotized; mesothoracic tergite weakly sclerotized, apart from the well-sclerotized dorsal part of the posterior margin; metathoracic tergite not sclerotized. Prothoracic spiracle distinct, with a sclerotized rim. Thoracic legs well developed; pretarsus with a squamiform seta adjacent to the claw (Fig. 6C). Abdomen: No distinctive pigmentation except a weakly sclerotized dorsal plate on the tenth segment. Prolegs reduced; crochets arranged as a transverse band consisting of two rows of spines: 9–12 larger posterior spines associated with 7–9 smaller anterior spines on segments 3, 4, 5, and 6, alongside two or three rows of 10–15 transverse spines on segment 10 (Fig. 6D). Number of crochets variable. Spiracles oval on the first to eighth segments.

Mature larva (Fig. 6E–H). Color: Yellowish-white.

Length: 4.2–4.4 mm (n = 3).

Body: Stout and fat. Head: Head capsule pale brown with brown area around the base of the antennae and the six pairs of stemmata; enclosed area of stemmata blackish-brown. Head capsule flattened. Posterior margin more bluntly V-shaped than that of pre-mature larva. Antenna with three weakly sclerotized segments. Thorax: Thoracic tergites not well-sclerotized. Prothoracic spiracle not pigmented. Pretarsus with a squamiform seta adjacent to the claw, almost the same size as that of the pre-mature larva. Abdomen: No distinctive pigmentation on the yellowish-white abdomen except a very weakly sclerotized dorsal plate on the tenth segment. Prolegs reduced; crochets with a transverse band consisting of a row of 7–9 spines on segments 3, 4, 5, and 6, and a row of 12–15 transverse spines on segment 10 (Fig. 6H) crochets evidently less than that of the pre-mature larva. Spiracles same as in the pre-mature larva.

Pupa: Not examined.

Etymology. The specific name is derived from the Latin *meridiana* (=southern), in reference to the southernmost distribution of the new species in the genus.

Barcode data. DNA barcodes of four specimens were generated (Table 1). A single female specimen (SaY89; Fig. 14) collected at Yonahadake, Kunigami-son, Okinawa Pref.—the holotype of *Vespina meridiana* (Fig. 1D)—showed 0.46–1.86% (SaY90, SaY91, SaY448) pairwise distance (in terms of the sequenced 658 bp COI barcoding region) from three larval specimens collected at Benoki and Hentona, Kunigami-son on *Morella rubra* leaves (Table 3). These distances were smaller than typical empirical interspecific distances (e.g., Hebert *et al*. 2003). Therefore, we concluded that the female from Yonahadake and the larvae from *Morella rubura* were the same species. The specimens collected from the two larger areas in the northern part of Okinawa Island (Benoki vs. Hentona and Yonahadake, ca. 10 km away) have some large intraspecific distances (1.70–2.02%), while the pairwise distances within the close areas (Yonahadake vs. Hentona) have small intraspecific distances (0.46%). Perhaps this represents the low migratory habits of adults.

Host plant. Myricaceae: *Morella rubra*.

Biology. In March 2017, we found a young larva of *Vespina meridiana* shouldering a thin case on a twig of *Morella rubra* (Fig. 13D), perhaps just after constructing the oval case. Later, the larva cut an oval section from the leaf and added it to the top of the old case, in the same manner as other species of *Vespina* (e.g., *V. quercivora* and *V. nielseni*).

Distribution. Japan (Okinawa Island and Amami-Oshima Island).

Remarks. One of the authors (T. Hirowatari) found portable larval cases of this species on *Morella rubra* (Myricaceae) on Amami-Oshima Island in March 1996. Since then, we have collected many portable larval cases of this species on the host plant in the northern part of Okinawa (Kunigami-son), and reared many larvae. However, we have failed to obtain pupae and adults under laboratory conditions in Osaka and Fukuoka, Japan. Most of the larvae collected in the spring survived for over four months; however, from spring to summer, many of them died in their pre-mature stage. By the end of summer, a small number of larvae appeared to be in the last instar phase and were alive until the end of the year, at which point they finally succumbed to death.

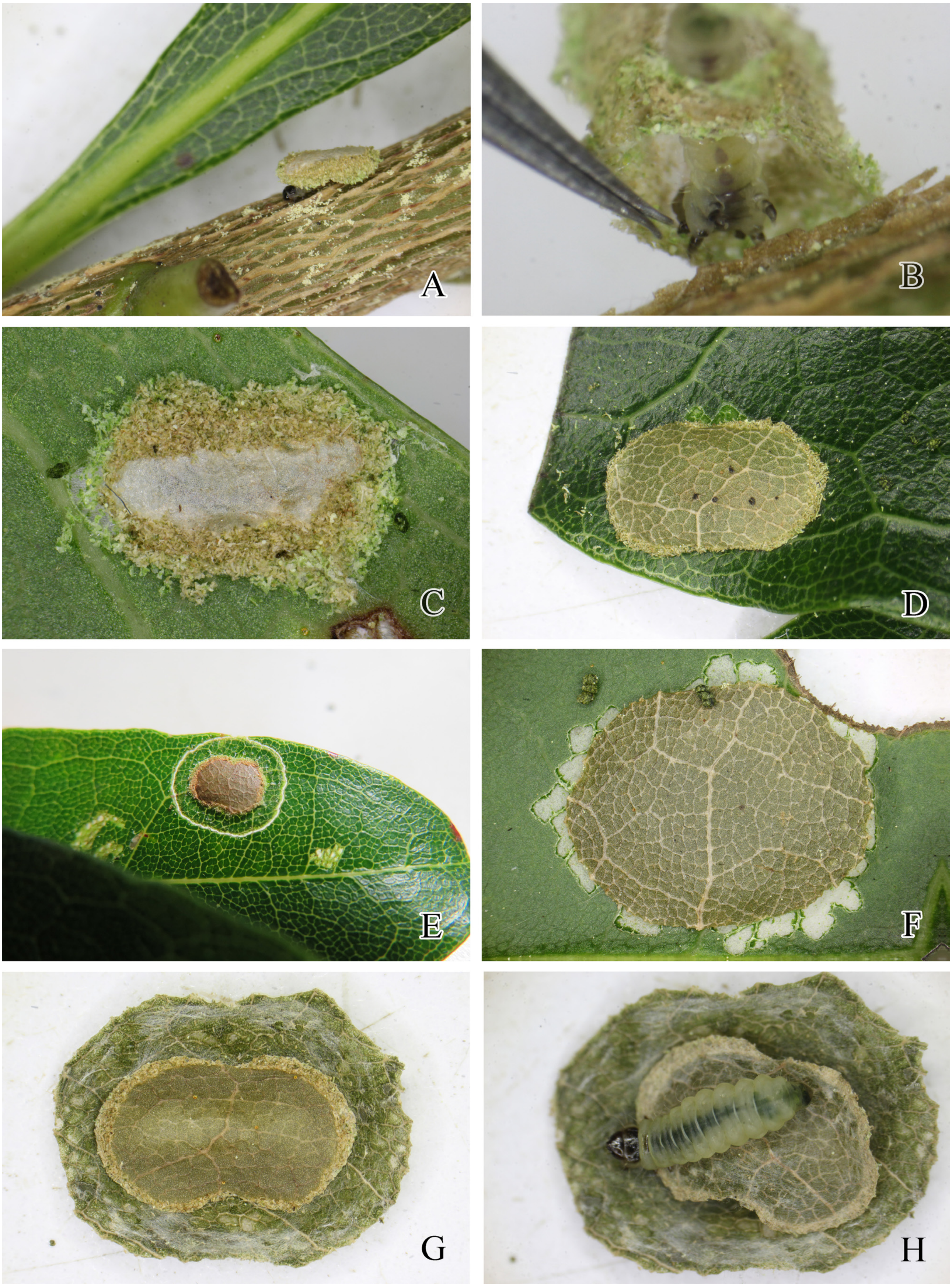

FIGURE 5. Larva and portable case of *Vespina meridiana* **sp. nov.** on the host plant *Morella rubra*. A–C, young instar larva; D, E, middle instar larva; F–H, pre-mature larva.

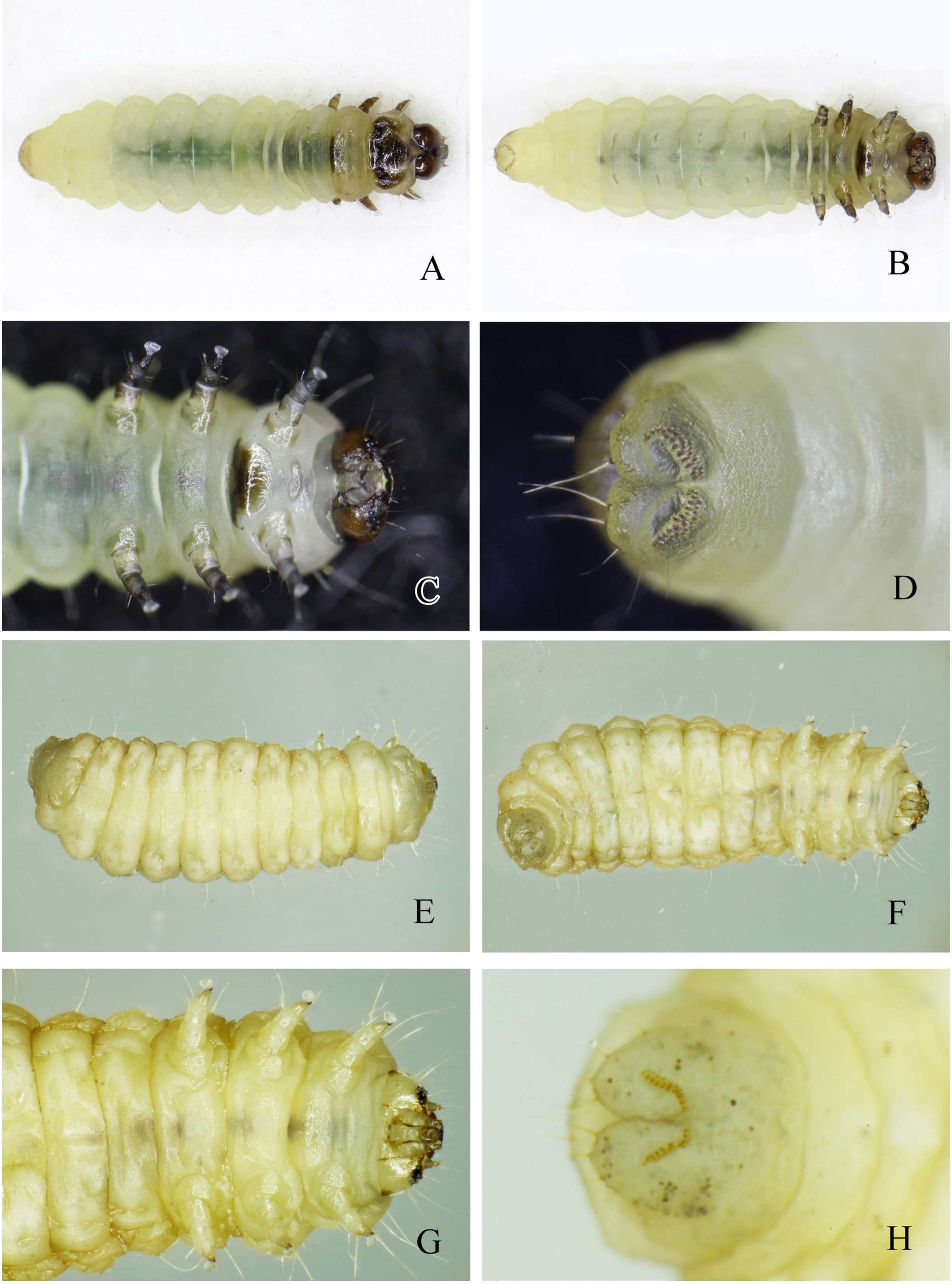

FIGURE 6. Larva of *Vespina meridiana* **sp. nov.** A–D, pre-mature larva, E–H, mature larva. A, E, dorsal view; B, F, ventral view; C, G, head and thorax, ventral view; D, H, terminal segment, ventral view, showing crochets of anal proleg.

No adults have been collected in the field. The larva of the holotype female within a portable case on an undetermined plant leaf (probably *Morella rubra*) was collected by Dr. Tatsuya Ueda in Okinawa in June 2004. It was in a non-feeding stage before pupation because no trace of feeding remained on the leaf. In the rearing condition, most premature larvae are observed to move from the leaves of the host plant to the wall of the rearing container and fix their case on the wall with a thread. The larva of the holotype also moved in such a manner for pupation. Then, the female emerged one week later. This species seems to undergo diapause before emergence, but the diapause-terminating cue is unclear.

Vespina sichuana **Hirowatari, Huang & Wang, sp. nov.**

(Figs 1E, F, 2E, F, 3E, F, 7–12, 13A, B)

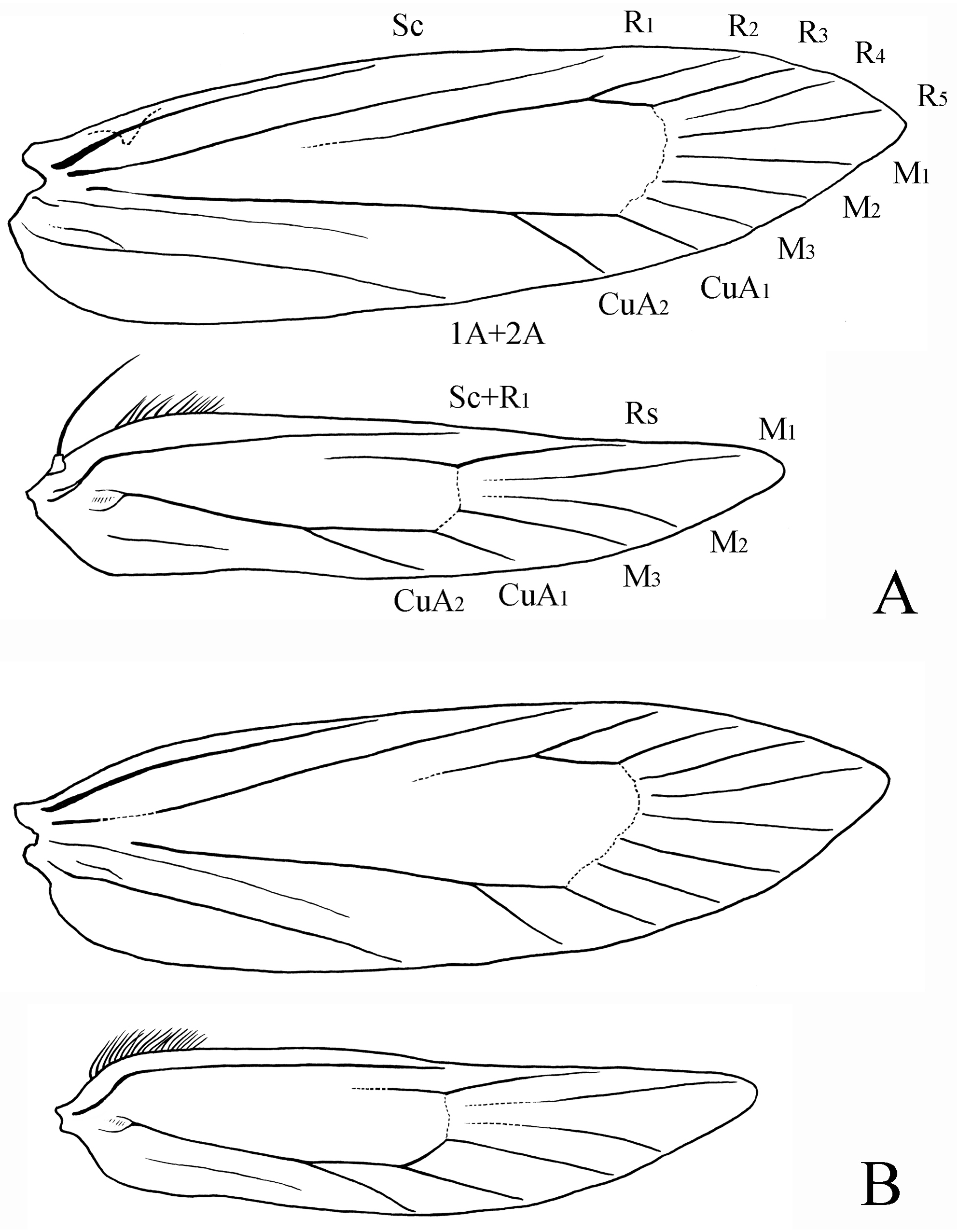

FIGURE 7. Wing venation of *Vespina sichuana* **sp. nov.** A, male; B, female.

Type material: Holotype ♂, "[China] Longcangou/ Ya'an Sichuan/ 17.vii.2017/ 25.vii.2017 em.", "G.H. Huang/M. Wang" in HUNAU.

Paratypes: 7 ♂, 11 ♀, same locality as holotype, larvae 18–24.vi.2016, emerged 15–29.vii.2016, G.H. Huang, host plant: *Castanopsis fargesii*, sample ID: SaY93 (HUNAU); 18 ♂, 11 ♀, larvae or pupae 17.vii.2017, emerged 18–26.vii.2017, G.H. Huang, M.Wang, host plant: *Castanopsis fargesii*, sample ID: SaY94 (♀), genitalia slide no. SY480, (HUNAU).

Other material. Larvae: 5 exs 18–24.vi.2016, Longcangou, Ya'an, Sichuan, China, G.H. Huang; pupae: 12 exs 17.vii.2017, Longcangou, Ya'an, Sichuan, China, G.H. Huang and M.Wang, sample ID SaY92 (a part of larvae and pupae were preserved in 80% ethanol; all collected on *Castanopsis fargesii*, Fagaceae).

Diagnosis. Distinguished from other *Vespina* species by the scattered blackish brown scales on the forewing and the indistinct dark-brown stria along the discal cell. In the male genitalia, the pecten of the valva is very long, nearly half the length of the valva, consisting of more than 30 spines. In the female genitalia, the anterior end of the apophysis posterioris is extremely swollen, 3–6 × as wide as the base.

Description.

Male (Figs 1E, 2E, 3E, 7A). Wingspan 9.0 mm in holotype, 8.0–9.0 mm in paratypes (n = 25).

Forewing length 4.2 mm in holotype, 4.0–4.7 mm in paratypes (n = 25).

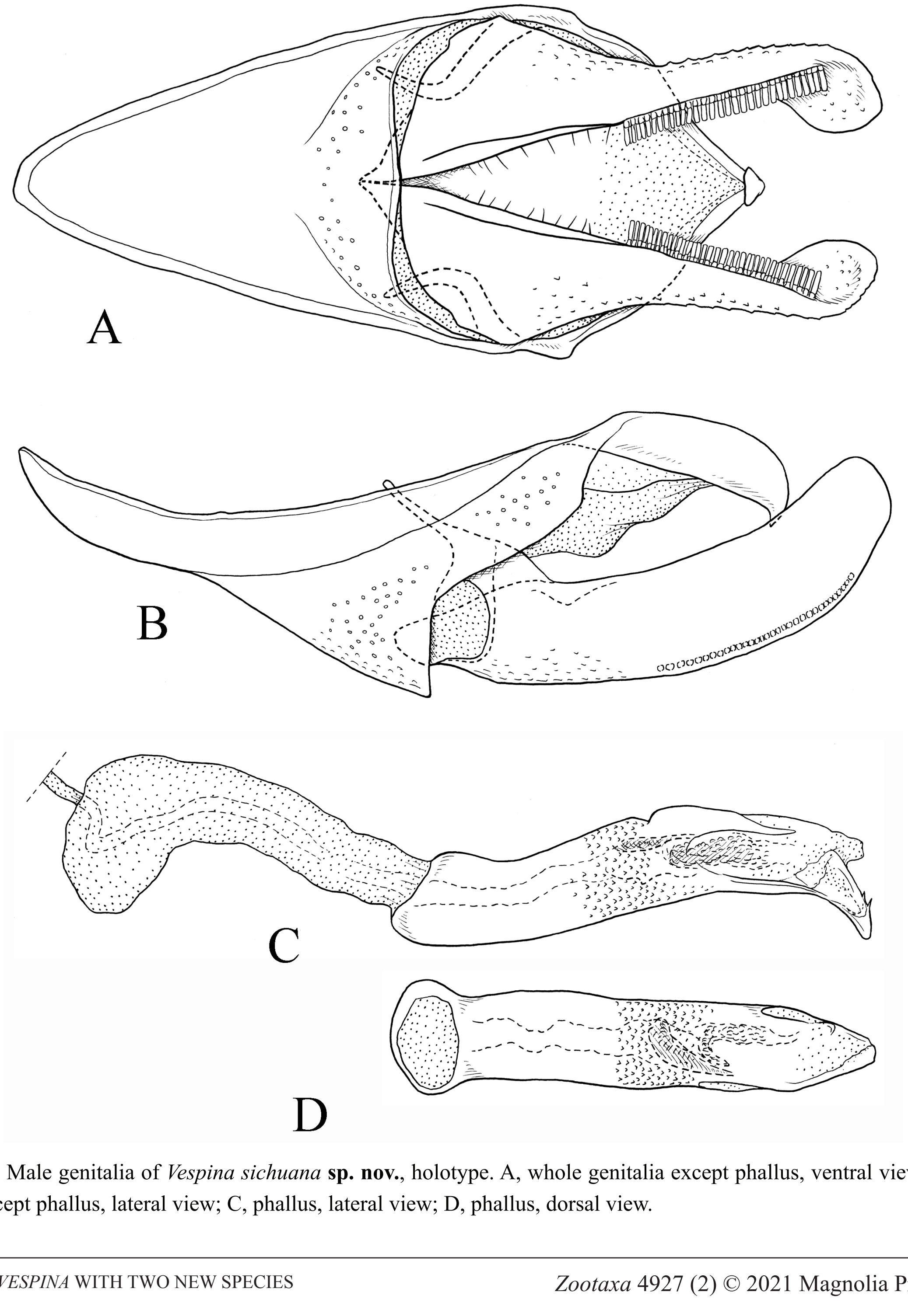

FIGURE 8. Male genitalia of *Vespina sichuana* **sp. nov.**, holotype. A, whole genitalia except phallus, ventral view; B, whole genitalia except phallus, lateral view; C, phallus, lateral view; D, phallus, dorsal view.

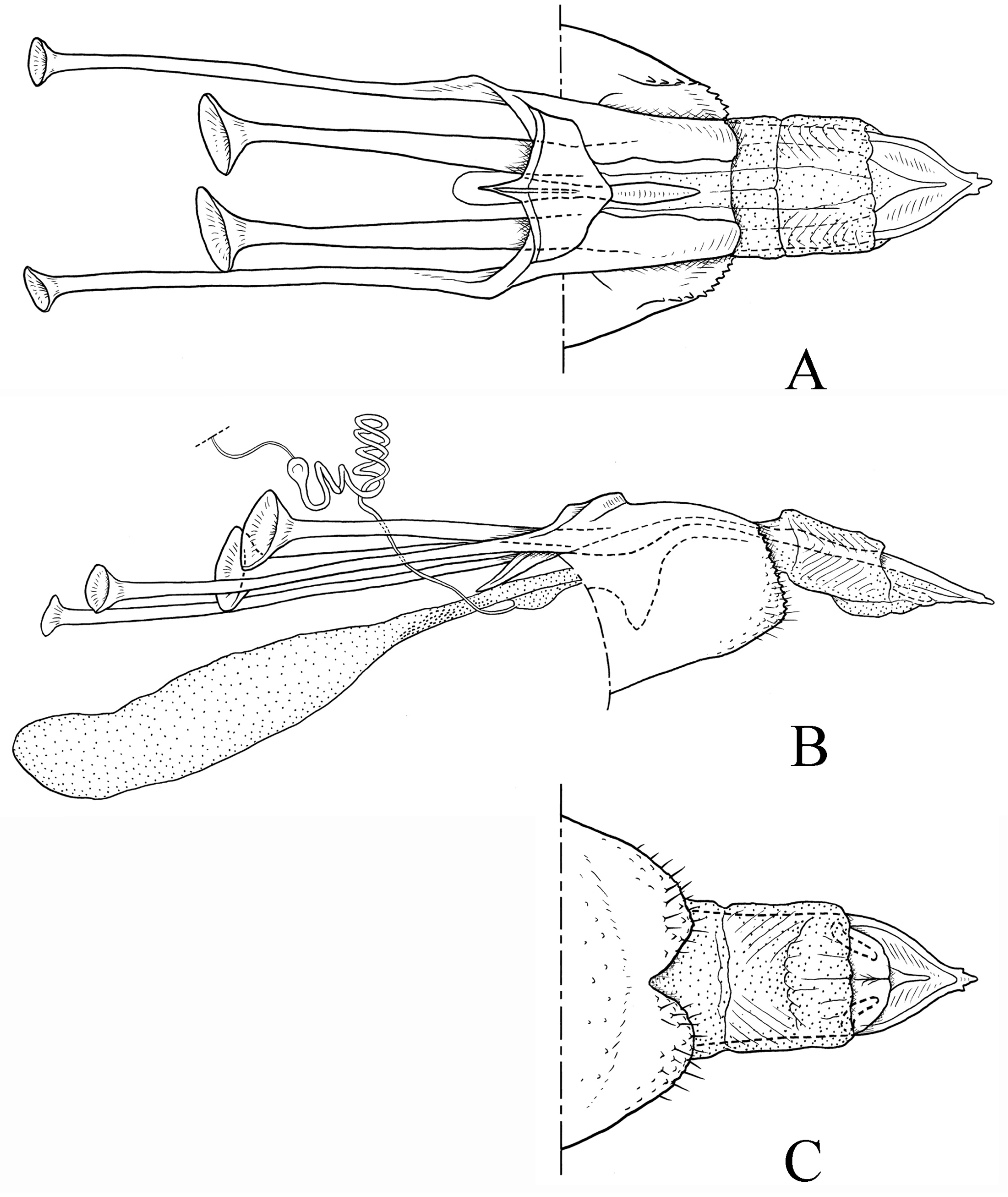

FIGURE 9. Female genitalia of *Vespina sichuana* **sp. nov.**, paratype. A, terminalia, dorsal view; B, terminalia, lateral view; C, terminalia (part), ventral view.

Male. Head: Vertex and frons with yellow hairs, mixed with light-brown hairs on the posterior, entirely rough (Fig. 2E); antenna 3/4 the length of the forewing. Ocellus absent. Compound eye large. Maxillary palpus short (slightly shorter than labial palpus), pale yellow mixed with dark brown. Labial palpus porrect, short and slender, pale yellow mixed with brown, second segment with several distal blackish-brown bristles.

Thorax: Tegula, prothorax and mesothorax dorsally dark brown with a weak purple gloss. Metathorax with dark brown scales on the posterior. Foreleg dark brown, partly mixed with pale yellow; midleg dark brown, partly mixed with pale yellow, with dark brown tibial spurs; hindleg ochreous brown dorsally, partly mixed with pale yellow, with dorsal and ventral pale yellow hairs on the tibia, and pale yellow tibial spurs. Wings narrow. Forewings dark brown with scattered blackish brown scales, those on the basal 1/3 rising; an indistinct short blackish-brown stria present at the end of the discal cell with 12 veins, all veins arising separately from the discal cell; accessory and intercalary cells, indistinct. Hindwing, dark brown. Frenulum consisting of a single large bristle followed by 12–15 pseudofrenular bristles.

Abdomen: Dorsal part dark brown with golden luster, terminally with brown tufts of long hairs. Ventral part similar to dorsal part, terminally with brown smooth scales.

Female (Figs 1F, 2F, 3F, 7B, 11G, H). Wingspan 8.0–11.0 mm (n = 22). Forewing length 4.4–5.0 mm (n = 22). Coloration of the head and wings similar to that of the male, but wings tend to be brighter than in males. Frenulum absent or reduced with 17–22 thin pseudofrenular bristles.

Male genitalia (Fig. 8): Uncus hooked. Vinculum and saccus triangular and slightly shorter than the valva in length. Valva spatulate over the apical 1/2, width 1/2 of the base. Sacculus not expanded; pecten long, nearly half the length of the valva, consisting of 30–36 spines arranged in a single row midway along the ventral margin. Transtilla present and horn-shaped. Phallus relatively short, slightly shorter than valva, anteriorly swollen, with a large spine-like subapical carina penis; cornuti consisting of many minute spines. Juxta, broad.

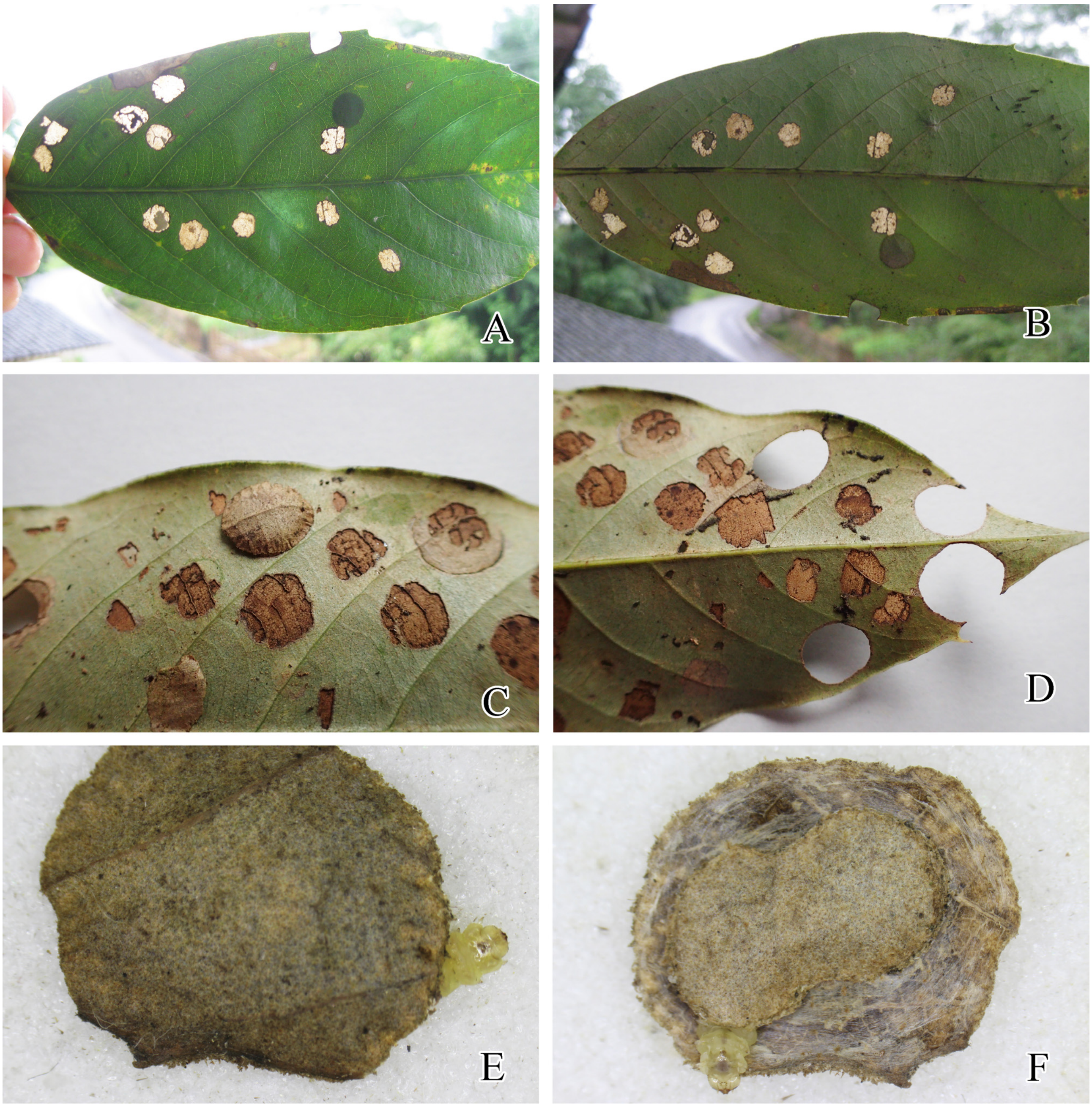

FIGURE 10. Larval portable case and mature larva of *Vespina sichuana* **sp. nov.** A–D, feeding traces; E, mature larva in portable case, dorsal view; F, mature larva in portable case, ventral view.

Female genitalia (Fig. 9): Apophyses stout, each anterior end swollen and trumpet-shaped; apophysis posterioris slightly shorter than apophysis anterioris, with the anterior end extremely swollen, 6 ×as wide as the base, and the posterior half depressed and expanded laterally. Apex of ovipositor dorsoventrally flattened with one median semicircular projection. Spermathecal vesicle small and roundish. Corpus bursae elongate ellipsoidal; signa, absent.

Ductus bursae relatively short, 1/2 as long as corpus bursae, weakly sclerotized near the caudal portion of the corpus bursae.

Immature stages.

Pre-mature larva: Not examined.

Mature larva (Figs 10E, F, 11A–C). Color yellowish-white.

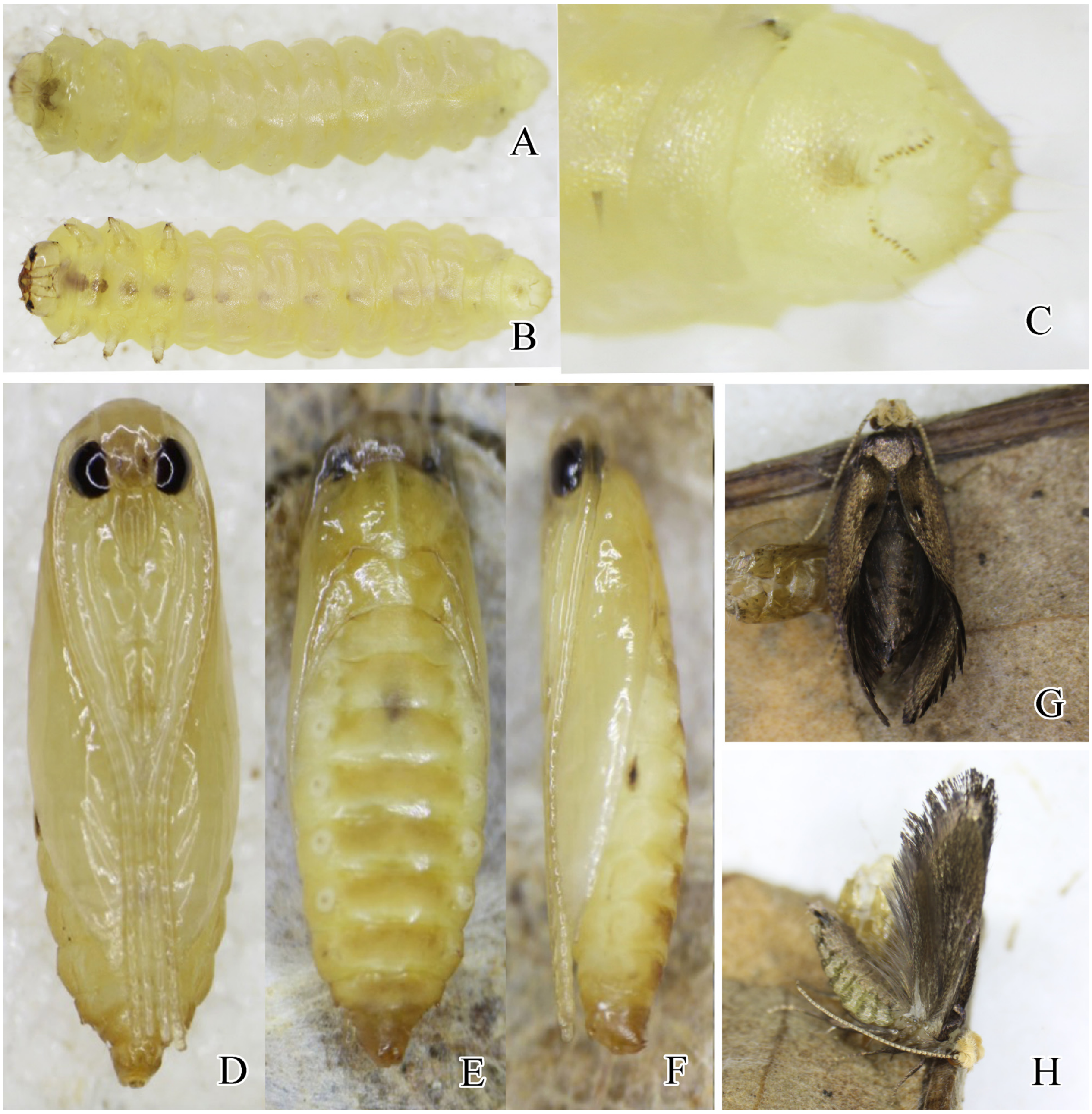

FIGURE 11. Immature stages of *Vespina sichuana* **sp. nov.** A, mature larva, dorsal view; B, mature larva, ventral view; C, terminal segment, ventral view, showing crochets of anal proleg; D, pupa, ventral view; E, pupa, dorsal view; F, pupa, lateral view; G, H; emerged female adult.

Length approximately 4.0–4.8 mm (n = 5). Body: Stout and fat. Head: Head capsule pale-yellow with pale-brown area around clypeus; enclosed area of six stemmata blackish-brown. Head capsule flattened. Posterior margin more bluntly V-shaped than that of the pre-mature larva. Antenna with three weakly sclerotized segments. Thorax: Thoracic tergites not well-sclerotized. Prothoracic spiracle not pigmented. Pretarsus with a squamiform seta adjacent to the claw. Abdomen: Yellowish-white with no distinctive pigmentation. Prolegs reduced; crochets reduced or present as an indistinct transverse band consisting of a row of 4–8 spines on segments 3, 4, 5, 6, and a row of 12–16 transverse spines on segment 10. Spiracles small oval on segments 1–8.

Pupa (Figs 11D–F, 12). Length 3.3–4.0 mm; width 1.2–1.4 mm; height 0.8–0.9 mm (n = 8). Color: Pale-yellow. Body flattened dorsoventrally. Vertex smooth. Galea short, shorter than the labial palpus. Antenna extending beyond wing tip. Wings extending to abdominal segment 8. Anterior half of abdominal segments, weakly pigmented and dorsally pale-brown. Abdominal segments 3–8 with minute scattered tergal spines; spines on abdominal segment 3 indistinct. A pair of dorsal hooked spines on the caudal margin of segment 8. Spiracles weakly protruded on abdominal segments 2–8, especially on 7 and 8.

Etymology. The specific name is derived from the type locality, Sichuan Province.

Barcode data. DNA barcodes of the three specimens were generated (Table 1) and their sequences showed no difference (Table 3). The closest sequences were *V. meridiana* **sp. nov.** (SaY448) and *V. nielseni* (SaY97) (pairwise distance: 7.7%).

Host plant. Fagaceae: *Castanopsis fargesii*.

Biology. All examined adults were reared from larvae or pupae within portable cases collected from host plants. In 2016, we collected portable cases of mature larvae during middle- to late-June. In 2017, we collected the pupae in portable cases during mid-July; all adults emerged in middle- to late-July during both years. This shows that the adults of this species fly in middle- to late-July in the type locality. However, we were unable to collect any flying adults during the daytime nor those attracted by light at night.

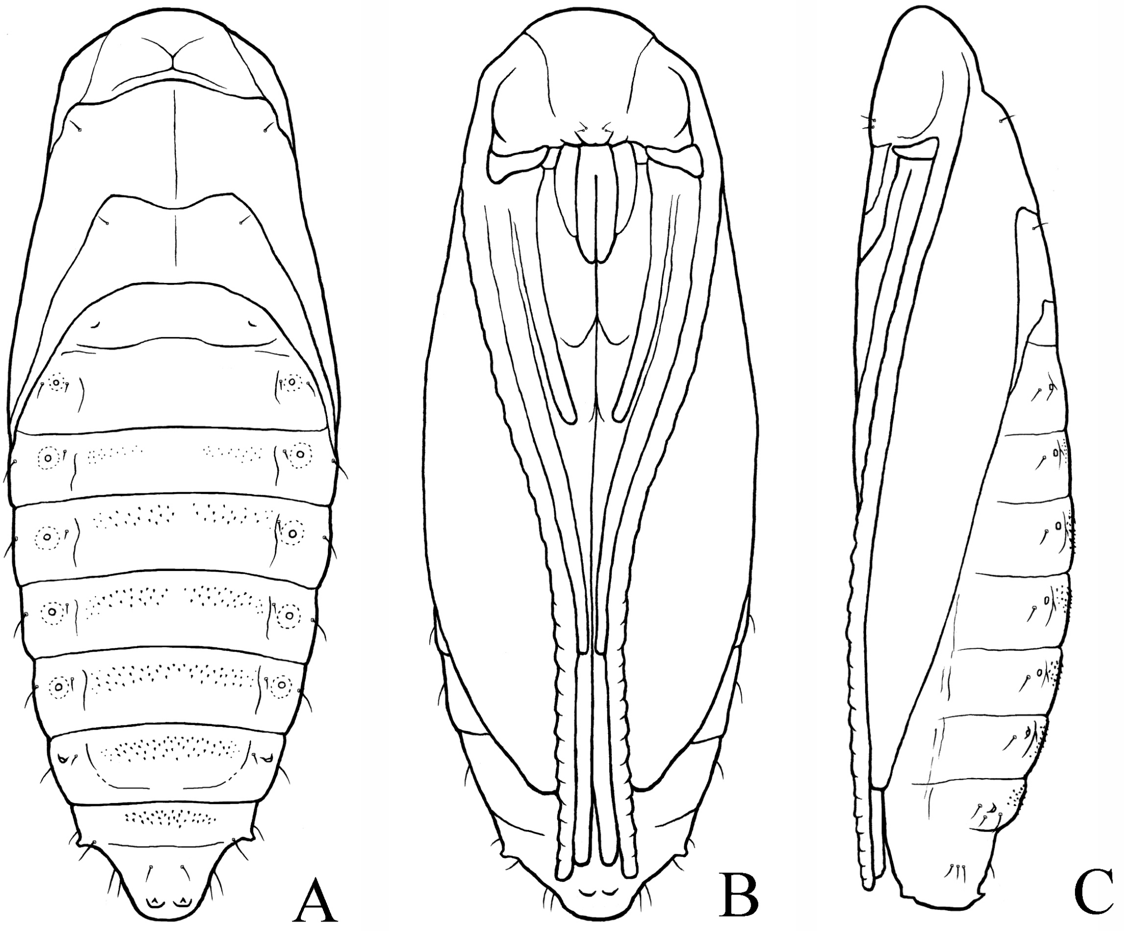

FIGURE 12. Male pupa of *Vespina sichuana* **sp. nov.** A, dorsal view; B, ventral view; C, lateral view.

Distribution. China (Sichuan Province).

Remarks. Although the host plant *Castanopsis fargesii* is widely distributed in southern China and Taiwan (Hong & Blackmore 2015), we have never found the larval portable case or larval feeding trace of *Vespina sichuana* anywhere other than in the Sichuan Province. However, the larval portable cases that seem to be of the genus *Vespina* are found in Taiwan on some evergreen oaks (S. Yagi, unpublished data).

FIGURE 13. Host plants and habitats of *Vespina* spp. in South and East Asia. A, habitat of *V. sichuana* **sp. nov.**, Longcangou, Sichuan, China; B, the host plant, *Castanopsis fargesii*; C, habitat of *V. meridiana* **sp. nov.**, Kunigami-son, Okinawa Is.; D, the host plant, *Morella rubura*; E, habitat of *V. nielseni*, Jiaoziping, Sichuan, China; F, the host plant, *Castanea crenata*.

DNA analysis

Based on the phylogenetic tree, the monophyly of the two new species was confirmed with high bootstrap values based on both MP and ML methods (Fig. 14). The topologies generated via MP and ML are mostly congruent, apart from the node showing a low bootstrap value.

Phylogenetic analysis suggested the monophyly of the genus *Vespina* (ML 92%; MP 97%), although the sequence data of *V. slovaciella* was not available. In contrast, we could not conclude the phylogenetic relationship within the genus *Vespina* and its related genera because of the low bootstrap values. However, pairwise distances between *V. quercivora* and other species suggested a close relationship with *V. nielseni*, which also utilizes *Quercus*. To confirm the relationships within species of the genus *Vespina*, further molecular analyses based on more regions are required.

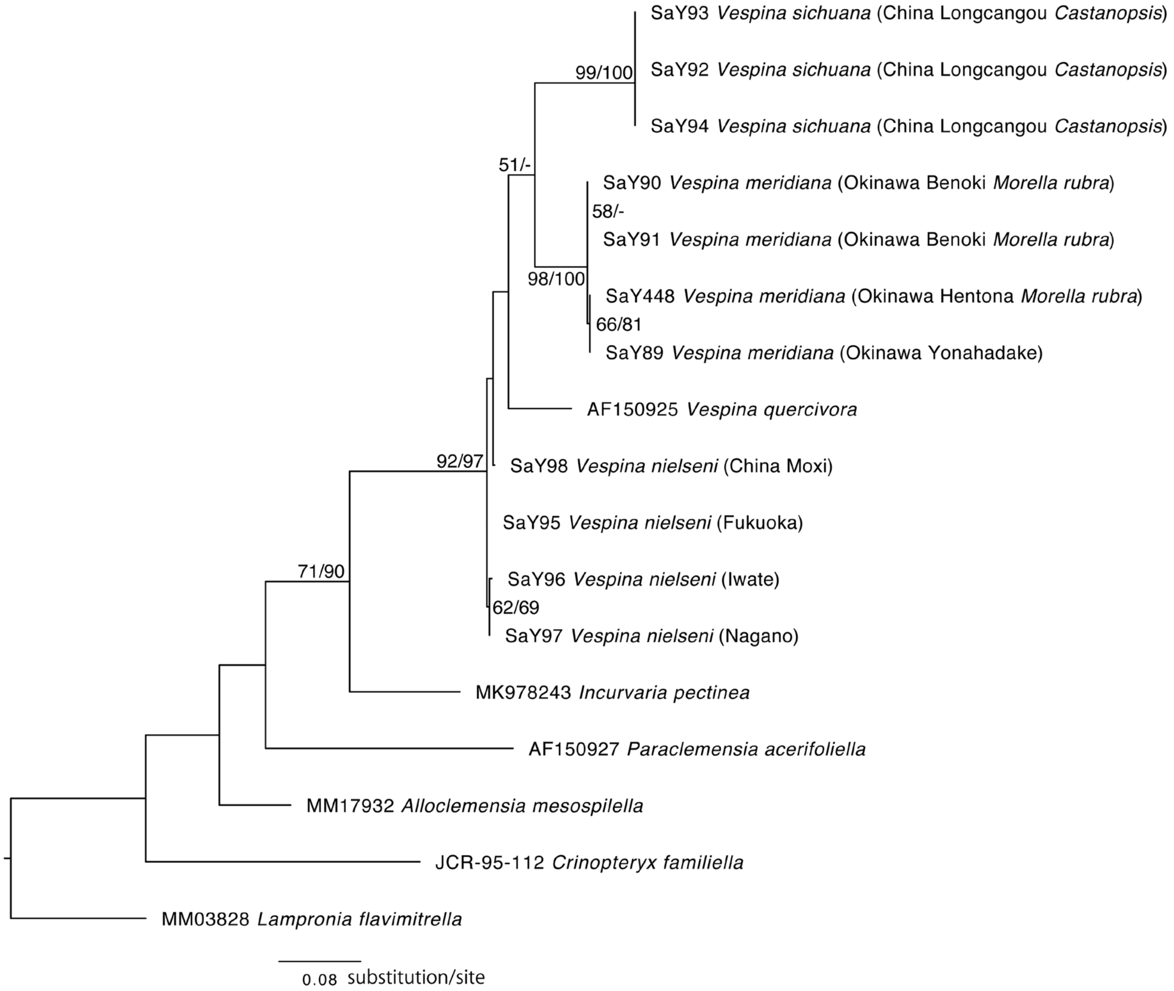

FIGURE 14. Maximum likelihood tree based on the COI sequences. Branch lengths are proportional to ML estimated genetic distances. Numbers associated with branches indicate bootstrap values higher than 50% (ML/MP). Within sample names, species names are followed by each sample ID. ML, maximum likelihood; MP, maximum parsimony.

Moreover, the pairwise distances between *Vespina* and *Incurvaria* (9.91–12.93%) were smaller than those with other incurvariid genera (12.55–17.77%). This, alongside the weak support of the ML tree, perhaps implies the close relationship of the two genera, although the COI barcoding region alone is not suitable for the inference of deeper clades. This affinity was supported by the similarity in the pupal tergal spines and bristles of the labial palpus and the absence (or reduction) of a frenulum in females (see Discussion); as in *Vespina*, bristles on the distal part of the second segment are also present in *Incurvaria takeuchii* and *I. alniella* (present study). This hypothesis is different from that of a previous study (Davis 1972a), which suggested that *Vespina* is similar to *Paraclemensia*. Further molecular analyses based on several nuclear genes will resolve these contradictions.

Discussion

Morphological characters of the genus

Adult morphology—Frenular and pseudofrenular bristles. The frenulum-retinaculum wing coupling is considered to be one of the autapomorphies shared in monotrysian and ditrysian Heteroneura. In males, the frenulum usually consists of a single large bristle, whereas in females, it usually consists of two or more thin frenular bristles (Davis 1999). However, the frenulum is sometimes absent even in monotrysian Heteroneura, as in Opostegidae (Nepticuloidea) (Davis 1989) and Cecidosidae (Adeloidea) (Davis 1999). In Opostegidae, dense rows of elongate

TABLE 3. Intraspecific and interspecific pairwise K2P distances in the COI barcoding region.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	SaY89 *Vespina meridiana* (Okinawa Yonahadake)																
2	SaY90 *Vespina meridiana* (Okinawa Benoki *Morella rubra*)	0.017															
3	SaY91 *Vespina meridiana* (Okinawa Benoki *Morella rubra*)	0.019	0.002														
4	SaY448 *Vespina meridiana* (Okinawa Hentona *Morella rubra*)	0.005	0.019	0.020													
5	SaY92 *Vespina sichuana* (China Longcangou *Castanopsis*)	0.079	0.089	0.087	0.077												
6	SaY93 *Vespina sichuana* (China Longcangou *Castanopsis*)	0.079	0.089	0.087	0.077	0.000											
7	SaY94 *Vespina sichuana* (China Longcangou *Castanopsis*)	0.079	0.089	0.087	0.077	0.000	0.000										
8	SaY95 *Vespina nielseni* (Fukuoka)	0.062	0.075	0.077	0.064	0.079	0.079	0.079									
9	SaY96 *Vespina nielseni* (Iwate)	0.065	0.079	0.081	0.067	0.079	0.079	0.079	0.003								
10	SaY97 *Vespina nielseni* (Nagano)	0.064	0.077	0.079	0.065	0.077	0.077	0.077	0.002	0.002							
11	SaY98 *Vespina nielseni* (China Moxi)	0.069	0.072	0.074	0.067	0.078	0.078	0.078	0.011	0.014	0.012						
12	AF150925 *Vespina quercivora*	0.085	0.085	0.083	0.083	0.088	0.088	0.088	0.069	0.072	0.071	0.064					
13	MK978243 *Incurvaria pectinea*	0.117	0.128	0.129	0.115	0.115	0.115	0.115	0.099	0.103	0.101	0.104	0.116				
14	AF150927 *Paraclemensia acerifoliella*	0.145	0.153	0.151	0.144	0.136	0.136	0.136	0.145	0.149	0.147	0.144	0.150	0.133			
15	MM17932 *Alloclemensia mesospilella*	0.149	0.153	0.151	0.151	0.155	0.155	0.155	0.125	0.129	0.127	0.129	0.152	0.140	0.142		
16	JCR-95-112 *Crinopteryx familiella*	0.159	0.172	0.170	0.157	0.172	0.172	0.172	0.170	0.170	0.168	0.178	0.174	0.165	0.146	0.161	
17	MM03828 *Lampronia flavimitrella*	0.161	0.168	0.166	0.159	0.157	0.157	0.157	0.157	0.157	0.155	0.157	0.164	0.184	0.159	0.158	0.164

pseudofrenular setae (=bristles) are present; these modified scales are considered to be autapomorphies shared with Nepticulidae (Davis 1989).

In the diagnoses of Adeloidea (as Incurvarioidea), Davis (1999) described the female frenulum as usually indistinct, consisting of two or more small, costal bristles along the base of the hindwing. However, in Adeloidea, the condition of the frenular and pseudofrenular bristles has never been studied comprehensively; specifically, the pseudofrenular bristles may have been particularly overlooked or not illustrated, even if present in many groups.

In publications of *Alloclemensia* (Nielsen 1981) and *Paraclemensia* (Nielsen 1982), pseudofrenular bristles are illustrated along the base of the hindwing in both sexes; in *Vespina* (Davis 1972; Kozlov 1997) and *Incurvaria* (Davis 1999; Hirowatari & Lee 2011), however, they are not illustrated. In the present study, we confirmed that pseudofrenular bristles are present in *Vespina* (*V. nielseni*, *V. meridiana,* and *V. sichuana*) but absent in both sexes of *Incurvaria* (*I. takeuchii* Issiki, 1957 and *I. alniella* (Issiki, 1957)). The pseudofrenular bristles are known to be present widely in monotrysian Heteroneura (Nielsen & Common 1991), but they may sometimes be lost in *Incurvaria*.

In female incurvariids of *Paraclemensia* and *Alloclemensia*, the pseudofrenular bristles are followed two thin frenula, but in the present study, we confirmed that distinct frenular bristles are not found and only 15–22 thin pseudofrenular bristles are present in female *Vespina* (*V. nielseni*, *V. meridiana,* and *V. sichuana*). This may be one of the autapomorphies of the genus *Vespina*. Davis (1999) noted that Crinopterygidae (= Crinopteriginae, Incurvariidae consisting of only one species, *Crinopteryx familiella*) have the following characters: "male frenulum a single large bristle accompanied by several smaller costal setae; female with a basal series of much smaller, undifferentiated costal setae. Since *Crinopteryx* may have similar condition to *Vespina*, further examination is required to confirm the homology of these bristles or setae.

Larval morphology. In *Vespina nielseni*, the mature larva is remarkably different from the premature larva, possessing a stouter body, shorter setae, less-sclerotized thoracic tergites, a smaller squamiform seta adjacent to the claws on the apices of the thoracic legs, fewer abdominal crochets, and a thinner and paler head capsule (Okamoto & Hirowatari 2000). All these traits, except for the reduction in size of the squamiform seta, were also confirmed in *Vespina meridiana*, for which we examined the pre-mature and mature larvae. In Heliozelidae, some remarkable reduction is observed in the last instar (mature) larva, as a non-feeding stage in the portable case, and the reduction is regarded as a general pattern (Kuroko 1961, 1987; Maier 1988; Lee *et al*. 2006). The last-instar larva seems to be a non-feeding stage in *Vespina* as well, but without the size reduction of the head capsule.

Pupal morphology. Okamoto & Hirowatari (2000) described the pupa of *V. nielseni* as possessing a "body flattened dorsoventrally. This characteristic was confirmed in *V. sichuana* in the present study, but was not indicated in *V. slovaciella* (Patočka & Turčáni 2005).

Posteriorly directed spines are a conspicuous trait of the most basal neolepidopteran pupae; they are instrumental in enabling the movement out of the cocoon/shelter before the final ecdysis (Hasenfuss & Kristensen 2003). The minute tergal spines are scattered on abdominal segments 3–8 in *V. sichuana* and *V. nielseni*, and have also been confirmed in the exuvium of the holotype of *V. meridiana* on sections 3–8, but indistinctly so on segment 3. The presence of the "band of spines is also shown on the middle abdominal segments of *V. slovaciella* (Patočka & Turčáni 2005).

Some Nepticulidae that had previously been recognized as Trifurculini (e.g., *Ectoedemia, Etainia*, and *Trifurcula*) have two large patches (fused in many species) with several spine rows on abdominal segments 2–8, while *Stigmella* has a single row on segments 3–8 (Johansson *et al*. 1990; Hasenfuss & Kristensen 2003; van Nieukerken *et al*. 2004). However, Opostegidae (e.g., *Notipostega atrata*) has two large patches of scattered minute spines on abdominal segments 1–8 (Davis & Stonis 2007).

In the Incurvariidae, *Alloclemensia* and *Paraclemensia* have a row of spines at the anterior margin on abdominal segments 3–8 (Nielsen 1981; Hirowatari & Lee 2011; Patočka & Turčáni 2005), but *Incurvaria takeuchii* has distinct tergal spines scattered on segments 3–8 (Hirowatari & Lee 2011).

In the Adeloidea, Prodoxidae and Adelidae also have a row of spines at the anterior margin of the dorsal abdominal segments (Mosher 1915; Patočka & Turčáni 2005). Moreover, *Antispila distyliella* and *Heliozela* sp. of Hirowatari (2013) (Heliozelidae) have minute tergal spines scattered widely on abdominal segments 1–8 (Lee *et al*. 2009; present study).

Thus, the condition of tergal spines in basal heteroneuran pupae is likely to change in the genus or a higher taxonomic rank level, but seems to be stable in each group. In *Vespina*, judging from the pupal exuviae, the pupa is protruded from the portable case, and the dorsal spines serve their function despite their minute size.

In summary, possible autapomorphies of *Vespina* are considered to be i) an absence or reduction of a female frenulum, instead consisting of approximately 20 thin pseudofrenular bristles, ii) a dorsoventrally flattened pupa, and iii) the minute tergal spines scattered on abdominal segments 3–8. Further phylogenetic studies are required to elucidate the evolution of these morphological characters in Incurvariidae.

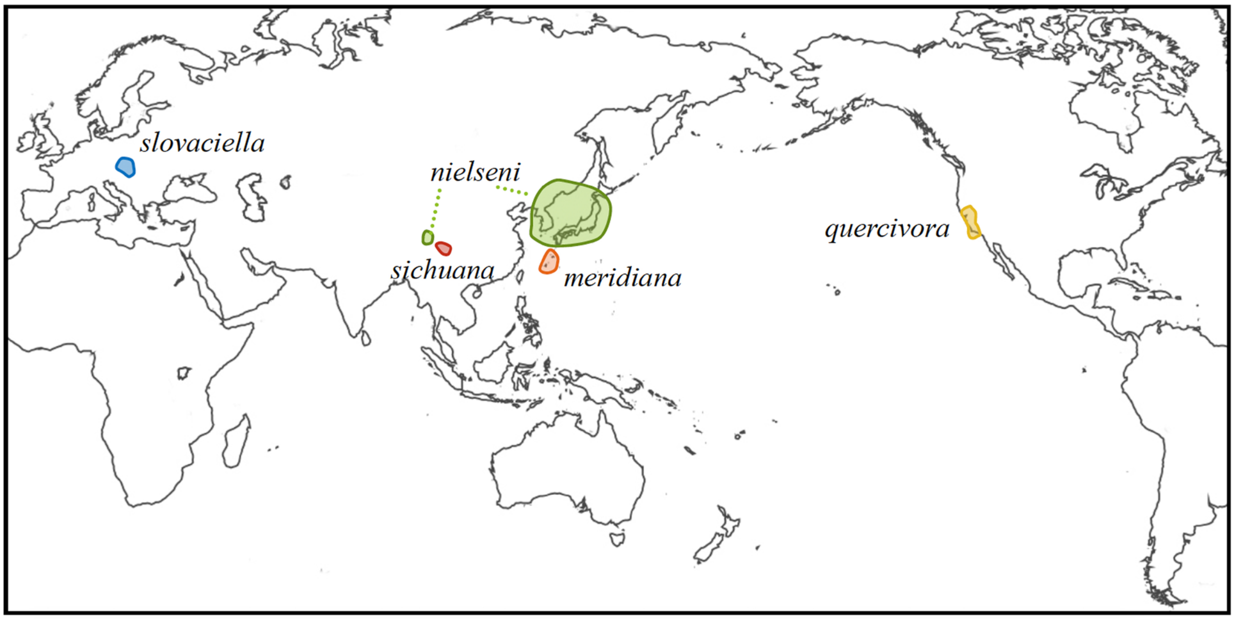

FIGURE 15. Distribution of *Vespina* spp.

Checklist

As a result of the present study, the following five species are recognized in the genus *Vespina*, distributed in restricted areas of the Holarctic region (Fig. 15).

Vespina Davis, 1972

quercivora (Davis, 1972)	USA (California)
nielseni Kozlov, 1987	Russian Far East, China (Sichuan), Korea, Japan
slovaciella (Zagulajev & Tokár, 1990)	Slovakia, Hungary
sichuana Hirowatari, Huang & Wang **sp. nov.**	China (Sichuan)
meridiana Hirowatari & Yagi **sp. nov.**	Japan (Ryukyus)

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