

# Integrative taxonomy of the Lauraceae-feeding species of the genus *Stephanitis* (Hemiptera, Heteroptera, Tingidae) from Japan

Jun Souma<sup>1,2</sup>

<sup>1</sup> Entomological Laboratory, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, Fukuoka, Japan

<sup>2</sup> Research Fellowship for Young Scientists (DC1), Japan Society for the Promotion of Science, Tokyo, Japan

<https://zoobank.org/BFE2BE47-59E9-450A-8070-79B702A38625>

Corresponding author: Jun Souma (kodokusignal@gmail.com)

Academic editor: Dávid Rédei ♦ Received 3 July 2022 ♦ Accepted 22 November 2022 ♦ Published 15 December 2022

## Abstract

*Stephanitis* Stål, 1873 (Hemiptera, Heteroptera, Tingidae, Tinginae, Tingini) is one of the most diverse lace bug genera in East Asia with over 50 species, many of them feeding on Ericaceae and Lauraceae. The Japanese species feeding on Lauraceae have high intra-specific and poor interspecific variation, so identification of some previous distribution records (mainly *S. (Norba) aperta* Horváth, 1912 and closely related taxa) is doubtful. In the present study, 5,080 specimens of Lauraceae-feeding species of *Stephanitis* from Japan were identified to species based on morphology, and DNA barcodes of the mitochondrial cytochrome *c* oxidase subunit (COI) region for 53 of those individuals were also obtained. The combined morphological and molecular evidence dataset showed that 10 species of *Stephanitis* feed on lauraceous trees in Japan: *S. (Stephanitis) ambigua* Horváth, 1912, *S. (Norba) aperta*, *S. (N.) exigua* Horváth, 1912, *S. (N.) hayashii* **sp. nov.**, *S. (N.) hiurai* Takeya, 1963, *S. (N.) ishikawai* **sp. nov.**, *S. (N.) mendica* Horváth, 1912, *S. (S.) tabidula* Horváth, 1912, *S. (S.) takeyai* Drake & Maa, 1955 and *S. (S.) tomokunii* **sp. nov.** Additionally, a new synonymy, *S. (S.) fasciicarina* Takeya, 1931, **syn. nov.** with *S. (S.) tabidula*, is proposed, a key for identifying the 10 species is provided and their distribution ranges and host plant relationships are presented.

## Key Words

East Asia, DNA barcoding, host plant, laurilignosa, new species, taxonomy

## Introduction

Lace bugs (Hemiptera, Heteroptera, Tingidae) are phytophagous insects that comprise over 2,600 species in 320 genera worldwide (Schuh and Weirauch 2020). Most tingids feed on the abaxial side of leaves of angiosperms and are monophagous or oligophagous (Schuh and Weirauch 2020). In Japan, a total of 86 species in 31 genera have been recorded to date (Yamada and Tomokuni 2012; Yamada and Ishikawa 2016; Souma and Kamitani 2021 etc.) and host plants of leaf-feeding genera are mostly known. The visible damage left on leaves during feeding (cf. Yasunaga et al. 1993) makes leaf-feeding tingids relatively easy to collect, but monophagous species feeding on rare plants are difficult to find. Therefore, leaf-feeding species that feed on common plants are very frequently

recorded, whereas those that feed on rare plants are not common in the historical record. In addition, the distribution of the commonly-collected species is localised to focused collecting events versus broad sampling across their host plant's distribution range. Moreover, although some tingids have been reported from fruits and vines (Souma 2019, 2020a, 2020b), these species are difficult to collect due to lacking visible damage.

The genus *Stephanitis* Stål, 1873 (Tinginae, Tingini) comprises 85 extant and a single extinct species in three subgenera—namely, *Menodora* Horváth, 1912, *Norba* Horváth, 1912 and *Stephanitis* s. str.—worldwide, with relatively large diversification in East Asia of over 50 species (cf. Péricart and Golub 1996; Souma 2020c, 2021a; Knudson et al. 2021). In Japan, 28 species have been reported to date (cf. Souma 2020c). To the best of

the author's knowledge and according to previous studies (e.g. Takeya 1951a; Takahashi 1990a; Yasunaga et al. 1993; Souma 2020c, 2021b, 2021c), all species for which the host plants are known feed on the abaxial side of leaves of angiosperms. Most Japanese species occur on Ericaceae or Lauraceae (Yamada and Tomokuni 2012). Many species feeding on Lauraceae are common in their distribution range, but their high intraspecific and poor interspecific variation result in taxonomic problems.

In Japan, the angiospermous family Lauraceae is one of the dominant taxa of the laurilignosa ecosystem (Tagawa 1995). To date, seven species of *Stephanitis*—*S. (Stephanitis) ambigua* Horváth, 1912, *S. (Norba) aperta* Horváth, 1912, *S. (N.) exigua* Horváth, 1912, *S. (S.) fasciicarina* Takeya, 1931, *S. (N.) mendica* Horváth, 1912, *S. (S.) tabidula* Horváth, 1912 and *S. (S.) takeyai* Drake & Maa, 1955—have been reported to feed on lauraceous trees (Takeya 1963; Yamada and Tomokuni 2012; Maehara 2014). Based on the best of the author's fieldwork, *S. (N.) hiurai* Takeya, 1963 also feeds on a lauraceous tree. Of these eight species, *S. (S.) fasciicarina* and *S. (S.) takeyai* are known as forest pests (Japanese Society of Applied Entomology and Zoology 1980, 2006). In the past 117 years, many taxonomic or faunistic studies of Lauraceae-feeding species of *Stephanitis* from Japan were conducted (Matsumura 1905; Horváth 1912; Takeya 1931, 1951b, 1953; Drake 1948; Drake and Maa 1955; Miyamoto 1964a, 1964b; Tomokuni 1981, 2006a; Tomokuni and Ishikawa 2002 etc.), but the distributional records of some species are doubtful in terms of identification. For instance, the general habitus of the population from the central and southern parts of the Ryukyu Islands identified as *S. (N.) aperta* in the literature is different from that of *S. (N.) aperta* described from “Sakuna” (cf. Horváth 1912; Takeya 1963; Miyamoto 1964a, 1964b; Yamada and Tomokuni 2012). Similarly, the general habitus of the populations from the southern part of the Ryukyu Islands, identified as *S. (N.) exigua* and *S. (N.) hiurai* in literature, is different from those of *S. (N.) exigua* and *S. (N.) hiurai* described from “Okinawa” and “Naze, Amami-Oshima”, respectively (cf. Takeya 1963; Miyamoto 1964a, 1964b; Yamada and Tomokuni 2012). In addition, the general habitus of a population from the southern part of the Izu Islands identified as *S. (S.) tabidula* in literature is different from that of *S. (S.) tabidula* described from “Kanagawa” (cf. Horváth 1912; Takeya 1963; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012). Moreover, the morphology of *S. (S.) fasciicarina* described from “Kyûshû, Chikuzen, Akama” is slightly different from that of the “true” *S. (S.) tabidula* (cf. Horváth 1912; Takeya 1931; Drake 1948; Takeya 1963; Yamada and Tomokuni 2012) and these species seem to be conspecific. One of the two subspecies of *S. (N.) hiurai*, *S. (N.) h. takaranis* Takeya, 1963, was synonymised with the nominotypical subspecies in a previous study (Miyamoto 1964b) and subsequent authors still treated it as valid without a formal restoration and any discussion (Péricart and Golub 1996; Yamada

and Tomokuni 2012; Yamada and Ishikawa 2016). Previous studies on Japanese species have often described new species using only a few specimens from a few localities, which may have contributed to the taxonomic confusion. Therefore, Lauraceae-feeding species of *Stephanitis* from Japan are in need of a revision using an adequate number of specimens from more localities.

In the present study, 5,080 individuals, including type specimens of Lauraceae-feeding species of *Stephanitis* from an area ranging from northern Honshu to the Ryukyu Islands, approximately corresponding to the entire distribution range of laurilignosa in Japan (Tagawa 1995), were collected from research institutions and by the author's and colleague's fieldwork. The specimens obtained in the author's survey were carefully examined for morphological characteristics and identified. Additionally, the author attempted to confirm morphological species identification by DNA barcoding using the mitochondrial cytochrome *c* oxidase subunit I (COI) sequence. Moreover, many new localities and host plants of each species were discovered.

The present study contributes to the taxonomy, distribution and biology of the Lauraceae-feeding species of *Stephanitis* from Japan. Three new species—*S. (N.) hayashii* sp. nov. from the central part of the Ryukyu Islands, *S. (N.) ishikawai* sp. nov. from the southern part of the Ryukyu Islands and northern Taiwan and *S. (S.) tomokunii* sp. nov. from the southern part of Izu Islands—are described. A new synonymy, *S. (S.) fasciicarina* syn. nov. with *S. (S.) tabidula*, is proposed. All 10 species recognised in Japan are diagnosed and the morphological characters relevant to their identification are discussed. Sexual dimorphism of *Stephanitis* species is reported in detail. Moreover, an identification key is presented to facilitate the identification of the ten species and their distribution range and host plant relationship are also presented and discussed. Finally, photographs of type and non-type specimens from the collection of the late Shonen Matsumura, the oldest important collection of lace bugs in Japan deposited in Hokkaido University and photographs of type specimens described by the late Choku Takeya deposited in Kyushu University are provided.

## Material and methods

A total of 57 specimens of 11 tingid species from Japan (Suppl. material 2), including *Cochlochila (Physodictyon) conchata* (Matsumura, 1913), which is placed into Tingini as well as *Stephanitis*, but differs from *Stephanitis* in the morphological characteristics, as an outgroup, were used for DNA extraction. DNA extraction was performed with the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). Most of the DNA samples were extracted from the whole body or abdomen of specimens using a non-destructive method; however, for Sample IDs JS1, JS2, JS5 and JS6, material from the abdomen of specimens was extracted using a destructive method.



Abdomens were preserved in small polyethylene vials containing 50% glycerine and 50% water solution. Other body parts are preserved as dried specimens and pinned down. PCR was carried out following protocols: initial denaturation at 98 °C for 3 min, denaturation at 98 °C for 10 s, annealing at 50 °C for 5 s and extension at 68 °C for 5 s for 33 cycles, with a final extension at 68 °C for 3 min. PCR products were purified with the ExoSAP IT kit (Amersham Biosciences, Amersham United Kingdom). A 758 bp fragment of the partial mitochondrial COI region was amplified using the primers C1-J-2183 (5'CAA CAT TTA TTT TGA TTT TTT GG 3') and TL2-N-3014 (5'TCC AAT GCA CTA ATC TGC CAT ATT A 3') (Simon et al. 1994). The edited COI sequences of the Japanese tingids were compared with related sequences from the database of the National Centre for Biotechnology Information (NCBI) (<http://www.ncbi.nlm.nih.gov>), using the Basic Local Alignment Search Tool (BLAST) algorithm (Altschul et al. 1997). Sequence alignment and pairwise sequence distances were generated using Mega 10.1.8 (Kumar et al. 2018). To identify similar species, pairwise sequence distances were calculated using the Kimura-two parameter (K2P) model. The average interspecific and intraspecific genetic distances of Heteroptera provided by the previous study (Jung et al. 2011) were 6.3% and 0.4%, respectively. In this study, the interspecific genetic distance of less than 1% and the intraspecific genetic distance of more than 2% are treated as small and large, respectively. Preliminary phylogenetic tree was constructed using Bayesian methods; model selection was performed using the Bayesian Information Criterion (BIC) using Kakusan 4 (Tanabe 2011). To decrease saturation and compositional bias, the RY coding (Woese et al. 1991) dataset for the third codon was used in the phylogenetic analyses. Bayesian analyses were performed using MrBayes v.3.2.7 (Ronquist et al. 2012) with two Markov Chain Monte Carlo (MCMC) runs of four chains for 1.3 million generations. Convergence of both runs, visualised by Tracer v. 1.6 (Rambaut et al. 2014), was judged to have occurred when the effective sample size (ESS) (Kass et al. 1998) increased above 200. The tree was visualised and edited using Figtree v. 1.4.4 (Rambaut 2014) and Adobe Photoshop 2021 ver. 22.5.1.

Morphological characteristics were observed, illustrated and measured under a stereoscopic microscope (SZ60; Olympus, Tokyo, Japan) equipped with an ocular grid. For the examination of the genitalia, the male terminalia was removed from the body after softening the specimens in hot water. The removed parts were immersed in a hot 15% potassium hydroxide (KOH) solution for 5 min and then soaked in 99% ethanol for further dissection. The male genitalia were observed by fixing the angles with a gel (Museum Gel Clear, Ready America, California, U.S.A) laid on the microscope slide and preserved in small polyethylene vials containing 50% glycerine and 50% water solution and mounted on a pin with the respective specimens. Measurements were obtained using a micrometer on the ocular grid. The specimens and living

individuals were photographed using digital microscopes (VHX-1100, Keyence, Osaka, Japan; Dino-Lite Premier M, Opto Science, Tokyo, Japan) and a compact digital camera (Tough TG-6, Olympus, Tokyo, Japan) and image stacks were processed using Adobe Photoshop 2021 ver. 22.5.1 when using Dino-Lite Premier M. Photographs of host plants were taken with a smartphone (iPhone 8, Apple, California, U.S.A.). Morphological terms were generally assigned in accordance with previous monographs (Drake and Davis 1960; Takeya 1962, 1963; Drake and Ruhoff 1965; Schuh and Weirauch 2020).

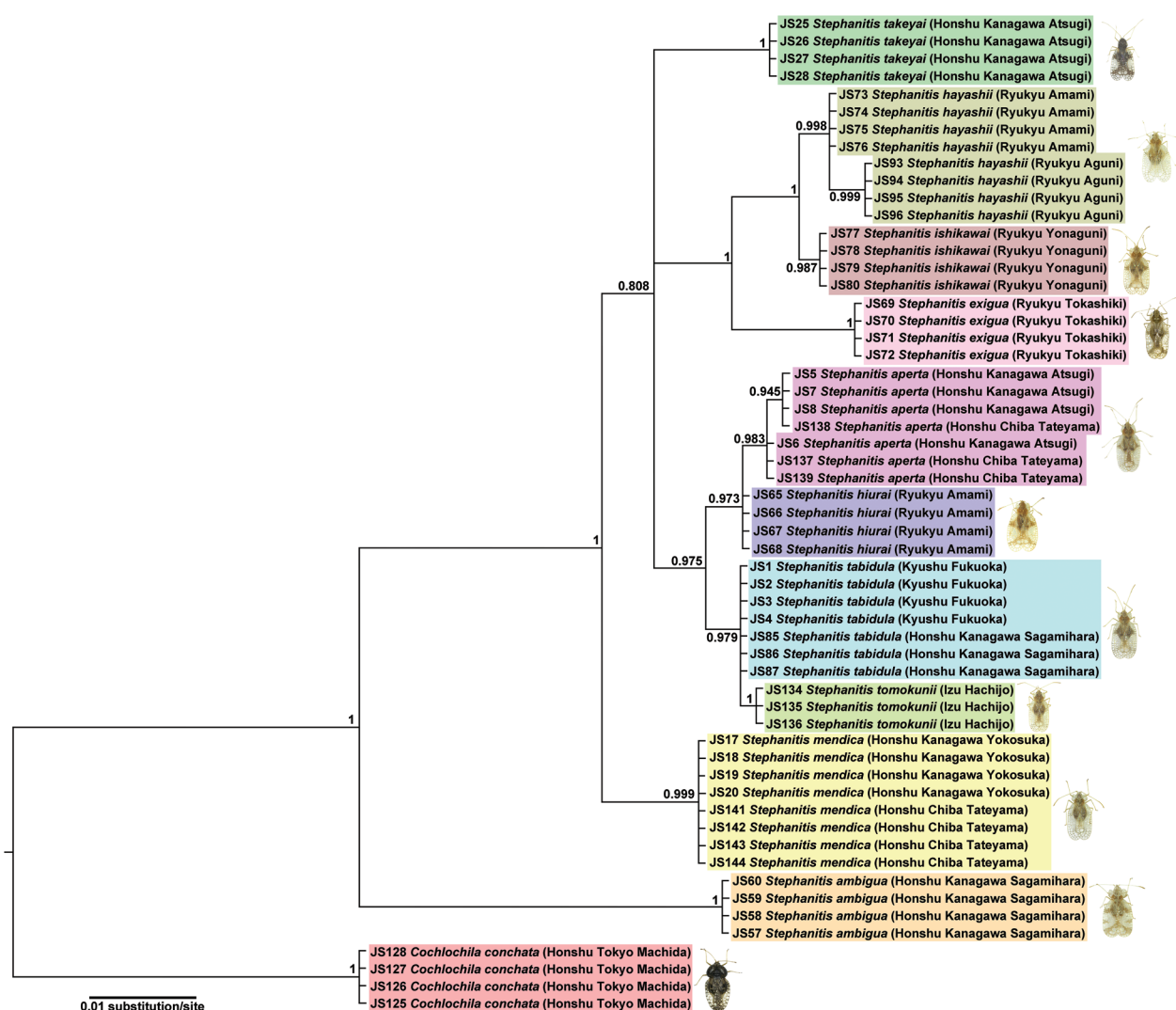
In accordance with a previous study (Takahashi et al. 2008), the author refers to Ryukyu Islands north of the Tokara Tectonic Strait as the northern part, between the Tokara Tectonic Strait and the Kerama Gap as the central part and south of the Kerama Gap as the southern part. Abbreviations for the institutions are as follows: ELHU: Laboratory of Systematic Entomology, Faculty of Agriculture, Hokkaido University, Sapporo, Japan; ELKU: Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan; HNHM: Hungarian Natural History Museum, Budapest, Hungary; KPMNH: Kanagawa Prefectural Museum of Natural History, Kanagawa, Japan; KUM: Kyushu University Museum, Fukuoka, Japan; NIAES: Institute of Agro-Environmental Sciences, NARO, Ibaraki, Japan; NMNS: National Museum of Natural Science, Taichung, Taiwan; NSMT: National Museum of Nature and Science, Ibaraki, Japan; OMNH: Osaka Museum of Natural History, Osaka, Japan; TUA: Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Kanagawa, Japan; USNM: United States National Museum of Natural History, Washington, D.C., U.S.A. All specimens used in this study are deposited in ELHU, ELKU, KPMNH, KUM, NIAES, NMNS, NSMT and TUA.

Distribution records of species were mapped using SimpleMapp (Shorthouse 2010). Geographical coordinates were obtained from Google Maps (<https://www.google.co.jp/maps>). The map was edited using Adobe Photoshop 2021 ver. 22.5.1. The scientific names of host plants were assigned according to Yonekura and Kajita (2003–2021).

## Results

### Molecular data

The interspecific and intraspecific distances of 57 individuals representing 11 Japanese tingid species were analysed, based on the K2P model of substitution of the partial COI gene (758 bp) (Suppl. material 3). The divergence between the ingroup (10 morphological species of *Stephanitis*) and outgroup (*Cochlochila* (*Physodictyon*) *conchata*) was 0.164559–0.193161. The interspecific divergences of ten morphological species of *Stephanitis*, except between *S. (Norba) aperta* and *S. (N.) hiurai* and between *S. (Stephanitis) tabidula* and *S. (S.) tomokunii* sp. nov. were 0.040983–0.170534. Contrarily,



**Figure 1.** Bayesian tree using the cytochrome *c* oxidase subunit I (COI) gene. Numbers associated with branches indicate posterior probabilities. Each sample ID is followed by a species name and collection locality.

the divergences between *S. (N.) aperta* and *S. (N.) hiurai* and between *S. (S.) tabidula* and *S. (S.) tomokunii* sp. nov. were only 0.006632–0.009310 and 0.002645–0.007978, respectively. However, all ten morphological species of *Stephanitis* formed monophyletic or independent clades in the Bayesian tree of the partial COI gene (Fig. 1; Suppl. material 1), including these two pairs, which could also be readily distinguished using morphological characteristics (see a diagnosis of each species). Thus, the 10 morphological species of *Stephanitis* herein studied, including *S. (N.) aperta*, *S. (N.) hiurai*, *S. (S.) tabidula* and *S. (S.) tomokunii* sp. nov., were treated as independent species.

The intraspecific divergences of 11 tingid species, except *S. (N.) hayashii* sp. nov., were 0–0.005305. However, the divergences between the populations of *S. (N.) hayashii* sp. nov. from Amami-Oshima and Aguni islands (Suppl. material 2) reached 0.022916 and the Bayesian tree of the partial COI gene shows separate clades with high posterior probability for each of these populations. Nevertheless, as no morphological difference was found

amongst the specimens from these Islands, both populations of *S. (N.) hayashii* sp. nov. are considered to be conspecific in the present study.

## Systematics

### Genus *Stephanitis* Stål, 1873

[Japanese name: Tsutsuji-gunbai-zoku]

*Stephanitis* Stål, 1873: 119. Type species: *Acanthia pyri* Fabricius, 1775, by subsequent designation (Oshanin 1912: 130). For other synonyms and detailed description, see Péricart (1983), Péricart and Golub (1996) and Souma (2020c).

**Remarks.** To date, only macropterous morphs are known for members of the genus *Stephanitis*. To the best of the author's knowledge, most species of this genus feed on the abaxial surface of angiospermous leaves, as do many lace bugs (Schuh and Weirauch 2020). The nominotypical subgenus *Stephanitis* is distinguished from the other

two subgenera, *Menodora* and *Norba*, by the following characteristics (Horváth 1912; Takeya 1963): pronotum tricarinate (unicarinate in *Norba*); lateral carina ridge-like or laminate (composed of a single row of areolae) (shell-like in *Menodora*); posterolateral angle of paranotum not protruding posteriad (protruding in *Menodora*); and hemelytral anterior margin not curved inwards in basal part (curved in *Menodora*). Nevertheless, four Japanese species—*S. (N.) aperta*, *S. (N.) mendica*, *S. (N.) morimotoi* Takeya, 1963 and *S. (S.) tabidula* [= *S. (S.) fasciicarina* syn. nov.]—have a unicarinate or tricarinate pronotum as intraspecific variation (Takeya 1931, 1963; Souma 2021c). *Stephanitis (Norba) mendica* is the type species of the subgenus *Norba* (Drake and Poor 1936). “*Stephanitis (Norba) aperta*” and “*S. (S.) tabidula*” possessing a unicarinate and tricarinate pronotum, respectively, reported in a previous study (Takeya 1963) are misidentifications of *S. (S.) tabidula* and *S. (N.) aperta*, respectively (see material examined of each species). However, *S. (S.) tabidula* possessing a unicarinate pronotum was confirmed in the present study. Therefore, the presence or absence of lateral carinae varies intraspecifically in at least three species. In conclusion, the number of the pronotal carinae is important for identifying most species, but insufficient for subgenus delimitation. Since the present author considers that molecular phylogenetic analysis using a high number of species and gene regions is necessary to synonymise *Norba* with the nominotypical subgenus *Stephanitis*, the subgeneric status of ten species treated in the present study follows the current classification.

### *Stephanitis (Stephanitis) ambigua* Horváth, 1912

[Japanese name: Yamakobashi-gunbai]

Figs 2A, 4A, 7A, 9A, 11A, 13A, 15A, 17A, 19A, 21A, 23A, 25A, 27A, 29A, 31A, 33, 40A–C

*Tingis pyrioides* Scott, 1874: Matsumura (1905: 33) (monograph). Misidentification (Horváth 1912: 328).

*Stephanitis pyri* Fabricius, 1775: Horváth (1906: 56) (monograph). Misidentification (Horváth 1912: 328).

*Stephanitis (Stephanitis) ambigua* Horváth, 1912: 328. Syntype(s): Japan: Kanagawa [= Honshu, Kanagawa-ken] and Akashi [= Honshu, Hyogo-ken, Akashi-shi]; HNHM.

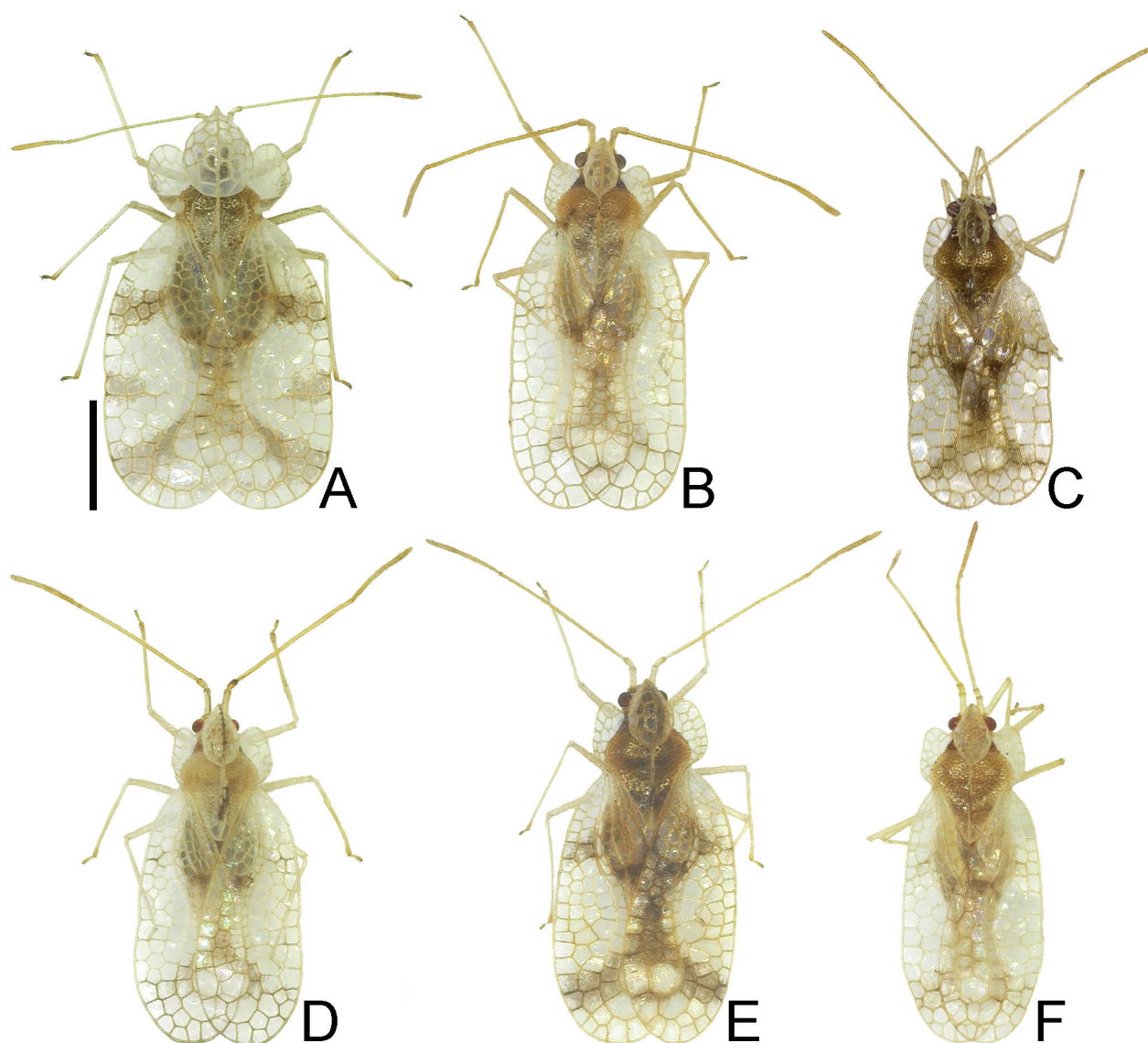
**References.** Esaki and Takeya (1931: 54) (host plant); Takeya (1932: 8) (distribution); Saito (1933: 6) (distribution); Drake (1938: 197) (distribution); Drake (1948: 54) (distribution); Takeya (1951b: 9) (checklist: Japan); Drake and Maa (1953: 100) (checklist: *Stephanitis*); Takeya (1953: 168) (distribution); Takeya (1963: 32) (distribution); Drake and Ruhoff (1965: 354) (catalog); Lee (1967: 106) (checklist: Korea); Lee (1969: 208) (nymph, male genitalia); Jing (1981: 355) (monograph); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Takahashi (1990b: 5) (checklist: Hyogo); Péricart and Golub (1996: 59) (catalogue: Palaearctic); Tomokuni (2006b: 67) (checklist: Taiwan); Yamada and Tomokuni

(2012: 205) (monograph); Yano et al. (2013: 25) (distribution); Maehara (2014: 60) (distribution); Yamada and Ishikawa (2016: 433) (checklist: Japan); Ahn et al. (2018: 64) (distribution); Ito and Sasaki (2018: 19) (checklist: Oita); Cho et al. (2020: 742) (distribution).

**Material examined. Non-types collected at type locality** (36 ♂♂ 34 ♀♀ 2 nymphs), JAPAN: HONSHU: Kanagawa-ken, Sagami-hara-Shi, Midori-ku, Yoshino (approximate coordinates: 35°37'54.8"N, 139°10'11.0"E), 9.viii.2017, leg. J. Souma (2 ♂♂, ELKU; 30 ♂♂ 28 ♀♀, TUA); Kanagawa-ken, Sagami-hara-Shi, Midori-ku, Naramoto For. Rd. (approximate coordinates: 35°37'48.6"N, 139°09'55.5"E), 4.ix.2020, leg. J. Souma (2 ♂♂ 2 ♀♀, ELKU; 2 ♂♂ 2 ♀♀ 2 nymphs, TUA). 64 adult individuals recorded above, matching the original description of the species (Horváth 1912), were collected from the type locality, “Kanagawa” [= Honshu, Kanagawa-ken (a prefecture) or Kanagawa-ku (a ward) of Yokohama-shi (a city) of Kanagawa-ken]. Identification of *S. (S.) ambigua* in the present work is mainly based on these 64 adults. A total of 8–10 syntypes of *S. (S.) ambigua* exist in the collection of HNHM (D. Rédei, pers. comm. 2021). **Non-types** (26 ♂♂ 22 ♀♀ 1 abdomen missing 2 nymphs), JAPAN: HONSHU: “群馬” [= Gunma-ken (approximate coordinates: 36°32'43.2"N, 139°01'07.5"E)], “20/5/914” [= 20.v.1914], “武井氏” [= leg. Takei] (2 ♂♂ 2 ♀♀, ELHU) (Fig. 33); Nagano, Ohya, 8.viii.1959, leg. S. Miyamoto (15 ♂♂ 10 ♀♀ 1 abdomen missing 2 nymphs, KUM); Nagano, Onasawa, 21.viii.1962, leg. Y. Miyatake (5 ♂♂, KUM); Nagano, Arayasu, 7.vii.1966, leg. Y. Miyatake (4 ♂♂ 9 ♀♀, KUM). Shikoku: Kagawa-ken, Takamatsu-shi, Nishiueta-cho, Donguri Land, Fujio Shrine, 4.vi.2020, leg. Y. Waki (2 ♀♀, TUA). KYUSHU: Bungo, Sobosan, 20.vii.1930, leg. Fujino & Yasumatsu (1 ♀, ELKU). Four specimens deposited in ELHU were labeled with an inscription of “Matsumura” (deposited in Matsumura’s collection).

**Diagnosis.** *Stephanitis (Stephanitis) ambigua* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral in various shades of brown (Figs 7A, 9A, 11A, 13A, 15A, 17A, 19A, 21A, 23A); calli light brown; body 1.8 times as long as maximum width across hemelytra (Figs 2A, 4A); rostrum reaching metasternum; pronotum tricarinate (Fig. 25A); hood pale, shorter than median carina of pronotum, wider than maximum width of head across eyes, completely covering eye, slightly higher than median carina of pronotum at highest part, with posterior margin extending to middle of pronotal disc; median carina of pronotum with 3 rows of areolae at highest part; pronotal disc opaque; paranotum more erect, not narrowed posteriorly, with 4 rows of areolae at widest part, with anterolateral angle protruding anteriorly, with outer margin angularly curved inward at posterolateral angle, maximum height longer than height of eye (Fig. 27A); apices of hemelytra separated from each other in rest; costal area with 5 rows of areolae at widest part; subcostal area with 2 rows of areolae at widest part;





**Figure 2.** Male habitus of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua* from Honshu; **B.** *S. (Norba) aperta* from Honshu; **C.** *S. (N.) exigua* from Minamidaito Island, Daito Islands; **D.** *S. (N.) hayashii* sp. nov. from Senaga Island, central part of Ryukyu Islands; **E, F.** *S. (N.) hiurai* from Kakeroma (**E**) and Takara (**F**) islands, central part of Ryukyu Islands. Scale bar: 1.0 mm.

discoïdal area with 4 rows of areolae at widest part; sutural area with 3 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore flat at centre of venter, with posterior margin emarginate in middle part (Fig. 29A); and paramere stout, weakly curved inwards at apex, with outer margin sinuate in middle part, inner margin not curved in basal part (Fig. 31A).

**Remarks.** Amongst the Japanese species of *Stephanitis*, *S. (Stephanitis) ambigua* is similar to *S. (S.) nashi* Esaki & Takeya, 1931, which feeds on deciduous rosaceous trees (Esaki and Takeya 1931; Yasunaga et al. 1993; Yamada and Tomokuni 2012), in its general habitus. However, the former is easily distinguished from the latter by the following characters: hood wider than maximum width of head across eyes (as wide as vertex at widest part in *S. (S.) nashi*), completely covering eye (not covering in *S. (S.) nashi*) (Figs 7A, 9A, 25A); costal

area of hemelytron with 5 rows of areolae at widest part (4 rows in *S. (S.) nashi*) (Figs 15A, 17A); and hypocostal lamina with a single row of areolae throughout its length (2 rows in basal part and a single row in remaining parts in *S. (S.) nashi*).

**Distribution.** Japan (Honshu; Shikoku; Kyushu) (Fig. 45); China; Korea (Esaki and Takeya 1931; Takeya 1932, 1963; Drake 1938, 1948; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016). A record from Taiwan (Drake 1948) does not list any examined specimen and appears to be erroneous. In Japan, *Stephanitis (Stephanitis) ambigua* inhabits deciduous broad-leaved forests in the temperate climatic zone of Japan proper (pertaining to the Palearctic Region).

**Host plants.** *Lindera erythrocarpa* Makino, “Kanakuginoki” (Cho et al. 2020); *L. glauca* (Siebold et Zucc.) Blume, “Yamakobashi” (Lauraceae) (Fig. 43A) (Takeya 1963; Yamada and Tomokuni 2012; present



study); *L. obtusiloba* Blume, “Dankobai” (Esaki and Takeya 1931; Takeya 1963; Yamada and Tomokuni 2012); *L. triloba* (Siebold et Zucc.) Blume, “Shiromoji” (Takeya 1963). *Stephanitis* (*Stephanitis*) *ambigua* feeds only on lauraceous trees and is oligophagous.

**Biology.** *Stephanitis* (*Stephanitis*) *ambigua* feeds on the abaxial surface of leaves of the three host plants in Japan (present study). In Japan, adults were collected in almost all seasons (Takeya 1953; Yamada and Tomokuni 2012; Yano et al. 2013; Maehara 2014; present study), whereas nymphs were collected in August and September (present study). The overwintering stage is the adult (Maehara 2014). One of the natural enemies of this lace bug is *Stethoconus japonicus* Schumacher, 1917 (Hemiptera, Heteroptera, Miridae) (Maehara 2014).

### *Stephanitis* (*Norba*) *aperta* Horváth, 1912

[Japanese name: Tabu-gunbai]

Figs 2B, 4B, 6A, 7B, 9B, 11B, 13B, 15B, 17B, 19B, 21B, 23B, 25B, 27B, 29B, 31B, 34A, B, 40D–G

*Stephanitis* (*Norba*) *aperta* Horváth, 1912: 335. Syntype(s): Japan: Sakuna [= Honshu, Chiba-ken, Sakuna of former Toyofusa-mura in early 20<sup>th</sup> Century (current Tateyama-shi, Sakuna)]; HNHM. “Sakuna” was considered to be a misspelling of “Satsuma” (Takeya 1931: 77).

*Stephanitis* (*Norba*) *vitrea* Takeya, 1931: 74. Holotype (Fig. 34A): Japan: Yakushima Is., Onoaida-Ambo [= Ryukyu Islands, Yakushima Island, between Onoaida and Anbo]; ELKU. Synonymised with *Stephanitis* (*Norba*) *exigua* Horváth, 1912 by Takeya (1953: 168), with *Stephanitis* (*Norba*) *aperta* Horváth, 1912 by Takeya (1963: 38).

*Stephanitis* *exigua* Horváth, 1912: Takeya (1953: 168) (distribution: part). Misidentification (Takeya 1963: 38).

**References.** Takeya (1931: 75) (distribution: part); Drake (1948: 54) (checklist: *Stephanitis*); Takeya (1951b: 13) (checklist: Japan); Drake and Maa (1953: 100) (checklist: *Stephanitis*); Takeya (1963: 38) (distribution: part); Miyamoto (1964a: 274) (distribution: part); Drake and Ruhoff (1965: 366) (catalog); Lee (1969: 246) (male genitalia); Jing (1981: 349) (monograph); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Yasunaga et al. (1993: 178) (monograph: part); Péricart and Golub (1996: 58) (catalogue: Palaearctic); Tomokuni et al. (2000: 38) (distribution); Tomokuni (2005: 400) (distribution); Tomokuni (2006a: 350) (distribution); Yamada and Tomokuni (2012: 205) (monograph: part); Yiu and Yip (2012: 83) (distribution); Yano et al. (2013: 25) (distribution); Tomokuni (2014: 362) (distribution); Nozaki et al. (2015: 9) (distribution); Yamada and Ishikawa (2016: 433) (checklist: Japan); Maehara (2017: 146) (distribution); Okochi (2019: 2) (distribution); Souma (2021b: 31) (distribution).

**Material examined. Holotype of *Stephanitis* (*Norba*) *vitrea* Takeya, 1931** (1 ♀, ELKU) (Fig. 34A), JAPAN: RYUKYU ISLANDS (northern part): “Yakushima Onoaida-Ambô” [= Yakushima Island, between Onoaida and Anbo (approximate coordinates: 30°16'08.3"N,

130°36'44.2"E)], 3.viii.1929, leg. H. Hori. The labels shown in Fig. 34A were created after (T. Mita, pers. comm. 2021), but the condition of the specimen matched the photograph of the original description (Takeya 1931). Therefore, the female individual seems to correspond to the holotype of *S. (N.) vitrea*. **Suspected syntype of *S. (Stephanitis) propinqua* Horváth, 1912** (1 ♀, ELHU) (Fig. 34B), JAPAN: KYUSHU: “カゴシマ” [= Kagoshima-ken (approximate coordinates: 31°35'59.5"N, 130°32'59.6"E)], “7/10” [= 10.vii]. This specimen was labelled as “*Stephanitis gratiosa* Horv.” (apparently an unpublished name) and “カゴシマグンバイ” (unknown Japanese name). According to the original description (Horváth 1912), the syntype(s) of *S. (S.) propinqua* was (were) deposited in ELHU and this female individual is the only specimen in Matsumura’s collection of ELHU matching the label data of syntype(s) of *S. (S.) propinqua*. However, the morphological characteristics of the specimen match the original description of *S. (N.) aperta* (Horváth 1912), but not that of *S. (S.) propinqua*. Conversely, the general habitus of *S. (S.) propinqua* recorded from Korea by previous studies (Takeya 1932, 1963) differs from that of all the East Asian species of *Stephanitis* (present study). Therefore, if there is no syntype of *S. (S.) propinqua* in other institutions, then *S. (S.) propinqua* should be synonymised with *S. (N.) aperta* and a new name should be given to “*S. (S.) propinqua*” distributed in Korea. **Non-types** (534 ♂♂ 777 ♀♀ 16 nymphs), JAPAN: HONSHU: Ibaraki-ken, Higashiibaraki-gun, Oarai-machi, Isohama-cho, 12.ix.2020, leg. J. Souma (7 ♂♂ 13 ♀♀ 3 nymphs, TUA); Tochigi Pref., Uchino, Watarase-yusuichi, 26.xi.2016, leg. S. Maehara (4 ♂♂ 2 ♀♀, TUA); as above but 2.x.2020 (4 ♂♂ 3 ♀♀, TUA); Chiba-ken, Tateyama-shi, Ohto (approximate coordinates: 34°58'19.8"N, 139°52'33.9"E), 22.v.2021, leg. J. Souma (1 ♀, TUA); Chiba-ken, Tateyama-shi, Shimosanagura, 22.v.2021, leg. J. Souma (1 ♂ 2 ♀♀, TUA); Chiba-ken, Tateyama-shi, Tateyama, 22.v.2021, leg. J. Souma (2 ♂♂ 6 ♀♀, TUA); as above but 23.v.2021 (4 ♀♀, ELKU; 2 ♂♂ 2 ♀♀ 1 nymph, TUA); Chiba-ken, Tateyama-shi, Sunozaki, 23.v.2021, leg. J. Souma (11 ♂♂ 32 ♀♀, TUA); Chiba-ken, Tateyama-shi, Sunozaki Shrine, 23.v.2021, leg. J. Souma (1 ♂ 2 ♀♀, TUA); Chiba-ken, Tateyama-shi, Masaki, 23.v.2021, leg. J. Souma (7 ♂♂ 14 ♀♀, TUA); Chiba-ken, Tateyama-shi, Higashinagata, 24.v.2021, leg. J. Souma (1 ♂ 1 ♀, TUA); Chiba-ken, Tateyama-shi, Yamogi (approximate coordinates: 34°58'08.7"N, 139°53'34.4"E), 24.v.2021, leg. J. Souma (2 ♂♂ 4 ♀♀, TUA); Chiba-ken, Minamiboso-shi, Chikura-cho, Minamiasai, 24.v.2021, leg. J. Souma (1 ♀, TUA); Chiba-ken, Kamogawa-shi, Yomogi, 25.v.2021, leg. J. Souma (1 ♀, TUA); Tokyo Met., Imperial Palace, 5.vi.1996, leg. A. Saito (7 ♂♂ 7 ♀♀, NSMT); as above but 16.x.1996, leg. M. Tomokuni (8 ♂♂ 15 ♀♀, NSMT); 19.xi.1997, leg. M. Tomokuni (9 ♂♂ 6 ♀♀, NSMT); as above but 25.v.1998 (2 ♀♀, NSMT); as above but 28.v.1998, leg. M. Tomokuni (4 ♂♂ 3 ♀♀, NSMT); as above but 16.vii.2009, leg. M. Tomokuni (1 ♀, NSMT);

- as above but 28.v.2012, leg. M. Tomokuni (1 ♀, NSMT); as above but 23.vii.2012, leg. M. Tomokuni (1 ♂ 2 ♀♀, NSMT); as above but 10.ix.2012, leg. M. Tomokuni (1 ♀, NSMT); Tokyo-to, Minato-ku, Shiba-koen, 8.vii.2022, leg. J. Souma (4 ♂♂ 1 ♀, TUA); Kanagawa-ken, Sagami-hara-shi, Minami-ku, Shimomizo, 15.xi.2021, leg. J. Souma (9 ♂♂ 8 ♀♀ 3 nymphs, TUA); Kanagawa-ken, Sagami-hara-shi, Chuo-ku, Tanashioda, 19.v.2019, leg. J. Souma (2 ♀♀, TUA); Kanagawa-ken, Sagami-hara-shi, Chuo-ku, Tana, 19.v.2019, leg. J. Souma (22 ♂♂ 16 ♀♀, TUA); as above but 17.xi.2021 (9 ♂♂ 11 ♀♀, TUA); Kanagawa-ken, Sagami-hara-shi, Midori-ku, Oshima, 17.xi.2021, leg. J. Souma (1 ♂ 3 ♀♀ 1 nymph, TUA); Kanagawa-ken, Zama-shi, Iriyanishi, 1.i.2022, leg. J. Souma (1 ♂ 14 ♀♀, TUA); Kanagawa-ken, Ebina-shi, Kamiimaizumi, 1.i.2022, leg. J. Souma (1 ♂ 1 ♀, TUA); Kanagawa-ken, Atsugi-shi, Funako, 29.v.2017, leg. J. Souma (37 ♂♂ 41 ♀♀, TUA); as above but 30.v.2017 (32 ♂♂ 30 ♀♀, TUA); as above but 31.v.2017 (4 ♀♀, ELKU; 52 ♂♂ 55 ♀♀, TUA); as above but 2.vi.2017 (6 ♂♂ 16 ♀♀, TUA); as above but 5.vi.2017 (30 ♂♂ 17 ♀♀, TUA); Kanagawa-ken, Atsugi-shi, Nanasawa, 6.vi.2017, leg. J. Souma (1 ♀, TUA); Kanagawa-ken, Aikogun, Aikawa-machi, Nakatsu, 26.v.2021, leg. J. Souma (3 ♂♂ 11 ♀♀, TUA); as above but 15.xi.2021 (3 ♀♀, TUA); Kanagawa-ken, Yokohama-shi, Isogo-ku, Negishihachiman Shrine, 31.v.1999, leg. M. Takakuwa (1 ♀, KPMNH); Kanagawa-ken, Yokohama-shi, Kanazawa-ku, Noukendaimori, 15.vi.2017, leg. J. Souma (3 ♂♂, TUA); Kanagawa-ken, Yokosuka-shi, Kamoi, 27.vi.2017, leg. J. Souma (4 ♀♀, TUA); Kanagawa-ken, Chigasaki-shi, Yanagishima, 1.vi.2019, leg. J. Souma (10 ♂♂ 7 ♀♀, TUA); Kanagawa-ken, Hadano-shi, Tsurumaki, Mt. Azuma, 19.xi.2021, leg. J. Souma (2 ♂♂ 5 ♀♀, TUA); Kanagawa-ken, Hadano-shi, Soya, Mt. Kobo, 19.xi.2021, leg. J. Souma (4 ♀♀, TUA); Kanagawa-ken, Ashigarashimo-gun, Manazuru-machi, Manazuru, 23.v.2021, leg. J. Souma (11 ♂♂ 30 ♀♀, TUA); Niigata-ken, Niigata-shi, Nishi-ku, Igarashi-2no-cho, 19.vii.2015, leg. K. Nakano (2 ♀♀, TUA); as above but 16.vi.2021, leg. G. Mashima (12 ♂♂ 14 ♀♀, TUA); Niigata-ken, Niigata-shi, Chuo-ku, Sekiya, Nishikaigan Park, 22.x.2016, leg. K. Nakano (4 ♂♂ 10 ♀♀, TUA); Niigata-ken, Niigata-shi, Chuo-ku, Seigoro, Toyonogata Park, 30.x.2016, leg. K. Nakano (1 ♂ 4 ♀♀, TUA); Niigata-ken, Niigata-shi, Higashi-ku, Matsuzono, 21.vii.2019, leg. K. Nakano (2 ♂♂ 1 ♀, TUA); Niigata-ken, Niigata-shi, Nishi-ku, Akatsuka, Sakata, 9.x.2019, leg. K. Nakano (1 ♂ 3 ♀♀, TUA); Niigata-ken, Niigata-shi, Kita-ku, Nigorikawa, 7.vi.2020, leg. K. Nakano (5 ♀♀, TUA); Niigata-ken, Niigata-shi, Chuo-ku, Nishifunami-cho, 12.vi.2021, leg. G. Mashima (12 ♂♂ 17 ♀♀, TUA); Niigata-ken, Niigata-shi, Chuo-ku, Bandaijima, 30.viii.2021, leg. J. Souma (18 ♂♂ 10 ♀♀, TUA); Shizuoka-ken, Shimoda-shi, Suzaki, Tsumekizaki, 21.vii.2020, leg. J. Souma (1 ♂, TUA); Shizuoka-ken, Hamamatsu-shi, Nishi-ku, Kamigaya-cho, 16.vi.2017, leg. J. Souma (15 ♂♂ 33 ♀♀, TUA); Shizuoka-ken, Numazu-shi, Kamikanuki, Higashihongo-cho, 27.xii.2021, leg. J. Souma (1 ♀, TUA); Yamaguchi-ken, Shimonoseki-shi, Mimosusogawa-cho, 16.ix.2022, leg. J. Souma (1 ♂ 3 ♀♀, ELKU). IZU ISLANDS (northern part): Izu-Oshima Island: Okada, Minatono-mieru-oka, 4.vi.2019, leg. Y. Tamadera (19 ♂♂ 37 ♀♀, TUA). JOGASHIMA ISLAND: 4.vi.2019, leg. J. Souma (11 ♂♂ 9 ♀♀, TUA). EBISU ISLAND: 21.vii.2020, leg. J. Souma (3 ♂♂, TUA). SHIKOKU: Ehime Pref., Kashima, 2.vi.1971, leg. M. Tomokuni (1 ♂ 1 ♀, NSMT); Tosa, Nakagawa, 19.viii.1953, leg. G. Yamamoto (1 ♂, ELKU); Kochi Pref., Cape Ashizuri, 7.vi.1971, leg. M. Tomokuni (1 ♀, NSMT); Kochi-ken, Kochi-shi, Hitsuzan-cho, 30.vi.2020, leg. J. Souma (1 ♀, TUA). OKINOSHIMA ISLAND (Kochi Prefecture): 11.viii.1951, leg. T. Esaki (1 ♀, ELKU; 1 ♀, KUM). KYUSHU: Prov. Buzen, Kokura, 20.xi.1951, leg. A. Yamasaki (1 ♂, KUM); Fukuoka, Tachibanayama, 23.vii.1961, leg. S. Miyamoto (6 ♂♂ 8 ♀♀, KUM); as above but 8.ix.1961 (1 ♀, KUM); Fukuoka-ken, Fukuoka-shi, Nishi-ku, Motooka, Kyushu University, 23.v.2020, leg. J. Souma (1 ♀, ELKU); Fukuoka-ken, Itoshima-shi, Tomari, 16.v.2022, leg. J. Souma (1 ♀, ELKU); as above but 10.vii.2022 (1 ♀, ELKU); Kumamoto-Pref., Kumamoto-City, Kuwamizuhonmachi, 4.i.2021, leg. K. Goto (2 ♀♀, ELKU); Ōita Pref., Saiki-shi, Yonouzu, Tsurumisaki, 2.vii.2017, leg. R. Ito (1 ♀, ELKU); Ōita Pref., Saiki-shi, Kamiura, Niinameura, 19.vii.2020, leg. R. Ito (1 ♂ 3 ♀♀, ELKU); Miyazaki Pref., Nichinan-shi, Miyauro, 12.v.2018, leg. R. Ito (1 ♂ 1 ♀, ELKU); Miyazaki Pref., Hyūga-shi, Okuragahama, 1.vi.2019, leg. R. Ito (2 ♀♀, ELKU); Kagoshima, 21.v.1953, leg. S. Miyamoto (1 ♂ 1 ♀, KUM); Oosumi, Izashiki~Ootomari, 25.v.1953, leg. Yoshida (1 ♂, ELKU); Osumi, Sata, 29.v.1953, leg. Yoshida (1 ♂ 1 ♀, ELKU); Osumi, Sata Cape, 30.v.1953, leg. I. Hiura (4 ♀♀, KUM); Kagoshima-ken, Kagoshima-shi, Shiroyama-cho, 4.vii.2017, leg. J. Souma (1 ♂, ELKU); Kagoshima, Minamiosumi-T., Sugiyama-dani Valley, 31.vii.2017, leg. N. Tsuji (1 ♀, ELKU); Kagoshima Pref., Minamiōsumi-chō, Sata, Hetsuka, 30.v.2020, leg. R. Ito (9 ♂♂ 6 ♀♀, ELKU). OKINOSHIMA ISLAND (Fukuoka Prefecture): 25–28.vii.1958, leg. Hirashima, Murakami & Y. Miyatake (35 ♂♂ 70 ♀♀, ELKU; 1 ♀, KUM). TSUSHIMA ISLAND: Izuhara-machi, Kitazato, Kamisaka, 27.vii.2022, leg. Y. Uehara (1 ♀, ELKU). AMAKUSA ISLANDS: Shimoshima Island: Tomioka, 12.ix.1931, leg. Hori & Chō (2 ♂♂ 4 ♀♀, ELKU; 1 ♀, KUM). GOTO ISLANDS: Fukue Island: 1. ix.1962, leg. S. Miyamoto (1 ♂ 1 ♀, KUM); as above but leg. S. Miyamoto & Kawarabata (1 ♀, ELKU); Inuyamaze, 2.ix.1962, leg. S. Miyamoto (2 ♂♂ 1 ♀, KUM); as above but (1 ♂ 1 ♀, KUM); Arakawa, 3. ix.1962, leg. S. Miyamoto (2 ♀♀, KUM). SAKURA ISLAND: Kurokami-cho, 27.vii.2021, leg. Y. Obae (18 ♂♂ 13 ♀♀, TUA). KOSHIKI ISLANDS: Kamikoshiki Island: Nakano, Mt. Tomeki, 2.v.2019, leg. N. Kaneko (1 ♂ 4 ♀♀ 1 nymph, TUA). Shimokoshiki Island: Teuchi, 27–29.viii.1960, leg. K. Morimoto (1 ♂ 2 ♀♀, ELKU); 25.v.1975, leg. Y. Watanabe (1 ♂ 1 ♀, TUA). RYUKYU ISLANDS (northern part): Tanegashima Island: Nishinoomote, 31.viii.1952, leg. C. Takeya & Y. Hirashima (2 ♂♂, ELKU; 2 ♂♂ 2 nymphs, KUM); Nakatane-cho, Masuda,

10.vii.2021, leg. T. Saeki (1 ♀, TUA). Yakushima Island: Onoaida, 26.viii.1952, leg. C. Takeya & Y. Hirashima (3 ♂♂ 1 ♀, ELKU); as above but 27.viii.1952 (8 ♂♂ 11 ♀♀ 1 nymph, ELKU); Miyanoura, 28.viii.1952, leg. C. Takeya & Y. Hirashima (1 ♂ 4 ♀♀, ELKU); as above but 18.v.2022, leg. J. Souma (1 ♀, TUA); Shiratani-un-suikyô, alt. 300–600 m, 14.vii.2017, leg. R. Ito (1 ♂, ELKU); Kurio, Koyojigawa For. Rd., 7.vii.2021, leg. T. Saeki (1 ♂, ELKU); Kurio, 15.viii.2021, leg. J. Souma (3 ♂♂, ELKU); Koseda, 17.viii.2021, leg. J. Souma (1 ♂, ELKU); as above but 19.v.2022, leg. J. Souma (10 ♂♂ 14 ♀♀, TUA); Funayuki, 17.viii.2021, leg. J. Souma (1 ♀, ELKU); Hirauchi, 19.viii.2021, leg. J. Souma (1 ♂ 4 ♀♀, ELKU); Anbo, 20.viii.2021, leg. J. Souma (9 ♂♂ 14 ♀♀, ELKU); Tabugawa, 18.v.2022, leg. J. Souma (1 ♂ 3 ♀♀, TUA). Nakanoshima Island: 3–13.vi.1953, leg. S. Miyamoto (1 ♀, ELKU); Okizaki, 5.vii.2017, leg. J. Souma (2 ♀♀, TUA); as above but 6.vii.2017 (1 ♀, TUA); Kusuki, 7.vii.2017, leg. J. Souma (4 ♂♂ 7 ♀♀, TUA). Taira Island: Shûraku, 8–10.x.2016, leg. H. Yoshitake (3 ♀♀, TUA); Higashinohama, 8–10.x.2016, leg. H. Yoshitake (1 ♀, TUA). Akuseki Island: 24.iv.1971, leg. M. Sakai (2 ♂♂ 3 ♀♀ 4 nymphs, NSMT); 17.vi.2016, leg. H. Yoshitake (1 ♀, NIAES); Yudomari, 8.vii.2017, leg. J. Souma (1 ♂ 3 ♀♀, TUA). Seven specimens collected from “Ohto” and “Yamogi” adjacent to the type locality “Sakuna” well match the original description of *Stephanitis (Norba) aperta* (Horváth 1912). In the present study, the author identified *S. (N.) aperta* based on these seven individuals. Syntype(s) of *S. (N.) aperta* exist(s) in the collection of HHNM (D. Rédei, pers. comm. 2021).

**Diagnosis.** *Stephanitis (Norba) aperta* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown (Figs 7B, 9B, 11B, 13B, 15B, 17B, 19B, 21B, 23B); calli dark brown; body in male 2.1 times (in female 2.0 times) as long as maximum width across hemelytra (Figs 2B, 4B, 6A); rostrum not reaching metasternum; pronotum unicarinate (Fig. 25B); hood pale, shorter than median carina of pronotum, as wide as vertex at widest part, not covering eye, as high as median carina of pronotum at highest part, with posterior margin not extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc opaque; paranotum less erect, narrowed posteriorly, with 3 rows of areolae at widest part, with anterolateral angle protruding anteriad, with outer margin gently curved inwards at posterolateral angle, maximum height shorter than height of eye (Fig. 27B); apices of hemelytra close to each other in rest; costal area with 3–4 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 3 rows) of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at centre of venter, with posterior margin slightly emarginate in middle part (Fig. 29B); and paramere stout, weakly curved inwards at

apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 31B).

**Remarks.** Amongst the Japanese species of *Stephanitis*, *S. (Norba) aperta* is similar to *S. (N.) exigua* in general habitus, but it is easily distinguished by the following characters: calli dark brown (light brown in *S. (N.) exigua*) (Figs 7B, C, 9B, C, 11B, C, 13B, C); pronotal disc opaque (lustrous in *S. (N.) exigua*); paranotum with 3 rows of areolae at widest part (2 rows in *S. (N.) exigua*), with anterolateral angle protruding anteriad (slightly protruding in *S. (N.) exigua*); and subcostal area of hemelytron in female with 3 rows of areolae at widest part (2 rows in *S. (N.) exigua*) (Figs 15B, C, 17B, C). The place name “Sakuna” was considered to be a misspelling of “Satsuma” [= Kyushu, Kagoshima-ken, former Satsuma-gun in the early 20th century (current Satsumasendai-shi and Satsuma-cho)] by Takeya (1931). However, the former is the name of an actual place in Honshu. The present author confirms the occurrence of *S. (N.) aperta* in “Ohto” and “Yamogi”, adjacent to “Sakuna” (see material examined). Therefore, “Sakuna” seems to correspond to the type locality of *S. (N.) aperta*.

**Teratological form.** The segmental oligomery of the antenna was confirmed in *Stephanitis (Norba) aperta*, and one examined specimen lacks the left antennal segment IV (Fig. 6A), as reported in many tingids (Štusák and Stehlík 1978; Souma 2020b, 2020d, 2020e). Additionally, the right paranotum of this teratological individual is shorter than that of its normal left side, with two rows of areolae at the widest part (three rows on the left side).

**Distribution.** Japan (Honshu; Izu Islands (northern part): Izu-Oshima Island; Jogashima Island; Ebisu Island; Shikoku; Okinoshima Island (Kochi Prefecture); Kyushu; Okinoshima Island (Fukuoka Prefecture); Tsushima Island; Amakusa Islands: Shimoshima Island; Goto Islands: Fukue Island; Sakura Island; Koshiki Islands: Kamikoshiki Island, Shimokoshiki Island; Ryukyu Islands (northern part): Tanegashima Island, Yakushima Island, Nakanoshima Island, Taira Island, Akuseki Island) (Fig. 45) (Horváth 1912; Takeya 1931, 1963; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016; present study). Previous records from China in the 20th century (Drake and Ruhoff 1965; Jing 1981) do not list the examined specimens and appear to be erroneous. Judging from the photographs, a recent record from Hong Kong (Yiu and Yip 2012) corresponds to another species, as the pronotum has lateral carina. Therefore, the presence of *S. (N.) aperta* in China remains unconfirmed. The previous record from the central part of the Ryukyu Islands (Miyamoto 1964b; Azuma and Kinjo 1987; Hayashi 2002) corresponds to *Stephanitis (Norba) exigua*, *S. (N.) hayashii* sp. nov. or *S. (N.) hiurai*. The previous records from the southern part of the Ryukyu Islands and northern Taiwan (Takeya 1963; Miyamoto 1964a; Azuma and Kinjo 1987; Hayashi 2002) correspond to *S. (N.) ishikawai* sp. nov., described below. Hundreds of specimens from the central and southern parts of the Ryukyu Islands possessing the unicarinate pronotum were examined, but all of them belong to *S. (N.) exigua*, *S. (N.) hayashii* sp. nov.,



*S. (N.) hiurai* or *S. (N.) ishikawai* sp. nov. Therefore, *S. (N.) aperta* is probably not distributed in the central and southern parts of Ryukyu Islands. *Stephanitis (Norba) aperta* inhabits the laurilignosa in a temperate climate of Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands and the northern part of the Izu and Ryukyu Islands, which is in the Palearctic Region.

**Host plants.** *Cinnamomum camphora* (L.) J.Presl, “Kusunoki” (Lauraceae) (Fig. 43D) (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; present study); *Neolitsea sericea* (Blume) Koidz., “Shirodamo” (Fig. 43C) (present study); *Machilus thunbergii* Siebold et Zucc., “Tabunoki” (Lauraceae) (Fig. 43B) (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Okochi 2019; present study). *Stephanitis (Norba) aperta* feeds only on lauraceous trees and is oligophagous. This lace bug was also collected from *Symplocos glauca* (Thunb.) Koidz., “Mimizubai” (Symplocaceae), without any data on its development (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012). This lace bug sometimes occurs on plantings of *C. camphora* and *M. thunbergii* in its distribution range (present study), suggesting that it can become a pest of both lauraceous trees.

**Biology.** *Stephanitis (Norba) aperta* feeds on the abaxial surface of leaves of the three known host plants (present study). Adults were collected in almost all seasons (Takeya 1931, 1953; Yasunaga et al. 1993; Yano et al. 2013; present study); nymphs were collected in April, May, August, September and November (present study); the overwintering stage is represented by the adult (present study).

### *Stephanitis (Norba) exigua* Horváth, 1912

[Japanese name: Himetabu-gunbai]

Figs 2C, 4C, 7C, 9C, 11C, 13C, 15C, 17C, 19C, 21C, 23C, 25C, 27C, 29C, 31C, 35, 40H, I

*Stephanitis (Norba) exigua* Horváth, 1912: 336. Syntype(s) (Fig. 34C):

Japan: Okinawa [= Ryukyu Islands, Okinawa-ken (an administrative area including a number of islands) or Okinawa Island (an island)] and Tateyama [= Honshu, Chiba-ken, Tateyama-shi, former Tateyama-machi in early 20<sup>th</sup> century (current Tateyama, Kamisanagura and Shimosanagura)]; ELHU and HNHM.

*Stephanitis (Norba) aperta* Horváth, 1912: Azuma and Kinjo (1987: 34) (distribution). Misidentification.

**References.** Drake (1937: 594) (distribution); Drake (1948: 55) (checklist: *Stephanitis*); Takeya (1951b: 13) (checklist: Japan); Drake and Maa (1953: 100) (checklist: *Stephanitis*); Takeya (1953: 168) (distribution: part); Takeya (1963: 38) (distribution: part); Drake and Ruhoff (1965: 367) (catalog); Miyamoto (1964a: 274) (distribution: part); Miyamoto (1964b: 524) (distribution: part); Lee (1969: 246) (male genitalia); Jing (1981: 348) (monograph); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Tomokuni (1994: 843) (type material); Péricart and Golub (1996: 58) (catalogue: Palearctic; Yamada

and Tomokuni (2012: 204) (monograph: part); Yamada and Ishikawa (2016: 433) (checklist: Japan); Nakatani (2021: 78) (distribution).

**Material examined. Syntype** (1 ♀, ELHU) (Fig. 34C), JAPAN: Honshu: “タテヤマ” [= Chiba-ken, Tateyama-shi, former Tateyama-machi in early 20<sup>th</sup> century (current Tateyama, Kamisanagura and Shimosanagura; approximate coordinates: 34°58'50.9"N, 139°51'27.1"E)], 11/VIII 1905 [= 11.viii.1905], “Matsumra” [sic; = collected by Shonen Matsumura and/or deposited in Matsumura's collection]. As pointed out in a previous study (Tomokuni 1994), this single female syntype corresponds to *Stephanitis (Stephanitis) pyrioides* (Scott, 1874) and does not match the original description of *S. (Norba) exigua* (Horváth 1912). Therefore, if the remaining syntypes are present in ELHU and/or HNHM, a lectotype should be designated. Nevertheless, the former curator of HNHM does not know if the syntype of *S. (N.) exigua* exists in the collection (D. Rédei, pers. comm. 2021). **Suspected syntypes** (2 ♂♂ 1 ♀ 1 nymph, ELHU) (Fig. 35), JAPAN: RYUKYU ISLANDS: “Okinawa” [= Okinawa-ken (a prefecture including a number of islands) or Okinawa Island (an island)], “6 29”. These four individuals were labelled with inscriptions of “*Stephanitis yaeyamae*” (unpublished name) and “Matsum” (collected by Shonen Matsumura and/or deposited in Matsumura's collection). The species epithet of the unpublished name seems to refer to the Yaeyama Islands, the southern part of the Ryukyu Islands, but this morphological species is only distributed in the Daito Islands and the central part of the Ryukyu Islands. The morphological characteristics and locality data of three adult specimens match the original description of *S. (N.) exigua* (Horváth 1912). However, the collector data of the four specimens are unclear and syntype(s) from “Okinawa” was (were) collected by “Kuroiwa” (Horváth 1912). Therefore, these three adults could correspond to syntypes of *S. (N.) exigua*. In the present study, the author identified *S. (N.) exigua* based on three adult individuals. **Non-types** (106 ♂♂ 189 ♀♀ 7 nymphs), JAPAN: RYUKYU ISLANDS (central part): Okinawa Island: 10.viii.1957, leg. T. Takara (1 ♀, NSMT); Kin, 14.vi.1958, leg. T. Takara (2 ♀♀, NSMT); Osato, 8.xi.1960, leg. K. Yasumatsu (2 ♂♂ 1 ♀, ELKU; 3 ♀♀, KUM); Yona, 14.xi.1960, leg. K. Yasumatsu (1 ♂, KUM); as above but 19.xi.1963, leg. H. Hasegawa (1 ♀, KUM); as above but 24.iii.1964, leg. Y. Miyatake (1 ♀, KUM); as above but 23.xi.1985, leg. M. Hayashi (2 ♂♂ 1 ♀, TUA); as above but 28.vi.1984, leg. M. Tomokuni (2 ♀♀, NSMT); Shuri, 2.vi.1961, leg. O. Nakoshi (1 ♂, KUM); Nago, 22.x.1963, leg. S. Uéno (1 ♂, KUM); Tamagusuku, 17.xi.1963, leg. H. Hasegawa (1 ♀, KUM); Kudaken, 20.iii.1964, leg. Y. Miyatake (2 ♂♂ 4 ♀♀, KUM); Izumi, 22.iii.1964, leg. T. Shirozu (9 ♂♂ 24 ♀♀, KUM); Izumi-Gogayama, 22.iii.1964, leg. S. Kimoto (1 ♂, KUM); as above but leg. Y. Miyatake (3 ♂♂ 2 ♀♀, KUM); Shoshi, 23.iii.1964, leg. S. Kimoto (1 ♂ 1 ♀, KUM); Nago, 23.iii.1964, leg. Y. Miyatake (1 ♂ 2 ♀♀, KUM); Hiji-Yonahadake, 25.iii.1964, leg. T. Shirozu (2 ♀♀, KUM); Hiji-gawa, 26.iii.1964, leg.



T. Shirozu (1 ♀, KUM); Chinen, Sefa utaki, 17.ii.1973, leg. H. Hasegawa (1 ♀, NIAES); Yona, 21.ii.1973, leg. H. Hasegawa (1 ♀, NIAES); Kunigami-son, Mt. Yonahadake, 29.vi.1984, leg. M. Tomokuni (3 ♀♀, NSMT); Hanejiokawa, 14.xi.1985, leg. M. Hayashi (1 ♂ 2 ♀♀, TUA); Kunigami, Mt. Nishime, 19.x.1987, leg. M. Tomokuni (1 ♀, NSMT); Kunigami, Hama, 20.x.1987, leg. M. Sakai (1 ♂ 3 ♀♀, NSMT); Kunigami, Ooguni-rindo, 8 km from Yona, alt. 300 m, 21.x.1987, leg. M. Tomokuni (3 ♂♂ 3 ♀♀, NSMT); Kunigami, Hiji–Hiji Fall, 22.x.1987, leg. M. Tomokuni (1 ♂, NSMT); Kudaken, Seifa-utaki, 8.x.1988, leg. M. Sakai (1 ♂ 1 ♀, NSMT); Kunigamison, 10–11.x.1988, leg. K. Konishi (1 ♀, NIAES); Nago City, 12.x.1988, leg. K. Konishi (1 ♀, NIAES); Nakijin, Uebaru, 23.x.1990, leg. M. Hayashi et al. (1 ♂, NSMT); Afuso, 3.iv.1991, leg. M. Hayashi (1 ♂, TUA); Mt. Terukubi, 5.v.1991, leg. M. Hayashi (1 ♀, TUA); Mt. Yonahadake, 3.iv.1999, leg. M. Hayashi (1 ♀, TUA); Hedo, 16.ix.2002, leg. M. Hayashi (1 ♀, TUA); Kisebaru, 10.xii.2010, leg. M. Hayashi (1 ♀, TUA); Manzamô, 30.iii.2013, leg. M. Hayashi (1 ♂, TUA); Nago, Katsuyama, Mt. Katsudake, 9.vi.2015, leg. H. Yoshitake (1 ♀, NIAES); Motobu, Namizato, Yaedake-sakura-no-mori-kôen, 30.iii.2018, leg. H. Yoshitake (4 ♂♂ 4 ♀♀, NIAES); Kunigami-son, Uka-rindô, 10.xi.2018, leg. H. Yoshitake (1 ♀, NIAES); Naha-shi, Shuri-sueyoshi-chô, Sueyoshi-kôen, 5.i.2019, leg. H. Yoshitake (1 ♀, NIAES); Yaese Park, 19.i.2019, leg. H. Shigetoh (4 ♂♂ 7 ♀♀ 1 nymph, TUA); as above but leg. H. Yoshitake (2 ♂♂ 1 ♀, NIAES); Nago-shi, Tanodake, 28.iv.2019, leg. R. Ito (1 ♂, TUA); Kunigami-gun, Kunigami-son, Sate, 6.v.2019, leg. R. Ito (1 ♂ 1 ♀, TUA); Nago, Genka Shisen For. Rd., 3.vi.2019, leg. T. Saeki (1 ♂ 1 ♀, TUA); Uruma-shi, Mt. Ishikawadake, 29.xii.2019, leg. H. Shigetoh (2 ♂♂ 1 ♀, TUA); Naha-shi, Ohnoyama Park, 8.iii.2020, leg. J. Souma (4 ♂♂ 5 ♀♀ 3 nymphs); Kunigami-son, Aha, 5.v.2019, leg. H. Yoshitake (1 ♀, NIAES); as above but 18.iv.2020 (1 ♂ 1 ♀, NIAES); as above but 18.iv.2020, leg. H. Shigetoh (3 ♀♀, TUA); Toyomigusuku, 6.xi.2020, leg. J. Souma (1 ♀, TUA); Tabaru, 6.xi.2020, leg. J. Souma (1 ♂ 9 ♀♀, TUA); Midorigaoka Park, 10.xi.2020, leg. J. Souma (5 ♂♂ 4 ♀♀ 1 nymph, TUA); Nanjô-shi, Chinen-jôseki, 30.i.2021, leg. H. Yoshitake (1 ♀, NIAES); Kitanakagusuku-son, Taguchi, 3.ii.2021, leg. H. Yoshitake (1 ♀, NIAES); Nakagusuku, Noborimata, 3.ii.2021, leg. H. Yoshitake (1 ♀, NIAES); Okinawa-shi, Yaeshima-kôen, 4.ii.2021, leg. H. Yoshitake (1 ♀, NIAES); Uruma-shi, Enobi, 4.ii.2021, leg. H. Yoshitake (1 ♀, NIAES); Yomitan-son, Zakimi-jôseki, 5.ii.2021, leg. H. Yoshitake (1 ♀, NIAES); Yonabaru-chô, Untamamori, 20.ii.2021, leg. H. Yoshitake (1 ♀, NIAES); Nago-shi, Makiya, 1–2.vi.2021, leg. T. Saeki (1 ♀, TUA). Aka Island: 13.viii.1977, leg. M. Kinjo (1 ♀, NSMT); as above but 14.viii.1977 (1 ♀, NSMT); as above but 14.viii.1977, leg. S. Azuma (2 ♂♂ 1 ♀, NSMT); Aka, 4.v.2021, leg. R. Ito (1 ♂ 3 ♀♀, TUA). Fukaji Island: 3.v.2021, leg. R. Ito (6 ♂♂ 6 ♀♀, TUA). Geruma Island: 10.viii.1977, leg. S. Azuma (1 ♀, NSMT); 2.viii.2019, leg. H. Shigetoh

(1 ♀, TUA); 4.v.2021, leg. R. Ito (4 ♂♂ 2 ♀♀, TUA). Kume Island: Une, Tonnaha-enchi, 27.iii.2018, leg. H. Yoshitake (1 ♀, NIAES); Daruma-yama, 28.iv.2018, leg. R. Ito (3 ♂♂ 4 ♀♀, TUA); Shirase-Riv., 29.iv.2018, leg. R. Ito (1 ♀, TUA); Yamashiro, 22–24.vii.2020, leg. H. Yoshitake (1 ♀, NIAES). Tokashiki Island: near Shuraku, 27.iv.2019, leg. H. Shigetoh (1 ♂, TUA); Tokashiki, 7.xi.2020, leg. J. Souma (2 ♂♂ 9 ♀♀, TUA); Aharen, 7.xi.2020, leg. J. Souma (2 ♂♂ 2 ♀♀, ELKU; 1 ♂ 3 ♀♀, TUA); Mt. Kumichizi, 8.xi.2020, leg. J. Souma (2 ♂♂ 4 ♀♀ 2 nymphs, TUA); Ôtani-path, 1.v.2018, leg. R. Ito (1 ♂ 2 ♀♀, TUA); Tokashiki, Ôtani road, 30.iv.2021, leg. R. Ito (1 ♀, TUA); as above but 1.v.2021 (4 ♂♂ 4 ♀♀, TUA). Tsuken Island: 16.iii.2019, leg. H. Shigetoh (1 ♀, TUA). Yabuchi Island: 5.iii.2020, leg. J. Souma (1 ♂ 1 ♀, TUA). Yagaji Island: Gabu, 9.iii.2020, leg. J. Souma (2 ♂♂ 2 ♀♀, TUA); Sumuide, 17.iv.2020, leg. H. Shigetoh (1 ♂, TUA). Zamami Island: near Mt. Otake, 20.iii.2020, leg. H. Shigetoh (1 ♂ 3 ♀♀, TUA); Asa Evacuation Route, 21.iii.2020, leg. H. Shigetoh (1 ♀, TUA); Ama, near Mt. Bansho, 21.iii.2020, leg. H. Shigetoh (1 ♂ 1 ♀, TUA); Inazaki–Kaminohama, 21.iii.2020, leg. H. Shigetoh (1 ♀, TUA); Ama, 3.vi.2020, leg. H. Shigetoh (1 ♀, TUA); Asa, 2.v.2018, leg. R. Ito (2 ♂♂ 2 ♀♀, TUA). DAITO ISLANDS: Kitadaito Island: Nakano, Daitôgû Shrine, 24.xi.2021, leg. T. Saeki (2 ♀♀, TUA). Minamidaito Island: Ikenosawa, 10.iii.2013, leg. H. Yoshitake (1 ♂ 1 ♀, NIAES); Zaisho, 6.vii.2014, leg. H. Ogai (5 ♂♂ 3 ♀♀, TUA); Daito Shrine, 9.ii.2018, leg. R. Ito (3 ♂♂ 2 ♀♀, TUA). Six specimens from Aka and Geruma islands collected in 1977 were considered to be recorded as “*Stephanitis aperta*” by a previous study (Azuma and Kinjo 1987).

**Diagnosis.** *Stephanitis (Norba) exigua* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown (Figs 7C, 9C, 11C, 13C, 15C, 17C, 19C, 21C, 23C); calli light brown; body in male 2.2 times (in female 2.1 times) as long as maximum width across hemelytra (Figs 2C, 4C); rostrum not reaching metasternum; pronotum unicarinate (Fig. 25C); hood pale, shorter than median carina of pronotum, as wide as vertex at widest part, not covering eye, as high as median carina of pronotum at highest part, with posterior margin not extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc lustrous; paranotum less erect, narrowed posteriorly, with 2 rows of areolae at widest part, with anterolateral angle slightly protruding anteriad, with outer margin gently curved inwards at posterolateral angle, maximum height shorter than height of eye (Fig. 27C); apices of hemelytra close to each other in rest; costal area with 3 rows of areolae at widest part; subcostal area with 2 rows of areolae at widest part; discoidal area with 3 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at cen-

tre of venter, with posterior margin slightly emarginate in middle part (Fig. 29C); and paramere stout, weakly curved inwards at apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 31C).

**Remarks.** Amongst the Japanese species of *Stephanitis*, *S. (Norba) exigua* is similar to *S. (N.) hiurai* in general habitus, but the former is easily distinguished from the latter by the following characters: hood as wide as vertex at widest part (wider than vertex in *S. (N.) hiurai*), not covering eye (incompletely covering in *S. (N.) hiurai*) (Figs 7C, E, F, 9C, E, F, 25C, E); paranotum with 2 rows of areolae at widest part (3 rows in *S. (N.) hiurai*), with anterolateral angle slightly protruding anteriad (protruding in *S. (N.) hiurai*); costal area of hemelytron with 3 rows of areolae at widest part (4 rows in *S. (N.) hiurai*) (Figs 15C, E, F, 17C, E, F); subcostal area in female with 2 rows of areolae at widest part (3 rows in *S. (N.) hiurai*); and R+M (radiomedial) vein in female carinate (not carinate in *S. (N.) hiurai*).

**Distribution.** Japan (Ryukyu Islands (central part): Okinawa Island, Aka Island, Fukaji Island, Geruma Island, Kume Island, Tokashiki Island, Tsuken Island, Yabuchi Island, Yagaji Island, Zamami Island; Daito Islands: Kitadaito Island, Minamidaito Island) (Fig. 45); China (Horváth 1912; Drake 1937; Takeya 1963; Miyamoto 1964a, 1964b; Azuma and Kinjo 1987; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016; Nakatani 2021; present study). The previous record from Honshu (Horváth 1912) is a misidentification of *Stephanitis (Stephanitis) pyrioides*. Hundreds of specimens from Honshu possessing the unicarinate pronotum were examined, but all of them belong to *S. (Norba) aperta*, *S. (N.) mendica* or *S. (S.) tabidula*. Therefore, *S. (N.) exigua* is probably not distributed in Honshu. The previous records from the southern part of the Ryukyu Islands and northern Taiwan (Takeya 1963; Miyamoto 1964a, 1964b, 1964c; Azuma and Kinjo 1987; Hayashi 2002) correspond to *S. (Norba) ishikawai* sp. nov., described below. Hundreds of specimens from the southern part of the Ryukyu Islands possessing the unicarinate pronotum were examined, but all of them belong to *S. (N.) ishikawai* sp. nov. Therefore, *S. (N.) exigua* is probably not distributed in the southern part of the Ryukyu Islands. In Japan, *S. (N.) exigua* inhabits the laurilignosa in a subtropical climate of the central part of the Ryukyu Islands, which is in the Oriental Region.

**Host plants.** *Cinnamomum camphora*, “Kusunoki” (Lauraceae) (Takeya 1963; present study); *C. yabunikkei* H. Ohba, “Yabunikkei” (present study); *Machilus thunbergii*, “Tabunoki” (Lauraceae) (Fig. 43E) (Takeya 1963; Yamada and Tomokuni 2012; present study). *Stephanitis (Norba) exigua* feeds only on lauraceous trees and is oligophagous. This lace bug sometimes occurs on plantings of *C. camphora* and *M. thunbergii* in its distribution range (present study), suggesting that it can become a pest of both lauraceous trees.

**Biology.** *Stephanitis (Norba) exigua* feeds on the abaxial surface of leaves of the three host plants in Japan (present study). In Japan, adults were collected in almost all seasons

(Miyamoto 1964a, 1964b; present study); nymphs were collected in January, March and November (present study).

### *Stephanitis (Norba) hayashii* sp. nov.

<https://zoobank.org/30B58A6E-39E6-4D6F-8660-8FE95E1E59C3>

[Japanese name: Hayashi-gunbai]

Figs 2D, 4D, 7D, 9D, 11D, 13D, 15D, 17D, 19D, 21D, 23D, 25D, 27D, 29D, E, 31D, E, 41A–D

*Stephanitis (Norba) aperta* Horváth, 1912: Miyamoto (1964b: 524) (distribution); Yamada and Ishikawa (2016: 433) (checklist: Japan). Misidentifications.

**Type series. Holotype** (♂, ELKU), “[JAPAN]: the Ryukyus, Okinawa Isls., Aguni Is., Hama” [=JAPAN: Ryukyu Islands (central part): Aguni Island: Hama (approximate coordinates: 26°34'50.7"N, 127°14'06.4"E)], 10.xi.2020, leg. J. Souma. **Paratypes** (47 ♂♂ 67 ♀♀), JAPAN: RYUKYU ISLANDS (central part): Amami-Oshima Island: Sokaru, 5.xi.2020, leg. J. Souma (7 ♂♂ 6 ♀♀, ELKU); Amami-shi, Kasari-cho, Wano 27.iv.2022, leg. J. Souma (4 ♂♂ 2 ♀♀, ELKU). Kakeroma Island: Osai, 3.xi.2020, leg. J. Souma (5 ♂♂ 2 ♀♀, ELKU). Yoron Island: Furusato, 11.xi.1966, leg. Y. Miyatake (1 ♂, KUM). Okinawa Island: Tamagusuku, 17.xi.1963, leg. H. Hasegawa (1 ♂, NIAES); Kudeken, 20.iii.1964, leg. Y. Miyatake (1 ♀, KUM); Yaese-chô, Yaese-kôen, 19.i.2019, leg. H. Yoshitake (1 ♀, NIAES); Rondon Forest Park, 20.i.2019, leg. H. Shigetoh (2 ♂, TUA); as above but leg. H. Yoshitake (1 ♀, NIAES); Uruma-shi, Ishikawayamashiro, 2.viii.2019, leg. H. Shigetoh (1 ♀, TUA); Kakazu, 9.xi.2020, leg. J. Souma (1 ♀, ELKU). Aguni Island: Bannyabaru, 7.iv.1999, leg. M. Hayashi et al. (1 ♀, TUA); Higashi, 6.iii.2020, leg. J. Souma (1 ♂ 3 ♀♀ ELKU, 14 ♂♂ 14 ♀♀, TUA); as above but 7.iii.2020 (5 ♂♂ 9 ♀♀, TUA); as holotype (3 ♂♂ 7 ♀♀, ELKU). Fukaji Island: 3.v.2021, leg. R. Ito (1 ♀, ELKU). Kouri Island: nr Amajafubaru-nôson-kôen, 7.iii.2020, leg. H. Yoshitake (1 ♀, NIAES). Senaga Island: 9.xi.2020, leg. J. Souma (2 ♂♂ 2 ♀♀, ELKU). Tokashiki Island: Tokashiki, 9.xi.2020, leg. J. Souma (7 ♀♀, ELKU). Yagaji Island: Gabu, 9.iii.2020, leg. J. Souma (2 ♂♂ 7 ♀♀, TUA). A single specimen collected in 1964 was recorded as “*Stephanitis aperta*” by the previous study (Miyamoto 1964b).

**Additional material examined** (27 nymphs). JAPAN: RYUKYU ISLANDS (central part): Kakeroma Island: Osai, 3.xi.2020, leg. J. Souma (3 nymphs, ELKU). Aguni Island: Higashi, 6.iii.2020, leg. J. Souma (6 nymphs, TUA); as above but 7.iii.2020 (1 nymph, TUA); as holotype (6 nymphs, ELKU). Tokashiki Island: Tokashiki, 9.xi.2020, leg. J. Souma (7 nymphs, ELKU). Yagaji Island: Gabu, 9.iii.2020, leg. J. Souma (2 nymphs, ELKU; 2 nymphs, TUA). All 27 nymphs recorded above are in poor condition and are thus not described in the present study.

**Diagnosis.** *Stephanitis (Norba) hayashii* sp. nov. is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc,

marking on hemelytra and ventral surface in various shades of brown (Figs 7D, 9D, 11D, 13D, 15D, 17D, 19D, 21D, 23D); calli light brown; body in male 2.1 times (in female 2.0 times) as long as maximum width across hemelytra (Figs 2D, 4D); rostrum reaching metasternum; pronotum unicarinate (Fig. 25D); hood pale, shorter than median carina of pronotum, wider than vertex at widest part, incompletely covering eye, as high as median carina of pronotum at highest part, with posterior margin extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc opaque; paranotum more erect, slightly narrowed posteriorly, with 3 rows of areolae at widest part, with anterolateral angle protruding anteriorly, with outer margin gently curved inwards at posterolateral angle, maximum height longer than height of eye (Fig. 27D); apices of hemelytra close to each other in rest; costal area with 3–4 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 3 rows) of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at centre of venter, with posterior margin slightly emarginate in middle part (Fig. 29D, E); and paramere slender, weakly curved inwards at apex, with outer margin not sinuate in middle part, inner margin slightly curved inwards in basal part (Fig. 31D, E).

**Description. Male.** Head, pronotal disc, marking on hemelytra and ventral surface various shades of brown; calli light brown; eye dark red; areolae of pronotum and hemelytron transparent; hood pale; pronotal disc opaque; pubescence on body yellowish (Figs 2D, 7D, 11D, 15D, 19D, 21D).

Body 2.1 times as long as maximum width across hemelytra (Fig. 2D). Head (Figs 7D, 11D, 19D, 25D) glabrous; pair of frontal spines close at apices, not reaching apex of clypeus; median spine as long as frontal spines, reaching bases of frontal spines; pair of occipital spines longer than median spine, reaching middle part of eyes; antenniferous tubercles obtuse, slightly curved inwards; clypeus smooth. Compound eye round in dorsal view. Antenna densely covered with pubescence; segment I cylindrical; segment II cylindrical, shortest amongst antennal segments; segment III longest amongst antennal segments; segment IV cylindrical, longer than segment I. Bucculae closed at anterior ends, with 3 rows of areolae throughout length. Rostrum reaching metasternum.

Pronotum (Figs 7D, 11D, 25D, 27D) unicarinate, 1.4 times as long as maximum width across paranota, sparsely covered with pubescence. Pronotal disc coarsely punctate. Hood shorter than median carina of pronotum, wider than vertex at widest part, incompletely covering eye, as high as median carina of pronotum at highest part, posterior margin extending to middle of pronotal disc, 4 rows of areolae at highest part, dorsal margin arched. Median carina straight, extending to apex of posterior process, 2 rows of areolae at highest part, dorsal margin arched. Calli

smooth. Paranotum more erect, slightly narrowed posteriorly, 3 rows of areolae at widest part, anterolateral angle protruding anteriorly, outer margin gently curved inwards at posterolateral angle, maximum height longer than height of eye. Posterior process triangular, obtuse at apex.

Hemelytron (Fig. 15D) 2.4 times as long as maximum width, extending beyond apex of abdomen, sparsely covered with pubescence; maximum width across hemelytra 1.7 times as wide as maximum width across paranota; apices close in rest; costal area with 3–4 rows of areolae at widest part; subcostal area with 2 rows of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; C (costal), R+M (radiomedial) and Cu (cubital) veins carinate.

Thoracic pleura (Fig. 11D) smooth in anterior part, coarsely punctate in posterior part. Ostiolar peritreme oblong. Sternal laminae (Fig. 19D) lower than bucculae; pro- and mesosternal laminae open in both anterior and posterior ends; metasternal laminae as high as mesosternal laminae, open at anterior ends, fused each other at posterior ends. Legs (Fig. 2D) smooth, densely covered with pubescence; femora thickest at middle.

Abdomen oblong in dorsal and ventral views. Pygophore (Figs 21D, 29D, E) compressed dorsoventrally, semicircular in ventral view, elevated at centre of venter, with posterior margin slightly emarginate in middle part, covered with pubescence. Paramere (Fig. 31D, E) slender, expanded in middle part, slightly curved inwards at apex, outer margin not sinuate in middle part, inner margin weakly curved inward in basal part, covered with pubescence in middle part of outer and inner margins.

Measurements ( $n = 20$ ). Body length with hemelytra 2.9–3.2 mm; maximum width across hemelytra 1.4–1.5 mm; length of antennal segments I to IV 0.2 mm, 0.1 mm, 1.2 mm and 0.6 mm, respectively; pronotal length 1.2–1.3 mm; pronotal width across paranota 0.8–0.9 mm; hemelytral length 2.2–2.5 mm; maximum width of hemelytron 1.0–1.1 mm.

**Female.** General habitus very similar to that of male (Figs 4D, 9D, 13D, 17D, 23D), except for the following characters: body 2.0 times as long as maximum width across hemelytra; antennal segment III shorter than in male; pronotum 1.5 times as long as maximum width across paranota; hood wider than in male; hemelytron 2.3 times as long as its maximum width; maximum width across hemelytra 1.9 times as much as maximum width across paranota; subcostal area wider than in male, with 3 rows of areolae at widest part; and apical part of abdomen pentagonal in ventral view.

Measurements ( $n = 20$ ). Body length with hemelytra 3.1–3.4 mm; maximum width across hemelytra 1.6–1.7 mm; length of antennal segments I to IV 0.2 mm, 0.1 mm, 1.0 mm and 0.6 mm, respectively; pronotal length 1.3–1.4 mm; pronotal width across paranota 0.9 mm; hemelytral length 2.4–2.5 mm; maximum width of hemelytron 1.0–1.1 mm.



**Remarks.** *Stephanitis (Norba) hayashii* sp. nov. was misidentified as *S. (N.) aperta* in a previous study (Miyamoto 1964b), as both species are very similar to each other. However, the former is easily distinguished from the latter by the following characters: calli light brown (dark brown in *S. (N.) aperta*) (Figs 7B, D, 9B, D, 11B, D, 13B, D); rostrum reaching metasternum (not reaching in *S. (N.) aperta*) (Fig. 19B, D); hood wider than vertex at widest part (as wide as in *S. (N.) aperta*), incompletely covering eye (not covering in *S. (N.) aperta*), slightly higher than median carina of pronotum at highest part (as high as in *S. (N.) aperta*), with posterior margin extending to middle of pronotal disc (not extending in *S. (N.) aperta*) (Fig. 25B, D); paranotum more erect (less erect in *S. (N.) aperta*), slightly narrowed posteriorly (strongly narrowed in *S. (N.) aperta*); and paramere slender (stout in *S. (N.) aperta*), with inner margin slightly curved inwards in basal part (nearly straight in *S. (N.) aperta*) (Fig. 31B, D, E).

**Distribution.** Japan (Ryukyu Islands (central part): Amami-Oshima Island, Kakeroma Island, Yoron Island, Okinawa Island, Aguni Island, Fukaji Island, Kouri Island, Senaga Island, Tokashiki Island, Yagaji Island) (Fig. 46) (Miyamoto 1964b; Yamada and Ishikawa 2016; present study). *Stephanitis (Norba) hayashii* sp. nov. inhabits the laurilignosa in a subtropical climate of the central part of the Ryukyu Islands, which is in the Oriental Region.

**Etymology.** This new species is named in honour of Masami Hayashi, a Japanese heteropterist who collected part of paratypes and taught the author how to conduct fieldwork.

**Host plants.** *Cinnamomum yabunikkei*, “Yabunikkei” (Fig. 43G) (present study); *Litsea japonica* (Thunb.) Juss., “Hamabiwa” (Lauraceae) (Fig. 43F) (present study). *Stephanitis (Norba) hayashii* sp. nov. feeds only on lauraceous trees and is oligophagous.

**Biology.** *Stephanitis (Norba) hayashii* sp. nov. feeds on the abaxial surface of leaves of the two known host plants (present study). Adults were collected from March to May and in January, August and November (Miyamoto 1964b; present study); nymphs were collected in March and November (present study).

### *Stephanitis (Norba) hiurai* Takeya, 1963

[Japanese name: Hiura-gunbai]

Figs 2E, F, 4E, F, 7E, F, 9E, F, 11E, F, 13E, F, 15E, F, 17E, F, 19E, 21E, 23E, 25E, 28A, 29F, 31F, 36A, 36B, 41E–G

*Stephanitis hiurai* Takeya, 1963: 34 (in *Norba* group). Holotype, ♀ (Fig. 36A): Japan: Amami-Oshima, Naze [= Ryukyu Islands, Amami-Oshima Island, Naze]; OMNH (not deposited), ELKU (currently deposited).

*Stephanitis hiurai takaranis* Takeya, 1963: 36 (in *Norba* group). Holotype, ♀ (Fig. 36B): Japan: Tokara Is., Takarajima [= Ryukyu Islands, Takara Island]; OMNH (not deposited), ELKU (currently deposited). Synonymised with *Stephanitis (Norba) hiurai* Takeya, 1963 by Miyamoto (1964b: 524).

*Stephanitis (Norba) aperta* Horváth, 1912: Hayashi (2002: 137) (distribution). Misidentification.

**References.** Miyamoto (1964a: 274) (distribution: part); Miyamoto (1964b: 524) (distribution: part); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Péricart and Golub (1996: 58) (catalogue: Palaearctic); Hayashi (2002: 137) (distribution); Yamada and Tomokuni (2012: 205) (monograph); Yamada and Ishikawa (2016: 433) (checklist: Japan).

**Material examined. Holotype** (1 ♀, ELKU) (Fig. 36A), JAPAN: RYUKYU ISLANDS (central part): “Amami Is. Naze” [= Amami-Oshima Island, Naze (approximate coordinates: 28°23'13.6"N, 129°29'38.2"E)], 4.v.1960, leg. T. Shibata. **Holotype of *Stephanitis (Norba) hiurai takaranis* Takeya, 1963** (1 ♀, ELKU) (Fig. 36B), JAPAN: RYUKYU ISLANDS (central part): “Tokara Is. Takarajima” [= Takara Island (approximate coordinates: 29°08'38.0"N, 129°12'27.8"E)], 5.vii.1960, leg. Y. Hama. **Paratype of *Stephanitis (Norba) hiurai takaranis* Takeya, 1963** (1 ♀, ELKU), JAPAN: RYUKYU ISLANDS (central part): “Tokara Is. Takarajima” [= Takara Island (approximate coordinates: 29°08'38.0"N, 129°12'27.8"E)], 5.vii.1960, leg. Y. Hama. The original description of *S. (N.) hiurai* and *S. (N.) hiurai takaranis* (Takeya 1963) states that their type specimens are deposited in OMNH, but these holotypes and paratype are now deposited in ELKU. **Non-types collected at type locality** (4 ♂♂ 6 ♀♀), JAPAN: RYUKYU ISLANDS (central part): Amami-Oshima Island: Amami-shi, Naze, Kaneku (approximate coordinates: 28°22'27.1"N, 129°29'43.6"E), 30.iv.2022, leg. J. Souma (3 ♂♂ 5 ♀♀, TUA); Amami-shi, Naze, Asani (approximate coordinates: 28°24'03.1"N, 129°29'25.3"E), 30.iv.2022, leg. J. Souma (1 ♂ 1 ♀, TUA). **Non-types** (50 ♂♂ 104 ♀♀ 16 nymphs), JAPAN: RYUKYU ISLANDS (central part): Takara Island: 26.v–1.vi.1953, leg. S. Miyamoto (1 ♂ 2 ♀♀, ELKU); 27.iv.1971, leg. M. Sakai (2 ♀♀ 1 nymph, NSMT). Kikai Island: Hyakunodai, 9.iii.2019, leg. H. Kojima (1 ♂ 3 ♀♀, TUA); between Keraji and Aden, 9.iii.2019, leg. H. Kojima (9 ♀♀, TUA). Amami-Oshima Island: Hatsuno, 11.xi.1962, leg. Y. Miyatake (1 ♂, ELKU); as above but 5.x.1988, leg. M. Tomokuni (1 ♂ 3 ♀♀, NSMT); Uragami, 31.x.1966, leg. Y. Miyatake (3 ♂♂ 2 ♀♀, KUM); Santaro-toge Pass, 2.xi.1966, leg. Y. Miyatake (1 ♀, KUM); as above but 30.vi.2000, leg. Y. Nakatani (1 ♂, NIAES); Yuwan, 3.xi.1966, leg. Y. Miyatake (5 ♂♂ 10 ♀♀, KUM); Naze, 21.iv.1971, leg. M. Sakai (3 ♀♀ 1 nymph, NSMT); Naze-shi, Akazaki, 2.xi.1984, leg. M. Tomokuni (1 ♂ 5 ♀♀, NSMT); Sumiyô-son, Kawauchi, Chûô-rindô, alt. 200 m, 3.x.1988, leg. M. Tomokuni (5 ♀♀, NSMT); Mt. Yuwandake, 4.x.1988, leg. M. Tomokuni (1 ♀, NSMT); Uken-son, Mt. Yuwan-dake, 23.iii.2019, leg. Y. Hisasue (1 ♀, TUA); Shinokawa, 2.xi.2020, leg. J. Souma (3 ♂♂ 1 ♀, ELKU; 5 ♂♂ 5 ♀♀, TUA); as above but 4.xi.2020 (1 ♂ 1 ♀ 8 nymphs, TUA); Konase, 2.xi.2020, leg. J. Souma (5 ♂♂ 5 ♀♀ 1 nymph, TUA); Sokaru, 5.xi.2020, leg. J. Souma (1 ♀, TUA); Uken-son, Yuwan, 28.iv.2022, leg. J. Souma (1 ♂ 2 ♀♀, TUA); Setouchi-cho, Amurogama, 29.iv.2022, leg. J. Souma



(3 ♀♀, TUA); Uken-son, Ikegachi, 30.iv.2022, leg. J. Souma (1 ♂, TUA); Amami-shi, Sumiyo-cho, Aoku, 30.iv.2022, leg. J. Souma (1 ♂ 1 ♀, TUA); Amami-shi, Sumiyo-cho, Santaro Pass, 1.v.2022, leg. J. Souma (1 ♂ 5 ♀♀ 4 nymphs, TUA); Amami-shi, Kasari-cho, Man-ya, 3.v.2022, leg. J. Souma (2 ♂♂ 2 ♀♀, TUA); Asani, Akazaki Park, 29.vi.2022, leg. S. Imada (1 ♀, TUA). Kakeroma Island: Shokazu, 3.xi.2020, leg. J. Souma (3 ♀♀, TUA); Kachiyuki, 3.xi.2020, leg. J. Souma (8 ♂♂ 10 ♀♀ 1 nymph, TUA). Tokunoshima Island: Asahigaoka, 11.xi.1966, leg. Y. Miyatake (2 ♀♀, KUM); Amagi-cho, Yonama, 2.x.1988, leg. M. Tomokuni (2 ♂ 1 ♀, NSMT). Okinoerabu Island: Mt. Koshiyama, 8.vii.2019, leg. Y. Tamadera (1 ♂ 3 ♀♀, TUA); Oyama Botanical Park, 23–26.vi.2022, leg. S. Imada (3 ♀♀, TUA). Okinawa Island: Yona, 19.x.1963, leg. S. Miyamoto (2 ♂♂, KUM); as above but leg. Y. Hirashima (1 ♀, KUM); as above but 25–27.v.1974, leg. M. Sato (2 ♀♀, NSMT); Izumi–Gogayama, 22.iii.1964, leg. S. Kimoto (1 ♂, KUM); as above but leg. Y. Miyatake (1 ♀, KUM); Aha, 26.xii.1973, leg. M. Hamakawa (1 ♂ 1 ♀, NSMT); Kunigami, Mt. Yonaha, 20.x.1987, leg. M. Sakai (1 ♀, NSMT); Kunigami, Ooguni-rindo, 8 km from Yona, alt. 300 m, 21.x.1987, leg. M. Tomokuni (1 ♂, NSMT); Okuni-Rindô, 16–21.iv.1997, leg. T. Ishikawa (1 ♀, TUA); Oku For. Rd., 12.ix.2005, leg. M. Hayashi (1 ♀, TUA).

**Diagnosis.** *Stephanitis (Norba) hiurai* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown (Figs 7E, F, 9E, F, 11E, F, 13E, F, 15E, F, 17E, F, 19E, 21E, 23E); calli light brown; body in male 2.0–2.1 times (in female 1.8–2.0 times) as long as maximum width across hemelytra (Figs 2E, F, 4E, F); rostrum not reaching metasternum; pronotum unicarinate (Fig. 25E); hood pale, shorter than median carina of pronotum, wider than vertex at widest part, incompletely covering eye, as high as median carina of pronotum at highest part, with posterior margin not extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc lustrous; paranotum less erect, narrowed posteriorly, 3 rows of areolae at widest part, anterolateral angle protruding anteriad, outer margin gently curved inwards at posterolateral angle, maximum height longer than height of eye (Fig. 28A); apices of hemelytra close to each other in rest; costal area with 4 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 3 rows) of areolae at widest part; discoidal area with 3 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein in male not carinate (in female carinate); pygophore elevated at centre of venter, posterior margin slightly emarginate in middle part (Fig. 29F); and paramere stout, weakly curved inwards at apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 31F).

**Intraspecific variation.** According to the original description (Takeya 1963), *Stephanitis (Norba) hiurai* is divided into two subspecies, *S. (N.) h. hiurai* Takeya, 1963 and *S. (N.) h. takaranis*. However, previous studies by Miyamoto (1964a, 1964b) used only a few specimens which included misidentified *S. (N.) ishikawai* sp. nov., described below, and synonymised *S. (N.) h. takaranis* with the nominotypical subspecies. Nevertheless, subsequent authors (Péricart and Golub 1996; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016) continued to treat *S. (N.) h. takaranis* as a valid subspecies without providing any justification. Many specimens of *S. (N.) hiurai* from various localities were observed in the present study and the differences in colouration and shape of the hood cited in the original description of the two subspecies (Takeya 1963) are herein considered to be intraspecific variations depending on individual and size, respectively. Therefore, the synonymy of *S. (N.) h. takaranis* with *S. (N.) hiurai*, proposed by Miyamoto (1964a, 1964b) is supported.

**Remarks.** The partial COI gene pairwise sequence distances between *Stephanitis (Norba) hiurai* and *S. (N.) aperta* are only 0.006632–0.009310 (Suppl. material 3) and both species resemble each other in general habitus. However, the former is easily distinguished from the latter by the following characters: hood wider than vertex at widest part (as wide as vertex in *S. (N.) aperta*), incompletely covering eye (not covering in *S. (N.) aperta*) (Figs 7B, E, F, 9B, E, F, 25B, E); pronotal disc lustrous (opaque in *S. (N.) aperta*); and R+M (radiomedial) vein in female carinate (not carinate in *S. (N.) aperta*) (Fig. 17B, E, F).

**Distribution.** Japan (Ryukyu Islands (central part): Takara Island, Kikai Island, Amami-Oshima Island, Kakeroma Island, Tokunoshima Island, Okinoerabu Island, Okinawa Island) (Fig. 46) (Takeya 1963; Miyamoto 1964a, 1964b, 1964c; Hayashi 2002; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016; present study). The previous record from Ishigaki Island, the southern part of the Ryukyu Islands (Miyamoto 1964a, 1964b), corresponds to *Stephanitis (Norba) ishikawai* sp. nov., described below. Hundreds of specimens from the southern part of the Ryukyu Islands possessing an unicarinate pronotum were examined, but all of them belonged to *S. (N.) ishikawai* sp. nov. Therefore, *S. (N.) hiurai* is probably not distributed in the southern part of the Ryukyu Islands. *Stephanitis (Norba) hiurai* inhabits the laurilignosa in a subtropical climate of the central part of the Ryukyu Islands, which is in the Oriental Region.

**Host plants.** *Machilus thunbergii*, “Tabunoki” (Lauraceae) (Fig. 43H) (present study). *Stephanitis (Norba) hiurai* feeds only on this lauraceous tree and is monophagous. This lace bug was also collected from *Symplocos myrtacea* Siebold et Zucc., “Hainoki” (Symplocaceae) without any data on its development (Yamada and Tomokuni 2012).

**Biology.** *Stephanitis (Norba) hiurai* feeds on the abaxial surface of leaves of *Machilus thunbergii* (present study). Adults were collected in almost all seasons (Takeya 1963; Miyamoto 1964a, 1964b; present study). Nymphs were collected in April and November (present study).

***Stephanitis (Norba) ishikawai* sp. nov.**

<https://zoobank.org/CC9E31D4-766C-4C48-ACBB-87D3297CA576>

[Japanese name: Ishikawa-gunbai]

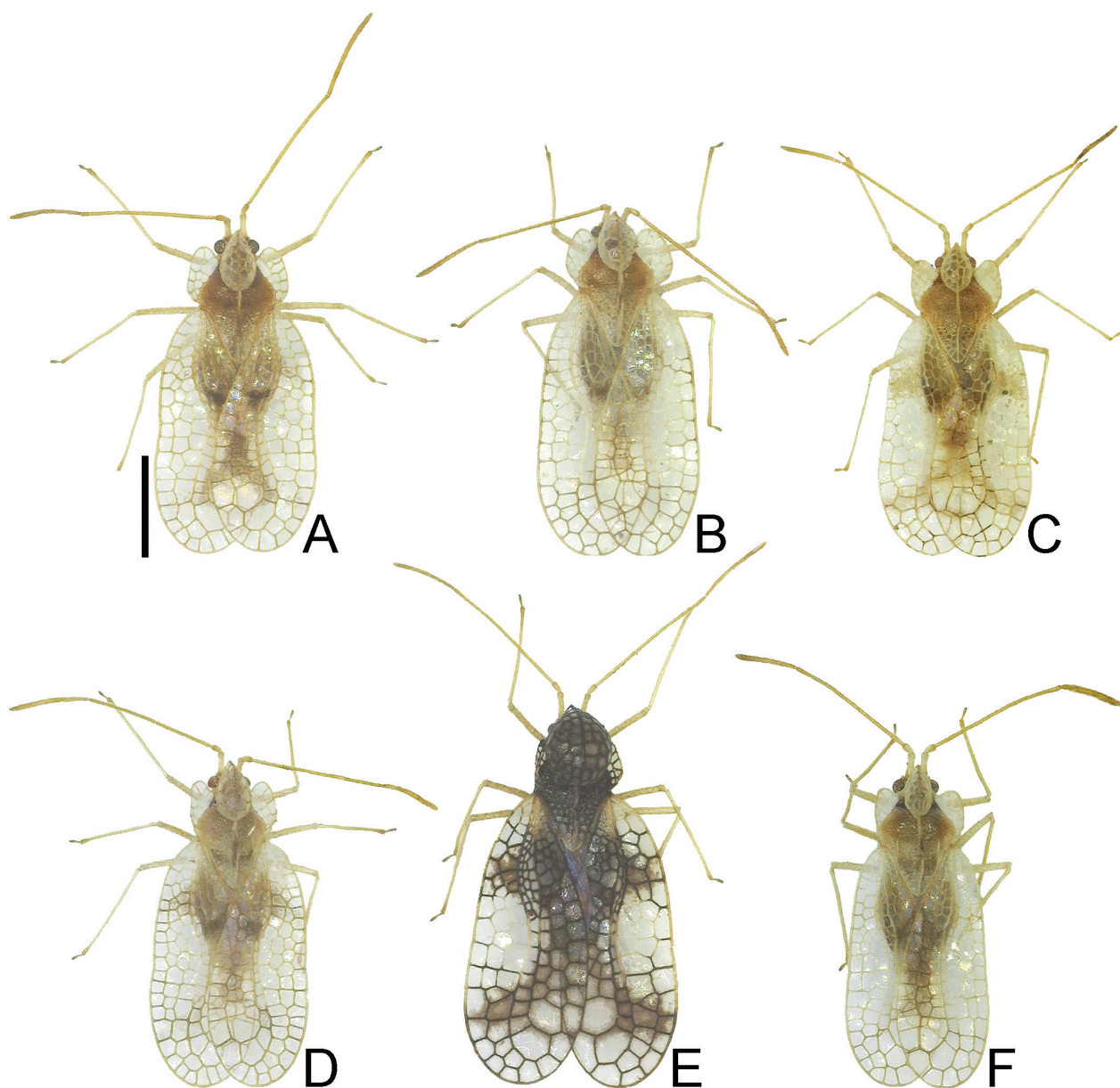
Figs 3A, 5A, 8A, 10A, 12A, 14A, 16A, 18A, 19F, 21F, 23F, 25F, 28B, 30A–C, 32A–C, 41H, I

*Stephanitis (Norba) aperta* Horváth, 1912: Takeya (1931: 75) (distribution: part); Maa (1957: 127) (nymph); Takeya (1963: 38) (distribution: part); Miyamoto (1964a: 274) (distribution: part); Miyamoto (1964b: 524) (distribution: part); Takara and Azuma (1972: 113) (distribution); Azuma and Kinjo (1987: 34) (distribution); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Yasunaga et al. (1993: 178) (monograph: part); Hayashi (2002: 137) (distribution); Tomokuni (2006b: 67) (checklist: Taiwan); Zheng and Lin (2013: 312) (distribution); Yamada and Tomokuni (2012: 205) (monograph: part); Yamada and Ishikawa (2016: 433) (checklist: Japan). Misidentifications.

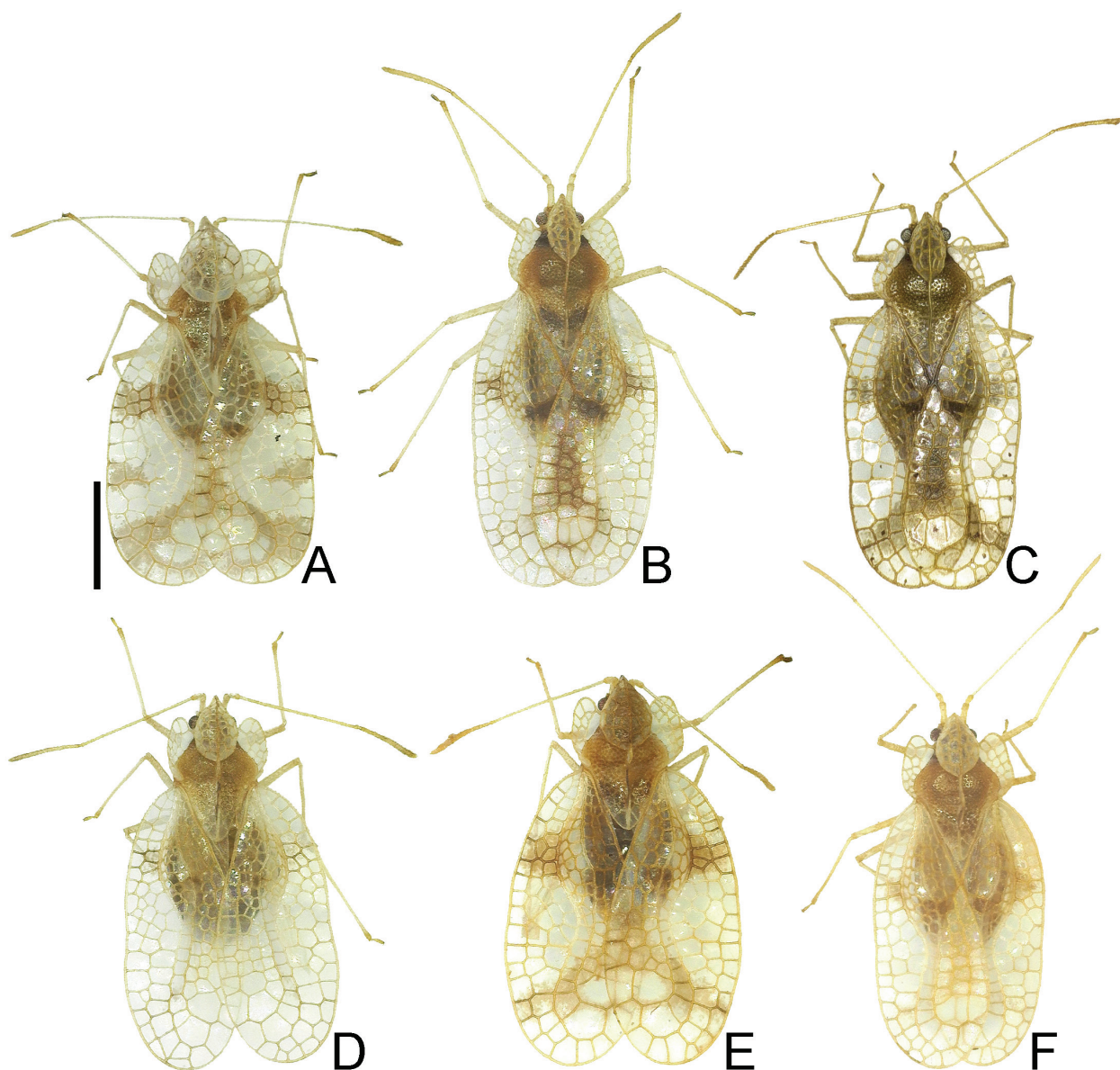
*Stephanitis (Norba) exigua* Horváth, 1912: Takeya (1963: 38) (distribution: part); Miyamoto (1964a: 274) (distribution: part); Miyamoto (1964b: 524) (distribution: part); Miyamoto (1964c: 105) (distribution); Takara and Azuma (1972: 113) (distribution); Azuma and Kinjo (1987: 34) (distribution); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Hayashi (2002: 137) (distribution); Tomokuni (2006b: 67) (checklist: Taiwan); Yamada and Tomokuni (2012: 204) (monograph: part); Yamada and Ishikawa (2016: 433) (checklist: Japan). Misidentifications.

*Stephanitis (Norba) hiurai* Takeya, 1963: Miyamoto (1964a: 272) (distribution: part); Miyamoto (1964b: 524) (distribution: part). Misidentifications.

**Type series. Holotype** (♂, ELKU), “[JAPAN]: the Ryukyu, Yaeyama Isls., Yonaguni Is., Mantabaru” [=JAPAN: RYUKYU ISLANDS (southern part): Yonaguni Island: Mantabaru (approximate coordinates: 24°27'27.6"N,



**Figure 3.** Male habitus of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) ishikawai* sp. nov. from Yonaguni Island, southern part of Ryukyu Islands; **B.** *S. (N.) mendica* from Honshu; **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai* from Shikoku; **F.** *S. (S.) tomokunii* sp. nov. from Miyake Island, southern part of Izu Islands. Scale bar: 1.0 mm.

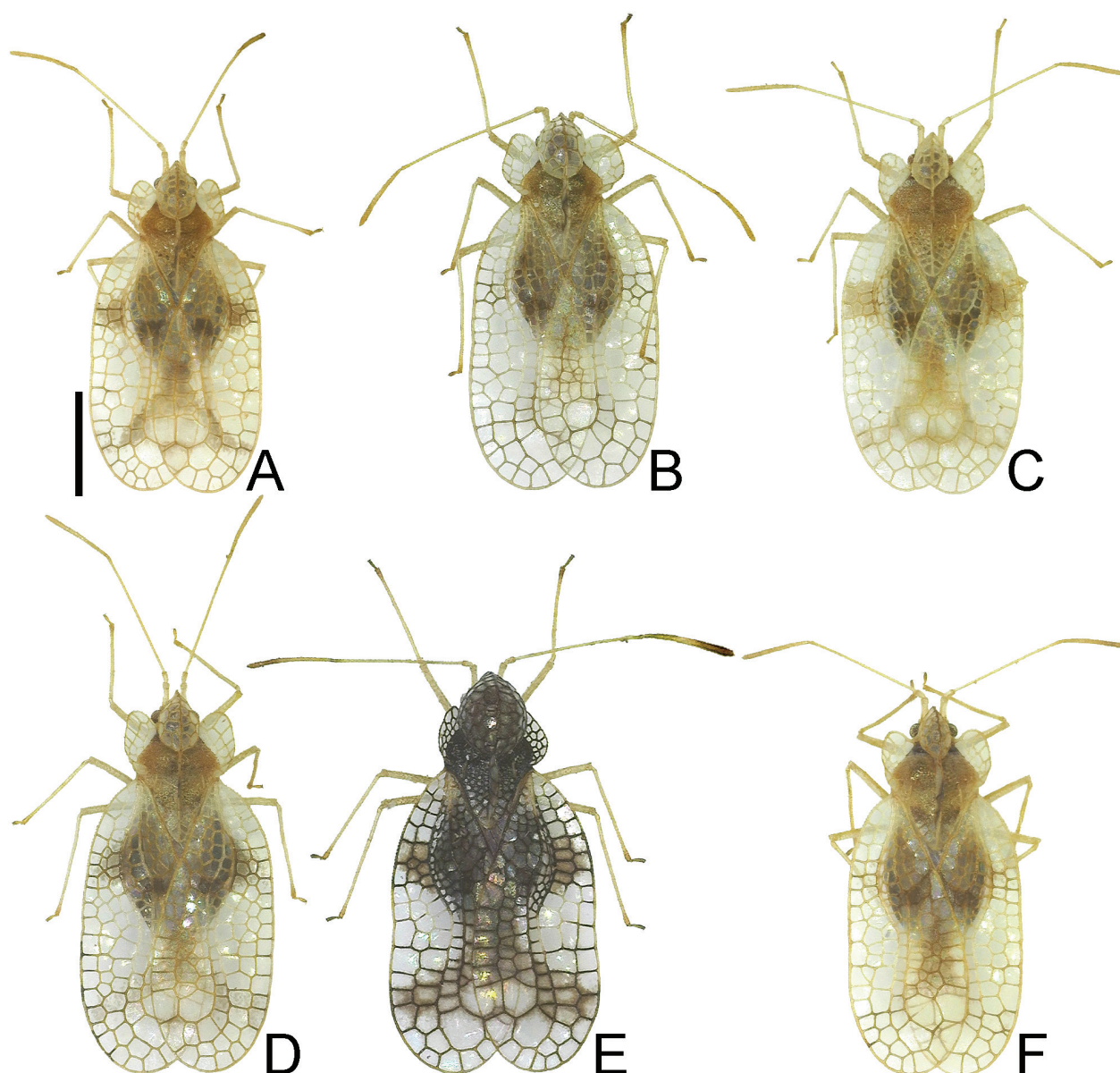


**Figure 4.** Female habitus of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua* from Honshu; **B.** *S. (Norba) aperta* from Honshu; **C.** *S. (N.) exigua* from Okinawa Island, central part of Ryukyu Islands; **D.** *S. (N.) hayashii* sp. nov. from Aguni Island, central part of Ryukyu Islands; **E, F.** *S. (N.) hiurai* from Okinawa (**E**) and Takara (**F**) Islands, central part of Ryukyu Islands. Scale bar: 1.0 mm.

122°58'16.6"E)], 11.xi.2020, leg. J. Souma. **Paratypes** (141 ♂♂ 252 ♀♀), JAPAN: RYUKYU ISLANDS (southern part): Miyako Island: Karimata, 2.ix.1958, leg. T. Hidaka (1 ♀, ELKU); Hirara, Karimata, 1.iv.1991, leg. M. Hayashi (1 ♀, TUA); as above but 21.xi.1992 (2 ♂♂ 1 ♀, ELKU); as above but 22.xi.1992 (1 ♀, TUA); Gusukube, Wipya, 2.iv.1991, leg. M. Hayashi (5 ♂♂ 9 ♀♀, TUA); Mt. Nobarudake, 2.iv.1991, leg. M. Hayashi (6 ♂♂ 12 ♀♀, TUA); as above, but 11.x.1993 (7 ♂♂ 21 ♀♀, TUA); as above, but 13.v.1995 (1 ♀, TUA); as above, but 24.vi.2008 (2 ♂♂ 1 ♀, TUA); as above but 9.xi.2018, leg. J. Souma (3 ♂♂ 2 ♀♀, TUA); Ono Mountain Forest, 18.v.1991, leg. M. Hayashi (3 ♀♀, TUA); as above but 7.xi.2018, leg. J. Souma (5 ♀♀, ELKU; 1 ♂ 2 ♀♀, TUA); Ueno-son, Mt. Nobarudake, 31.x.1999, leg. T. Ishikawa (3 ♂♂ 4 ♀♀, TUA); as above but leg. M. Tomokuni (2

♂♂ 1 ♀, NSMT); Karimata, Ôno-sanrin, 1.xi.1999, leg. T. Ishikawa (1 ♂, TUA); Hirara, Higashi-sokobaru, 2.xi.1999, leg. T. Ishikawa (1 ♂ 1 ♀, TUA); Kamamamine Park, 28.iv.2002, leg. M. Hayashi (1 ♀, TUA); Ueno, Mt. Nobarudake, 27.xii.2017, leg. H. Yoshitake (2 ♂♂ 3 ♀♀, TUA); Gusukube, Yoshino, 8.xi.2018, leg. J. Souma (1 ♂ 7 ♀♀, TUA). Irabu Island: Irabu, 10.xi.2018, leg. J. Souma (1 ♂, ELKU); Makiyama, 10.xi.2018, leg. J. Souma (1 ♂ 2 ♀♀, ELKU); as above but 25.vii.2022, leg. S. Shimamoto (1 ♂ 3 ♀♀, TUA); near Makiyama-tenbôdai, 26.ix.2020, leg. H. Yoshitake (1 ♂ 1 ♀, NIAES). Kurima Island: 31.x.2007, leg. M. Hayashi (1 ♀, TUA). Ogami Island: 9.vi.2009, leg. M. Hayashi (1 ♂, TUA); 27.xii.2017, leg. H. Yoshitake (2 ♂♂ 6 ♀♀, TUA). Ishigaki Island: 5.ix.1957, leg. T. Takara (2 ♀♀, NSMT); 20.iii.1960, leg. T. Takara (1 ♂ 1 ♀, KUM); Nanbadake, 24.xi.1960, leg.



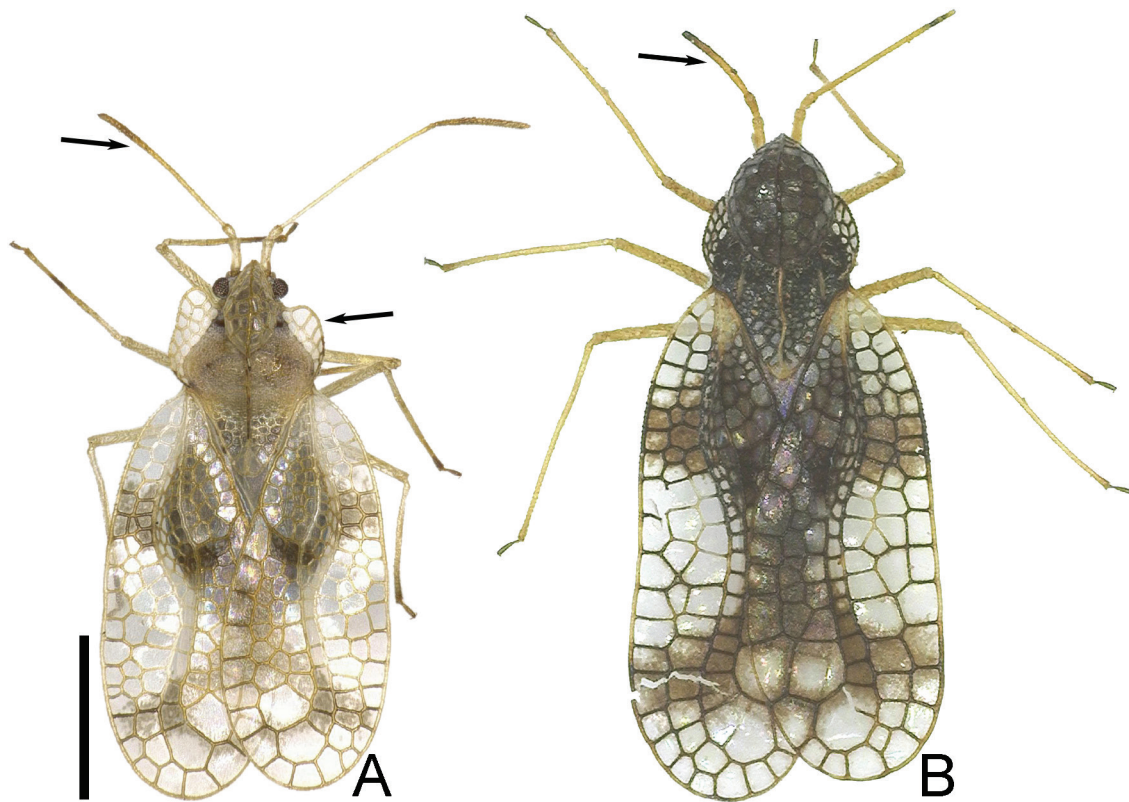


**Figure 5.** Female habitus of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) ishikawai* sp. nov. from Miyako Island, southern part of Ryukyu Islands; **B.** *S. (N.) mendica* from Honshu; **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai* from Kyushu; **F.** *S. (S.) tomokunii* sp. nov. from Miyake Island, southern part of Izu Islands. Scale bar: 1.0 mm.

K. Yasumatsu (1 ♀, KUM); Kawara, 28.x.1963, leg. Y. Hirashima (2 ♀♀, KUM); Mt. Omoto, alt. 100–526 m, 17.xi.1963, leg. G. A. Samuelson (1 ♀, KUM); Yonehara, 15.iii.1964, leg. Taira (1 ♂ 1 ♀, NIAES); Kahara-yama, 14.iii.1964, leg. Y. Miyatake (4 ♂♂ 1 ♀, KUM); as above but leg. S. Kimoto (1 ♂, KUM); as above but 18.iii.1964 (1 ♀, KUM); Yonehara, 15.iii.1964, leg. T. Shirozu (1 ♂ 3 ♀♀, KUM); as above but leg. Y. Miyatake (1 ♂ 1 ♀, KUM); as above but 12.vi.2008, leg. M. Hayashi (1 ♀, TUA); Omoto-san, 16.iii.1964, leg. Y. Miyatake (2 ♂♂ 6 ♀♀, KUM); Takada, 10.iv.1981, leg. K. Baba (1 ♀, NIAES); as above but 10.xi.1985, leg. M. Hayashi (2 ♀♀, TUA); Omoto, 15.x.1988, leg. M. Hayashi (1 ♀, TUA); as above but 2.vii.1998, leg. M. Hayashi (1 ♀, TUA); Ban-

na-dake, 12.v.1975, leg. Y. Notsu (1 ♂, NSMT); as above but 16.xi.1984, leg. M. Tomokuni (2 ♀♀, NSMT); Mt. Bannadake, 2.iv.1976, leg. K. Murakami (1 ♂, NSMT); as above but 19.vii.2022, leg. S. Shimamoto (3 ♂♂ 6 ♀♀, TUA); Banna Park, 17.iii.1993, leg. M. Hayashi (1 ♀, TUA); Nosoko, 1.v.1998, leg. K. Takahashi (1 ♂, NSMT); Mt. Yarabu-dake, 23.iv.1999, leg. T. Ishikawa (1 ♀, TUA); as above but 6–9.v.2016, leg. N. Tsuji (2 ♀♀, ELKU); as above but 13.xi.2018, leg. J. Souma (1 ♂, TUA); Takeda-rindo, 23.v.2000, leg. H. Mizushima (1 ♂, TUA); Mt. Omoto-dake, 18.vi.1991, leg. S. Miyakawa (4 ♀♀, NSMT); as above but 22.vi.1991 (1 ♀, NSMT); as above but 12.v.1993, leg. M. Hayashi (1 ♀, TUA); as above but 24.v.2000, leg. T. Ishikawa (1 ♀, TUA); Mt. Maesedake,

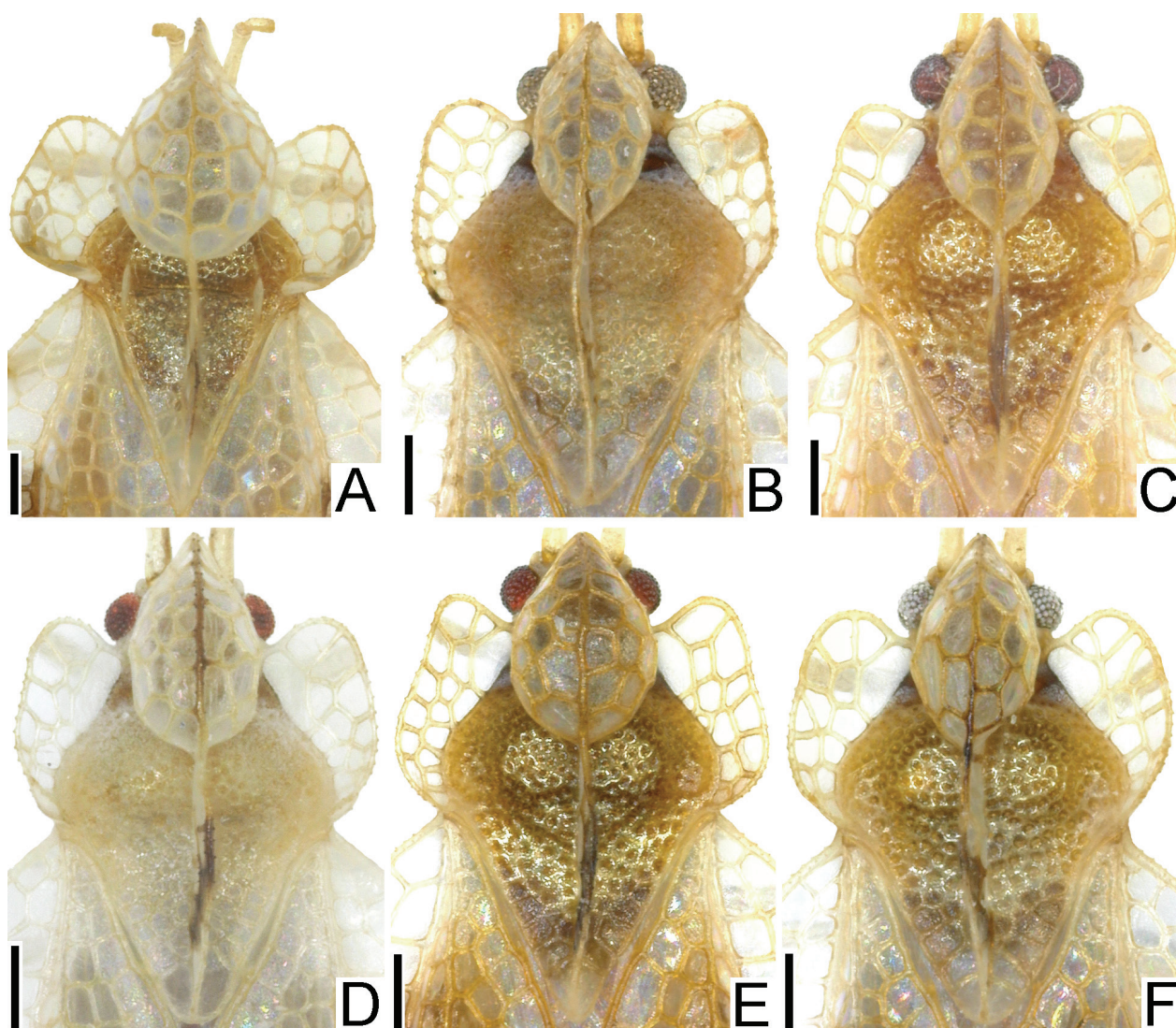




**Figure 6.** Teratological forms of two *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) aperta* from Izu-Oshima Island, northern part of Izu Islands; **B.** *S. (Stephanitis) takeyai* from Kyushu. Arrows indicate antennae with segmental oligomery and malformed paranotum. Scale bar: 1.0 mm.

20.iv.2005, leg. M. Hayashi (3 ♂♂ 3 ♀♀, TUA); as above but 21.ii.2006 (2 ♂♂ 4 ♀♀, TUA) as above but 22.iii.2006 (1 ♂, TUA); as above but 16.xi.2018, leg. J. Souma (1 ♀, TUA); as above but 6.iii.2022, leg. T. Saeki (1 ♂, TUA); as above but 20.vii.2022, leg. S. Shimamoto (5 ♀♀, TUA); Shiramizu, 29.x.2007, leg. M. Hayashi (1 ♀, TUA); Kabira, 29.x.2007, leg. M. Hayashi (1 ♀, TUA); as above but 8.x.2013, leg. R. Ito (1 ♂ 1 ♀, ELKU); Hirae, Takeda-rindō, 4.x.2013, leg. R. Ito (1 ♀, ELKU); Hirae, Omoto-dake, 7.x.2013, leg. R. Ito (1 ♂, ELKU); Nagura, 7.x.2013, leg. R. Ito (3 ♂♂ 2 ♀♀, ELKU); Yarabu, Yarabu-dake, 8.x.2013, leg. R. Ito (1 ♀, ELKU); Yarabu, 8.x.2013, leg. R. Ito (1 ♀, ELKU); Okawa, 11.xi.2018, leg. J. Souma (1 ♂, TUA); Oganaki, 13.xi.2018, leg. J. Souma (1 ♀, ELKU); Nosoko, 14.xi.2018, leg. J. Souma (1 ♂, ELKU); Itona, 14.xi.2018, leg. J. Souma (1 ♂, TUA); Inoda, 14.xi.2018, leg. J. Souma (1 ♀, ELKU); Hirae, 17.xi.2018, leg. J. Souma (1 ♀, TUA); Sakieda, 1.iii.2020, leg. Y. Obae (2 ♂♂ 1 ♀, ELKU). Iriomote Island: 24.iv.1951, leg. T. Takara (1 ♀, NSMT); Ōhara, 22.xi.1960, leg. K. Yasumatsu (1 ♂, ELKU); Ushikumori, 4.x.1963, leg. S. Miyamoto (1 ♂, KUM); as above but 9.iii.1964, leg. Y. Miyatake (2 ♂♂ 1 ♀, KUM); as above leg. T. Shirozu (1 ♂ 4 ♀♀, KUM); as above but 11.iii.1964, leg. Y. Miyatake (3 ♂♂ 2 ♀♀, KUM); as above but 24.iii.1973, leg. S. Azuma (1 ♂ 2 ♀♀, NSMT); Sonai,

6.x.1963, leg. S. Miyamoto (1 ♂, KUM); as above but 8.x.1963 (1 ♂ 1 ♀, KUM); Komi, 12.vii.1963, leg. Y. Miyatake (4 ♀♀, KUM); as above but 2.iv.1978, leg. K. Baba (1 ♀, NIAES); as above but 10.xi.1984, leg. M. Tomokuni (1 ♀, NSMT); as above but 11.xi.1984, leg. M. Tomokuni (1 ♂, NSMT); as above but 20.xi.1998, leg. T. Ishikawa (1 ♀, TUA); as above but 20–23.iii.2015, leg. R. Ito (1 ♀, ELKU); as above but 24.viii.2020, leg. Y. Hisasue (1 ♂, ELKU); Shirahama, 5.xi.1963, leg. H. Hasegawa (1 ♀, NIAES); Shirahama–Sonae, 5.xi.1963, leg. H. Hasegawa (1 ♀, KUM); Shirahama–Hoshidate, 8.iii.1964, leg. Y. Miyatake (2 ♂♂ 2 ♀♀, KUM); as above but leg. S. Kimoto (1 ♀, KUM); Upstream of Nakara-gawa Riv., 12.iii.1964, leg. Y. Miyatake (1 ♀, KUM); as above but leg. S. Kimoto (1 ♂ 1 ♀, KUM); as above but leg. S. Higashihirachi (1 ♂, NIAES); Ohara, 20.viii.1971, leg. S. Azuma (1 ♂, NSMT); Funaura, 28.iii.1973, leg. S. Azuma (1 ♂, NSMT); as above but 21.viii.1976, leg. K. Kyoda (1 ♀, NSMT); as above but 8.x.1977, leg. M. Taniguchi (1 ♀, NSMT); as above but 9.x.1977, leg. M. Kinjo (1 ♀, NSMT); as above but 9.x.1977, leg. M. Arasaki (1 ♀, NSMT); as above but 11.xi.1984, leg. M. Tomokuni (1 ♀, NSMT); as above but 31.iii.1996, leg. M. Hayashi (1 ♂, TUA); Hoshidate, 7.xi.1985, leg. M. Hayashi (1 ♂, TUA); Monpanare, 29.ix.1993, leg. M. Hayashi (1 ♀, TUA); Takana, Yutsun Riv., 22.xi.1997, leg. M. Tomokuni (1 ♀,

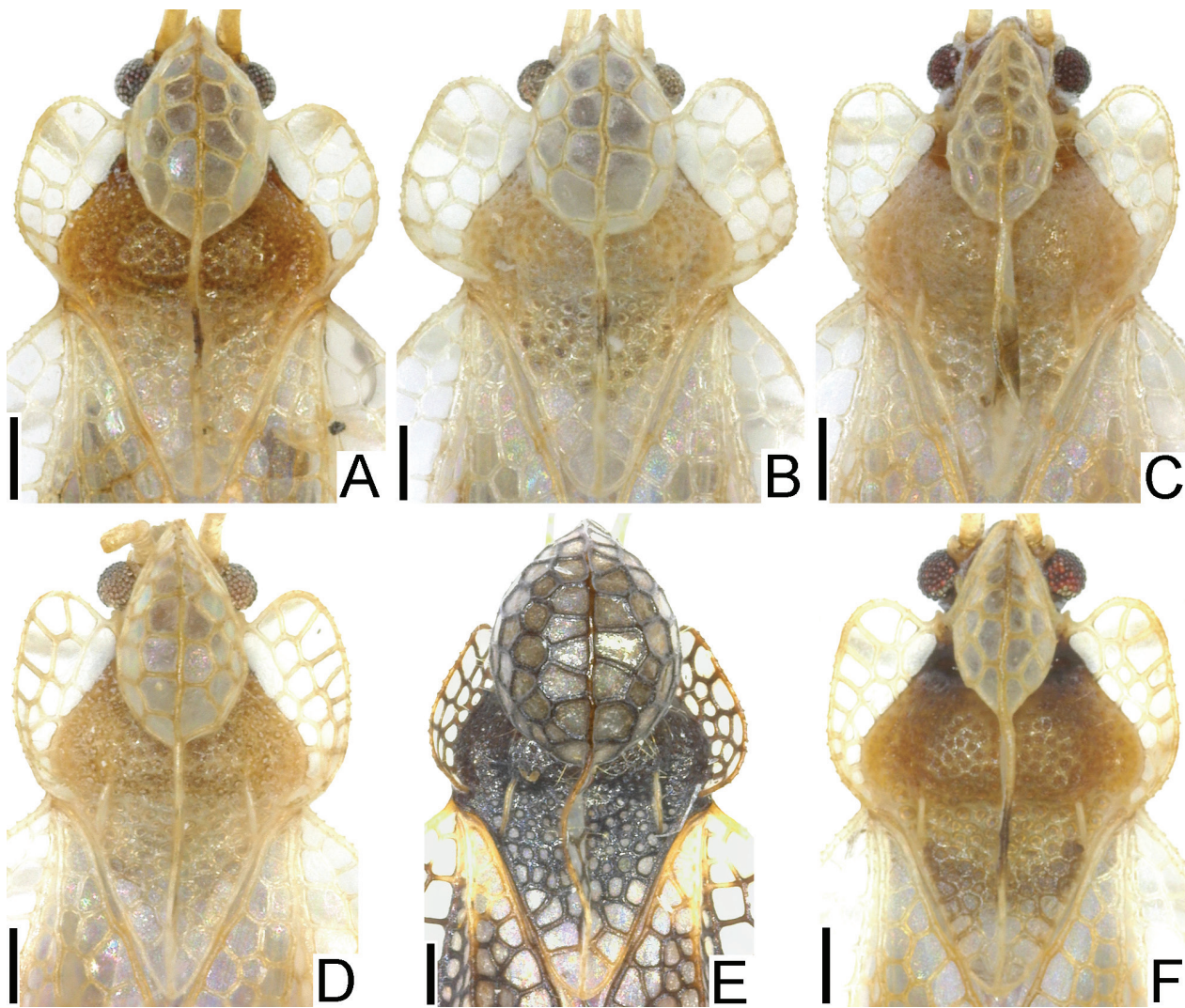


**Figure 7.** Male pronota of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E, F.** *S. (N.) hiurai* from Amami-Oshima (**E**) and Kikai (**F**) Islands, central part of Ryukyu Islands. Scale bars: 0.2 mm.

NSMT); Urauchi, 19.vi.1998, leg. T. Ishikawa (1 ♀, TUA); Shirahama-rindō, 1.iii.2002, leg. T. Ishikawa (2 ♀, TUA); Mt. Sonaidake, 1.iii.2002, leg. T. Ishikawa (2 ♂♂ 1 ♀, TUA); Ōhara, Fusatoruba, 3.iii.2002, leg. T. Ishikawa (4 ♂♂ 1 ♀, TUA); Aira-gawa Rev., 7.x.2009, leg. T. Ishikawa (1 ♂, TUA); Haiminaka, 21–23.iii.2015, leg. R. Ito (1 ♀, ELKU); Sonai, 19.xi.2018, leg. J. Souma (1 ♀, ELKU); Otomi For. Rd., 20.xi.2018, leg. J. Souma (1 ♂, TUA); Unarizaki, 20.xi.2018, leg. J. Souma (1 ♂, ELKU); Ōtomi-path, 21.ii.2020, leg. R. Ito (3 ♂♂ 3 ♀♀, ELKU); Mt. Tedo-san, 14.x.2020, leg. Y. Hisasue (1 ♀, ELKU); Inaba Trail, 16.x.2020, leg. Y. Hisasue (1 ♀, ELKU). Yonaguni Island: Mt. Kubura-dake, 2.vii.1973, leg. K. Shigematsu (1 ♂, NSMT); as above but 30.iii.2020, leg. R. Ito (1 ♀, ELKU); Mt. Urabu-dake, 28.iii.1997, leg. T. Ishikawa (5 ♂♂ 1 ♀♀, TUA); as holotype (6 ♂♂ 13 ♀♀, ELKU); as holotype but 14.xi.2020 (2 ♂♂ 8 ♀♀, ELKU); Mt. Inbidake, 11.xi.2020, leg. J. Souma (1 ♂ 3 ♀♀,

ELKU); as above but 13.xi.2020, leg. J. Souma (11 ♂♂ 16 ♀♀, ELKU); Higawa, 11.xi.2020, leg. J. Souma (4 ♀♀, ELKU); Iranda For. Rd., 25.iii.2021, leg. T. Saeiki (1 ♂, ELKU); Promenade of Atlas Moth Museum, 26.iii.2021, leg. K. Saito (2 ♂♂ 1 ♀, ELKU). A single paratype collected in 1958 was recorded as “*Stephanitis aperta*”, four paratypes collected in 1960 as “*Stephanitis exigua*” by Takeya (1963). Of 12 paratypes collected in 1963, eight were recorded as “*Stephanitis exigua*” or “*Stephanitis hiurai*” by Miyamoto (1964a). Of 42 paratypes collected in 1964, 38 individuals were recorded as “*Stephanitis exigua*” by Miyamoto (1964b). Four paratypes from Iriomote Island collected by Y. Miyatake in 1963 were recorded as “*Stephanitis exigua*” by Miyamoto (1964c). Six paratypes from Iriomote Island collected by S. Azuma or M. Kinjo were considered to be recorded as “*Stephanitis aperta*” or “*Stephanitis exigua*” by Azuma and Kinjo (1987).





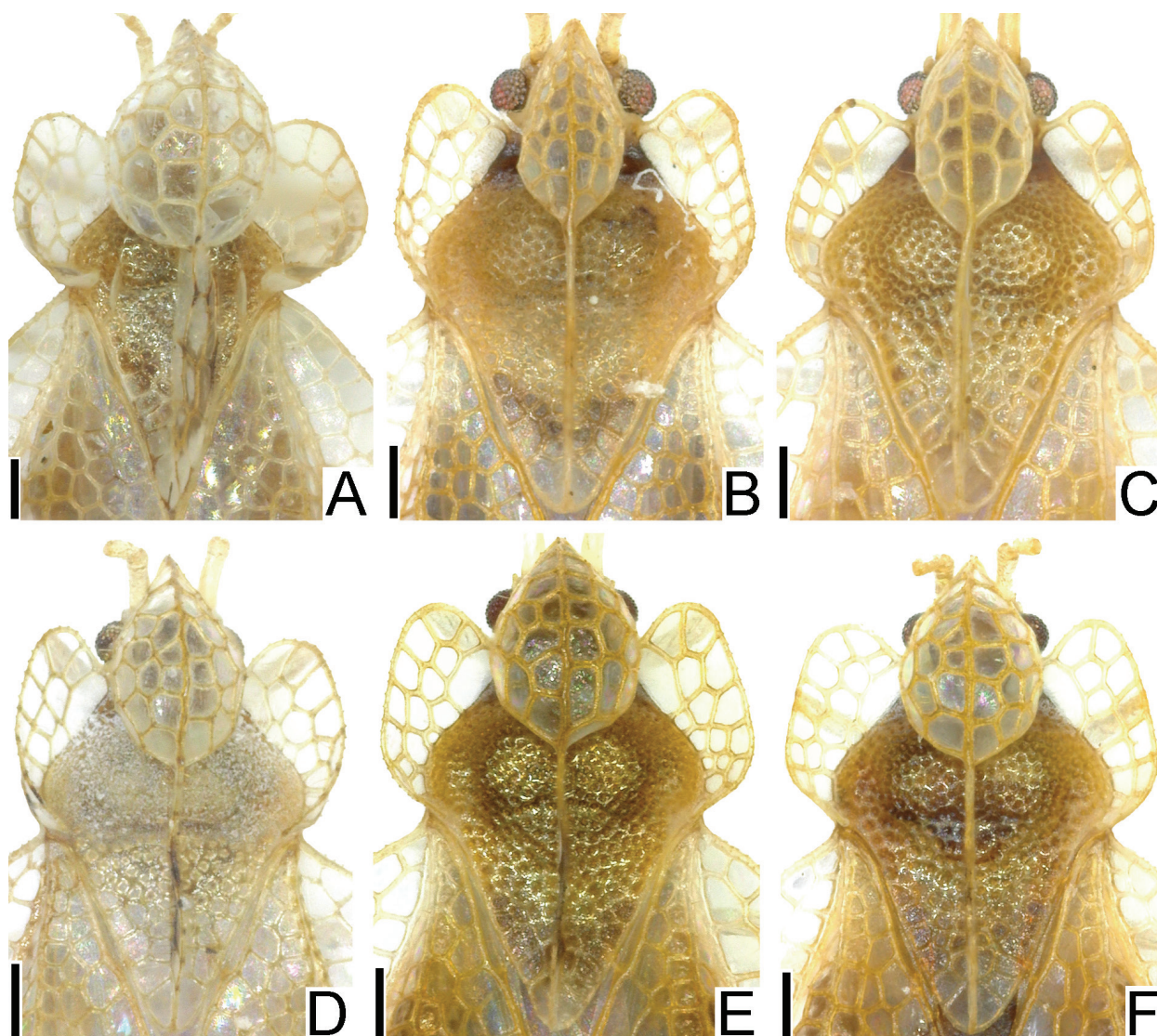
**Figure 8.** Male pronota of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) ishikawai* sp. nov.; **B.** *S. (N.) mendica* lacking lateral carina; **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai*; **F.** *S. (S.) tomokunii* sp. nov.. Scale bars: 0.2 mm.

**Additional material examined. Non-types** (13 ♂♂ 8 ♀♀ 13 nymphs), JAPAN: RYUKYU ISLANDS: (southern part): Iriomote Island: Shirahama–Hoshidate, 8.iii.1964, leg. Y. Miyatake (1 nymph); Ōhara, Fusatoruba, 3.iii.2002, leg. T. Ishikawa (4 nymphs, TUA). Yonaguni Island: as holotype (1 nymph). TAIWAN: TAIPEI CITY: Taihoku [= Taipei], 16.iv.1917, leg. M. Maki (2 ♂♂, ELKU); as above but 15.i.1927, leg. R. Takahashi (1 ♀, ELKU); as above but 2.iv.1930, leg. C. Takeya (1 ♂ 1 ♀, ELKU); as above, but 10.ii.1932, leg. R. Takahashi (4 ♂♂ 2 ♀♀, ELKU; 1 ♂, KUM); Da'an District, 5.x.2021, leg. Y.-J. Tsai (3 ♂♂ 1 ♀ 7 nymphs, NMNS); as above but 22.xi.2021 (2 ♂♂ 3 ♀♀, NMNS). Twelve specimens collected from Taiwan in the early 20<sup>th</sup> century were recorded as “*Stephanitis aperta*” or “*Stephanitis exigua*” by Takeya (1931, 1963). The Taiwanese specimens are most similar to *Stephanitis (Norba) ishikawai* sp. nov. in morphological characteristics and were provisionally identified as pertaining to the new species in

the present study. All 13 nymphs recorded above are in poor condition and are thus not described here.

**Diagnosis.** *Stephanitis (Norba) ishikawai* sp. nov. is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown (Figs 8A, 10A, 12A, 14A, 16A, 18A, 19F, 21F, 23F); calli light brown; body in male 2.1 times (in female 2.0 times) as long as maximum width across hemelytra (Figs 3A, 5A); rostrum reaching metasternum; pronotum unicarinate (Fig. 25F); hood pale, shorter than median carina of pronotum, wider than vertex at widest part, incompletely covering eye, as high as median carina of pronotum at highest part, posterior margin extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc opaque; paranotum less erect, slightly narrowed posteriorly, with 3 rows of areolae at widest part, anterolateral angle protruding anteriad, outer margin gently curved inwards at





**Figure 9.** Female pronota of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E, F.** *S. (N.) hiurai* from Amami-Oshima (**E**) and Kikai (**F**) Islands, central part of Ryukyu Islands. Scale bars: 0.2 mm.

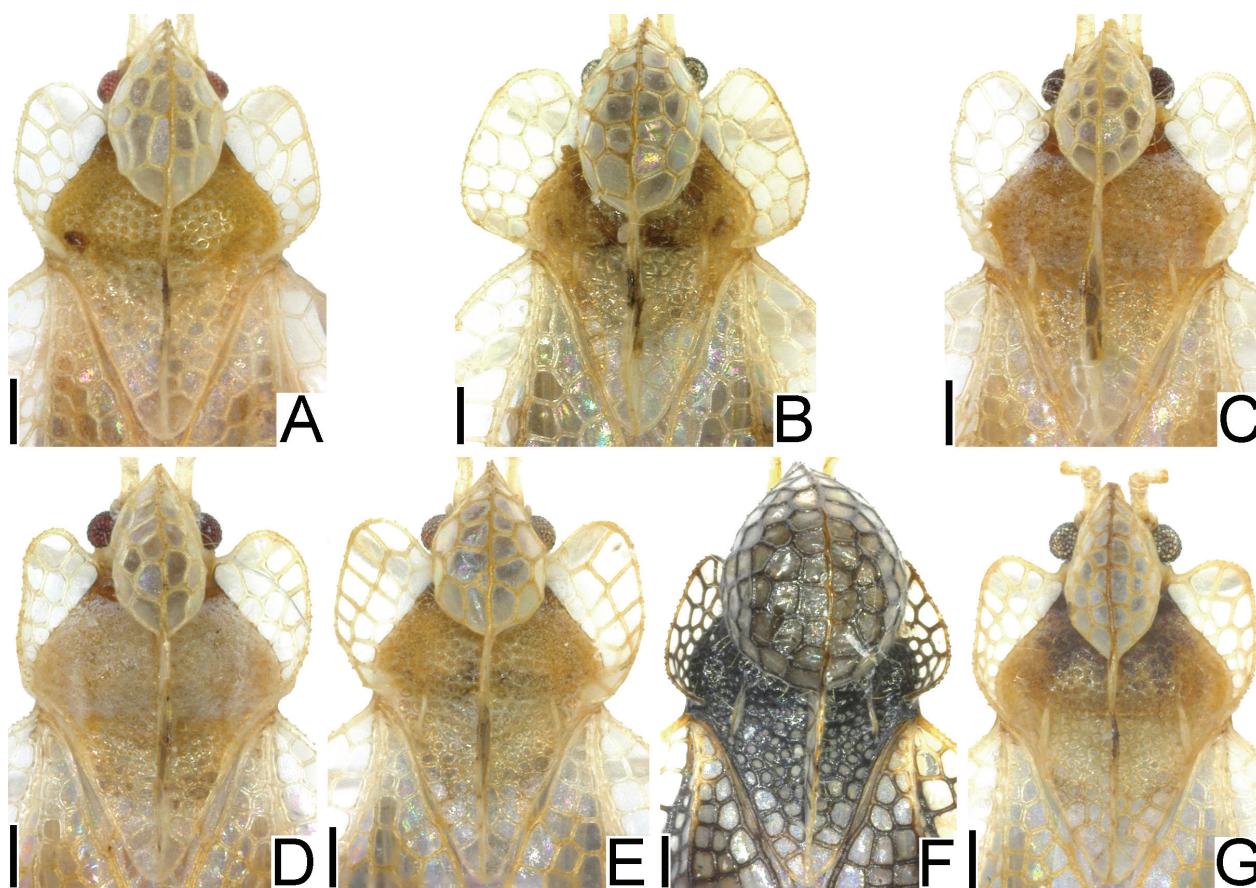
posterolateral angle, maximum height longer than height of eye (Fig. 28B); apices of hemelytra close to each other in rest; costal area with 3–4 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 3 rows) of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at centre of venter, posterior margin slightly emarginate in middle part (Fig. 30A–C); and paramere stout, weakly curved inwards at apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 32A–C).

**Description. Male.** Head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown; calli light brown; eye dark red; areolae of pronotum and hemelytron transparent; hood pale; pronotal disc opaque; pubescence on body yellowish (Figs 3A, 8A, 12A, 16A, 19F, 21F).

Body 2.1 times as long as maximum width across hemelytra (Fig. 3A). Head (Figs 8A, 12A, 19F, 25F) glabrous; a pair of frontal spines close to each other at apices, not reaching apex of clypeus; median spine as long as frontal spines, reaching bases of frontal spines; pair of occipital spines longer than median spine, reaching middle part of eyes; antenniferous tubercles obtuse, slightly curved inwards; clypeus smooth. Compound eye round in dorsal view. Antenna densely covered with pubescence; segment I cylindrical; segment II cylindrical, shortest among antennal segments; segment III longest amongst antennal segments; segment IV cylindrical, longer than segment I. Bucculae closed at anterior ends, with 3 rows of areolae throughout length. Rostrum reaching metasternum.

Pronotum (Figs 8A, 12A, 25F, 28B) unicarinate, 1.3 times as long as maximum width across paranota, sparsely covered with pubescence. Pronotal disc coarsely punctate. Hood shorter than median carina of pronotum, wider than vertex at widest part, incompletely covering eye, as high





**Figure 10.** Female pronota of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) ishikawai* sp. nov.; **B.** *S. (N.) mendica* possessing lateral carina; **C–E.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**E**) possessing lateral carina and from Honshu (**D**) lacking lateral carina; **F.** *S. (S.) takeyai*; **G.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

as median carina of pronotum at highest part, posterior margin extending to middle of pronotal disc, 4 rows of areolae at highest part, dorsal margin arched. Median carina straight, extending to apex of posterior process, 2 rows of areolae at highest part, dorsal margin arched. Calli smooth. Paranotum less erect, slightly narrowed posteriorly, with 3 rows of areolae at widest part, anterolateral angle protruding anteriorly, outer margin gently curved inwards at posterolateral angle, maximum height longer than height of eye. Posterior process triangular, obtuse at apex.

Hemelytron (Fig. 16A) 2.4 times as long as its maximum width, extending beyond apex of abdomen, sparsely covered with pubescence; maximum width across hemelytra 1.6 times as much as maximum width across paranota; apices close to each other in rest; costal area with 3–4 rows of areolae at widest part; subcostal area with 2 rows of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; C (costal), R+M (radiomedial) and Cu (cubital) veins carinate.

Thoracic pleura (Fig. 12A) smooth in anterior part, coarsely punctate in posterior part. Ostiolar peritreme oblong. Sternal laminae (Fig. 19F) lower than bucculae; pro- and mesosternal laminae open in both anterior and posterior ends; metasternal laminae as high as

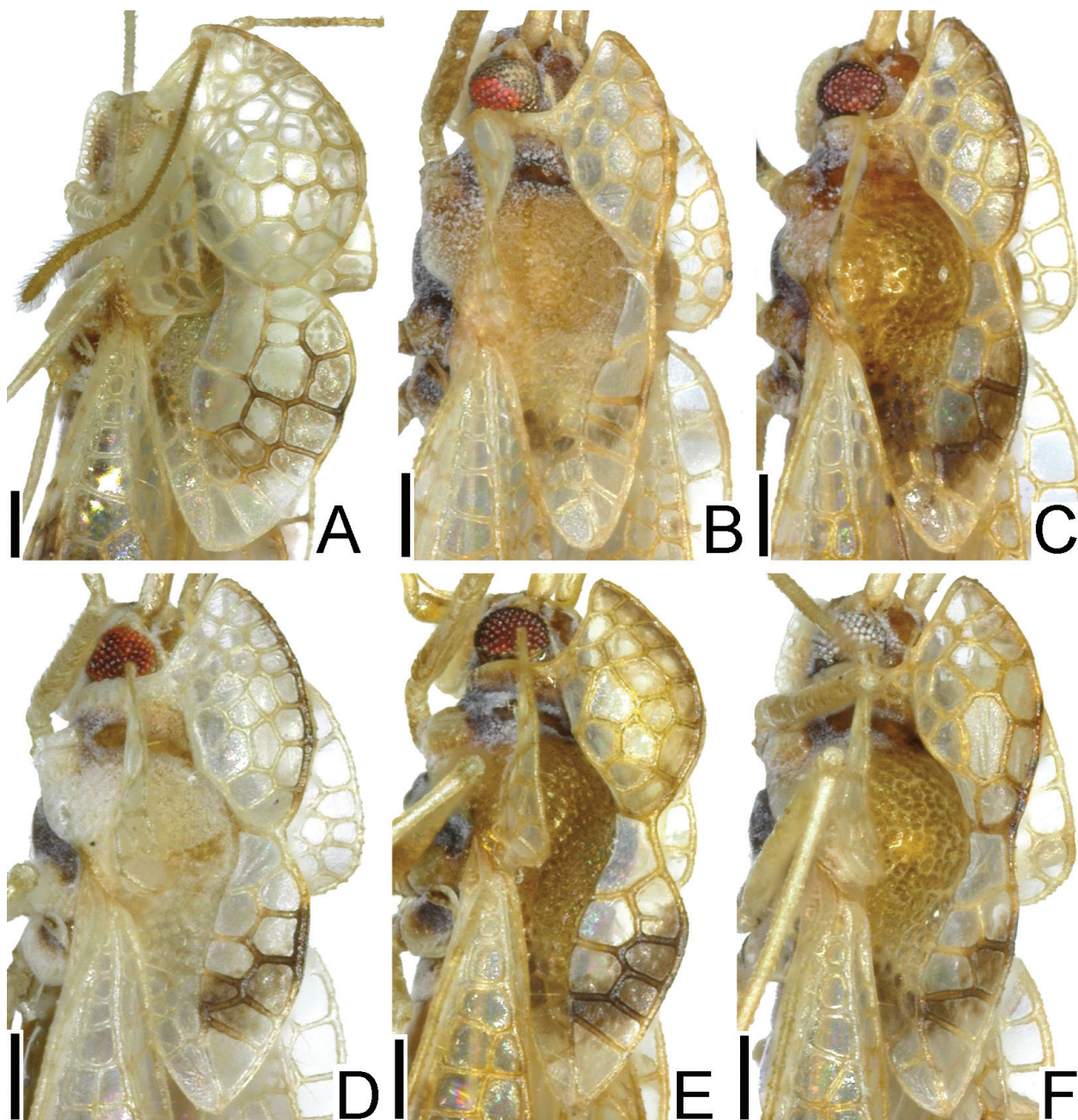
mesosternal laminae, open at anterior ends, fused each other at posterior ends. Legs (Fig. 3A) smooth, densely covered with pubescence; femora thickest at middle.

Abdomen oblong in dorsal and ventral views. Pygophore (Figs 21F, 30A–C) compressed dorsoventrally, semicircular in ventral view, elevated at centre of venter, with posterior margin slightly emarginate in middle part, covered with pubescence. Paramere (Fig. 32A–C) stout, expanded in middle part, weakly curved inwards at apex, outer margin not sinuate in middle part, inner margin nearly straight in basal part, covered with pubescence in middle part of outer and inner margins.

Measurements ( $n = 20$ ). Body length with hemelytra 2.9–3.2 mm; maximum width across hemelytra 1.4–1.6 mm; length of antennal segments I to IV 0.2 mm, 0.1 mm, 1.2 mm and 0.7–0.8 mm, respectively; pronotal length 1.2–1.3 mm; pronotal width across paranota 0.8–1.0 mm; hemelytral length 2.2–2.5 mm; maximum width of hemelytron 0.9–1.1 mm.

**Female.** General habitus very similar to that of male (Figs 4D, 9D, 13D, 17D, 23D), except for the following characters: body 2.0 times as long as maximum width across hemelytra; antennal segment III shorter than in male; pronotum 1.4 times as long as maximum width across paranota; hood wider than in male; hemelytron 2.3 times as long as maximum width; maximum width across





**Figure 11.** Male pronota of five *Stephanitis* species from Japan, dorsolateral view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E, F.** *S. (N.) hiurai* from Amami-Oshima (**E**) and Kikai (**F**) Islands, central part of Ryukyu Islands. Scale bars: 0.2 mm.

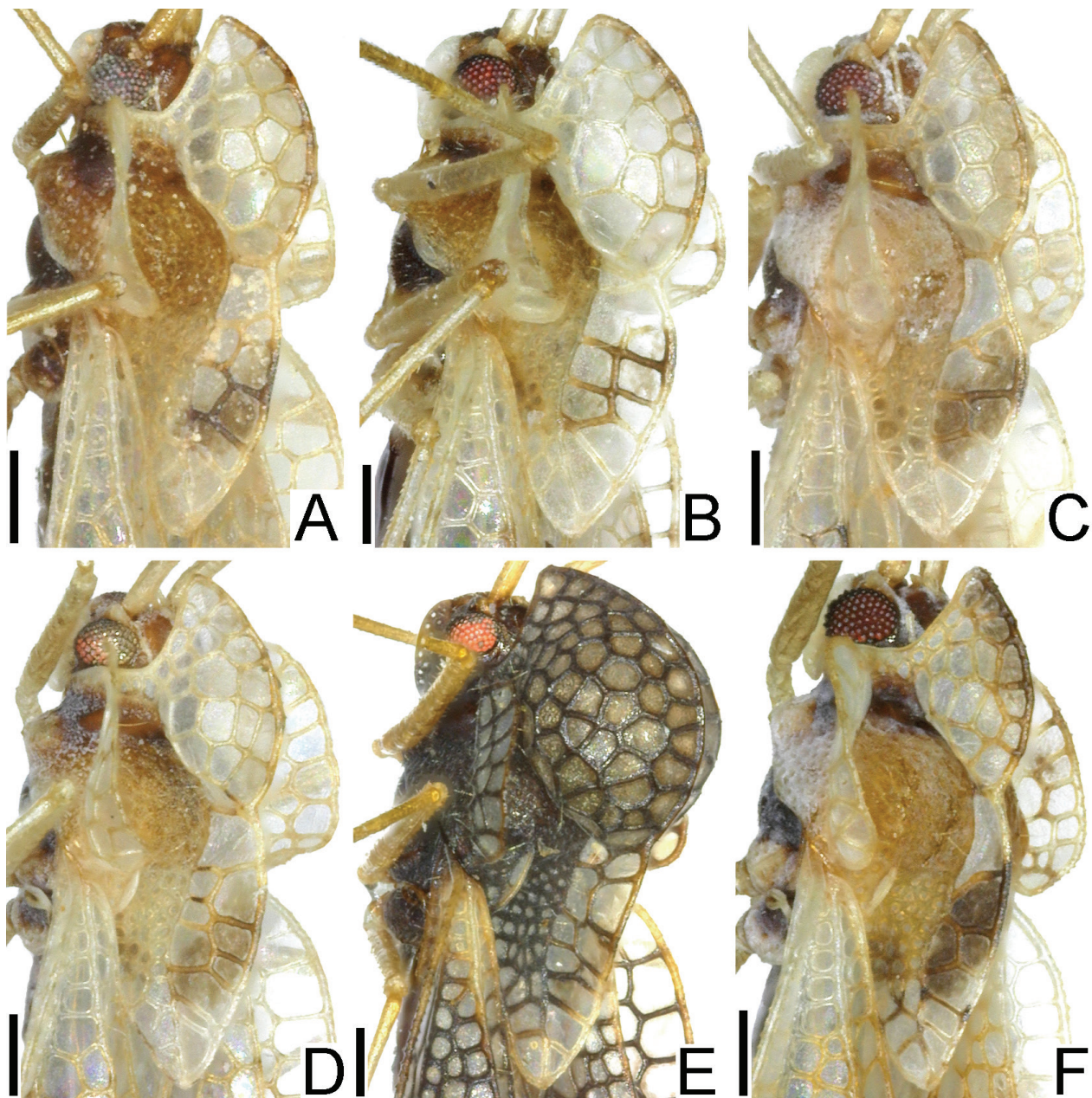
hemelytra 1.7 times as much as maximum width across paranota; subcostal area wider than in male, with 3 rows of areolae at widest part; and apical part of abdomen pentagonal in ventral view.

Measurements ( $n = 20$ ). Body length with hemelytra 3.0–3.4 mm; maximum width across hemelytra 1.5–1.7 mm; length of antennal segments I to IV 0.2 mm, 0.1 mm, 1.0 mm and 0.7–0.8 mm, respectively; pronotal length 1.2–1.4 mm; pronotal width across paranota 0.9–1.0 mm; hemelytral length 2.3–2.5 mm; maximum width of hemelytron 1.0–1.1 mm.

**Remarks.** Amongst the Japanese species of *Stephanitis*, *S. (Norba) ishikawai* sp. nov. is most similar to

*S. (N.) hayashii* sp. nov. in general habitus, but the former is easily distinguished from the latter by the following characters: length of antennal segment IV 0.7–0.8 mm (0.6 mm in *S. (N.) hayashii* sp. nov.); paranotum less erect (more erect in *S. (N.) hayashii* sp. nov.) (Figs 7D, 8A, 9D, 10A, 11D, 12A, 13D, 14A); and paramere stout (slender in *S. (N.) hayashii* sp. nov.), with inner margin nearly straight in basal part (slightly curved inward in *S. (N.) hayashii* sp. nov.) (Figs 31C, D, 32A–C). Moreover, the partial COI gene pairwise sequence distances between both species are 0.042503–0.048201 (Suppl. material 3). *Stephanitis (Norba) ishikawai* sp. nov. was misidentified as *S. (N.) aperta*, *S. (N.) exigua* and *S. (N.) hiurai* in previous studies





**Figure 12.** Male pronota of five *Stephanitis* species from Japan, dorsolateral view: **A.** *S. (Norba) ishikawai* sp. nov.; **B.** *S. (N.) mendica* lacking lateral carina; **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai*; **F.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

(Takeya 1931, 1963; Maa 1957; Miyamoto 1964a, 1964b; Takara and Azuma 1972; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Zheng and Lin 2013), as these four species are very similar to each other. However, *S. (N.) ishikawai* sp. nov. is easily distinguished from the three species by the following characters: rostrum reaching metasternum (not reaching in *S. (N.) aperta*, *S. (N.) exigua* and *S. (N.) hiurai*) (Fig. 19B, C, E, F); and hood slightly higher than median carina of pronotum at highest part (as high as *S. (N.) aperta*, *S. (N.) exigua* and *S. (N.) hiurai*), with posterior margin extending to middle of pronotal disc (not extending in *S. (N.) aperta*, *S. (N.) exigua* and *S. (N.) hiurai*) (Figs 7B, C, E, F, 8A, 9B, C, E, F, 10A, 11B, C, E, F, 12A, 13B, C, E, F, 14A, 25B, C, E, F).

**Distribution.** Japan (Ryukyu Islands (southern part): Miyako Island, Irabu Island, Kurima Island, Ogami Island, Ishigaki Island, Iriomote Island, Yonaguni Island); Taiwan (northern part) (Fig. 47) (Takeya 1931, 1963; Maa 1957; Miyamoto 1964a, 1964b, 1964c; Takara and Azuma 1972; Azuma and Kinjo 1987; Yasunaga et al. 1993; Hayashi 2002; Yamada and Tomokuni 2012; Zheng and Lin 2013; Yamada and Ishikawa 2016; present study). Judging from the photographs, living individuals identified as “*Stephanitis (Norba) aperta*” or “*S. (N.) exigua*” in previous studies (Yasunaga et al. 1993; Yamada and Tomokuni 2012; Zheng and Lin 2013) corresponded to the new species. *Stephanitis (Norba) ishikawai* sp. nov. inhabits the laurilignosa in a subtropical climate of the

southern part of the Ryukyu Islands and northern Taiwan, which is in the Oriental Region.

**Etymology.** The new species is named in honour of Tadashi Ishikawa, a Japanese heteropterist who collected part of paratypes and taught the author how to describe new species.

**Host plants.** *Cinnamomum camphora*, “Kusunoki” (Lauraceae) (present study); *Litsea japonica*, “Hama-biwa” (Lauraceae) (Fig. 43I) (present study); *Machilus thunbergii*, “Tabunoki” (Lauraceae) (present study). *Stephanitis* (*Norba*) *ishikawai* sp. nov. feeds only on lauraceous trees and is oligophagous.

**Biology.** *Stephanitis* (*Norba*) *ishikawai* sp. nov. feeds on the abaxial surface of leaves of the three host plants (present study). Adults were collected in almost all seasons (Miyamoto 1964a, 1964b, 1964c; Takara and Azuma 1972; Yasunaga et al. 1993; Yamada and Tomokuni 2012; present study); nymphs were collected in March and November (present study).

### *Stephanitis* (*Norba*) *mendica* Horváth, 1912

[Japanese name: Yabunikkei-gunbai]

Figs 3B, 5B, 8B, 10B, 12B, 14B, 16B, 18B, 20A, 22A, 24A, 26A, B, 28C, 30D, 32D, 42A, B

*Stephanitis* (*Norba*) *mendica* Horváth, 1912: 334. Syntype(s): Japan: Sakuna [= Honshu, Chiba-ken, Sakuna of former Toyofusa-mura in early 20<sup>th</sup> Century (current Tateyama-shi, Sakuna)] and Satsuma [= Kyushu, Kagoshima-ken, former Satsuma-gun in early 20<sup>th</sup> Century (current Satsumasendai-shi and Satsuma-cho)]; ELHU (not deposited), HNHM.

*Stephanitis* (*Stephanitis*) *fasciicarina* Takeya, 1931: Takara and Hidaka (1960: 188) (distribution). Misidentification.

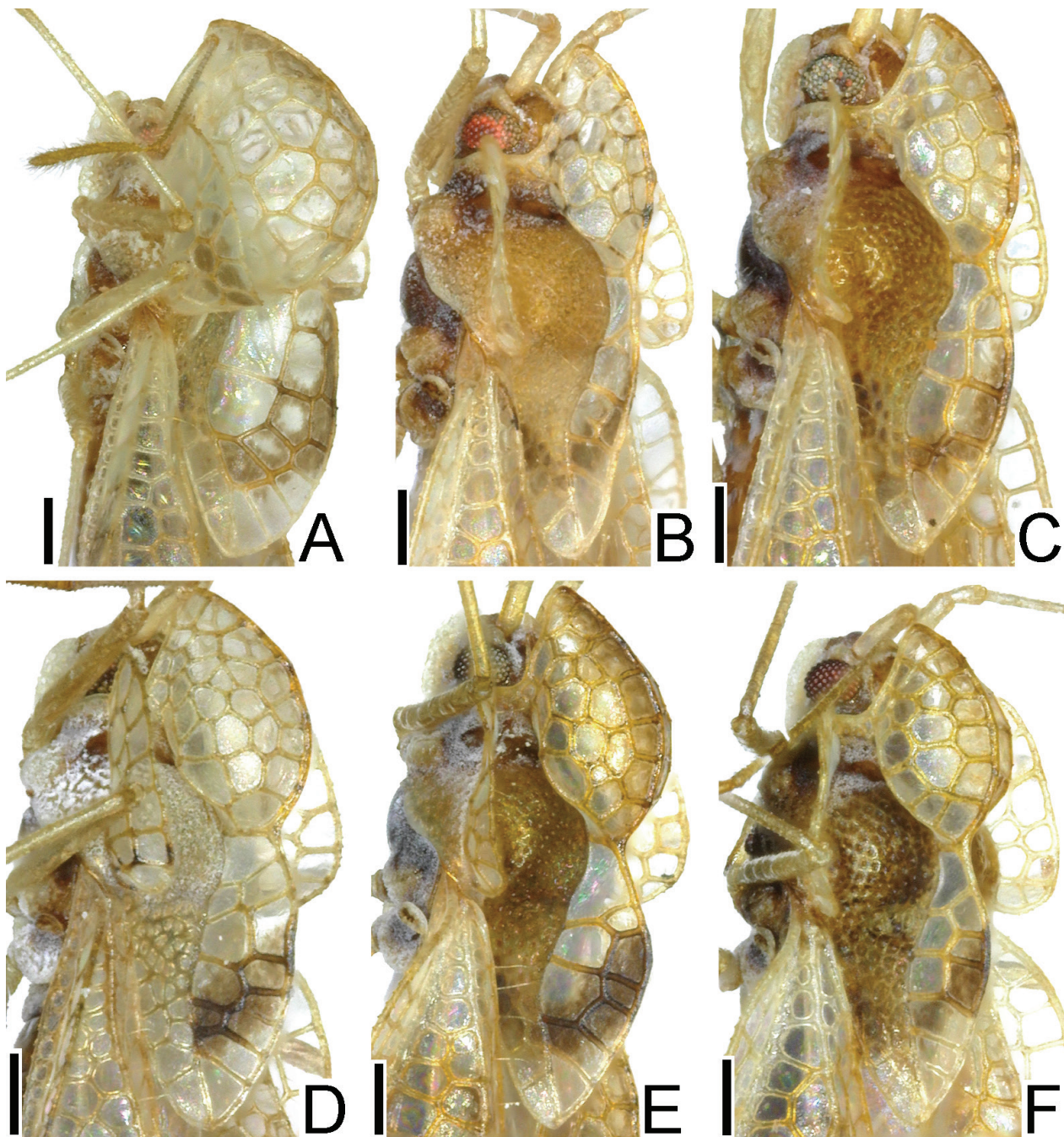
**References.** Takeya (1931: 77) (distribution); Drake (1948: 55) (checklist: *Stephanitis*); Takeya (1951b: 13) (checklist: Japan); Drake and Maa (1953: 100) (checklist: *Stephanitis*); Takeya (1953: 168) (distribution); Takeya (1963: 38) (distribution); Drake and Ruhoff (1965: 367) (catalog); Jing (1981: 346) (monograph); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Péricart and Golub (1996: 58) (catalogue: Palaearctic); Yamada and Tomokuni (2012: 205) (monograph); Yamada and Ishikawa (2016: 433) (checklist: Japan); Okochi (2019: 2) (distribution); Souma (2021d: 26) (distribution).

**Material examined. Non-types** (186 ♂♂ 291 ♀♀ 9 nymphs), JAPAN: HONSHU: Chiba-ken, Tateyama-shi, Shimosanagura, 22.v.2021, leg. J. Souma (19 ♂♂ 16 ♀♀ 1 nymph, TUA); Chiba-ken, Tateyama-shi, Tateyama, 22.v.2021, leg. J. Souma (8 ♂♂ 1 ♀ 5 nymphs); as above but 23.v.2021 (7 ♂♂ 7 ♀♀, TUA); Chiba-ken, Tateyama-shi, Sunozaki, 23.v.2021, leg. J. Souma (1 ♂ 3 ♀♀); Chiba-ken, Tateyama-shi, Yamogi (approximate coordinates: 34°58'08.9"N, 139°53'33.4"E), 24.v.2021, leg. J. Souma (3 ♂♂ 1 nymph, ELKU; 1 ♂ 4 ♀♀, TUA); Kanagawa-ken, Yokohama-shi, Kanazawa-ku, Noukendaimori, 15.vi.2017, leg. J. Souma (45 ♂♂ 61 ♀♀, TUA);

Kanagawa-ken, Yokosuka-shi, Kamoi, 27.vi.2017, leg. J. Souma (1 ♂ 3 ♀♀, ELKU; 38 ♂♂ 98 ♀♀, TUA). JOGASHIMA ISLAND: 4.vi.2019, leg. J. Souma (7 ♂♂ 13 ♀♀, TUA). SHIKOKU: Kochi Pref., Ashizuri-misaki, 29.v.1999, leg. T. Befu (1 ♂, NSMT); Kochi Pref., Mt. Oodo, 3.vi.1971, leg. M. Tomokuni (2 ♂♂ 2 nymphs, NSMT). KYUSHU: Chikuzen, Fukuoka, 27.vi.1931, leg. C. Takeya (1 ♂, ELKU; 5 ♂♂ 5 ♀♀, KUM); Chikuzen, Aburayama, 6.vii.1952, leg. C. Takeya (4 ♀♀, KUM); Fukuoka, Atagoyama, 26.vi.1959, leg. Y. Miyatake (1 ♂, KUM); as above but 4.viii.1961, leg. S. Miyamoto (1 ♀, KUM); Fukuoka, Hirao, 4.vii.1959, leg. Y. Miyatake (4 ♂♂ 4 ♀♀, KUM); Fukuoka-ken, Itoshima-shi, Shimakeya, 14.vi.2021, leg. J. Souma (6 ♂♂ 11 ♀♀, ELKU); Ōita Pref., Saiki-shi, Kamiura, Niinameura, 19.vii.2020, leg. R. Ito (1 ♂ 5 ♀♀, ELKU); Miyazaki Pref., Takanabe-chō, Mochida, Omarugawa, 12.v.2019, leg. R. Ito (13 ♂♂ 8 ♀♀, ELKU); Miyazaki Pref., Hyūga-shi, Okuragahama, 1.vi.2019, leg. R. Ito (4 ♂♂ 6 ♀♀, ELKU); Kagoshima-ken, Kagoshima-shi, Shiroyama-cho, 4.vii.2017, leg. J. Souma (4 ♀♀, TUA); Kagoshima Pref., Sō-shi, Sueyoshi-chō, Minaminogō, 8.vi.2019, leg. R. Ito (1 ♀, ELKU); Kagoshima Pref., Kanoya-shi, Aira-chō, Kamimiyō, 7.vi.2020, leg. R. Ito (1 ♀, ELKU). NOKONOSHIMA ISLAND: 27.vi.1987, leg. S. Miyamoto (2 ♀♀, KUM). RYUKYU ISLANDS (northern and central parts): Yakushima Island: Tabugawa, 18.v.2022, leg. J. Souma (13 ♂♂ 12 ♀♀, TUA); Kusugawa, 18.v.2022, leg. J. Souma (5 ♂♂ 6 ♀♀, TUA); Kosedo, 19.v.2022, leg. J. Souma (3 ♂♂ 1 ♀, TUA). Amami-Oshima Island: Amami-shi, Sumiyo-cho, Ishihara, 2.v.2022, leg. J. Souma (4 ♂♂ 2 ♀♀, TUA); Amami-shi, Kasari-cho, Many, 3.v.2022, leg. J. Souma (2 ♂♂ 12 ♀♀, TUA). Okinawa Island: 20.iv.1958, leg. T. Takara (2 ♂♂ 2 ♀♀, NSMT). Eight adult specimens collected from “Yamogi”, which is adjacent to one of the type localities, “Sakuna”, match the original description of *Stephanitis* (*Norba*) *mendica* (Horváth 1912). The author identified *S. (N.) mendica* based on these eight adults in the present study. Syntype(s) of *S. (N.) mendica* exist in the collection of HNHM (D. Rédei, pers. comm. 2021). Four specimens collected from Okinawa Island were recorded as “*Stephanitis fasciicarina*” by Takara and Hidaka (1960).

**Diagnosis.** *Stephanitis* (*Norba*) *mendica* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown (Figs 8B, 10B, 12B, 14B, 16B, 18B, 20A, 22A, 24A); calli light brown; body in male 2.2 times (in female 2.0 times) as long as maximum width across hemelytra (Figs 3B, 5B); rostrum reaching metasternum; pronotum unicarinate or tricarinate (Fig. 26A, B); hood pale, shorter than median carina of pronotum, wider than vertex at widest part, incompletely covering eye, higher than median carina of pronotum at highest part, with posterior margin extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc opaque; paranotum more erect, not narrowed





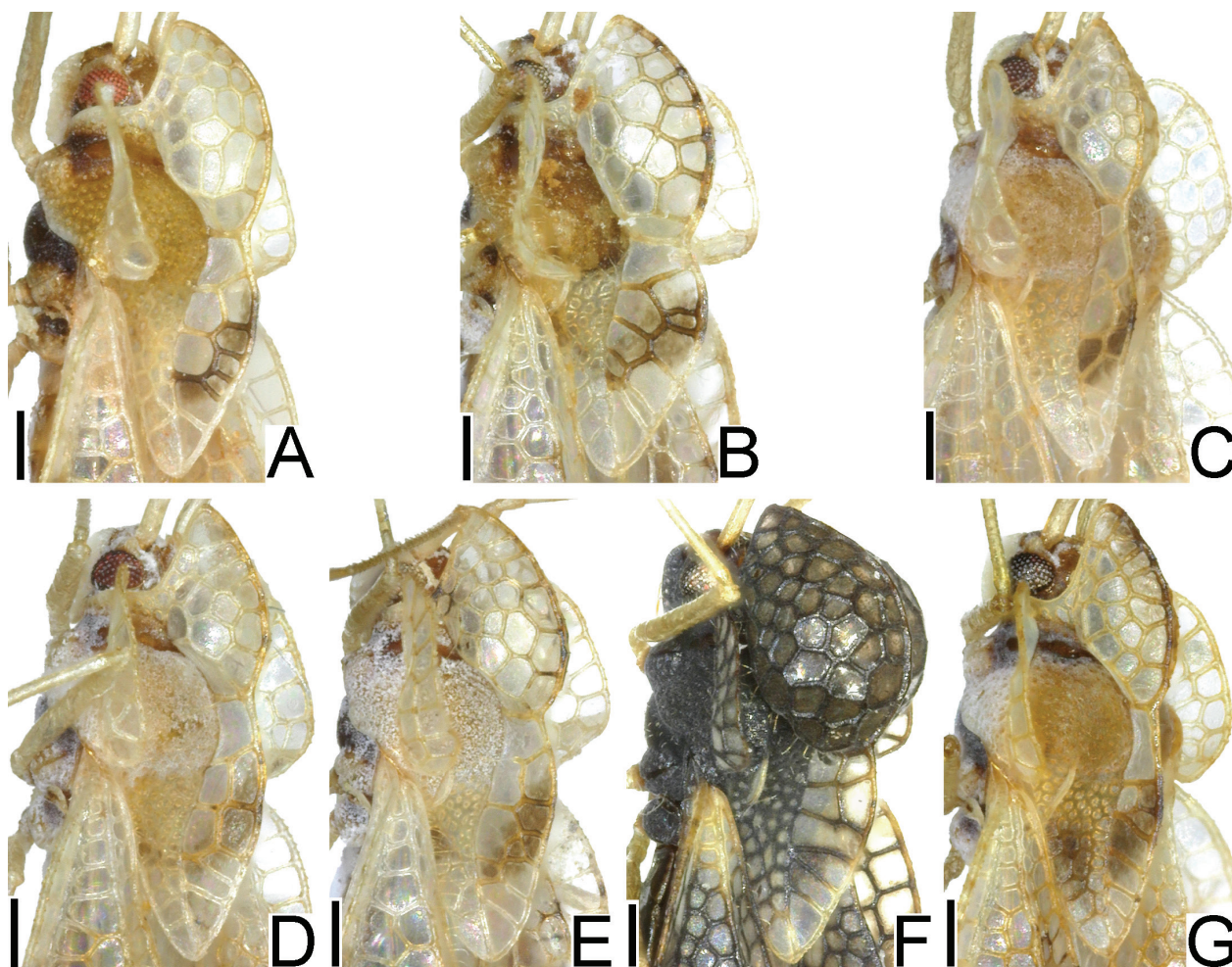
**Figure 13.** Female pronota of five *Stephanitis* species from Japan, dorsolateral view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E, F.** *S. (N.) hiurai* from Amami-Oshima (**E**) and Kikai (**F**) Islands, central part of Ryukyu Islands. Scale bars: 0.2 mm.

posteriorly, with 3 rows of areolae at widest part, with anterolateral angle protruding anteriad, with outer margin angularly curved inwards at posterolateral angle, maximum height longer than height of eye (Fig. 28C); apices of hemelytra close to each other in rest; costal area with 3–4 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 2–3 rows) of areolae at widest part; discoidal area with 3 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypostostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein not carinate; pygophore

elevated at centre of venter, with posterior margin slightly emarginate in middle part (Fig. 30D); and paramere stout, weakly curved inwards at apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 32D).

**Remarks.** Amongst the Japanese species of *Stephanitis*, *S. (Norba) mendica* is similar to *S. (N.) hiurai* in general habitus, but it is easily distinguished by the following characters: hood slightly higher than median carina of pronotum at highest part (as high as in *S. (N.) hiurai*), with posterior margin extending middle





**Figure 14.** Female pronota of five *Stephanitis* species from Japan, dorsolateral view: **A.** *S. (Norba) ishikawai* sp. nov.; **B.** *S. (N.) mendica* possessing lateral carina; **C–E.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**E**) possessing lateral carina and from Honshu (**D**) lacking lateral carina; **F.** *S. (S.) takeyai*; **G.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

of pronotal disc (not extending in *S. (N.) hiurai*) (Figs 7E, F, 8B, 9E, F, 10B, 11E, F, 12B, 13E, F, 14B, 25E, 26B); pronotal disc opaque (lustrous in *S. (N.) hiurai*); paranotum more erect (less erect in *S. (N.) hiurai*), not narrowed posteriorly (narrowed in *S. (N.) hiurai*), with outer margin angularly curved inwards at posterolateral angle (gently curved in *S. (N.) hiurai*); and R+M (radiomedial) vein in female carinate (not carinate in *S. (N.) hiurai*) (Figs 17E, F, 18B). The place name of one of the type localities “Sakuna” was considered to be a misspelling of “Satsuma” by Takeya (1931). However, both place names were listed together in the original description and the former is the name of an actual place in Honshu. The present author confirms the occurrence of *S. (N.) mendica* in “Yamogi”, adjacent to “Sakuna” (see material examined). Therefore, “Sakuna” seems to indeed correspond to one of the type localities of *S. (N.) mendica*.

**Distribution.** Japan (Honshu; Jogashima Island; Shikoku; Kyushu; Nokonoshima Island; Ryukyu Islands (northern and central parts): Yakushima Island, Amami-Oshima Island, Okinawa Island) (Fig. 47) (Horváth 1912; Takeya 1931, 1963; Yamada and Tomokuni 2012;

Yamada and Ishikawa 2016; present study). Judging from the description and illustration provided by Jing (1981), Chinese individuals identified as *Stephanitis (Norba) mendica* differ from Japanese specimens in the structure of the pronotum, suggesting that they pertain to another species. *Stephanitis (N.) mendica* inhabits the laurilignosa in a temperate climate of Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands, which are in the Palearctic Region.

**Host plants.** *Cinnamomum yabunikkei* H. Ohba, “Yabunikkei” (Lauraceae) (Fig. 44A) (Takeya 1931, 1963; Yamada and Tomokuni 2012; Okochi 2019; Souma 2021d; present study). *Stephanitis (Norba) mendica* feeds only on this lauraceous tree and is monophagous.

**Biology.** *Stephanitis (Norba) mendica* feeds on the abaxial surface of leaves of *Cinnamomum yabunikkei* (present study). This lace bug occurs only around “Tsuyu” (rainy season in Japan) (present study) and seems to be univoltine; adults were collected from April to August (Yamada and Tomokuni 2012; Okochi 2019; Souma 2021d; present study); nymphs were collected in May and June (present study); the overwintering stage is unknown.

***Stephanitis (Stephanitis) tabidula* Horváth, 1912**

[Japanese name: Kusu-gunbai]

Figs 3C, D, 5C, D, 8C, D, 10C–E, 12C, D, 14C–E, 16C, D, 18C, D, 20B, 22B, 24B, 26C, D, 28D, 30E, F, 32E, F, 37A, 38, 42C–G

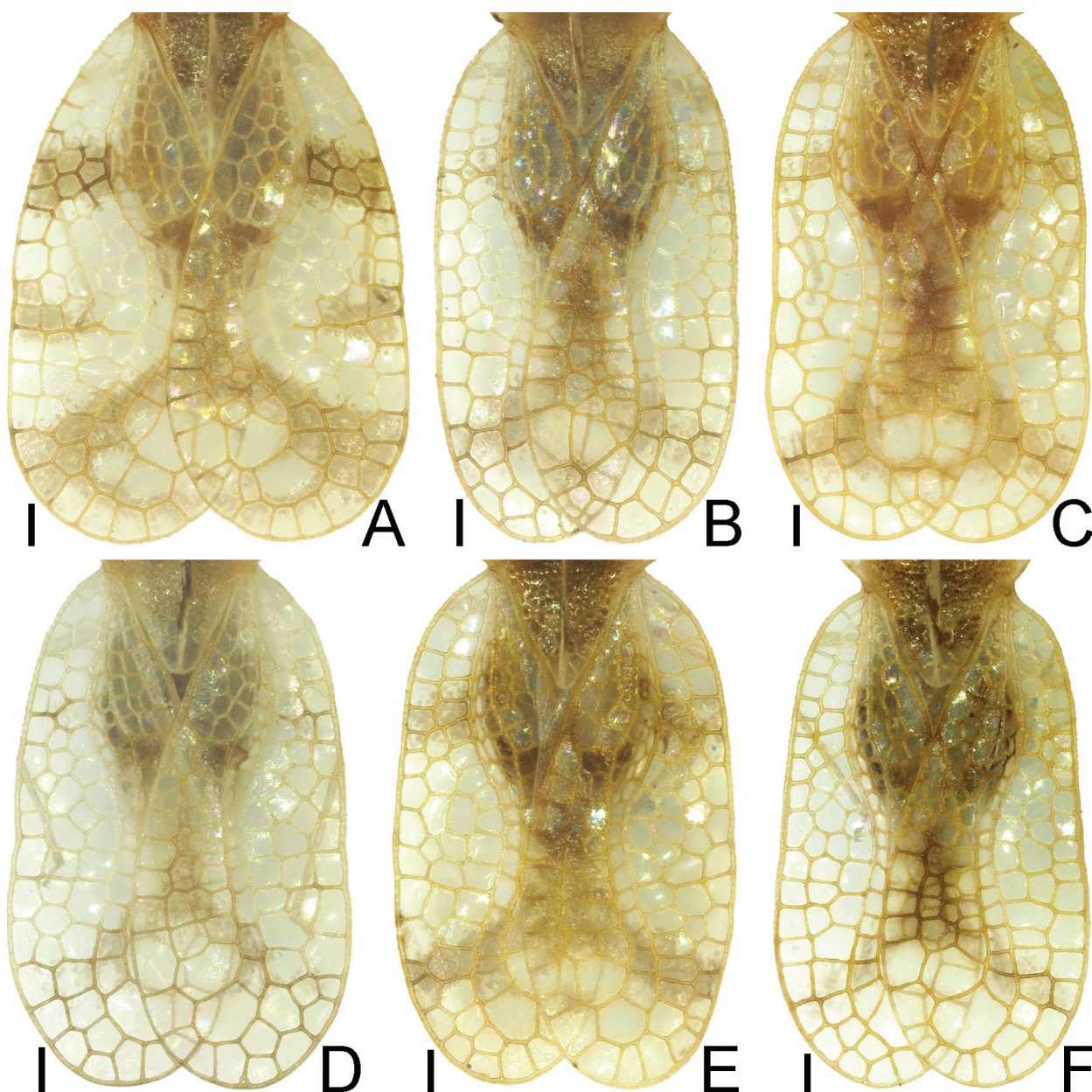
*Stephanitis (Stephanitis) tabidula* Horváth, 1912: 333. Syntype(s): Japan: Kanagawa [Honshu, Kanagawa-ken (a prefecture) or Kanagawa-ku (a ward) of Yokohama-shi (a city) of Kanagawa-ken]; HNHN.*Stephanitis (Stephanitis) fasciicarina* Takeya, 1931: 70. Holotype, ♂: Japan: Kyushu, Chikuzen, Akama [= Kyushu, Fukuoka-ken, Munakata-shi, Akama]; ELKU (not found, mislabeling of paratype collected at type locality?). New subjective synonym.*Stephanitis kyushuana* Drake, 1948: 52. Holotype, ♂: Japan: Kyushu, Moje [= Kyushu, Fukuoka-ken, Kitakyushu-shi, Moji-ku]; USNM. Synonymised with *Stephanitis (Stephanitis) fasciicarina* Takeya, 1931 by Takeya (1951b: 11).

**References.** Drake and Poor (1937: 403) (distribution); Drake (1948: 56) (checklist: *Stephanitis*); Takeya (1951b: 12) (checklist: Japan); Drake and Maa (1953: 101) (checklist: *Stephanitis*); Takara and Hidaka (1960: 188) (distribution); Takeya (1963: 42) (distribution: part); Miyamoto (1964a: 275) (checklist: Ryukyu Islands); Drake and Ruhoff (1965: 363) (catalog); Miyamoto (1965: 91) (monograph); Lee (1969: 215) (nymph, male genitalia); Miyamoto (1976: 497) (distribution); Japanese Society of Applied Entomology and Zoology (1980: 194) (pest); Jing (1981: 353) (monograph); Tomokuni (1981: 109) (distribution); Tomokuni (1985: 156) (distribution); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Yasunaga et al. (1993: 178) (monograph); Péricart and Golub (1996: 63) (catalogue: Palaearctic); Japanese Society of Applied Entomology and Zoology (2006: 250) (pest); Tomokuni and Hayashi (2006: 293) (distribution); Miyamoto (2008: 157) (monograph); Yamada and Tomokuni (2012: 208) (monograph: part); Yano et al. (2013: 25) (distribution); Maehara (2014: 60) (distribution); Yamada and Ishikawa (2016: 434) (checklist: Japan); Ahn et al. (2018: 65) (distribution); Okochi (2019: 3) (distribution); Cho et al. (2020: 742) (distribution); Souma (2021b: 31) (distribution).

**Material examined. Non-types collected at type locality of *S. (S.) tabidula* Horváth, 1912** (77 ♂♂ 69 ♀♀ 8 nymphs), JAPAN: HONSHU: Kanagawa-ken, Sagami-hara-shi, Chuo-ku, Tanashioda (approximate coordinates: 35°32'03.6"N, 139°20'57.7"E), 19.v.2019, leg. J. Souma (43 ♂♂ 22 ♀♀ 8 nymphs, TUA); as above but 25.v.2019 (4 ♂♂, ELKU; 22 ♂♂ 31 ♀♀, TUA); as above but 25.ii.2020, leg. J. Souma (1 ♂ 12 ♀♀, TUA); as above but 17.xi.2021 (3 ♂♂ 3 ♀♀, TUA); “Mt. Ohokusu” [= Kanagawa-ken, Yokosuka-shi, Ashina, Mt. Ogusu (approximate coordinates: 35°15'00.8"N, 139°37'40.6"E)], 7.viii.1973, leg. K. B. S. (1 ♂, KPMNH); “三崎” [= Kanagawa-ken, Miura-shi, Misaki (approximate coordinates: 35°08'31.5"N, 139°36'55.1"E)], “21–18/4/1911” [= 18–21.iv.1911], “Matsumura” (collected by Shonen Matsumura and/or deposited in Matsumura’s collection) (1 ♂ 1 ♀, ELHU) (Fig. 38); Kanagawa-ken, Oiso-machi, Terasaka, Nagayama, 9.vi.1991, leg. M. Enju (1 ♂, TUA);

Kanagawa Pref., Ashigarashimo-gun, Manazuru-hantou, 11.xi.2000, leg. S. Nagashima (1 ♂, TUA). The type locality of *Stephanitis (Stephanitis) tabidula* is “Kanagawa” [= Honshu, Kanagawa-ken (a prefecture) or Kanagawa-ku (a ward) of Yokohama-shi (a city) of Kanagawa-ken] and the 146 adult individuals recorded above match the original description of the species (Horváth 1912). The author identified *S. (S.) tabidula* based on the 146 adults in the present study. **Paratypes of *S. (S.) fasciicarina* Takeya, 1931 collected at type locality** (40 ♂♂ 45 ♀♀, ELKU; 1 ♀, KUM) (Fig. 37A), JAPAN: KYUSHU: “Chikuzen Akama” [= Fukuoka-ken, Munakata-shi, Akama (approximate coordinates: 33°48'26.1"N, 130°35'31.2"E)], 31.v.1931, leg. C. Takeya. The male holotype of *S. (S.) fasciicarina* is currently missing (Souma 2021b). However, the labels shown in Fig. 37A were created after the original description (T. Mita, pers. comm. 2021). As mentioned in the section below, some of the non-types were labelled as “paratype”. Therefore, since labelling errors are suspected to have occurred for some of the type specimens, one of the 40 male paratypes collected at the type locality recorded above may correspond to the holotype. **Paratypes of *S. (S.) fasciicarina*** (59 ♂♂ 46 ♀♀, ELKU), JAPAN: HONSHU: “Nagato Shimonoseki” [= Yamaguchi-ken, Shimonoseki-shi (approximate coordinates: 33°57'09.1"N, 130°55'16.8"E)], 22.viii.1930, leg. K. Yasumatsu (8 ♂♂ 5 ♀♀), KYUSHU: “Fukuoka” [= Fukuoka-ken (a prefecture) or Fukuoka-shi (a city) of Fukuoka-ken (approximate coordinates: 33°35'06.7"N, 130°22'43.4"E)], 14.v.1930, leg. C. Takeya (7 ♂♂ 1 ♀♀); as above but 21.v.1930 (6 ♂♂ 7 ♀♀); as above, but 22.v.1930 (21 ♂♂ 14 ♀♀); as above, but 30.vi.1930 (1 ♂ 1 ♀); as above but 7.vii.1930 (16 ♂♂ 18 ♀♀). Although the labels of the 105 specimens were created after (T. Mita, pers. comm. 2021), their locality data match that of the original description of *S. (S.) fasciicarina* (Takeya 1931). **Non-types collected at type locality of *S. (S.) fasciicarina*** (4 ♀♀, TUA), JAPAN: KYUSHU: Fukuoka-ken, Munakata-shi, Akama (approximate coordinates: 33°48'26.1"N, 130°35'31.2"E), 26.ix.2021, leg. J. Souma. **Non-types collected at type locality of *S. (S.) kyushuana* Drake, 1948** (1 ♀, TUA), JAPAN: KYUSHU: Fukuoka-ken, Kitakyushu-shi, Moji-ku, Motokiyotaki (approximate coordinates: 33°56'18.9"N, 130°57'42.7"E), 16.ix.2022, leg. J. Souma. **Non-types** (518 ♂♂ 653 ♀♀ 60 nymphs), JAPAN: HONSHU: Miyagi-ken, Oshika-gun, Onagawa-cho, Kirigasaki, 20.ix.2020, leg. H. Konno (2 ♂♂ 3 ♀♀, TUA); Miyagi-ken, Miyagi-gun, Rifu-cho, Akanuma, Tanbazawa, 22.ix.2020, leg. H. Konno (1 ♀, TUA); Ibaraki, Choshi, 15.vi.1981, leg. M. Miyazaki (13 ♂♂ 24 ♀♀ 1 nymph, NIAES); Tochigi Pref., Uchino, Watarase-yusuichi, 29.v.2001, leg. S. Maehara (2 ♂♂ 1 ♀, TUA); as above but 5.xi.2012 (1 ♂, TUA); Tochigi, Simotsuke City, Motoyoshida, 12.x.2013, leg. S. Maehara (2 ♀♀, TUA); as above, but 28.xi.2016 (1 ♂ 2 ♀♀); as above but 12.xi.2019 (1 ♂ 2 ♀♀, TUA); as above, but 15.x.2020 (4 ♂♂ 1 ♀, TUA); Saitama Pref., Nihongi Pass, 3.vii.1984, leg. M. Hayashi et al. (1 ♂, TUA);



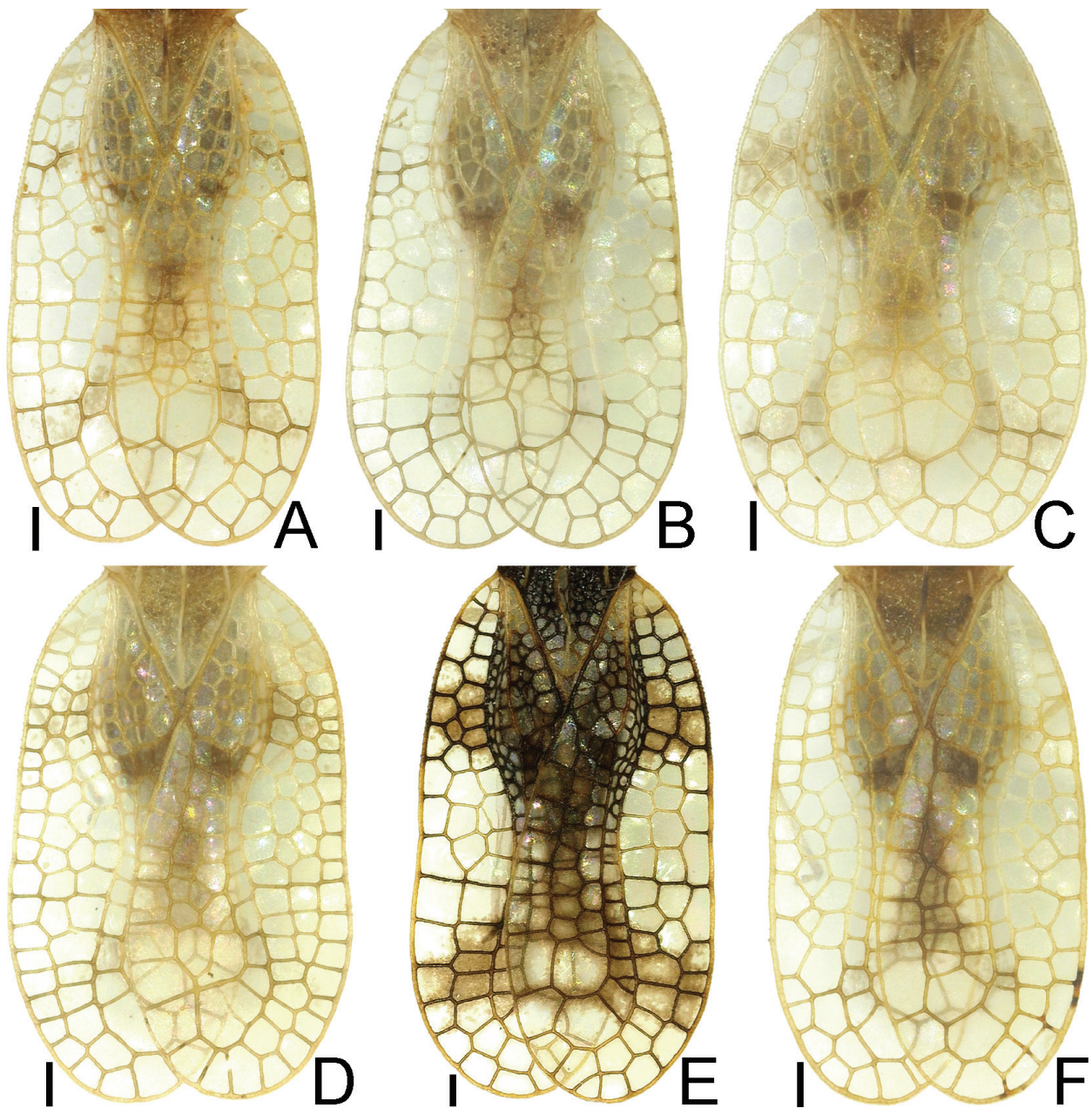


**Figure 15.** Male hemelytra of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E, F.** *S. (N.) hiurai* from Amami-Oshima (**E**) and Kikai (**F**) Islands, central part of Ryukyu Islands. Scale bars: 0.2 mm.

Saitama-ken, Iruma-gun, Moroyama-machi, Takinoiri, Shobo-goya, 28.v.2021, leg. J. Souma (2 ♂♂ 4 ♀♀, TUA); Saitama-ken, Iruma-gun, Moroyama-machi, Takinoiri, Kanikusa-hashii, 28.v.2021, leg. J. Souma (8 ♂♂ 9 ♀♀, TUA); Tokyo, 22.viii.1949, leg. R. Takahashi (1 ♂ 1 ♀, ELKU); Chiba, Tateyama, Susaki, 11.x.2001, leg. M. Tomokuni (5 ♂♂ 5 ♀♀, NSMT); Tokyo, Kiyosumi-koen, 24.vi.1972, leg. H. Hasegawa (11 ♂♂ 22 ♀♀, NIAES); Niigata-ken, Kitakanbara-gu, Seiro-machi, Mano, 14–15.vi.2013, leg. K. Nakano (1 ♂, TUA); Niigata-ken, Murakami-shi, Kashio, 13.vi.2015, leg. K. Nakano (1 ♂ 4 ♀♀, TUA); as above but 1.x.2016, leg. K. Nakano (1 ♂ 4 ♀♀, TUA); Niigata-ken, Niigata-shi, Nishi-ku, Igarashi-2no-cho, 19.vii.2015, leg. K. Nakano (1 ♀, TUA); Niigata-ken, Kariwa-gun, Kariwa-mura, Takiya, 13.

vi.2021, leg. G. Mashima (1 ♂ 1 ♀, TUA); Niigata-ken, Kashiwazaki-shi, Miyagawa, 13.vi.2021, leg. G. Mashima (2 ♂♂, TUA); Ishikawa, Sekidoyama, 2.viii.1960, leg. T. Hidaka (1 ♀, ELKU); Fukui Pref., Otomi, 12.vii.1981, leg. O. Kishimoto (1 ♀, KUM); Fukui Pref., Mt. Aoba, 20.ix.1981, leg. O. Kishimoto (1 ♀, KUM); Mino, Utsumi, 21.x.1952, leg. Yasumatsu (1 ♂ 1 ♀, ELKU); Izu, Kuren, 16.x.1952, leg. Yasumatsu (3 ♀♀, ELKU); Izu, Suzaki, 30.ix.1980, leg. M. Tomokuni (7 ♂♂ 7 ♀♀, NSMT); Izu, Ohno-yama, nr. Ohsawa, 1.x.1980, leg. M. Tomokuni (3 ♀♀, NSMT); Shizuoka-ken, Hamamatsu-shi, Nishi-ku, Kamigaya-cho, 16.vi.2017, leg. J. Souma (1 ♀, TUA); Aichi-ken, Kitashitara-gun, Shitara-cho, Taguchi, 17.vi.2017, leg. J. Souma (1 ♀, TUA); Mie Pref., Oosugidani, 11.viii.1970, leg. M. Tomokuni (1 ♂,



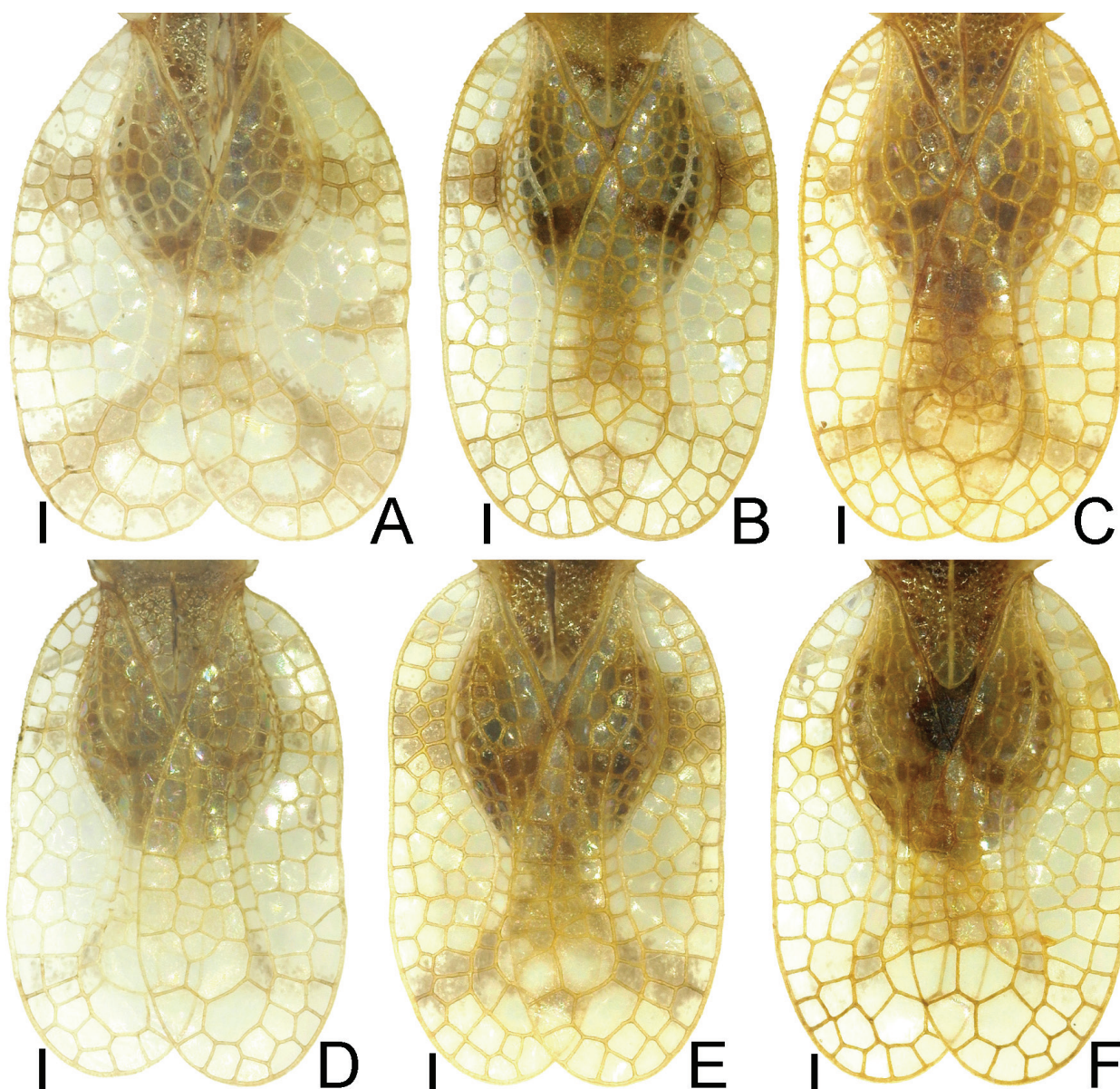


**Figure 16.** Male hemelytra of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) ishikawai* sp. nov.; **B.** *S. (N.) mendica*; **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai*; **F.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

NSMT); Mie Pref., Ise-shi, Shimogu, 1.xi.2000, leg. T. Ishikawa (1 ♀, TUA); Kyoto Pref., Kurama-Kibune, 12.vii.1970, leg. M. Tomokuni (1 ♀, NSMT); Osaka Pref., Higashi-Sumiyoshi, Nagai, 2.vi.1985, leg. T. Kishimoto (1 ♀, TUA); Kobe, 29.v.1941, leg. Kurosa (1 ♂, ELKU); Tajima, Sekinomiya, 8.vii.1952, leg. R. Morimoto (7 ♂♂ 6 ♀♀, ELKU); Hyogo-ken, Kobe-shi, Suma-ku, Higashisuma, 8.x.2022, leg. J. Souma (3 ♂♂ 3 ♀♀, TUA); Yamato, Nara, 14.x.1951, leg. C. Takeya (3 ♂♂ 3 ♀♀, ELKU); as above but 16.x.1951 (23 ♂♂ 30 ♀♀, ELKU; 1 ♂ 1 ♀, KUM); Prov. Kii, Wakayama, 15.x.1951, leg. S. Goto (2 ♀♀, ELKU); Wakayama, Nachi-Irokawa, 2.ix.1998, leg. leg. S. Gotoh (1 ♂, NSMT); Okayama-ken, Okayama-shi, Kita-ku, Heidan, 20.v.2022, leg. J. Souma (1 ♀, TUA); Yamaguchi-ken, Yamagu-

chi-shi, Atou, Shinome, 25.x.2008, leg. M. Hayashi (1 ♀, TUA); Yamaguchi-ken, Shimonoseki-shi, Hon-machi, 24.ix.2022, leg. J. Souma (6 ♂♂ 3 ♀♀, TUA). TASHIRO ISLAND: Shikishima, near Manga Island, 10.xi.2019, leg. H. Konno (1 ♂ 1 ♀, TUA). SADO ISLAND: Kitaikari, 26.viii.2021, leg. J. Souma (2 ♂♂ 1 ♀, TUA); Kubota, 27.viii.2021, leg. J. Souma (2 ♀♀, TUA); Ishida, 27.viii.2021, leg. J. Souma (2 ♂♂ 8 ♀♀, TUA); Anyoji, 28.viii.2021, leg. J. Souma (1 ♀, TUA); Kujikawachi, 29.viii.2021, leg. J. Souma (1 ♀, TUA); Kawasaki, 29.viii.2021, leg. J. Souma (3 ♂♂ 4 ♀♀, TUA). AWA ISLAND: Uramura, Uchiura, 3.x.2021, leg. J. Souma (9 ♂♂ 7 ♀♀, TUA). IZU ISLANDS (northern part): Izu-Oshima Island: Kasamatsu, 4.x.2002, leg. M. Tomokuni (1 ♂♂ 2 ♀♀, NSMT). AWAJI ISLAND: Fukura, 29.ix.1972, leg. M.



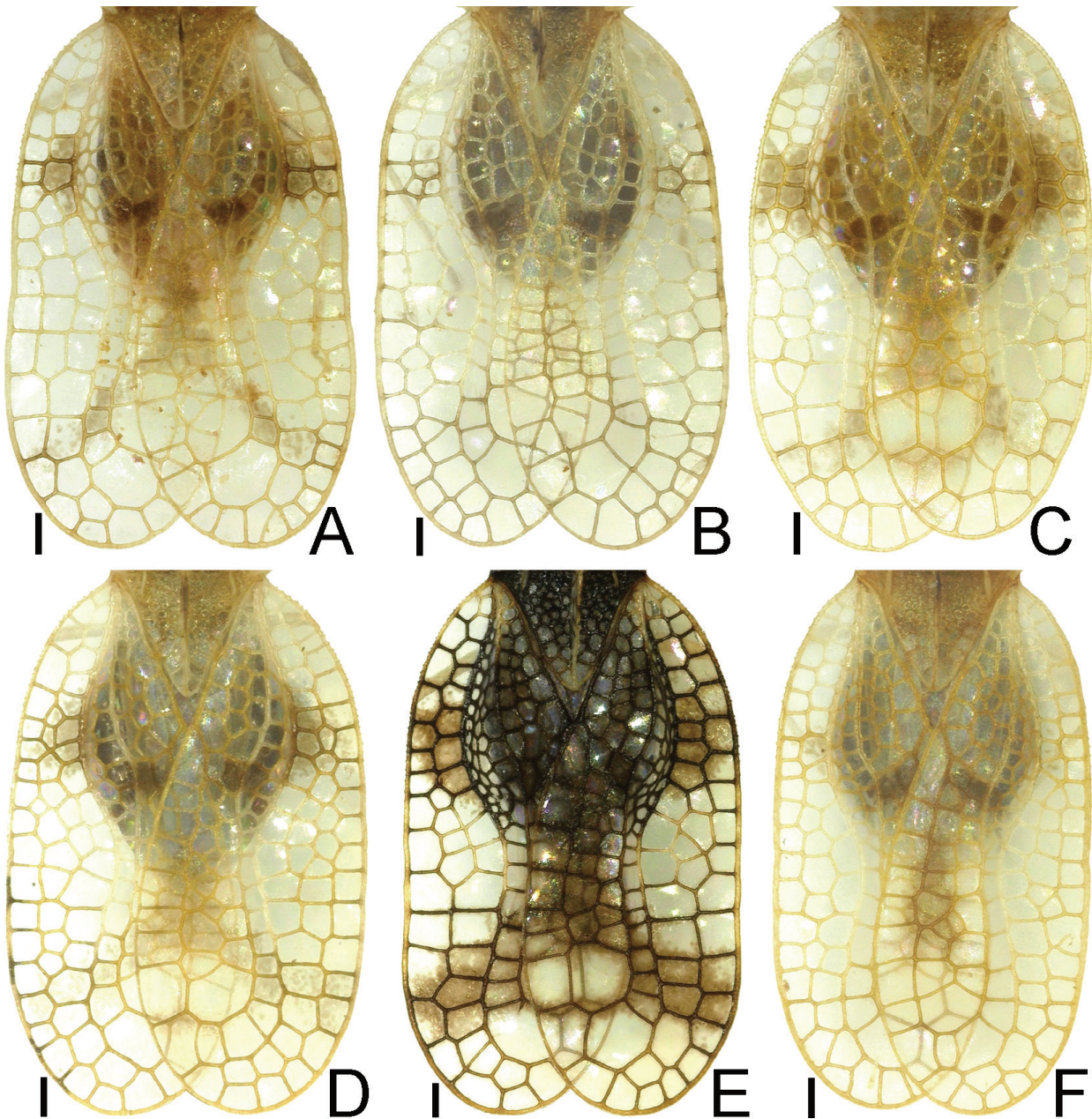


**Figure 17.** Female hemelytra of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E, F.** *S. (N.) hiurai* from Amami-Oshima (**E**) and Kikai (**F**) Islands, central part of Ryukyu Islands. Scale bars: 0.2 mm.

Tomokuni & M. Sakai (1 ♀, NSMT); Mt. Mikuma, 30. ix.1972, leg. M. Tomokuni & M. Sakai (1 ♀, NSMT). OKI ISLANDS: Dogo Island: Saigo-cho, Mt. Daimanji, 12.ix.1984, leg. M. Tomokuni (3 ♀♀, NSMT). SHIKOKU: Tokushima-ken, Tokushima-shi, Bizan-cho, Mosukegahara, 2.x.2022, leg. J. Souma (1 ♂ 1 ♀, TUA); “Sanuki Wada-mura” [= Kagawa-ken, Kannonji-shi, Toyohama-cho, Wada], 10.vi.1930, leg. M. Hanada (2 ♂ 3 ♀♀, ELKU; 1 ♀, KUM); Tosa, Yamakita-mura, 10.xi.1951, leg. K. Yasumatsu (3 ♂♂ 2 ♀, ELKU); Ehime P., Matsuyama C., 25.x.1972, leg. H. Hasegawa (11 ♂♂ 7 ♀♀ 4 nymphs, NIAES). KYUSHU: as paratype collected at type locality (1 nymph, ELKU); Fukuoka, Hirao, 22.x.1931, leg. Fujino & Hashimoto (1 ♀, ELKU); as above but 16.x.1932, leg. T. Shrozu (1 ♂ 1 ♀, ELKU); as above but 3.vi.1951, leg. Matsuda (1 ♀, ELKU); as above but 21.

vi.1957, leg. Y. Miyatake (1 ♀, KUM); Chikuzen, Inunakiyama, 25.x.1931, leg. K. Yasumatsu (1 ♀, KUM); as above, but 15.vi.1969, leg. S. Miyamoto (1 ♀, KUM); Chikuzen, Tsutsugatake, 6.xii.1931, leg. C. Takeya (1 ♂ 14 ♀♀, ELKU); Tikuzen, Kyûdai-Kasuya-Ensyûrin, 20–22.vi.1944, leg. S. Ito (1 ♀, ELKU); Buzen, Hikosan, 12.vii.1948, leg. S. Miyamoto (1 ♀, KUM); as above, but 5.viii.1951, leg. C. Takeya (5 ♂♂ 9 ♀♀, ELKU); as above, but 6.viii.1951, leg. C. Takeya (8 ♂♂ 15 ♀♀, ELKU); as above but 15.vii.1958, leg. Y. Miyatake (2 ♂♂ 1 ♀, KUM); as above, but 6.vi.1959, leg. Y. Miyatake (1 ♂, KUM); as above but 7.vi.1959, leg. Y. Miyatake (1 ♀, KUM); as above, but 14.vi.1959 (3 ♀♀, KUM); as above, but 14.vi.1959, leg. K. Yasumatsu (1 ♀, ELKU); Chikugo, Korasan, 25.vii.1951, leg. C. Takeya (3 ♂♂ 3 ♀♀, ELKU); as above, but 7.viii.1951, leg. S. Miyamoto (1 ♂



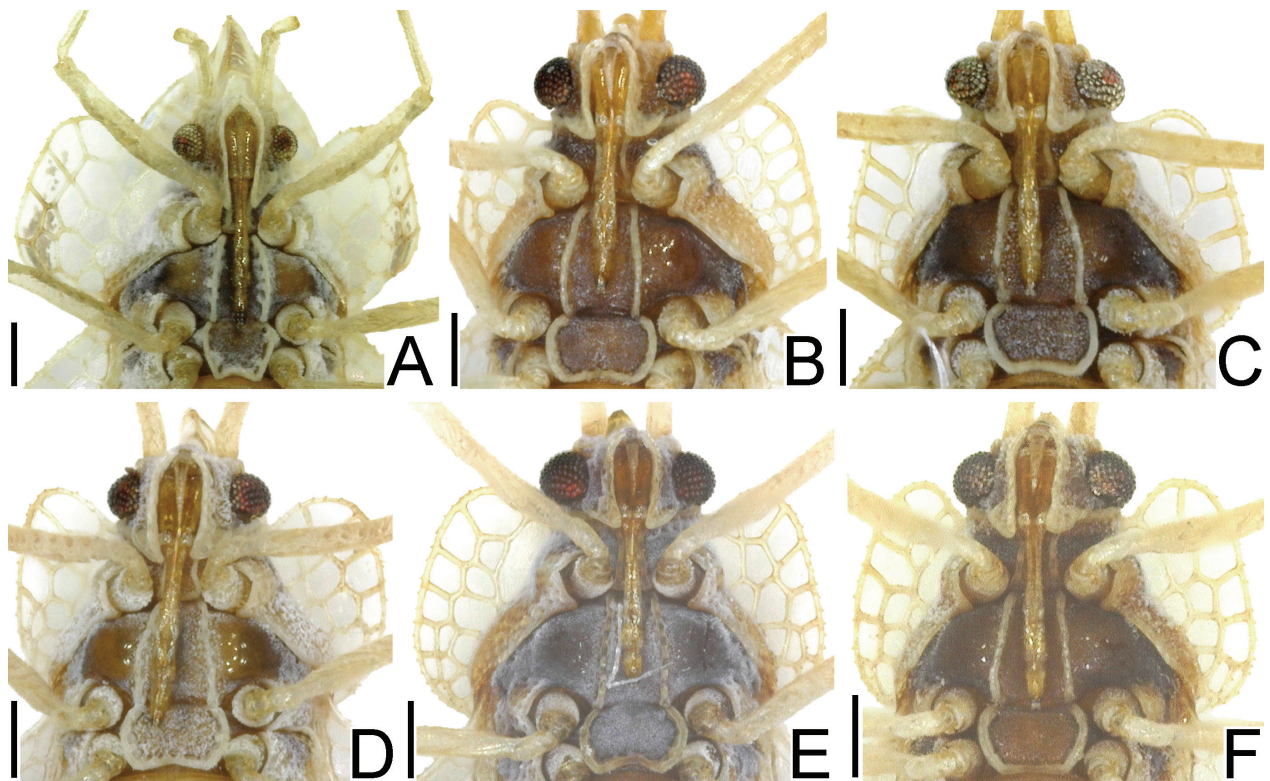


**Figure 18.** Female hemelytra of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) ishikawai* sp. nov.; **B.** *S. (N.) mendica*; **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai*; **F.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

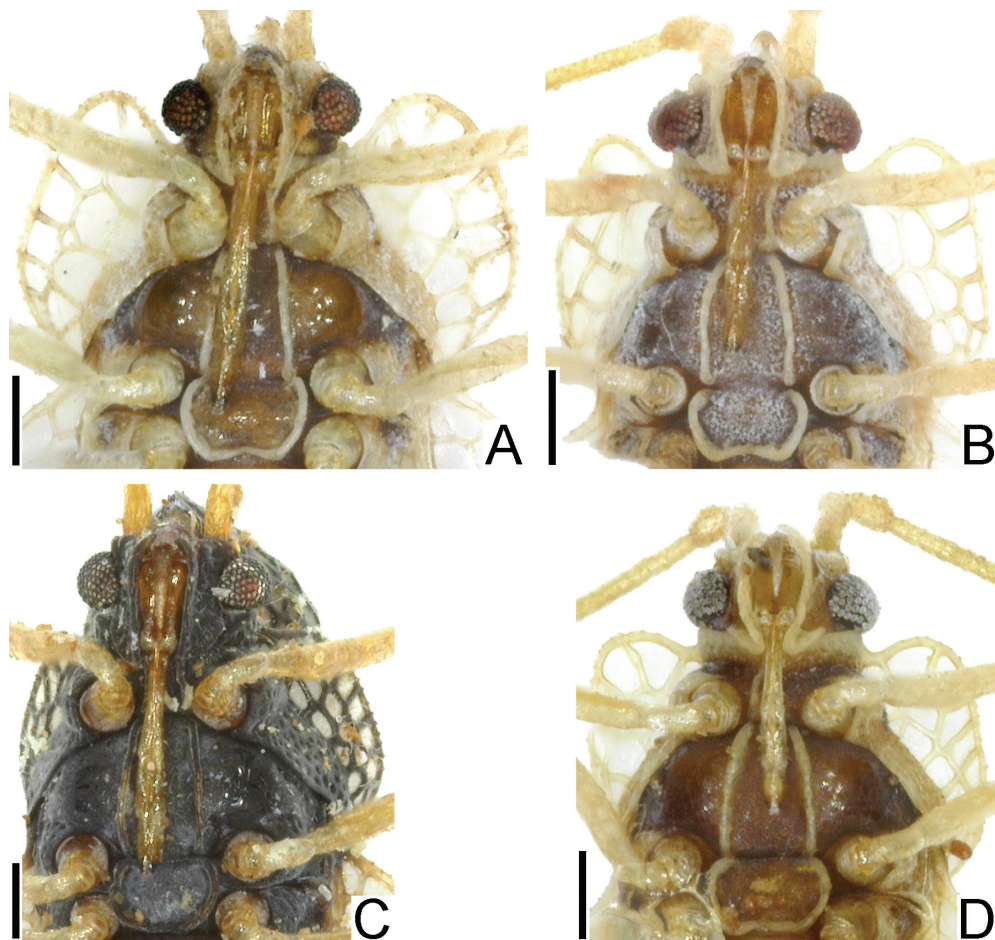
1 ♀, ELKU); as above, but 1.ix.1951, leg. C. Takeya (1 ♂ 3 ♀♀, ELKU); as above but 26.v.1953 (4 ♂♂ 5 ♀♀, ELKU); Fukuoka, Fukuoka, Korasan, 25.vii.1951, leg. S. Miyamoto (1 ♂ 3 ♀♀, KUM); as above but 7.viii.1951 (2 ♀♀, KUM); as above, but 11.vi.1961 (3 ♀, KUM); Chikuzen, Fukuoka, 27.vii.1951, leg. C. Takeya (6 ♂♂ 7 ♀♀, ELKU); Chikuzen, Narutake-yama, 19.viii.1951, leg. Y. Hirashima (1 ♀, ELKU); as above but 8.vi.1961, leg. C. Takeya (1 ♀, ELKU); Fukuoka, Mt. Kumado, 23.viii.1952, leg. S. Miyamoto (4 ♂♂ 3 ♀♀, ELKU; 9 ♂♂ 6 ♀♀ 5 nymphs, KUM); Aburayama, 28.viii.1952, leg. C. Takeya (1 ♀, ELKU); as above, but 5.v.1961, leg. S. Miyamoto (5 ♂♂ 9 ♀♀ 17 nymphs, KUM); as above, but 11.v.1961, leg. S. Miyamoto (16 ♂♂ 11 ♀♀, KUM); as above, but 4.vi.1961, leg. S. Miyamoto (1 ♀, KUM);

Fukuoka, Magarifuchi, 23.ix.1952, leg. C. Takeya (6 ♂♂ 4 ♀♀, ELKU); as above, but 16.vii.1961, leg. S. Miyamoto (3 ♂♂ 4 ♀♀, KUM); Chikuzen, Mt. Kosho, 14.vi.1953, leg. C. Takeya (1 ♀, ELKU); Chikugo, Himeharu, 3.vi.1954, leg. Gyotoku (3 ♂♂ 3 ♀♀, ELKU); Fukuoka, Sasayama, ix.1954, leg. S. Miyamoto (1 ♂ 2 ♀♀, KUM); Fukuoka, Gokoku Shrine, 5.ix.1959, leg. S. Miyamoto (39 ♂♂ 36 ♀♀, KUM); as above, but 24.vii.1961 (9 ♂♂ 8 ♀♀, KUM); Fukuoka, Kashii, 6.ix.1959, leg. S. Miyamoto (1 ♀, KUM); as above, but 2.xi.1961 (1 ♂, KUM); Fukuoka, Nogochi, 16.vi.1961, leg. S. Miyamoto (13 ♂♂ 9 ♀♀ 3 nymphs, KUM); Fukuoka, Tachibanayama, 23.vii.1961, leg. S. Miyamoto (2 ♂♂ 7 ♀♀, KUM); Fukuoka, 24.vii.1961, leg. S. Miyamoto (2 ♂♂ 6 ♀♀, KUM); Fukuoka, Atagoyama, 4.viii.1961, leg. S.



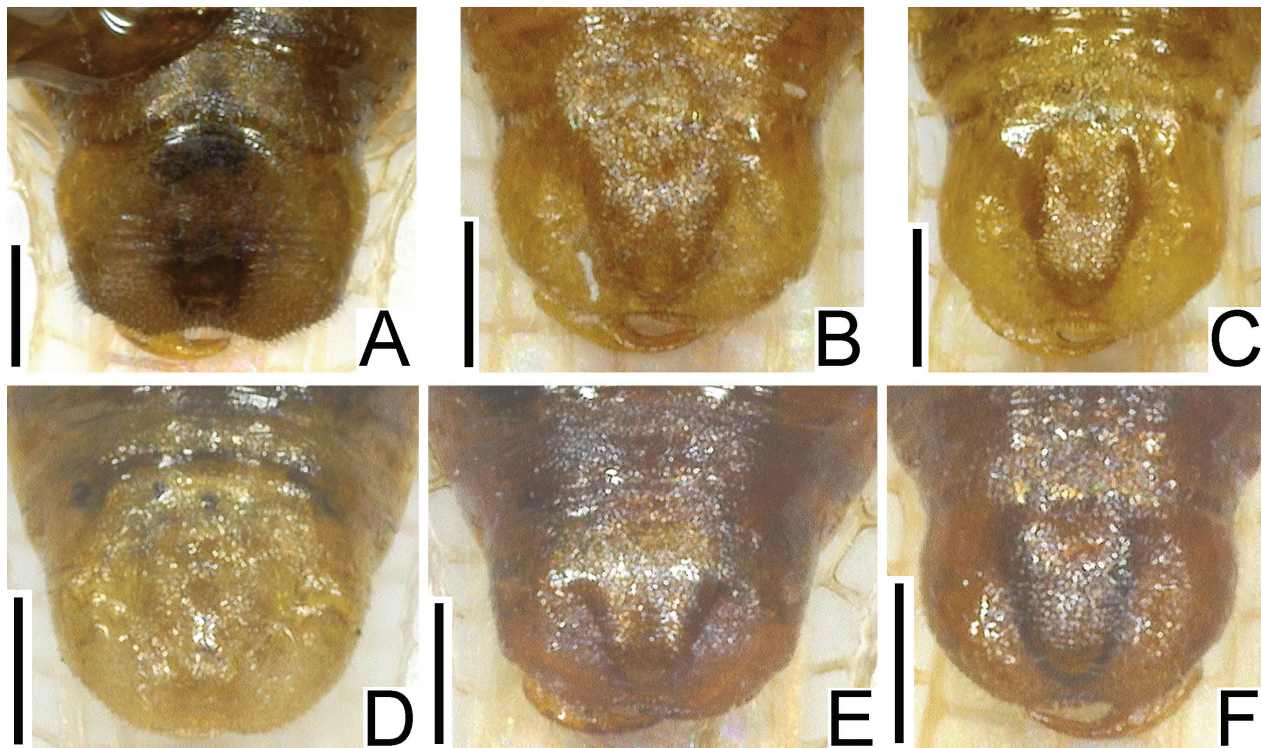


**Figure 19.** Rostra of six *Stephanitis* species from Japan, dorsal view: A. *S. (Stephanitis) ambigua*; B. *S. (Norba) aperta*; C. *S. (N.) exigua*; D. *S. (N.) hayashii* sp. nov.; E. *S. (N.) hiurai*; F. *S. (N.) ishikawai* sp. nov. Scale bars: 0.2 mm.

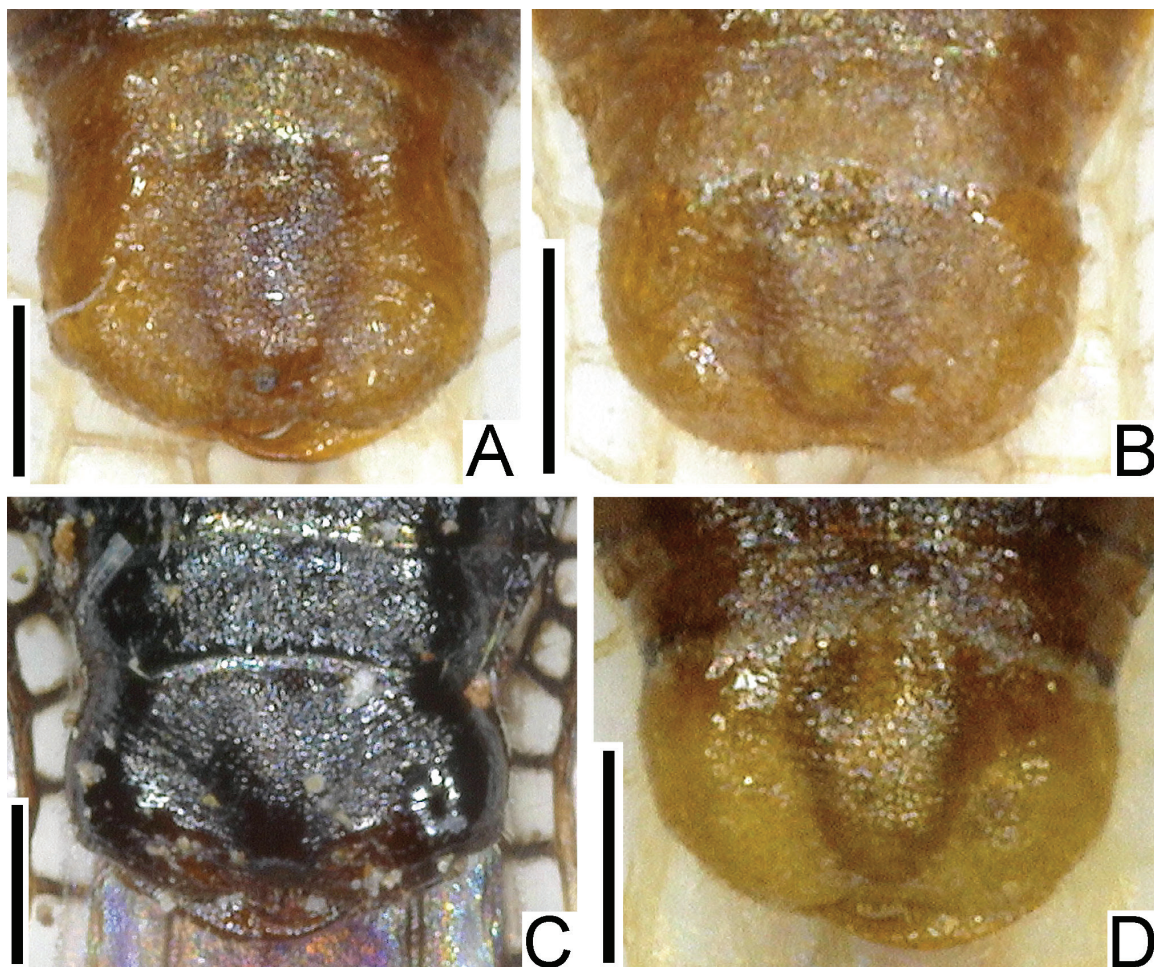


**Figure 20.** Rostra of four *Stephanitis* species from Japan, dorsal view: A. *S. (Norba) mendica*; B. *S. (Stephanitis) tabidula*; C. *S. (S.) takeyai*; D. *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.



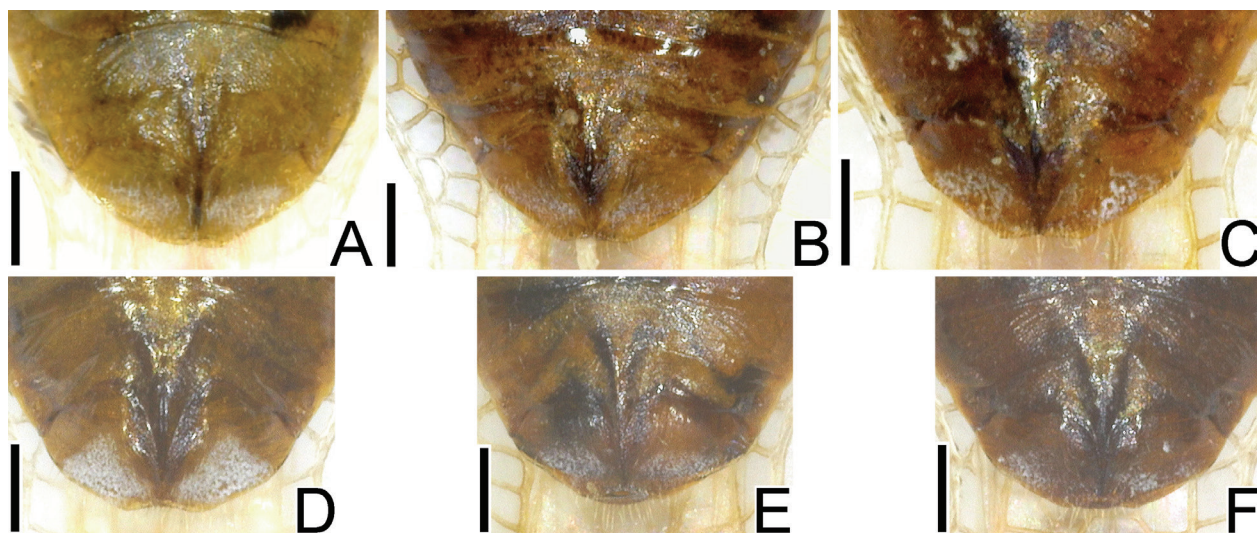


**Figure 21.** Male terminalia of six *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E.** *S. (N.) hiurai*; **F.** *S. (N.) ishikawai* sp. nov. Scale bars: 0.2 mm.

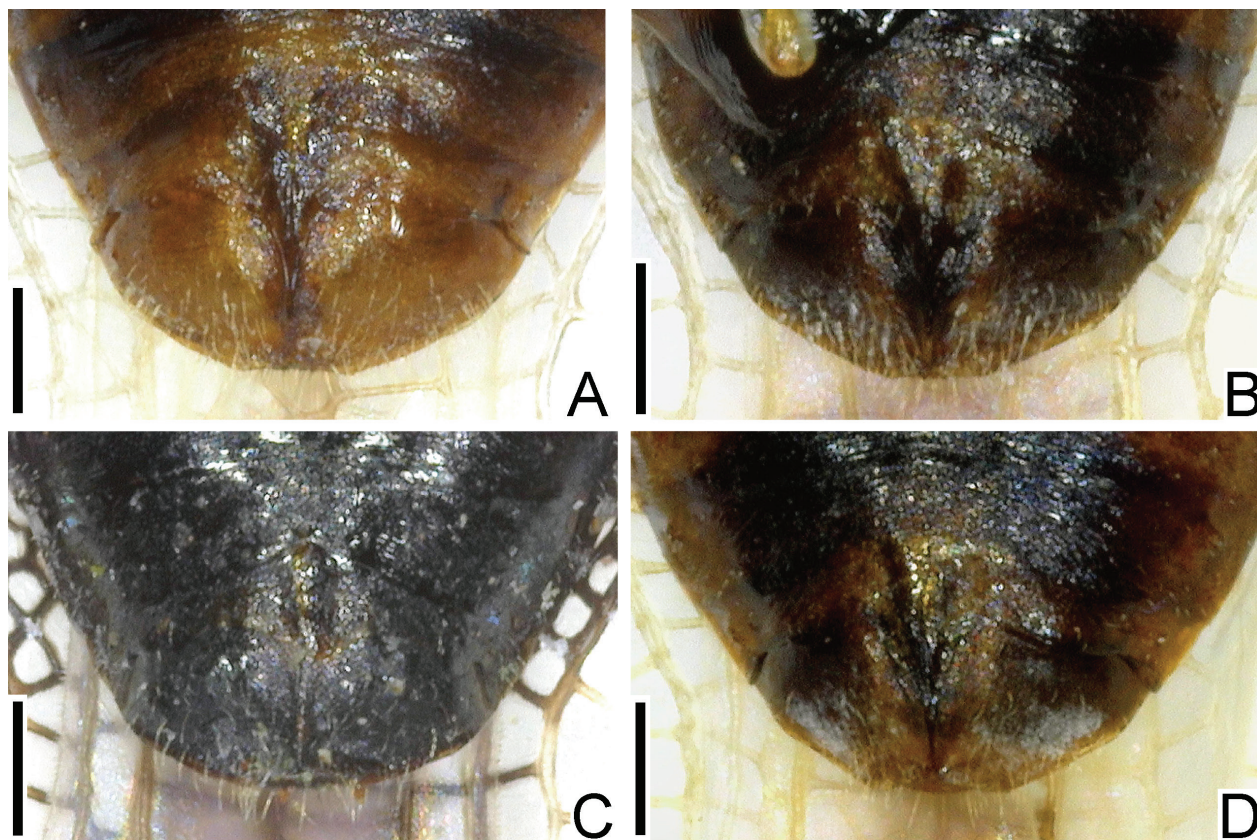


**Figure 22.** Male terminalia of four *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) mendica*; **B.** *S. (Stephanitis) tabidula*; **C.** *S. (S.) takeyai*; **D.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.





**Figure 23.** Female terminalia of six *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E.** *S. (N.) hiurai*; **F.** *S. (N.) ishikawai* sp. nov. Scale bars: 0.2 mm.

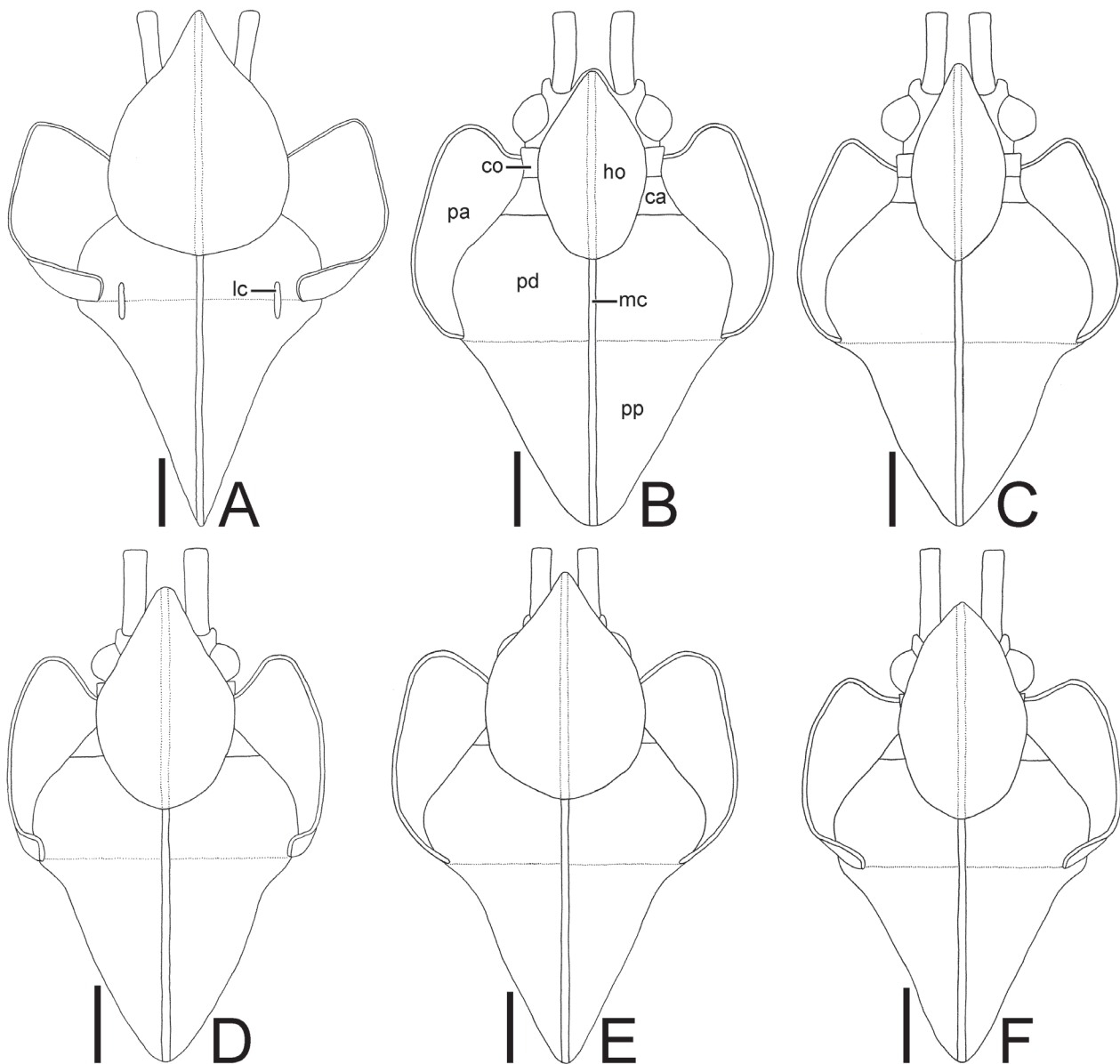


**Figure 24.** Female terminalia of four *Stephanitis* species from Japan, dorsal view: **A.** *S. (Norba) mendica*; **B.** *S. (Stephanitis) tabidula*; **C.** *S. (S.) takeyai*; **D.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

Miyamoto (1 ♂ 1 ♀, KUM); Fukuoka, Hakozaki, Kyushu University, 12.viii.1961, leg. S. Miyamoto (134 ♂♂ 124 ♀♀ 14 nymphs, KUM); Fukuoka, Kanetake, 13.ix.1969, leg. S. Miyamoto (5 ♂♂ 12 nymphs, KUM); Fukuoka, Kamado Shrine, 27.ix.1977, leg. S. Miyamoto (2 ♂♂, KUM); as above, but 5.xi.1977 (1 ♀, KUM); Fukuoka, Tenmangu, 6.x.1977, leg. S. Miyamoto (1 ♀, KUM); Fukuoka-ken, Munakata-shi, Yamada, 28.viii.2017, leg. J. Souma (1 ♀, TUA); Fukuoka-ken, Fukuoka-shi, Nishi-ku,

Motooka, Kyushu University, 23.v.2020, leg. J. Souma (2 ♂♂ 1 ♀, ELKU); as above, but 21.ix.2020 (3 ♂♂ 1 ♀, ELKU); Fukuoka-ken, Fukuoka-shi, Nishi-ku, Kusaba, 24.v.2020, leg. J. Souma (1 ♂, ELKU); Fukuoka-ken, Itoshima-shi, Shimanokita, 24.v.2020, leg. J. Souma (14 ♂♂ 28 ♀♀, ELKU); Fukuoka-ken, Fukuoka-shi, Sawaraku, Itaya, Mt. Sefuri, 30.v.2020, leg. S. Yagi (1 ♀, ELKU); Fukuoka-ken, Dazaifu-shi, Kitadani, Mt. Homan, 4.vi.2020, leg. J. Souma (7 ♂♂ 11 ♀♀, ELKU; 1 ♂ 4 ♀♀,

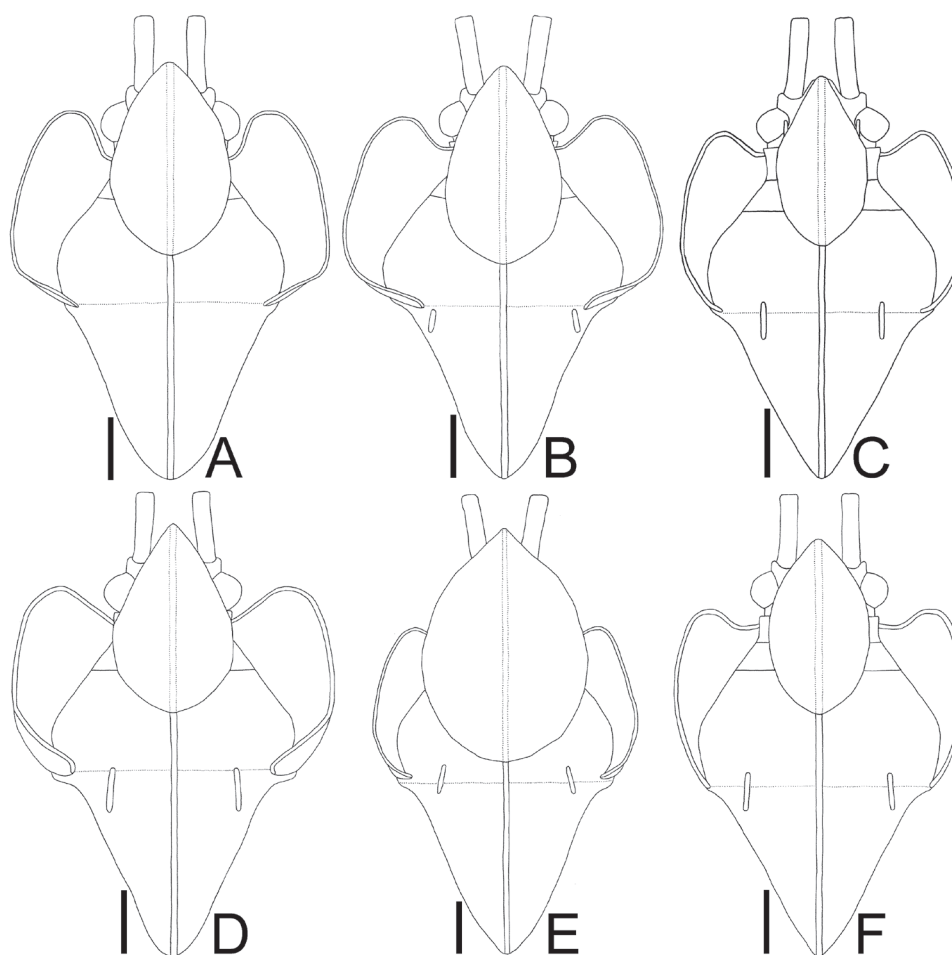




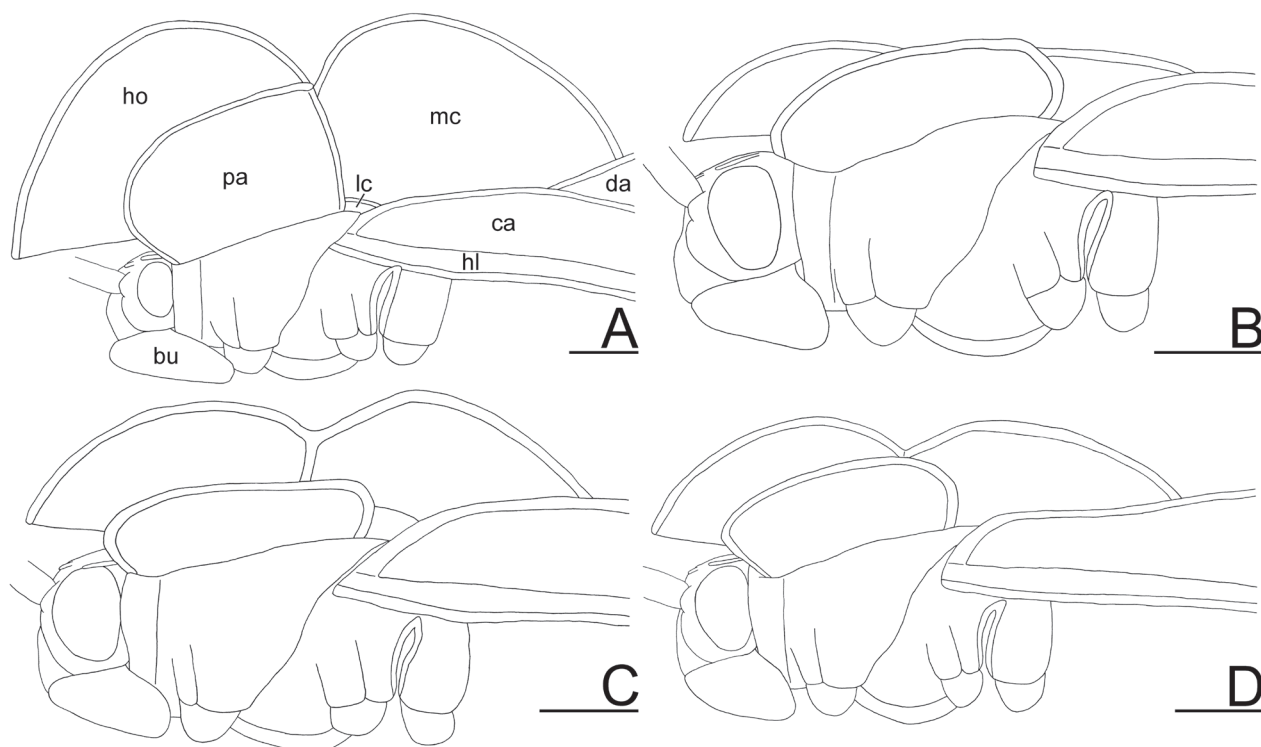
**Figure 25.** Line drawings of the pronota of six *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov.; **E.** *S. (N.) hiurai*; **F.** *S. (N.) ishikawai* sp. nov. Abbreviations: ca, calli; co, collar; ho, hood; lc, lateral carina; mc, median carina; pa, paranotum; pd, pronotal disc; pp, posterior process. Scale bars: 0.2 mm.

TUA); Fukuoka-ken, Kasuya-gun, Sasaguri-machi, Tsubakuro, 5.vi.2020, leg. J. Souma (2 ♂♂ 1 ♀, TUA); Fukuoka-ken, Itoshima-shi, Nijofukui, Nijo Forest Park, 20.vi.2020, leg. S. Chuman (4 ♂♂ 2 ♀♀, TUA); Fukuoka-ken, Tagawa-gun, Soeda-machi, Mt. Hikosan, 21.vi.2020, leg. J. Souma (3 ♀♀, TUA); as above but 20.vi.2020, leg. S. Yagi (1 ♀, ELKU); Fukuoka-ken, Itoshima-shi, Tomari, 29.v.2022, leg. J. Souma (1 ♀, ELKU); as above, but 10.vii.2022, leg. J. Souma (1 ♂, TUA); Saga Pref., Fujitsu-gun, Tara-cho, Oura, Ushioro, alt. 100 m, 12.vii.2021, leg. M. Nishida (1 ♂, ELKU); Hizen, Kunimiyama, 16.vi.1950, leg. T. Shrozu (1 ♂ 2 ♀♀, ELKU); Higo, Yatsushiro, 8.x.1953, leg. C. Takeya (1 ♀, ELKU); Kumamoto, Yuyama, Mt. Ichifusa, 5.viii.1985, leg. M. Miyazaki (3 ♀♀, NIAES); as above, but 6.viii.1985 (2 ♂♂ 4 ♀♀, NIAES); Bungo, Tsukumi, 29.

vii.1951, leg. R. Matsuda (2 ♂♂ 1 ♀, ELKU); Bungo, Hachiya, 11.x.1951, leg. S. Nakao (1 ♀, KUM); Ōita Pref., Saiki-shi, Ume, Minamitabarū, Takadoya-jinja, 26.v.2019, leg. R. Ito (1 ♂, TUA); Ōita Pref., Saeki-shi, Ume, Kitagawa dam, 25–26.v.2019, leg. N. Tsuji & S. Imada (1 ♀, TUA); Hyuga, Takaoka, 25.viii.1952, leg. A. Ema (6 ♂♂ 10 ♀♀, ELKU); Hyuga, Mt. Kirishima, 12.ix.1952, leg. Nakao & Ogata (1 ♂, ELKU); Miyazaki Pref., Hinokage-chō, Mt. Tansuke-dake, 1.vi.2019, leg. R. Ito (1 ♀, TUA); Miyazaki-ken, Higashimorokata-gun, Aya-cho, Takeno, Omoridake For. Rd., 8.x.2021, leg. T. Saeki (1 ♂, ELKU); Kagoshima Pref., Mianmiōsumi-chō, Sata, Hetsuka, 30.v.2020, leg. R. Ito (1 ♀, TUA). NOKONOSHIMA ISLAND: 27.vi.1987, leg. S. Miyamoto (1 ♀, KUM). TSUSHIMA ISLAND: Izuhara–Sasutōge, 7.vi.1941, leg. T. Shirōzu (1 ♀, ELKU); Izuhara, 31.x.1962,

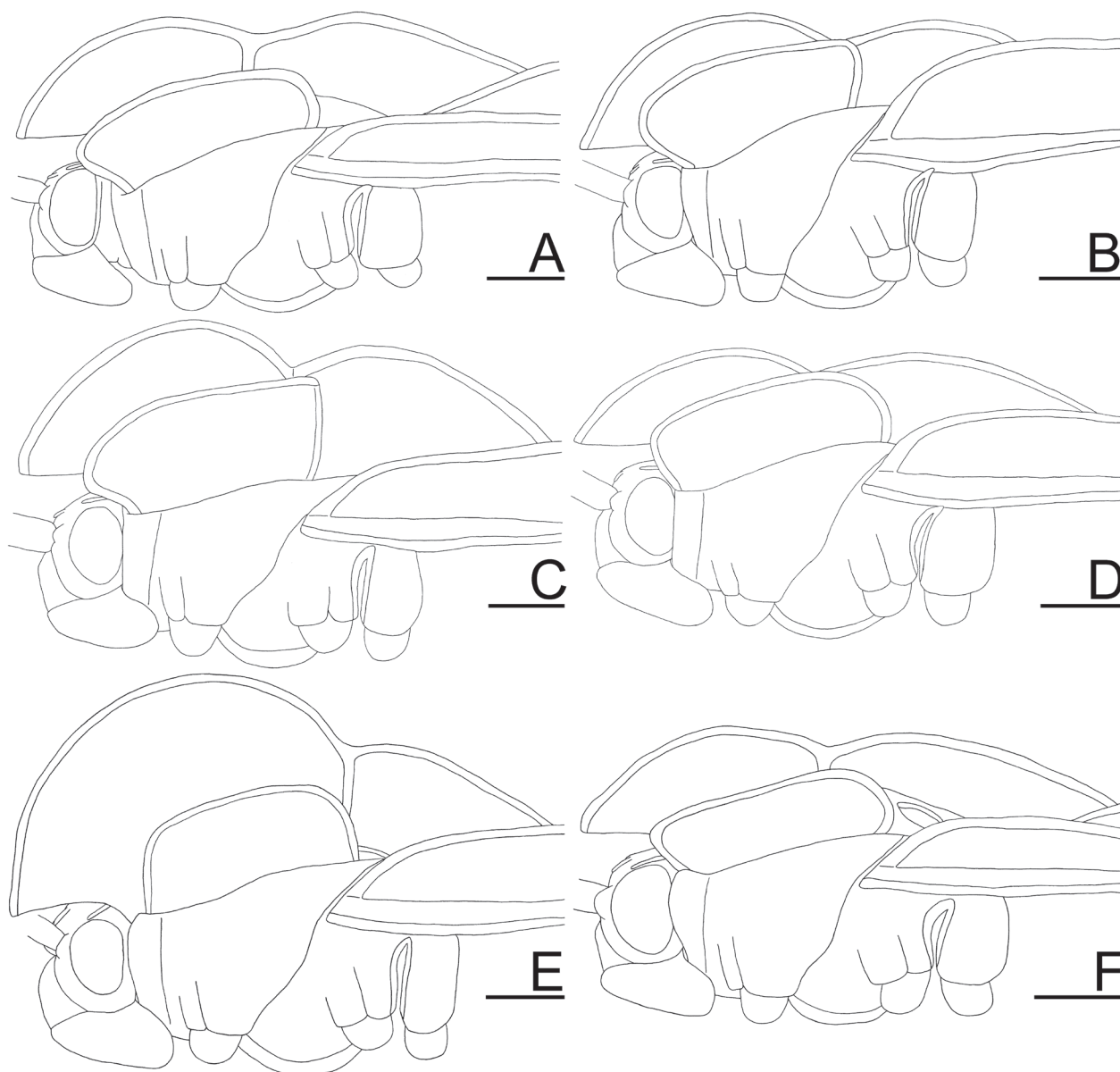


**Figure 26.** Line drawings of the pronota of four *Stephanitis* species from Japan, dorsal view: **A, B.** *S. (Norba) mendica* lacking lateral carina (**A**) and possessing lateral carina (**B**); **C, D.** *S. (Stephanitis) tabidula* from Honshu (**C**) and Kyushu (**D**); **E.** *S. (S.) takeyai*; **F.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.



**Figure 27.** Line drawings of the pronota of four *Stephanitis* species from Japan, lateral view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D.** *S. (N.) hayashii* sp. nov. Abbreviations: bu, buccula; ca, costal area; da, discoidal area; hl, hypocostal lamina; ho, hood; lc, lateral carina; mc, median carina; pa, paranotum. Scale bars: 0.2 mm.



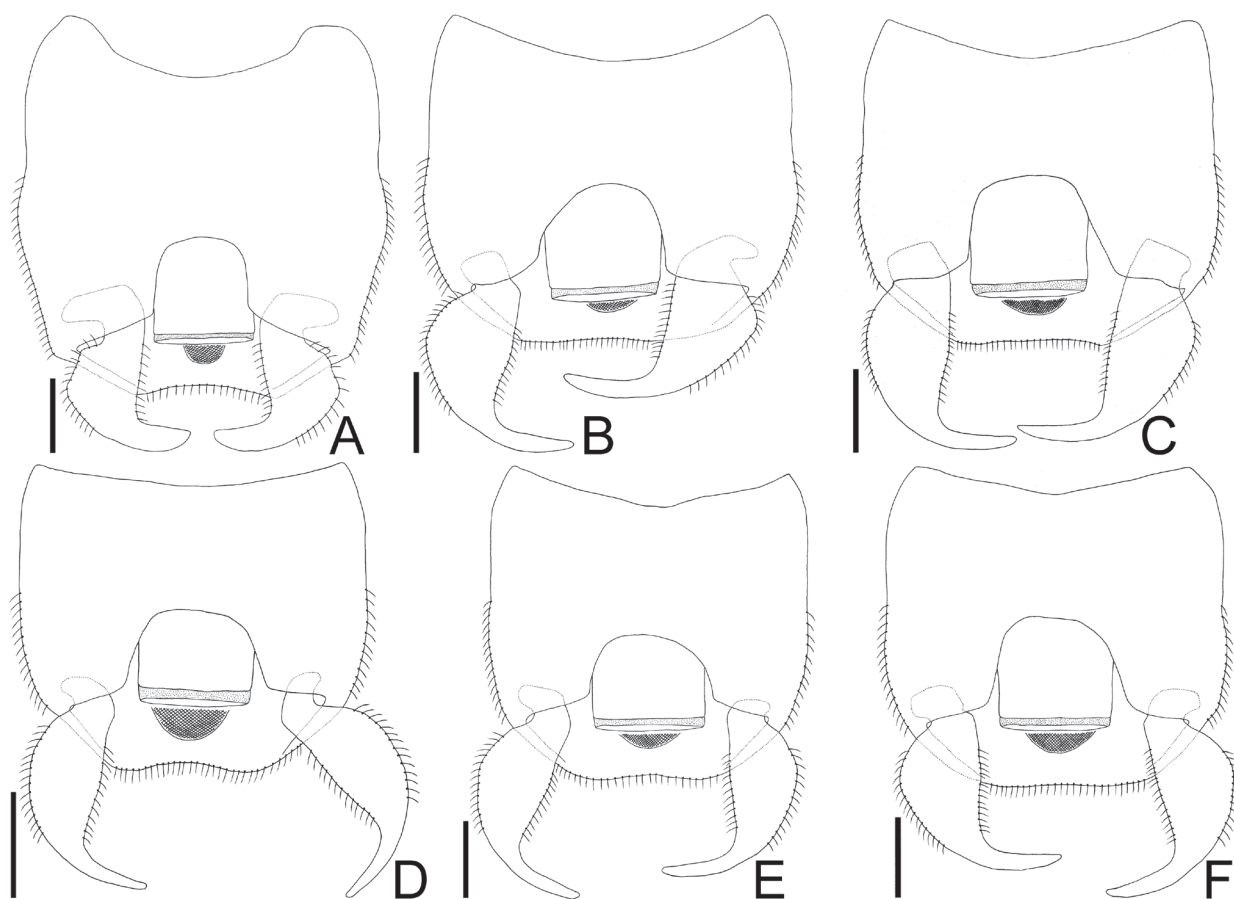


**Figure 28.** Line drawings of the pronota of six *Stephanitis* species from Japan, lateral view: **A.** *S. (Norba) hiurai*; **B.** *S. (N.) ishi-kawai* sp. nov.; **C.** *S. (N.) mendica* lacking lateral carina; **D.** *S. (Stephanitis) tabidula* lacking lateral carina from Honshu; **E.** *S. (S.) takeyai*; **F.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.2 mm.

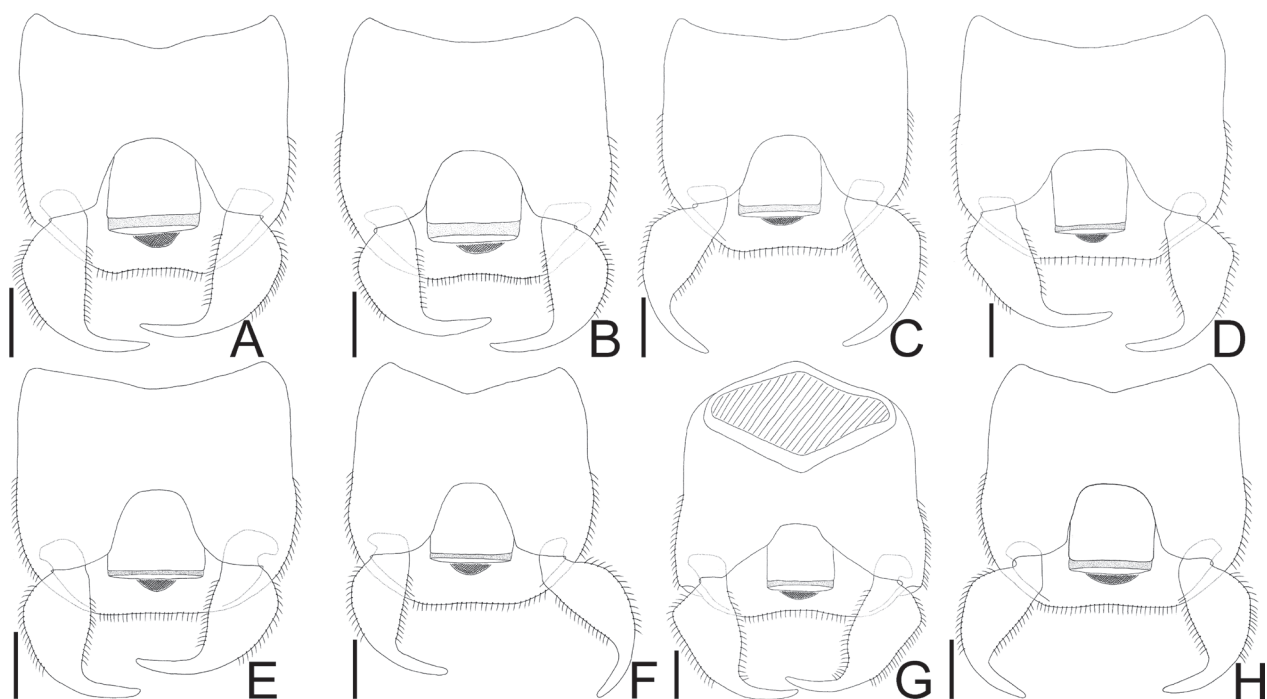
leg. S. Miyamoto (1 ♀, ELKU; 1 ♂, KUM); Mt. Ariake, 12.vii.1968, leg. S. Miyamoto & A. Nakanishi (1 ♀, KUM); Observatory, 28.viii.1988, leg. S.+ K. M. (1 ♀, KUM); Kuda, 29.viii.1988, leg. S. + K. M. (1 ♂ 1 ♀, KUM); Kamiagata-cho, Sago, 6.ix.2017, leg. J. Souma (5 ♂♂ 4 ♀♀, TUA); as above but 8.ix.2017 (3 ♀♀, TUA); Izuhara-cho, Tsutsu, Mount Tatera, 7.ix.2017, leg. J. Souma (1 ♂, TUA); Kamiagata-machi, near Mt. Kōnoki-yama, 8.ix.2017, leg. T. Ishikawa (11 ♂♂ 8 ♀♀ 3 nymphs, TUA); Mitsushima-machi, Kechi, 8.ix.2017, leg. J. Souma (12 ♂♂ 17 ♀♀, TUA). IKI ISLAND: Gōnoura-chō, Katabaruhure, Takenotsuji, 16–18.vii.2016, leg. R. Ito (1 ♂, TUA). AMAKUSA ISLANDS: Shimoshima Island: “Kakuyama” [= Miyajidake-machi, Mt. Kakuyama], 18.ix.1931, leg. H. Hori (1 ♂ 1 ♀, ELKU). GOTO ISLANDS: Fukue Island: Miiraku-Kahara, 4.viii.1933, leg. T. Shirozu (2 ♀, KUM). RYUKYU ISLANDS (northern part):

Yakushima Island: Kosugidani, 23.viii.1952, leg. C. Takeya & Y. Hirashima (2 ♂♂ 5 ♀♀, ELKU); Koseda, 21.ix.2013, leg. N. Tsuji (1 ♀, ELKU). Eight specimens from “Sanuki Wada-mura” and “Kakuyama” were labelled as “paratype” of *S. (S.) fasciicarina*. However, their labels were created subsequently (T. Mita, pers. comm. 2021) and the locality data of these eight individuals do not match those of the original description of *S. (S.) fasciicarina* (Takeya 1931). Therefore, the eight specimens do not seem to have paratype status. Four specimens from “Tachibanayama” were identified as “*S. (N.) aperta* possessing lateral carina” in a previous study (Takeya 1963).

**Diagnosis.** *Stephanitis (Stephanitis) tabidula* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, calli, pronotal disc, marking on hemelytra and ventral surface in

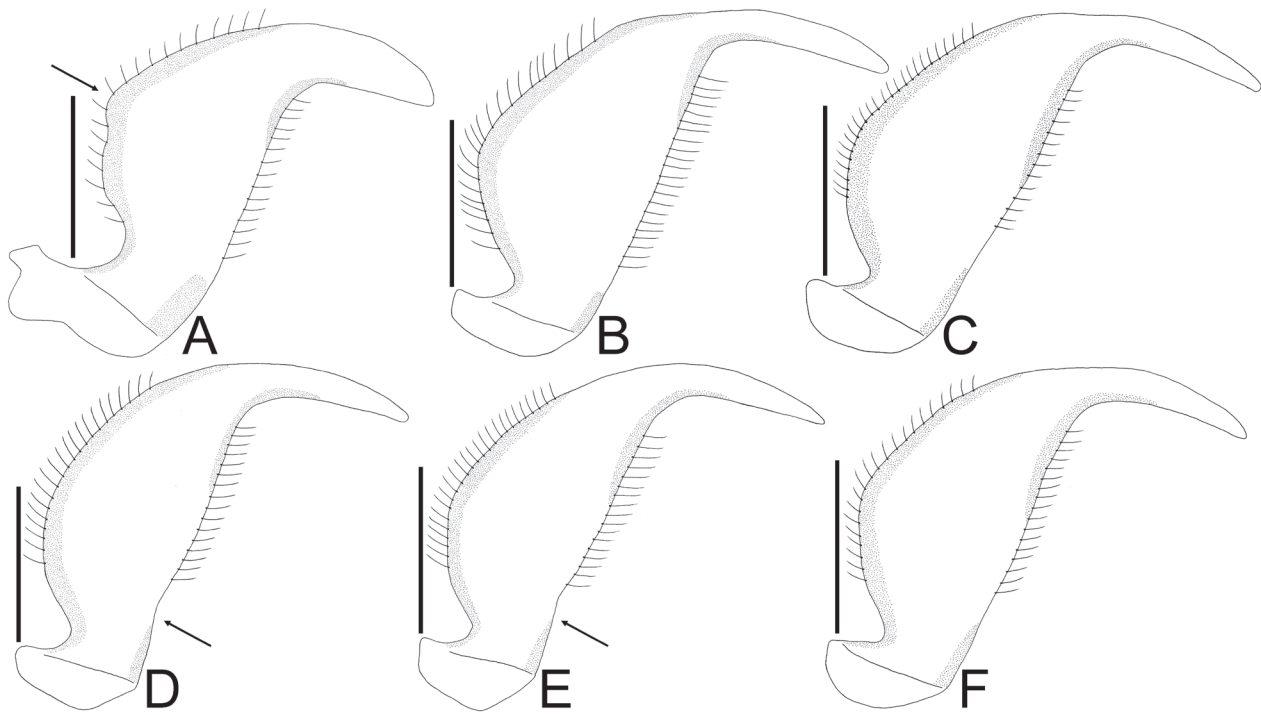


**Figure 29.** Line drawings of the pygophore of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D, E.** *S. (N.) hayashii* sp. nov. from Kakeroma (**D**) and Aguni (**E**) Islands, central part of Ryukyu Islands; **F.** *S. (N.) hiurai*. Scale bars: 0.1 mm.



**Figure 30.** Line drawings of the pygophore of five *Stephanitis* species from Japan, dorsal view: **A–C.** *S. (Norba) ishikawai* sp. nov. from Miyako (**A**) and Yonaguni (**B**) Islands, central part of Ryukyu Islands and Taiwan (**C**); **D.** *S. (N.) mendica*; **E, F.** *S. (Stephanitis) tabidula* from Honshu (**E**) and Tsushima Islands (**F**); **G.** *S. (S.) takeyai*; **H.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.1 mm.



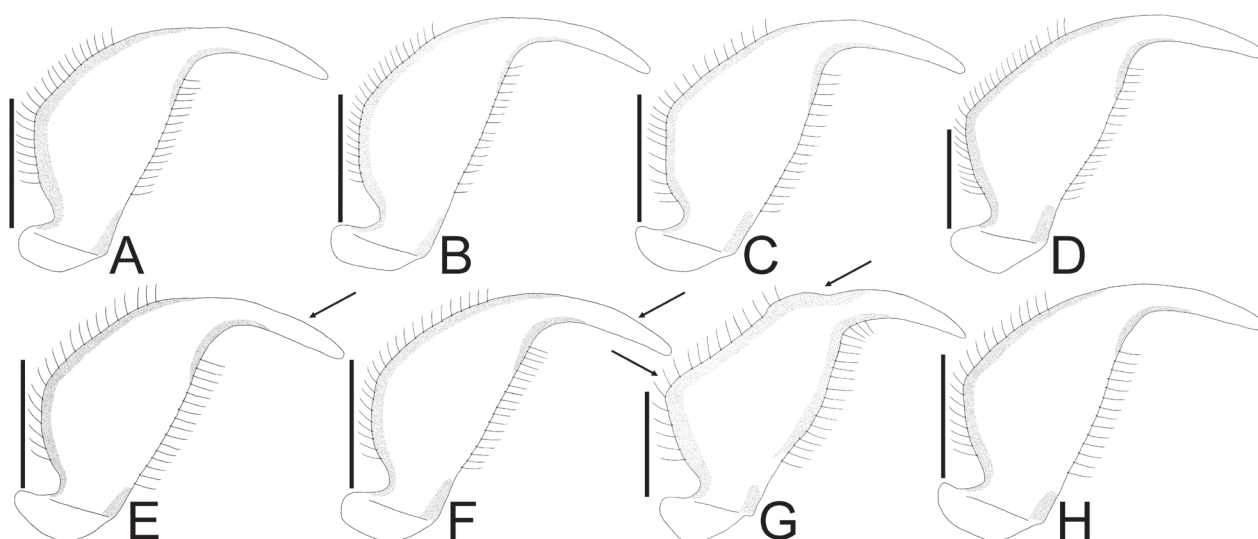


**Figure 31.** Line drawings of the paramere of five *Stephanitis* species from Japan, dorsal view: **A.** *S. (Stephanitis) ambigua*; **B.** *S. (Norba) aperta*; **C.** *S. (N.) exigua*; **D, E.** *S. (N.) hayashii* sp. nov. from Kakeroma (**D**) and Aguni (**E**) Islands, central part of Ryukyu Islands; **F.** *S. (N.) hiurai*. Scale bars: 0.1 mm. Arrows indicate important morphological differences.

various shades of brown (Figs 8C, D, 10C–E, 12C, D, 14C–E, 16C, D, 18C, D, 20B, 22B, 24B); body in male 2.1 times (in female 2.0 times) as long as maximum width across hemelytra (Figs 3C, D, 5C, D); rostrum not reaching metasternum; pronotum unicarinate or tricarinate (Fig. 26C, D); hood pale, shorter than median carina of pronotum, as wide as or wider than vertex at widest part, not or incompletely covering eye, as high as median carina of pronotum at highest part, with posterior margin not extending to middle of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc opaque; paranotum more erect, slightly narrowed posteriorly, with 3 rows of areolae at widest part, anterolateral angle protruding anteriorly, outer margin gently curved inwards at posterolateral angle, maximum height longer than height of eye (Fig. 28D); apices of hemelytra close to each other in rest; costal area with 3–5 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 2–3 rows) of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at centre of venter, with posterior margin slightly emarginate in middle part (Fig. 30E, F); and paramere stout, strongly curved inwards at apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 32E, F).

**Intraspecific variation.** *Stephanitis (Stephanitis) fasciicarina* (including its junior synonym *S. (S.) kyushuana*)

was previously distinguished from *S. (S.) tabidula* by the following characters (Takeya 1931; Drake 1948): body larger (smaller in *S. (S.) tabidula*); antennal segment III less than 2.0 times as long as antennal segment IV (2.0 times in *S. (S.) tabidula*); anterior margin of hood extending beyond clypeus (slightly extending in *S. (S.) tabidula*); markings on hemelytron indistinct (distinct in *S. (S.) tabidula*); and costal area with 4 rows of areolae at widest part (3 rows in *S. (S.) tabidula*). The author's examination of 1,496 adults from various localities in Japan, including the type localities of *S. (S.) tabidula* and *S. (S.) fasciicarina*, together with the photographs of the holotype of *S. (S.) kyushuana* (United States National Museum of Natural History 2021) revealed that no other significant differences in the external morphology could be found between the two forms and these characters have considerable intraspecific variability, with transitional individuals between the extreme forms (Figs 3C, D, 5C, D, 8C, D, 10C–E, 12C, D, 14C–E, 16C, D, 18C, D, 20B, 22B, 24B, 26C, D, 30E, F, 32E, F, 32D, E, 37A, 38, 42C–F). In addition, the partial COI gene pairwise sequence distances between the two forms from the vicinity of the type localities of *S. (S.) tabidula* and *S. (S.) fasciicarina* (Suppl. material 2) were only 0.001321–0.003973 (Suppl. material 3). Furthermore, the Bayesian tree (Fig. 1), based on the partial COI gene, shows that the two forms are monophyletic with a high posterior probability. In conclusion, *S. (S.) tabidula* and *S. (S.) fasciicarina* are currently impossible to distinguish, based on morphological and molecular data either at the species or subspecies



**Figure 32.** Line drawings of the paramere of five *Stephanitis* species from Japan, dorsal view: **A–C.** *S. (Norba) ishikawai* sp. nov. from Miyako (**A**) and Yonaguni (**B**) Islands, central part of Ryukyu Islands and Taiwan (**C**); **D.** *S. (N.) mendica*; **E, F.** *S. (Stephanitis) tabidula* from Honshu (**E**) and Tsushima Islands (**F**); **G.** *S. (S.) takeyai*; **H.** *S. (S.) tomokunii* sp. nov. Scale bars: 0.1 mm. Arrows indicate important morphological differences.

level. Therefore, the following new subjective synonymy is proposed: *Stephanitis (Stephanitis) tabidula* Horváth, 1912 = *Stephanitis (Stephanitis) fasciicarina* Takeya, 1931 syn. nov.

**Remarks.** *Stephanitis (Stephanitis) tabidula* and *S. (Norba) aperta* are distributed in the same regions and feed on the same host plants (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; present study), but the former can be readily distinguished by the tricarinate pronotum (unicarinate in *S. (N.) aperta*) (Figs 7B, 8C, D, 9B, 10C, E, 25B, 26C, D). However, individuals of *S. (S.) tabidula* rarely have an unicarinate pronotum (Fig. 10D). Such specimens, although they strongly resemble *S. (N.) aperta* in general habitus, can still be easily differentiated from the latter species by the following characteristics: paranotum more erect (less erect in *S. (N.) aperta*), slightly narrowed posteriorly (narrowed in *S. (N.) aperta*), with maximum height longer than height of eye (shorter in *S. (N.) aperta*) (Figs 11B, 13B, 14D, 27B, 28D); and apex of paramere strongly curved inwards (slightly curved in *S. (N.) aperta*) (Figs 31B, 32E).

**Teratological form.** As mentioned in the above section, *Stephanitis (Stephanitis) tabidula* rarely has a unicarinate pronotum (Figs 10D, 14D).

**Distribution.** Japan (Honshu; Izu Islands (northern part): Izu-Oshima Island; Tashiro Island; Sado Island; Awa Island; Awaji Island; Oki Islands: Dogo Island; Shikoku; Kyushu; Nokonoshima Island; Tsushima Island; Iki Island; Amakusa Islands: Shimoshima Island; Goto Islands: Fukue Island; Ryukyu Islands (northern part): Yakushima Island) (Fig. 48); southern Korea (Horváth 1912; Takeya 1931, 1963; Takara and Hidaka 1960; Miyamoto 1976; Tomokuni 1985; Yasunaga et al. 1993; Tomokuni and Hayashi 2006; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016; Ahn et al. 2018; present study). Judging from the description and illustration (Jing 1981), the Chi-

nese population differs from the Japanese population in the structure of the pronotum and seems to correspond to another species. According to the present author's examination, the specimens previously recorded from Okinawa Island (the central part of the Ryukyu Islands) (Takara and Hidaka 1960) correspond to *Stephanitis (Norba) mendica*. Judging from the photographs and specimens, the previous records from the southern part of the Izu Islands (Takeya 1963; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012) correspond to *S. (S.) tomokunii* sp. nov., described below. In Japan, *S. (S.) tabidula* inhabits the laurilignosa in a temperate climate of Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands and the northern part of Izu and Ryukyu Islands, which is located in the Palaearctic Region.

**Host plants.** *Cinnamomum camphora*, “Kusunoki” (Lauraceae) (Fig. 44D) (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; present study); *C. yabunikkei*, “Yabunikkei” (Yasunaga et al. 1993; present study); *Laurus nobilis* L., “Gekkeiju” (Lauraceae) (Takeya 1963; Yamada and Tomokuni 2012); *Neolitsea sericea*, “Shirodamo” (Fig. 44C) (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Okochi 2019; present study); *Machilus japonica* Siebold et Zucc. ex Blume, “Aogashi” or “Hosobatabu” (Lauraceae) (Takeya 1963; Yamada and Tomokuni 2012; Okochi 2019; present study); *M. thunbergii*, “Tabunoki” (Fig. 44B) (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Okochi 2019; present study). *Stephanitis (Stephanitis) tabidula* feeds only on lauraceous trees and is oligophagous. This lace bug sometimes occurs on plantings of *C. camphora* and *M. thunbergii* in its distribution range (present study). This tingid species has been known to be a pest of *C. camphora* (Japanese Society of Applied Entomology and Zoology 1980, 2006) and occasionally also causes harm on *M. thunbergii*.





Figure 33. Non-type specimens of *Stephanitis* (*Stephanitis*) *ambigua* deposited in Matsumura's collection of ELHU and their labels.

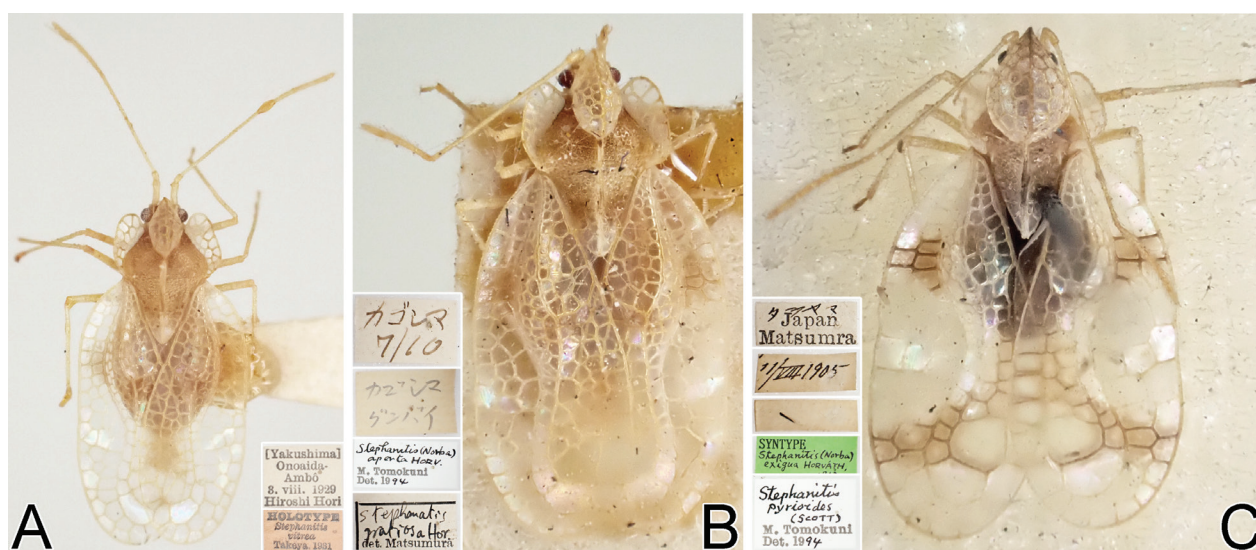


Figure 34. Three specimens of *Stephanitis* species from Japan. A. Holotype of *S. (Norba) vitrea* [= *S. (N.) aperta*] deposited in ELHU and its labels; B. Suspected syntype of *S. (Stephanitis) propinqua* [= *S. (N.) aperta*] deposited in Matsumura's collection of ELHU and its labels; C. Syntype of *S. (N.) exigua* [= *S. (S.) pyrioides*] deposited in Matsumura's collection of ELHU and its labels.



Figure 35. Suspected syntype of *Stephanitis* (*Norba*) *exigua* deposited in Matsumura's collection of ELHU and its labels.





**Figure 36.** Holotypes of *Stephanitis (Norba) hiurai* (A) and *S. (N.) hiurai takaranis* [= *S. (N.) h. hiurai*] (B) deposited in ELKU and its labels.

**Biology.** *Stephanitis (Stephanitis) tabidula* feeds on the abaxial surface of leaves of the five host plants in Japan (present study). In Japan, adults were collected in almost all seasons (Takeya 1931; Miyamoto 1976; Tomokuni 1981, 1985; Yasunaga et al. 1993; Tomokuni and Hayashi 2006; Yano et al. 2013; Okochi 2019; present study); nymphs were collected from May to July and in September and October (present study); the overwintering stage is the adult (present study).

#### *Stephanitis (Stephanitis) takeyai* Drake & Maa, 1955

[Japanese name: Tosaka-gunbai]

Figs 3E, 5E, 6B, 8E, 10F, 12E, 14F, 16E, 18E, 20C, 22C, 24C, 26E, 28E, 30G, 32G, 37B, 42H–J

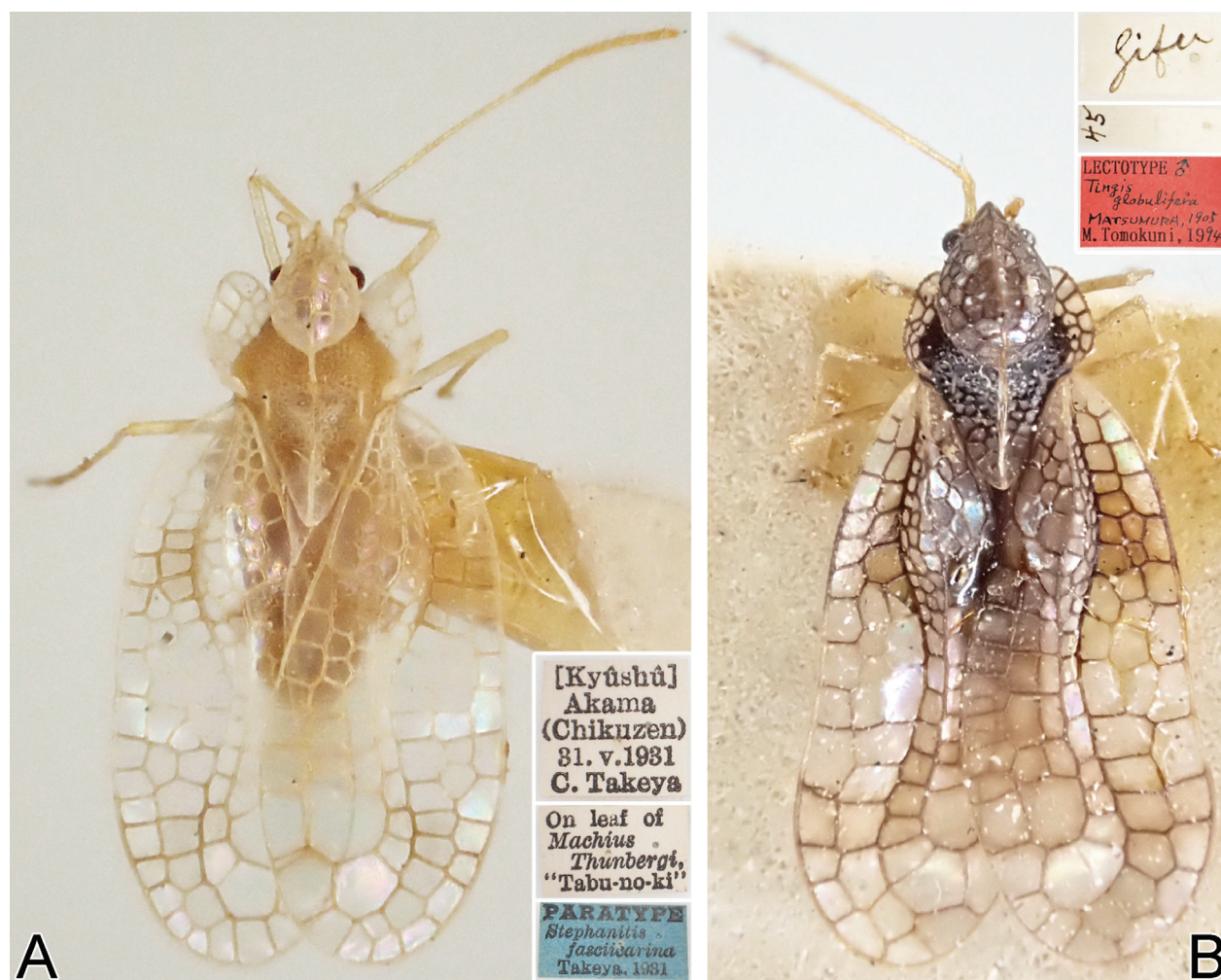
*Tingis globurifera* Matsumura, 1905: 36 (junior primary homonym of *Tingis globurifera* Walker, 1873). Lectotype by subsequent designation (Tomokuni 1994: 842), ♂ (Fig. 37B): Japan: Gifu [= Honshu, Gifu-ken]; ELHU.

*Stephanitis globurifera*: Matsumura (1907: 148) (new combination).

*Stephanitis takeyai* Drake & Maa, 1955: 10. New name for *Stephanitis globurifera* (Matsumura, 1905).

**References.** Horváth (1912: 330) (distribution); Drake (1923: 104) (distribution); Takeya (1930: 72) (host plant); Drake and Poor (1937: 403) (distribution); Drake (1948: 55) (checklist: *Stephanitis*); Bailey (1950: 148) (invasion); Takeya (1951b: 11) (checklist: Japan); Drake and Maa (1953: 100) (checklist: *Stephanitis*); Takeya (1953: 168) (distribution); Takeya (1963: 50) (distribution); Drake and Ruhoff (1965: 364) (catalog); Miyamoto (1965: 91) (monograph); Lee (1969: 226) (nymph, male genitalia); Tomokuni (1981: 109) (distribution); Japanese Society of Applied Entomology and Zoology (1980: 134) (pest); Tomokuni (1985: 156) (distribution); Ichita (1989: 33) (distribution); Miyamoto and Yasunaga (1989: 168) (checklist: Japan); Takahashi (1990a: 28) (checklist: Hyogo); Yasunaga et al. (1993: 179) (monograph); Tsukada (1994: 221) (biology); Péricart and Golub (1996: 63) (catalogue: Palearctic); Japanese Society of Applied Entomology and Zoology (2006: 183) (pest); Miyatake (2006:





**Figure 37.** Two specimens of *Stephanitis* species from Japan. **A.** Paratype of *S. (Stephanitis) fasciicarina* syn. nov. [= *S. (S.) tabidula*] collected at type locality deposited in ELKU and its labels; **B.** Lectotype of *Tingis globulifera* [= *S. (S.) takeyai*] deposited in Matsumura's collection of ELHU and its labels.

27) (host plant); Miyamoto (2008: 158) (monograph); Tsukada (2008: 349) (biology); Yamada and Tomokuni (2012: 208) (monograph); Véték et al. (2012: 22) (distribution); Aukema et al. (2013: 72) (checklist: Palaearctic); Yano et al. (2013: 26) (distribution); Machara (2014: 61) (distribution); Barta and Bideň (2016: 195) (distribution); Yamada and Ishikawa (2016: 434) (checklist: Japan); Ito and Sasaki (2018: 20) (checklist: Oita); Okochi (2019: 3) (distribution); Grosso-Silva et al. (2020: 371) (distribution).

**Material examined. Lectotype** (1 ♂, ELHU) (Fig. 37B), JAPAN: Honshu: Gifu [= Honshu, Gifu-ken (approximate coordinates: 35°26'05.5"N, 136°46'16.6"E)]. **Non-types** (157 ♂♂ 169 ♀♀ 2 nymphs), JAPAN: HONSHU: Saitama-ken, Iruma-gun, Moroyama-machi, Takinoiri, Kanikusa-hashi, 28.v.2021, leg. J. Souma (3 ♀♀, TUA); Tokyo-to, Hachioji-shi, Uratako-machi, Kogesawa-rindo, 6.ix.2016, leg. J. Souma (11 ♂♂ 7 ♀♀, TUA); as above but 12.v.2017 (1 ♂ 1 ♀, TUA); as above 22.v.2017, leg. Y. Kato (1 ♀, TUA); Kanagawa-ken, Sagami-hara-shi, Minami-ku, Asamizodai, 4.vi.2017, leg. J. Souma (2 ♂♂ 1 ♀, TUA); Kanagawa-ken, Sagami-hara-shi, Minami-ku, Shimomizo, 10.ix.2020, leg. J. Souma (1 ♀, TUA); Kanagawa-ken, Atsugi-shi, Funako, 12.v.2016, leg. J. Souma (1 ♂, TUA); as

above but 7.iii.2017 (1 ♀, TUA); as above, but 5.v.2017 (23 ♂♂ 18 ♀♀, TUA); as above but 6.v.2017 (20 ♂♂ 9 ♀♀, TUA); as above, but 7.v.2017, leg. H. Shigetoh (1 ♂, TUA); as above but 11.v.2017 (43 ♂♂ 52 ♀♀, TUA); as above, but 31.v.2017 (4 ♀♀, ELKU); as above but 5.vi.2017 (1 ♀, TUA); Kanagawa-ken, Atsugi-shi, Nanasawa, 6.vi.2017, leg. J. Souma (8 ♂♂ 5 ♀♀, TUA); Kanagawa-ken, Isehara-shi, Oyama, 31.v.2017, leg. Y. Yamada (1 ♂, TUA); Yamanashi-ken, Hokuto-shi, Takane-cho, Kiyosato, 5.ix.2022, leg. J. Souma (1 ♂, TUA); Nagano-ken, Matsumoto-shi, Azumi, 7.ix.2022, leg. J. Souma (2 ♂♂ 1 ♀, TUA); Hiroshima Pref., Kitahiroshima, Nakaso, 23.vii.2022, leg. Y. Uehara (1 ♂, TUA); as above but leg. H. Hashimoto (1 ♂, TUA). SADO ISLAND: Chigusa, 28.viii.2021, leg. J. Souma (1 ♂ 2 ♀♀, TUA); Kamiyokoyama, 28.viii.2021, leg. J. Souma (3 ♂♂ 5 ♀♀, TUA); Kujikawachi, 29.viii.2021, leg. J. Souma (2 ♀♀, TUA); Noura, 29.viii.2021, leg. J. Souma (3 ♀♀, TUA). SHIKOKU: Kagawa-ken, Takamatsu-shi, Nishiueta-cho, Fujio, 28.iv.2020, leg. Y. Waki (1 ♂, TUA); Kagawa-ken, Takamatsu-shi, Nishiueta-cho, Donguri Land, 23.v.2021, leg. Y. Waki (1 ♀, TUA); Kochi-ken, Kochi-shi, Shigekura, 2.vii.2020, leg. J. Souma (2 ♂♂ 1 ♀ 2 nymphs, ELKU). KYUSHU: Fukuoka-ken,





**Figure 38.** Non-types of *Stephanitis* (*Stephanitis*) *tabidula* collected at type locality deposited in Matsumura's collection of ELHU and their labels.

Kasuya-gun, Sasaguri-machi, Tsubakuro, 5.vi.2020, leg. N. Tsuji (5 ♂♂ 9 ♀♀, ELKU); Fukuoka Pref., Tagawa, Soeda, Mt. Hiko-san, Takanosubar, 28.v.2022, leg. Y. Uehara (1 ♂ 1 ♀, TUA); Oita-ken, Kusu-gun, Kokonoe-machi, 12.vii.2017, leg. S. Imada (1 ♀, ELKU); Kumamoto Pref., Aso, Minamiaso, Kain, 12.vi.2022, leg. H. Hashimoto (1 ♀, TUA); Kumamoto-ken, Kuma-gun, Mizukami-mura, Mt. Ichifusa-yama, 27.vii.2022, leg. S. Inoue (1 ♀, TUA); Oita-ken, Hita-shi, Maetsue-machi, Ono, 21.viii.2022, leg. J. Souma (1 ♂ 1 ♀, TUA); Oita-ken, Hita-shi, Maetsue-machi, Yugi, 21.viii.2022, leg. J. Souma (1 ♂, TUA). RYUKYU ISLANDS (northern part): Yakushima Island: Kosugidani, 23.viii.1952, leg. C. Takeya & Y. Hirashima (2 ♂♂ 3 ♀♀, ELKU); as above, but 29.vii.1963, leg. T. Okada (1 ♀, KUM); Hananoego, 24.viii.1952, leg. C. Takeya & Y. Hirashima (17 ♂♂ 19 ♀♀, ELKU; 1 ♀, KUM); as above, but 26.x.1979, leg. S. Makihara (4 ♂♂ 7 ♀♀, NSMT); Onoaida, 20.viii.2021 (3 ♂♂ 5 ♀♀, ELKU).

**Diagnosis.** *Stephanitis* (*Stephanitis*) *takeyai* is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, calli, pronotal disc, marking on hemelytra and ventral surface black (Figs 8E, 10F, 12E, 14F, 16E, 18E, 20C, 22C, 24C); body in male 2.1 times (in female 1.9 times) as long as maximum width across hemelytra (Figs 3E, 5E, 6B); rostrum reaching metasternum; pronotum tricarinate (Fig. 26E); hood dark,

longer than median carina of pronotum, wider than maximum width of head across eyes, completely covering eye, higher than median carina of pronotum at highest part, with posterior margin extending near posterior margin of pronotal disc; median carina of pronotum with 2 rows of areolae at highest part; pronotal disc opaque; paranotum more erect, not narrowed posteriorly, 3 rows of areolae at widest part, anterolateral angle slightly protruding anteriorly, outer margin gently curved inwards at posterolateral angle, maximum height longer than height of eye (Fig. 28E); apices of hemelytra close to each other in rest; costal area with 3–4 rows of areolae at widest part; subcostal area in male with 3 rows (in female with 4 rows) of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at centre of venter, with posterior margin slightly emarginate in middle part (Fig. 30G); and paramere stout, weakly curved inwards at apex, with outer margin cuspidate in middle part, inner margin slightly curved inwards in basal part (Fig. 32G).

**Remarks.** Amongst the Japanese species of *Stephanitis*, *S.* (*Stephanitis*) *takeyai* is similar to *S.* (*S.*) *sven-soni* Drake, 1948, which feeds on *Illicium anisatum* L. (Schisandraceae) (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012), in general habitus, but



the former is easily distinguished from the latter by the following characters: hood longer than median carina of pronotum (shorter in *S. (S.) svensoni*), wider than maximum width of head across eyes (narrower in *S. (S.) svensoni*), completely covering eye (incompletely covering in *S. (S.) svensoni*) (Figs 8E, 10F, 26E); and subcostal area of hemelytron in male with 3 rows (in female 4 rows) of areolae at widest part (in male 4 rows and in female 5 rows in *S. (S.) svensoni*) (Figs 16E, 18E).

**Teratological form.** Segmental oligomery of the antenna was confirmed in *S. (S.) takeyai* and one examined specimen lacked the left antennal segment IV (Fig. 6B), as reported in many tingids (Štůsák and Stehlík 1978; Souma 2020b, 2020d, 2020e).

**Distribution.** Japan (Honshu; Sado Island; Oki Islands: Dogo Island; Shikoku; Kyushu; Ryukyu Islands (northern part): Yakushima Island) (Fig. 48); Austria; Belgium; Canada; Czech Republic; France; Great Britain; Germany; Hungary; Italy; Netherlands; Poland; Portugal; Slovakia; Switzerland; U.S.A. (Takeya 1963; Yamada and Tomokuni 2012; Véték et al. 2012; Aukema et al. 2013; Barta and Bideň 2016; Yamada and Ishikawa 2016; Grosso-Silva et al. 2020; present study). *Stephanitis (Stephanitis) takeyai* is native to Japan, but it has invaded many countries in Europe and North America (Yamada and Tomokuni 2012). The previous record from India (Drake and Ruhoff 1965) is an error resulting from the confusion between the type locality of *Tingis globulifera* Walker, 1873 [= *Cochlochila (Physodictyon) bullita* (Stål, 1873)] described from India and *T. globulifera* Matsumura, 1905 [= *S. (S.) takeyai* Drake & Maa, 1955] described from Japan (cf. Drake and Maa 1955). The previous records from Amami-Oshima Island, the central part of the Ryukyu Islands (Takeya 1963), are misidentifications of *S. (S.) pyrioides* and a nymph pertaining to another genus. In Japan, *S. (S.) takeyai* inhabits the deciduous broad-leaved forest in a temperate climate of Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands, which is in the Palearctic Region.

**Host plants.** *Aesculus turbinata* Blume, “Tochinoki” (Sapindaceae) (Takeya 1963); *Cerasus jamasakura* (Siebold ex Koidz.) H. Ohba, “Yamazakura” (Rosaceae) (Takeya 1963; Yamada and Tomokuni 2012); *Cinnamomum camphora*, “Kusunoki” (Lauraceae) (Takeya 1930, 1963; Yamada and Tomokuni 2012; Okochi 2019); *Diospyros kaki* Thunb., “Kaki” (Ebenaceae) (Takeya 1963; Yasunaga et al. 1993); *Elliottia paniculata* (Siebold et Zucc.) Hook.f., “Hotsutsuji” (Ericaceae) (Takeya 1963); *Hydrangea hydrangeoides*, “Iwagarami” (Siebold et Zucc.) B. Schulz (Hydrangeaceae) (Takeya 1963; Yamada and Tomokuni 2012); *Illicium anisatum*, “Shikimi” (Schisandraceae) (Takeya 1963; Yamada and Tomokuni 2012); *Lindera obtusiloba*, “Dankobai” (Lauraceae) (Takeya 1963; Yamada and Tomokuni 2012; present study); *L. praecox* (Siebold et Zucc.) Blume, “Aburachan” (Takeya 1963); *L. triloba*, “Shiromoji” (Takeya 1963); *Litsea cubeba* (Lour.) Pers., “Aomoji” (Lauraceae) (Takeya 1930, 1963; Yamada and Tomokuni 2012); *Lit. umbellata* Thunb., “Kuromoji” (Fig. 44E) (Takeya 1930, 1963; Yamada and Tomokuni 2012; Okochi 2019; present study); *Lit. sericea*

(Siebold et Zucc.) Blume, “Kekuromoji” (Takeya 1963; Yamada and Tomokuni 2012); *Lyonia ovalifolia* (Wall.) Drude, “Nejiki” (Ericaceae) (Takeya 1963; Yamada and Tomokuni 2012; Maehara 2014; Okochi 2019); *Machilus thunbergii*, “Tabunoki” (Lauraceae) (present study); *Pieris japonica* (Thunb.) D. Don ex G. Don, “Asebi” (Ericaceae) (Takeya 1930, 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Maehara 2014); *Platanus* spp., “Suzukakenoki” or “Puratanasu” (Platanaceae) (Miyatake 2006); *Pourthiaea villosa* (Thunb.) Decne. “Ushikoroshi” (Rosaceae) (Takeya 1963; Yamada and Tomokuni 2012); *Rhododendron japonoheptamerum* Kitam. var. *hondoense* (Nakai) Kitam., “Honshakunage” (Okochi 2019); *Salix* sp., “Yanagi” (Salicaceae) (Takeya 1963; Yamada and Tomokuni 2012); *Styrax japonicus* Siebold & Zucc., “Egonoki” (Styracaceae) (Takeya 1930, 1963). *Stephanitis (Stephanitis) takeyai* feeds on an extremely wide range of angiosperms and is euryphagous, unlike many tingids (Schuh and Weirauch 2020). However, some records of this species, collected from Hydrangeaceae, Rosaceae, Salicaceae, Sapindaceae, Schisandraceae and Styracaceae (Takeya 1930, 1963; Yamada and Tomokuni 2012), do not include data on the insect’s development. As this lace bug is the most common Japanese lace bug (Yamada and Tomokuni 2012), some of the previous host records may be of plant families from which *S. (S.) takeyai* was accidentally collected. This lace bug sometimes occurs on plantings of *C. camphora*, *D. kaki* and *P. japonica* in its distribution range (present study). This tingid species has been known to be a pest of *D. kaki* and *P. japonica* (Japanese Society of Applied Entomology and Zoology 1980, 2006) and, occasionally, it can also cause harm on *C. camphora*.

**Biology.** *Stephanitis (Stephanitis) takeyai* feeds on the abaxial surface of leaves of the various host plants in Japan (present study). In Japan, this lace bug is trivoltine (Tsukada 1994, 2008); adults were collected in almost all seasons (Takeya 1953; Tomokuni 1981, 1985; Ichita 1989; Yasunaga et al. 1993; Tsukada 1994, 2008; Yamada and Tomokuni 2012; Yano et al. 2013; Maehara 2014; Ito and Sasaki 2018; present study); nymphs were collected from April to October (Tsukada 1994, 2008; Maehara 2014; present study); the overwintering stage is the egg, but third-generation adults are found until March of the following year (Tsukada 1994; present study).

### *Stephanitis (Stephanitis) tomokunii* sp. nov.

<https://zoobank.org/62534AF0-5030-4CC3-BD68-D008D9D6C3AE>

[Japanese name: Tomokuni-gunbai]

Figs 3F, 5F, 8F, 10G, 12F, 14G, 16F, 18F, 20D, 22D, 24D, 26F, 28F, 30H, 32H, 39, 42K, L

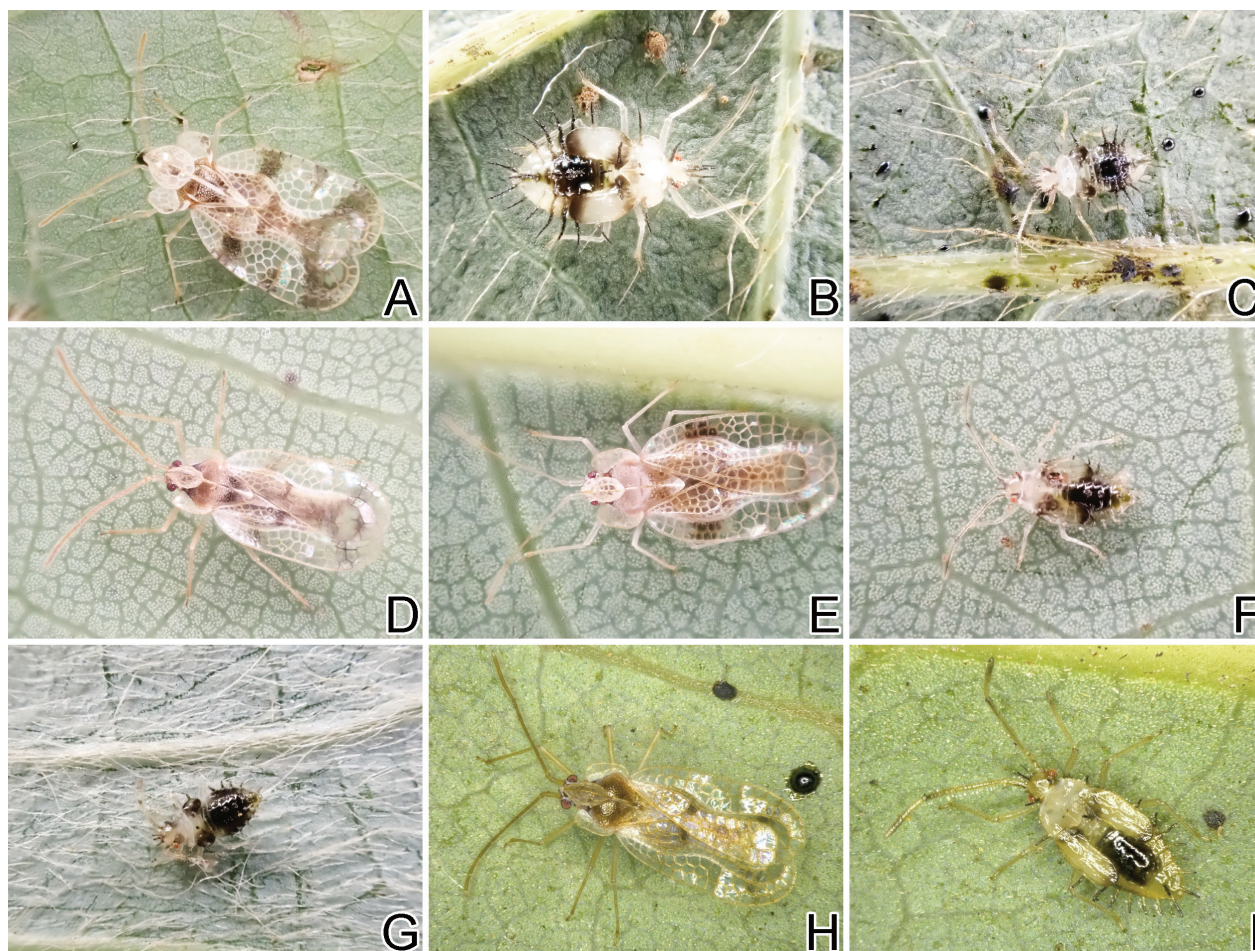
*Stephanitis (Stephanitis) tabidula* Horváth, 1912: Takeya (1963: 42) (distribution: part); Tomokuni and Ishikawa (2002: 170) (distribution); Yamada and Tomokuni (2012: 208) (monograph: part); Yamada and Ishikawa (2016: 434) (checklist: Japan). Misidentifications.

**Type series.** **Holotype** (♂, ELKU), “[JAPAN]: Izu Isls., Hachijo, Is., Mitsune” [=JAPAN: IZU ISLANDS (southern part): Hachijo Island: Mitsune (approximate coordinates:





**Figure 39.** Paratypes of *Stephanitis (Stephanitis) tomokunii* sp. nov. deposited in Matsumura's collection of ELHU and their labels.

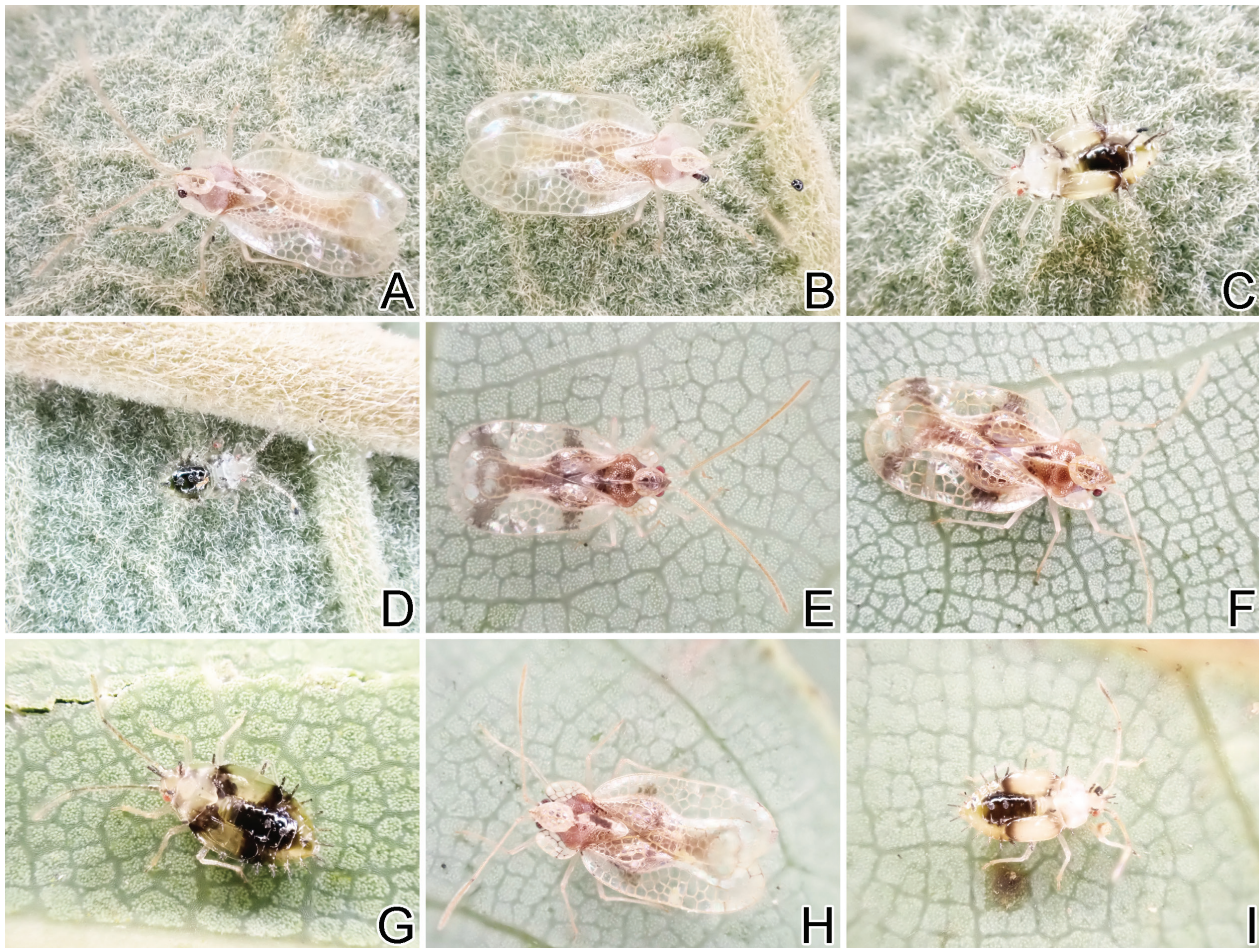


**Figure 40.** Living individuals of three species of *Stephanitis* from Japan: **A–C.** *S. (Stephanitis) ambigua* from Honshu, male (**A**) and fifth (**B**) and fourth (**C**) instar nymphs; **D–G.** *S. (Norba) aperta* from Honshu, male (**D**), female (**E**) and fifth (**F**) and fourth (**G**) instar nymphs; **H, I.** *S. (N.) exigua* from Okinawa Island, central part of Ryukyu Islands, male (**H**) and fifth instar nymph (**I**).

33°07'16.3"N, 139°48'21.6"E)], 17.v.2021, leg. J. Souma. **Paratypes** (66 ♂♂ 134 ♀♀), JAPAN: IZU ISLANDS: (southern part): Miyake Island: Ako, 15.v.1999, leg. T. Kishimoto (1 ♂ 1 ♀); Izu, 12.v.2018, leg. T. Ishikawa (8 ♂♂ 12 ♀♀, TUA); Tosa For. Rd., 12.v.2018, leg. J. Souma (2 ♂♂ 8 ♀♀, TUA); as above but leg. T. Saeki (1 ♂ 1 ♀, TUA); Sannomiya For. Rd., 12.v.2018, leg. J. Souma (20

♂♂ 18 ♀♀, TUA); Nanto For. Rd., 13.v.2018, leg. J. Souma (1 ♂ 2 ♀♀, TUA). Hachijo Island: “八丈” [= Hachijo Island], Arakawa, “20/V/909” [= 20.v.1909] (1 ♂ 2 ♀♀, ELHU) (Fig. 39); Minemura, 7.viii.1948, leg. Fujiyama (1 ♀, ELKU); Kaminato, 24.v.1949, leg. I. Fujiyama (1 ♀, NIAES); Mitsune Beach, 28.v.1949, leg. T. Aoki (1 ♀, NIAES); Noboryo Pass, 11.viii.1949, leg. I. Fujiyama





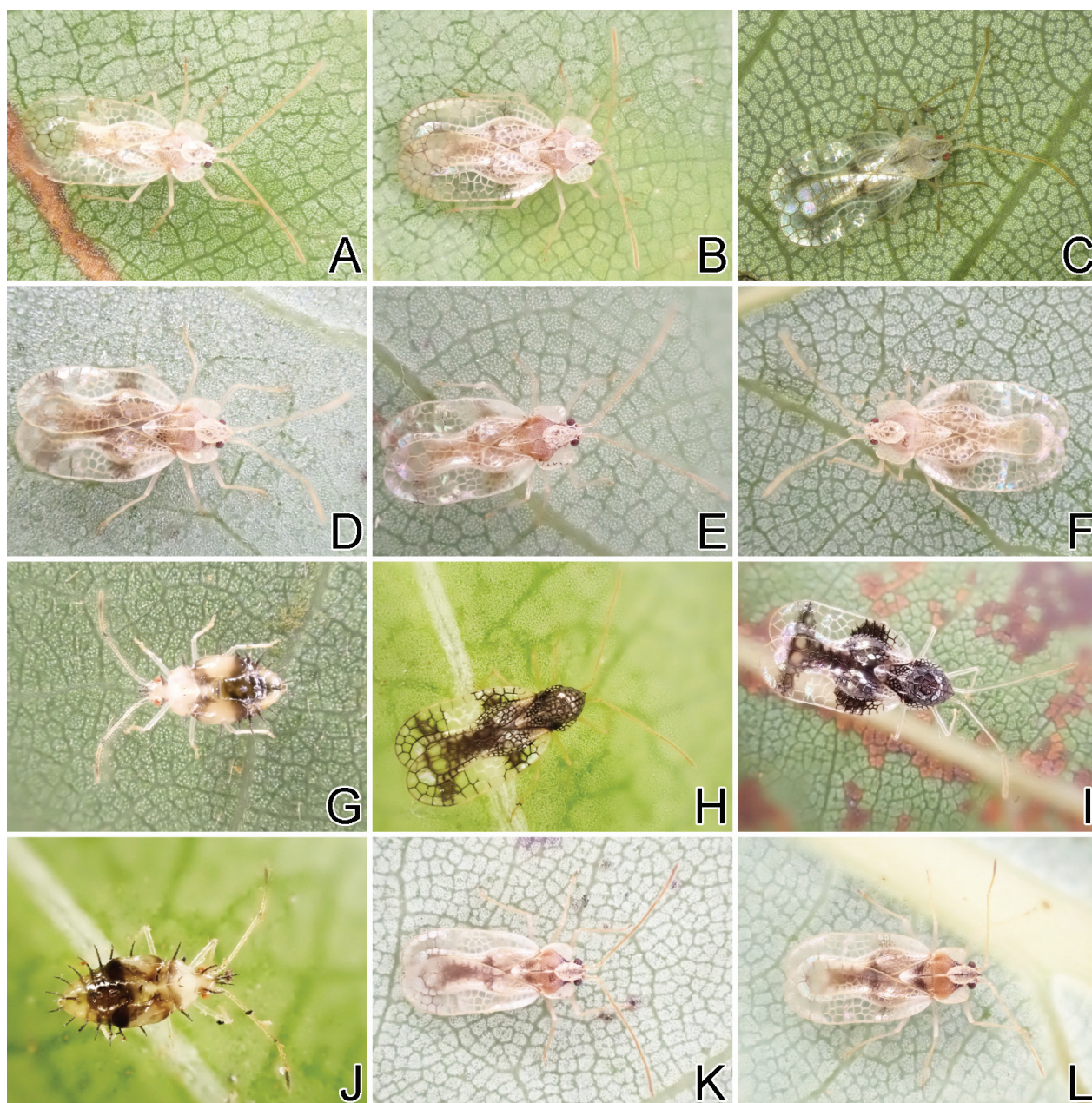
**Figure 41.** Living individuals of three species of *Stephanitis* from Japan: **A–D.** *S. (Norba) hayashii* sp. nov. from the central part of Ryukyu Islands, male (**A**), female (**B**) and fifth (**C**) and fourth (**D**) instar nymphs from Kakeroma Island; **E–G.** *S. (N.) hiurui* from Amami-Oshima Island, central part of Ryukyu Islands, male (**E**) and female (**F**) and fifth instar nymph (**G**); **H, I.** *S. (N.) ishikawai* sp. nov. from Yonaguni Island, southern part of Ryukyu Islands, female (**H**) and fifth instar nymph (**I**).

(1 ♀, NIAES); as above but alt. 350 m, 5.vii.2001, leg. M. Tomokuni (3 ♂♂ 3 ♀♀, NSMT); 19.vii.1957, leg S. Hisamatsu (1 ♀, NSMT); as holotype but 16.v.2021 (4 ♀♀, ELKU); Mt. Miharayama, alt. 200–560 m, 2.vii.2001, leg. M. Tomokuni (1 ♂ 2 ♀♀, NSMT); Mt. Hachijo-fuji, alt. 250–530 m, 4.vii.2001, leg. M. Tomokuni (3 ♀♀, NSMT); as above but alt. 560–850 m, 3.vii.2001 (3 ♀♀, NSMT); as holotype (4 ♂♂ 5 ♀♀, ELKU); as holotype but 18.v.2021 (10 ♂♂ 30 ♀♀, ELKU); as holotype but 19.v.2021, leg. J. Souma (1 ♂ 1 ♀, ELKU; 5 ♂♂ 16 ♀♀, TUA); as holotype but 20.v.2021 (6 ♂♂ 14 ♂♂, TUA); Mistune, Mihara For. Rd., 17.v.2021, leg. J. Souma (2 ♂♂ 7 ♀♀, ELKU); Sueyoshi, 17.v.2021, leg. J. Souma (1 ♂ 2 ♀♀, ELKU). Three paratypes collected in 1909 are deposited in Matsumura's collection. A single paratype collected in 1948 and 12 paratypes collected in 3–5.vii.2001, were recorded as “*Stephanitis tabidula*” in previous studies (Takeya 1963; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012).

**Diagnosis.** *Stephanitis (Stephanitis) tomokunii* sp. nov. is recognised amongst other species of *Stephanitis* by a combination of the following characters: head, pronotal disc, marking on hemelytra and ventral surface

in various shades of brown (Figs 8F, 10G, 12F, 14G, 16F, 18F, 20D, 22D, 24D); calli dark brown; body in male 2.3 times (in female 2.1 times) as long as maximum width across hemelytra (Figs 3F, 5F); rostrum not reaching metasternum; pronotum tricarinate (Fig. 26F); hood pale, shorter than median carina of pronotum, as wide as vertex at widest part, not covering eye, as high as median carina of pronotum at highest part, posterior margin not extending to middle of pronotal disc; median carina of pronotum with 1–2 rows of areolae at highest part; pronotal disc; paranotum less erect, narrowed posteriorly, 3 rows of areolae at widest part, anterolateral angle slightly protruding anteriad, outer margin gently curved inwards at posterolateral angle, maximum height shorter than height of eye (Fig. 28F); apices of hemelytra close to each other in rest; costal area with 3 rows of areolae at widest part; subcostal area in male with 2 rows (in female with 2–3 rows) of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; R+M (radiomedial) vein carinate; pygophore elevated at centre of venter, posterior margin slightly





**Figure 42.** Living individuals of four species of *Stephanitis* from Japan: **A, B.** *S. (Norba) mendica* from Honshu, male (**A**) and female (**B**); **C–G.** *S. (Stephanitis) tabidula*, male (**C**) and female (**D**) from Honshu and male (**E**), female (**F**) and fifth instar nymph (**G**) from Kyushu; **H–J.** *S. (S.) takeyai*, male (**H**) and fifth instar nymph (**J**) from Shikoku and female from Honshu (**I**); **K, L.** *S. (S.) tomokunii* sp. nov. from Hachijo Island, southern part of Izu Islands, male (**K**) and female (**L**).

emarginate in middle part (Fig. 30H); and paramere stout, weakly curved inward at apex, with outer margin not sinuate in middle part, inner margin nearly straight in basal part (Fig. 32H).

**Description. Male.** Head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown; calli dark brown; eye dark red; areolae of pronotum and hemelytron transparent; hood pale; pronotal disc opaque; pubescence on body yellowish (Figs 3F, 8F, 12F, 16F, 20D, 22D).

Body 2.3 times as long as maximum width across hemelytra (Fig. 3F). Head (Figs 8F, 12F, 20D, 26F) glabrous; pair of frontal spines close to each other at apices, not reaching apex of clypeus; median spine as long as

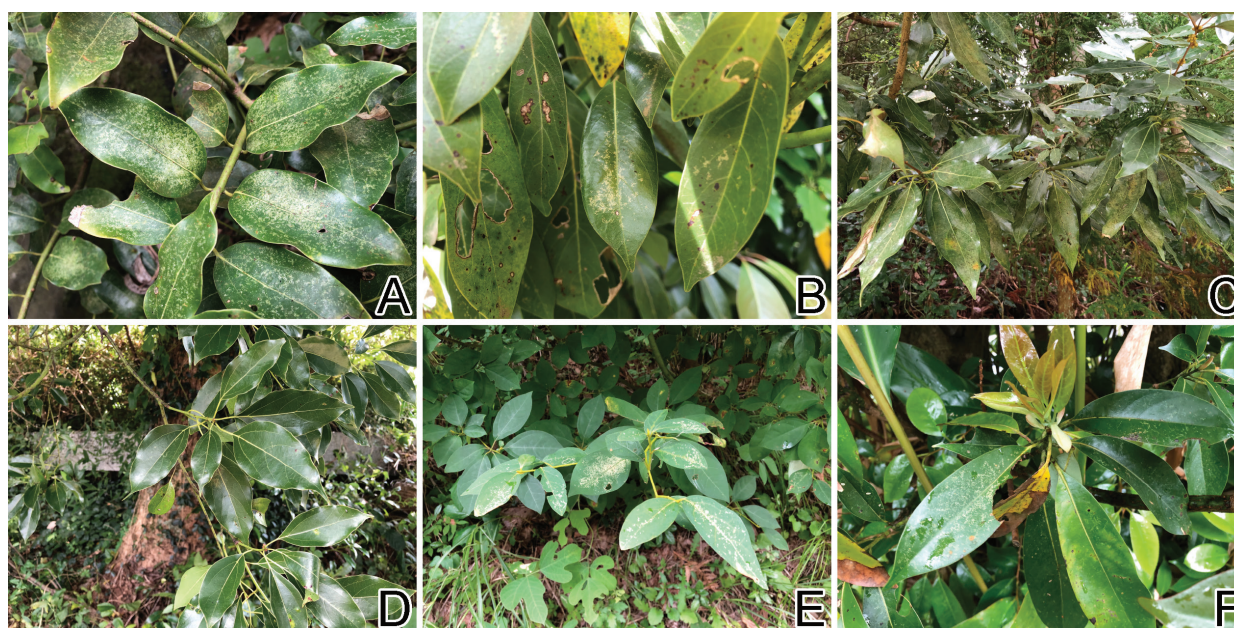
frontal spines, reaching bases of frontal spines; pair of occipital spines longer than median spine, reaching middle part of eyes; antenniferous tubercles obtuse, slightly curved inwards; clypeus smooth. Compound eye round in dorsal view. Antenna densely covered with pubescence; segment I cylindrical; segment II cylindrical, shortest amongst antennal segments; segment III longest amongst antennal segments; segment IV cylindrical, longer than segment I. Bucculae closed to each other at anterior ends, with 2 rows of areolae throughout its length. Rostrum not reaching metasternum.

Pronotum (Figs 8F, 12F, 26F, 28F) unicarinate, 1.3 times as long as maximum width across paranota, sparsely covered with pubescence. Pronotal disc coarsely



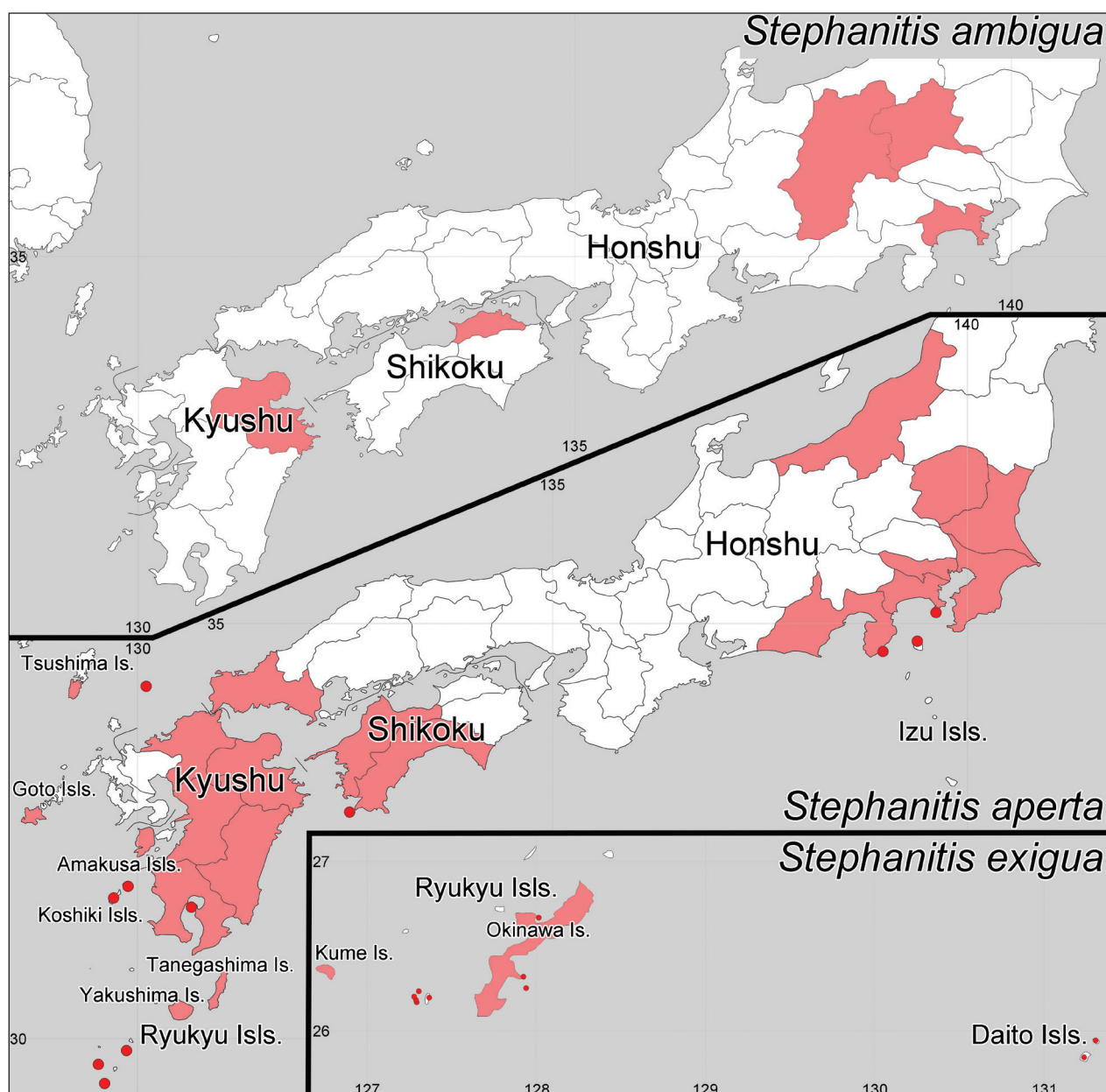


**Figure 43.** Lauraceous host plants of six species of *Stephanitis* from Japan: **A.** *Lindera glauca* from Honshu, damaged by *S. (Stephanitis) ambigua*; *Machilus thunbergii* (**B**), *Neolitsea sericea* (**C**) and *Cinnamomum camphora* (**D**) from Honshu, all damaged by *S. (Norba) aperta*; **E.** *M. thunbergii* from Okinawa Island, damaged by *S. (N.) exigua*; *Litsea japonica* (**F**) from Kakeroma Island and *C. yabunikkei* (**G**) from Tokashiki Island, both damaged by *S. (N.) hayashii* sp. nov.; **H.** *M. thunbergii* from Amami-Oshima Island, damaged by *S. (N.) hiurai*; **I.** *Lit. japonica* from Miyako Island, damaged by *S. (N.) ishikawai* sp. nov.



**Figure 44.** Lauraceous host plants of four species of *Stephanitis* from Japan: **A.** *Cinnamomum yabunikkei* from Kyushu, damaged by *S. (Norba) mendica*; *Machilus thunbergii* (**B**) from Honshu, *Neolitsea sericea* (**C**) from Sado Island and *C. camphora* (**D**) from Kyushu, all damaged by *S. (Stephanitis) tabidula*; **E.** *Lindera umbellata* from Sado Island, damaged by *S. (S.) takeyai*; **F.** *M. thunbergii* from Hachijo Island, damaged by *S. (S.) tomokunii* sp. nov.





**Figure 45.** Collection sites of *Stephanitis* (*Stephanitis*) *ambigua*, *S. (Norba)* *aperta* and *S. (N.)* *exigua* used in the present study. Red-filled areas = localities; circles = small isolated islands.

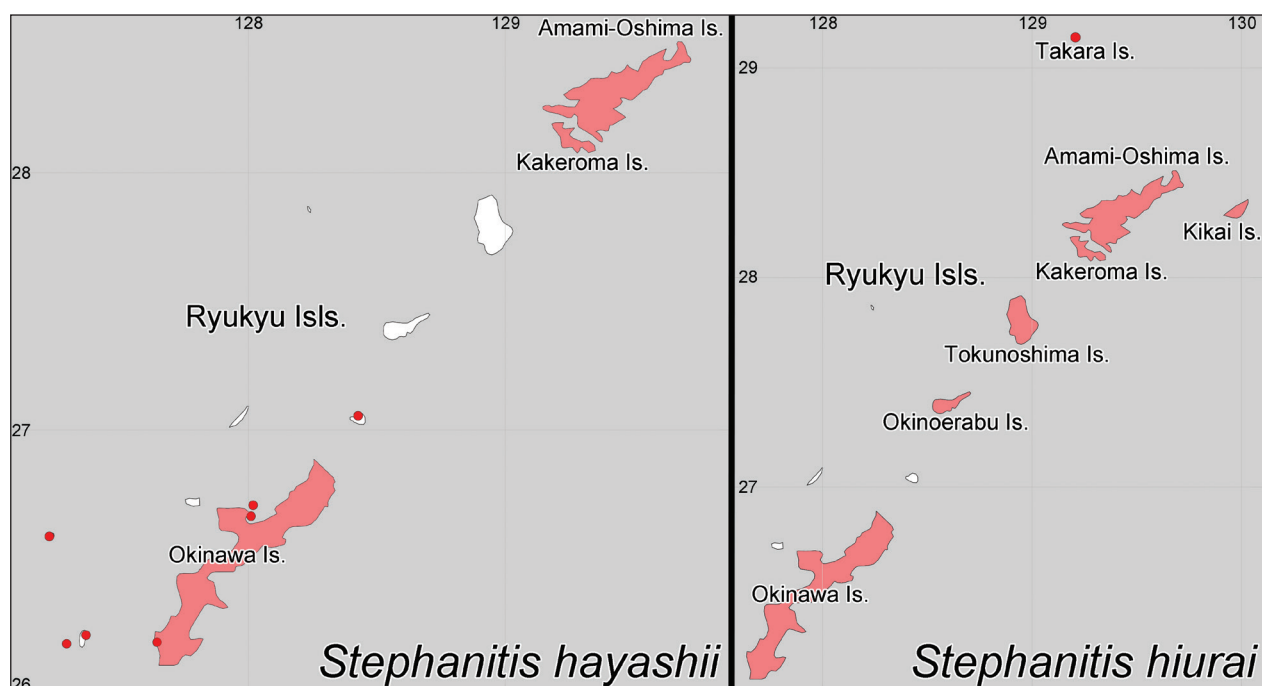
punctate. Hood shorter than median carina of pronotum, as wide as vertex at widest part, not covering eye, as high as median carina of pronotum at highest part, posterior margin not extending to middle of pronotal disc, 4 rows of areolae at highest part, dorsal margin slightly arched. Median carina straight, extending to apex of posterior process, 1–2 rows of areolae at highest part, dorsal margin arched. Calli smooth. Paranotum less erect, narrowed posteriorly, 3 rows of areolae at widest part, with anterolateral angle slightly protruding anteriad, outer margin gently curved inwards at posterolateral angle, maximum height shorter than height of eye. Posterior process triangular, obtuse at apex.

Hemelytron (Fig. 16F) 2.5 times as long as its maximum width, extending beyond apex of abdomen, glabrous; maximum width across hemelytra 1.6 times as

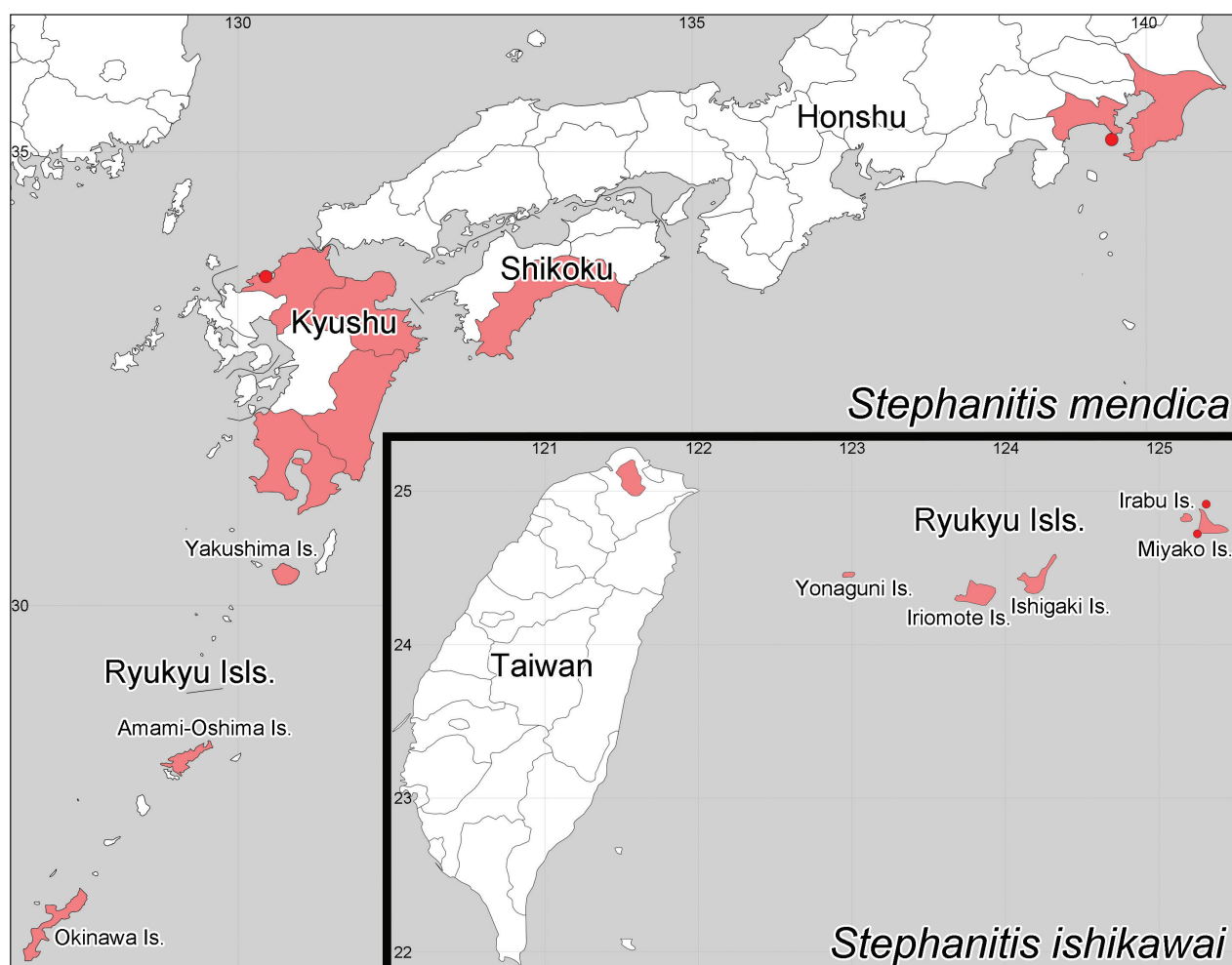
much as maximum width across paranota; apices close to each other in rest; costal area with 3 rows of areolae at widest part; subcostal area with 2 rows of areolae at widest part; discoidal area with 3–4 rows of areolae at widest part; sutural area with 3–4 rows of areolae at widest part; hypocostal lamina with a single row of areolae throughout its length; C (costal), R+M (radiomedial) and Cu (cubital) veins carinate.

Thoracic pleura (Fig. 12F) smooth in anterior part, coarsely punctate in posterior part. Ostiolar peritreme oblong. Sternal laminae (Fig. 20D) lower than bucculae; pro- and mesosternal laminae open in both anterior and posterior ends; metasternal laminae as high as mesosternal laminae, open at anterior ends, fused each other at posterior ends. Legs (Fig. 3F) smooth, densely covered with pubescence; femora thickest at middle.

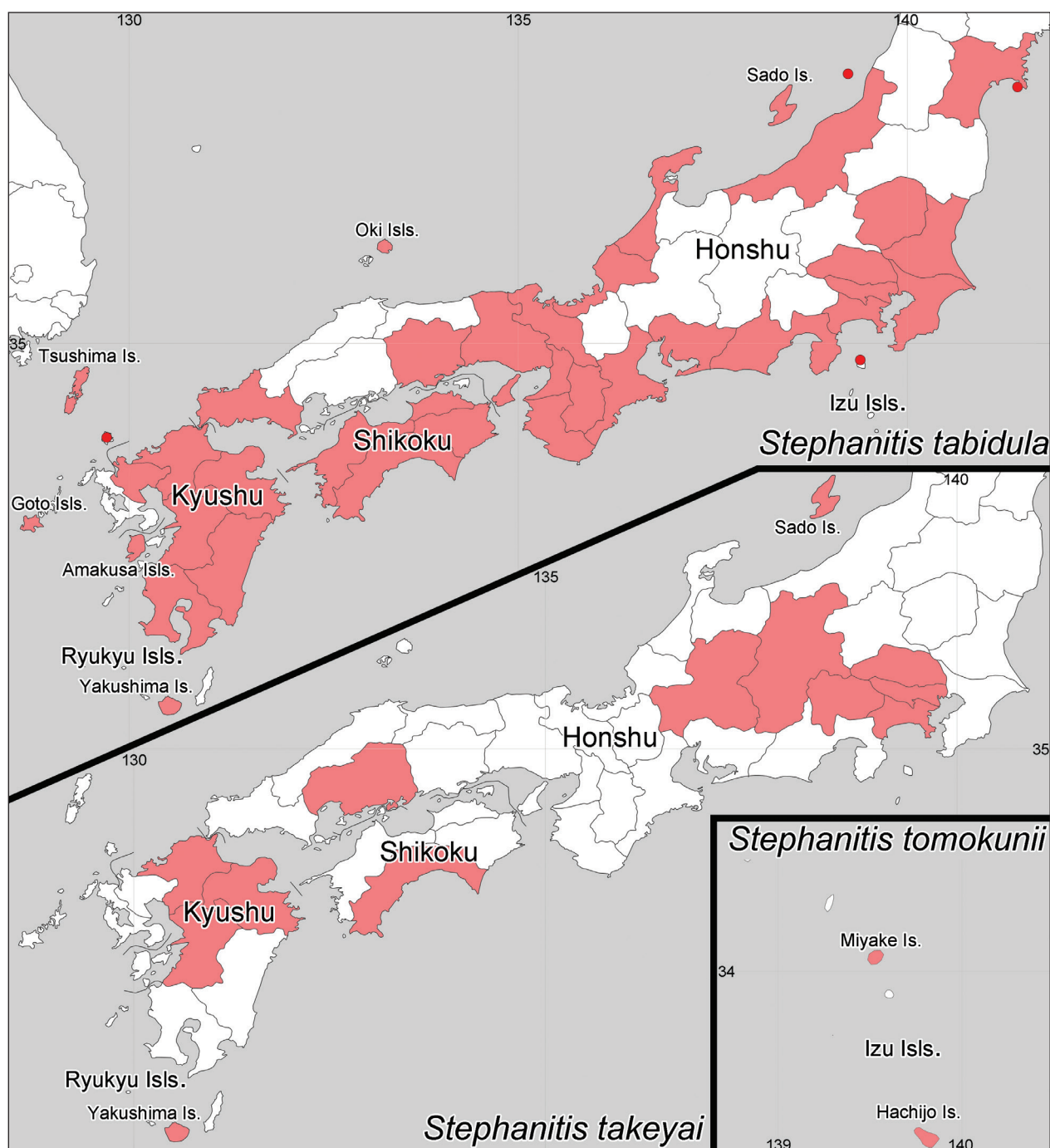




**Figure 46.** Collection sites of *Stephanitis (Norba) hayashii* sp. nov. and *S. (N.) hiurai* used in the present study. Red-filled areas = localities; circles = small isolated islands.



**Figure 47.** Collection sites of *Stephanitis (Norba) ishikawai* sp. nov. and *S. (N.) mendica* used in the present study. Red-filled areas = localities; circles = small isolated islands.



**Figure 48.** Collection sites of *Stephanitis* (*Stephanitis*) *tabidula*, *S. (S.) takeyai* and *S. (S.) tomokunii* sp. nov. used in the present study. Red-filled areas = localities; circles = small isolated islands.

Abdomen oblong in dorsal and ventral views. Pygophore (Figs 22D, 30H) compressed dorsoventrally, semicircular in ventral view, elevated at centre of venter, posterior margin slightly emarginate in middle part, covered with pubescence. Paramere (Fig. 32H) stout, expanded in middle part, weakly curved inwards at apex, outer margin not sinuate in middle part, inner margin nearly straight in basal part, covered with pubescence in middle part of outer and inner margins.

Measurements ( $n = 20$ ). Body length with hemelytra 3.1–3.4 mm; maximum width across hemelytra 1.4–1.5 mm; length of antennal segments I to IV 0.2 mm, 0.1 mm, 1.2–1.3 mm and 0.6 mm, respectively; pronotal length

1.2–1.4 mm; pronotal width across paranota 0.8–0.9 mm; hemelytral length 2.4–2.6 mm; maximum width of hemelytron 1.0–1.1 mm.

**Female.** General habitus very similar to that of male (Figs 5F, 10G, 14G, 18F, 24D) except for the following characters: body 2.1 times as long as maximum width across hemelytra; antennal segment III shorter than in male; pronotum 1.4 times as long as maximum width across paranota; hood wider than in male; maximum width across subcostal area wider than in male, with 2–3 rows of areolae at widest part; and apical part of abdomen pentagonal in ventral view.



Measurements ( $n = 20$ ). Body length with hemelytra 3.3–3.6 mm; maximum width across hemelytra 1.5–1.7 mm; length of antennal segments I to IV 0.2 mm, 0.1 mm, 1.0–1.1 mm and 0.6 mm, respectively; pronotal length 1.3–1.5 mm; pronotal width across paranota 0.9–1.0 mm; hemelytral length 2.5–2.7 mm; maximum width of hemelytron 1.0–1.2 mm.

**Remarks.** The partial COI gene pairwise sequence distances between *Stephanitis (Stephanitis) tomokunii* sp. nov. and *S. (S.) tabidula* are only 0.002645–0.007978 (Suppl. material 3) and both species are very similar in general habitus. In fact, *S. (S.) tomokunii* sp. nov. was misidentified as *S. (S.) tabidula* in previous studies (Takeya 1963; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012). However, the former is easily distinguished from the latter by the following characters: body in male 2.3 times (in female 2.1 times) as long as maximum width across hemelytra (in male 2.1 times and in female 2.0 times in *S. (S.) tabidula*) (Figs 3C, D, F, 5C, D, F); paranotum less erect (more erect in *S. (S.) tabidula*), narrowed posteriorly (slightly narrowed in *S. (S.) tabidula*), with anterolateral angle slightly protruding antierad

(protruding in *S. (S.) tabidula*), with maximum height shorter than height of eye (longer in *S. (S.) tabidula*) (Figs 8C, D, F, 10C–E, G, 12C, D, F, 14C–E, G, 26C, D, F, 28, D, F); and apex of paramere weakly curved inwards (strongly curved in *S. (S.) tabidula*) (Fig. 32E, F, H).

**Distribution.** Japan (Izu Islands (southern part): Miyake Island, Hachijo Island) (Fig. 48) (Takeya 1963; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012; present study). *Stephanitis (Stephanitis) tomokunii* sp. nov. inhabits the laurilignosa in a temperate climate of the southern part of the Izu Islands, which is in the Palaearctic Region.

**Etymology.** The new species is named in honour of Masaaki Tomokuni, a Japanese heteropterist who collected some of the paratype specimens.

**Host plants.** *Machilus thunbergii*, “Tabunoki” (Fig. 44F) (present study). *Stephanitis (Stephanitis) tomokunii* sp. nov. feeds only on this lauraceous tree and is monophagous.

**Biology.** *Stephanitis (Stephanitis) tomokunii* sp. nov. feeds on the abaxial surface of leaves of *Machilus thunbergii* (present study). Adults were collected in May, July and August (Takeya 1963; Tomokuni and Ishikawa 2002; present study); the nymph and overwintering stage are unknown.

## Key to Lauraceae-feeding species of *Stephanitis* from Japan

- 1 Pronotum tricarinate (Figs 7A, 8C–F, 9A, 10B, C, E–G, 25A, 26B–F)..... 2
- Pronotum unicarinate (Figs 7B–F, 8A, B, 9B–F, 10A, D, 25B–F, 26A)..... 6
- 2 Head, pronotal disc, marking on hemelytra and ventral surface black (Figs 12E, 14F, 16E, 18E, 20C, 22C, 24C); hood dark, longer than median carina of pronotum (Figs 8E, 10F, 26E); known from Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands, and northern part of Ryukyu Islands ..... *Stephanitis (Stephanitis) takeyai* Drake & Maa, 1955
- Head, pronotal disc, marking on hemelytra and ventral surface in various shades of brown (Figs 11A, 12C, D, F, 13A, 14B, C, E, G, 15A, 16B–D, F, 17A, 18B–D, F, 19A, 20A, B, D, 21A, 22A, B, D, 23A, 24A, B, D); hood pale, shorter than median carina of pronotum (Figs 7A, 8C, D, F, 9A, 10C, E, G, 25A, 26B–D, F) ..... 3
- 3 Body 1.8 times as long as maximum width across hemelytra (Figs 2A, 4A); hood completely covering eye (Figs 7A, 9A, 25A); median carina of pronotum with 3 rows of areolae at highest part (Figs 11A, 13A); paranotum with 4 rows of areolae at widest part; apices of hemelytra separated from each other in rest (Figs 15A, 17A); costal area of hemelytron with 5 rows of areolae at widest part; pygophore flat at centre of venter (Fig. 21A) ; known from Japan proper (Honshu, Shikoku and Kyushu).....*Stephanitis (Stephanitis) ambigua* Horváth, 1912
- Body at least 2.0 times as long as maximum width across hemelytra (Figs 3C, D, F, 5B, C, D, F); hood incompletely or not covering eye (Figs 8C, D, F, 10B, C, E, G, 26B–D, F); median carina of pronotum with 1–2 rows of areolae at highest part (Figs 12C, D, F, 14B, C, E, G); paranotum with 3 rows of areolae at widest part; costal area of apices of hemelytra close to each other in rest (Figs 16B–D, F, 18B–D, F); hemelytron with 3–4 rows of areolae at widest part; pygophore elevated at centre of venter (Figs 21B–F, 22A, B) ..... 4
- 4 Rostrum reaching metasternum (Fig. 20A); hood higher than median carina of pronotum at highest part, with posterior margin extending to middle of pronotal disc (Figs 10B, 14B, 26B, 28C); paranotum not narrowed posteriorly, with outer margin angularly curved inward at posterolateral angle; known from Japan proper (Honshu, Shikoku, and Kyushu) and its surrounding islands, and northern and central parts of Ryukyu Islands; feeding only on *Cinnamomum yabunikkei*; occurring only around “Tsuyu” (rainy season in Japan) .....*Stephanitis (Norba) mendica* Horváth, 1912
- Rostrum not reaching metasternum (Fig. 20B, D); hood as high as median carina of pronotum at highest part, with posterior margin not extending to middle of pronotal disc (Figs 10C, E, G, 14C, E, G, 26C, D, F, 28D, F); paranotum narrowed posteriorly, with outer margin gently curved inward at posterolateral angle..... 5
- 5 Body in male 2.1 times (in female 2.0 times) as long as maximum width across hemelytra (Figs 3C, D, 5C, D); paranotum more erect, slightly narrowed posteriorly, with anterolateral angle protruding antierad (Figs 8C, D, 10C, E, 12C, D, 14C, E, 26C, D); apex of paramere curved inwards (Fig. 32E, F); known from Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands and northern part of Izu and Ryukyu Islands.....*Stephanitis (Stephanitis) tabidula* Horváth, 1912
- Body in male 2.3 times (in female 2.1 times) as long as maximum width across hemelytra (Figs 3F, 5F); paranotum less erect, narrowed posteriorly, with anterolateral angle slightly protruding antierad (Figs 8F, 10G, 12F, 14G, 26F); apex of paramere weakly curved inward (Fig. 32H); endemic to southern part of Izu Islands.....*Stephanitis (Stephanitis) tomokunii* sp. nov.

- 6 Paranotum with 2 rows of areolae at widest part, with anterolateral angle slightly protruding anteriorly (Figs 7C, 9C, 25C); subcostal area of hemelytron in female with 2 rows of areolae at widest part (Fig. 17C); known from Daito Islands and central part of Ryukyu Islands ..... *Stephanitis (Norba) exigua* Horváth, 1912
- Paranotum with 3 rows of areolae at widest part, with anterolateral angle protruding anteriorly (Figs 7B, D–F, 8A, B, 9B, D–F, 10A, D, 25B, D–F); subcostal area of hemelytron in female with 3 rows of areolae at widest part (Figs 17B, D–F, 18A–C) ..... 7
- 7 Pronotal disc lustrous (Fig. 7E, F); R+M (radiomedial) vein of hemelytron in female not carinate (Fig. 17E, F); endemic to central part of Ryukyu Islands ..... *Stephanitis (Norba) hiurai* Takeya, 1963
- Pronotal disc opaque (Figs 7B, D, 8A, B, 9B, D, 10A, D); R+M (radiomedial) vein of hemelytron in female carinate (Figs 17B, D, 18A, C) ..... 8
- 8 Hood higher than median carina of pronotum at highest part (Fig. 28C); paranotum not narrowed posteriorly, with outer margin angularly curved inwards at posterolateral angle (Figs 8B, 26A); known from Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands, and northern and central parts of Ryukyu Islands; feeding only on *Cinnamomum yabunikkei*; occurring only around “Tsuyu” (rainy season in Japan) ..... *Stephanitis (Norba) mendica* Horváth, 1912
- Hood as high as median carina of pronotum at highest part (Figs 27B, D, 28B, D); paranotum narrowed posteriorly, with outer margin gently curved inward at posterolateral angle (Figs 7B, D, 8A, 9B, D, 10A, D, 25B, D, F) ..... 9
- 9 Rostrum not reaching metasternum (Figs 19B, 20B); hood as high as median carina of pronotum at highest part, with posterior margin not extending to middle of pronotal disc (Figs 7B, 9B, 10D, 11B, 13B, 14D, 25B); known from Japan proper (Honshu, Shikoku, and Kyushu) and its surrounding islands, and northern part of Izu and Ryukyu Islands ..... 10
- Rostrum reaching metasternum (Fig. 19D, F); hood slightly higher than median carina of pronotum at highest part, with posterior margin extending to middle of pronotal disc (Figs 7D, 8A, 9D, 10A, 11D, 12A, 13D, 14A, 25D, F); known from central and southern parts of Ryukyu Islands ..... 11
- 10 Paranotum less erect, narrowed posteriorly, maximum height shorter than height of eye (Figs 7B, 9B, 11B, 13B, 25B, 27B); apex of paramere weakly curved inward (Fig. 31B) ..... *Stephanitis (Norba) aperta* Horváth, 1912
- Paranotum more erect, slightly narrowed posteriorly, maximum height longer than height of eye (Figs 10D, 14D, 28D); apex of paramere strongly curved inward (Fig. 32E); teratological form .... *Stephanitis (Stephanitis) tabidula* Horváth, 1912
- 11 Length of antennal segment IV 0.6 mm; paranotum more erect (Figs 7D, 9D, 11D, 13D); paramere slender, inner margin slightly curved inwards in basal part (Fig. 31C, D); endemic to central part of Ryukyu Islands ..... *Stephanitis (Norba) hayashii* sp. nov.
- Length of antennal segment IV 0.7–0.8 mm; paranotum less erect (Figs 8A, 10A, 12A, 14A); paramere stout, inner margin nearly straight in basal part (Fig. 32A–C); endemic to southern part of Ryukyu Islands ..... *Stephanitis (Norba) ishikawai* sp. nov.

## Discussion

### Morphological characters for species identification

Several authors diagnosed *Stephanitis* species, based on characteristics such as colouration, length of antennal segments and rostrum, the shape of pronotum and hemelytron, number of pronotal and hemelytral areolae and the structure of male genitalia (Horváth 1912; Takeya 1931, 1963; Drake 1948; Jing 1981; Péricart 1983; Souma 2020c etc.). In the present study, the author confirmed the utility of these characteristics for the identification of Lauraceae-feeding species of *Stephanitis* from Japan. However, the colouration of the hemelytron, which was used for identification in previous studies, often based on few specimens from few localities (e.g. Horváth 1912; Drake 1948; Takeya 1963), has high intraspecific variation and is useless for identification. For example, while *S. (Stephanitis) tabidula* was generally considered to have hemelytra with indistinct markings in previous studies (Drake 1948; Takeya 1963), some individuals were herein observed to have hemelytra with distinct markings (Fig. 42D). Additionally, although sexual dimorphism in *Stephanitis* can be observed in the length of antennal

segment III and the number of areolae of the hemelytral subcostal area, as mentioned in the below section, previous studies (Horváth 1912; Takeya 1931, 1963; Drake 1948; Yamada and Tomokuni 2012; Souma 2020c etc.) have identified species without considering these aspects. Therefore, the descriptions and identification keys provided by previous studies (Horváth 1912; Takeya 1931, 1963; Drake 1948; Yamada and Tomokuni 2012; Souma 2020c etc.) are at least partially unworkable. Lee (1969) tried to identify *Stephanitis* species, based on differences in the structure of the phallus. The differences observed are judged to be small and partly subjective; many close relatives of the treated species were not illustrated. Lee’s collection seems to be mostly lost (Cho et al. 2020), making it impossible to re-examine the material. Thus, the structure of the phallus was not compared in the present study. The structure of the pygophore and paramere is confirmed to be certainly useful for identifying some species (*S. (S.) ambigua*, *S. (Norba) hayashii* sp. nov., *S. (S.) tabidula* and *S. (S.) takeyai*). The structure of male genitalia is not used in the current taxonomic studies on Tingidae (e.g. Guilbert 2015; Guilbert and Guidotti 2018; Guilbert et al. 2018), despite previous studies indicating that the phallus possesses a complex structure (Lis 2004). A future comprehensive and detailed examination



of the male genitalia of Tingidae may improve taxonomic studies. Conversely, no morphological difference was herein found in the shape of female terminalia in Lauraceae-feeding species of *Stephanitis* from Japan (Figs 23, 24). In conclusion, the taxonomic confusion regarding *Stephanitis* species may have been caused by the misidentification of some specimens from some localities without considering intraspecific variation and sexual dimorphism. Future taxonomic studies should identify *Stephanitis* species, based on many specimens from various localities, using enough morphological characters.

## Sexual dimorphism

In the genus *Stephanitis*, sexual dimorphism in the structure of antennae has been described for *S. (Stephanitis) nashi* (Wang et al. 2020): long antennal sensilla denser in males than in females; antennal segment III longer in males than in females. Additionally, the following sexually dimorphic features were found in nine species, except *S. (S.) ambigua*, in the present study (Figs 2–5, 7–10, 15–18): body narrower in males than in females; hood often narrower in males than in females; subcostal area of hemelytron narrower in males than in females; and the number of rows of the subcostal area usually one less in males than in females. Sexual dimorphism was not considered in previous taxonomic studies on *Stephanitis*, even though the sexually dimorphic structures of the pronotum and hemelytron are important characters for identifying species. Therefore, some species cannot be accurately identified using the identification keys provided by previous studies (Takeya 1963; Yamada and Tomokuni 2012). For instance, male *S. (Norba) aperta* cannot be distinguished from male *S. (N.) exigua*, based on the number of areolae in the subcostal area of the hemelytron, unlike in previous studies (Takeya 1963; Yamada and Tomokuni 2012). However, females of the former species can be distinguished from those of the latter, based on their character, as in previous studies (Takeya 1963; Yamada and Tomokuni 2012). In conclusion, sexual dimorphism must be considered in future taxonomic studies on *Stephanitis*.

## DNA barcoding

To date, taxonomic studies on Tingidae (e.g. Guilbert 2015; Guilbert and Guidotti 2018; Guilbert et al. 2018) have been conducted considering morphological characters such as those mentioned in the previous section. However, part of the characteristics used to identify species have high intraspecific variation depending on the genus and/or species. Interspecies differences among the Lauraceae-feeding species of *Stephanitis* from Japan are sometimes difficult to judge, based on the available morphological characters. In the present study, phylogenetic analyses and species delimitation, based on DNA barcoding of the COI region, were performed for 53 individuals of 10 provision-

ally identified morphological species of *Stephanitis*, with four individuals of *Cochlochila (Physodictyon) conchata* as the outgroup. Although only minor genetic differences were confirmed, based on the pairwise distances from the K2P model (Suppl. material 3) between *S. (Norba) aperta* and *S. (N.) hiurai* and between *S. (Stephanitis) tabidula* and *S. (S.) tomokunii* sp. nov., all the 10 morphological species formed monophyletic or independent clades in the Bayesian tree (Fig. 1; Suppl. material 1). This tree does not define the phylogeny of the genus *Stephanitis*, but it indicates that the DNA barcoding of the COI region is an effective method for identifying the Lauraceae-feeding species of *Stephanitis* from Japan, which are very similar to each other. Future morphology-based taxonomic studies on Tingidae could be improved by the DNA barcoding of the COI region.

## Distribution range of species in Japan

To the best of the present author's knowledge and based on previous studies (Matsumura 1905; Horváth 1912; Takeya 1931, 1951b, 1953; Drake 1948; Drake and Maa 1955; Miyamoto 1964a, 1964b; Tomokuni 1981, 2006a; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012; Yamada and Ishikawa 2016 etc.), the distribution range of Lauraceae-feeding species of *Stephanitis* in Japan can be divided into six environments and/or regions (Figs 45–48): (1) Two species—*S. (Stephanitis) ambigua* and *S. (S.) takeyai*—are distributed in the deciduous broad-leaved forest of Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands and the northern part of the Ryukyu Islands (*S. (S.) takeyai*), which is located in the Palearctic Region; (2) Two species—*S. (Norba) aperta*, and *S. (S.) tabidula*—are distributed in the laurilignosa of Japan proper and its surrounding islands and the northern part of the Izu and Ryukyu Islands, which is located in the Palearctic Region; (3) Only one species—*S. (N.) mendica*—is widely distributed in the laurilignosa of the Palearctic and Oriental Regions (Japan proper and its surrounding islands and the northern and central parts of the Ryukyu Islands); (4) Only one species—*S. (S.) tomokunii* sp. nov.—is distributed in the laurilignosa of the southern part of the Izu Islands, which is located in the Palearctic Region; (5) Three species—*S. (N.) exigua*, *S. (N.) hayashii* sp. nov., and *S. (N.) hiurai*—are distributed in the laurilignosa of the central part of the Ryukyu Islands and the Daito Islands (*S. (N.) exigua*), which is located in the Oriental Region; (6) only one species—*S. (N.) ishikawai* sp. nov.—is distributed in the laurilignosa of the southern part of the Ryukyu Island, which is located in the Oriental Region. Outside Japan, *S. (S.) ambigua* and *S. (S.) tabidula* are distributed in southern Korea, which is in the Palearctic Region (Ahn et al. 2018; Cho et al. 2020) and *S. (N.) ishikawai* sp. nov. is distributed in northern Taiwan, which is in the Oriental Region (Takeya 1931, 1963; present study). Additionally, *S. (N.) esakii* Takeya, 1931 and *S. (S.) gallarum* Horváth, 1906

also feed on lauraceous trees in Taiwan (Takeya 1963). Therefore, Lauraceae-feeding species of *Stephanitis* are distributed in different regions and/or environments in Japan and its surrounding regions. The eight species inhabiting laurilignosa in Japan are similar in their morphology and may be closely related. However, the discussion of possible geographic speciation of these eight species must be based on further studies on the phylogenetic relationships amongst East Asian species of *Stephanitis*.

## Making public awareness

All species of *Stephanitis* for which the host plants are known to feed on the abaxial side of leaves of angiosperms (e.g. Takeya 1951a; Takahashi 1990a; Yasunaga et al. 1993; Souma 2020c, 2021b, 2021c) make visible damage left on leaves during feeding similar to many tingids (Figs 43, 44). From the author's experience in fieldwork, most species of *Stephanitis* are relatively abundant in their habitats and collecting a number of individuals during emergence time is easy. Thus, oligophagous species feeding on common plants (e.g. *S. (Norba) aperta* and *S. (Stephanitis) tabidula*) or euryphagous species (*S. (S.) takeyai*) are very frequently recorded amongst the Japanese Tingidae (Takeya 1963; Maehara 2014; Okochi 2019; Souma 2021b etc.). However, monophagous species collected from rare plants (e.g. *S. (Menodora) formosa* Horváth, 1912) (Souma 2020f) or having a limited distribution range (e.g. *S. (N.) hiurai*) (present study) are difficult to find and are not common in historical records. Additionally, the distribution of the commonly collected species of *Stephanitis* is localised to focused collecting events versus broad sampling across their host plant's distribution range. To the best of the author's knowledge, only a few leaf-feeding tingids of other genera can be easily collected and are frequently recorded in Japan. Moreover, some species of other genera (*Baeochila* Drake & Poor, 1937, *Physatocheila* Fieber, 1844 and *Tingis* Fabricius, 1803) have been reported from fruits and vines (Souma 2019, 2020a, 2020b), but these species are difficult to collect due to lack of visible damage. In Japan, only a few common leaf-feeding lace bugs mainly composed of *Stephanitis* species are recognised by the public. In the present study, multiple species confused in the common species of *Stephanitis* were described as new species. In other words, some of the most common Japanese tingids have been considered to be recognised by the public, but have actually been poorly known. Although monophagous species of *Stephanitis* feeding on endemic plants of Japan (e.g. *S. (S.) drakei* Takeya, 1963) have been known as endemic species (Souma 2021b), this study reveals that monophagous or oligophagous species feeding on non-endemic plants of Japan (*S. (N.) aperta*, *S. (N.) exigua*, *S. (N.) hayashii* sp. nov., *S. (N.) hiurai*, *S. (N.) ishikawai* sp. nov., *S. (N.) mendica* and *S. (S.) tomokunii* sp. nov.) or euryphagous species (*S. (S.) takeyai*) have

sometimes limited distribution ranges. Since most species of *Stephanitis* from Japan are relatively easy to collect and have clear relationships with host plants, they will provide good research material for considering the characteristics of the phytophagous heteropteran fauna in Japan. Making the public aware of the existence of endemic species of *Stephanitis* may promote the public's appreciation of nature in the Japanese archipelago, a global biodiversity hotspot (Conservation International 2021). As a result of taxonomic issues that hinder the identification of some tingids, even common species, presenting an easy method of identification is essential for clarifying the current diversity of the taxon and increasing public awareness of the Japanese Tingidae.

## Host plant relationship

Of the 10 Lauraceae-feeding species of *Stephanitis* from Japan, seven—*S. (Norba) aperta*, *S. (N.) exigua*, *S. (N.) hiurai*, *S. (N.) ishikawai* sp. nov., *S. (Stephanitis) tabidula*, *S. (S.) takeyai*, and *S. (S.) tomokunii* sp. nov.—were collected from *Machilus thunbergii*; six of these species (except for *S. (S.) takeyai*) were confirmed to feed on this lauraceous tree (Takeya 1931, 1963; Drake 1948; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Maehara 2014; present study). According to the observations made in the present study, *M. thunbergii* was damaged by *Stephanitis* species in its entire approximate distribution range in Japan, which almost corresponds to the distribution range of laurilignosa in the country (cf. Tagawa 1995; Tanaka and Matsui 2007–2021). In Japan proper (Honshu, Shikoku and Kyushu) and its surrounding islands and the northern part of the Izu and Ryukyu Islands, *M. thunbergii* is damaged by two species, *S. (N.) aperta* and *S. (S.) tabidula* (Takeya 1931, 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; Maehara 2014; Okochi 2019; present study). The present author has frequently collected *S. (N.) aperta* along the coast and *S. (S.) tabidula* inland, but the habitat isolation of these species is ambiguous as many exceptions were confirmed. In the central part of the Ryukyu Islands, *M. thunbergii* is damaged by two species, *S. (N.) exigua* and/or *S. (N.) hiurai* (Takeya 1963; Yamada and Tomokuni 2012; present study); however, habitat isolation in Okinawa Island, where both species are distributed, is unknown. In the southern part of Izu and Ryukyu Islands, *M. thunbergii* is damaged by only one species each, *S. (S.) tomokunii* sp. nov. and *S. (N.) ishikawai* sp. nov., respectively (Yasunaga et al. 1993; present study). Therefore, *M. thunbergii*, which is one of the dominant species of the Japanese laurilignosa (Tagawa 1995), is considered an important host plant for Lauraceae-feeding species of *Stephanitis* from Japan. The remaining lauraceous host plants except *Cinnamomum yabunikkei* are damaged by *Stephanitis* species only in limited regions of Japan (Takeya 1963; Yasunaga et al. 1993; Yamada and Tomokuni 2012; present study).



## Conclusions

In the present study, a total of 5,080 specimens of Lauraceae-feeding species of *Stephanitis* from Japan were identified to 10 species, based on morphological characteristics. The results of the DNA barcoding of the COI region for 53 individuals of these 10 species matched the identification using morphological characters. In conclusion, 10 species of *Stephanitis* feeding on Lauraceae were identified in Japan: *S. (Stephanitis) ambigua*, *S. (Norba) aperta*, *S. (N.) exigua*, *S. (N.) hayashii* sp. nov., *S. (N.) hiurai*, *S. (N.) ishikawai* sp. nov., *S. (N.) mendica*, *S. (S.) tabidula*, *S. (S.) takeyai* and *S. (S.) tomokunii* sp. nov. The host plants of these 10 species are herein recorded and *Machilus thunbergii* seems to be one of the most important host plants for the Japanese species feeding on Lauraceae. Extensive fieldwork revealed that different Lauraceae-feeding species of *Stephanitis* are distributed in different regions and/or environments in Japan. The 10 lace bugs herein studied are common species in their distribution range, but the three new species described were previously misidentified (Takeya 1931, 1963; Miyamoto 1964a, 1964b; Yasunaga et al. 1993; Tomokuni and Ishikawa 2002; Yamada and Tomokuni 2012). Integrative taxonomy, based on DNA barcoding and morphological characters, improved the identification of Lauraceae-feeding species of *Stephanitis* with a high intraspecific and poor interspecific variation. A high number of specimens from various localities with host records are necessary for future taxonomic studies on *Stephanitis*.

## Acknowledgements

I sincerely thank Dávid Rédei (National Chung Hsing University, Taichung, Taiwan), Toshiharu Mita and Naomichi Ohara (ELKU) for the useful advice on the existence of type specimens and Alexander H. Knudson (North Dakota State University, Fargo, U.S.A.) and Dávid Rédei for critical comments to the manuscript. I acknowledge Kazunori Yoshizawa, Masahiro Ohara (ELHU), Kyohei Watanabe (KPMNH), Munetoshi Maruyama, Junna Matsumoto (KUM), Yukinobu Nakatani (NIAES), Masaaki Tomokuni, Takuya Kiyoshi (NSMT) and Tadashi Ishikawa (TUA) for the loan of valuable materials. I owe my deepest gratitude to Masami Hayashi (KUM), Hiraku Yoshitake (NIAES), Hiroaki Konno (Miyagi, Japan), Satoshi Mae-hara (Tochigi, Japan), Yoshihiro Yamada (Chiba, Japan), Yu Kato, Hiroaki Shigetoh (Kanagawa, Japan), Kiyoshi Nakano, Gô Mashima (Niigata, Japan), Ryudai Ito (Nara, Japan), Yuta Waki (Tokushima, Japan), Kiyoshiro Goto (Kumamoto, Japan), Reo Ito (Oita, Japan), Hideo Ogai (Okinawa, Japan), Yuito Obae (Tottori University, Tottori, Japan), Yutaka Tamadera (ELHU), Sadahisa Yagi, Naomichi Tsuji, Shota Inoue, Shunsuke Imada, Yu Hisasue, Yutaro Uehara, Shogo Chuman (ELKU), Hiroaki Kojima, Shusuke Shimamoto, Tomoya Saeki (TUA) and Yao-Jin Tsai (Taipei City, Taiwan) for kindly providing valuable

materials and information on the collection sites. I appreciate Jing-Fu Tsai (NMNS) for the depository of the specimens and Naoki Kaneko (Tokyo, Japan), Hiroki Nagano (Osaka, Japan), Kenji Hagiwara, Takumi Koshizawa (Chiba, Japan), Hiroaki Yoshikawa (Kagoshima, Japan), Shota Inoue (ELKU), Hiroaki Kojima, Masami Yamada (TUA) and Hiraku Yoshitake (NIAES) for accompanying me on fieldwork. I am grateful to Kazutaka Yamada (Tokushima Prefectural Museum, Tokushima, Japan) for connecting me to Hideo Ogai. This work was partially supported by a Grant-in-Aid for JSPS Fellows (JP20J20483) to the author from the Japan Society for the Promotion of Science, Tokyo, Japan. I would like to thank Editage ([www.editage.com](http://www.editage.com)) for English language editing.

## References

- Ahn SJ, Kim WG, Kim SS, Park CG (2018) The Terrestrial Heteroptera of Korea. Nature & Ecology, Seoul, Korea, 632 pp. [in Korean]
- Altschul SF, Madden TL, Schaffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: A new generation of protein database search programs. *Nucleic Acids Research* 25(17): 3389–3402. <https://doi.org/10.1093/nar/25.17.3389>
- Aukema B, Rieger C, Rabitsch W (2013) Catalogue of the Heteroptera of the Palaearctic Region. Vol. 6, Supplement. Netherlands Entomological Society, Amsterdam, Netherlands, [xxiv +] 629 pp.
- Azuma S, Kinjo M (1987) Check-list of the insects of Okinawa. The Biological Society of Okinawa, Nishihara, Okinawa, Japan, 422 pp.
- Bailey NS (1950) An Asiatic tingid new to North America (Heteroptera). *Psyche* (New York) 57(4): 143–145. <https://doi.org/10.1155/1950/85276>
- Barta M, Bideň T (2016) *Stephanitis takeyai* and *S. rhododendri* (Heteroptera: Tingidae) in Slovakia: First record and economic importance. *Journal of Plant Protection Research* 56(2): 193–198. <https://doi.org/10.1515/jppr-2016-0022>
- Cho G, Kim W, Kwon YS, Lee S (2020) Check list of lace bugs (Hemiptera: Tingidae) of Korea. *Journal of Asia-Pacific Entomology* 23(3): 736–745. <https://doi.org/10.1016/j.aspen.2020.04.005>
- Conservation International (2021) Biodiversity Hotspots. <https://www.conservation.org/priorities/biodiversity-hotspots> [Accessed: 2021-11-1]
- Drake CJ (1923) Some Tingitidae from Japan (Hemip.). *The Ohio Journal of Science* 23(2): 102–106.
- Drake CJ (1937) Tingitidae from South China (Hemiptera). *Lingnan Science Journal* 16(3): 591–594.
- Drake CJ (1938) Chinese Tingitidae (Hemiptera). *Lingnan Science Journal* 17(2): 195–197.
- Drake CJ (1948) New species of *Stephanitis* Stål including a list of species of the World. *Notes d'Entomologie Chinoise* 12(6): 45–56.
- Drake CJ, Davis NT (1960) The morphology, phylogeny, and higher classification of the family Tingidae, including the description of a new genus and species of the subfamily Vianaidinae (Hemiptera: Heteroptera). *Entomologica Americana* 39: 1–100.
- Drake CJ, Maa TC (1953) Chinese and other Oriental Tingoidae (Hemiptera). *Quarternary Journal of Taiwan Museum* 6(2): 87–101.
- Drake CJ, Maa TC (1955) Chinese and other Oriental Tingoidae (Hemiptera). Part III. *Quarternary. Journal of Taiwan Museum* 8(1): 1–11.

- Drake CJ, Poor ME (1936) The genera and genotypes of Tingitoidea of the Western Hemisphere. *Iowa State College Journal of Science* 10(4): 381–390.
- Drake CJ, Poor ME (1937) Some Tingitidae (Hemiptera) from Oceania. *Iowa State College Journal of Science* 11(4): 397–404. <https://doi.org/10.5962/p.234850>
- Drake CJ, Ruhoff FA (1965) Lacebugs of the world, a catalog (Hemiptera: Tingidae). *Bulletin of the United States National Museum* 243: [i–viii +] 1–634[. pls. frontis piece + 1–56]. <https://doi.org/10.5479/si.03629236.243.1>
- Esaki T, Takeya C (1931) Identification of a Japanese Tingid injurious to the pear tree. *Mushi* 4: 51–59[. tab. 4].
- Grosso-Silva JM, Frias I, van der Heyden T (2020) *Stephanitis takeyai* Drake & Maa, 1955 (Hemiptera: Tingidae), new species for Portugal. *Arquivos entomológicos* 22: 371–372.
- Guilbert E (2015) New species and new records of Tingidae (Hemiptera: Heteroptera) from Vietnam. *Zootaxa* 3956(4): 531–546. <https://doi.org/10.11646/zootaxa.3956.4.5>
- Guilbert E, Guidoti M (2018) New species and new records of Tingidae (Hemiptera: Heteroptera) from Thailand. *Zootaxa* 4482(2): 274–296. <https://doi.org/10.11646/zootaxa.4482.2.3>
- Guilbert E, Pham HT, Soulier-Perkins A (2018) New species and new records of Tingidae (Insecta: Heteroptera) from Vietnam. *Zootaxa* 4387(3): 591–600. <https://doi.org/10.11646/zootaxa.4387.3.11>
- Hayashi M (2002) Heteroptera. In: Azuma S, Yafuso M, Kinjo M, Hayashi M, Kohama T, Sasaki T, Kimura M, Kawamura F (Eds.) 沖縄産昆虫目録 [Check List of the Insect of the Ryukyu Islands (2<sup>nd</sup> Edn.)]. The Biological Society of Okinawa, Nishihara, Okinawa, Japan, 127–150. [in Japanese]
- Horváth G (1906) Synopsis Tingitidarum Regionis palaearticae. *Annales Historico-Naturales Musei Nationalis Hungarici* 4: 1–117.
- Horváth G (1912) Species generis Tingitidarum *Stephanitis*. *Annales Historico-Naturales Musei Nationalis Hungarici* 10: 319–339.
- Ichita T (1989) 青森県のカメムシ (II) [True bugs from Aomori-ken, Honshu, Japan. (II)]. *Celastrina* 22: 29–38. [in Japanese]
- Ito R, Sasaki S (2018) 大分県のカメムシ (グンバイムシ科) [Tingidae from Oita-ken, Kyushu, Japan (Heteroptera)]. *Niho-no-Mushi* 56: 17–24 [in Japanese]
- Japanese Society of Applied Entomology and Zoology [Ed.] (1980) Major Insect and other Pests of Economic Plants in Japan. Japan Plant Protection Association, Tokyo, Japan, 307 pp. [in Japanese]
- Japanese Society of Applied Entomology and Zoology [Ed.] (2006) Major insect and other pests of economic plants in Japan (Revised edition). Japan Plant Protection Association, Tokyo, Japan, 387 pp. [in Japanese]
- Jing HL (1981) Tingidae. In: Hsiao TY, Ren SZ, Zheng LY, Jing HL, Zou HG, Liu SL: A handbook for the determination of the Chinese Hemiptera-Heteroptera (Volume II). Science Press, Beijing, China, 271–368[. pls. 42–50]. [in Chinese with English summary].
- Jung S, Duwal RK, Lee S (2011) COI barcoding of true bugs (Insecta, Heteroptera). *Molecular Ecology Resources* 11(2): 266–270. <https://doi.org/10.1111/j.1755-0998.2010.02945.x>
- Kass RE, Carlin BP, Gelman A, Neal R (1998) Markov chain Monte Carlo in practice: A roundtable discussion. *The American Statistician* 52(2): 93–100. <https://doi.org/10.1080/00031305.1998.10480547>
- Knudson AH, Rider DA, Knodel JJ (2021) Two new species of Tingidae (Hemiptera: Heteroptera) from Panama. *Zootaxa* 4958(1): 334–344. <https://doi.org/10.11646/zootaxa.4958.1.20>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Lee CE (1967) Tingidae from Korea (Heteroptera). *Mushi* 41: 91–111.
- Lee CE (1969) Morphological and phylogenetic studies on the larvae and male genitalia of the East Asiatic Tingidae (Heteroptera). *Journal of the Faculty of Agriculture, Kyushu University* 15(2): 137–256[. pl. 1–16]. <https://doi.org/10.5109/22784>
- Lis B (2004) Comparative studies on the ductus seminis of aedeagus in Tingioidea (Hemiptera: Heteroptera). *Polish Journal of Entomology* 73: 245–258.
- Maa TC (1957) Nymphal stages of certain Oriental Tingidae (Hemiptera). *Quarterly Journal of Taiwan Museum* 10(3,4): 117–133.
- Machara S (2014) 栃木県のカメムシについて [Tingidae from Tochigi-ken, Honshu, Japan]. *Insekuto* 65(1): 57–64. [in Japanese]
- Machara S (2017) 栃木県で採集されたカメムシ類について [True bugs collected from Tochigi-ken, Honshu, Japan]. *Insekuto* 68(2): 144–149. [in Japanese]
- Matsumura S (1905) Thousand insects of Japan II. Keiseisha, Tokyo, Japan, 213 pp.[ + 17 pls.] [in Japanese]
- Matsumura S (1907) Konchu bunrui-gaku Jokan. Keiseisha, Tokyo, Japan, 344 pp. [in Japanese]
- Miyamoto S (1964a) Tingidae and Nabidae of the South-West Islands, Lying Between Kyushu and Formosa (Hemiptera). *Kontyû* 32(2): 271–280.
- Miyamoto S (1964b) Additions to the tingid fauna of the South-West Islands, lying between Kyushu and Formosa (Hemiptera). *Kontyû* 32(4): 523–528.
- Miyamoto S (1964c) Heteroptera collected by the Second Kyushu University Expedition to the Yaeyama Group, 1963 (excluding the Lygaeidae and Reduviidae). *Reports of the Committee on Foreign Scientific Research. Kyushu University* 2: 99–110.
- Miyamoto S (1965) グンバイムシ科 [Tingidae]. In: Yasumatsu K, Asahina S, Ishihara T (Eds) *Iconographia Insectorum Japonicorum Colore Naturali Edita Vol. III. Hokuryukan, Tokyo, Japan*, 90–92[. pl. 45–46]. [in Japanese]
- Miyamoto S (1976) 対馬産異翅半翅類 (2) —トコジラミ型類その他— [Heteroptera of Tsushima (2) Cimicomorpha and the others]. In: The Nagasaki Biological Society (Ed.) 対馬の生物 [The creatures of Tsushima Island, Kyushu, Japan]. The Nagasaki Biological Society, Nagasaki, Japan, 497–510. [in Japanese]
- Miyamoto S (2008) グンバイムシ科 [Tingidae]. In: Hirashima Y, Morimoto K (Eds) *Iconographia Insectorum Japonicorum Colore Naturali Edita Vol. III (New Edition). Hokuryukan, Tokyo, Japan*, 156–159[. pl. 54–55]. [in Japanese]
- Miyamoto S, Yasunaga T (1989) Heteroptera. In: Hirashima Y (Ed.) A Check List of Japanese Insects. I. Laboratory of Entomology, Faculty of Agriculture, Kyushu University, Fukuoka, Japan, 151–188. [in Japanese]
- Miyatake Y (2006) *Stephanitis takeyai* (Tingidae) injured the plane-tree (Platanaceae) in Honshu, Japan. *Rostria* 52: 27–28. [in Japanese with English Summary]
- Nakatani Y (2021) Terrestrial heteropterans collected from Daito Islands, the Ryukyus. *Rostria* 66: 77–80. [in Japanese]
- Nozaki T, Nozaki Y, Uki K, Tsukada T (2015) The heteropteran fauna of Shimokoshiki Island, Kagoshima Prefecture, Japan. *Rostria* 58: 1–40. [in Japanese with English summary]
- Okochi A (2019) 山陰地方で採集したグンバイムシ [Tingidae collected from Sanin district, Honshu, Japan]. *Sukashiba* 66: 1–4. [in Japanese]



- Oshanin B (1912) Katalog der Paläarktischen Hemipteren 1 (Heteroptera, Homoptera-Auchenorrhyncha und Psylloidea). Friedländer, Berlin, Germany, [xiv +] 187 pp. <https://doi.org/10.5962/bhl.title.13940>
- Péricart J (1983) Faune de France 69. Hémiptères Tingidae euro-méditerranéens. Fédération Française des Sociétés de Sciences Naturelles, Paris, France, 620 pp.
- Péricart J, Golub VB (1996) Superfamily Tingioidea Laporte, 1832. In: Aukema B, Rieger C (Eds) Catalogue of the Heteroptera of the Palaearctic Region. Vol. 2, Cimicomorpha I. Netherlands Entomological Society, Amsterdam, Netherlands, 3–78.
- Rambaut A (2014) FigTree Ver. 1.4.4. <http://tree.bio.ed.ac.uk/software/figtree/> [Accessed: 2021-6-24]
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer. Version 1.6. <http://beast.bio.ed.ac.uk/Tracer> [Accessed: 2021-6-24]
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Saito K (1933) 朝鮮産軍配蟲ノ一新變種及一未記録種ニ就テ (附、朝鮮産軍配蟲ノ食餌植物) [On a new variety and unrecorded species of Tingidae from Korea, with brief notes on their host plants]. *Journal of the Chosen Natural History Society* 15: 5–7. [in Japanese]
- Schuh RT, Weirauch C (2020) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history (2<sup>nd</sup> edn.). Siri Scientific Press, Manchester, UK, 768 pp., [32 pls]
- Shorthouse DP (2010) SimpleMapp, an online tool to produce publication-quality point maps. <http://www.simplemapp.net> [Accessed: 2022-6-28]
- Simon C, Rati FF, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87(6): 651–701. <https://doi.org/10.1093/aesa/87.6.651>
- Souma J (2019) *Physatocheila nigrintegerrima* sp. nov. from Japan: a first fruit-feeder of the genus (Hemiptera: Heteroptera: Tingidae). *Zootaxa* 4638(2): 264–272. <https://doi.org/10.11646/zootaxa.4638.2.6>
- Souma J (2020a) Discoveries of the genera *Baeochila* and *Idiocysta* from Japan, with descriptions of two new species (Hemiptera: Heteroptera: Tingidae). *Zootaxa* 4731(3): 388–402. <https://doi.org/10.11646/zootaxa.4731.3.7>
- Souma J (2020b) Taxonomic study of the subgenus *Tropidocheila* of the lace bug genus *Tingis* (Hemiptera: Heteroptera: Tingidae) from Japan, with description of *Tingis* (*Tropidocheila*) *yamaboushi* sp. nov. collected from *Cornus kousa* (Cornaceae). *Zootaxa* 4868(2): 284–294. <https://doi.org/10.11646/zootaxa.4868.2.8>
- Souma J (2020c) *Stephanitis* (*Stephanitis*) *raphiolepidis* sp. nov. (Hemiptera: Heteroptera: Tingidae) from Japan: First representative of the genus feeding on the evergreen rosaceous plant. *Journal of Insect Biodiversity* 17(2): 36–47. <https://doi.org/10.12976/jib/2020.17.2.2>
- Souma J (2020d) The monocotyledon-feeding lace bugs of the genus *Agramma* from Japan (Hemiptera: Heteroptera: Tingidae). *Acta Entomologica Musei Nationalis Pragae* 60(2): 527–536. <https://doi.org/10.37520/aemnp.2020.035>
- Souma J (2020e) Notes on habitat, 5<sup>th</sup> instar nymph, teratological form and emergence of *Tingis* (*Tingis*) *lasiocera* Matsumura, 1907 (Heteroptera: Tingidae). *Rostria* 64: 34–37. [in Japanese]
- Souma J (2020f) Rediscovery of *Stephanitis* (*Menodora*) *formosa* Horváth, 1912 (Heteroptera, Tingidae) from Japan after an interval of 58 years, with a new record from Iriomote Island, the Ryukyu Islands. *Rostria* 64: 31–33. [in Japanese]
- Souma J (2021a) *Stephanitis* (*Norba*) *syotii* sp. nov. (Hemiptera: Heteroptera: Tingidae) from Taiwan, China. *Journal of Insect Biodiversity* 23(1): 17–22. <https://doi.org/10.12976/jib/2021.23.1.3>
- Souma J (2021b) Lace bugs from Yakushima Island, Ryukyu Archipelago, Japan (Hemiptera: Heteroptera: Tingidae). *Fauna Ryukyuna* 63: 29–39. [in Japanese with English Summary]
- Souma J (2021c) Notes on infraspecific variation and host plant of *Stephanitis* (*Norba*) *morimotoi* Takeya, 1963 (Heteroptera: Tingidae). *Rostria* 66: 45–50.
- Souma J (2021d) Distributional record of the lace bug species *Stephanitis* (*Norba*) *mendica* Horváth, 1912 (Heteroptera, Tingidae) from Kanto District, Honshu, Japan. *Rostria* 66: 26–27. [in Japanese]
- Souma J, Kamitani S (2021) Taxonomic review of the lace bug genus *Omoplax* (Hemiptera: Heteroptera: Tingidae) endemic to “Oriental Galapagos” (the Ogasawara Islands, Japan) with the description of its new allied genus and species. *Entomological Science* 24(1): 3–11. <https://doi.org/10.1111/ens.12445>
- Stål C (1873) Enumeratio Hemipterorum. 3. Kungliga Svenska Vetenskapsakademiens Handlingar (N. F.) 11(2): 1–163.
- Štusák JM, Stehlík JL (1978) Second contribution to the teratology of Tingidae (Heteroptera) Antennal anomalies. *Acta Musei Moraviae. Scientiae Biologicae* 63: 89–105.
- Tagawa H (1995) Distribution of lucidophyll oak-laurel forest formation in Asia and other areas. *Tropics* 5(1/2): 1–40. <https://doi.org/10.3759/tropics.5.1>
- Takahashi T (1990a) 兵庫県のグンバイムシ (2) [Tingidae from Hyogo-ken, Honshu, Japan. 2]. *Kiberihamushi* 18(2): 27–31. [in Japanese]
- Takahashi T (1990b) 兵庫県のグンバイムシ (1) [Tingidae from Hyogo-ken, Honshu, Japan. 1]. *Kiberihamushi* 18(1): 1–5. [in Japanese]
- Takahashi A, Otsuka H, Ota H (2008) Systematic Review of Late Pleistocene Turtles (Reptilia: Chelonii) from the Ryukyu Archipelago, Japan, with Special Reference to Paleogeographical Implications. *Pacific Science* 62(3): 395–402. [https://doi.org/10.2984/1534-6188\(2008\)62\[395:SRLOPT\]2.0.CO;2](https://doi.org/10.2984/1534-6188(2008)62[395:SRLOPT]2.0.CO;2)
- Takara T, Azuma S (1972) Fauna of the Iriomote Island, Ryukyus. II. List of the insects (2). Order Hemiptera (Heteroptera). The Science Bulletin of the Faculty of Agriculture. University of the Ryukyus 19: 99–121.
- Takara T, Hidaka T (1960) Provisional list of Hemiptera-Heteroptera in the Ryukyu Islands. Supplemental notes 1. The Science Bulletin of the Division of Agriculture, Home Economics & Engineering. University of the Ryukyus 7: 181–188.
- Takeya C (1930) トサカグンバイの寄主植物 [Host plants for *Stephanitis* (*Stephanitis*) *takeyai* Drake & Maa, 1955]. *Mushi* 3: 72. [in Japanese]
- Takeya C (1931) Some Tingitidae of the Japanese Empire. *Mushi* 4: 65–84.
- Takeya C (1932) Some Korean lace-bugs. *Mushi* 5: 8–13, [tab. 1].
- Takeya C (1951a) Notes on *Stephanitis typica* (Distant) in Japan (Hemiptera: Tingidae). *Kurume University Journal* 4(2): 39–46. [Natural Sciences]
- Takeya C (1951b) A tentative list of the Tingidae of Japan and her adjacent territories (Hemiptera). *Kurume University Journal* 4(1): 5–28. [Natural Sciences]

- Takeya C (1953) Notes on the Tingidae of Shikoku, Japan (Hemiptera). Transactions of the Shikoku Entomological Society 3(7): 167–176. [., pl. 6]
- Takeya C (1962) Taxonomic revision of the Tingidae of Japan, Korea, the Ryukyus and Formosa Part 1 (Hemiptera). Mushi 36(5): 41–75.
- Takeya C (1963) Taxonomic revision of the Tingidae of Japan, Korea, the Ryukyus and Formosa Part 2 (Hemiptera). Mushi 37(4): 27–52.
- Tanabe AS (2011) Kakusan4 and Aminosan: Two programs for comparing nonpartitioned, proportional, and separate models for combined molecular phylogenetic analyses of multilocus sequence data. Molecular Ecology Resources 11(5): 914–921. <https://doi.org/10.1111/j.1755-0998.2011.03021.x>
- Tanaka N, Matsui T (2007–2021) PRDB: Phytosociological Relevé Database. <http://www.ffpri.affrc.go.jp/labs/prdb/index.html> [Accessed: 2021-12-6]
- Tomokuni M (1981) Heteroptera of the Izu peninsula, Central Japan. Memoirs of the National Science Museum 14: 103–116. [in Japanese with English summary]
- Tomokuni M (1985) Heteroptera of the Oki Islands, Shimane Prefecture, Japan. Memoirs of the National Science Museum 18: 153–161. [in Japanese with English summary]
- Tomokuni M (1994) Type materials of several Japanese and Korean Tingidae (Heteroptera), with designation of Lectotypes and notes on Matsumura's collection. Japanese Journal of Entomology 62(4): 839–844.
- Tomokuni M (2005) Heteroptera (Insecta) from the Akasaka Imperial Gardens and the Tokiwamatsu Imperial Villa, Tokyo, Japan. Memoirs of the National Science Museum 39: 397–408. [in Japanese with English summary]
- Tomokuni M (2006a) Additional material of Heteroptera (Insecta) collected at the Imperial Palace, the Akasaka Imperial Gardens, and the Tokiwamatsu Imperial Villa, Tokyo Japan. Memoirs of the National Science Museum 43: 349–354. [in Japanese with English summary]
- Tomokuni M (2006b) A small collection of Tingidae (Insecta, Heteroptera) from Taiwan, with a checklist of the known species. Memoirs of the National Science Museum 44: 59–69.
- Tomokuni M (2014) Heteroptera from the Garden of the Imperial Palace, Tokyo, Japan. Memoirs of the National Science Museum 50: 359–369. [in Japanese with English summary]
- Tomokuni M, Hayashi M (2006) Hemiptera (Insecta) in the Coastal Areas on the Sagami Sea, Central Japan. Memoirs of the National Science Museum 42: 285–310. [in Japanese with English summary]
- Tomokuni M, Ishikawa T (2002) Hemiptera (Insecta) of Hachijo Island, the Izu Islands, Japan. Memoirs of the National Science Museum 38: 169–178. [in Japanese with English summary]
- Tomokuni M, Hayashi M, Usui T (2000) Hemiptera excluding Sternorrhyncha from the Garden of the Imperial Palace, Tokyo, Japan. Memoirs of the National Science Museum 36: 35–55. [in Japanese with English summary]
- Tsukada M (1994) Seasonal host alternation by the andromeda lace bug, *Stephanitis takeyai* (Heteroptera: Tingidae) between its two main host-plant species. Researches on Population Ecology 36(2): 219–224. <https://doi.org/10.1007/BF02514938>
- Tsukada M (2008) Life history evolution of the andromeda lace bug, *Stephanitis takeyai*, induced by the simplification of vegetation in Nara Park, caused by browsing of the sika deer, *Cervus nippon*. Nihon Shinrin Gakkaishi 90(5): 348–355. <https://doi.org/10.4005/jjfs.90.348> [in Japanese with English Summary]
- United States National Museum of Natural History (2021) *Stephanitis kyushuana* Drake, 1948. <http://n2t.net/ark:/65665/3d0b59aeb-f291-40c8-b236-9c06e7099e82> [Accessed: 2021-11-3]
- Vétek G, Kondorosy E, Marácz L (2012) First record of the andromeda lace bug (*Stephanitis takeyai* Drake et Maa) (Heteroptera: Tingidae) in Hungary. Novenyvedelem 48(1): 21–26. [in Hungarian with English Summary]
- Wang Y, Brožek J, Dai W (2020) Functional morphology and sexual dimorphism of antennae of the pear lace bug *Stephanitis nashi* (Hemiptera: Tingidae). Zoologischer Anzeiger 286: 11–19. <https://doi.org/10.1016/j.jcz.2020.03.001>
- Woese CR, Achenbach L, Rouviere P, Mandelco L (1991) Archaeal phylogeny: Reexamination of the phylogenetic position of *Archaeoglobus fulgidus* in light of certain composition-induced artifacts. Systematic and Applied Microbiology 14(4): 364–371. [https://doi.org/10.1016/S0723-2020\(11\)80311-5](https://doi.org/10.1016/S0723-2020(11)80311-5)
- Yamada K, Ishikawa T (2016) Family Tingidae. In: Hayashi M, Tomokuni M, Yoshizawa K, Ishikawa T (Eds) Catalogue of the insects of Japan Volume 4 Paraneoptera. Touka-shobo, Fukuoka, Japan, 429–435. [in Japanese]
- Yamada K, Tomokuni M (2012) Family Tingidae Laporte, 1832. In: Ishikawa T, Takai M, Yasunaga T (Eds) A field guide to Japanese bugs. Terrestrial heteropterans III. Zenkoku Noson Kyoiku Kyokai, Publishing Co., Ltd., Tokyo, Japan, 180–213. [., pl. 2–13] [in Japanese]
- Yano S, Takechi L, Kikuhara Y (2013) Heteroptera of Ehime Prefecture, Shikoku, Japan (Insecta, Hemiptera) I. Bulletin of Omogo mountain museum 5: 23–52. [in Japanese]
- Yasunaga T, Takai M, Yamashita I, Kawamura M, Kawasaki T (1993) A field guide to Japanese bugs. Terrestrial heteropterans. Zenkoku Noson Kyoiku Kyokai, Publishing Co., Ltd., Tokyo, Japan, 380 pp. [in Japanese]
- Yiu V, Yip CH (2012) A photographic guide to Hong Kong true bugs. Hong Kong Entomological Society, Hong Kong, China, 263 pp. [in Chinese]
- Yonekura K, Kajita T (2003–2021) BG Plants Wamei-Gakumei Index (YList). <http://ylist.info> [Accessed: 2021-11-1] [in Japanese]
- Zheng S, Lin Y (2013) 椿象圖鑑 [Encyclopedia of Heteroptera from Taiwan]. Morning Star Publishing Co., Ltd., Taichung, Taiwan, 381 pp. [in Chinese]

## Supplementary material 1

### Bayesian tree

Authors: Jun Souma

Data type: figure (PDF file)

Explanation note: Bayesian tree using the cytochrome c oxidase subunit I (COI) gene.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/dez.69.89864.suppl1>



## Supplementary material 2

### Sample IDs and GenBank Accession numbers

Authors: Jun Souma

Data type: table (excel document)

Explanation note: Sample IDs and GenBank Accession numbers for 57 individuals of 11 tingid species used for DNA barcoding.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/dez.69.89864.suppl2>

## Supplementary material 3

### Pairwise genetic divergence

Authors: Jun Souma

Data type: table (excel document)

Explanation note: Pairwise genetic divergence (Kimura-two parameter) for 57 individuals of 11 tingid species, based on the cytochrome *c* oxidase subunit I (COI) gene sequence.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/dez.69.89864.suppl3>