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RESEARCH PAPER

The tribe Anthocorini in Japan (Hemiptera: Anthocoridae): descriptions of new species, review of distribution and bionomics

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Abstract. Japanese Anthocorini are reviewed. A total of five genera and 13 species were identified, including two new species described below: *Temnostethus mirificus* sp. nov. and *Anthocoris venustus* sp. nov. Previous records of *Anthocoris miyamotoi* Hiura, 1959 from Japan are considered to be confused with *A. venustus* sp. nov. *Anthocoris nemoralis* (Fabricius, 1794), which is a common and widespread species in Europe, is recorded in Japan for the first time; it is assumed to have been accidentally introduced into Japan recently. *Temnostethus distans* Kerzhner, 1973 and *Anthocoris kalopanacis* Kerzhner, 1977 are newly recorded in Japan proper. Male and female genitalia are illustrated and described for most of the treated species. Identification keys to the genera and species that occur in Japan are provided. Bionomics are provided for each species. Detailed locality information and distribution maps in Japan are presented for all Japanese species and their zoogeography is discussed.

Key words. Hemiptera, Heteroptera, Anthocoridae, Anthocorini, taxonomy, new species, new record, bionomics, zoogeography, Japan, Palaearctic Region

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Introduction

Anthocorini Fieber, 1836 is the most species-rich tribe in the family Anthocoridae, currently comprising 11 genera and approximately 150 described species worldwide (cf. Ford 1979, Henry 1988, Péricart 1996, Carpintero 2002, Ballal et al. 2018). As evidenced by both the number of species and the distribution of the genera, Anthocorini undoubtedly represents a Holarctic group. *Anthocoris* Fallén, 1814 is the largest genus in the Anthocorini, with nearly 80 species distributed mainly in the Palaearctic Region. Other well-known taxa such as *Elatophilus* Reuter, 1884, *Temnostethus* Fieber, 1860, *Acompocoris* Reuter, 1875, and *Tetraphleps* Fieber, 1860 also occur in the Holarctic, but with more species in the Palaearctic.

A taxonomic study of the Japanese Anthocorini had its beginnings in the work of Poppius (1909) who described *Anthocoris japonicus* from Kanagawa. In the following 50 years, no taxonomic work on the tribe was conducted in Japan, but Hiura (1959, 1966) composed a monograph of its fauna, with descriptions of four new species. Subsequently, Yasunaga et al. (1999) and Yasunaga (2001b) added a few species to the Japanese Anthocorini fauna. To date, five genera and 10 species have been identified in Japan (Yamada et al. 2016). However, there has been no comprehensive review of the Japanese Anthocorini.

Through careful examination of materials deposited in several institutions, as well as specimens collected by the authors of this study and their colleagues, we found undescribed species of *Temnostethus* and *Anthocoris* from Japan. The latter was recognized from specimens previously identified as *A. miyamotoi* Hiura, 1959, based on examination of specimens from various parts of Japan and a study of type specimens. In addition, an adventive species, *Anthocoris nemoralis* (Fabricius, 1794), was discovered in Japan for the first time and also represents the first record from eastern Asia.

This paper reviews the Japanese species of Anthocorini. Five genera and 13 species are identified in total. These 13 species are documented, including two species described as new. Male and female genitalia are illustrated and described for most treated species based on specimens from Japan. Identification keys for genera and species are provided. Bionomics are provided for each species. Distribution maps of all Japanese species are presented, and their zoogeography is discussed.

Material and methods

Examinations of external characters and genitalia were performed using a binocular microscope (Stereoscopic Zoom Microscope SMZ1500; Nikon). Male genitalia were dissected after maceration in hot 10% potassium hydroxide solution until the organs became transparent (approximately 5 min). Female genitalia were dissected after being heated in hot 1% potassium hydroxide solution, stained with chlorazol black E, following the method of Ke & Bu (2007). These genital structures were dissected with micropins in glycerin on a well-glass slide under a binocular microscope (Stereoscopic Zoom Microscope SMZ1500; Nikon). Photographs (Figs 1, 4, 7, 8) were obtained using a digital camera (EOS 70D; Canon) with an extreme macro lens (MP-E 65 mm F2.8 1–5×; Canon) and a flashlight (Speedlite 430EX III-RT; Canon), and then combined using the automontage software CombineZP (Alan Hadley, UK). To examine the detailed surface structures, scanning electron microscopy images were obtained using a JEOL JSM-5300 housed in the Tokushima Prefectural Museum (with platinum coating; Figs 2D, 5, 9A–C,E–G, 10–11) and a Hitachi Tabletop Microscope® TM3030 (without metalic vapor deposition; Figs 2A–C, 9D). Line drawings (Figs 3, 6, 12–15) were prepared principally with the aid of an eyepiece grid. All digital images were edited and assembled using Adobe Photoshop CC 2018. All measurements were recorded using a micrometer eyepiece and are given in millimeters. Terminology generally follows that of Bu & Zheng (2001) and Yamada et al. (2010) for external morphology and of Horton & Lewis (2011) for genital structures. Label data of type specimens are presented verbatim, lines are separated by a backslash (\), and the two sides of the label by single quotation marks (‘’). An asterisk (*) immediately after the name of a locality indicates new distributional data.

Depositories of the specimens are abbreviated as follows:

AMNH	American Museum of Natural History, New York, USA;
BMNH	Natural History Museum, London, United Kingdom;
ELKU	Entomological Laboratory, Kyushu University, Fukuoka, Japan;
EUM	Ehime University Museum, Matsuyama, Ehime, Japan;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
MNHN	Muséum National d’Histoire Naturelle, Paris, France;
MZHF	Zoological Museum, University of Helsinki, Finland;
NKUM	Nankai University, Department of Biology, Tianjin, P. R. China;
NMPC	National Museum, Prague, Czech Republic;
NSMT	National Museum of Nature and Sciences, Tsukuba, Ibaraki, Japan;
NWHS	Nagasaki West High School, Biology, Nagasaki, Japan;
OMNH	Osaka Museum of Natural History, Osaka, Japan;
RMNH	National Museum of Natural History (Naturalis), Leiden, The Netherlands;
TKPM	Tokushima Prefectural Museum, Tokushima, Japan;
TYCN	Tomohide Yasunaga collection, Nagasaki, Japan;
ZMAN	Zoölogisch Museum, University of Amsterdam, Amsterdam, The Netherlands (currently merged with National Museum of Natural History (Naturalis), Leiden, The Netherlands);
ZMAS	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark;
ZMUH	Zoologisches Museum, Universität Hamburg, Germany.

Taxonomy

Tribe Anthocorini Fieber, 1836

Diagnosis. Anthocorini is primarily recognized by a combination of the following characters: Macrochetae on head and pronotum absent or indistinct; antennal segments III and IV generally fusiform, almost same width as segment II; length of each seta less than twice the diameter of the segment; pronotal collar generally wide and distinct; fossula spongiosa present on apex of pro- and mesotibiae, sometimes on the metatibiae; protibiae lacking teeth on ventral surface; protarsi always with pulvillus; male abdominal segment VIII symmetrical; paramere variable in shape, but generally horn-shaped or falcate; endosoma very long, in the form of a copulatory fiber, covered with small spinules; ectospermalege formed as copulatory tube; copulatory tube opens to the exterior on ventral side between abdominal segments VII and VIII, membranous and very long, correlated with the length of endosoma; and sperm pouch more or less spherical. Detailed characteristics of the tribe were provided by Carayon (1972).

Discussion. The Anthocorini currently contains 11 genera: *Acompocoris* Reuter, 1875 (Holarctic), *Anthocoris* Fallén, 1814 (Northern Hemisphere, with a few exceptions), *Arnulphus* Distant, 1904 (Myanmar), *Coccivora* McAtee & Malloch, 1925 (USA), *Compsobiella* Poppius, 1909 (Afrotropical), *Elatophilus* Reuter, 1884 (Holarctic), *Galchana* Distant, 1910 (India), *Macrotrachelia* Reuter, 1871 (Neotropical), *Melanocoris* Champion, 1900 (New World), *Temnostethus* Fieber, 1860 (Palaearctic, with one Holarctic species), and *Tetraphleps* Fieber, 1860 (Holarctic). The majority of species in the tribe occur in the Holarctic Region, especially the Palaearctic, where approximately 90 species are reported (Péricart 1996, Aukema et al. 2013a). Considering the distribution of each species, the Anthocorini seem to have originated in the Palaearctic, with subsequent dispersal to the Oriental and across the Bering Strait into the Nearctic (Ford 1979). As stated by Ford (1979), the Anthocorini represent a more recent group than other anthocorid tribes, based on their phylogeny and their distribution pattern. Her opinion is also supported by recent molecular analyses, which suggested that the tribe originated in the Early Cretaceous (Jung & Lee 2011).

Exhibiting great similarity in the female genitalia (e.g., the ectospermalege formed as copulatory tube, connecting to a spherical sperm pouch), the Anthocorini and the Oriini Carayon, 1958 are presumably derived from a common ancestor. The composition of the copulatory

Fig. 1. Habitus, dorsal (A, C, E) and lateral (B, D, F) views. A–B – *Temnostethus distans* Kerzhner, 1973, female; C–D – *T. mirificus* sp. nov., holotype, male; E–F – *Elatophilus nipponensis* Hiura, 1966, male. Scale bars: 1.0 mm.

tube is similar in females of the tribes Scolopini Carayon, 1954 and Blaptostethini Carayon, 1972; therefore, these four tribes might form a closely related or a monophyletic group within the Anthocoridae or Cimicoidea. However, their morphological similarity in female genitalia is not in accordance with the recent molecular-based phylogenetic analyses of relationships among these tribes (Jung et al. 2010, Jung & Lee 2011).

Carpintero & Dellapé (2008) transferred *Dufouriellus* Kirkaldy, 1906 from the tribe Dufouriellini to the Anthocorini based on the following: 1) the ocelli placed behind the line of the eyes, 2) antennae with length of each seta less than twice the diameter of the segment, 3) a transverse row of setae on the head absent, 4) tibial teeth or spines absent, and 5) dorsal surface subglabrous (Carpintero & Dellapé 2008). However, the above diagnostic features 1), 3), and 5), at least, are also found in Scolopina of the Scolopini, and character 4) is also shared with some genera of the Dufouriellini [= Cardiastethini *sensu* Carpintero & Dellapé (2008)] and some genera of the Scolopini. In addition, Anthocorini has a unique copulatory mechanism, in which the very long endosoma is in the form of a copulatory fiber and inserts through a very long female copulatory tube to the sperm pouch. These characteristic states are regarded as synapomorphies, which strongly support the monophyly of Anthocorini. The female genitalia of *Dufouriellus* are reduced and have no ectospermalege-shaped copulatory tube (lacking ectospermalege itself) (Carayon 1972, Péricart 1972, Carpintero & Dellapé 2008; Yamada, unpubl. data). The morphological features

proposed to isolate *Dufouriellus* from Cardiastethini by Carpintero & Dellapé (2008) seem to be highly homoplastic. Nevertheless, with the exception of *Dufouriellus*, the Anthocorini are almost certainly monophyletic, based on the above-mentioned synapomorphies. Furthermore, *Dufouriellus* should not be treated as a member of the Anthocorini until a phylogenetic analysis based on all known genera of Anthocoridae is undertaken.

Key to the genera of Anthocorini occurring in Japan

1. Metasternum apically truncate or weakly rounded; metacoxae widely separated from each other. 2
– Metasternum apically triangular; metacoxae contiguous with each other. 3
2. Labium usually extending to mesocoxae (Fig. 1B); lateral margin of pronotum notched at the border of collar and callus (Figs 1A,C); ostiolar peritreme protruding, directed transversely toward the outer margin of metapleuron and almost truncated or obtuse at its apex (Figs 2A–B). ..... ***Temnostethus*** Fieber, 1860
– Labium reaching or barely exceeding procoxae (Fig. 1F); lateral margin of pronotum straight (Fig. 1E); ostiolar peritreme subplanate, directed obliquely toward the outer margin of metapleuron and gently acute at its apex (Fig. 2C). ..... ***Elatophilus*** Reuter, 1884
3. Hemelytra impunctate or shallowly punctate; abdominal sternum with a pair of membranous areas on segments II–III (Fig. 12). ... ***Anthocoris*** Fallén, 1814
– Hemelytra densely covered with setigerous punctures; abdominal sternum without membranous area. 4
4. Ostiolar peritreme protruding slightly at the apex but not prolonged tongue-like, its apex continued by a fine carina (Fig. 5A). ..... ***Acompocoris*** Reuter, 1875
– Ostiolar peritreme apically projected, tongue-like and protruding above the surface of evaporatorium, its apex not continued by a fine carina (Fig. 5D). .... ***Tetraphleps*** Fieber, 1860

Genus *Temnostethus* Fieber, 1860

Temnostethus Fieber, 1860: 263. Type species by subsequent designation (Kirkaldy 1906: 120): *Anthocoris pusillus* Herrich-Schaeffer, 1835.

Ectemnus Fieber, 1860: 264 (as genus; downgraded to valid subgenus by Péricart 1972: 84). Type species by monotypy: *Anthocoris reduvinus* Herrich-Schaeffer, 1850.

Tmetostethus T. A. Marshall, 1868: 281. Unnecessary new name.

Stethotomus T. A. Marshall, 1868: 281. Unnecessary new name.

Montandoniella Puton, 1888: 255 (as genus; downgraded to valid subgenus by Péricart 1972: 81). Type species by monotypy: *Montandoniella dacica* Puton, 1888.

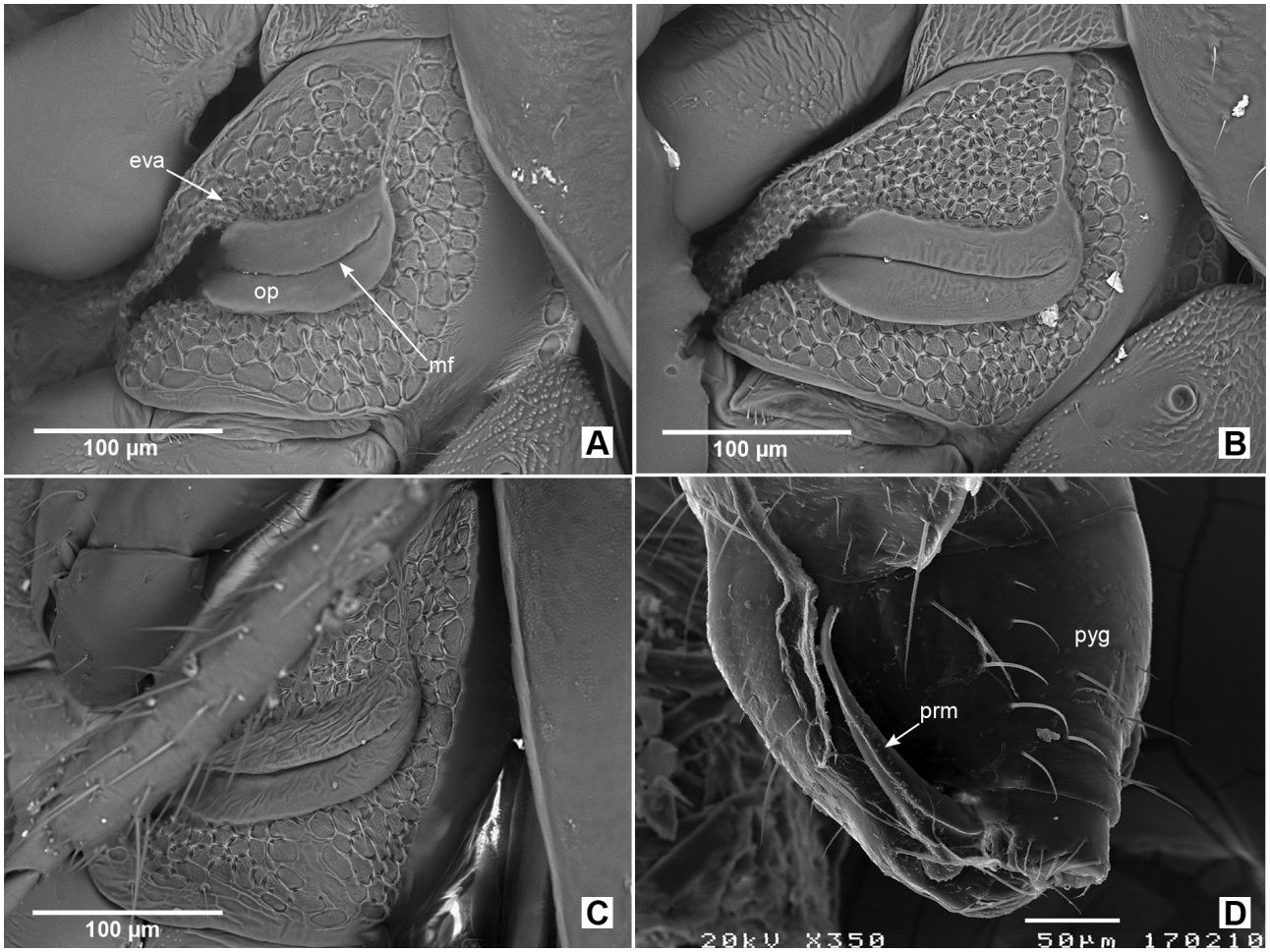

Fig. 2. Scanning electron micrographs of diagnostic characters of Japanese anthocorids. A – *Temnostethus distans* Kerzhner, 1973, female; B, D – *T. mirificus* sp. nov., female (B) and male (D), paratypes; C – *Elatophilus nipponensis* Hiura, 1966, female. A–C – ostiolar peritreme and evaporatorium, left lateroventral view; D – pygophore with paramere, lateral view. Abbreviations: eva – evaporatorium; mf – median furrow; op – ostiolar peritreme; prm – paramere; pyg – pygophore.

Temnostethus (selected references): Fieber (1861): 38, 136 (in key, redescription); Reuter (1875): 64 (in key); Reuter (1884): 55, 60 (in key, redescription); Poppius (1909): 27 (in key); Stichel (1958): 12 (in key); Stichel (1960): 356 (catalogue, fauna of Palaearctic); Kerzhner (1964): 696–697 (in key, diagnosis); Carayon (1972): 345 (listed); Péricart (1972): 78–79 (in key, redescription, fauna of W. Palaearctic); Herring (1976): 145–146 (figure, in key); Elov (1976): 369 (in key); Kelton (1978): 17–18 (in key, redescription, fauna of Canada and Alaska); Ford (1979): 58 (check list of the world); Önder (1982): 28, 59 (in key, redescription, fauna of Turkey); Henry (1988): 16 (catalogue, N. America); Kerzhner (1988): 770, 772 (in key, note); Péricart (1996): 118 (catalogue, Palaearctic); Bu & Zheng (2001): 108, 166 (in key, redescription, fauna of China); Yasunaga (2001b): 282 (diagnosis, fauna of Japan); Wachmann et al. (2006): 199 (diagnosis, habitat); Horton (2008): 2403 (listed); Falamarzi et al. (2009): 36 (in key).

Diagnosis. Distinguished from other genera of Anthocorini by the combination of the following characters: body shiny, almost glabrous; head longer than width across eyes, covered with short setae; eyes small; labium usually extending to mesocoxae; lateral margin of pronotum notched at the border of collar and callus; collar well developed; callus swollen, finely sculptured; metasternum apically truncate or weakly rounded; metacoxae widely separated from each other; ostiolar peritreme (Figs 2A–B) protruding, directed transversely toward the outer margin of metapleuron and almost truncated or obtuse at its apex.

Remarks. *Temnostethus* currently contains 11 species and three subspecies and is widely distributed in the Palaearctic Region (cf. Péricart 1996, Ballal et al. 2018). The species with the widest distribution, *T. gracilis* Horváth, 1907, is also present in the Nearctic Region (Henry 1988). Drake & Harris (1926) described *T. fastigiatus* from California, U.S.A. as the first American record of *Temnostethus*; later, this species was synonymized with *Elatophilus dimidiatus* (Van Duzee, 1921) by Lattin (2001). Three subgenera, *Ectemnus* Fieber, 1860, *Montandoniella* Puton, 1888, and *Temnostethus* s. str., are included in this genus (Péricart 1972). Wing polymorphism in *Temnostethus* appears to be common, and at least eight polymorphic species are known (Wagner 1940, Péricart 1972).

Species of *Temnostethus* generally occur on broad-leaved trees and are often found on mosses and lichens that cover the bark, branches, and twigs (Péricart 1972). *Temnostethus wichmanni* Wagner, 1961, occurs only on the conifer *Picea* species (Pinaceae) in central Europe (Péricart 1972).

Subgenus *Temnostethus* Fieber, 1860

Temnostethus distans Kerzhner, 1973

(Figs 1A–B, 2A, 3A–D, 18)

Temnostethus distans Kerzhner, 1973: 277. Holotype: ♂ (macropterous), Kuril Is., Shikotan (ZMAS). Note. The published year of this species has long been treated as 1972 in previous papers; however, it was corrected by Aukema et al. (2013a), who confirmed Kerzhner's paper formally published in 1973 (Kerzhner 1973).

Temnostethus distans: Kerzhner (1988): 772–773 (in key, figures); Péricart (1996): 119 (catalogue, distribution); Yasunaga (2001b): 283 (record, diagnosis, habitat); Kanyukova & Marusik (2006): 168 (record); Gapon & Konstantinov (2008): 26 (listed); Vinokurov et al. (2010): 58 (catalogue, distribution); Aukema et al. (2013a): 88 (catalogue, distribution); Maehara (2015): 29 (recorded as *Temnostethus* sp., habitat); Yamada et al. (2016): 422 (catalogue, distribution).

Type material examined. Holotype: ♂, Kuril Islands, Shikotan, nr Kurilsk, 24.VIII.1963, G. O. Krivolutskaya (ZMAS, image examined). Paratype: sex unknown, Iturup, nr Lesozavodsk, 28.VIII.1961, G. O. Krivolutskaya (ZMAS, image examined).

Additional material examined. JAPAN: Hokkaido: 1 ♀ (Figs 1A–B, 2A), Lake Mashû-ko to Teshikaga-cho, 2.x.1993, M. Tomokuni (NSMT); 1 ♀, Akkeshi-cho, Bekanbeushi Marsh, 43.05.42N 144.51.30E, 3.–24. viii.2004, Malaise trap, R. Matsumoto (OMNH). **Honshu:** Tochigi Pref.: 4 ♀♀, Nikko-shi, Noguchi, 30.x.2019, S. Maehara (TKPM); 1 ♂ (Figs 3A–C), Nikko-shi, Shôbugahama, 5.viii.2010, S. Maehara (TKPM); 1 ♀, same locality, 25.v.2011, S. Maehara (TKPM). Nara Pref.: 1 ♀, Kamikitayama-mura, Ôdaigahara, 9.ix.1962, N. Ohtani (OMNH). **Kyushu:** Fukuoka Pref.: 1 ♀ (Fig. 3D), Soeda-machi Mt. Hikosan, 8.vii.1957, M. Miyatake (EUM).

Differential diagnosis. Recognized by the following combination of characters: Body (Figs 1A–B) always macropterous, generally blackish brown, shiny; head as long as or slightly longer than width across eyes; antennal segment II (Figs 1A–B) pale yellow, with fuscous base and apex; labium uniformly blackish brown, reaching to metasternum; hemelytra (Fig. 1A) somber blackish brown, strongly shining; endocorium with antero-median portion mostly whitish or off-white (Fig. 1A); embolium with anterior portion narrowly whitish or off-white, excepting darkened basal extreme portion (Fig. 1A); whitish area on endocorium located posteriad in comparison with whitish area on embolium (Fig. 1A); membrane of hemelytra smoky dark brown, with basal and innermost portions and area behind apex of cuneus greyish white (Fig. 1A); legs blackish brown to reddish brown, with pro- and mesotibiae pale yellow (Figs 1A–B). Most similar in appearance to *T. gracilis* but distinguished from that species by the metatibiae being blackish brown to reddish brown (in *T. gracilis*, all tibiae pale yellow) and the paramere being moderately curved and slightly constricted at middle (in *T. gracilis*, more slender and very slightly curved, not constricted at middle). This species is similar to *T. pusillus* (Herrich-Schaeffer, 1835) in the coloration of hemelytra, but the latter has uniformly darkened antennae and a straight paramere.

Redescription. ***Male genitalia*** (Figs 3A–C): Pygophore (Fig. 3A) cone-shaped, somewhat flattened, covered with three long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest setae are shorter than half length of pygophore; mid-dorsal surface hirsute with short, suberect setae; paramere (Figs 3B–C) very short, moderately curved, slightly constricted at middle, strongly bent at the base, with broad groove in form of shallow depression.

Female genitalia (Fig. 3D): Copulatory tube fused on middle of intersegmental membrane between sterna VII and VIII, extremely expanded and twisted with clearly visible rugosities on basal 1/3, and then gradually narrowing toward apex with less obvious rugosities; sperm pouch unfortunately broken off during the dissection; trunk of conductive tissue not pronounced (or possibly dissolved).

Measurements [mm; ♂ (n = 1) / ♀♀ (n = 6)]. Body length 3.35 / 2.85–3.18; head length (excl. neck) 0.46 / 0.46–0.49; head width across eyes 0.46 / 0.42–0.45; vertex width 0.25 / 0.26–0.29; length of antennal segments I – 0.16 / 0.16–0.19, II – 0.54 / 0.49–0.56, III – 0.31 / 0.29–0.34, and IV – 0.36 / 0.35–0.37; length of labial segments II – 0.20 /

0.24–0.26, III – 0.67 / 0.67–0.75, and IV – unmeasurable / 0.36–0.40; anterior pronotal width 0.36 / 0.37–0.39; mesal pronotal length 0.40 / 0.42–0.44; basal pronotal width 0.97 / 0.88–1.01; length of embolial margin 1.00 / 0.82–1.01; length of cuneal margin 0.62 / 0.52–0.62; maximum width across hemelytra unmeasurable / 1.05–1.16.

Bionomics. *Temnostethus distans* is found on various trees [e.g., *Alnus maximowiczii* Callier (Betulaceae)] (Kerzhner 1973, 1988). Maehara (2015) collected this species (as *Temnostethus* sp.) from lichens that cover the bark of broad-leaved trees in Tochigi Prefecture, central Honshu, Japan. He also mentions that this species was found on *Aesculus turbinata* Blume (Sapindaceae), *Prunus* species (Rosaceae), *Magnolia kobus* DC. (Magnoliaceae), and *Zelkova serrata* (Thunb.) Makino (Ulmaceae) in a low mountainous area (Satoshi Maehara, pers. comm.).

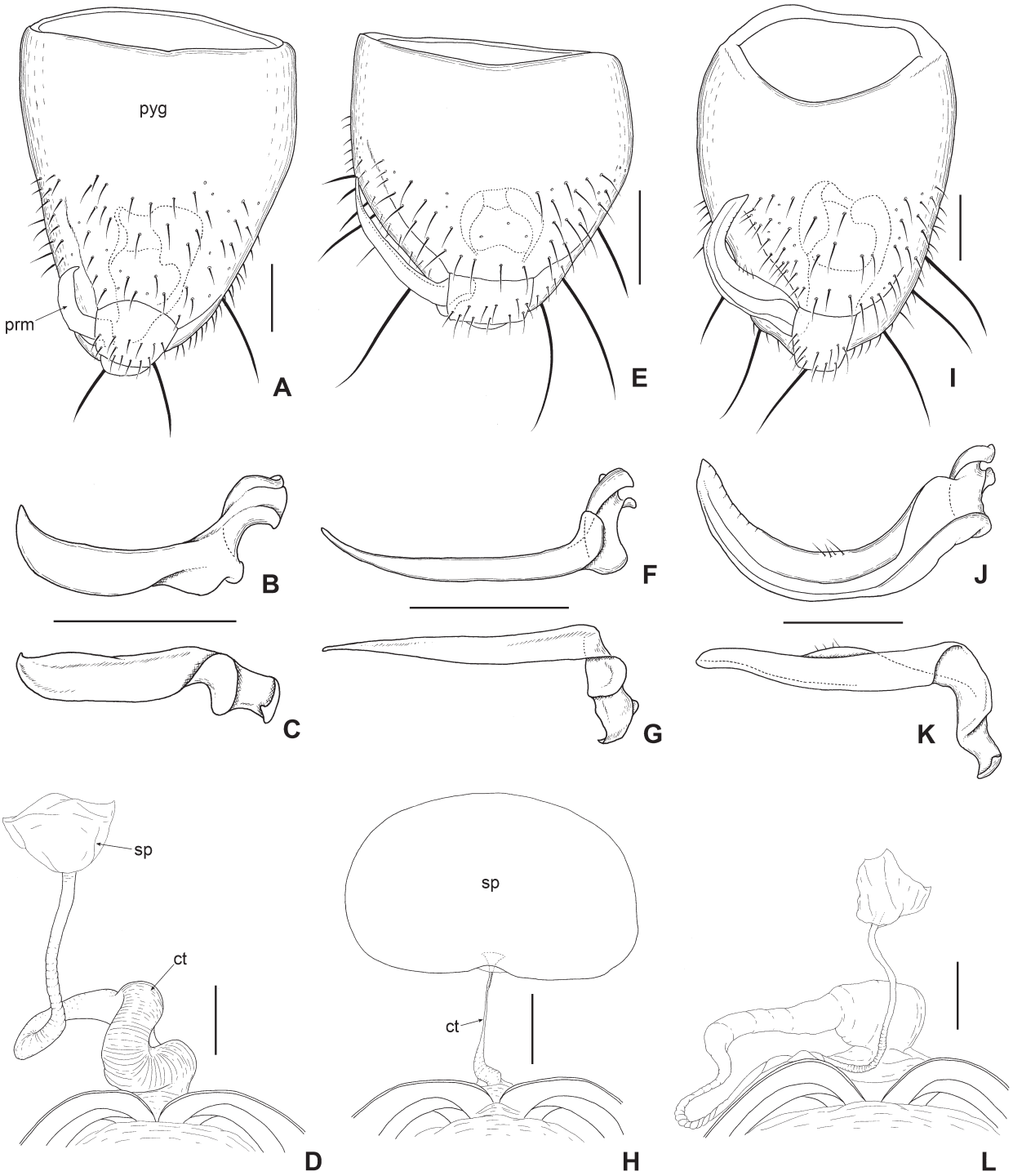

Fig. 3. Male (A–C, E–G, I–K) and female (D, H, L) genitalia. A–D –*Temnostethus distans* Kerzhner, 1973; E–H – *T. mirificus* sp. nov., paratype; I–L – *Elatophilus nipponensis* Hiura, 1966. A, E, I – pygophore with paramere (ejaculatory bulb omitted), dorsal view; B–C, F–G, J–K – paramere, two different views; D, H, L – copulatory tube and sperm pouch (D, L, sperm pouch broken off), dorsal view. Abbreviations: ct – copulatory tube; prm – paramere; pyg – pygophore; sp – sperm pouch. Scale bars: 0.1 mm.

Distribution. Japan: Hokkaido*; Honshu*: Tochigi, Nara; Kyushu*: Fukuoka. Chishima (Kuril) Islands: Iturup Is. (Kerzhner 1973), Kunashir Is. (Kanyukova & Marusik 2006), and Shikotan Is. (Kerzhner 1973). Russia: Far East: Sakhalin (Kerzhner 1973, Vinokurov et al. 2010). The species is known to occur in the Chishima Islands and the Russian Far East (Péricart 1996); however, we present the first record of this species in Japan proper (Fig. 18).

Temnostethus mirificus sp. nov.

(Figs 1C–D, 2B,D, 3E–H, 18)

Type locality. Japan, Aichi Prefecture, Toyota-shi, Odo-cho, riverbed of Yahagi-gawa River.

Type material. Holotype: ♂ (Figs 1C–D), '[JAPAN: AICHI] \ Toyota, Odo \ (Yahagi Riv.) \ 15-June-2012 \ M. YAZAKI leg.' [printed], [a card with locality data in Chinese script, printed]; mounted on a triangular card, in intact condition (TKPM). Paratypes: **JAPAN: Honshu:** Tochigi Pref.: 1 ♀, Sano-shi, Mt. Karasawa, 26.vi.2020, S. Maehara (TKPM). Chiba Pref.: 1 ♂ 1 ♀, Matsudo-shi, Sendabori, 4.x.2014, N. Muro (TKPM). Aichi Pref.: 1 ♀, same locality as holotype, 17.vi.2007, M. Yazaki (TKPM); 4 ♂♂ (one in Fig. 2D, one in Figs 3E–G) 6 ♀♀ (one in Fig. 2B, one in Fig. 3H), same data as holotype (TKPM, TYCN); 3 ♂♂ 2 ♀♀, same locality as holotype, 18.vi.2013, M. Yazaki.

Differential diagnosis. Recognized by the following combination of characters: body (Figs 1C–D) always brachypterous, generally blackish brown; labium roughly reaching abdominal sternum III; hemelytra (Fig. 1C) mostly dark brown to blackish brown, with anterior half of corium brown to light brown; claval suture vestigial; costal fracture and membrane completely absent; hind wing greatly reduced; paramere (Figs 2D, 3E–G) slender, straight or very slightly curved but curved at apex, with longitudinal groove in form of shallow depression; apex of paramere reaching to approximately halfway along the outer margin of pygophore. Distinctive among *Temnostethus* species in having only the brachypterous form characterized by the vestigial claval suture and the lack of a membrane. The morphology of the hemelytra clearly distinguishes the new species from other congeners. In general appearance, the new species is most similar to the brachypterous form of *T. gracilis*, but it is distinguished from the latter by the primarily dark brown to blackish-brown hemelytra (in *T. gracilis*, brownish with pale band on anterior portion of corium), the yellowish-brown tibiae being apically tinged with fuscous (in *T. gracilis*, entirely pale yellow), and the paramere being slender and straight or very slightly curved (in *T. gracilis*, stout, and moderately curved).

Description. ***Coloration.*** Body (Figs 1C–D) generally blackish brown. Head (Fig. 1C) blackish brown to dark orangish brown; clypeus sometimes yellowish brown; eyes and ocelli reddish black; margin of ocellus red to reddish brown. Antennal segment I uniformly blackish brown; segment II yellowish brown on basal 2/3, fuscous distally; segments III and IV fuscous (Figs 1C–D). Labium (Fig. 1D) yellowish brown to dark brown. Pronotum and scutellum (Fig. 1C) entirely blackish brown. Hemelytra (Fig. 1C) mostly dark brown to blackish brown; anterior half of corium brown to light brown. Legs (Fig. 1C) yellowish brown; coxae, trochanters, and femora darker brown; tibiae apically tinged with fuscous. Venter of thorax and abdomen (Fig. 1D) uniformly blackish brown. Pygophore blackish brown with pale yellow paramere (Figs 1C–D). Ovipositor and area around ovipositor brown to light brown.

Structure. Body (Figs 1C–D) oblong oval, shiny on dorsal and ventral surfaces. Head (Fig. 1C) cylindrical, impunctate, slightly longer than width across eyes, sparsely covered with suberect, yellowish setae; three pairs of long, erect trichobothria on the dorsal surface of the head, one on anterior clypeus, one in front of eye, and one between eye and ocellus; anteocular region approximately twice as long as length of eye in dorsal view; vertex approximately 2.7 times as wide as width of eye in dorsal view in male, 4.0–4.5 times as wide as width of eye in female; postocular region weakly constricted, demarcated by transverse shallow furrow; neck long, smooth, highly polished; eye not exceeding level of dorsal and ventral surface of head in lateral view. Antennae (Figs 1C–D) densely covered with short, decumbent, yellowish setae interspersed with long, erect setae, of which the longest are as long as or slightly shorter than width of corresponding segment; segment I not reaching apex of head, sparsely covered with short setae; segment II gradually thickened toward apex, male thicker than female, approximately 1.2 times as long as head width across eyes; segment III 0.52–0.55 as long as segment II; segment IV longer than segment III. Labium (Fig. 1D) reaching to approximately abdominal sternum III, sparsely covered with short, suberect setae; segment III medially constricted in ventral view, moderately curved in lateral view, approximately twice as long as or longer than segment II; segment IV approximately 0.5 times as long as segment III.

Pronotum (Fig. 1C) flattened, with a pair of long, erect trichobothria on midline of collar; anterior margin weakly concave, slightly shorter than mesal length; lateral margin sinuate, anteriorly rounded; lateral carina strongly expanded anteriad; collar short, transversely rugose, with scattered, yellowish setae; callus not swollen, impunctate; posterior lobe behind callus sparsely covered with suberect, yellowish setae and punctures; posterior margin concave, wider than twice the anterior margin. Scutellum (Fig. 1C) sub-equilateral, slightly wider at base than long, deeply depressed posteriad; anterior half smooth, posterior half strongly rugose. Hemelytra (Fig. 1C) attaining abdominal tergum III, sparsely covered with suberect, yellowish setae, and with punctures on posterior part of corium and along inner margin of clavus; costal margin and medial fracture strongly convex; claval suture vestigial (weakly demarcated by shallow groove); costal fracture and membrane completely absent; hind wing greatly reduced. Ostiolar peritreme (Fig. 2B) broad, very slightly curved anteriorly at apex, continued by a fine carina that reaches anterior margin of metapleuron; outer margin of ostiolar peritreme weakly raised above level of surrounding evaporatorium. Legs covered with sparse suberect, yellowish setae; fossula spongiosa present, but very small on apex of protibiae, indistinct on meso- and metatibiae.

Abdomen (Figs 1C–D) covered with recumbent, yellowish setae; dorsal laterotergites not fused with mediotergites on abdominal segment II.

Male genitalia (Figs 2D, 3E–G): Pygophore (Fig. 3E) broadly cone-shaped, somewhat flattened, covered with 5–7 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest setae are approximately half length of pygophore; mid-dorsal surface with suberect setae; paramere (Figs 2D, 3F–G) slender, straight or very slightly curved but curved at apex, strongly bent at the base, with longitudinal groove in the form of shallow depression; apex of paramere reaching to approximately halfway along outer margin of pygophore.

Female genitalia (Fig. 3H): Copulatory tube fused on middle of intersegmental membrane between sterna VII and VIII, approximately 0.15 mm in length, basally thickened, and gradually narrowed toward apex, with weak rugosities at basal 1/3; sperm pouch large; trunk of conductive tissue not pronounced (or possibly dissolved).

Measurements [mm; ♂♂ (n = 5) / ♀♀ (n = 9), holotype in parentheses]. Body length 2.25–2.45 (2.45) / 2.30–2.70; head length (excl. neck) 0.42–0.46 (0.45) / 0.44–0.48; head width across eyes 0.41–0.44 (0.44) / 0.39–0.45; vertex width 0.24–0.26 (0.26) / 0.26–0.29; length of antennal segments I – 0.14–0.15 (0.15) / 0.13–0.15, II – 0.51–0.56 (0.56) / 0.45–0.51, III – 0.26–0.30 (0.30) / 0.25–0.28, and IV – 0.31–0.34 (0.33) / 0.30–0.34; length of labial segments II – 0.32–0.35 (0.32) / 0.34–0.40, III – 0.63 (unmeasurable) / 0.68–0.75, and IV – 0.30 (unmeasurable) / 0.31–0.34; anterior pronotal width 0.34–0.36 (0.36) / 0.34–0.38; mesal pronotal length 0.36–0.38 (0.37) / 0.35–0.40; basal pronotal width 0.70–0.79 (0.75) / 0.70–0.83; length of hemelytron 0.54–0.66 (0.60) / 0.48–0.67; maximum width across hemelytra 0.90–1.02 (0.97) / 0.90–1.05.

Etymology. From Latin, *mirificus* (= strange, amazing), referring to the vestigial wings of the new species, which represent an unknown morphological condition among its congeners; an adjective.

Bionomics. *Temnostethus mirificus* sp. nov. is associated with lichens on the trunk surface of deciduous broadleaf trees, similar to the habitat of its congeners. This new species was collected from only three localities in the Tochigi, Chiba and Aichi Prefectures, Honshu. In Tochigi, one female specimen was collected from the trunk of *Quercus* species covered with lichens and/or mosses (Satoshi Maehara, pers. comm.). The Aichi population of *T. mirificus* was found along the riverbank of the Yahagi-gawa River in a low mountainous area (Mitsuhiko Yazaki, pers. comm.). The Chiba population was discovered in an urban park, where its habitat appears to be restricted to a few broad-leaved trees (Noriyuki Muro, pers. comm.). This area, prior to its conversion into a park, used to be a paddy field at the bottom of a valley surrounded by deciduous forests. Presumably, *T. mirificus* may prefer the border areas around mountain foothills and the rural areas of low mountains; however at present, we have insufficient data to determine whether or not the Chiba population is native. Regarding the species' phenology, according to Muro's observations, active adults (walking or mating) and active nymphs (walking) were present for six months between the middle of June to early December. Consequently, univoltine or bivoltine life cycles are assumed for this species; however, no detailed information is available on the overwintering stage.

Distribution. Japan: Honshu: Tochigi, Chiba, Aichi. This species is endemic to Japan, representing only three populations known to date from Tochigi, Chiba, and Aichi Prefectures (Fig. 18).

Genus *Elatophilus* Reuter, 1884

Elatophilus Reuter, 1884: 61. Type species by subsequent designation (Kirkaldy 1906: 120, misprinted "*nigellus*"): *Anthocoris nigrella* Zetterstedt, 1838.

Euhadrocerus Reuter, 1884: 65 (as valid subgenus of *Elatophilus*). Type species by monotypy: *Temnostethus crassicornis* Reuter, 1875.

Xenotracheliella Drake & Harris, 1926: 38 Type species by original designation: *Xenotracheliella inimica* Drake & Harris, 1926. Synonymized by Kelton & Anderson (1962: 1306).

Elatophilus (selected references): Poppius (1909): 28 (in key); Blatchley (1928): 86 (diagnosis); Stichel (1958): 12 (in key); Stichel (1960): 356 (catalogue, fauna of Palaearctic); Kerzhner (1964): 696, 698 (in key, diagnosis); Péricart (1967): 52 (taxonomic history); Carayon (1972): 345 (listed); Péricart (1972): 78, 97 (in key, description, fauna of W. Palaearctic); Herring (1976): 145–146 (figure, in key); Kelton (1978): 17, 19 (in key, description, fauna of Canada and Alaska); Ford (1979): 57 (check list of the world); Önder (1982): 28, 71 (in key, redescription, fauna of Turkey); Henry (1988): 15 (catalogue, N. America); Kerzhner (1988): 770, 772 (in key, note); Lattin & Stanton (1992): 434 (diagnosis, habitat, prey); Péricart (1996): 116 (catalogue, Palaearctic); Lattin (2000): 616 (bionomics); Bu & Zheng (2001): 109, 163 (in key, redescription, fauna of China); Yasunaga (2001b): 282 (diagnosis, fauna of Japan); Carpintero (2002): 36 (fauna of Neotropical Region); Wachmann et al. (2006): 193 (distribution, habitat); Horton (2008): 2403 (listed).

Diagnosis. Distinguished from the other genera of Anthocorini by the combination of the following characters: body flattened, shining; head elongate; eyes prominent, sexually dimorphic; antennal segment II linear (subgenus *Elatophilus*) or enlarged (subgenus *Euhadrocerus* Reuter, 1884); labium reaching or barely exceeding procoxae; pronotal collar narrow; lateral margin of pronotum straight; hemelytra usually dark with some pale markings, sometimes brachypterous; membrane with four veins; ostiolar peritreme (Fig. 2C) subplanate, directed slightly obliquely toward the outer margin of metapleuron and gently narrowed at its apex; apex of metasternum weakly rounded; metacoxae widely separated from each other; paramere short, broad, and curved.

Remarks. *Elatophilus* contains 19 species distributed throughout the Holarctic Region, 11 species of which are known from the Palaearctic Region, seven from North America, and one from Mexico (cf. Kelton 1976, Henry 1988, Lattin & Stanton 1993, Péricart 1996). This genus is divided into two subgenera, *Elatophilus* s. str. and *Euhadrocerus*, based especially on the antennal structure (the second segment is rather slender in *Elatophilus* s. str., whereas it is remarkably enlarged in *Euhadrocerus*) (Péricart 1972).

Bionomics. Species of *Elatophilus* are restricted to conifers, especially on various species of *Pinus* (Pinaceae). Several species of *Elatophilus* are known to be associated with species of the magarodid scale *Matsucoccus* Cockerell, 1909, which are serious pests of pines in the Old and

New World (e.g., Bliotti & Riom 1967, Drooz 1985). For some of these scales, species of *Elatophilus* [e.g., *E. nigricornis* (Zetterstedt, 1838) and *E. inimicus* (Drake & Harris, 1926)] have been well studied as effective predators (Bliotti & Riom 1967; Mendel et al. 1991, 1995a,b).

Subgenus *Elatophilus* Reuter, 1884

Elatophilus nipponensis Hiura, 1966

(Figs 1E–F, 2C, 3I–L, 18)

Elatophilus nipponensis Hiura, 1966: 29. Holotype: ♂, Japan, Nagano Pref., Sugadaira (OMNH).

Elatophilus nipponensis: Ford (1979): 58 (listed, distribution); Zhang & Lin (1985): 192 (habitat, redescription, distribution); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Zheng & Bu (1990): 25 (listed); Péricart (1996): 117 (catalogue, distribution); Sonobe (1997): 54 (record, as *Anthocoris chibi*); Takeno (1998): 44 (listed); Fabre et al. (2000): 791 (bionomics); Hua (2000): 198 (listed, distribution, habitat); Bu & Zheng (2001): 164–165 (figures, in key, redescription); Yasunaga (2001b): pl. 94, 282 (photo, diagnosis, habitat); Shimonoya (2001): 68, 74 (record, photo); Maehara (2009): 65 (record, habitat, photo); Asahi et al. (2010): 68 (record, bionomics); Maehara (2011): 123 (record, habitat); Maehara (2012): 35 (record, distribution, habitat, bionomics); Konno (2012a): 54 (record, photo, habitat); Hao & Ma (2013): 36 (listed); Nozaki & Nozaki (2013): 33 (record); Konno (2014): 4 (record, habitat); Yamada (2015): 381 (distribution, habitat); Maehara (2015): 29 (record, distribution, habitat); Yamada et al. (2016): 422 (catalogue, distribution); Yazaki (2016): 81–82 (listed, photo); Sawada (2018): D-36 (listed); Maehara (2018): 679 (photo, diagnosis, distribution, habitat); Konno (2020): 18 (record, habitat).

Type material examined. Paratype: ♀, '[Kyûshû] \ Sanguzan \ (Chikuzen) \ 10. v. 1931 \ K. Yasumatsu' [printed], 'Elatophilus [handwritten] \ nipponensis ♀ [handwritten] \ n. sp. [handwritten] \ Det. I. Hiura, 1966 [printed]', 'PARATYPE \ ♀' [handwritten] (ELKU).

Additional material examined. JAPAN: Honshu: Yamagata Pref.: 1 ♂ (Figs 3I–K), Yamagata-shi, Kamisakurada, Kamisakurada forest road, 8.xii.2009 (nymph collected), H. Konno. Tochigi Pref.: 1 ♂ (Figs 1E–F), Mashiko-cho, Takatateyama, 14.iv.2010, S. Maehara; 1 ♀ (Figs 2C, 3L), Sano-shi, Toyoshiro, 26.iv.2008, S. Maehara (all in TKPM).

Differential diagnosis. Recognized by the following combination of characters: body (Figs 1E–F) generally blackish brown; head much longer than width across eyes; vertex approximately 2.5 times as width of eye in dorsal view in male, approximately three times as width of eye in female; labium extending to procoxae; lateral margin of pronotum (Fig. 1E) straight or very slightly curved, slightly explanate on anterior half; pronotal callus weakly swollen, posteriorly demarcated by transverse depression; posterior lobe behind callus transversely rugose; hemelytra (Fig. 1E) with whitish marking on clavus, membrane smoky dark brown with basal portion whitish; pro- and mesotibiae tinged with yellowish brown. Most similar in general appearance to *E. matsucocciphagus* Bu & Zheng, 2001, but distinguished from that species by the lateral margin of pronotum being slightly explanate on the anterior half (in *E. matsucocciphagus*, lateral margin entirely explanate) and the hemelytra with whitish marking on clavus (in *E. matsucocciphagus*, median part of clavus, and inner 1/3 to 1/2 of endocorium grayish white). In addition, the paramere of this species is slender and longer than that of *E. matsucocciphagus*.

Redescription. ***Male genitalia*** (Figs 3I–K): Pygophore (Fig. 3I) covered with 6–7 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest setae are approximately half the length of the pygophore; paramere (Figs 3J–K) curved, basally twisted, with a few very short, erect setae on middle portion; pronounced groove present, formed by weakly rolled anterior and posterior edge; apical portion of anterior edge weakly dentate.

Female genitalia (Fig. 3L): Copulatory tube fused on middle of intersegmental membrane between sterna VII and VIII; basal 1/3 of copulatory tube extremely expanded and bulbous with rugosities and then gradually narrowed apically; apical 2/3 much thinner than basal 1/3 portion with many twists; sperm pouch broken off during the dissection; trunk of conductive tissue not pronounced (or possibly dissolved).

Measurements [mm; ♂♂ (n = 2) / ♀♀ (n = 2)]. Body length 4.00–4.25 / 4.13–4.25; head length (excl. neck) 0.55–0.57 / 0.57–0.58; head width across eyes 0.51–0.52 / 0.47; vertex width 0.24–0.27 / 0.28–0.29; length of antennal segments I – 0.22 / 0.23–0.24, II – 0.78–0.80 / 0.75–0.83, III – 0.38–0.39 / 0.40–0.42, and IV – 0.40 / 0.41–0.42; length of labial segments II – 0.28–0.30 / 0.32–0.33, III – 0.55 / 0.60–0.65, and IV – 0.30–0.31 / 0.36; anterior pronotal width 0.38–0.39 / 0.39–0.43; mesal pronotal length 0.40 / 0.42–0.45; basal pronotal width 1.05–1.13 / 1.12–1.15; length of embolial margin 1.30–1.35 / 1.27–1.37; length of cuneal margin 0.66–0.72 / 0.65–0.70; maximum width across hemelytra 1.12–1.35 / 1.25–1.27.

Bionomics. Although previous studies, including the original description, mentioned that *E. nipponensis* was collected under the bark of *Pinus densiflora* Siebold & Zucc., almost nothing is known about the biology of the species, because of limited collection records (e.g., Hiura 1966, Yasunaga 2001b). However, the meticulous field observations by Maehara (2011) revealed that this species inhabits the fragmented, flake-like bark of young branches. Since his report, the species has been discovered mainly in the Tohoku district in the northern part of Honshu, where Japanese red pine forests are preserved in good condition over a wide area (Konno 2012a, 2020; Maehara 2015). Thus, *E. nipponensis* has an undoubtedly strong association with *P. densiflora*. The population of *P. densiflora* seems to be decreasing in various parts of Japan owing to pine wilt disease and chemical spraying. Therefore, Japanese populations of *E. nipponensis* are currently designated as a Near Threatened Species Category in the Red-List by the Ministry of the Environment (Yamada 2015).

Distribution. Japan: Honshu: Aomori (Konno 2020), Miyagi (Konno 2012a), Yamagata (Konno 2012a), Tochigi (Maehara 2009), Tokyo (Hiura 1966), Fukui (Shimonoya 2001), Yamanashi (Hiura 1966), Nagano (Hiura 1966), Aichi (Asahi et al. 2010), Hiroshima (Nozaki & Nozaki 2013); and Kyushu: Fukuoka (Hiura 1966). China: Liaoning (Bu & Zheng 2001). In Japan, this species is presently restricted to Honshu and Kyushu (Fig. 18). Recent records are concentrated in the northern part of Honshu, such as Tochigi and the Tohoku district (Konno 2012a, 2020; Maehara 2015).

Remarks. Nearly no information is currently available on the morphology of the female genitalia of *Elatophilus* because they had never been described and illustrated. The female genitalia of *E. nipponensis* are characterized by having the basal part of the copulatory tube being extremely expanded and bulbous with rugosities. This character state somewhat resembles that of *Temnostethus distans*. Similar traits have also been found in *Anthocoris* species (e.g., *A. thibetanus* Poppius, 1909) (Ke & Bu 2007). The similarity of the copulatory tube between these species in different genera implies that this structure varies greatly among species in the same genus. To the best of our knowledge, it seems difficult to define each genus of Anthocorini based only on female genitalia.

Genus *Acompocoris* Reuter, 1875

Acompocoris Reuter, 1875: 63. Type species by subsequent designation (Kirkaldy 1906: 120): *Lygaeus pygmaeus* Fallén, 1807.

Acompocoris (selected references): Reuter (1884): 56, 87 (in key, redescription); Poppius (1909): 28 (in key); Harris & Shull (1944): 207 (listed); Stichel (1958): 13 (in key); Stichel (1960): 358 (catalogue, fauna of Palaearctic); Kerzhner (1964): 696, 698 (in key, diagnosis); Carayon (1972): 345 (listed); Péricart (1972): 78, 146 (in key, redescription, fauna of W. Palaearctic); Herring (1976): 145–146 (figure, in key); Kelton (1978): 18, 32 (in key, redescription, fauna of Canada and Alaska); Ford (1979): 55 (check list of the world); Önder (1982): 28, 75 (in key, redescription, fauna of Turkey); Henry (1988): 13 (catalogue, N. America); Kerzhner (1988): 770, 774 (in key, note); Lattin & Stanton (1992): 427 (diagnosis, habitat, prey); Péricart (1996): 108 (catalogue, Palaearctic); Lattin (2000): 612 (bionomics); Bu & Zheng (2001): 45, 109 (distribution, in key, redescription, fauna of China); Yasunaga (2001b): 280 (diagnosis, fauna of Japan); Wachmann et al. (2006): 182 (distribution, habitat); Horton (2008): 2403 (listed).

Diagnosis. Distinguished from the other genera of Anthocorini by the combination of the following characters: body shiny, generally pubescent; labium almost reaching or exceeding metacoxae, but reaching near middle of mesosternum in *A. brevirostris* Kerzhner, 1979; hemelytra densely covered with setigerous punctures; ostiolar peritreme (Fig. 5A) broad, slightly curved forward, slightly protruding at apex but not prolonged tongue-like, apex not reaching outer margin of metapleuron and continued by a fine carina; metasternum apically triangular; metacoxae contiguous with each other.

Remarks. *Acompocoris* comprises six species in the Holarctic Region (Péricart 1972, 1996; Henry 1988). Four of these species are native to the Palaearctic, one in the Nearctic, and one species, *A. pygmaeus* (Fallén, 1807), is widespread in Eurasia and has been introduced in eastern Canada.

Species of this genus are found on conifers (e.g., *Pinus*, *Abies*, *Picea*, and *Larix* species), where they feed on aphids (Rozhkov 1966, Péricart 1972, Lattin & Stanton 1992).

Acompocoris brevirostris Kerzhner, 1979

(Figs 4A–D, 5A–C, 6A–D, 16A–B, 19)

Acompocoris brevirostris Kerzhner, 1979: 23. Holotype: ♂, Kuril Is., Urup, Kaymen (ZMAS).

Acompocoris brevirostris: Kerzhner (1988): 773–774 (figures, in key); Péricart (1996): 109 (catalogue, distribution); Yasunaga et al. (1999): 8 (record, distribution, photo); Yasunaga (2001b): pl. 85, 280 (photo, diagnosis, habitat, prey, phenology); Togashi (2002): 8 (record, photo); Iijima (2004): 134 (record); Khomentovsky (2004): 182 (listed); Kanyukova & Marusik (2006): 164, 168 (listed); Gapon & Konstantinov (2008): 26 (listed); Vinokurov et al. (2010): 56 (catalogue, distribution); Aukema et al. (2013a): 84 (catalogue, distribution); Vinokurov & Golub (2016): 350–351 (listed, figure); Yamada et al. (2016): 422 (catalogue, distribution); Vinokurov (2020): 39 (catalogue, distribution); Vinokurov & Khruleva (2021): 22 (distribution, habitat).

Material examined. JAPAN: Hokkaido: 1 ♂ (Figs 4A–B) 1 ♀ (Figs 4C–D), Nakagawa-cho, Mt. Panke, 300–630 m, 31.vii.1997, T. Yasunaga (TKPM); 1 ♂ (Figs 6A–C) 2 ♀♀ (one in Fig. 5A, one in Fig. 6D), same locality and date, S. Yamashita (TKPM); 1 ♂ 2 ♀♀, Kamikawa-cho, Mts. Taisetsu, Mt. Midori-dake, 1500–1700 m alt., 43.640N 142.923E, *Pinus pumila*, 7.viii.2001, T. Yasunaga (TYCN); 1 ♀, Kamikawa-cho, Goshikigahara, 12.viii.1998, A. Yamamoto (TKPM); 1 ♂, Mt. Antaroma-dake, 11.viii.1967, A. Nakanishi (ELKU); 1 ♂, Mt. Satsunai-dake, 28.vii.1967, A. Nakanishi (ELKU). **Honshu:** Yamagata Pref.: 2 ♀♀, Mt. Chôkai, 17.ix.1971, M. Tomokuni (NSMT). Gunma Pref.: 1 ♀, Katashina-mura, Tokura, 17.x.2014, K. Takahashi (TKPM). Nagano Pref.: 1 ♀, South Alps, Mt. Senjôga-take, 2.x.2011, S. Shiyake (OMNH); 3 ♂♂ (one in Figs 5B–C) 14 ♀♀, Ôtaki-mura, Tanohama, 7. viii.2010, T. Ban (TKPM). Gifu Pref.: 1 ♂ 1 ♀, Mt. Norikura-dake, 7.ix.1951, H. Hasegawa (OMNH).

Differential diagnosis. Recognized by the following combination of characters: body (Figs 4A–D, 16A–B) generally blackish brown; antennal segment II approximately 1.2 times as long as head width across eyes; labium (Figs 4B,D) reaching near middle of mesosternum; hemelytra (Figs 4A,C) tinged with reddish brown, female (Fig. 4C) much paler with dark spot near middle of endocorium; membrane of hemelytra smoky dark brown, with area behind apex of cuneus and area along four veins grayish white; apex of femora and entire tibiae reddish brown to yellowish brown. Similar to Holarctic *A. pygmaeus* (Fallén, 1807) and Palaearctic *A. alpinus* Reuter, 1875, but distinguished from both by labium reaching near middle of mesosternum (in *A. pygmaeus* and *A. alpinus*, labium extending or almost reaching metacoxae) and paramere basally widened (in *A. pygmaeus* and *A. alpinus*, narrower). The form of female genitalia of *A. brevirostris* is similar to that of *A. alpinus* with a copulatory tube possessing a lateral process at base but separated from that species by the copulatory tube being fused on the left side of the intersegmental membrane between sterna VII and VIII in dorsal view (in *A. alpinus*, fused on the mesal part of the intersegmental membrane) and the copulatory tube being rather short (in *A. alpinus*, much longer).

Redescription. ***Male genitalia*** (Figs 5B–C, 6A–C): Pygophore (Fig. 6A) broadly cone-shaped, covered with 4–5 long, stout setae (missing in Fig. 6A) intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest setae are approximately half the length of pygophore; mid-dorsal surface very hirsute with short, suberect setae; paramere (Figs 5C, 6B–C) lamellate, short, strongly curved near apex, basally widened, with a few very short, erect setae on middle portion, without distinct groove but weak depression near base formed by inflection of posterior edge.

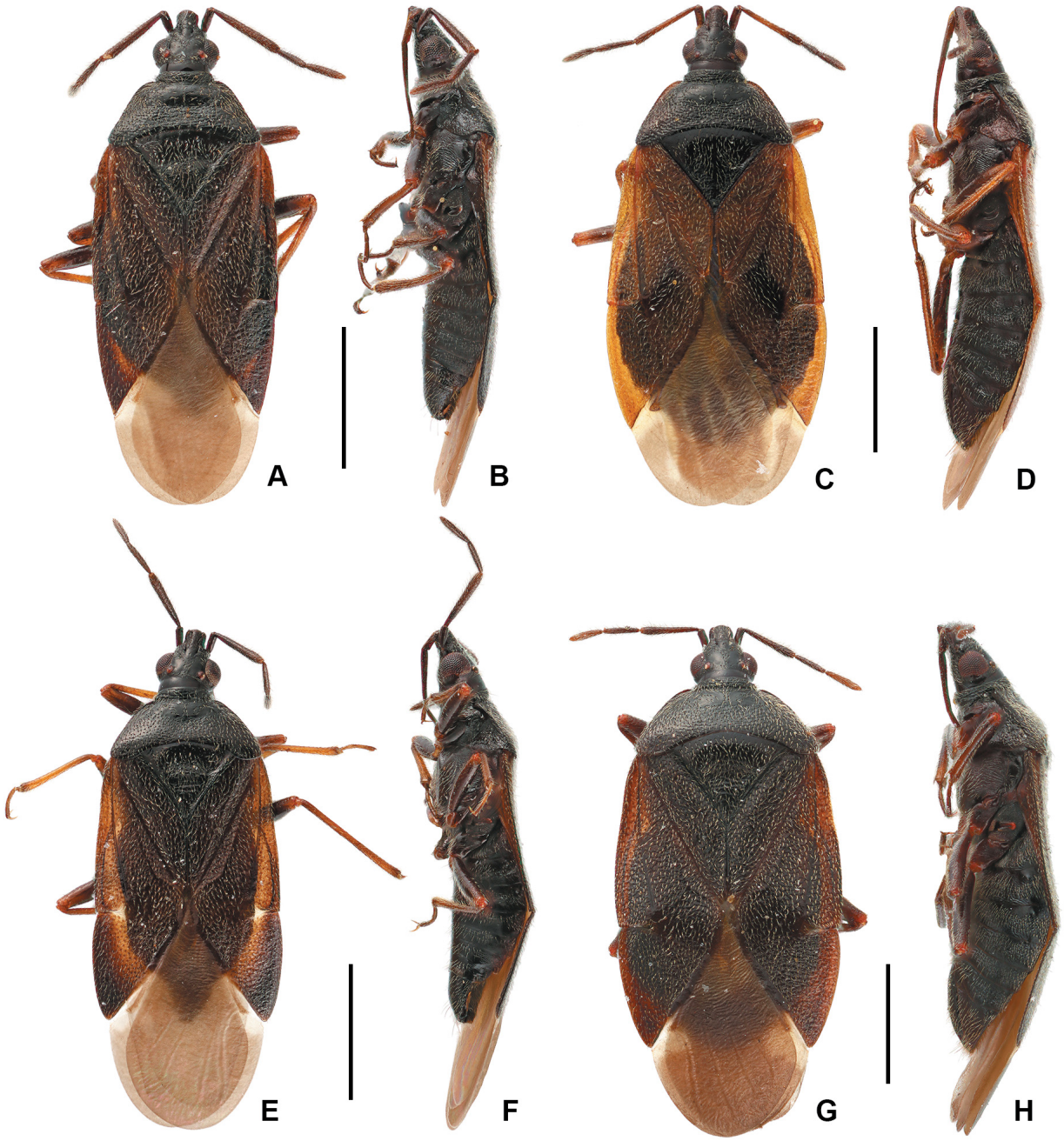

Fig. 4. Habitus, dorsal (A, C, E, G) and lateral (B, D, F, H) views. A–B – *Acompocoris brevirostris* Kerzhner, 1979, male; C–D – same, female; E–F – *Tetraphleps aterrima* (J. Sahlberg, 1878), male; G–H – same, female. Scale bars: 1.0 mm.

Female genitalia (Fig. 6D): Copulatory tube fused on left lower surface of intersegmental membrane between sterna VII and VIII in dorsal view, approximately 0.3 mm in length, with lateral process at base, somewhat narrowing toward apex, entire copulatory tube with rugosities; thin-walled, annular structures of unknown function visible within sperm pouch at junction of pouch and copulatory tube; trunk of conductive tissue not pronounced (or possibly dissolved).

Measurements [mm; ♂♂ (n = 5) / ♀♀ (n = 10)]. Body length 3.85–4.00 / 4.10–4.50; head length (excl. neck) 0.46–0.50 / 0.45–0.51; head width across eyes 0.51–0.56 / 0.53–0.58; vertex width 0.29–0.33 / 0.31–0.34; length of antennal segments I – 0.20–0.23 / 0.20–0.23, II – 0.63–0.69 / 0.60–0.65, III – 0.36–0.39 / 0.36–0.41, and IV – 0.35–0.40 / 0.35–0.43; length of labial segments II – 0.20–0.23 / 0.21–0.26, III – 0.69–0.75 / 0.65–0.80, and IV – 0.29–0.31 / 0.30–0.35; anterior pronotal width 0.43–0.45 / 0.44–0.50; mesal pronotal length 0.48–0.53 / 0.50–0.55; basal pronotal width 1.18–1.25 / 1.28–1.44; length of embolial margin 1.22–1.31 / 1.22–1.48; length of cuneal margin 0.90–0.95 / 1.00–1.15; maximum width across hemelytra 1.46–1.55 / 1.63–1.85.

Bionomics. *Acompocoris brevirostris* is associated with *Pinus pumila* (Pall.) Regel (e.g., Kerzhner 1979, 1988; Yasunaga 2001b; Togashi 2002; Khomentovsky 2004).

In the treeless areas of the Chukotka Autonomous Okrug (tundra zone and the elfin wood subzone) in Far East Russia, it was collected on a swamp river terrace with sedge-sphagnum-moss cover and shrubs of dwarf pine and alder (Vinokurov & Khruleva 2021).

Distribution. Japan: Hokkaido (Yasunaga et al. 1999); Honshu: Yamagata*, Gunma*, Ishikawa (Togashi 2002), Nagano*, Gifu*. Chishima (Kuril) Islands: Kunashir Is., Iturup Is., Urup Is., Simushir Is., Ketoi Is., Shiashkotan Is., Paramushir Is., Shumshu Is. (Kerzhner 1979, Kanyukova & Marusik 2006). Russia: Far East: Magadan, Kamchatka, Sakhalin, Primorsky Kray (Kerzhner 1988, Vinokurov et al. 2010, Vinokurov & Golub 2016). In Japan, this species is apparently restricted to the subalpine coniferous forests of the central and northern parts of the country, generally at high elevations but also in the lowland areas of Hokkaido where *Pinus pumila* subalpine forests can be found.

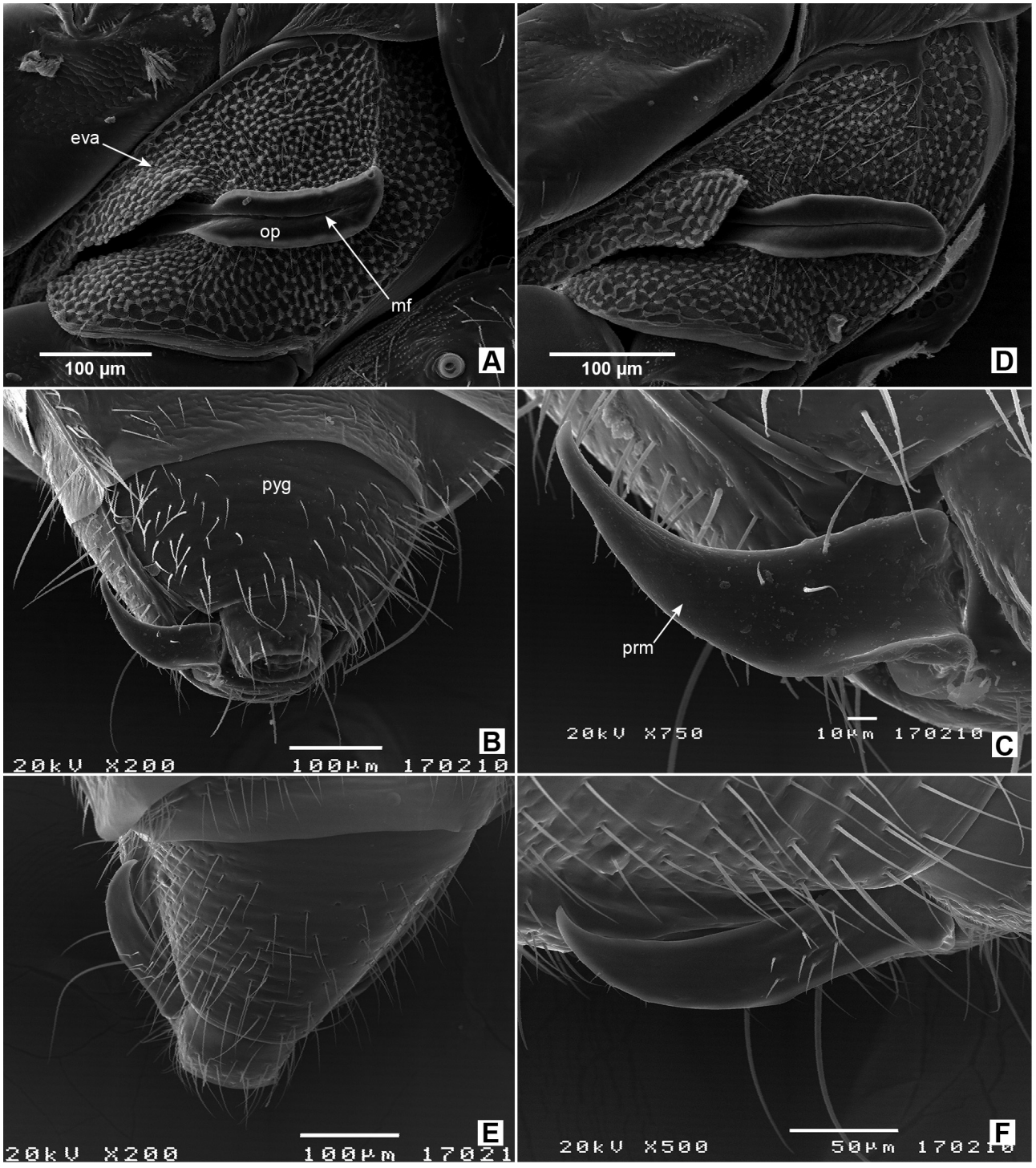

Fig. 5. Scanning electron micrographs of diagnostic characters of Japanese anthocorids. A–C – *Acompocoris brevirostris* Kerzhner, 1979, female (A) and male (B–C); D–F – *Tetraphleps aterrima* (J. Sahlberg, 1878), male. A, D – ostiolar peritreme and evaporatorium, left lateroventral view; B, E – pygophore with paramere, dorsal view; C, F – paramere, dorsal views. Abbreviations: eva – evaporatorium; mf – median furrow; op – ostiolar peritreme; prm – paramere; pyg – pygophore.

Genus *Tetraphleps* Fieber, 1860

Tetraphleps Fieber, 1860: 262. Type species by monotypy: *Anthocoris vittatus* Fieber, 1836 (= *Anthocoris bicuspis* Herrich-Schaeffer, 1835).

Tetraphleps (selected references): Fieber (1861): 38, 135 (in key, redescription); Reuter (1875): 62–63 (in key); Reuter (1884): 56, 85 (in key, description); Lethierry & Severin (1896): 245 (catalogue); Kirkaldy (1906): 120 (listed); Poppius (1909): 28 (in key); Stichel (1958): 12 (in key); Stichel (1960): 358 (catalogue, fauna of Palaearctic); Kelton & Anderson (1962): 1307 (diagnosis, list of N. America); Kerzhner (1964): 696, 698 (in key, diagnosis); Carayon (1972): 345 (listed); Péricart (1972): 78, 154 (in key, description, fauna of W. Palaearctic); Elov (1976): 370 (in key); Herring (1976): 145–146 (figure, in key); Kelton (1978): 18, 25 (in key, description, fauna of Canada and Alaska); Muraleedharan & Ananthakrishnan (1978): 8 (in key); Ford (1979): 58 (check list of the world); Henry (1988): 17 (catalogue, N. America); Kerzhner (1988): 770, 774 (in key, note); Péricart (1996): 120 (catalogue, Palaearctic); Lattin (2000): 622 (bionomics); Bu & Zheng (2001): 109, 169 (in key, redescription, fauna of China); Yasunaga (2001b): 283 (diagnosis, fauna of Japan); Wachmann et al. (2006): 202 (distribution, habitat); Horton (2008): 2403 (listed); Jung et al. (2013): 422 (listed); Jung & Lee (2017): 34, 39 (in key, listed, fauna of Korea).

Diagnosis. Distinguished from the other genera of Anthocorini by the combination of the following characters: body shiny, generally pubescent; labium almost reaching or exceeding procoxae; hemelytra densely covered with setigerous punctures; ostiolar peritreme (Fig. 5D) apically projected, tongue-like and protruding above the surface of evaporatorium, its apex sometimes reaching outer margin of metapleuron and not continued by a fine carina; metasternum apically triangular; metacoxae contiguous with each other.

Remarks. *Tetraphleps* currently contains 16 species distributed in the Northern Hemisphere. Ten of them are known from the Palaearctic, five from the Nearctic, and one from India and Kenya (Henry 1988, Péricart 1996, Bu & Zheng 2001, Tong & Nonnaizab 2008, Ballal et al. 2018). *Tetraphleps raoi* Ghauri, 1965, known from Kenya, was introduced in India as a biological control agent against serious pests of *Pinus* spp. (Chacko 1973, Karanja & Aloo 1990).

Species of the genus are found exclusively on conifers (e.g., mostly on *Pinus*, sometimes on *Abies*, *Larix*, *Picea*, and *Pseudotsuga* species), where they feed mainly on aphids (Reuter 1908, Péricart 1972, Kelton 1978, Lattin & Stanton 1992).

Tetraphleps aterrima (J. Sahlberg, 1878)

(Figs 4E–H, 5D–F, 6E–H, 16C, 19)

Anthocoris aterrimus J. Sahlberg, 1878: 31. Lectotype (designated by Péricart 1970: 740): ♀, Russia (ES), Yenisei Valley, Imbatsk (MZHF).

Tetraphleps aterrimus var. *piceipennis* Reuter, 1883a: 27. Syntypes: Russia: West Siberia: Tyumen Prov., "Leusch" (= Leushi) (MZHF).

Tetraphleps ezoensis Hiura, 1959: 2. Holotype: ♂, Japan, Hokkaido, Mt. Meakandake (OMNH). Synonymized by Kerzhner (1978: 48).

Tetraphleps aterrimus (selected references): Reuter (1884): 86 (redescription); Lethierry & Severin (1896): 244 (listed, taxonomic status); Péricart (1972): 155–157 (in key, figures, redescription, distribution); Elov (1976): 371–372, 377 (figure, in key, note); Elov & Kerzhner (1977): 212 (record, bionomics); Ford (1979): 58 (listed, distribution); Bu & Zheng (1991b): 198, 202 (record, taxonomic status); Hua (2000): 199 (listed, distribution); Bu & Zheng (2001): 170 (in key, redescription, figures); Coulianos (2005): 18 (record, distribution); Ke & Bu (2005): 393 (description of female genitalia); Hao & Ma (2013): 36 (listed).

Tetraphleps aterrima (selected references): Stichel (1958): 30 (in key, diagnosis); Stichel (1960): 358 (listed, distribution); Kerzhner (1988): 769, 774 (figure, in key); Miyamoto & Yasunaga (1989): 166 (listed, distribution); Vinokurov & Kanyukova (1995): 12 (listed); Péricart (1996): 120 (catalogue, distribution); Mizoi (1999): 45, 46 (record); Mizoi & Haga (1999): 64 (listed); Kwon et al. (2001): 81 (catalogue, record, distribution); Yasunaga (2001b): pl. 85, 283 (photo, diagnosis, habitat, phenology); Coulianos (2003): 61 (record, distribution); Hoffmann & Melber (2003): 243 (distribution); Vinokurov et al. (2003): 58 (listed); Ichita (2009): 68 (listed); Vinokurov et al. (2010): 59 (catalogue, distribution); Rintala & Rinne (2011): 170 (diagnosis, habitat, distribution, photo); Suzuki (2011): 8 (distribution); Aukema et al. (2013a): 88 (catalogue, distribution); Esenbekova (2013): 59 (habitat, distribution); Jung et al. (2013): 422 (catalogue, diagnosis, distribution); Albrecht et al. (2015): 24 (listed); Maehara (2015): 28 (recorded as *Acompocoris* sp., bionomics); Maehara (2016): 126 (recorded as *Acompocoris brevirostris*, distribution, habitat); Tochigi Prefectural Museum (2016): 60 (recorded as *Acompocoris brevirostris*, photo, habitat, phenology); Yamada et al. (2016): 423 (catalogue, distribution); Jung & Lee (2017): 39 (distribution); Vinokurov (2020): 40 (catalogue, distribution); Vinokurov & Khruleva (2021): 22–23 (distribution).

Tetraphleps ezoensis: Miyamoto (1961): 220 (morphology of alimentary organ); Togashi (1985): 97–99 (listed).

Type material examined. *Tetraphleps ezoensis*: Holotype: ♂, '5. VII. 1958 \ Mt. MEAKAN \ HOKKAIDO \ Ezomatsu [= *Picea jezoensis*, in Chinese script], Todomatsu [= *Abies sachalinensis* in Chinese script]' [handwritten], 'Holotype ♂ [handwritten] \ Tetraphleps [handwritten] \ ezoensis [handwritten] \ HIURA, 1959 [handwritten] \ I. HIURA Det. [printed]', 'OMNH TI 188' [handwritten] (OMNH). Paratopotype: ♀ (Figs 4G–H), '5. VII. 1958 \ Mt. MEAKAN \ HOKKAIDO \ Ezomatsu [= *Picea jezoensis*, in Chinese script], Todomatsu [= *Abies sachalinensis* in Chinese script] \ S. MIYAMOTO' [handwritten], 'Paratopotype \ Tetraphleps [handwritten] \ ezoensis [handwritten] \ HIURA, 1959 ♀ [handwritten] \ I. HIURA Det. [printed]' (OMNH).

Additional material examined. JAPAN: Hokkaido: 1 ♂ 2 ♀♀, Kamikawa-cho, Mts. Taisetsu, Mt. Midori-dake, 1500–1700 m alt., 43.640N 142.923E, *Pinus pumila*, 7.viii.2001, T. Yasunaga (TYCN); 1 ♂, Kamikawa-cho, Aizankei, 19.vii.1962, Y. Miyatake (OMNH); 1 ♀, Higashikawa-cho, Mt. Asahi-dake, 10.vii.1970, H. Hasegawa (OMNH); 3 ♂♂ (one in Figs 5D–F) 1 ♀, Kuchanbetu Riv., Taisetsu Natural Park, 1000–1100 m, 26.vii.2000, T. Yasunaga (TKPM); 1 ♂ (Figs 6E–G) 1 ♀ (Fig. 6H), Kamishihoro-cho, Mikuni-tôge, 17.vii.2000, K. Yamada (TKPM); 1 ♂, Mt. Upepesanke, 20.vii.1967, A. Nakanishi (ELKU); 2 ♂♂, Mt. Satsunai-dake, 28.vii.1967, A. Nakanishi (ELKU). Rishiri-tô Is.: 1 ♂ (Figs 4E–F), Kutsukata, 27.–28.vii.1994, T. Yasunaga (TKPM); 1 ♂, no detailed locality, 7.viii.1954, T. Nakane (OMNH). **Honshu:** Aomori Pref.: 1 ♀, Towada-shi, Kasamatsu-tôge, 18.vii.1998, T. Ichita (TKPM). Tochigi Pref.: 1 ♀, Nikko-shi, Yumoto, 25.vi.2010, S. Maehara (TKPM); 1 ♀, same locality, 16.vi.2015, S. Maehara (TKPM); 1 ♀, same locality, 24.vii.2019, S. Maehara (TKPM); 1 ♂ 1 ♀, Nikko-shi, Yumoto, Mt. Yusengatake, 2280 m alt., N36°49′23.3″ E139°24′12.4″, 14.ix.2013, T. Kurihara (TKPM). Yamanashi Pref.: 2 ♀♀, Koufu-shi, Oodarumi-tôge to Mt. Kinpusan, 2360–2500 m, 18.vii.2010, H. Kojima (TKPM). Nagano Pref.: 1 ♀, Mt. Yatsuga-take, 18.vii.1939, H. Hasegawa (OMNH); 2 ♀♀, South Alps, Kitazawa to Mt. Senjôga-take, 27.vii.1959, Y. Miyatake (OMNH); 2 ♀♀, Ôtaki-mura, Tanohama, 7.viii.2010, T. Ban (TKPM). Gifu Pref.: 1 ♀, Mt. Norikura-dake, Dohyôgahara to Sarutobihacchô, 2400–2600 m, 16.vii.1960, I. Hiura (OMNH); 1 ♂, Mt. Norikura-dake, 8.ix.1951, H. Hasegawa (OMNH). No data: 4 ♀♀ (TKPM).

Differential diagnosis. Recognized by the following combination of characters: body (Figs 4E–H, 16C) generally blackish brown; anteocular region as long as the length of eye in dorsal view; antennal segment II approximately as long as head width across eyes; labium (Figs 4F,H) just reaching but not exceeding to procoxae; hemelytra (Figs 4E,G) sometimes tinged with reddish brown; membrane of hemelytra smoky dark brown, with area behind apex of cuneus,

with four distinct veins grayish white; apex of femora and entire tibiae reddish brown to yellowish brown. Similar in general appearance to *T. bicuspis* (Herrich-Shaeffer, 1835) from the western to central Palaearctic Region, but distinguished from that species by the anteocular region being as long as the length of eye in dorsal view (in *T. bicuspis*, considerably longer than length of eye), labium reaching but not exceeding the procoxae (in *T. bicuspis*, reaching middle of mesosternum), and hemelytral membrane with grayish pale or whitish markings on area behind apex of cuneus (in *T. bicuspis*, grayish pale or whitish along four distinct veins). Resembling also *Acompocoris brevirostris* in appearance but distinguished from that species by the length of labium and the shape of ostiolar peritreme (Figs 4F,H, 5D).

Redescription. ***Male genitalia*** (Figs 5E–F, 6E–G): Pygophore (Fig. 6E) elongate-conical, covered with 4–5 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest setae are shorter than half the length of pygophore; mid-dorsal surface very hirsute with short, suberect setae; paramere (Figs 5F, 6F–G) moderately curved, acute at apex, basally twisted, with a few very short, erect setae on middle portion, without longitudinal groove.

Female genitalia (Fig. 6H): Copulatory tube fused on middle part of intersegmental membrane between sterna VII and VIII in dorsal view, approximately 1.3 mm in length, entirely very thin but expanded at base, with many twists; thin-walled, annular structures of unknown function slightly visible within sperm pouch at junction of pouch and copulatory tube; trunk of conductive tissue not pronounced (or possibly dissolved).

Measurements [mm; ♂♂ (n = 9) / ♀♀ (n = 12)]. Body length 4.10–4.75 / 4.20–5.00; head length (excl. neck) 0.48–0.53 / 0.54–0.60; head width across eyes 0.54–0.58 / 0.58–0.66; vertex width 0.28–0.30 / 0.33–0.36; length of antennal segments I – 0.15–0.19 / 0.18–0.23, II – 0.56–0.60 / 0.50–0.69, III – 0.31–0.36 / 0.31–0.40, and IV – 0.35–0.39 / 0.34–0.41; length of labial segments II – 0.15–0.18 / 0.16–0.20, III – 0.46–0.53 / 0.55–0.68, and IV – 0.26–0.29 / 0.28–0.36; anterior pronotal width 0.43–0.46 / 0.48–0.55; mesal pronotal length 0.49–0.58 / 0.56–0.65; basal pronotal width 1.21–1.38 / 1.38–1.66; length of embolial margin 1.29–1.50 / 1.50–1.75; length of cuneal margin 0.88–1.03 / 1.00–1.18; maximum width across hemelytra 1.54–1.75 / 1.81–2.13.

Bionomics. *Tetraphleps aterrima* was collected from *Picea jezoensis* (Sieb. & Zucc.) Carrière and *Abies sachalinensis* (F. Schmidt) Masters in Hokkaido (Hiura 1959), and from *Abies homolepis* Sieb. & Zucc., *A. mariesii* Mast., and *Picea jezoensis* var. *hondoensis* (Mayr) Rehder in the northern part of Tochigi Prefecture, at 1600 to 2300 m

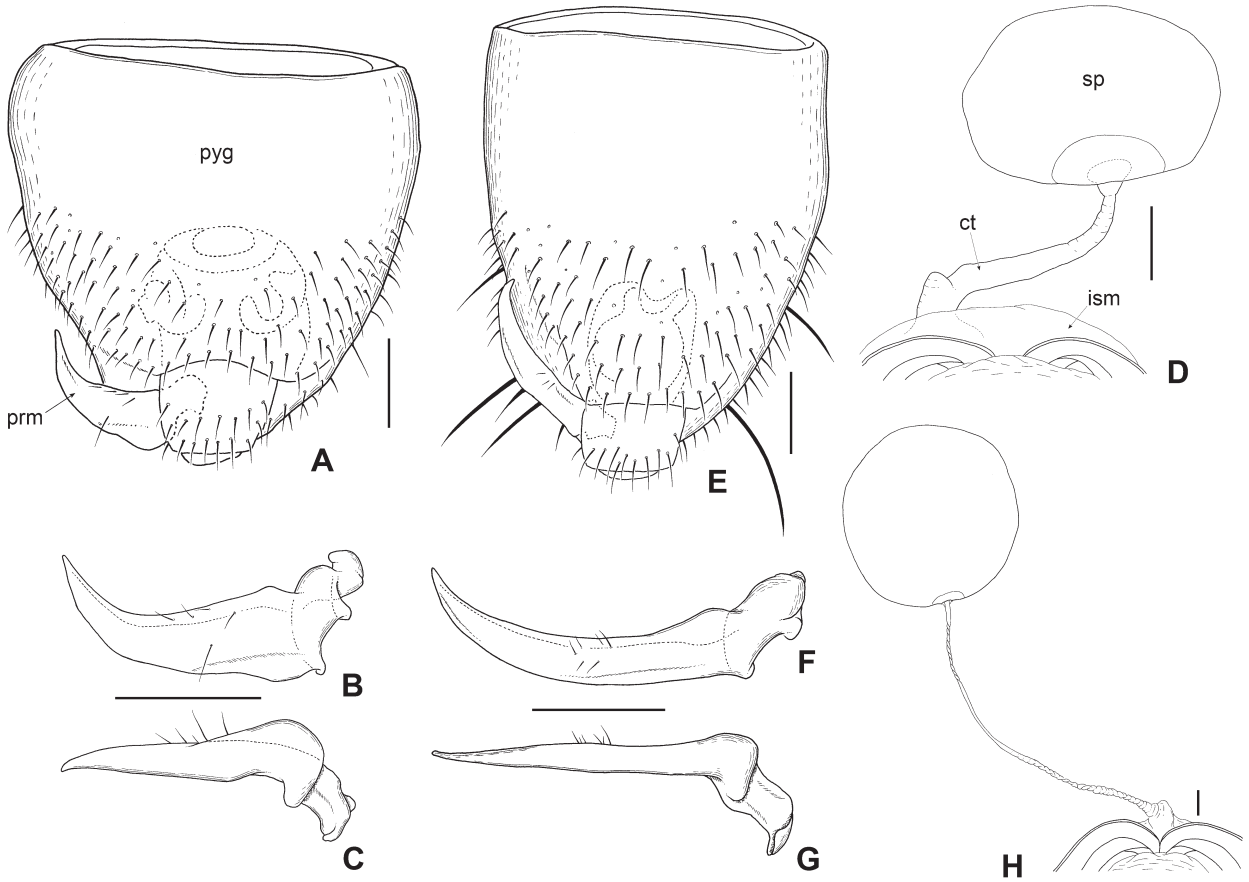

Fig. 6. Male (A–C, E–G) and female (D, H) genitalia. A–D – *Acompocoris brevirostris* Kerzhner, 1979; E–H – *Tetraphleps aterrima* (J. Sahlberg, 1878). A, E – pygophore with paramere (ejaculatory bulb omitted), dorsal view; B–C, F–G – paramere, two different views; D, H – copulatory tube and sperm pouch, dorsal view. Abbreviations: ct – copulatory tube; ism – intersegmental membrane; prm – paramere; pyg – pygophore; sp – sperm pouch. Scale bars: 0.1 mm.

elevation (Maehara 2016, Tochigi Prefectural Museum 2016). The species was also found on *Pinus pumila* in the alpine zone of Hokkaido and central Honshu. *Tetraphleps aterrima* was collected from *Abies sibirica* Ledeb. in Europe and Russia (Péricart 1972), and from *Larix* species in Siberia (Kerzhner 1988).

Distribution. Japan: Hokkaido (Hiura 1959), Rishiri-tô Is.*; Honshu: Aomori (Yasunaga 2001b), Tochigi (Maehara 2016), Ishikawa (Togashi 1985), Yamanashi (Mizoi 1999), Nagano*, Gifu*. Korea: North (Kwon et al. 2001). Mongolia (Péricart 1972). China: Jilin, Hebei, Ningxia, Shanxi, Xinjiang (Bu & Zheng 2001). Russia (whole territories) (Kerzhner 1988, Vinokurov et al. 2010). Finland (Linnavuori 1951, Albrecht et al. 2015). Germany (Jordan 1963, Hoffmann & Melber 2003). Estonia (Coulianos 2003). Kazakhstan: Asian part (Péricart 1996, Esenbekova 2013). Kirgizia (Péricart 1996). In Japan, this species is apparently restricted to subalpine coniferous forests of high mountain regions in central and northern Japan and frequently co-occurs with *Acompocoris brevirostris* (Fig. 19). This species is also strongly associated with subalpine conifers, similar to *A. brevirostris*.

Genus *Anthocoris* Fallén, 1814

Anthocoris Fallén, 1814: 9. Type species by subsequent designation (Westwood 1840: 122): *Cimex nemorum* Linnaeus, 1761. Placed on the Official List of Generic Names (ICZN 1928: 25, Opinion 104).

Hylophila Stephens, 1829: 65. Type species by monotypy: *Cimex nemorum* Linnaeus, 1761. Junior homonym of *Hylophila* Hübner, 1825 (Lepidoptera). Synonymized by Westwood (1840: 122).

Rhynarius Hahn, 1832: 104. Type species by subsequent designation (Kirkaldy 1906: 120): *Rhynarius sylvestris* sensu Hahn, 1832 (= *Cimex nemorum* Linnaeus, 1761). Synonymized by Hahn (1833: 233).

Leptomeris Laporte, 1832: 10. Type species by monotypy: *Leptomeris picta* Laporte, 1832 (? = *Cimex nemorum* Linnaeus, 1761). Junior homonym of *Leptomeris* Hübner, 1825 (Lepidoptera). Synonymized by Kirkaldy (1906: 120).

Phyllocoris A. Costa, 1847: 25. Type species by monotypy: *Cimex nemorum* Linnaeus, 1761. Synonymized by Baerensprung (1860: 11).

Anthocoris (selected references): Fieber (1836): 106 (redescription); Fieber (1860): 263 (redescription); Fieber (1861): 38, 136 (in key, redescription); Reuter (1875): 63 (in key); Reuter (1883b): 78 (taxonomic history); Reuter (1884): 56, 66 (in key, redescription); Lethierry & Severin (1896): 243 (catalogue); Champion (1900): 323 (distribution, fauna of C. America); Poppius (1909): 28 (in key); Distant (1910): 298 (distribution, diagnosis); Van Duzee (1916): 34 (fauna of America); Priesner & Alfieri (1953): 81 (in key); Gross (1954): 131, 133 (in key, redescription, fauna of Australia); Stichel (1958): 12 (in key); Stichel (1960): 357 (catalogue, fauna of Palaearctic); Hiura (1959): 3 (fauna of Japan and Far East of USSR); Kerzhner (1964): 696, 698 (in key, diagnosis); Carayon (1972): 345 (listed); Péricart (1972): 78, 110 (in key, redescription, fauna of W. Palaearctic); Herring (1976): 145–146 (figure, in key); Elov (1976): 369–370 (in key, note); Muraleedharan (1977): 231 (diagnosis); Kelton (1978): 18, 34 (in key, redescription, fauna of Canada and Alaska); Muraleedharan & Ananthakrishnan (1978): 8 (in key); Ford (1979): 55 (checklist of the world); Önder (1982): 27–28, 77 (in key, redescription, fauna of Turkey); Henry (1988): 14 (catalogue, N. America); Kerzhner (1988): 770, 772 (in key, note); Lattin & Stanton (1992): 429 (diagnosis, habitat, prey); Cassis & Gross (1995): 27 (catalogue, Australia); Péricart (1996): 109 (catalogue, Palaearctic); Lattin (2000): 612 (bionomics); Bu & Zheng (2001): 45, 109, 111 (distribution, in key, redescription, fauna of China); Yasunaga (2001b): 280 (diagnosis, fauna of Japan); Carpintero (2002): 36 (fauna of Neotropical Region); Wachmann et al. (2006): 184 (distribution, habitat); Horton (2008): 2403 (listed); Falamarzi et al. (2009): 36 (in key); Jung et al. (2013): 422 (listed); Jung & Lee (2017): 34–35 (in key, listed, fauna of Korea).

Diagnosis. Distinguished from other genera of Anthocorini by a combination of the following characters: body shiny or pruinose, generally pubescent; distinctly porrect head; labium not or rarely exceeding procoxae; pronotal collar broad and distinct, situated in front of anterior angles of pronotum; callus developed; hemelytra smooth or shallowly punctate; ostiolar peritreme (Fig. 9) wide, slightly curved forward at apex, distinctly continued by a fine carina, which reaches anterior margin of metapleuron; metasternum apically triangular; metacoxae contiguous with each other; and abdominal sternum with a pair of membranous areas on segments II–III.

Remarks. A species-rich genus currently including nearly 80 species worldwide (Henry 1988; Cassis & Gross 1995; Péricart 1996; Bu & Zheng 2001; Carpintero 2002; Péricart 2007; Yamada et al. 2010; Lewis & Horton 2012; Moulet et al. 2017, 2018). Most of them occur in the Northern Hemisphere, but the genus is the most speciose in Asia; approximately 40 species are known from China (Bu & Zheng 2001).

Anthocoris species are principally arboreal and are usually found on broad-leaved plants, particularly on trees, where they feed on aphids, psyllids, thrips, mites, and other small arthropods (Péricart 1972, Lattin & Stanton 1992, Lattin 2000). Most Japanese species are associated with broadleaf trees, except for the pine-inhabiting *A. chibi*.

Key to Japanese species of *Anthocoris*

1. Hemelytra uniformly black or dark, without whitish markings (Fig. 7). 2
– Hemelytra with some whitish markings (Fig. 8). 7
2. Anterior half of hemelytra densely covered with recumbent whitish silver setae (Fig. 7A); antennal segment III mostly pale brown (Fig. 7A). .... ***A. chibi*** Hiura, 1959
– Anterior half of hemelytra without whitish silver setae (Figs 7C,G,I,K), or covered with pruinose setae (Fig. 7E); antennal segment III uniformly blackish or darkish brown (Figs 7C–L). 3
3. Hemelytra more or less brown or reddish brown at base or in basal half (Figs 7C,I); antennal segment II mostly pale brown (Figs 7C,I). 4
– Hemelytra uniformly black (Figs 7E,G,K); antennal segment II black or blackish brown (Figs 7E,G,K). .. 5
4. Pronotum uniformly blackish brown (Fig. 7C); a strip along the inner embolioum dull or pruinose, the outer portion of the embolium shiny; tibiae mostly pale brown (Figs 7C–D); paramere subapically with a sharply defined projection (Figs 10D, 13E–F). .... ***A. confusus*** Reuter, 1884
– Pronotum light brown or reddish brown on posterior half (Fig. 7I); embolium entirely shiny; tibiae mostly reddish brown to blackish brown (Figs 7I–J); paramere slender, curved, gradually acute at apex (Figs 13K–L). ..... ***A. nemoralis*** (Fabricius, 1794)

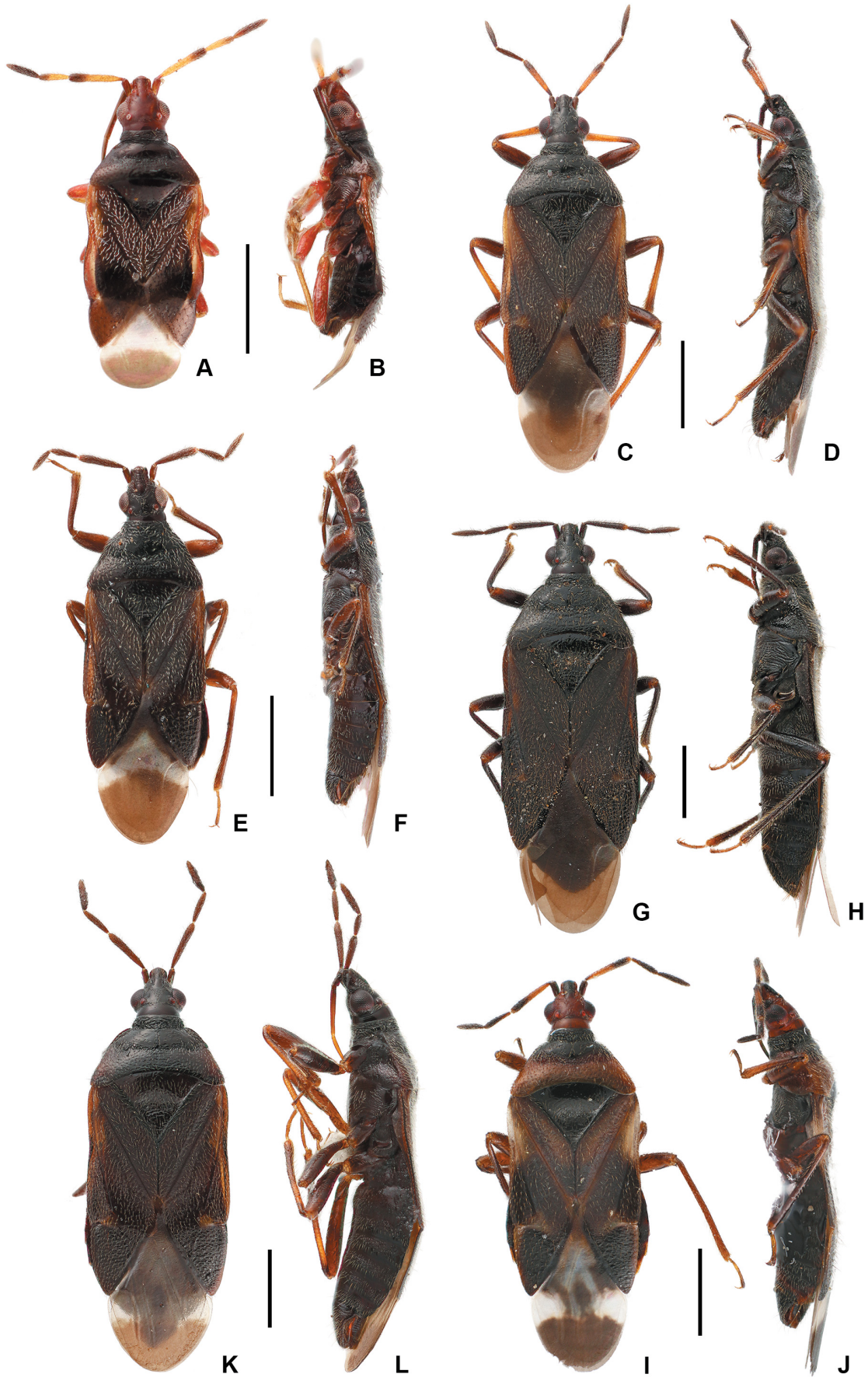

Fig. 7. Habitus of *Anthocoris* spp., dorsal (A, C, E, G, I, K) and lateral (B, D, F, H, J, L) views. A–B – *A. chibi* Hiura, 1959, male; C–D – *A. confusus* Reuter, 1884, male; E–F – *A. japonicus* Poppius, 1909, male; G–H – *A. kalopanacis* Kerzhner, 1977, female; I–J – *A. nemoralis* (Fabricius, 1794), male; K–L – *A. takahashii* Hiura, 1959, male. Scale bars: 1.0 mm.

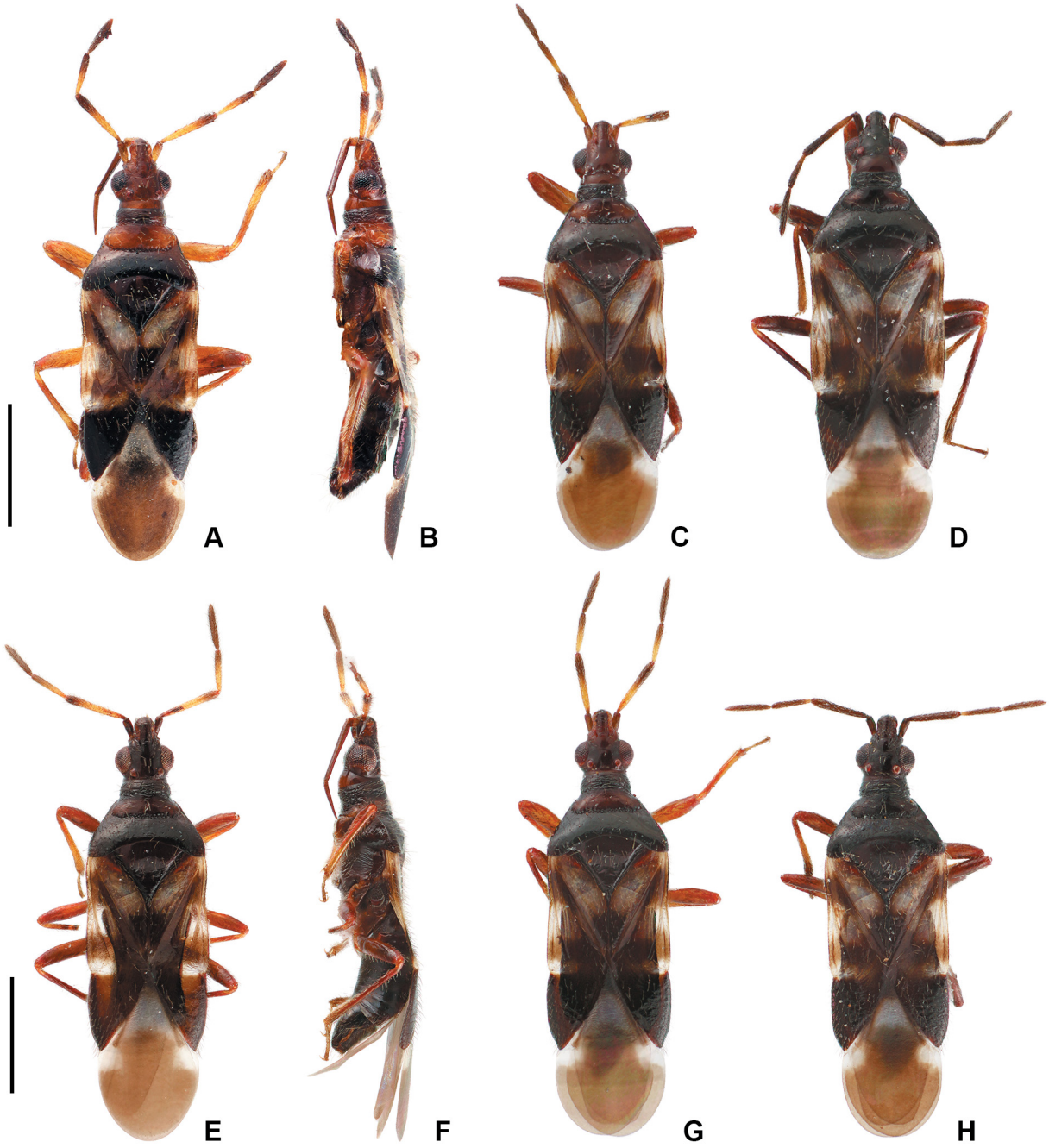

Fig. 8. Habitus of *Anthocoris* spp., male, dorsal (A, C–E, G–H) and lateral (B, F) views. A–B – *A. miyamotoi* Hiura, 1959, holotype (Nakanoshima Is., Tokara Isls.); C – same (Wakayama, Honshu); D – same (Kagoshima, Kyushu); E–F – *A. venustus* sp. nov., holotype (Hokkaido); G – same, paratype (Tochigi, Honshu); H – same, paratype (Nara, Honshu). Scale bars: 1.0 mm.

5. Membrane with broad whitish band on basal part (Fig. 7E); body 3.3–4.0 mm in length. .... ***A. japonicus*** Poppius, 1909
– Membrane with two or three whitish or greyish pale markings (Figs 7G,K); body 4.0–5.0 mm in length. ... 6
6. Membrane with two small, indistinct grayish pale markings (Fig. 7G); labium reaching to middle of prosternum (not reaching procoxae) (Fig. 7H). .... ***A. kalopanacis*** Kerzhner, 1977
– Membrane with three large, irregular-shaped whitish markings (Fig. 7K); labium just reaching procoxae (Fig. 7L). ..... ***A. takahashii*** Hiura, 1959
7. Head and callus of pronotum usually orangish brown to reddish brown (Figs 8A–B); paramere sickle-shaped, rather widened (Figs 14A–C); copulatory tube approximately 0.25 mm in length, very thick and wrinkled at basal 2/3 (Fig. 15F). .... ***A. miyamotoi*** Hiura, 1959
– Head and pronotum uniformly blackish (Figs 8E–H); paramere slender, very slightly curved (Figs 14D–F); copulatory tube approximately 0.8 mm in length, basally thickened with a few twists (Fig. 15G). .... ***A. venustus*** **sp. nov.**

Anthocoris chibi Hiura, 1959

(Figs 7A–B, 9A, 10A–B, 12A, 13A–C, 15A, 20)

Anthocoris chibi Hiura, 1959: 5. Holotype: ♂, Japan, Tokyo (OMNH).

Anthocoris chibi: Miyamoto (1961): 220 (morphology of alimentary organ); Miyamoto (1965): 96, pl. 48 (diagnosis, habitat, distribution, photo); Shimizu (1969): 244 (record); Tawara (1970): 67 (record); Ford (1979): 55 (listed, distribution); Otsuka (1982): 138 (record); Zheng (1984): 66, 68 (record); Ichita (1988): 132 (record); Kerzhner (1988): 774 (in key); Hayashi (1989): 217 (record); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Otsuka & Aramaki (1989): 29 (record); Asaoka & Ieki (1990): 155 (listed, distribution); Zheng & Bu (1990): 23 (listed); Lee et al. (1994): 5 (record); Kwon et al. (1996a): 109 (record); Péricart (1996): 110 (catalogue, distribution); Hayashi (1998): 165 (record); Yasunaga (1999): 22 (listed, distribution); Yasunaga et al. (1999): 8 (record, distribution); Hua (2000): 198 (listed, distribution); Tomokuni (2000): 39 (record); Bu & Zheng (2001): 120, 158 (in key, redescription, figures); Kwon et al. (2001): 79 (catalogue, record, distribution); Yasunaga (2001b): pl. 85, 281 (photo, diagnosis, habitat, prey); Okayama Prefecture (2003): 65 (listed, distribution); Hayashi & Ozaki (2004): 223 (distribution); Nozaki & Nozaki (2006): 11 (record); Ke & Bu (2007): 90–91 (figure, description of female genitalia); Miyamoto (2008): 164, pl. 57 (diagnosis, habitat, distribution, photo); Aoki (2010): 72 (record); Vinokurov et al. (2010): 56 (catalogue, distribution); Yano et al. (2012): 87 (record, distribution); Aukema et al. (2013a): 88 (catalogue, distribution); Hao & Ma (2013): 36 (listed); Jung et al. (2013): 422 (catalogue, diagnosis, distribution, habitat, prey); Iwasaki (2014): 24 (record); Tomokuni (2014): 363 (record); Maehara (2015): 28 (record, habitat, prey); Nozaki et al. (2015): 18 (record); Miyake (2018): 56 (record); Sawada (2018): D-36 (listed); Komatsu (2016): 97 (record); Yamada et al. (2016): 422 (catalogue, distribution); Jung & Lee (2017): 35, 70 (diagnosis, redescription, prey, distribution, photo, figure); Hayashi et al. (2018): 182 (distribution); Ito et al. (2020): 113 (record); Shizuoka Prefecture (2020): 128 (listed).

Type material examined. Holotype: ♂, '12. VII. 1957 \ Yodobashi-Jyôsuijyô [= Yodobashi water purification plant, in Chinese script] \ TOKYO \ Y. NISHIOKA' [handwritten], 'HOLOTYPE ♂ [handwritten] \ Anthocoris [handwritten] \ chibi [handwritten] \ HIURA, 1959 [handwritten] \ I. HIURA Det. [printed]', 'OMNH TI 190' [handwritten] (OMNH).
Additional material examined. JAPAN: Hokkaido: 1 ♀, Tomakomai-shi, Hokkaido Univ. Exp. Forest, 30.vii.1998, T. Yasunaga (TYCN); 1 ♂ 4 ♀♀, Hakodate-shi, Mt. Esan, 15.–16.vii.1970, M. Sakai (NSMT). **Honshu:** Aomori Pref.: 1 ♂, Tsugaru-shi, around Hirataki-numa, 17.vi.2016, T. Yoshida (TKPM). Kanagawa Pref.: 1 ♀, Manazuru-cho, Manazuru Cape, 16.v.2009, T. Ban (TKPM). Nagano Pref.: 1 ♀, Matsumoto-shi, Johyama Park, 8.vi.1991, M. Tomokuni (NSMT). Aichi Pref.: 1 ♀, Tahara-shi, Atsumi, 16.vi.2005, T. Ueda (TKPM). Hyogo Pref.: 11 ♂♂ (one in Figs 7A–B, one in Figs 10A–B, one in Figs 12A, 13A–C) 6 ♀♀ (one in Fig. 15A), Miki-shi, Miki SA, 27.vi.2002, T. Ueda (TKPM) 7 ♀♀ (one in Fig. 9A), same locality, 26.iii.2002, T. Ueda (TKPM); 1 ♂ 6 ♀♀, same locality, 21.x.2002, T. Ueda (TKPM). Tottori Pref.: 1 ♀, Mt. Daisen, Masumizuhara, 13.ix.1984, M. Tomokuni (NSMT). **Shikoku:** Tokushima Pref.: 6 ♂♂ 2 ♀♀, Tokushima-shi, Ôbara-cho, Ômiko, 18.v.2010, K. Yamada (TKPM); 3 ♀♀, Mima-shi, Sôgo, 4.vi.2010, K. Yamada (TKPM). Kagawa Pref.: 6 ♂♂ 5 ♀♀, Takamatsu-shi, Kinbuchi Forest Park, 19.–20.vii.2003, K. Yamada (TKPM); 1 ♀, Shôdoshima-cho, Shihouzashi, 750 m, 16.vii.1999, M. Tomokuni (NSMT).

Differential diagnosis. Recognized by the following combination of characters: Body (Figs 7A–B) reddish brown to blackish brown; head reddish brown; antennae (Fig. 7A) pale brown to yellowish brown; segment I brown, apices of segments II and III and entire segment IV dark brown; anterior half of hemelytra (Fig. 7A) densely covered with recumbent whitish-silver setae; membrane (Fig. 7A) smoky dark brown, with broad whitish band on basal part; legs (Fig. 7A) reddish brown, tibiae uniformly pale brown to yellowish brown; ostiolar peritreme (Fig. 9A) straight, curved anteriorly at apex; abdominal sternum II (Fig. 12A) with a pair of kidney-shaped membranous areas on posterior half. Similar to the general appearance of *A. notatotibialis* Bu & Zheng, 2001 from China, but distinguished from the latter by the tibiae being uniformly pale brown to yellowish brown (in *A. notatotibialis* blackish brown, with outer side of basal half grayish white) and the apex of paramere being strongly curved (in *A. notatotibialis* smoothly curved).

Redescription. ***Male genitalia*** (Figs 10A–B, 13A–C): Pygophore (Fig. 13A) turbinate, slightly wider than long, covered with 4–8 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface; mid-dorsal surface very hirsute with short, suberect setae; paramere (Figs 10B, 13B–C) wide, gradually narrowed toward apex, apex strongly bent, with a few very short, erect setae on median portion; longitudinal groove in form of shallow depression.

Female genitalia (Fig. 15A): Copulatory tube fused on left upper surface of intersegmental membrane between sterna VII and VIII, approximately 0.4 mm in length, almost same width from just anteriad of the base to apex (junction to trunk of conductive tissue), basally slightly thickened; trunk of conductive tissue visible.

Measurements [mm; ♂♂ (n = 10) / ♀♀ (n = 10)]. Body length 2.50–2.88 / 2.75–3.40; head length (excl. neck) 0.38–0.45 / 0.42–0.49; head width across eyes 0.43–0.46 / 0.45–0.52; vertex width 0.25–0.27 / 0.26–0.32; length of antennal segments I – 0.14–0.17 / 0.15–0.18, II – 0.42–0.50 / 0.46–0.56, III – 0.25–0.31 / 0.25–0.32, and IV – 0.32–0.35 / 0.32–0.36; length of labial segments II – 0.12–0.17 / 0.15–0.21, III – 0.50–0.53 / 0.54–0.62, and IV – 0.27–0.32 / 0.29–0.35; anterior pronotal width 0.34–0.38 / 0.37–0.44; mesal pronotal length 0.38–0.44 / 0.42–0.52; basal pronotal width 0.83–1.02 / 0.86–1.13; length of embolial margin 0.87–1.04 / 0.87–1.15; length of cuneal margin 0.42–0.54 / 0.46–0.60; maximum width across hemelytra 0.95–1.08 / 0.96–1.27.

Bionomics. Hiura (1959) reported that this species inhabits *Pinus* forests, where it preys on aphids. In particular, it has been found on *P. densiflora* (e.g., Kerzhner 1988, Bu & Zheng 2001). Yasunaga et al. (1999) recorded this species from Hokkaido based on a specimen from *P. koraiensis* Siebold & Zucc. He suggested that the specimen may have been introduced together with young trees of *Pinus* species from Honshu (Yasunaga et al. 1999, Yasunaga 2001b). A few specimens deposited in NSMT were obtained from Hakodate, in the southern part of Hokkaido in 1970. These specimens may also represent a population introduced from Honshu; therefore, it is probable that artificial introduction from Honshu to Hokkaido occurred repeatedly in the past.

Distribution. Japan: Hokkaido (Yasunaga et al. 1999); Honshu: Aomori (Ichita 1988), Tochigi (Maehara 2015), Saitama (Hayashi 1989), Chiba (Aoki 2010), Tokyo (Hiura 1959), Kanagawa (Hayashi & Ozaki 2004), Nagano*, Shizuoka (Shizuoka Prefecture 2020), Aichi (Asaoka & Ieki 1990), Osaka (Iwasaki 2014), Hyogo*, Tottori*, Okayama (Nozaki & Nozaki 2006); Izu Islands: Ôshima Is. (Hiura 1959); Shikoku: Tokushima (Hiura 1959), Kagawa*, Ehime (Yano et al. 2012); Kyushu: Fukuoka

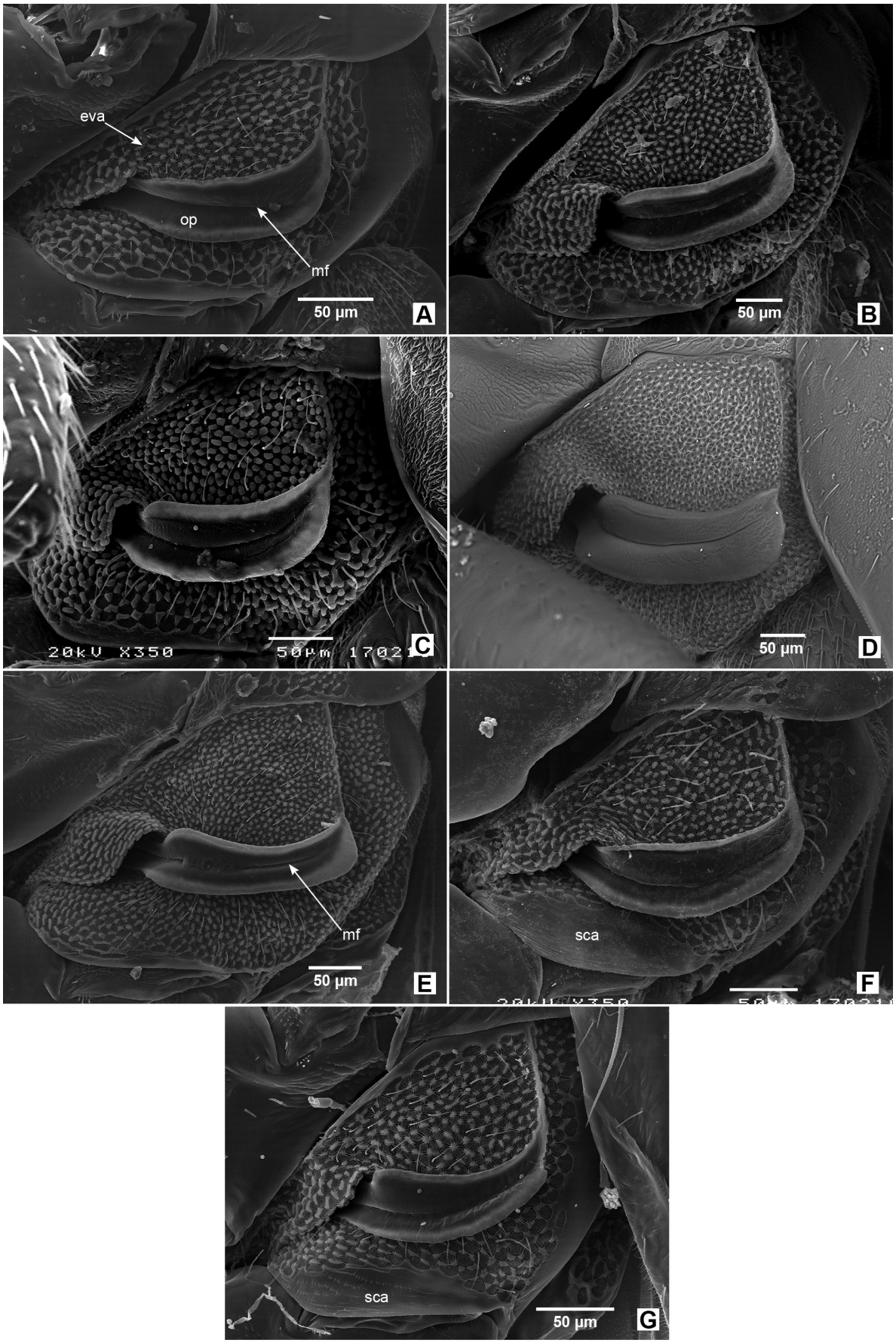

Fig. 9. Scanning electron micrographs of ostiolar peritreme and evaporatorium of *Anthocoris* spp, left lateroventral view. A – *A. chibi* Hiura, 1959, female; B – *A. confusus* Reuter, 1884, male (from India); C – *A. japonicus* Poppius, 1909, female; D – *A. kalopanacis* Kerzhner, 1977, female; E – *A. takahashii* Hiura, 1959, female; F – *A. miyamotoi* Hiura, 1959, female; G – *A. venustus* sp. nov., paratype, male. Abbreviations: eva – evaporatorium; mf – median furrow; op – ostiolar peritreme; sca – supracoxal area.

(Hiura 1959), Kumamoto (Otsuka 1982), Oita (Miyake 2018), Miyazaki (Tawara 1970, Komatsu 2016), Kagoshima (Hiura 1959, Ito et al. 2020); Tsushima Island (Yasunaga 1999). Korea: South: Gyeongsangbuk-do, Jeollanam-do (Kwon et al. 1996a, 2001), Jeollanam-do (Jung et al. 2013). China: Heilongjiang, Jilin, Gansu, Shandong (Bu & Zheng 2001). Russia: Far East: Primorsky Kray (Kerzhner 1988). According to the collection records, this species mainly inhabits the lowland areas of Honshu, Shikoku, and Kyushu, Japan (Fig. 20).

Anthocoris confusus Reuter, 1884

(Figs 7C–D, 9B, 10C–D, 12B, 13D–F, 15B, 16D, 20)

Anthocoris confusus Reuter, 1884: 194. Lectotype (Péricart 1970: 738): ♂, France, Vosges (MNHN).

Anthocoris confusus var. *funestus* Horváth, 1896: 329. Holotype: unsexed, Germany, Bavaria, Neu-Ulm (HNHM).

Anthocoris confusus ab. *aterrimus* Gravestein, 1945: 122. Holotype: ♀, The Netherlands, Prov. Limburg, Geulem (= Geulhem) (ZMAN → RMNH). Junior primary homonym of *Anthocoris aterrimus* J. Sahlberg, 1878, unavailable name.

Anthocoris confusus f. *gravesteini* Stichel, 1958: 22. New name for *aterrimus* Gravestein, 1945, unavailable name.

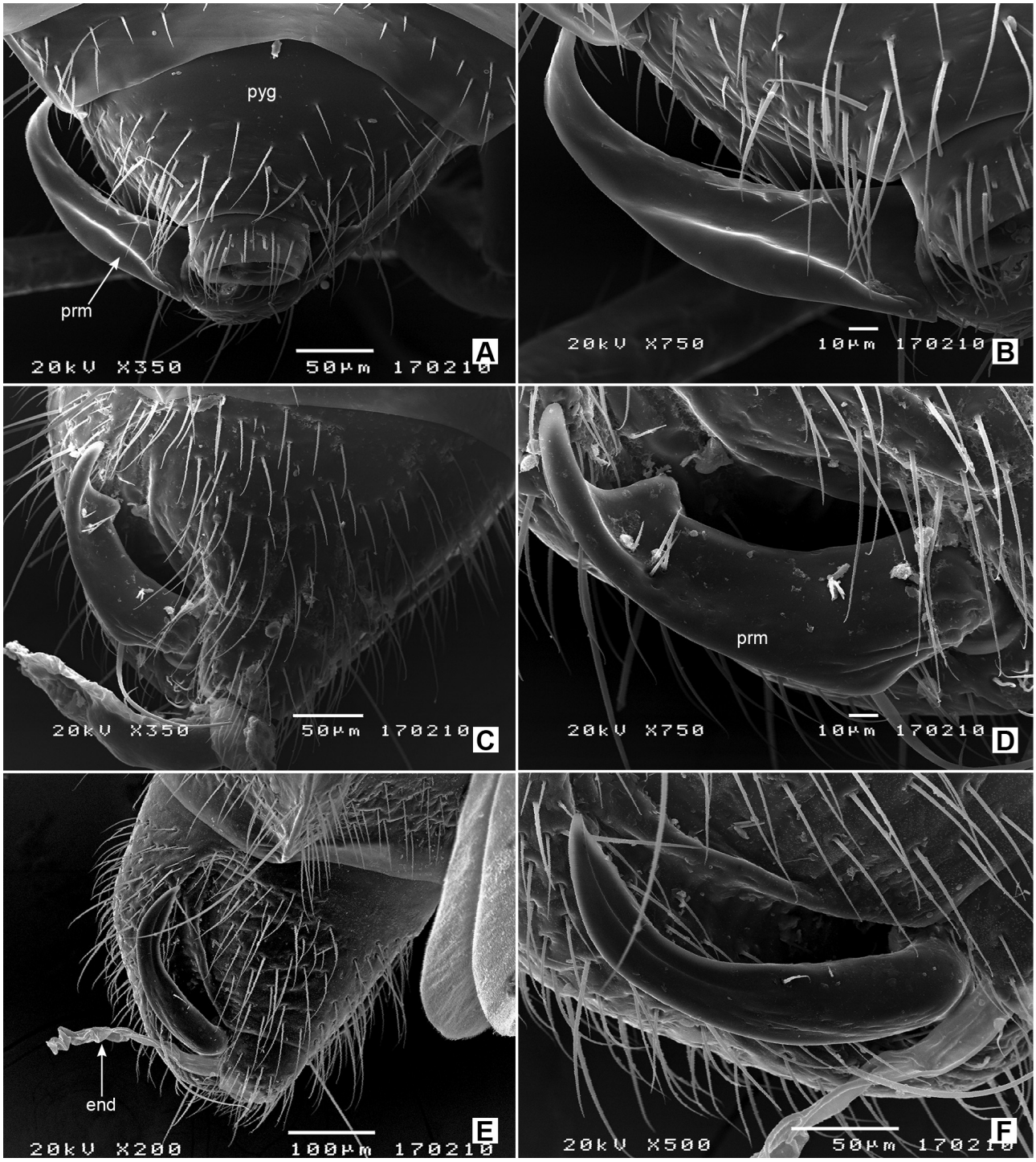

Fig. 10. Scanning electron micrographs of male genitalia of *Anthocoris* spp. A–B – *A. chibi* Hiura, 1959; C–D – *A. confusus* Reuter, 1884 (from India); E–F – *A. japonicus* Poppius, 1909. A, C, E – pygophore with paramere, dorsal (A, C) and laterodorsal (E) views; B, D, F – paramere, dorsal (B, D) and laterodorsal (F) views. Abbreviations: end – endosoma; prm – paramere; pyg – pygophore.

Anthocoris confusus f. *pallipes* Péricart, 1972: 135. Holotype: ♂, Georgia, Antsal-Or River, Signakhi Distr. (ZMAS).

Anthocoris confusus (selected references): Edwards (1890): 236 (in key, redescription); Lethierry & Severin (1896): 243 (listed, taxonomic status); Lindberg (1927): 21 (listed); Halbert (1935): 257 (records, life cycle, habitat); Procter (1946): 77 (record); Sands (1957): 300 (description of immature stages); Stichel (1958): 21–22 (in key, diagnosis); Hiura (1959): 6, pls. 3–4 (record, distribution, figures); Stichel (1960): 357 (listed, distribution); Anderson (1962): 75 (bionomics); Anderson & Kelton (1963): 439 (record); Josifov (1964): 85 (record); Kerzhner (1964): 698 (in key); Hill (1965): 245 (bionomics); Servadei (1967): 215 (distribution); Josifov (1970): 839 (distribution); Péricart (1972): 114, 134–135 (in key, redescription, figures); Coulianos & Ossiannilsson (1976): 150 (listed, distribution); Elov (1976): 370–371, 376 (in key, figure, diagnosis); Elov & Kerzhner (1977): 209 (record, bionomics); Heiss (1977): 42–43 (record, distribution, habitat); Hoberlandt (1977): 65 (listed); Kelton (1978): 35, 43, 71, 82, 92 (in key, redescription, figures, photo); Ford (1979): 55 (listed, distribution); Drosopoulos (1980): 171 (listed); Gidayatov et al. (1980): 90 (habitat); Önder (1982): 17, 79, 92–93 (in key, redescription, prey, habitat, distribution); Roşca & Popov (1982): 129 (listed); Scudder (1986): 64 (record); Henry (1988): 14 (catalogue, distribution); Kerzhner (1988): 773 (in key, figure); Bosmans & Péricart (1989): 41 (distribution, records); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Péricart & Halperin (1989): 92 (listed); Zheng & Bu (1990): 24 (listed); Reichling & Gerend (1994): 282 (listed); Vinokurov & Kanyukova (1995): 12 (listed); Péricart (1996): 111 (catalogue, distribution); Putshkov & Putshkov (1996): 16 (distribution); Carapezza (1997): 201 (records, distribution); Lukashuk (1997): 9 (distribution); Coulianos (1998): 25 (listed, distribution); Protić (1998): 42 (records, distribution, habitat); Kondorosy (1999): 138 (listed); Nonnaizab (1999): 55 (distribution); Hua (2000): 198 (listed, distribution); Lattin (2000): 613 (bionomics); Bu & Zheng (2001): 120, 155 (in key, redescription, figures); Yasunaga (2001b): pl. 85, 281 (photo, diagnosis, habitat, phenology); Hoffmann & Melber (2003): 243 (distribution); Gogala (2004): 248 (records); Coulianos (2005): 18 (record, distribution); Lewis et al. (2005): 61 (taxonomic history, record); Rabitsch (2005): 35 (listed); Abd-Rabou & Ghahari (2006): 43 (listed as predator of whitefly, associated plant); Önder et al. (2006): 28 (listed, distribution); Wachmann et al. (2006): 186 (distribution, habitat, photo); Bryja & Kment (2007): 32 (record); Ke & Bu (2007): 91–92 (figure, description of female genitalia); Horton & Lewis (2009): 610 (summary of N. American records); Ghahari et al. (2009): 46 (catalogue, distribution); Söderman & Rintala (2009): 18 (record); Neimorovets (2010): 21 (records); Vinokurov et al. (2010): 56 (catalogue, distribution); Ghahari et al. (2011): 4 (record); Farzaneh et al. (2011): 338 (record, photo); Heckmann & Blöchlinger (2011): 108 (records); Horton & Lewis (2011): 1262, 1265, 1268–1270, 1273 (description of male and female genitalia, photo, figures); Kment & Kejval (2011): 38 (listed); Malenovský et al. (2011): 144 (record, prey, habitat, associated plant); Rintala & Rinne (2011): 170 (diagnosis, habitat, distribution, photo); Cuppen (2012): 159 (listed); Kment & Baňař (2012): 509 (record, distribution); Aukema et al. (2013a): 84 (catalogue, distribution); Esenbekova (2013): 56–57 (habitat, distribution); Hao & Ma (2013): 36 (listed); Jerinić-Prodanović & Protić (2013): 171 (record, distribution, prey); Jung et al. (2013): 422 (record, diagnosis, distribution, habitat); Albrecht et al. (2015): 24 (listed); Ballal & Yamada (2016): 191 (record); Protić (2016): 366 (listed); Yamada et al. (2016): 422

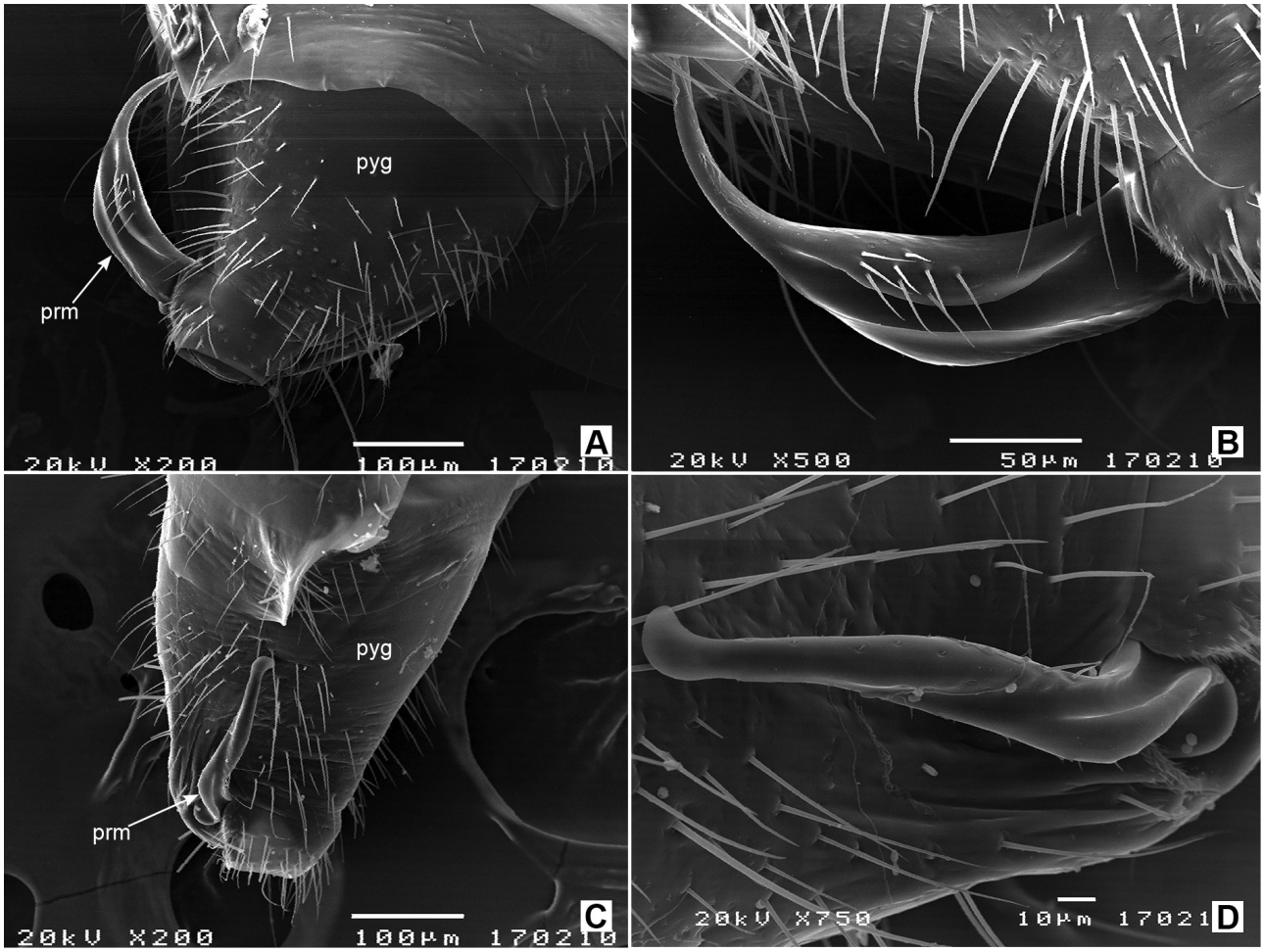

Fig. 11. Scanning electron micrographs of male genitalia of *Anthocoris* spp. A–B – *A. miyamotoi* Hiura, 1959; C–D – *A. venustus* sp. nov., paratype. A, C – pygophore with paramere, dorsal (A) and lateral (C) views; B, D – paramere, dorsal (B) and lateral (D) views. Abbreviations: prm – paramere; pyg – pygophore.

(catalogue, distribution); Jung & Lee (2017): 36, 70 (diagnosis, redescription, associated plant, distribution, photo, figure); Ostovan et al. (2017): 453 (distribution, habitat, prey); Aukema et al. (2018): 22 (record); Ballal et al. (2018): 209 (catalogue, distribution); Morkel et al. (2018): 229 (record); Moulet et al. (2018): 135, 139 (listed, distribution, in key); Ryan (2018): 26 (listed); Vinokurov (2019): 21 (record); Goula et al. (2020): 12 (listed); Vinokurov (2020): 39 (catalogue, distribution).

Material examined. JAPAN: Hokkaido: 1 ♀, Horokanai-cho, Uen-nai Dam, 20.viii.2000, T. Yasunaga (TYCN); 1 ♂ (Figs 12B, 13D–F), Sapporo-shi, Hitsujigaoka, 15.v.1992, collector unknown (TKPM). **Honshu:** Tochigi Pref.: 1 ♂ (Figs 7C–D), Nikko-shi, Yumoto, 16.xi.2006, S. Maehara (TKPM); 1 ♀, same locality, 18.vi.2010, S. Maehara (TKPM); 1 ♂, same locality, 4.ix.2017, S. Maehara (TKPM). Yamanashi Pref.: 1 ♀ (Fig. 15B), Hokuto-shi, Kanayamadaira, 27.ix.2007, T. Ban (TKPM). – **FRANCE:** 1 ♀, Forêt de Fontainebleau, 20.viii.1966, J. Péricart (MNHN). **THE NETHERLANDS:** 2 ♂♂, Leiden near 'Naturalis', 19.vii.2006, K. Yamada (TKPM). **INDIA: Himachal Pradesh:** 2 ♂♂ (one in Fig. 9B, one in Figs 10C–D) 2 ♀♀, unknown date and collector (TKPM).

Differential diagnosis. Recognized by the following combination of characters: head and pronotum (Figs 7C–D) blackish brown; antennal segments I, III, and IV blackish brown, segment II pale brown or yellowish brown and darkened at base and apex (Figs 7C–D); hemelytra (Figs 7C, 16D) more or less brown or reddish brown at base, a strip along the inner embolioum dull or pruinose, the outer portion of the embolium shiny; membrane (Fig. 7C) smoky dark brown, with three whitish markings on basal and innermost portions and area behind apex of cuneus; tibiae (Figs 7C–D) mostly pale brown; ostiolar peritreme (Fig. 9B) straight, almost same width throughout, curved slightly anteriad at apex; abdominal sternum II (Fig. 12B) with a pair of small triangle-shaped membranous areas along posterior margin. Most similar in appearance to Palaearctic *A. minki* Dohrn, 1860 and European *A. simulans* Reuter, 1884, but distinguished from both by antennal segment II mostly pale brown and darkened at base and apex (in *A. minki*, pale yellow with fuscous tinge at apex; in *A. simulans*, uniformly darkened) and each tibia mostly pale brown (in *A. minki*, reddish brown to blackish brown; in *A. simulans*, blackish brown). The shape of the paramere is also most similar to both above mentioned species by the possession of a subapical projection. However, these species might not be clearly separated by relying solely on the form of the paramere.

Redescription. ***Male genitalia*** (Figs 10C–D, 13D–F): Pygophore (Fig. 13D) turbinate, longer than wide, covered with 8–12 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest are approximately half length of pygophore; mid-dorsal surface very hirsute with suberect setae; paramere (Figs 10D, 13E–F) lamellate, slender, acute at apex, subapically with a sharply defined projection, with a few very short, erect setae on median portion, strongly curved at base in posterolateral view; longitudinal groove lacking.

Female genitalia (Fig. 15B): Copulatory tube fused on middle of intersegmental membrane between sterna VII and VIII, approximately 1.5 mm in length, very thin and almost same width from base to apex (junction to trunk of conductive tissue), with few distinct twists at apex and base; trunk of conductive tissue pronounced.

Measurements [mm; ♂♂ (n = 2) / ♀♀ (n = 3)]. Body length 4.50–4.60 / 4.33–4.63; head length (excl. neck) 0.53–0.56 / 0.50–0.56; head width across eyes 0.57–0.58 / 0.55–0.57; vertex width 0.30–0.31 / 0.30–0.33; length of antennal segments I – 0.18–0.19 / 0.16–0.20, II – 0.56–0.57 / 0.53–0.55, III – 0.32–0.35 / 0.31–0.33, and IV – 0.40 / 0.36–0.39; length of labial segments II – 0.15–0.17 / 0.15–0.16, III – 0.56–0.57 / 0.52–0.59, and IV – 0.30–0.31 / 0.30–0.34; anterior pronotal width 0.48–0.50 / 0.46–0.48; mesal pronotal length 0.60–0.63 / 0.60–0.62; basal pronotal width 1.32–1.35 / 1.30–1.35; length of embolial margin 1.40–1.44 / 1.35–1.48; length of cuneal margin 0.82–0.84 / 0.73–0.80; maximum width across hemelytra 1.45–1.49 / 1.45–1.55.

Bionomics. *Anthocoris confusus* is found on various broad-leaved trees, including *Acer*, *Betula*, *Alnus*, *Salix*, *Populus*, *Quercus*, *Fagus*, *Carpinus*, *Ulmus*, *Fraxinus*, and *Tilia* (Péricart 1972). This species was collected from *Fagus grandifolia* Ehrhart and *Tilia* sp. in North America (Lattin 2000, Horton & Lewis 2009) and in Japan, from *Cerasus sargentii* (Rehder) H. Ohba var. *sargentii*, *Betula platyphylla* Sukaczev, and *Alnus japonica* (Thunb.) Steud. (Yasunaga 2001b). A specimen from Tochigi Prefecture, Japan, was collected from under the bark of *Betula ermanii* Cham. in November (Satoshi Maehara, pers. comm.). In South Korea (Seoul), hibernating specimens were discovered under the bark of *Zelkova serrata* (Jung et al. 2013).

Distribution. Japan: Hokkaido (Hiura 1959); Honshu*: Tochigi, Yamanashi. We present the first record from Honshu (Fig. 20); however, it is rare. The species is widely distributed throughout the Palaearctic Region (Péricart 1996) and is also introduced into North America (Anderson & Kelton 1963, Horton & Lewis 2009).

Summary of known records: **ASIA:** Armenia (Péricart 1972). Azerbaijan (Gidayatov et al. 1980, Péricart 1996). China: Nei Mongol, Hebei, Sichuan (Zheng & Bu 1990, Bu & Zheng 2001). Georgia (Péricart 1972). India: Himachal Pradesh (Ballal & Yamada 2016, Ballal et al. 2018). Iran (Linnavuori & Hosseini 2000, Ostovan et al. 2017). Israel (Péricart & Halperin 1989). Kazakhstan: Asian part (Péricart 1972, Esenbekova 2013). Korea: Chungcheongnam-do, Seoul (Jung et al. 2013, Jung & Lee 2017). Mongolia: (Péricart 1972, Elov & Kerzhner 1977). Russia: West and East Siberia, Far East (Lindberg 1927, Vinokurov et al. 2010). Turkey: Asian part (Péricart 1996, Önder et al. 2006). Turkmenistan (Péricart 1996). **EUROPE:** Albania (Josifov 1970). Andorra (Péricart 1996). Austria (Heiss 1977, Rabitsch 2005). Belgium (Stichel 1958, Bosmans & Péricart 1989). Bosnia and Herzegovina (Péricart 1972). Bulgaria (Stichel 1958, Josifov 1964). Belarus (Péricart 1972, Lukashuk 1997). Croatia (Horváth 1896, Péricart 1972). Czech Republic (Hoberlandt 1977, Kment & Baňař 2012). Denmark (Péricart 1972). Estonia (Coulianos 2005). Finland (Reuter 1884, Albrecht et al. 2015). France (Reuter 1884, Péricart 1972). Germany (Horváth 1896, Hoffmann & Melber 2003).

Greece (Stichel 1958, Drosopoulos 1980). Hungary (Péricart 1972, Kondorosy 1999). Ireland (Halbert 1935). Italy (Reuter 1884, Servadei 1967). Latvia (Péricart 1996). Lithuania (Söderman & Rintala 2009). Luxembourg (Péricart 1996). Moldavia (Péricart 1996). Montenegro (Stichel 1958, Protić 2016). The Netherlands (Reuter 1884, Gravestein 1945, Aukema et al. 2018). North Macedonia (Wagner 1962). Norway (Stichel 1958, Coulianos 1998). Poland (Stichel 1958). Romania (Péricart 1972, Roşca & Popov 1982). Russia: South, Central and North European Territories (Stichel 1958, Neimorovets 2010). Serbia (Protić 1998). Slovakia (Hoberlandt 1977, Péricart1996, Bryja & Kment 2007). Slovenia (Gogala 2004). Spain (Stichel 1958, Goula et al. 2020). Sweden (Stichel 1958, Péricart 1972). Switzerland (Stichel 1958, Heckmann & Blöchlinger 2011). Ukraine (Putshkov & Putshkov 1996). United Kingdom (Edwards 1890, Sands 1957). **NORTH AFRICA:** Tunisia (Péricart 1972). **NORTH AMERICA:** Canada: Nova Scotia, Newfoundland, British Columbia (Procter 1946, Horton & Lewis 2009). USA: Maine, New York, North Carolina, Michigan, Tennessee, Washington (Lewis et al. 2005, Horton & Lewis 2009).

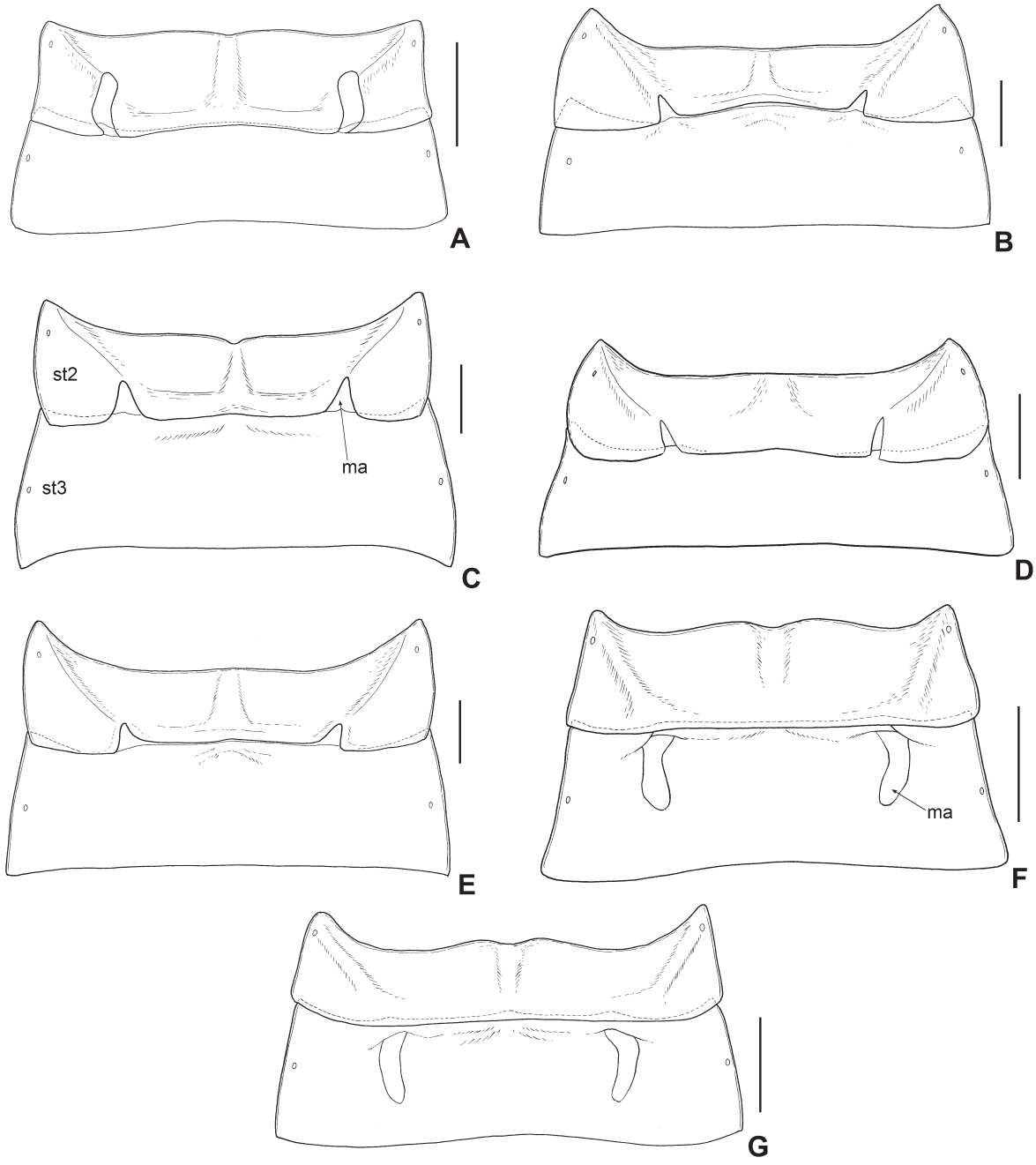

Fig. 12. Abdominal sterna II–III of *Anthocoris* spp., male, ventral view (setae omitted). A – *A. chibi* Hiura, 1959; B – *A. confusus* Reuter, 1884; C – *A. japonicus* Poppius, 1909; D – *A. nemoralis* (Fabricius, 1794); E – *A. takahashii* Hiura, 1959; F – *A. miyamotoi* Hiura, 1959; G – *A. venustus* sp. nov., paratype. Abbreviations: ma – membranous area; st2–3 – abdominal sternum II to III. Scale bars: 0.2 mm.

Anthocoris japonicus Poppius, 1909

(Figs 7E–F, 9C, 10E–F, 12C, 13G–I, 15C, 17C–E, 21)

Anthocoris japonicus Poppius, 1909: 33. Holotype: ♀, Japan, Honshu, Kanagawa (HNHM).

Anthocoris japonicus (selected references): Esaki (1950): 257 (redescription, habitus, distribution); Miyamoto (1957): 76 (ovariole number); Esaki et al. (1959): 105 (description of fifth instar nymph, habitus, habitat); Hiura (1959): 4, pls. 3–4 (distribution, habitat, phenology, figures); Takakura (1959): 14 (record, habitat); Stichel (1960): 357 (listed, distribution); Miyamoto (1965): 96, pl. 48 (diagnosis, habitat, prey, distribution, photo); Miyamoto & Lee (1966): 375–376 (record); Lee (1971): 358–359, 552 (redescription, photo, record, distribution); Hiura (1977): pl. 32, 122 (photo, bionomics); Nozawa (1978): 373 (record); Ford (1979): 56 (listed, distribution); Iwasaki (1983): 14 (record); Tachikawa (1983): 106, 255 (photo, diagnosis, bionomics); Hayashi (1984): 427 (record); Kim & Nam (1984): 309 (record); Takakura (1984): 5 (record); Lee et al. (1985): 364 (record); Sasaji (1985): 58 (record); Otsuka & Yoshizaki (1987): 596 (record); Ichita (1988): 132 (record); Kerzhner (1988): 773–774 (figure, in key); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Asaoka & Ieki (1990): 155 (listed, distribution); Yoon et al. (1990): 106 (record); Zheng & Bu (1990): 24 (record); Bu & Zheng (1991a): 94, 98 (listed); Lee & Kwon (1991): 13 (record); Lee et al. (1991): 39–40 (record); Kim (1993): 290 (record); Lee et al. (1993): 10 (record); Nozawa (1993): 6 (record); Otsuka (1993): 70 (listed); Ichita (1994): 201 (listed); Lee & Kwon (1994): 63 (listed); Yoshitomi (1994): 25–26 (record); Kim (1995): 216 (listed); Otsuka (1995): 45 (record); Otsuka (1996): 282 (record); An (1996): 28 (record); Kwon et al. (1996a): 109 (listed); Péricart (1996): 112 (catalogue, distribution); Nakamura et al. (1997): 163 (distribution); Sonobe (1997): 54 (record, habitat); Hayashi (1998): 165 (record); Kishimoto et al. (1998): 84 (listed); Yasunaga (1999): 22 (listed, distribution); Hua (2000): 198 (listed, distribution); Osaka Prefecture (2000): 62 (listed, distribution); Yano & Yamamoto (2000): 168 (listed); Bu & Zheng (2001): 121, 160 (in key, redescription, figures); Iwate Prefecture (2001): 179 (listed); Kwon et al. (2001): 79 (catalogue, record, distribution); Yasunaga (2001b): pl. 85, 281 (photo, diagnosis, habitat, phenology); Maruyama et al. (2000): 252 (record); Suzuki (2003): 147 (distribution); Kagawa & Higuchi (2003): 205 (record, distribution); Hayashi & Ozaki (2004): 223 (distribution); Kanyukova & Marusik (2006): 168 (listed); Tago (2006): 29 (record); Ke & Bu (2007): 91–92 (figure, description of female genitalia); Tachikawa (2009): 4 (record); Miyamoto (2008): 164, pl. 57 (diagnosis, habitat, prey, distribution, photo); Ichita (2009): 68 (listed); Vinokurov et al. (2010): 56 (catalogue, distribution); Torigoe (2011): 69 (record); Yamazaki & Takakura (2011): 79 (record); Ushirokita et al. (2012): 16 (record); Aukema et al. (2013a): 85 (catalogue, distribution); Enju et al. (2013): 245 (photo, distribution, habitat); Hao & Ma (2013): 36 (listed); Jung et al. (2013): 422 (catalogue, diagnosis, distribution, habitat); Iwasaki (2014): 24 (record); Suzuki (2014a): 7 (distribution); Maehara (2015): 28–29 (record, distribution, habitat, phenology); Yazaki (2015): 144 (record); Nozaki et al. (2016): 82 (record); Yamada et al. (2016): 422 (catalogue, distribution); Jung & Lee (2017): 36–37, 70 (diagnosis, redescription, associated plant, prey, distribution, photo, figure); Ito & Imasaka (2018): 15 (record); Hayashi et al. (2018): 182 (distribution); Sawada (2018): D-36 (listed); Yasunaga et al. (2018): 33, 58 (photo); Takai & Sakou (2019): 114 (listed, distribution); Tanaka (2019): 64, 111 (listed); Urayama et al. (2019): 79, 81–82 (record, photo, habitat, phenology); Miyazaki et al. (2020): 65–66 (synthetic diet); Okuda (2020): 44 (listed); Shizuoka Prefecture (2020): 128 (listed).

Material examined. JAPAN: Honshu: Aomori Pref.: 2 ♂♂ 1 ♀, Mutsu-shi, Sekine, 26.viii.1986, B. Tanaka. Fukushima Pref.: 1 ♀, Inawashiro-cho, Mt. Bandai-san, 31.iv.1999, T. Shimada. Ibaraki Pref.: 2 ♂♂ 4 ♀♀, Tsukuba-shi, 12.i.2000, K. Takahashi; 1 ♀, Tsukuba-shi, 1.iv.2000, K. Takahashi. Tochigi Pref.: 3 ♂♂ 1 ♀, Nikko-shi, Shichiri, 21.vi.2020, S. Maehara; 1 ♂, Utsunomiya-shi, Yanagita-ryokuchi, 23.iii.2018, S. Maehara; 9 ♂♂ 9 ♀♀, Tochigi-shi, Kashiwagura, 18.iii.1991, H. Yoshitomi (EUM); 5 ♀♀, Tochigi-shi, Oominagawa, 6.i.1994, H. Yoshitomi (EUM); 1 ♂ 1 ♀, Tochigi-shi, Minagawajonai, 6.i.1994, H. Yoshitomi (EUM); 1 ♂ 1 ♀, Tochigi-shi, Shiriuch, 4.i.1994, H. Yoshitomi (EUM); 6 ♂♂ 10 ♀♀, Tochigi-shi, Tochigi-koukou, 28.ii.1991, H. Yoshitomi (EUM); 1 ♂ 1 ♀, Tochigi-shi, Yanagibashi-cho, 9.iii.1994, S. Nagashima; 1 ♂, Tochigi-shi, Fujioka-machi, Fujioka, 26.xi.2020, S. Maehara; 2 ♂♂ (one in Figs 7E–F) 3 ♀♀, Ôyama-shi, Shimada, 6.i.1994, S. Nagashima. Saitama Pref.: 2 ♀♀, Toda-shi, Doman, 27.xii.1998, S. Arai. Chiba Pref.: 1 ♀, Narita-shi, Ôtake, 29.iv.2015, R. Nakamura. Tokyo-to: 6 ♂♂ (one in Figs 10E–F, one in Figs 12C, 13G–I) 11 ♀♀ (one in Fig. 15C), Setagaya-ku, Kinuta Park, 10.viii.2001, J. Ikuta; 1 ♂, Chitose-funabashi, Karasuyama-ryokudo, no date, J. Narukawa. Kanagawa Pref.: 3 ♀♀, Atugi-shi, Funako, 13.iv.2001, S. Nagashima; 1 ♀, Yokosuka-shi, Tsukui, Mt. Miurafuji, 5.v.1988, S. Miyakawa. Aichi Pref.: 1 ♂ 4 ♀♀, Kasugai-shi, no date, S. Nagashima. Osaka Pref.: 3 ♂♂ 6 ♀♀, Ibaraki-shi, Niwakubo, 14.vii.2004, T. Ueda; 1 ♀, Sakai-shi, Izumigaoka, 25.xi.2000, M. Yoshio. Nara Pref.: 1 ♀, Nara-shi, Yagyû-kaidô, 4.v.2001, T. Tsuru; 2 ♂♂ 3 ♀♀, Nara-shi, Nakamachi, 6.vi.2000, K. Yamada; 1 ♂, Gojô-shi, Yoshino-gawa Riv., 29.vi.2000, T. Ueda; 1 ♀, Gojô-shi, Minamiada-cho, 28.xi.2000, K. Yamada. Wakayama Pref.: 1 ♀, Wakayama-shi, Myo-oji, 3.vii.2001, Y. Miyamoto. **Shikoku:** Tokushima Pref.: 1 ♀, Tokushima-shi, Hachiman-cho, Mukôterayama, Bunka-no-Mori Park, 34.040278N 134.527222E, 1.iii.2008, K. Yamada; 11 ♂♂ 16 ♀♀ (one in Fig. 9C), same locality, 18.iii.2011, K. Yamada; 2 ♂♂ 2 ♀♀, Tokushima-shi, Jôroku-cho, Jôroku-Higashi Park, 30.xii.2013, T. Nakanishi. Kochi Pref.: 1 ♀, Tôyô-cho, None, 22.iv.2000, M. Takai. **Kyushu:** Kumamoto Pref.: 1 ♀, Chôyô-mura, Tochinoki, 27.iv.2002, T. Ueda. Nagasaki Pref.: 2 ♂♂ 2 ♀♀, Nagasaki-shi, Kawaguchi-Park, 32.76684N 129.86353E, under flakes of bark of *Zelkova serrata*, 21.ii.2020, T. Yasunaga et al. (NWHS); 3 ♂♂ 3 ♀♀, Omura-shi, Omura High School garden, 24.ii.2021, under flakes of bark of *Zelkova serrata*, 32.8970N 129.9631E, T. Yasunaga (NWHS). All in TKPM except for EUM and NWHS.

Differential diagnosis. Recognized by the following combination of characters: body (Figs 7E–F) generally black, covered with pruinose setae on dorsal surface; hemelytra and legs (Figs 7E–F) sometimes tinged with reddish brown; membrane (Fig. 7E) smoky dark brown with broad whitish band on basal part; ostiolar peritreme (Fig. 9C) straight, curved anteriorly at apex; abdominal sternum II (Fig. 12C) with a pair of triangle-shaped membranous areas along posterior margin. General appearance similar to that of *A. takahashii*, but readily distinguished from the latter by the rather smaller body, the coloration of the hemelytral membrane, the shape of the paramere, and the overall structure of female genitalia.

Redescription. ***Male genitalia*** (Figs 10E–F, 13G–I): Pygophore (Fig. 13G) turbinate, longer than wide, covered with 8–12 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface; mid-dorsal surface very hirsute with suberect setae; paramere (Figs 10F, 13H–I) slender, very slightly curved, apically acute, and bent anteriad, with a few very short setae on median portion; longitudinal groove lacking, but a weak longitudinal edge present on anterior half.

Female genitalia (Fig. 15C): Copulatory tube fused on intersegmental membrane slightly left to the middle, between sterna VII and VIII, approximately 1.4–1.5 mm in length, very thin and almost same width from base to apex (junction to trunk of conductive tissue), with few distinct twists; trunk of conductive tissue invisible (possibly dissolved).

Measurements [mm; ♂♂ (n = 10) / ♀♀ (n = 10)]. Body length 3.45–4.08 / 3.43–4.25; head length (excl. neck) 0.45–0.53 / 0.45–0.55; head width across eyes 0.49–0.55 / 0.48–0.56; vertex width 0.27–0.30 / 0.26–0.32; length of antennal segments I – 0.15–0.19 / 0.15–0.20, II – 0.44–0.52

/ 0.39–0.50, III – 0.26–0.32 / 0.26–0.32, and IV – 0.33–0.37 / 0.32–0.39; length of labial segments II – 0.13–0.17 / 0.14–0.19, III – 0.46–0.54 / 0.47–0.56, and IV – 0.27–0.34 / 0.29–0.35; anterior pronotal width 0.43–0.46 / 0.42–0.50; mesal pronotal length 0.49–0.63 / 0.52–0.66; basal pronotal width 1.15–1.27 / 1.05–1.35; length of embolial margin 1.08–1.26 / 1.00–1.35; length of cuneal margin 0.63–0.74 / 0.57–0.75; maximum width across hemelytra 1.20–1.38 / 1.06–1.40.

Bionomics. *Anthocoris japonicus* is frequently collected from *Zelkova serrata* (Miyamoto 1965, Yasunaga 2001b), where its prey consists of aphids, *Paracolopha morrisoni* (Baker, 1919) (Hemiptera: Sternorrhyncha: Aphididae), living on the leaves. They also prey on the Japanese pine blast scale, *Matsucoccus matsumurae* (Kuwana, 1905) (Coccomorpha: Matsucoccidae) (Bu & Zheng 2001). Almost nothing is known about this species' movements once it departs *Zelkova serrata* generally before summer, but a few individuals have been collected from *Elaeagnus umbellata* Thunb. var. *umbellata* in June at Nikko, in the northern part of Tochigi. Males and females hibernate under bark flakes of *Z. serrata* (Fig. 17C), *Ulmus parvifolia* Jacq., and *Aphananthe aspera* (Thunb.) Planch. (Hiura 1959, Enju et al. 2013, Jung et al. 2013, Urayama et al. 2019). The adults appear to be active in winter when temperatures are sufficiently warm, and even mating pairs have been observed during this season (Figs 17D–E). The searching male encounters a female and attempts to mount her. After mounting the female's dorsum, the male curves his abdomen from the female's right side and inserts his paramere to median part of ventral side between abdominal segment VII and VIII. The female does not struggle once the male has mounted her. Duration of copulation was generally at least 10 minutes, as seen in the other *Anthocoris* species (Horton et al. 2000, 2002; Horton & Lewis 2005).

Distribution. Japan: Honshu: Aomori (Ichita 1988), Iwate (Iwate Prefecture 2001), Fukushima*, Ibaraki*, Tochigi (Sonobe 1997, Maehara 2015), Saitama (Nozawa 1978), Chiba (Maruyama et al. 2000, Suzuki 2003), Tokyo (Hiura 1959), Kanagawa (Poppius 1909, Suzuki 1981, Hayashi et al. 2018), Fukui (Sasaji 1985), Gifu (Takai & Sakou 2019), Shizuoka (Shizuoka Prefecture 2020), Aichi (Asaoka & Ieki 1990), Osaka (Yamazaki & Takakura 2011), Hyogo (Ushirokita et al. 2012), Nara (Hiura 1959), Wakayama*, Tottori (Hiura 1959), Okayama (Okayama Prefecture 2020), Hiroshima (Nakamura et al. 1997), Yamaguchi (Hiura 1959); Shikoku: Tokushima*, Ehime (Yano & Yamamoto 2000), Kochi*; Kyushu: Fukuoka (Takakura 1959), Nagasaki (Urayama et al. 2019), Kumamoto (Otsuka & Yoshizaki 1987), Oita (Takakura 1984); Tsushima Island (Yasunaga 1999). Chishima (Kuril) Islands: Kunashir Is. (Kerzhner 1988, Kanyukova & Marusik 2006). Russia: Far East: Primorsky Kray (Kerzhner 1988, Vinokurov et al. 2010). Korea: Gangwon-do, Gyeonggi-do, Chungcheongbuk-do, Chungcheongnam-do, Gyeongsangbuk-do, Gyeongsangnam-do, Jeollabuk-do, Jeollanam-do, Jeju-do (Kerzhner 1988, Kwon et al. 2001, Jung & Lee 2017). China: Zhejiang (Zheng & Bu 1990, Bu & Zheng 2001). This species is one of the more common species of Japanese Anthocoridae and is widespread in the lowland areas of Honshu, Shikoku, and Kyushu, Japan (Fig. 21). In addition, it extends to the Korean Peninsula and to a few localities in the Russian Far East and east China. Distribution records of the species in Japan seem to be associated with the distribution pattern of *Zelkova serrata*, a well-known tree planted in various urbanized areas such as parks and roadsides. In urbanized zones in Nagasaki Prefecture, this anthocorid is evidently expanding its habitat, utilizing *Zelkova serrata* planted in parks and school campuses for landscaping (Figs 17A–B) (cf. Urayama et al. 2019).

Anthocoris kalopanacis Kerzhner, 1977

(Figs 7G–H, 9D, 21)

Anthocoris kalopanacis Kerzhner, 1977: 8. Holotype: ♂, Kuril Is, Kunashir, Tretyakovo (ZMAS). Note: The published year of this species has long been treated as 1976 in previous papers; however, it was corrected by Aukema et al. (2013a), who confirmed Kerzhner's paper formally published in 1977 (Kerzhner 1977).

Anthocoris kalopanacis: Kerzhner (1988): 773 (in key, figure); Péricart (1996): 112 (catalogue, distribution); Yasunaga (2001b): 281 (record, diagnosis, habitat); Kanyukova & Marusik (2006): 168 (record); Gapon & Konstantinov (2008): 26 (listed); Vinokurov et al. (2010): 57 (catalogue, distribution); Aukema et al. (2013a): 85 (catalogue); Yamada et al. (2016): 422 (catalogue, distribution).

Type material examined. Holotype: ♂, Tretyakovo, Kunashir, 17.VI.1973, I. M. Kerzhner (ZMAS, image examined). Paratype: ♀, Alekhino, Kunashir 15.VI.1973, I. M. Kerzhner (ZMAS, image examined).

Additional material examined. JAPAN: Hokkaido: 1 ♀, Otaru-shi, Tenjin-josuijo, 22.vii.1999, A. Yamamoto; 1 ♀, Otaru-shi, Okusawa-suigenchi, 27.vii.2004, A. Yamamoto (all in TKPM). **Honshu:** Tochigi Pref.: 1 ♀ (Figs 7G–H, 9D), Nikko-shi, Shôbugahama, 11.vi.2005, S. Maehara; 1 ♀, same locality, 11.vi.2010, S. Maehara; 1 ♀, same locality, 25.v.2011, S. Maehara (all in TKPM).

Differential diagnosis. Recognized by the following combination of characters: Body (Figs 7G–H) uniformly black; labium (Fig. 7H) reaching to middle of prosternum (not reaching procoxae); membrane (Fig. 7G) smoky dark brown, with two small indistinct grayish pale markings on innermost portion and behind apex of cuneus; ostiolar peritreme (Fig. 9D) straight, almost same width throughout, obtuse at apex and slightly curved forward; legs (Figs 7G–H) black, but apices of femora and tibiae tinged with yellowish brown. Most similar in general appearance to *A. takahashii*, but separable from that species by the uniformly black hemelytra, labium reaching the middle of prosternum, and membrane with two small indistinct grayish pale markings on the innermost portion and behind apex of cuneus.

Redescription. ***Measurements*** [mm; ♀♀ (n = 5)]. Body length 4.85–5.40; head length (excl. neck) 0.56–0.63; head width across eyes 0.60–0.65; vertex width 0.35–0.38; length of antennal segments I – 0.20–0.23, II – 0.54–0.60, III – 0.31–0.35, and IV – 0.39–0.44; length of labial segments II – 0.14–0.19, III – 0.49–0.53, and IV – 0.28–0.31; anterior pronotal width 0.50–0.59; mesal pronotal length 0.74–0.80; basal pronotal width 1.54–1.69; length of embolial margin 1.58–1.78; length of cuneal margin 0.84–0.94; maximum width across hemelytra 1.60–1.75.

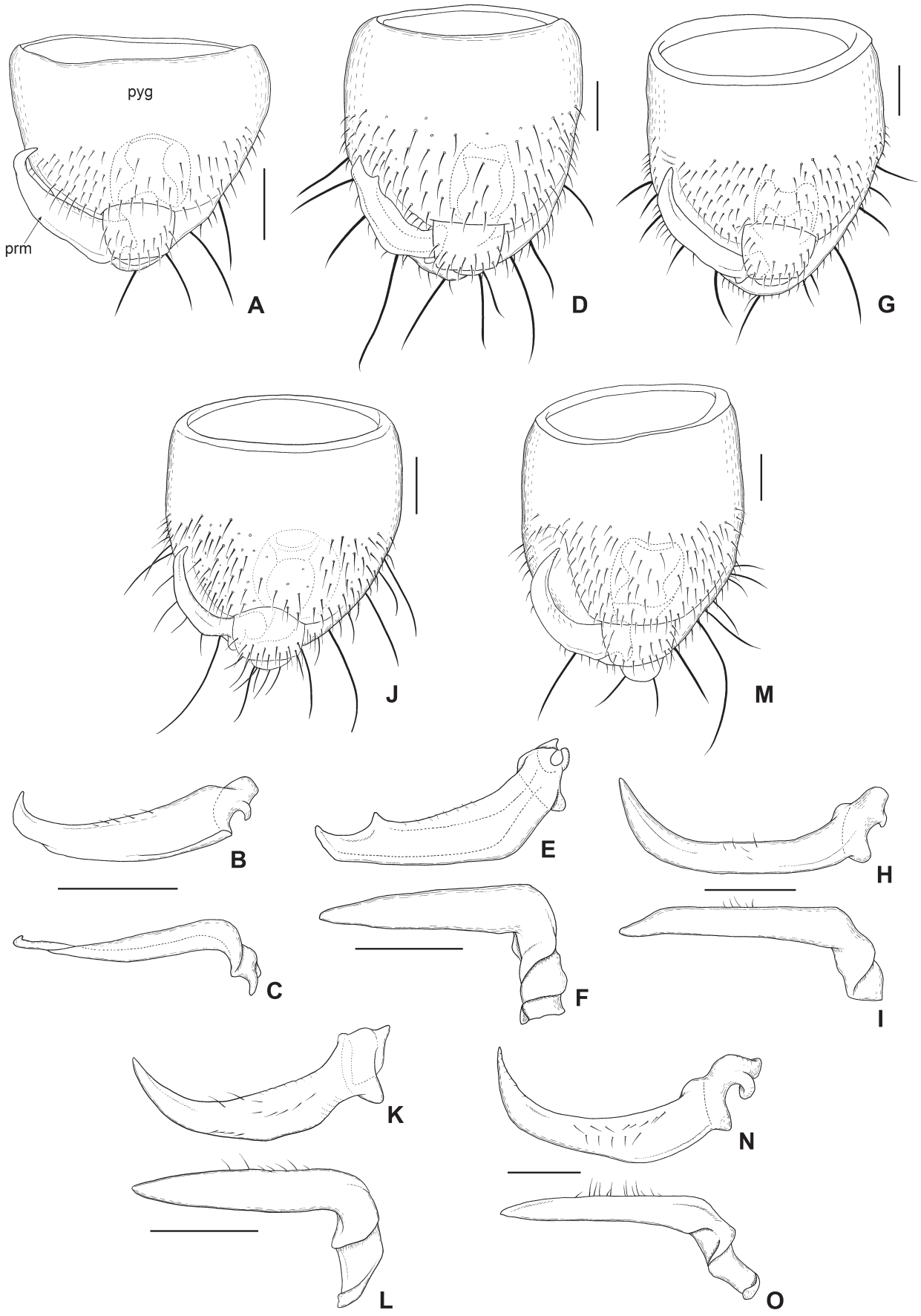

Fig. 13. Male genitalia of *Anthocoris* spp. A–C – *A. chibi* Hiura, 1959; D–F – *A. confusus* Reuter, 1884; G–I – *A. japonicus* Poppius, 1909; J–L – *A. nemoralis* (Fabricius, 1794); M–O – *A. takahashii* Hiura, 1959. A, D, G, J, M – pygophore with paramere (ejaculatory bulb omitted), dorsal view; B–C, E–F, H–I, K–L, N–O – paramere, two different views. Abbreviations: prm – paramere; pyg – pygophore. Scale bars: 0.1 mm.

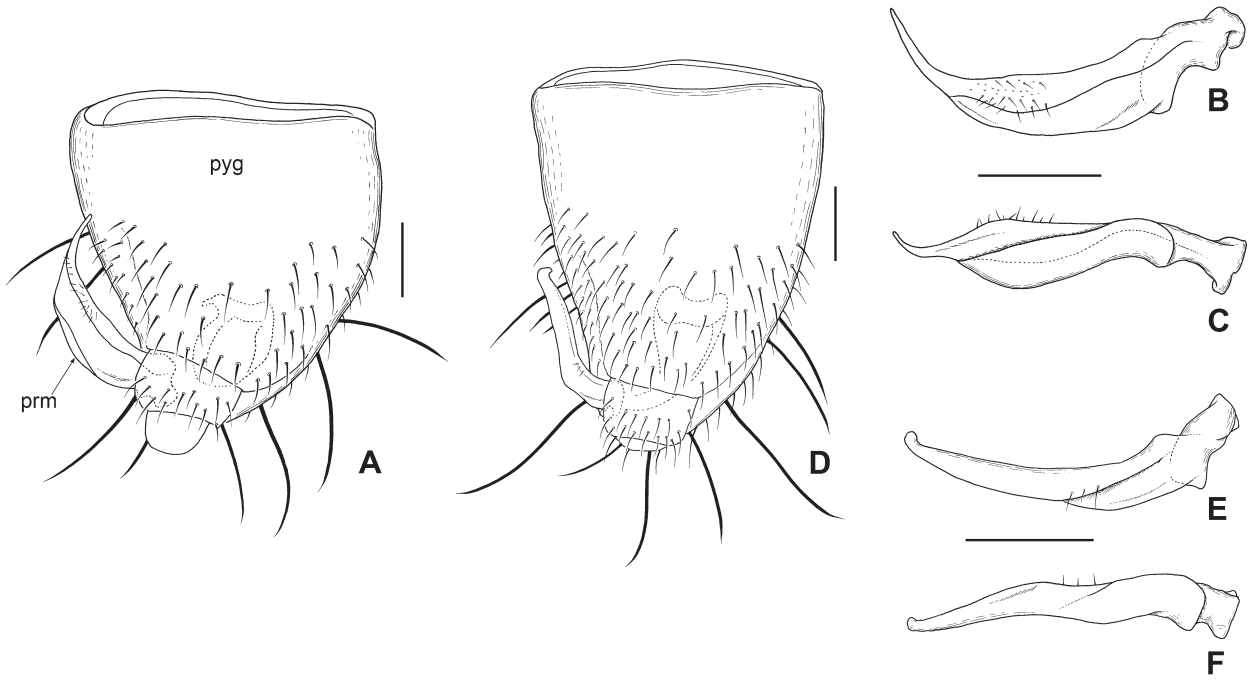

Fig. 14. Male genitalia of *Anthocoris* spp. A–C – *A. miyamotoi* Hiura, 1959; D–F – *A. venustus* sp. nov., paratype. A, D – pygophore with paramere (ejaculatory bulb omitted), dorsal view; B–C, E–F – paramere, two different views. Abbreviations: prm – paramere; pyg – pygophore. Scale bars: 0.1 mm.

Bionomics. *Anthocoris kalopanacis* is found on *Kalopanax septemlobus* (Thunb.) Koidz. (Araliaceae) (Kerznher 1977, Yasunaga 2001b).

Distribution. Japan: Hokkaido*; Honshu*: Tochigi. Chishima (Kuril) Islands: Kunashir Is. (Kerznher 1977, Kanyukova & Marusik 2006, Vinokurov et al. 2010). The species has been restricted to Kunashir Island to date; however, we confirm that it occurs on mainland Japan (Fig. 21).

Anthocoris nemoralis (Fabricius, 1794)

(Figs 7I–J, 12D, 13J–L, 15D)

?Cimex silvarum Rossi, 1790: 251. Syntypes: Italy. Synonymized by Reuter (1888: 317, suspected).

Acanthia nemoralis Fabricius, 1794: 76. Lectotype (designated by Péricart 1972: 120): ♂, Denmark (ZMUC).

Cimex triguttatus Schrank, 1796: 165. No types verified. Junior primary homonym of *C. triguttatus* Linnaeus, 1767 and *C. triguttatus* Fabricius, 1775; synonymized by Reuter (1888: 317).

Lygaeus austriacus Fabricius, 1803: 239. Syntypes: Austria (lost) (Zimsen 1964: 331). Synonymized by Fieber (1861: 137).

Anthocoris nemoralis var. *superbus* Westhoff, 1881: 78. Syntypes: Germany, Westfalia (lost).

Anthocoris dohrni Le Quesne, 1958: 125. Holotype: ♂, Spain, Gibraltar (BMNH). Synonymized by Péricart (1971: 95).

Anthocoris pemphigi Wagner, 1960: 91. Holotype: ♂, Egypt, Mansoura (ZMUH). Synonymized by Péricart (1971: 95).

Anthocoris nemoralis (selected references): Fieber (1860): 263 (listed); Fieber (1861): 137 (in key); Garbiglietti (1869): 122 (listed); Reuter (1871): 316 (listed); Reuter (1879): 13 (in key, taxonomic status); Horváth (1883): 29 (listed); Reuter (1884): 67, 72 (in key, redescription); Edwards (1890): 236 (in key); Lethierry & Severin (1896): 244 (listed, taxonomic status); Halbert (1935): 258 (records, life cycle, habitat); Seabra (1941): 22 (listed); Sands (1957): 297, 298 (figure, description of immature stages); Stichel (1958): 22–23 (in key, diagnosis); Stichel (1960): 357 (listed, distribution); Carayon (1961): 546 (prey, remark for record of S. Africa); Linnavuori (1961): 35 (record, habitat, distribution); Anderson (1962): 75 (bionomics); Anderson & Kelton (1963): 439 (record); Josifov (1964): 85 (record, habitat); Kerzhner (1964): 698 (in key); Eckerlein & Wagner (1965): 213 (records); Ribes (1965): 80 (record); Servadei (1967): 219 (distribution); Eckerlein & Wagner (1969): 180 (records); Josifov (1970): 834, 894 (record, distribution). Péricart (1970): 737 (taxonomic history); Carayon (1972): 312, 327 (figures, morphology of male reproductive system); Péricart (1972): 113, 120–122 (in key, redescription, figures, distribution); Misja (1973): 139 (record); Coulianos & Ossiannilsson (1976): 150 (listed, distribution); Georghiou (1977): 114 (record); Heiss (1977): 41–42 (record, distribution, habitat); Hoberlandt (1977): 65 (listed); Kelton (1978): 35, 42, 71, 81, 91 (in key, redescription, figures, photo); Ford (1979): 56 (listed, distribution); Adlbauer & Heiss (1980): 9 (record, distribution); Drosopoulos (1980): 171 (listed); Önder (1982): 14–15, 17, 24, 79, 107 (figures, in key, redescription, prey, habitat, distribution); Roşca & Popov (1982): 129 (listed); Dioli (1983): 6 (prey); Henry (1988): 14 (catalogue, distribution); Bosmans & Péricart (1989): 42 (distribution, records); Péricart & Halperin (1989): 92 (listed); Hagen & Dreistadt (1990): 323 (record); Bernhardt (1992): 305 (listed, habitat); Reichling & Gerend (1994): 282 (listed); Dioli (1995): 10, 23 (listed, distribution); Péricart (1996): 113 (catalogue, Palaearctic); Putshkov & Putshkov (1996): 17 (distribution); Derzhansky (1997): 5 (listed); Lukashuk (1997): 9 (distribution); Coulianos (1998): 25 (listed, distribution); Protić (1998): 43 (records, distribution, habitat); Kondorosy (1999): 138 (listed); Horton et al. (2000): 663 (mating preference, mating propensity, reproductive traits); Lattin (2000): 613 (bionomics); Ostovan & Niakan (2000): 6, 9, 11 (record, in key, photo); Horton et al. (2002): 47 (copulation duration); Morkel (2002): 108 (record); Hoffmann & Melber (2003): 243 (distribution); Wyniger & Burckhardt (2003): 65 (records, distribution, habitat); Gogala (2004): 248; Horton et al. (2004): 18 (full summary of N. American records); Coulianos (2005): 18 (record, distribution); Horton et al. (2005): 331 (ovarian development, lipid reserves); Lewis et al. (2005): 62 (taxonomic history, record); Rabitsch (2005): 36 (listed); Ribes & Borges (2005): 191 (record); Abd-Rabou & Ghahari (2006): 43 (listed as predators of whitefly, associated plant); Morkel (2006): 228 (record); Önder et al. (2006): 28 (listed, distribution); Wachmann et al. (2006): 188 (distribution, habitat, photo); Ke & Bu (2007): 93–94 (figure, description of female genitalia); Ghahari et al. (2008): 16 (record, distribution); Horton (2008): 2406, 2410 (photo, economic im-

portance); El-Meghrabi (2009): 755 (habitat, distribution); Ghahari et al. (2009): 47 (catalogue, distribution); Hassanzadeh et al. (2009): 21 (record); Hassanzadeh Awal & Modarres Awal (2010): 659 (listed, in key, figure); Neimorovets (2010): 20 (records); Ghahari et al. (2011): 5 (record); Heckmann & Blöchlinger (2011): 108 (records); Horton & Lewis (2011): 1266, 1268–1269, 1271–1274 (description of male and female genitalia, photo, figures); Malenovský et al. (2011): 144 (record, prey, habitat, associated plant); Rintala & Rinne (2011): 170 (diagnosis, habitat, distribution, photo); Cuppen (2012): 159 (listed); Kment & Baňař (2012): 510 (record, distribution); Rabitsch (2012): 270, 292 (listed); Aukema et al. (2013a): 86 (catalogue, distribution); Aukema et al. (2013b): 462 (record); Esenbekova (2013): 58 (habitat, prey, distribution); Horton et al. (2013): 488, 492 (listed); Jerinić-Prodanović & Protić (2013): 175 (record, distribution, prey); Khaghaninia et al. (2013): 469 (record, distribution); Yildirim et al. (2013): 56 (record); Albrecht et al. (2015): 24 (listed); Carapezza & Mifsud (2015): 34 (record); Carpintero (2015): 229 (listed, photo); Ghahari et al. (2015): 506 (record, distribution, prey); Ballal & Yamada (2016): 186, 198, 200–201 (review of bionomics); Protić (2016): 367 (listed); Farshbaf Pour-Abad et al. (2017): 337 (record); Ostovan et al. (2017): 456 (distribution, habitat, prey); Morkel et al. (2018): 229 (record); Moulet et al. (2018): 136, 140 (listed, distribution, in key); Ryan (2018): 26 (listed); Günther & Günther (2019): 231 (records); Goula et al. (2020): 12 (listed); Hassanzadeh Awal et al. (2020): 1671–1672, 1675 (photo, diagnosis).

Type material examined. *Anthocoris dohrni*: Holotype: ♂, 'Gibraltar' [printed], 'A. minki' [handwritten], 'Type' [printed circle with red border], 'Champion \ Coll. B. M. \ 1927-409.' [printed], 'Anthocoris \ dohrni Le Q \ TYPE' [handwritten], 'Anthocoris [handwritten] \ nemoralis [hand written] \ J. PERICART, det. 1969 [printed + handwritten]', '♂' [printed], 'BMNH(E) \ 1254856' [printed] (BMNH).

Additional material examined. JAPAN: Honshu: Osaka Pref.: 1 ♂ (Figs 7I–J), Osaka-shi, Taishô-ku, Kobayashi-nishi, Rinkôryokuchi Park, 19.v.2020, A. Ichikawa; 1 ♂ 1 ♀ (Fig. 15D), same locality, 23.ix.2020, A. Ichikawa; 1 ♂ (Figs 12D, 13J–L), Osaka-shi, Taishô-ku, Kobayashi-nishi, 15.vi.2020, on *Lantana* spp., A. Ichikawa; Hyogo Pref.: 1 ♀, Kobe-shi, Higashinada-ku, Kôyô-chô, Naka, 22.ix.2020, A. Ichikawa (all in TKPM).

Differential diagnosis. Recognized by the following combination of characters: head (Figs 7I–J) blackish brown to black, sometimes mostly reddish brown; antennal segments I, III, and IV blackish brown, segment II pale brown or yellowish brown and darkened at extreme base and apical half (Fig. 7I); labium (Fig. 7J) generally reddish brown to blackish brown; pronotum (Fig. 7I) blackish brown with light brown or reddish brown on posterior half; scutellum uniformly black, shiny; hemelytra (Fig. 7I) blackish brown, but brown or reddish brown on basal half; clavus and endocorium matted or dull, the remainder of corium shiny; embolium and endocorium somewhat semi-transparent mostly at the base; membrane (Fig. 7I) smoky black, with large whitish markings on basal portion and area behind apex of cuneus, and whitish area along veins; legs (Figs 7I–J) generally reddish brown to blackish brown; ostiolar peritreme straight, almost same width throughout, obtuse at apex; abdominal sternum II (Fig. 12D) with a pair of narrow triangle-shaped membranous areas along posterior margin. Most similar in general coloration to *A. butleri* Le Quesne, 1954 from Europe, but distinguished from it by the shorter antennae and the paramere being shorter and strongly bent at base (in *A. butleri*, much longer, moderately curved at base). It is also similar in appearance to *A. confusus* but distinguished from it by the light-brown or reddish-brown posterior half of pronotum, mostly reddish-brown to blackish-brown tibiae, embolium and endocorium being somewhat semi-transparent mostly at the base, and the greater contrast between shiny embolium and dull endocorium.

Redescription. ***Male genitalia*** (Figs 13J–L): Pygophore (Fig. 13J) turbinate, longer than wide, covered with 8–12 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest are approximately half the length of pygophore; mid-dorsal surface very hirsute with suberect setae; paramere (Figs 13K–L) slender, curved, gradually becoming acute at apex, sub-basally slightly constricted, with a few short, suberect setae on median portion, angulate at base in posterolateral view; longitudinal groove lacking.

Female genitalia (Fig. 15D): Copulatory tube fused on left side of intersegmental membrane between sterna VII and VIII, approximately 1.1 mm in length, thickest at base (cystiform) and gradually narrowing toward apex; trunk of conductive tissue invisible (or possibly dissolved).

Measurements [mm; ♂♂ (n = 3) / ♀♀ (n = 2)]. Body length 3.85–4.25 / 4.00–4.35; head length (excl. neck) 0.46–0.53 / 0.54–0.55; head width across eyes 0.51–0.58 / 0.56–0.58; vertex width 0.29–0.33 / 0.33–0.34; length of antennal segments I – 0.13–0.16 / 0.19, II – 0.50–0.55 / 0.53–0.54, III – 0.29–0.33 / 0.34–0.35, and IV – 0.34–0.39 / 0.38–0.39; length of labial segments II – 0.10–0.14 / 0.13–0.15, III – 0.40–0.45 / 0.45–0.49, and IV – 0.28–0.30 / 0.28; anterior pronotal width 0.43–0.45 / 0.48–0.50; mesal pronotal length 0.56–0.63 / 0.65–0.69; basal pronotal width 1.20–1.36 / 1.45–1.50; length of embolial margin 1.25–1.41 / 1.39–1.44; length of cuneal margin 0.69–0.83 / 0.79–0.85; maximum width across hemelytra 1.29–1.44 / 1.46–1.55.

Bionomics. In Europe, *A. nemoralis* is common on many trees and shrubs, and is known to prey on psyllids, aphids, thrips, eggs and larvae of moths, and on some mites. This species has been studied extensively in Europe as a major predator of pear psyllids. In North America, this species was accidentally introduced from Europe to the eastern areas before 1958 and was possibly intentionally introduced to pear growing regions of western North America during the 1960s (Horton et al. 2004).

In Japan, this species was discovered in the harbor areas along Osaka Bay for the first time. Specimens were first collected from several sites in port areas of Osaka Prefecture from May to July 2020, where they were found on various broadleaf trees planted for landscaping (Akihiko Ichikawa, pers. comm.). In September 2020, in addition to the Osaka populations, a few specimens were collected from a port area (landfill) in Kobe, Hyogo Prefecture. It is assumed that this species was accidentally introduced into Japan very recently. This discovery is the first record not only from Japan but also from East Asia; however, the origin of the Japanese populations cannot be determined at present.

Distribution. Japan: Honshu*: Osaka, Hyogo. *Anthocoris nemoralis* is widespread in the Western Palaearctic (Péricart 1996, Aukema et al. 2013a), and has also been introduced to North America (Horton et al. 2004). Very recently, this species has been found in Japan. This discovery represents the first East Asian record of this species.

Summary of known records: **ASIA:** Azerbaijan (Péricart 1996). Armenia (Péricart 1996). Turkey: Asian part (Horváth 1883, Önder et al. 2006). Georgia (Péricart 1996). Iran (Linnavuori & Hosseini 2000, Ostovan et al. 2017). Israel (Bodenheimer 1937, Péricart & Halperin 1989). Jordan (Péricart 1996). Kazakhstan (Esenbekova 2013). Syria (Reuter 1884, Stichel 1958). **EUROPE:** Albania (Stichel 1958, Misja 1973). Andorra (Péricart 1996). Austria (Stichel 1958, Rabitsch 2005). Belgium (Stichel 1958, Bosmans & Péricart 1989). Bosnia and Herzegovina (Péricart 1996). Bulgaria (Stichel 1958, Josifov 1964). Belarus (Lukashuk 1997). Croatia (Péricart 1996). Cyprus (Georghiou 1977). Czech Republic (Hoberlandt 1977, Kment & Baňař 2012). Denmark (Fabricius 1794, Stichel 1958). Estonia (Coulianos 2005). Finland (Reuter 1884, Albrecht et al. 2015). France (Reuter 1884, Stichel 1958). Germany (Stichel 1958, Hoffmann & Melber 2003). Greece (Drosopoulos 1980, Péricart 1996). Hungary (Stichel 1958, Kondorosy 1999). Ireland (Halbert 1935). Italy (Stichel 1958, Dioli 1983). Latvia (Stichel 1958). Liechtenstein (Bernhardt 1992). Luxembourg (Péricart 1996). Malta (Péricart 1996, Carapezza & Mifsud 2015). Moldavia (Péricart 1972, Derzhansky 1997). Montenegro (Protić 1998, 2016). The Netherlands (Stichel 1958). North Macedonia (Péricart 1996). Norway (Stichel 1958, Coulianos 1998). Poland (Stichel 1958). Portugal (Seabra 1941). Romania (Stichel 1958, Roşca & Popov 1982). Russia: Central and South European Territories (Stichel 1958). Serbia (Protić 1998). Slovakia (Hoberlandt 1977, Péricart 1996). Slovenia (Gogala 2004). Spain (Le Quesne 1958, Goula et al. 2020). Sweden (Reuter 1884, Stichel 1958). Switzerland (Stichel 1958, Heckmann & Blöchlinger 2011). Ukraine (Péricart 1996). United Kingdom (Edwards 1890, Stichel 1958). Turkey: European part (Péricart 1996, Önder et al. 2006). **NORTH AFRICA:** Algeria (Stichel 1958, Eckerlein & Wagner 1965). Azores (Ribes & Borges 2005). Canary Islands (Stichel 1958, Péricart 1972). Egypt (Stichel 1958, Wagner 1960). Libya (Stichel 1958, El-Meghrabi 2009). Morocco (Stichel 1958). Tunisia (Reuter 1884, Stichel 1958). **NORTH AMERICA:** Canada: Ontario, British Columbia (Anderson & Kelton 1963, Horton et al. 2004). USA: Washington, Oregon, California (Horton et al. 2004).

Anthocoris takahashii Hiura, 1959

(Figs 7K–L, 9E, 12E, 13M–O, 15E, 16E, 21)

Anthocoris takahashii Hiura, 1959: 6. Holotype: ♂, Japan, Hokkaido, Ashoro (OMNH).

Anthocoris takahashii: Ford (1979): 56 (listed, distribution); Kerzhner (1988): 773–774 (figures, in key); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Péricart (1996): 115 (catalogue, distribution); Iijima (1997): 15 (record); Bu & Zheng (2001): 120, 162 (in key, figures, redescription); Yasunaga (2001a): 231 (listed, habitat); Yasunaga (2001b): pl. 85, 282 (photo, diagnosis, habitat, phenology); Kanyukova & Marusik (2006): 168 (record); Ke & Bu (2007): 92–93 (figure, description of female genitalia); Maehara (2009): 65 (record, distribution, photo); Vinokurov et al. (2010): 58 (catalogue, distribution); Konno (2012b): 32 (record, photo, associated plant); Maehara (2012): 35 (record, associated plant, distribution); Hao & Ma (2013): 36 (listed); Komatsu & Nagai (2014): 43 (record, habitat, photo); Maehara (2015): 29 (record, distribution, habitat); Komatsu (2016): 97 (listed); Yamada et al. (2016): 422 (catalogue, distribution).

Type material examined. Holotype: ♂, 'ASHORO \ HOKKAIDO \ 28. V. 1957 \ M. TAKAHASHI' [handwritten], 'HOLOTYPE ♂ [handwritten] \ Anthocoris [handwritten] \ takahashii [handwritten] \ HIURA, 1959 [handwritten] \ I. HIURA Det. [printed]', 'OMNH TI 191' [handwritten] (OMNH).

Additional material examined. JAPAN: Hokkaido: 1 ♂, Horokanai-cho, Uen-nai Dam, 20.viii.2000, T. Yasunaga (TYCN); 1 ♀, Kamikawa-cho, Aizankei, 19.vii.1962, Y. Miyatake (ELKU); 2 ♂♂ (one in Figs 7K–L), Asahikawa-shi, Kasuga near Mt. Inoh, 19.vii.1998, T. Yasunaga (TKPM); 1 ♀, Kamishihoro-cho, Nukabira, 23.vii.1959, K. Morimoto (ELKU); 1 ♀, Tobetsu-cho, Yon-ban-gawa Riv., 13.vi.1997, S. Yamashita (TYCN); 2 ♂♂ 1 ♀, same locality, 15.vii.1997, T. Akiba (TKPM); 1 ♂ (Figs 12E, 13M–O) 3 ♀♀ (one in Fig. 9E, one in Fig. 15E), same locality, 15.vii.1997, A. Hiranuma (TKPM); 1 ♀, Otaru-shi, Katsuraoka, 14.viii.2005, A. Yamamoto (TKPM); 1 ♂, Otaru-shi, Asari Pass, 20.vi.1996, H. Maeda (TKPM); 1 ♂, Otaru-shi, Okusawa-Suigenchi, 31.v.1995, M. Ôhara (TKPM). Rishiri-tô Is.; 1 ♀, Hime-numa, 18.ix.1991, M. Tomokuni (NSMT). **Honshu:** Tochigi Pref.: 2 ♀♀, Nikko-shi, Nakamiyori, 17.v.2010, S. Maehara (TKPM); 1 ♀, Nikko-shi, Yumoto, 1.viii.2006, S. Maehara (TKPM). Niigata Pref.: 1 ♀, Yuzawa-machi, Asakai, 18.vi.1957, K. Baba (ELKU). Nagano Pref.: 1 ♀, Karuizawa, 3.–7.viii.1959, S. Miyamoto (ELKU).

Differential diagnosis. Recognized by the following combination of characters: body (Figs 7K–L, 16E) generally black; antennae (Figs 7K–L) blackish brown; labium (Fig. 7L) just reaching to procoxae; hemelytra (Fig. 7K) black, sometimes with brownish tinge on anterior half; membrane (Fig. 7K) smoky dark brown, with basal and innermost portions and area behind apex of cuneus whitish, large and irregularly shaped markings; legs (Fig. 7L) reddish brown to blackish brown, tibiae sometimes yellowish brown; ostiolar peritreme (Fig. 9E) straight, slightly narrowed at middle, obtuse at apex and slightly curved forward; abdominal sternum II (Fig. 12E) with a pair of small triangular membranous areas along posterior margin. A similar general appearance to eastern Palaearctic *A. ussuriensis* Lindberg, 1927, but distinguished from that species by the uniformly blackish-brown antennal segment II (in *A. ussuriensis*, basal half of segment II yellowish brown), slightly brownish on anterior half of hemelytra (in *A. ussuriensis*, rather paler on anterior half of hemelytra), and copulatory tube fused on upper surface of intersegmental membrane between sterna VII and VIII, slightly to left of the middle of the membrane (in *A. ussuriensis*, fused on middle of intersegmental membrane).

Redescription. ***Male genitalia*** (Figs 13M–O): Pygophore (Fig. 13M) turbinate, longer than wide, covered with 8–12 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest is approximately half the length of pygophore; mid-dorsal surface very hirsute with short, suberect setae; paramere (Figs 13N–O) sickle-shaped, sub-basally widened, with several short setae on median portion; longitudinal groove lacking.

Female genitalia (Fig. 15E): Copulatory tube fused slightly left of middle on upper surface of intersegmental membrane between sterna VII and VIII, approximately 0.6–0.7 mm in length, basal 1/3 thickened, very thin and almost same width on apical 2/3; trunk of conductive tissue visible.

Measurements [mm; ♂♂ (n = 5) / ♀♀ (n = 10)]. Body length 4.60–5.25 / 4.70–5.35; head length (excl. neck) 0.56–0.60 / 0.54–0.63; head width across eyes 0.64–0.70 / 0.63–0.69; vertex width 0.33–0.36 / 0.34–0.38; length of antennal segments I – 0.19–0.21 / 0.19–0.23, II – 0.54–0.65 / 0.53–0.60, III – 0.36–0.38 / 0.35–0.38, and IV – 0.39–0.44 / 0.38–0.44; length of labial segments II – 0.18–0.20 / 0.16–0.20, III – 0.58–0.63 / 0.58–0.65, and IV – 0.35–0.40 / 0.38–0.43; anterior pronotal width 0.53–0.58 / 0.54–0.58; mesal pronotal length 0.66–0.76 / 0.70–0.81; basal pronotal width 1.43–1.60 / 1.50–1.75; length of embolial margin 1.54–1.78 / 1.63–1.85; length of cuneal margin 0.86–0.95 / 0.83–0.96; maximum width across hemelytra 1.55–1.78 / 1.63–1.88.

Bionomics. *Anthocoris takahashii* has been collected from *Alnus* spp. (Betulaceae) and *Ulmus davidiana* Planch. var. *japonica* (Rehder) Nakai (Ulmaceae) (Yasunaga 2001a,b; Konno 2012b; Maehara 2015). This species feeds on psyllids (Bu & Zheng 2001).

Distribution. Japan: Hokkaido (Hiura 1959), Rishiri-tô Is.*; Honshu: Yamagata (Konno 2012b), Tochigi (Maehara 2009), Niigata*, Nagano*; Kyushu: Miyazaki (Komatsu & Nagai 2014). Chishima (Kuril) Islands: Kunashir Is. (Kerzhner 1988, Kanyukova & Marusik 2006). Russia: Far East: Sakhalin (Kerzhner 1988, Vinokurov et al. 2010). China: Guizhou, Zhejiang (Bu & Zheng 2001). This species is distributed mainly in Hokkaido and the Russian Far East, with scattered records from northern Honshu and Kyushu in Japan, and China (Fig. 21).

Anthocoris miyamotoi Hiura, 1959

(Figs 8A–D, 9F, 11A–B, 12F, 14A–C, 15F, 17F–G, 22)

Anthocoris miyamotoi Hiura, 1959: 3. Holotype: ♂, Japan, Tokara Islands, Nakanoshima Is. (OMNH).

Anthocoris miyamotoi: Ford (1979): 56 (listed, distribution); Tomokuni (1981): 109 (record); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Tomokuni (1993): pl. 27, 168 (photo, diagnosis, habitat, distribution); Péricart (1996): 113 (catalogue, Palaearctic); Yasunaga (1997a): 32 (listed); Yasunaga (1999): 22 (listed, distribution); Yasunaga (2001b): 282 (listed); Hayashi (2002): 136 (listed, distribution); Tomokuni & Ishikawa (2002): 173 (record); Tomokuni & Hayashi (2006): 293 (record); Aukema et al. (2013a): 86 (catalogue); Yamada et al. (2016): 422 (catalogue, distribution); Yasunaga et al. (2018): 138 (photo); Urayama et al. (2019): 79, 81–82 (record, photo, habitat); Miyazaki et al. (2020): 65–66 (rearing method).

? *Anthocoris miyamotoi* (doubtful identifications, not verified): Miyamoto (1965): 96, pl. 48 (diagnosis, habitat, distribution, photo); Nakajima (1968): 46 (record); Shimizu (1969): 244 (record); Tawara (1970): 67 (record); Nakajima (1976): 97 (record); Miyata et al. (1977): 566 (record); Iwasaki (1983): 14 (record); Takakura & Tsutsumi (1983): 178 (record); Takakura (1984): 6 (record); Sasaji (1985): 58 (record); Otsuka & Yoshizaki (1987): 596 (record); Otsuka & Aramaki (1989): 29 (record); Ichita (1988): 132 (record); Asaoka & Ieki (1990): 155 (listed, distribution); Lee & Kwon (1991): 13 (record); Ichita & Suzuki (1993): 199 (distribution); Lee et al. (1993): 10 (record); Lee & Kwon (1994): 63 (listed); Kwon (1994): 177 (listed); Kwon et al. (1996a): 109 (listed); Kwon et al. (1996b): 453 (record); Hayashi (1998): 165 (record); Ichita (1998): 27 (record); Kishimoto et al. (1998): 84 (distribution); Hua (2000): 198 (listed, distribution); Ichita et al. (2000): 110 (record); Yano & Yamamoto (2000): 168 (record); Bu & Zheng (2001): 118, 146 (in key, redescription, figures); Iwate Prefecture (2001): 179 (listed); Kwon et al. (2001): 80 (catalogue, record, distribution); Yasunaga & Higuchi (2002): 88 (record, associated plant); Kagawa & Higuchi (2003): 205 (record, distribution); Suzuki (2003): 147 (distribution); Hayashi & Ozaki (2004): 223 (distribution); Hayashi & Ishikawa (2005): 94 (photo of fifth instar larva and adult, diagnosis, habitat, prey, distribution); Wachi (2006): 66 (record); Tago (2006): 29 (record); Enju (2007): 89 (distribution); Ke & Bu (2007): 92–93 (figure, description of female genitalia); Miyamoto (2008): 164, pl. 57 (diagnosis, habitat, distribution, photo); Ichita (2009): 68 (listed); Aoki (2010): 72 (record); Ogawa et al. (2012): 8 (record); Yano et al. (2012): 87 (record); Hao & Ma (2013): 36 (listed); Jung et al. (2013): 422 (catalogue, diagnosis, distribution); Nozaki & Nozaki (2013): 33 (record); Zheng & Lin (2013): 298 (redescription, photo); Suzuki (2014b): 7 (record); Maehara (2015): 29 (record, habitat, phenology); Nozaki et al. (2015): 18 (record); Komatsu (2016): 97 (listed); Nozaki et al. (2016): 82 (record); Jung & Lee (2017): 37–38, 71 (diagnosis, redescription, distribution, photo, figure); Hayashi et al. (2018): 182 (distribution); Hayashi & Kadowaki (2019): 19 (listed); Tanaka (2019): 64, 111 (listed); Komatsu & Hidaka (2020): 108–109 (record, photo); Ito et al. (2020): 113 (record); Okuzono & Yamamoto (2020): 82 (record); Shizuoka Prefecture (2020): 128 (listed).

Type material examined. Holotype: ♂ (Figs 8A–B), 'Osaka Mun. Mus. \ Tokara Is. Exp. \ Nakanoshima \ 3–13. vi. 1953 \ T. Nakane' [printed], 'HOLOTYPE ♂ [handwritten] \ Anthocoris [handwritten] \ miyamotoi [handwritten] \ HIURA, 1959 [handwritten] \ I. HIURA Det. [printed]', 'OMNH TI 189' [handwritten] (OMNH).

Additional material examined. JAPAN: Honshu: Chiba Pref.: 2 ♂♂ 1 ♀, Tateyama-shi, Mera, 15.vi.2002, M. Tomokuni (NSMT). Kanagawa Pref.: 2 ♀♀, Yokosuka-shi, Sarushima, 7.viii.1999, S. Arai (TKPM); 1 ♀, Yokosuka-shi, Mt. Take-yama, 12.ii.1990, K. Aoki (TKPM). Mie Pref.: 1 ♀, Shima-shi, Daiô-cho, Tomoyama-Nakiri, 11.viii.1996, T. Konishi (EUM). Shiga Pref.: 8 ♀♀, Ôtsu-shi, Seta-gawa Riv., 28.vii.2004, K. Yamada (TKPM). Hyogo Pref.: 2 ♀♀, Minamiawaji-shi, Nada-Yoshino, 25.v.2017, H. Inoue (TKPM). Wakayama Pref.: 1 ♂ (Fig. 8C), Kushimoto-cho, Hashikui, 22.xi.2001, K. Yamada (TKPM). Yamaguchi Pref.: 2 ♀♀, Hikari-shi, Mt. Senbou-san, 18.vii.2010, T. Ban (TKPM); 2 ♂♂, Kaminoseki-cho, Nagashima Is., 23.–25.vi.2000, S. Nagashima (TKPM). **Izu Islands:** Ôshima Is.: 1 ♀, 17.iv.1974, Y. Furuki (EUM). Miyake-jima Is.: 2 ♀♀, 15.v.1999, T. Kishimoto (TKPM). Hachijô-jima Is.: 4 ♂♂ 10 ♀♀, Mt. Hachijôfuji, 560–850 m, 2.–5.vii.2001, M. Tomokuni (NSMT); 2 ♂♂ 1 ♀, same locality, 3.viii.2001, T. Ishikawa (TKPM); 1 ♂, Mt. Mihara-yama, 24.vii.2001, J. Ogawa (EUM). **Shikoku:** Tokushima Pref.: 1 ♀, Tokushima-shi, Ichinomiya-cho, 20.iii.2017, T. Nakanishi (TKPM); 1 ♂ 2 ♀♀, Ôbara-cho, 24.v.2016, T. Nakanishi (TKPM); Sanagouchi-son, Ozakai, 34.005000N 134.478889E: 1 ♀, 16.x.2013; 1 ♀, 27.xii.2013; 1 ♂, 18.v.2015; 2 ♂♂ 4 ♀♀, 7.x.2016, T. Nakanishi (all in TKPM); 5 ♂♂ 2 ♀♀, Kamiyama-cho, Orono, 33.987778N 134.398611E, 13.v.2016, T. Nakanishi (TKPM); Katsuura-cho, Nue, 33.940278N 134.541944E: 1 ♂, 29.iv.2013; 2 ♂♂, 14.v.2013; 3 ♂♂, 30.v.2013; 1 ♀, 25.ii.2014; 3 ♂♂ 3 ♀♀ (one in Fig. 15F), 26.iv.2016; 1 ♂ 2 ♀♀, 8.v.2016; 1 ♂ 2 ♀♀, 21.v.2017, T. Nakanishi (all in TKPM); 1 ♀, Katsuura-cho, Hoshidani, 29.x.2013, T. Nakanishi (TKPM); 3 ♂♂ 7 ♀♀ (one in Fig. 9F), Anan-shi, Kuwano-cho, 33.870833N 134.610278E, 29.iv.2016, T. Nakanishi (TKPM); 1 ♀, Kaiyô-cho, Kôno, 6.vi.2012, K. Yamada (TKPM). Kagawa Pref.: 1 ♀, Shôdoshima Is., Tonosyô-chô, Oobe, 27.iii.2020, G. Kisaki (TKPM). Ehime Pref.: 1 ♂ 1 ♀, Matsuyama-shi, Kashima, 29.iii.1953, M. Miyatake (EUM); 1 ♂, Matsuyama-shi, Takahama-machi, 14.v.2002, T. Kurihara (EUM). Kochi Pref.: 3 ♀♀, Tôyô-cho, None, 3.v.2000, M. Takai (TKPM); 1 ♀, Tosashimizu-shi, Ashizuri Cape, 25.–26.vii.1967, M. Miyatake et al. (EUM); 1 ♀, same locality, 23.v.1983, M. Miyatake (EUM); 1 ♀, Tosashimizu-shi, Ashizuri-hantô, 29.vi.2001, M. Takai (TKPM). **Kyushu:** Fukuoka Pref.: 1 ♀, Sasaguri-machi, Mt. Wakasugi-yama, 1.iv.1959, Y. Miyatake (OMNH); 1 ♀, Fukuoka-shi, Hakozaki, 17.iv.1958, Y. Miyatake (OMNH); 1 ♀, Fukuoka-shi, Hirao, 29.v.1959, Y. Miyatake (OMNH). Nagasaki Pref.: 1 ♀, Nagasaki-shi, Kônoura, 4.viii.1996, T. Yasunaga (TKPM); 1 ♀, Nagasaki-shi, Nomozaki, 7.iv.1978, M. Sakai (TKPM); 1 ♀, Nagasaki-shi, Nomozaki, Kabashima Is., 32.5555N 129.7768E, male flower of *Mallotus japonicus*, 24.viii.2013, T. Yasunaga (TYCN); 1 ♂, Nagasaki-shi, Kawaguchi-Park, 32.76685N 129.86355E, under flakes of bark of *Zelkova serrata*, 2.ii.2018, T. Yasunaga et al. (NWHS); 1 ♀, Nagasaki-shi, 4.iv.1973, Y. Furuki (EUM); 1 ♂ (Figs 11A–B), Nagasaki-shi, 24.iv.2012, T. Yasunaga (TKPM); 1 ♀, Saikai-

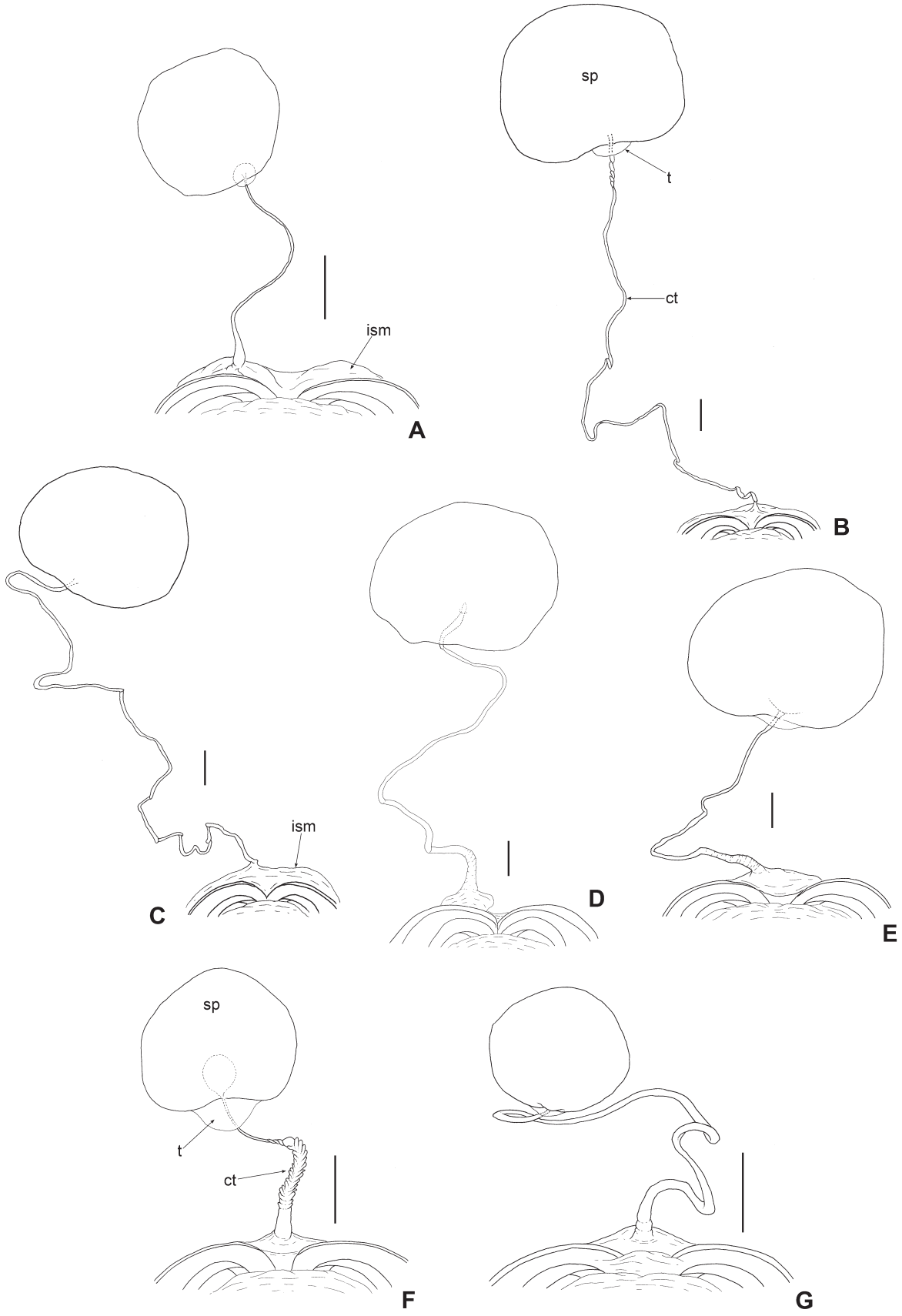

Fig. 15. Female genitalia of *Anthocoris* spp., dorsal view. A – *A. chibi* Hiura, 1959; B – *A. confusus* Reuter, 1884; C – *A. japonicus* Poppius, 1909; D – *A. nemoralis* (Fabricius, 1794); E – *A. takahashii* Hiura, 1959; F – *A. miyamotoi* Hiura, 1959; G – *A. venustus* sp. nov., paratype. Abbreviations: ct – copulatory tube; ism – intersegmental membrane; sp – sperm pouch; t – trunk of conductive tissue (C–D, trunk of conductive tissue dissolved). Scale bars: 0.1 mm.

-shi, Seihi-cho, Nagasaki Biopark, 32.988073N 129.78233E, *Ligustrum japonicum* inflorescens, 29.vi.2013, T. Yasunaga (TYCN). Kagoshima Pref.: 2 ♂♂ (one in Fig. 8D) 5 ♀♀, Satsumasendai-shi, Kashima-cho, Imuta, 24.iv.2012, H. Inoue (TKPM); 1 ♀, Minamiôsumi-cho, Ôdomari, 19.iii.1973, M. Miyatake (EUM). **Tsushima Island:** 1 ♀, Kamiagata-cho, Saozaki Park, 15.–16.vii.2000, J. Ogawa (EUM); 1 ♂, Kamiagata-cho, Mt. Mitake, 15.vii.2000, J. Ogawa (EUM); 1 ♀, Toyotama-cho, Waita, 30.vi.2008, T. Nakayama (TKPM). **Ryukyu Islands:** Yakushima Is.: 1 ♂, Miyanoura, 16.iv.1954, Y. Kurosawa (TKPM); 2 ♂♂ 2 ♀♀, Onoaida, 3.i.1965, I. Hiura (OMNH). Kuchinoshima Is.: 1 ♂, 21.v.1962, M. Sato (EUM). Nakanoshima Is.: 4 ♂♂ (one in Figs 12F, 14A–C) 1 ♀ 1 unsexed, Takamoto-rindô, 6.–10.vi.2005, T. Mita (TKPM); 1 ♂, 2.v.1971, M. Sakai (EUM). Amami-Ôshima Is.: 1 ♀, Tatsugô-cho, 24.iii.2011, S. Kudo (TKPM); 2 ♂♂ 4 ♀♀, Tatsugô-cho, 17.iv.2016, S. Kudo (TKPM); 1 ♀, Amami-shi, Daikuma-cho, 10.iv.1971, M. Sakai (EUM); 1 ♀, Amami-shi, Mt. Ogami-yama, 30.iv.1977, A. Oda (NSMT); 7 ♂♂ 4 ♀♀, Amami-shi, Asado, 31.v.1993, T. Yasunaga (TKPM); 1 ♀, Chûou-rindô, 18.vi.1995, Y. Sawada (TKPM); 1 ♀, Amami-shi, Sumiyô, Hatsuno-bashi, 5.vii.2005, light trap, T. Ishikawa (TKPM); 1 ♂ 2 ♀♀, Yamato-son, Mt. Yuwan-dake, 17.–19.iv.1971, M. Sakai (EUM); 1 ♀, same locality, 30.v.1993, T. Yasunaga (TKPM); 2 ♀♀ 1 unsexed, Setouchi-cho, Mt. Yui-dake, 24.iv.1997, T. Ishikawa (TKPM); 1 ♂, 25.v.2004, T. Mita (TKPM); 1 ♀, Ikari, 6.v.1960, T. Shibata (OMNH). Okinawa-hontô Is.: 1 ♀, Kunigami-son, Mt. Nishime-dake, 25.v.1993, T. Yasunaga (TKPM); 1 ♂, Kunigami-son, Sate, 24.v.1993, T. Yasunaga (TKPM); 2 ♀♀, Kunigami-son, Yona, 20.v.1993, T. Yasunaga (TKPM); 1 ♀, 12.iv.1996, Y. Nakatani (TKPM); 2 ♂♂ 1 ♀, 18.v.2002, K. Yamada (TKPM); 1 ♀, Kunigami-son, Mt. Terukubi-yama, 23.v.1993, T. Yasunaga (TKPM); 2 ♀♀, Kunigami-son, Hentona, Shinrin Park, 31.iii.2001, K. Yamada (TKPM); 1 ♀, Kunigami-son, Mt. Yonaha-dake, 13.vi.2003, T. Tsuru (TKPM).

Differential diagnosis. Recognized by the following combination of characters: head and callus of pronotum orangish brown to reddish brown (Figs 8A–B); clavus with basal and apical portions blackish brown, inner margin narrowly darkened; endocorium with basal and apical portions mostly blackish brown; embolium with basal and apical portions blackish brown; median portion of clavus and outer part of median portion of endocorium and remaining area of embolium whitish and subhyaline; area in front of cuneal fracture narrowly whitish or subhyaline; outer (posterior) margin of ostiolar peritreme touching or close to supracoxal area (Fig. 9F); paramere (Figs 11A–B, 14B–C) sickle-shaped, widened at basal 2/3, apical 1/3 needle-like, with distinct longitudinal groove; and copulatory tube (Fig. 15F) approximately 0.25 mm in length, basal 2/3 very thick and wrinkled and then rapidly becoming narrow apically. Most closely resembling *A. venustus* sp. nov. in general appearance but distinguished from that species by the orangish brown to reddish-brown head and pronotal callus, sickle-shaped and rather widened paramere, and a shorter copulatory tube, at the basal 2/3 of which is very thickened and wrinkled. It is also similar to *A. dividens* Bu & Zheng, 2001 from China, but clearly distinguished by the yellowish-brown antennal segment II, which has the base and apical 1/4 to 1/3 dark brown (in *A. dividens*, uniformly blackish brown), membrane with basal and innermost portions and area behind apex of cuneus off-white (in *A. dividens*, membrane with grayish-white V-shaped marking on basal part), and sickle-shaped paramere (in *A. dividens*, lamellate).

Redescription. ***Coloration.*** Head (Figs 8A–D) reddish brown to blackish brown; eyes reddish black; margin of ocellus red to reddish brown. Antennal segment I dark brown, sometimes yellowish brown on basal half; segment II yellowish brown, dark brown on base and apical 1/4 to 1/3; segment III yellowish brown, dark brown on apical half; segment IV dark brown. Labium (Fig. 8B) uniformly black to blackish brown. Pronotum (Figs 8A–D) generally blackish brown; callus usually orangish brown to reddish brown, sometimes mostly blackish brown but reddish tinge at median part. Scutellum overall black to blackish brown. Clavus with basal and apical portions blackish brown, inner margin narrowly darkened (Figs 8A,C–D); endocorium with basal and apical portions mostly blackish brown (Figs 8A,C–D); embolium with basal and apical portions blackish brown (Figs 8A,C–D); cuneus wholly blackish brown; median portion of clavus and outer part of median portion of endocorium and remaining area of embolium whitish or subhyaline (Figs 8A,C–D); area in front of cuneal fracture narrowly whitish or subhyaline; membrane smoky dark brown, with basal and innermost portions and area behind apex of cuneus off-white (Figs 8A,C–D). Legs yellowish brown to reddish brown; trochanters tinged with yellowish brown; apical half or apical 2/3 of tibiae sometimes paler. Venter of the thorax reddish brown to blackish brown. Abdomen black to blackish brown. Pygophore blackish brown with light brown paramere.

Structure. Body (Figs 8A–D, 17G) elongate, shiny on dorsal and ventral surfaces, sparsely covered with suberect, simple, yellowish setae. Head (Figs 8A–D) cylindrical, impunctate, approximately as long as width across eyes; three pairs of long, erect trichobothria on dorsal surface of head, one on anterior clypeus, one in front of eye, and one behind ocellus; anteocular region slightly longer than length of eye in dorsal view; vertex approximately twice as wide as eye in dorsal view in male, approximately 2.2 times as wide as eye in female; postocular region constricted, demarcated by transverse shallow furrow; neck long, smooth, highly polished; eye oblong, not exceeding level of dorsal surface of head in lateral view in both sexes, but exceeding level of ventral surface of head in male and not exceeding in female. Antennae (Figs 8A–D) densely covered with short, decumbent, yellowish setae interspersed with long, erect setae, of which the longest are as long as or slightly shorter than width of corresponding segment; segment I barely reaching apex of head, sparsely covered with short setae; segment II gradually thickened toward apex, a little thicker in the male than in the female, approximately as long as head width across eyes; segment III approximately 0.6–0.7 times as long as segment II; segment IV longer than segment III. Labium (Fig. 8B) just reaching procoxae; segment III approximately 4.0 times as long as segment II; segment IV approximately 0.58 times as long as segment III.

Pronotum (Figs 8A,C–D) with pairs of long, erect trichobothria on midline of collar and on each anterior and posterior angle; anterior margin very slightly curved, approximately 0.7 times as long as mesal length; lateral margin slightly sinuate; lateral carina slightly expanded anteriorly, more obscure posteriad; posterior margin emarginate, approximately 2.5 times as wide as anterior margin; collar long, transversely rugose, with scattered

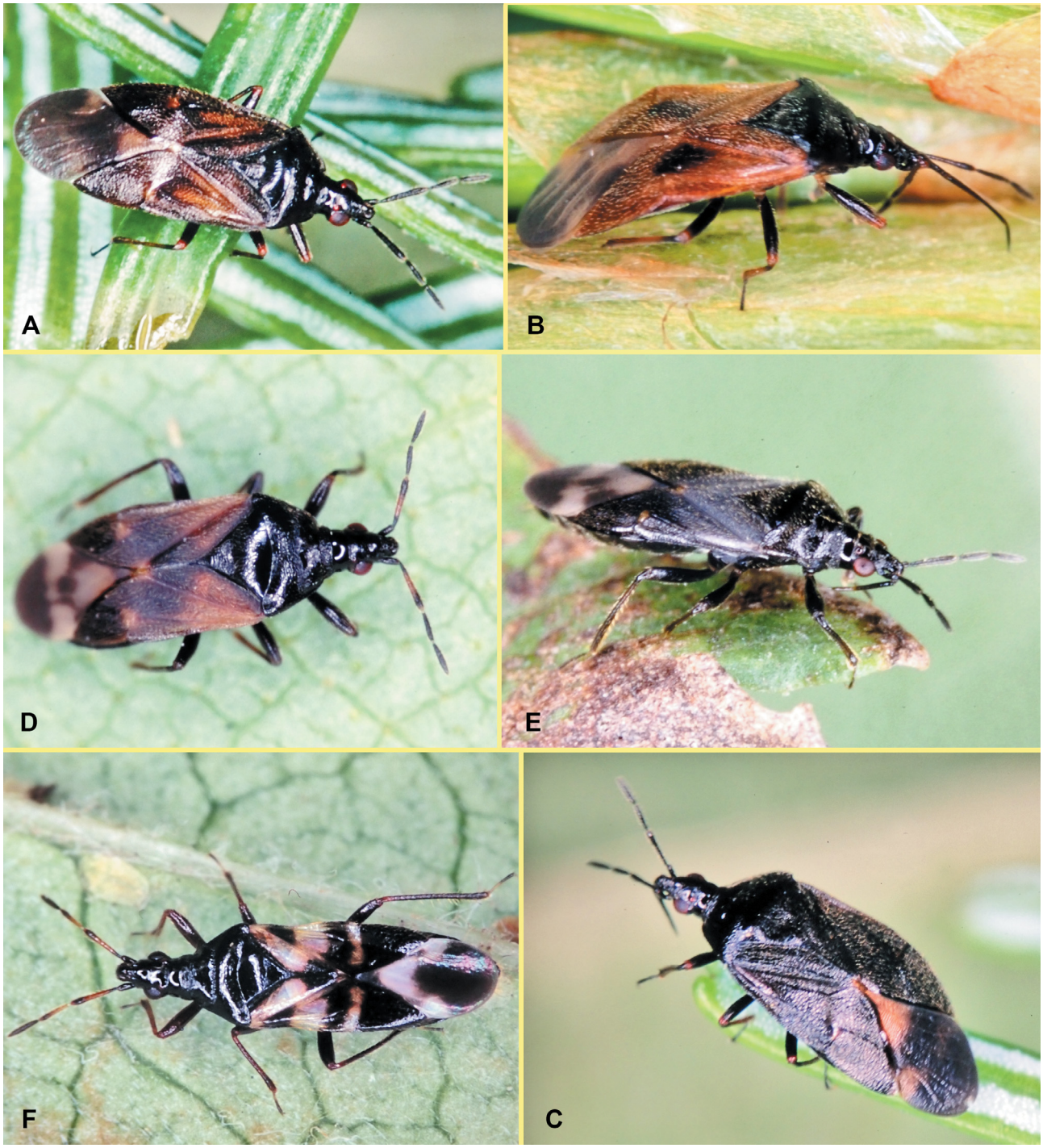

Fig. 16. Habitus images of living individuals of Japanese Anthocorini spp. A – *Acompocoris brevirostris* Kerzhner, 1979, male; B – same, female; C – *Tetraphleps aterrima* (J. Sahlberg, 1878); D – *Anthocoris confusus* Reuter, 1884; E – *A. takahashii* Hiura, 1959; F – *A. venustus* sp. nov. (courtesy of M. Takai).

long setae; callus extremely swollen, polished, impunctate, sides strongly bulging, demarcated posteriorly by deep impression; deep impression with short parallel carinae and coarse punctures; posterior lobe behind callus densely covered with minute punctures. Scutellum (Figs 8A,C–D) smooth, sub-equilateral, wider at base than long, depressed through middle. Hemelytra (Figs 8A–D) sparsely covered with long, erect, simple, yellowish setae, and with minute punctures; costal margin slightly sinuate; maximum width of endocorium approximately 1.6 times that of maximum width of embolium; cuneal margin approximately 0.6 times as long as embolial margin; membrane with three veins, outermost vein distinct and slightly curved, inner two veins obscure and very slightly curved. Ostiolar peritreme (Fig. 9F) wide, gently curved anteriorly, narrowing toward apex, and then continuing to a fine carina that reaches the anterior margin of metapleuron; outer (posterior) margin of ostiolar peritreme touching or close to supracoxal area; evaporatorium sparsely covered with long, recumbent setae. Fossula spongiosa present on apex of all tibiae, enlarged on

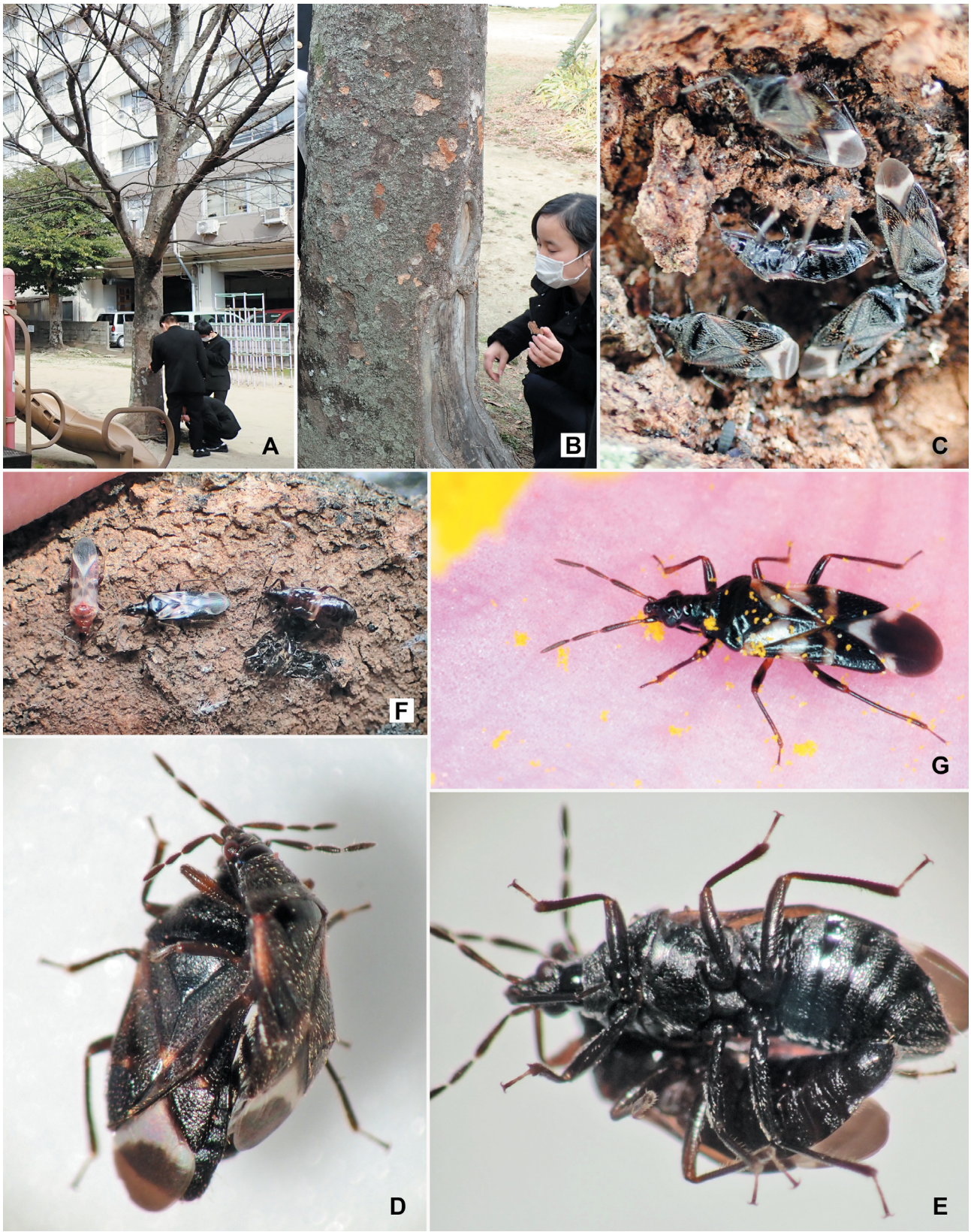

Fig. 17. Habitats, overwintering individuals, and mating pair of *Anthocoris* spp. A–B – Field survey on hibernating anthocorids under bark-flakes of *Zelkova serrata* at urbanized zone of Nagasaki City (Kawaguchi Park) in early February; C – *A. japonicus* Poppius, 1909, overwintering adults under the bark-flake of *Z. serrata*; D–E – same, mating pair; F – *A. miyamotoi* Hiura, 1959, adult males and final instar immature (right), overwintering individuals under the bark of *Z. serrata*; G – same, active male adult on flower of *Camellia sasanqua* in winter (observed on Jan. 4, 2020).

protibiae and small on meso- and metatibiae; apical 1/4 of metatibiae bearing small spines on ventral side. Abdominal sternum III (Fig. 12F) with a pair of banana-shaped membranous areas on anterior half, membranous area slightly constricted at middle; dorsal laterotergites not fused with mediotergites on abdominal segments II and III.

Male genitalia (Figs 11A–B, 14A–C): Pygophore (Fig. 14A) rather pointed apically, asymmetrical, covered with 6–8 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest are approximately half length of pygophore; mid-dorsal surface hirsute with suberect setae; paramere (Figs 11B, 14B–C) sickle-shaped, widened at basal 2/3, needle-like at apical 1/3, with several setae on subapical portion, apex exceeding half of left outer margin of pygophore; longitudinal groove distinct, formed by inflection of anterior and posterior edge of paramere.

Female genitalia (Fig. 15F): Copulatory tube fused on middle of intersegmental membrane between sterna VII and VIII, approximately 0.25 mm in length, very thick and wrinkled at basal 2/3 and then rapidly becoming narrow apically; trunk of conductive tissue strongly pronounced.

Measurements [mm; ♂♂ (n = 10) / ♀♀ (n = 10)]. Body length 3.08–4.00 / 3.15–4.20; head length (excl. neck) 0.44–0.49 / 0.44–0.52; head width across eyes 0.47–0.55 / 0.48–0.56; vertex width 0.24–0.29 / 0.27–0.30; length of antennal segments I – 0.13–0.17 / 0.14–0.19, II – 0.46–0.59 / 0.43–0.55, III – 0.30–0.37 / 0.29–0.36, and IV – 0.37–0.42 / 0.36–0.41; length of labial segments II – 0.12–0.15 / 0.10–0.17, III – 0.50–0.56 / 0.50–0.62, and IV – 0.28–0.33 / 0.30–0.35; anterior pronotal width 0.38–0.44 / 0.39–0.45; mesal pronotal length 0.52–0.60 / 0.52–0.62; basal pronotal width 0.89–1.10 / 0.94–1.18; length of embolial margin 0.90–1.20 / 0.90–1.25; length of cuneal margin 0.56–0.75 / 0.57–0.79; maximum width across hemelytra 0.94–1.16 / 0.97–1.27.

Bionomics. No specific plant associations are known for *Anthocoris miyamotoi*, as it is collected from various deciduous and evergreen broadleaf trees. The species is found on *Salix* spp., *Quercus* spp., *Castanopsis* spp., *Zelkova serrata*, *Mallotus japonicus* (L. f.) Müll. Arg., *Eriobotrya japonica* (Thunb.) Lindl., *Elaeagnus macrophylla* Thunb., *Rhus javanica* L. var. *chinensis* (Mill.) T. Yamaz., *Schima wallichii* (DC.) Korth. subsp. *noronhae* (Reinw. ex Blume) Bloemb., and *Albizia julibrissin* Durazz. Additionally, this species was collected from different parts of the same tree, such as flowers, leaves, stems, peduncles, and bud scales; therefore, it may walk around very actively and does not seem to stay on one particular part of a tree.

In Tokushima, eastern Shikoku, this species is frequently found on *Eriobotrya japonica* (Rosaceae), where it preys on the psyllid *Cacopsylla biwa* Inoue, 2014 (Hemiptera: Psyllidae), a serious pest of the loquat. Both nymphs and adults of *A. miyamotoi* are usually observed on the stems, peduncles, and bud scales, and are present for two months, from early April to the end of May. *Anthocoris miyamotoi* is easily found on loquat when *C. biwa* is present, but often disappears from the tree when the psyllid is not abundant. From the end of May to June, *A. miyamotoi* regularly disappears from loquat, as a consequence of the seasonal decrease in psyllid numbers. Presumably, *A. miyamotoi* moves between various broad-leaved trees for breeding or when seeking food. Individuals are observed again on loquat in February. Thus, after departing loquat in summer, individuals of the next generations apparently return in autumn or winter, and overwinter there.

In Nagasaki, south-western Kyushu (belonging to warm-temperate climatic zones), this anthocorid seems to complete two or three generations per year, and the adults have been found throughout the year. During winter (December–February), adults and late instar immature forms were observed to co-occur and hibernate under bark flakes of *Zelkova serrata*, sometimes together with *Anthocoris japonicus* (Urayama et al. 2019) (Fig. 17F). The adults appear to be active even in winter when temperature is high (Fig. 17G).

Based on the above, no specificity for associated plant or specific overwintering sites were recognized in *A. miyamotoi*. Although the prey preference of *A. miyamotoi* has been studied insufficiently, this species is certainly a polyphagous predator, and its frequency of occurrence seems to be affected by the amount of food resources.

Distribution. Japan: Honshu: Chiba (Tomokuni & Hayashi 2006, material verified), Kanagawa; Shizuoka (Tomokuni 1981, material verified), Mie, Shiga, Wakayama, Hyogo, Yamaguchi; Izu Islands: Ôshima Is., Miyake-jima Is., Hachijô-jima Is. (Tomokuni & Ishikawa 2002, material verified); Shikoku: Tokushima (Hiura 1959, material verified), Kagawa, Ehime, Kochi; Kyushu: Fukuoka (Hiura 1959, material verified), Nagasaki (Yasunaga et al. 1989, Yasunaga 1997a, material verified), Kagoshima (Hiura 1959, material verified); Tsushima Island (Yasunaga et al. 1989); Ryukyu Islands: Yakushima Is., Kuchinoshima Is., Nakanoshima Is. (Hiura 1959, material verified), Amami-Ôshima Is. (Tomokuni 1993), Okinawa-hontô Is. (Hayashi 2002), Ishigaki-jima Is. (Hayashi 2002), Iriomote-jima Is (Hayashi 2002) (Fig. 22). The specimens, including previously published ones from Ishigaki-jima and Iriomote-jima Islands, were not examined in the present study; however, the species is distributed on both islands. Based on the specimens verified, this species is currently distributed along the coastal areas of Honshu west of the Kanto district, Shikoku, Kyushu, and the Ryukyu Islands, as well as some small islands (Izu Islands and Tsushima Island) (Fig. 22).

Remarks. *Anthocoris miyamotoi* is known to occur in Japan, Chishima (Kuril) Islands (Shikotan Is., Kunashir Is., Iturup Is.), Russia (Primorsky Kray, Sakhalin), Korea (Gyeonggi-do, Gyeongsangbuk-do, Gyeongsangnam-do, Jeju-do), China (Shaanxi), and Taiwan (e.g., Kerzhner 1988, Péricart 1996, Bu & Zheng 2001, Kanyukova & Marusik 2006, Zheng & Lin 2013, Jung & Lee 2017). During this study, however, our careful examinations based on the holotype of *A. miyamotoi* revealed that the previous records of this species, at least from Japan, included some misidentifications with *A. venustus* sp. nov. The records from the Chishima Islands and Russian Far East should probably be assigned to *A. venustus* sp. nov. based on their

distribution. Judging from the figures of Bu & Zheng (2001: p. 145, fig. 220) and Jung & Lee (2017: p. 71, fig. 98), the shape of the paramere somewhat resembles that of *A. venustus* sp. nov.; therefore, *A. miyamotoi* as studied by Bu & Zheng (2001) and Jung & Lee (2017) is presumed to represent *A. venustus* sp. nov., or an undescribed species. Chinese and Korean records of *A. miyamotoi* require careful verification based on their genital structures. The Taiwanese record is probably a misidentification because the habitus photo of Zheng & Lin (2013: p. 298) is different from specimens collected in Japan in the coloration of hemelytra. This species appears to be an undescribed species closely related to *A. miyamotoi*.

Hiura (1959) noted that 'Specimens from Tokara Is. and lower land of Kyushu are light, from mountainous region of Shikoku and Hokkaido are blackish, some of from Kyushu are of intermediate colour pattern'. Examination of the type series of *A. miyamotoi* specimens from Tokara Islands and the lowland of Kyushu has proven them to be *A. miyamotoi*, while the blackish specimens of the mountainous region of Shikoku and Hokkaido are shown to be *A. venustus* sp. nov. Among Hiura's type series, specimens from Mt. Hikosan, Fukuoka Prefecture were assigned to *A. venustus* sp. nov., but the remainder of the paratypes from Kyushu were all *A. miyamotoi*. Thus, the intermediate color pattern of this species as indicated by Hiura (1959), includes *A. venustus* sp. nov. Remarkable color variation, particularly in the head and pronotum, is seen in both species (Figs 8, 16F, 17G); it is therefore difficult to identify the species accurately by coloration alone, and the genital structures are currently the only reliable character for clear determination of the species (Fig. 14).

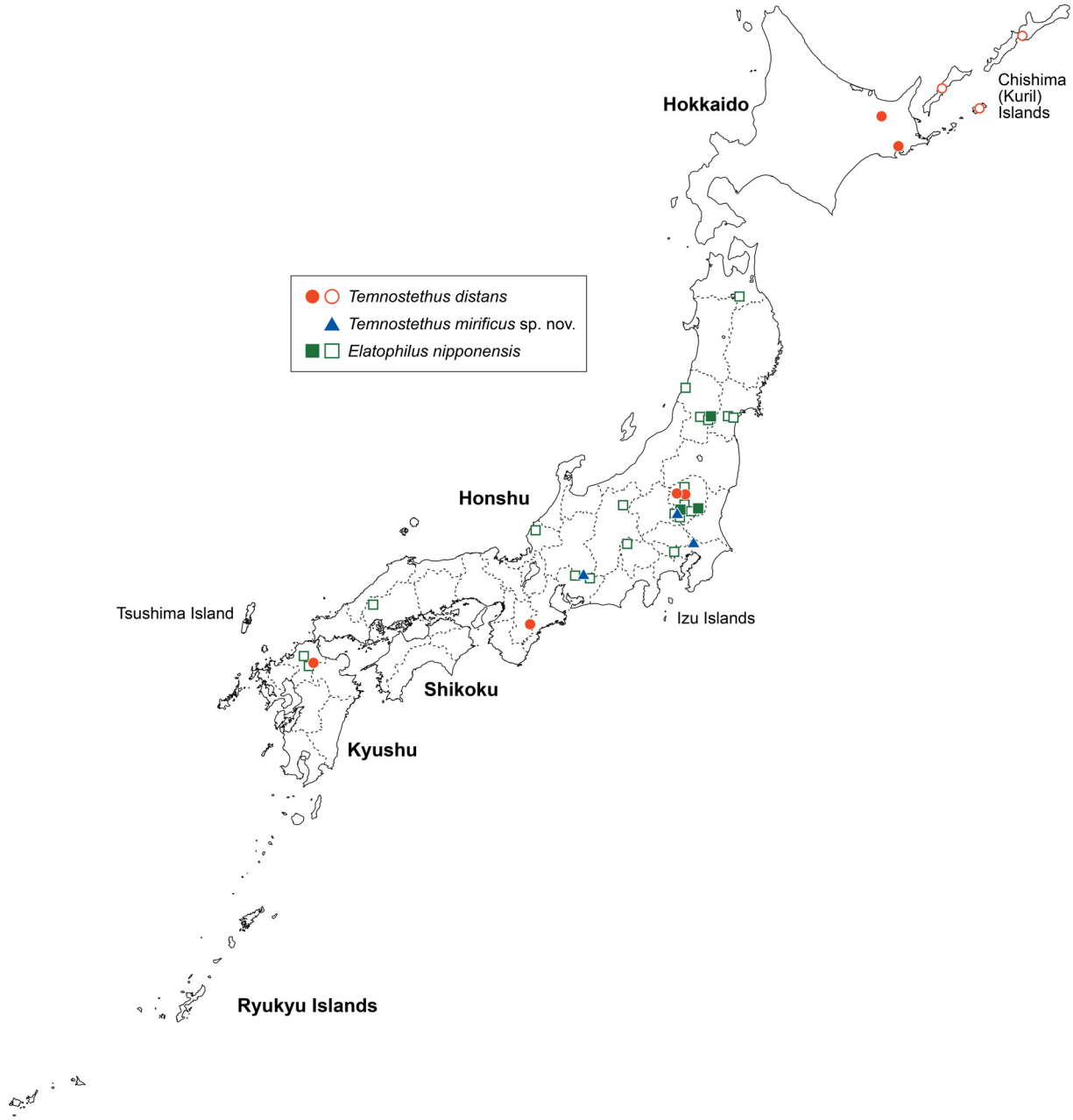

Fig. 18. Distribution of *Temnostethus distans* Kerzhner, 1973 (circles), *T. mirificus* sp. nov. (triangles), and *Elatophilus nipponensis* Hiura, 1966 (squares) in Japan. Filled symbols represent records based on specimens examined by us, open symbols represent literature records.

Anthocoris venustus sp. nov.

(Figs 8E–H, 9G, 11C–D, 12G, 14D–F, 15G, 16F, 22)

Anthocoris miyamotoi (misidentification): Hiura (1959): 3 (description, in part); Kerzhner (1988): 774 (in key); Miyamoto & Yasunaga (1989): 165 (listed, distribution); Tomokuni (1992): 158 (record); Tomokuni (1993): 168 (diagnosis, habitat, distribution); Yoshitomi (1994): 26 (record); Péricart (1996): 113 (catalogue, distribution); Iijima (1997): 15 (record); Yamamoto (1997): 15 (record); Yasunaga (1997b): 224 (record); Takeno (1998): 44 (listed, associated plant); Yamamoto (1999): 94 (record); Yamamoto (2001): 5 (record); Kanyukova & Marusik (2006): 168 (record); Vinokurov et al. (2010): 57 (catalogue, distribution); Yamamoto (2011): 4 (record); Yamada et al. (2016): 422 (catalogue, distribution); Nakatani (2019): 94 (record).

Type locality. Japan, Hokkaido, Hiyama-gun, Kaminokuni-cho, Yunotai.
Type material. Holotype: ♂ (Figs 8E–F), 'JAPAN/ Hokkaido \ Yunotai, Hiyama \ 19. viii. 1994 \ T. Yasunaga leg.' [printed], 'On *Salix* sp.' [printed]; mounted on a triangular card, in intact condition (TKPM).

Paratypes: **JAPAN: Hokkaido:** 2 ♂♂ 1 ♀, Wakkanai-shi, 15.ix.1974, Y. Furuki (EUM); 4 ♂♂ 1 ♀, Horokanai-cho, Moshiri, 3.viii.1994, on *Salix* sp., Y. Tôdo (1 ♂ 1 ♀ TKPM, 2 ♂♂ NMPC); 1 ♂ 2 ♀♀, Horokanai-cho, Moshiri-Shirakaba, 2.–7.viii.1994, on *Salix* sp., T. Yasunaga (2 ♀♀ TKPM, 1 ♂ ZMAS); 1 ♂, Monbetsu-shi, Kônomai, 3.viii.1997, S. Yamashita (TKPM); 1 ♂ 2 ♀♀, Higashikawa-cho, Mt. Asahi-dake, 200–800 m, 9.–10.viii.1994, on *Salix* sp., Y. Tôdo (1 ♂ 2 ♀♀ TKPM, 1 ♀ ZMAS); 1 ♂, Higashikawa-cho, Mt. Asahi-dake, 800 m, 9.viii.1994, R. Matsumoto (TKPM); 1 ♂ 1 ♀, Higashikawa-cho, Tennin-kyô Valley, 11.viii.1994, on *Salix* sp., Y. Tôdo (TKPM); 1 ♂ 1 ♀, Shintotsukawa-cho, 26.vii.1998, S. Gotoh (TKPM); 3 ♂♂ 4 ♀♀ (one in Fig. 15G), Shari-cho, Mt. On-nebetsu-dake, Opekepu-rindô, 31.viii.–1.ix.1995, T. Yasunaga & Y. Tôdo (1 ♂ 3 ♀♀ TKPM, 2 ♂♂ 1 ♀ AMNH); 1 ♂, Akkeshi-cho, Suminoe, 4.viii.2004, R. Matsumoto (OMNH); 1 ♂ 2 ♀♀, Kushiro-cho, Takkobu, 30.viii.1995, on *Salix* sp., Y. Tôdo (1 ♂ TKPM, 2 ♀♀ NMPC); 1 ♀, Kushiro-cho, Iwabokki-suimon, 28.viii.1995, on *Salix* sp., M. Ozaki (TKPM); 4 ♂♂ (one in Figs 9G, 11C–D, one in Figs 12G, 14D–F) 1 ♀, Makubetsu-cho, Chûrui, Kimontô, 21.viii.1995, on *Salix* sp., T. Yasunaga

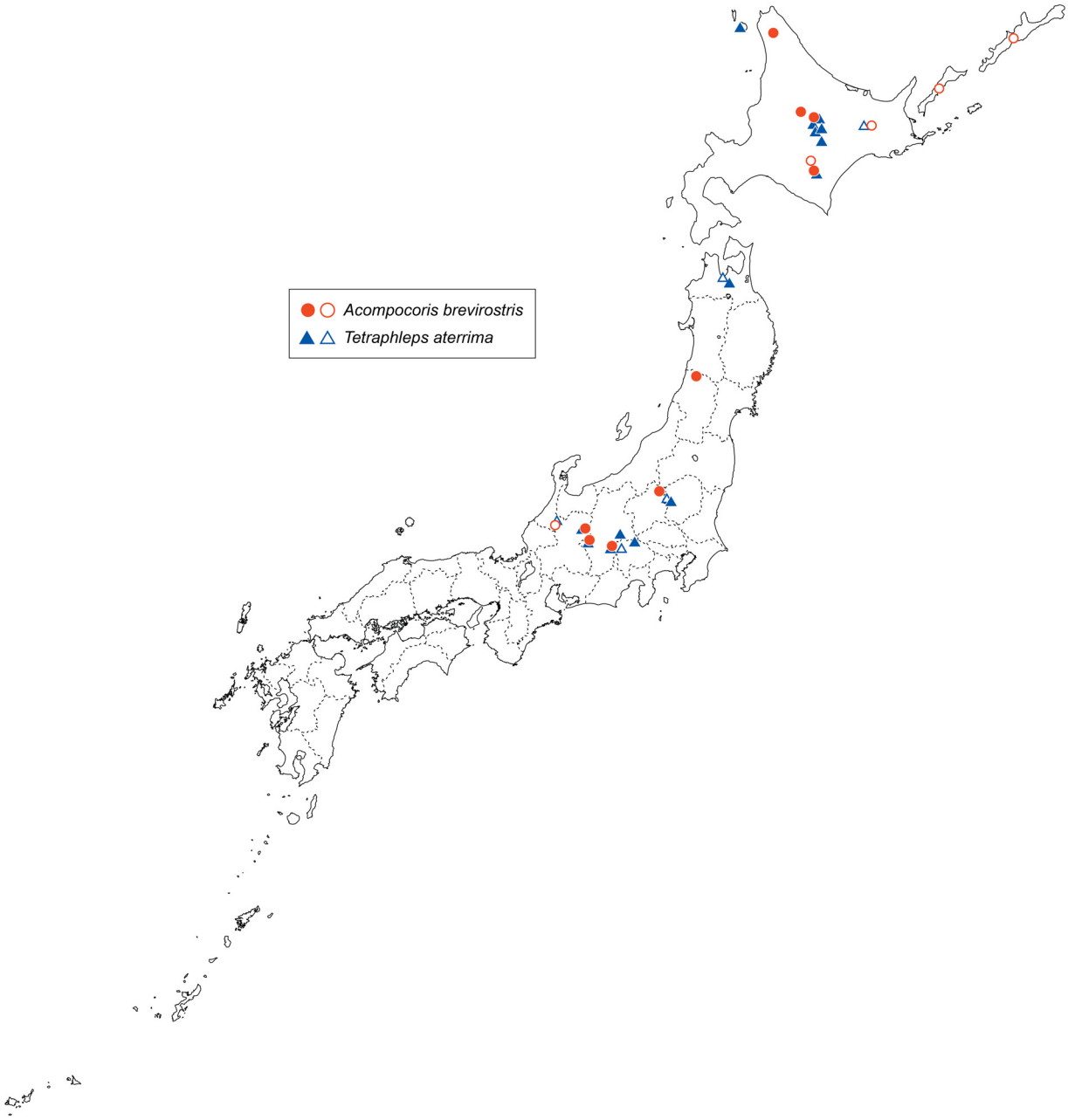

Fig. 19. Distribution of *Acompocoris brevirostris* Kerzhner, 1979 (circles) and *Tetraphleps aterrima* (J. Sahlberg, 1878) (triangles) in Japan. Filled symbols represent records based on specimens examined by us, open symbols represent literature records.

& Y. Tôdo (TKPM); 1 ♀, Nakasatsunai-mura, Pyoutan-no-Taki Fall, 16.vii.2000, light trap, K. Yamada (TKPM); 1 ♂, Urakawa-cho, Nishicha, Hidaka-horobetsu-gawa Riv., 18.viii.1995, on *Salix* sp., Y. Tôdo (TKPM); 1 ♀, Tobetsu-cho, Aoyama, 14.vii.1997, A. Makino (TKPM); 1 ♂, same locality, on *Fraxinus mandshurica*, 26.vii.1997, T. Yasunaga (TYCN); 1 ♀, Atsuta Village, Hatsutari, on *Juglans mandshurica*, 7.viii.1998, T. Yasunaga (TYCN); 1 ♀, Tobetsu-cho, Ishikari-gawa Riv., 17.vii.1997, A. Makino (TKPM); 1 ♀, Sapporo-shi, Mt. Moiwa, 3.viii.1970, S. Kinoshita (EUM); 1 ♂, Sapporo-shi, Otarunai-gawa-oku-rindô, 43.082N, 141.106E, 28.vii.2019, A. Yamamoto (TKPM); 1 ♀, Otaru-shi, Nagahashi-Naebo, 43.213N, 140.977E, 18.v.2018, A. Yamamoto (TKPM); 2 ♀♀, Otaru-shi, Asari-tôge, 23.vii.1995, on *Salix* sp., Y. Tôdo (TKPM); 1 ♂, same locality, 18.viii.1996, on Alder, collector unknown (TKPM); 1 ♀, Niseko, Mt. Chise-nupuri, 500–600 m, 9.vii.1994, on *Quercus crispula*, T. Yasunaga (TKPM); 1 ♀, Chitose-shi, Lake side of Shikotsu-ko, 5.–6.viii.1984, Y. Honda (EUM); 1 ♀, Toyo-ura-cho, Iburi, 21.viii.1997, T. Yasunaga (TYCN). Rebun-tô Is.: 2 ♂♂, Hamanaka, 22.ix.1991, M. Tomokuni (NSMT); 1 ♂, Kabukai, Rebun-rindô, 23.ix.1991, M. Tomokuni (NSMT). Rishiri-tô Is.: 2 ♂♂ 1 ♀, Oshidomari, 17.ix.1991, M. Tomokuni (NSMT); 1 ♀, Oniwaki, 28.–29.vii.1994, on *Salix* sp., Y. Tôdo (TKPM); 1 ♂, no detailed locality, 16.–17.ix.1974, Y. Furuki (EUM). **Honshu:** Aomori Pref.: 1 ♀, Mutsu-shi, Sekine, 31.v.1982, B. Tanaka (TKPM). Iwate Pref.: 1 ♀, Yahaba-cho, Mt. Nansyou-zan, 1.vii.2004, T. Ishizaki (TKPM). Tochigi Pref.: 1 ♂, Nasushiobara-shi, Nakagawa-kahan-kôen, 4.viii.2016, S. Maehara (TKPM); 1 ♂, Nikko-shi, Kawamata, 27.ix.2019, S. Maehara (TKPM); 1 ♀, Nikko-shi, Yumoto, 21.v.2007, S. Maehara (TKPM); 1 ♂ (Fig. 8G), Nikko-shi, Ryû-oh-kyô, 19.vii.2010, S. Maehara (TKPM); 1 ♂ 1 ♀, Nikko-shi, Shôbugahama, 5.viii.2010, S. Maehara (TKPM); 1 ♀, Nikko-shi, Chûgûshi, Asegata, 18.ix.2020, S. Maehara (TKPM); 1 ♀, Shimotsuke-shi, Hosoya, 4.xi.2000, S. Maehara (TKPM); 1 ♀, Mooka-shi, Isagahara, 6.vi.2018, S. Maehara (TKPM); 1 ♀, Tochigi-shi, Hoshino-machi, 6.iii.1991, H. Yoshitomi (EUM); 1 ♀, Tochigi-shi, Oominagawa,

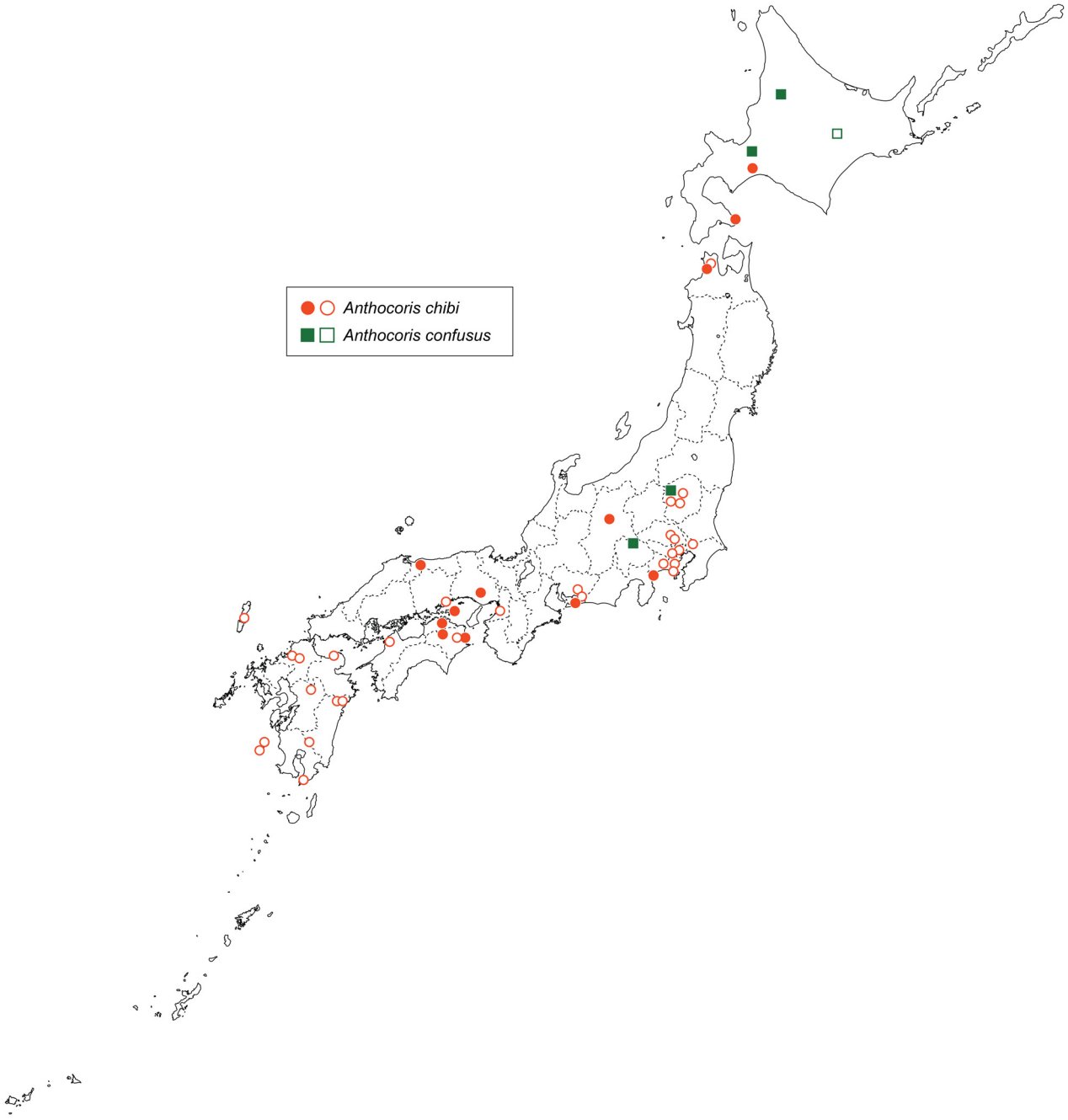

Fig. 20. Distribution of *Anthocoris chibi* Hiura, 1959 (circles) and *A. confusus* Reuter, 1884 (squares) in Japan. Filled symbols represent records based on specimens examined by us, open symbols represent literature records.

6.i.1994, H. Yoshitomi (EUM). Nagano Pref.: 1 ♀, Kijimadaira-mura, Kayanodaira, 1.v.2000, Y. Kita (TKPM). Gifu Pref.: 1 ♀, Takayama-shi, Hirayu, 28.vii.1959, M. Miyatake (EUM). Aichi Pref.: 1 ♀, Toyone-mura, Mt. Chausu-yama, 15.–16.vii.1974, Y. Hori (TKPM). Nara Pref.: 1 ♂ (Fig. 8H), 2 ♀♀, Kamikitayama-mura, Ôdaigahara, 16.viii.2004, K. Yamada (TKPM); 1 ♂ 2 ♀♀, same locality, 14.–15.xi.2004, K. Yamada (TKPM); 1 ♀, Nosegawa-mura, Mt. Obako-dake, 25.v.2000, K. Yamada (TKPM). **Shikoku:** Tokushima Pref.: 2 ♂♂ 1 ♀, Naka-cho, Kisawa, 16.viii.1998, M. Takai (TKPM); 1 ♀, Naka-cho, Kawanari-tôge, 6.vii.2011, K. Yamada (TKPM); 1 ♂, Naka-cho, Iwakura, 23.viii.2010, K. Yamada (TKPM); 1 unsexed, Naka-cho, Ichinomori to Nishijima, 16.vii.1984, M. Miyatake (EUM); 1 ♂, Mt. Tsurugi, 14.viii.1959, I. Hiura (OMNH). Ehime Pref.: 1 ♀, Kumakôgen-cho, Omogo-kei, 26.iv.1958, Y. Takaishi (EUM); 1 ♀, Kumakôgen-cho, Ishizuchi-san, 13.vii.2021, H. Yoshitomi (EUM). Kochi Pref.: 1 ♂, Ôtoyo-cho, Mt. Kajigamori, 20.viii.1959, K. Morimoto (ELKU). **Kyushu:** Fukuoka Pref.: 2 ♂♂ 2 ♀♀, Soeda-machi, Mt. Hikosan, 8.–11.ix.1997, T. Ishikawa (TKPM); 1 ♀, same locality and date, T. Shimada (TKPM). Oita Pref.: 1 ♀, Yufu-shi, Syônai-cho, Oike, 27.vii.1995, Y. Nakatani (TKPM); 1 ♀, Mt. Kujyû, 9.iv.1959, Y. Miyatake (OMNH). Miyazaki Pref.: 1 ♀, Gokase-cho, Mt. Shiraiwayama, 22.–24.vii.2016, T. Yoshida (TKPM).

Differential diagnosis. Recognized by the following combination of characters: head and pronotum uniformly black to blackish brown (Figs 8E–H); clavus with basal and apical portions blackish brown, inner margin narrowly darkened; endocorium with basal and apical portions mostly blackish brown; embolium with basal and apical portions blackish brown; median portion of clavus and outer part of median portion of endocorium and remaining area of

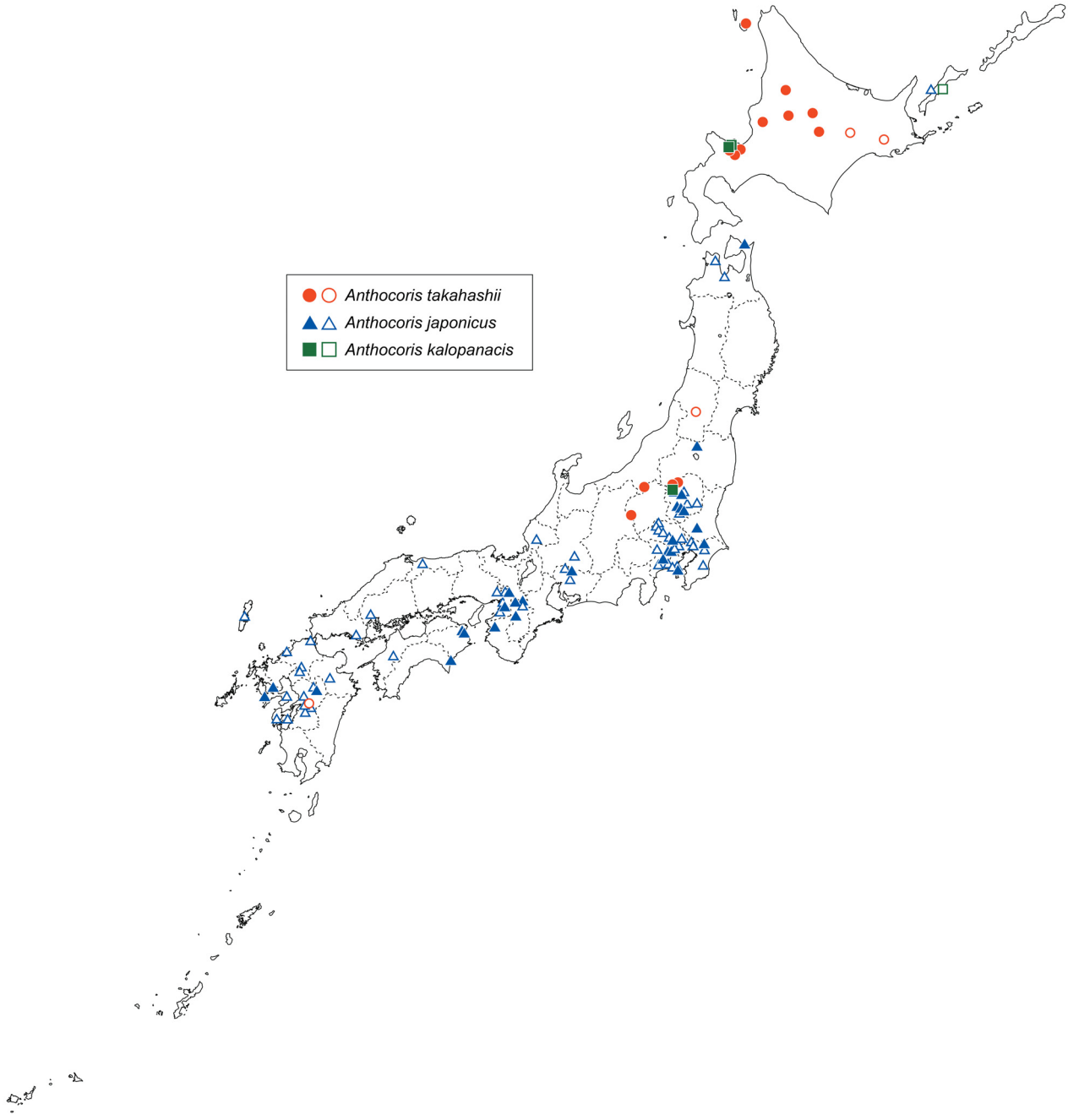

Fig. 21. Distribution of *Anthocoris takahashii* Hiura, 1959 (circles), *A. japonicus* Poppius, 1909 (triangles), and *A. kalopanacis* Kerzhner, 1977 (squares) in Japan. Filled symbols represent records based on specimens examined by us, open symbols represent literature records.

embolium whitish and subhyaline; area in front of cuneal fracture whitish or subhyaline; outer (posterior) margin of ostiolar peritreme not close to supracoxal area (Fig. 9G); paramere (Figs 11C–D, 14E–F) slender and very slightly curved, with longitudinal groove in form of shallow depression; copulatory tube (Fig. 15G) approximately 0.8 mm in length, basally thickened, with a few twists. Closely related to *A. miyamotoi* but distinguished from that species by the uniformly blackish head and pronotum, slender and very slightly curved paramere, and copulatory tube longer and basally thickened with a few twists.

Description. ***Coloration.*** Body (Figs 8E–H, 16F) generally black to blackish brown. Head and pronotum (Figs 8E, G–H) blackish brown, sometimes vertex and callus tinged with reddish brown; eyes reddish black; margin of ocellus red to reddish brown. Antennal segment I dark brown; segment II yellowish brown, dark brown on base and apical 1/4 to 1/3; segment III yellowish brown, dark brown on apical half; segment IV dark brown. Labium (Fig. 8F) uniformly black to blackish brown. Scutellum overall black to blackish brown. Clavus with basal portion and apex blackish brown, inner margin narrowly darkened (Figs 8E,G–H);

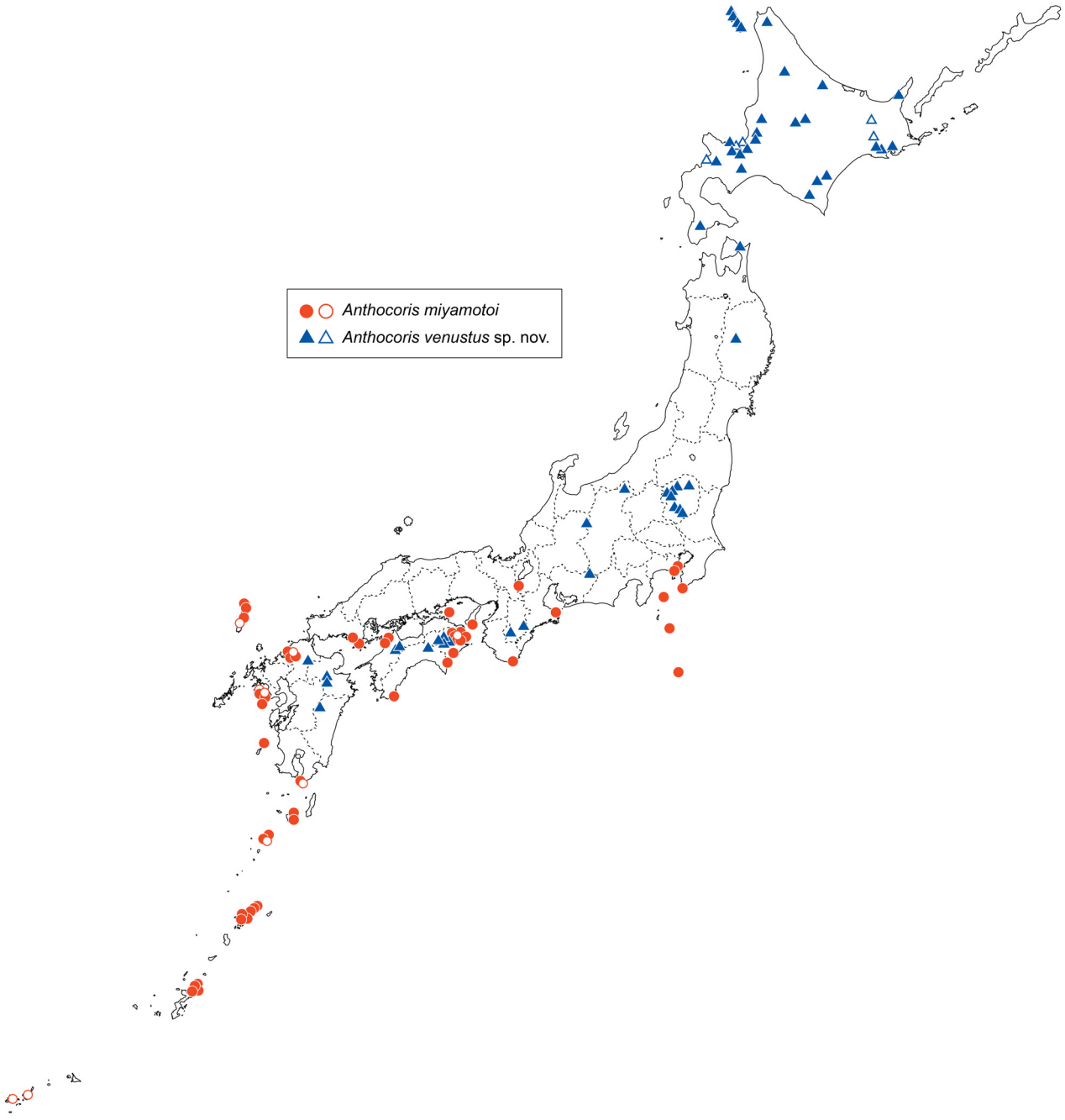

Fig. 22. Distribution of *Anthocoris miyamotoi* Hiura, 1959 (circles) and *A. venustus* sp. nov. (triangles) in Japan. Filled symbols represent records based on specimens examined by us, open symbols represent literature records.

endocorium with basal and apical portions mostly blackish brown (Figs 8E,G–H); embolium with basal and apical portions blackish brown (Figs 8E,G–H); cuneus wholly blackish brown; median portion of clavus and outer part of median portion of endocorium and remaining area of embolium whitish and subhyaline (Figs 8E,G–H); area in front of cuneal fracture whitish or subhyaline; membrane smoky dark brown, with basal and innermost portions and area behind apex of cuneus off-white (Figs 8E,G–H). Legs dark reddish brown; trochanters tinged with yellowish brown; apical half or apical 2/3 of protibiae sometimes tinged with yellowish brown. Venter of thorax uniformly blackish brown. Abdomen black to blackish brown. Pygophore blackish brown with pale yellow paramere.

Structure. Body (Figs 8E–H) elongate, shiny on dorsal and ventral surfaces, sparsely covered with suberect, simple, yellowish setae. Head (Figs 8E–H) cylindrical, impunctate, approximately as long as width across eyes; three pairs of long, erect trichobothria on the dorsal surface of head, one on anterior clypeus, one in front of eye, and one behind ocellus; anteocular region as long as length of eye in dorsal view in male, slightly longer than length of eye in female; vertex approximately twice as wide as eye in dorsal view in male, approximately 2.5 times as wide as eye in female; postocular region constricted, demarcated by transverse shallow furrow; neck long, smooth, highly polished; eye oblong, not exceeding level of dorsal surface of head in lateral view but exceeding level of ventral surface of head. Antennae (Figs 8E–H) densely covered with short, decumbent, yellowish setae interspersed with long, erect setae, of which the longest are as long as or slightly shorter than width of corresponding segment; segment I just reaching apex of head, sparsely covered with short setae; segment II gradually thickened toward apex, slightly thicker in the male than in the female, approximately as long as head width across eyes; segment III approximately 0.7 times as long as segment II; segment IV longer than segment III. Labium (Fig. 8F) just reaching procoxae; segment III approximately 4.0–5.0 times as long as segment II; segment IV approximately half as long as segment III.

Pronotum (Figs 8E,G–H) with pairs of long, erect trichobothria on midline of collar and on each anterior and posterior angle; anterior margin very slightly curved, approximately 0.7 times as long as mesal length; lateral margin very slightly curved; lateral carina slightly expanded anteriorly, more obscure posteriad; posterior margin concave inwardly, approximately 2.5 times as wide as anterior margin; collar long, transversely rugose, with scattered long setae; callus extremely swollen, polished, impunctate, sides strongly bulging, demarcated posteriorly by deep transverse impression; deep impression with short parallel carinae and coarse punctures; posterior lobe behind callus densely covered with minute punctures. Scutellum (Figs 8E,G–H) smooth, sub-equilateral, wider at base than long, depressed through middle. Hemelytra (Figs 8E–H) sparsely covered with long, erect, simple, yellowish setae, and with minute punctures; costal margin slightly sinuate; endocorium approximately 1.6 times as wide as maximum width of embolium; cuneal margin approximately 0.7 times as long as embolial margin; membrane with three veins, outermost vein distinct and slightly curved, inner two veins obscure and very slightly curved. Ostiolar peritreme (Fig. 9G) wide, gently curved anteriorly, gradually narrowing toward apex and then continued by a fine carina that reaches the anterior margin of metapleura; outer (posterior) margin of ostiolar peritreme not close to supracoxal area; evaporatorium bearing a small number of long, recumbent setae. Fossula spongiosa present on apex of all tibiae, enlarged on protibiae and small on meso- and metatibiae; apical 1/4 of metatibiae bearing small spines on ventral side. Abdominal sternum III (Fig. 12G) with a pair of banana-shaped membranous areas on anterior half, membranous area somewhat widened near base; dorsal laterotergites not fused with mediotergites on abdominal segments II and III.

Male genitalia (Figs 11C–D, 14D–F): Pygophore (Fig. 14D) rather pointed apically, asymmetrical, covered with 6–8 long, stout setae intermixed with short, suberect setae along outer margin and on posteroventral surface, of which the longest are approximately half length of pygophore; mid-dorsal surface hirsute with suberect setae; paramere (Figs 11D, 14E–F) slender, very slightly curved but bent at basal 1/3, with a few very short, erect setae on sub-basal portion, the apex hooked and reaching nearly half of the left outer margin of pygophore; longitudinal groove in form of shallow depression, twisted basally.

Female genitalia (Fig. 15G): Copulatory tube fused on middle of intersegmental membrane between sterna VII and VIII, approximately 0.8 mm in length, basally thickened, gradually narrowing toward apex, with a few loops; trunk of conductive tissue not pronounced (or possibly dissolved).

Measurements [mm; ♂♂ (n = 10) / ♀♀ (n = 10), holotype in parentheses]. Body length 3.50–4.18 (3.75) / 3.50–4.08; head length (excl. neck) 0.47–0.50 (0.47) / 0.48–0.55; head width across eyes 0.47–0.54 (0.54) / 0.48–0.53; vertex width 0.24–0.27 (0.26) / 0.28–0.30; length of antennal segments I – 0.15–0.18 (0.17) / 0.16–0.19, II – 0.48–0.56 (0.55) / 0.47–0.53, III – 0.32–0.39 (0.36) / 0.32–0.38, and IV – 0.39–0.42 (0.41) / 0.37–0.41; length of labial segments II – 0.12–0.16 (0.12) / 0.13–0.17, III – 0.54–0.62 (0.60) / 0.58–0.65, and IV – 0.30–0.35 (0.33) / 0.32–0.38; anterior pronotal width 0.36–0.41 (0.40) / 0.39–0.45; mesal pronotal length 0.51–0.57 (0.55) / 0.55–0.62; basal pronotal width 0.92–1.13 (1.04) / 0.99–1.17; length of embolial margin 0.91–1.15 (1.03) / 0.97–1.13; length of cuneal margin 0.65–0.80 (0.70) / 0.64–0.78; maximum width across hemelytra 0.96–1.18 (1.07) / 1.05–1.26.

Etymology. From Latin, *venustus* (= beautiful, graceful), referring to the beautiful and graceful body color of the new species; an adjective.

Bionomics. *Anthocoris venustus* sp. nov. has been frequently collected from *Salix* spp. in Hokkaido and Tochigi. It was also collected from *Quercus crispula* Blume, *Kalopanax* sp., and *Alnus japonica*, and sometimes from the herbaceous plant *Fallopia sachalinensis* (F. Schmidt) Ronse Decr. in Hokkaido. This species was collected from *Mallotus japonicus* in Tokushima and from *Quercus serrata* Murray at Mt. Hikosan, Fukuoka (Takeno 1998).

Distribution. Japan: Hokkaido, Rebun-tô Is., Rishiri-tô Is.; Honshu: Aomori, Iwate, Tochigi, Nagano, Gifu, Aichi, Nara; Shikoku: Tokushima, Ehime, Kochi; Kyushu: Fukuoka, Oita, Miyazaki (Fig. 22). Compared to the distribution pattern of *A. miyamotoi*, the new species is widely distributed throughout Hokkaido and is restricted to the mountainous areas of Honshu, Shikoku, and Kyushu (Fig. 22). This species shows an apparently allopatric distribution with *A. miyamotoi*. The allopatric distribution in both species might be influenced by differences in life history traits such as diapause and cold tolerance.

Discussion

The present study discovered that five genera and 13 species comprise the fauna of Japanese Anthocorini. These species could be grouped into two main biogeographical elements: East Asian elements and widespread Palaearctic elements. Most members (10 species) include East Asian elements that occur in Japan, the Russian Far East, the Korean Peninsula, China, and Mongolia. Of these, *Temnostethus distans*, *Acompocoris brevirostris*, *Anthocoris kalopanacis*, *A. takahashii*, and *A. venustus* sp. nov. inhabit mainly cold-temperate and subalpine climatic zones in northern Japan (Figs 18–19, 21–22) and the marginal areas of the Russian Far East. *Anthocoris venustus* sp. nov. is currently confirmed only from Japan, but the records of *A. miyamotoi* from the Russian Primorsky Kray and Sakhalin and the Chishima Islands are likely to be *A. venustus* sp. nov. *Elatophilus nipponensis*, *Anthocoris chibi*, and *A. japonicus* are distributed in the warm-temperate zone of mainland Japan (Figs 18, 20–21), with the exception of a few boreal or disjunct records in adjacent eastern Asia. These three species are native to the Sino-Japanese region. *Anthocoris miyamotoi* is the sole species that spreads southward in Japan (Fig. 22). This species is associated with warm-temperate deciduous forests in south-western Japan, and subtropical semi-evergreen and deciduous forests in the Ryukyu Islands. *Temnostethus mirificus* sp. nov. is endemic to Japan and inhabits deciduous forests in the warm-temperate zone of central Honshu, but its distribution is quite fragmented and limited (Fig. 18). Although a similar species, *T. gracilis*, is widely distributed in the Palaearctic Region, no presumed sister species are known from the neighboring areas in eastern Asia and the external features of *T. mirificus* sp. nov. are remarkably distinctive among congeneric species; therefore, the new species appears to represent a relict endemic.

The species widespread over the Palaearctic Region, *Anthocoris confusus* and *Tetraphleps aterrima*, also occur in the northern part of Japan (Figs 19–20). Judging from known records, *A. confusus* seems to be native to Europe or the western Palaearctic, and to have later dispersed to the eastern Palaearctic. The current distribution of *Tetraphleps aterrima* implies a Siberian origin, with a subsequent spread throughout the Palaearctic Region. In Japan and eastern Asia, both species are restricted to cold-temperate and subalpine zones, similar to those of *Acompocoris brevirostris*, *Anthocoris kalopanacis*, and *A. takahashii*.

Acompocoris brevirostris and *T. aterrima* also inhabit mountainous regions such as the Japan Alps and Mt. Hakusan (Ishikawa Prefecture), at an altitude of 2300–2600 m, in central Honshu, far from their primary distribution area (Fig. 19). The distribution pattern of such glacial relicts depends primarily on high altitude (or cold climatic condition) and the availability of subalpine vegetation such as *Pinus pumila*, which is strongly associated with both species. These distribution patterns suggest that both species represent glacial relicts in this area, as a result of ancient southward migrations from boreal regions during glacial periods, and later surviving in higher altitude areas during interglacial periods of the Pleistocene.

The modern distribution pattern between related species suggests that their habitats appear to be clearly demarcated. *Anthocoris japonicus*, *A. takahashii*, and the related species *A. ussuriensis* Lindberg, 1927 are undoubtedly a sister group based on the great similarity of genital structures (e.g., Bu & Zheng 2001). As mentioned above, *A. japonicus* and *A. takahashii* are warm-temperate and cold-temperate inhabitants throughout Japan and in the marginal areas of eastern Asia (Far East Russia, the Korean Peninsula, and China), respectively. In contrast, *A. ussuriensis* is distributed in continental East Asia (Far East Russia, Mongolia, northern and central China, and North Korea) (Péricart 1996, Jung & Lee 2017).

The *Anthocoris miyamotoi* group (*sensu* Bu & Zheng 2001) also exhibits a distinct allopatric distribution pattern (Fig. 22). Species in this group include *A. miyamotoi*, *A. venustus* sp. nov., and *A. dividens* Bu & Zheng, 2001. *Anthocoris miyamotoi* and *A. venustus* sp. nov. show clear habitat boundaries; the former inhabits the warm-temperate and subtropical zones of coastal areas in southwestern Japan, and the latter the cold temperate zones, mainly in northern Japan (as mentioned above, Fig. 22). In contrast, *A. dividens* is distributed in the high-altitude areas of Sichuan and Yunnan Provinces, southwestern China (Bu & Zheng 2001), quite far from the distribution of Japanese species. It is remarkable that species related to *A. miyamotoi* are widely distributed in the Oriental Region: *A. muraleedharani* Yamada, 2010 is known from southern India (Yamada et al. 2010, Ballal et al. 2018), and a few undescribed species in Nepal and the Indochina Peninsula. The members of the *A. miyamotoi* group represent the Eastern Himalayan-Japanese and Oriental widespread elements and seem to diversify from a center of origin in the Hengduan Mountains, eastern Himalayas, as in the *A. nemorum* group (Li et al. 2012).

Based on these observations, the Japanese Anthocorini fauna is posited to have been established by colonization from mainland Asia through landbridges that formed during glacial periods. Although there appears to be low endemicity of the anthocorid fauna in Japan, at least *A. japonicus*, *A. chibi*, *A. takahashii*, and *E. nipponensis* possibly originate in Japan, and later dispersed to neighboring areas such as mainland China and the Korean Peninsula.

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