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RESEARCH PAPER

The monocotyledon-feeding lace bugs of the genus *Agramma* from Japan (Hemiptera: Heteroptera: Tingidae)

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Abstract. In this paper, I revise the taxonomy of the lace bug genus Agramma Stephens, 1829 (Hemiptera: Heteroptera: Tingidae: Tinginae) from Japan. Two species are recognized and re-described: A. japonicum (Drake, 1948) described previously from Japan, and A. abruptifrons Golub, 1990, newly recorded from Japan. The previous records of A. nexile (Drake, 1948) from Japan are confirmed as misidentifications of A. japonicum. The host plant relationship is discussed for A. abruptifrons and A. japonicum. Photographs of living individuals for A. abruptifrons and A. japonicum are presented. A key is provided to facilitate the identification of the two species of Agramma distributed in Japan.

Key words. Hemiptera, Heteroptera, Tingidae, Tinginae, taxonomy, key to species, biology, host plant, distribution, Japan, eastern Asia, Palaearctic Region

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Introduction

In Japan, a number of monocotyledons are confirmed as host plants for various phytophagous insects (e.g. Kawai 1980; Moritsu 1983; Japanese Society of Applied Entomology and Zoology 2006). Among the Japanese members of the family Tingidae (Hemiptera: Heteroptera) or lace bugs, which are phytophagous and comprise 82 species in 29 genera (Kerzhner 1978; Miyamoto & Yasunaga 1989; Péricart & Golub 1996; Yamada & Tomokuni 2012; Aukema et al. 2013; Yamada & Ishikawa 2016; Souma 2019a, b, 2020a, b; Souma & Ishikawa 2020), only *Agramma nexile* (Drake, 1948) has so far been confirmed to feed on monocotyledons (Takeya 1962, Yamada & Tomokuni 2012).

The genus *Agramma* Stephens, 1829 comprises a number of species feeding on the monocotyledons known from the Old World (cf. Drake & Ruhoff 1965a; Putshkov 1974; Péricart 1983; Göllner-Scheiding 2004; Rintala & Rinne 2011). Although over 1,000 monocotyledonous species are known in Japan (Yano 2018, Shutoh et al. 2019), only two species of *Agramma*, *A. japonicum* (Drake, 1948) and *A. nexile*, have been recorded from the country to date (Yanda & Ishikawa 2016). On other

hand, a total of eight species, A. abruptifrons Golub, 1990, A. femorale Thomson, 1871, A. minutum Horváth, 1874, A. mongolicum Golub, 1990, A. neimongolicum Qi, 1996, A. nigrum Fieber, 1844, A. ruficorne (Germar, 1835), and A. tropidopterum Flor, 1860, are known from the adjacent regions of Japan proper, i.e. eastern part of Russia, Korean Peninsula, and northern and northeastern parts of China, but have not yet been recorded from Japan (PÉRICART & GOLUB 1996; VINOKUROV et al. 2010; AUKEMA et al. 2013; CHO et al. 2020). Thus, more extensive field research may provide discoveries of additional unknown species of Agramma in Japan.

Recently, an indeterminate species of *Agramma* was collected from the monocotyledonous herb *Juncus* sp. (Juncaceae) in the wetland of Honshu, Japan by me and my colleague, Mr. Yoichi Yazaki. The photographs of the holotype (Henry 2020a) indicated distinct differences from the Japanese population of *A. nexile*, making the distribution records of the species in Japan dubious. Moreover, *A. japonicum* and *A. nexile* from Japan are difficult to distinguish according to their general appearance (Yamada & Tomokuni 2012), and the Japanese species of *Agramma* should therefore be taxonomically revised.



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After careful morphological examination, I concluded that the above-mentioned indeterminate species was *A. abruptifrons*, which has not been previously recorded from Japan. Furthermore, the previous records of *A. nexile* in Japan are likely misidentifications of *A. japonicum*. Herein, I record *A. abruptifrons* from Japan for the first time and correct the previous records of *A. nexile* in the country to *A. japonicum*. I also diagnose *Agramma*, and redescribe *A. abruptifrons* and *A. japonicum*. Consequently, two species of *Agramma* are now recognized from Japan. In addition, I discuss the host plant relationship of these two species. Furthermore, I present photographs of living individuals for *A. abruptifrons* and *A. japonicum*, and a key to the Japanese species of the genus.

Material and methods

The specimens were naturally dried at room temperature. For examination of the genitalia, the male terminalia were removed from the body after the specimens had been softened using hot water. The removed parts were immersed in hot 15% KOH solution for 5 minutes and then soaked in 70% ethanol for further dissection.

Morphological characteristics were observed under a stereoscopic microscope (SZ60, Olympus, Tokyo, Japan) and drawn using an ocular grid. The genitalia were then preserved in small glass tubes filled with glycerin and mounted on a pin with the respective specimens. Ratios of lengths for antennal segments were measured using an ocular micrometer. Photographs of the specimens were taken using a digital microscope (VHX-1100, Keyence, Osaka, Japan). The distribution range of the species was mapped using SimpleMappr (Shorthouse 2010), and geographical coordinates were obtained from Google Maps (https://www.google.co.jp/maps) if they were not provided on the specimen labels.

Abbreviations for the relevant institutions are as follows:

ELKU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan;

NMPC National Museum, Prague, Czech Republic;

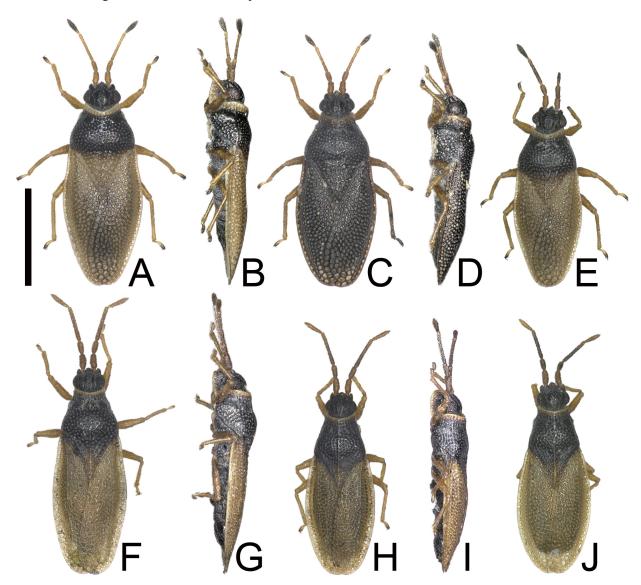


Fig 1A–J. Two species of Agramma from Japan, dorsal and lateral views: A–E – A. abruptifrons Golub, 1990: A, B – macropterous female, C, D – submacropterous female, E – macropterous male with segmental oligomery of right antenna. F–J – A. japonicum (Drake, 1948): F, G – macropterous male, H, I – submacropterous male, J – submacropterous female. Scale bar = 1.0 mm.

TUA Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Kanagawa, Japan;

USNM United States National Museum of Natural History, Washington, D.C., U.S.A.;

ZIAS Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

The scientific names of the host plants were assigned in accordance with YONEKURA & KAJITA (2003–2020).

Taxonomy

Agramma Stephens, 1829

Agramma Stephens, 1829: 64. Type species by monotypy: *Tingis laeta* Fallén, 1807.

Agramma: PÉRICART & GOLUB (1996): 11–12 (catalogue, synonymy); AUKEMA et al. (2013): 59–60 (catalogue, synonymy).

Diagnosis. Recognized among other tingid genera by a combination of the following characters: body oblong; head shorter than its maximum width across compound eyes, with a pair of anterior spines reaching level far remote from tip of clypeus; vertex coarsely punctate; antenniferous tubercles obtuse, slightly curved inward; antenna covered with pubescence throughout its length and tiny tubercles in segments I to II; segment I longer than segment II, separated from each other at their bases; segment II shortest among antennal segments, extending beyond tip of clypeus; segment III longest among antennal segments; segment IV longer than segment I; bucculae contiguous at anterior ends; pronotum unicarinate or without carina; anterior margin of pronotum curved inward; lateral margin of pronotum gently curved outward throughout its length; pronotal disc coarsely punctate; hood absent; collar coarsely punctate; calli smooth; median carina ridge-shaped; posterior process well-developed, flattened, triangular; anterior margin of hemelytron gently curved outward throughout its length, without spines; clavus reduced; costal area present; subcostal area subhorizontal; discoidal area flat; delimiting veins present; sutural area well-developed; hypocostal lamina with a single row of areolae throughout its length; ostiolar peritreme well-developed; metasternum as wide as mesosternum at widest part of each; sternal laminae nearly straight throughout its length; legs smooth, covered with pubescence; abdominal sternites without transverse furrow; apical part of abdomen in both sexes covered with pubescence; pygophore smooth, not elevated at center of venter; outer and inner margins of paramere covered with pubescence in middle part; suspensory arm of paramere completely visible in dorsal view; ovipositor with well-developed ovivalvula at base; paratergite IX unilobed.

Remarks. In the genus *Agramma*, three subgenera are currently recognized: *Aexiloma* Drake & Ruhoff, 1965 from Papua New Guinea and Madagascar, *Lisia* Koçak & Kemal, 2010 from Iran, and the nominotypical *Agramma* Stephens, 1829 from the Old World (Drake & Ruhoff 1965a, b; Lis 2003; Koçak & Kemal 2010). A total of 88 extant species and a single fossil species are known from the Old World (Drake & Ruhoff 1965a, b; Wagner 1973; Zhang 1989; Péricart 1991, 1992; Livingstone & Jeyanthibai 1994; Péricart & Golub 1996; Lis 2003;

GÖLLNER-SCHEIDING 2004; GUILBERT 2007, 2015; AUKEMA et al. 2013; GUILBERT & GUIDOTI 2018), of which two species, *A. japonicum* and *A. nexile*, have been recorded from Japan to date (YAMADA & ISHIKAWA 2016). *Agramma* species were diagnosed by previous authors based on the differences of various morphological characters, such as presence or absence of the paranota, arrangement of areolae on the hemelytron, shape of the paramere, and structure of the female terminalia (e.g. DRAKE & RUHOFF 1965b; PÉRICART 1983; GOLUB 1990; LIS 2003). These characteristics are also useful in the identification of the Japanese species. Conclusively, I recognize two species belonging to the nominotypical subgenus in Japan, namely *A. abruptifrons* and *A. japonicum*.

Agramma strongly resembles Ceratinoderma Stål, 1873 in general appearance, but the former is distinguished from the latter by the presence of the costal area of hemelytron (in contrast, in Ceratinoderma the costal area of hemelytron is absent).

Agramma abruptifrons Golub, 1990

(Figs 1A-E, 2A, C, F, G, 3A-C, 4A, B)

Agramma nexile (non Drake, 1948): Kerzhner (1972): 291 (distribution); Golub (1977): 252 (distribution). Misidentifications (Golub 1990: 48).

Agramma gibbum (non Fieber, 1844): JING (1981): 280 (distribution). Misidentification (GOLUB 1990: 51).

Agramma abruptifrons Golub, 1990: 41. Holotype: & (macropterous), Mongolia: E Aimak, Khalkh-Gol River, 33 km SE of Khalkh-Gol (ZIAS). Agramma abruptifrons: Péricart & Golub (1996): 12 (check-list, Palaearctic); VINOKUROV et al. (2010): 151 (check-list: eastern Russia).

Diagnosis. Recognized among other species of Agramma by a combination of the following characters: frons convex, descending to base of clypeus; a pair of frontal spines obliquely protruding downward, touching clypeus at apices, separated from each other at apices; distance between apices of frontal spines as long as their length; pubescence on body less than 0.5 times as long as diameter of compound eye; rostrum reaching middle part of mesosternum; median carina of pronotum indistinct throughout its length; costal area with a single row of areolae throughout its length, narrower than tibia; areolae of costal area less than 2 times as long as its maximum width at middle of hemelytron; subcostal-discoidal boundary vein present in basal part and absent in remaining parts; subcostal area with 4 rows of areolae at widest part; discoidal-sutural boundary vein absent; discoidal-sutural area with 8 rows of areolae at widest part; outer and inner margins of paramere gently curved in middle part (Figs 3B, C); female terminalia pentagonal in ventral view (Figs 2F, G); and posterior margin of female terminalia not protruding posteriad in middle part.

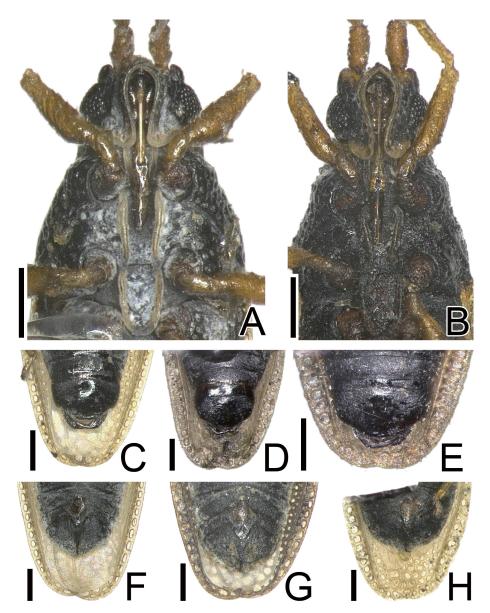


Fig. 2. A–B – rostra and sternal laminae, ventral view: A – A. abruptifrons Golub, 1990; B – A. japonicum (Drake, 1948). C–H – apical part of abdomen, ventral view: C, F, G – A. abruptifrons: C – macropterous male, F – macropterous female, G – submacropterous female; D, E, H – A. japonicum: D – macropterous male, E – submacropterous male, H – submacropterous female. Scale bars = 0.2 mm.

Redescription. Coloration. Head, antennal segment IV, calli, pronotal disc, basal part of posterior process, thoracic pleura, apical part of tarsi and abdomen black; antennal segments I to III, bucculae, rostrum, collar, sternal laminae, legs except apical part of tarsi brown; apical part of posterior process, hemelytron brown or black; compound eyes dark red; pubescence on body yellowish (Figs 1A–E, 2A, C, F, G).

Macropterous morph. Body (Figs 1A, B, E) approximately 2.6 times as long as maximum width across hemelytra. Ratios of lengths from antennal segments I to IV as 1.3:1.0:2.9:1.6. Bucculae 2.5 times as long as its maximum height, with 2 rows of areolae throughout its length. Rostrum (Fig. 2A) 0.6 times as long as antennae.

Pronotum (Figs 1A, B, E, 3A) 1.2 times as long as maximum width across humeri, without paranota. Pronotal disc as high as hemelytron at highest part of each. Collar lower than pronotal disc at highest part of each; anterior

margin gently curved inward. Median carina indistinct throughout its length. Posterior process 0.8 time as long as its maximum width.

Hemelytron (Figs 1A, B, E) 2.9 times as long as its maximum width; maximum width across hemelytra 1.2 times as wide as maximum width across humeri; apices of hemelytra overlapping each other in rest.

Abdomen 1.5 times as long as its maximum width. Pygophore (Figs 2C, 3C) compressed dorsoventrally, semicircular in ventral view, reaching beyond apex of subcostal area of hemelytron; anterior margin of dorsum gently curved inward. Paramere (Fig. 3B) expanded in middle part. Female terminalia (Fig. 2F) reaching apex of subcostal area of hemelytron.

Submacropterous morph. General appearance very similar to that of macropterous morph except for the following characters: body (Figs 1C, D) approximately 2.5 times as long as maximum width across hemelytra;

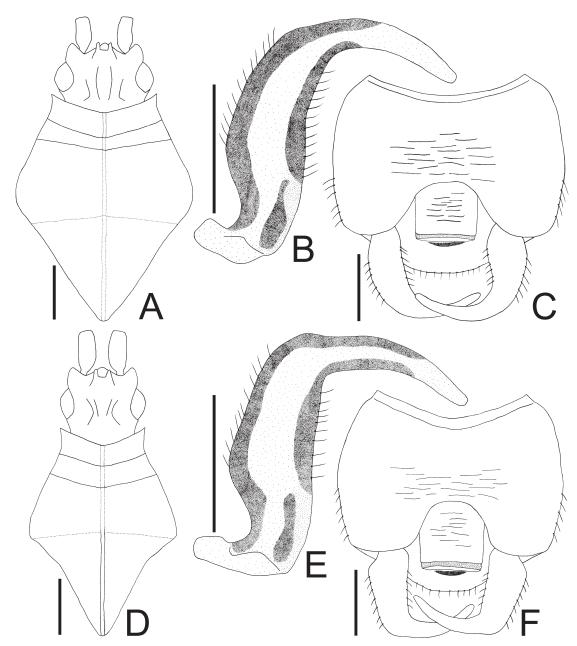


Fig. 3. A, D – heads and pronota, dorsal view: B, C, E, F – parameres and pygophores, dorsal view: A, B, C – *A. abruptifrons* Golub, 1990; D, E, F – *A. japonicum* (Drake, 1948). Scale bars: A, D = 0.2 mm; B, C, E, F = 0.1 mm

hemelytron 2.7 times as long as its maximum width; female terminalia (Fig. 2G) reaching beyond apex of subcostal area of hemelytron.

Measurements (12 macropterous and 9 submacropterous morphs). Body length with hemelytra 1.8–2.1 mm; maximum width across hemelytra 0.7–0.8 mm; pronotal width across paranota 0.6–0.7 mm.

Remarks. The above-recorded specimens well match the original description (GOLUB 1990) of *Agramma abruptifrons* described from Mongolia in terms of general appearance.

Segmental oligomery of antenna is confirmed in *A. abruptifrons* (Fig. 1E), and this individual lack antennal segment III. In other species of *Agramma*, similar teratological form has been known in *A. atricapillum* (Spinola,

1837) and *A. confusum* (Puton, 1879) (ŠTUSÁK & STEHLÍK 1978). Therefore, segmental oligomery of antenna may be common in the genus *Agramma*.

In Japan, *Agramma abruptifrons* inhabits wetlands with a warm-temperate climate.

Host plant. *Juncus* sp. (Juncaceae) (Fig. 4C) has been confirmed as a host plant for *Agramma abruptifrons* in Japan by me and one of my colleagues Mr. Yoichi Yazaki.

Biology. Although many tingids generally feed on the abaxial surface of leaves of host plants (SCHUH & SLATER 1995), a number of individuals of *A. abruptifrons* were collected from stems of the host plant *Juncus* sp. (Fig. 4C) in Japan. In Japan, adults were collected in April, July and October. **Distribution.** China: Beijing City, Hebei Province, Shanxi Province, Inner Mongolia Autonomous Region,

Ningxia Hui Autonomous Region (JING 1981; GOLUB 1990; PÉRICART & GOLUB 1996); Mongolia (GOLUB 1990); Russia: East Siberia (GOLUB 1990); Japan (Honshu) (new record).

Agramma japonicum (Drake, 1948)

(Figs 1F-J, 2B, D, E, H, 3D-F, 4D, E)

Serenthia japonica Drake, 1948: 174. Holotype: ♀ (submacropterous), Japan: Sapporo [= Japan: Hokkaido, Sapporo-shi] (USNM: see HENRY 2020b). Synonymized with Agramma nexile (Drake, 1948) by Takeya (1962: 52) and with A. ruficorne (Germar, 1835) by Péricart (1983: 531). Restored by GOLUB (1990: 48).

Agramma nexile (non Drake, 1948): Drake (1948): 174 (paratypes); Takeya (1951): 23 (check-list: eastern Asia); Esaki (1952): 238 (distribution); Takeya (1953): 167 (distribution); Miyamoto (1965): 90 (distribution); Lee (1967): 92 (distribution); Lee (1969): 162 (nymph, male genitalia); Kerzhner (1978): 47 (distribution); Tomokuni (1979): 135 (distribution); Tomokuni (1987): 115 (distribution); Takahashi (1990): 2 (distribution); Tomokuni & Ishikawa (2002): 170 (distribution); Miyamoto (2008): 156 (distribution); Yamada & Tomokuni (2012): 188 (monograph); Yano et al. (2013): 24 (distribution); Maehara (2014): 58 (distribution); Tomokuni (2014): 362 (distribution); Yamada & Ishikawa (2016): 429 (check-list: Japan); Окосні (2019): 1 (distribution). Misidentifications.

Agramma ruficorne (non Germar, 1835): PÉRICART (1983): 531 (monograph); GOLUB (1988): 148 (key to species); MIYAMOTO & YASUNAGA (1989): 167 (check-list: Japan); TOMOKUNI (2005): 400 (distribution). Misidentifications (GOLUB 1990: 48).

Agramma japonicum: Takeya (1951): 23 (check-list: eastern Asia); Drake & Maa (1953): 23 (distribution); Golub (1988): 148 (key to species); Miyamoto & Yasunaga (1989): 167 (check-list: Japan); Kerzhner & Marusik (1996): 26 (check-list: Kuril Islands); Péricart & Golub (1996): 14 (check-list: Palaearctic); Kwon et al. (2001): 186 (check-list: Korea); Kerzhner et al. (2004): 239 (check-list: Kuril Islands); Kanyukova & Marusik (2006): 171 (check-list: Kuril Islands); Tomokuni (2006): 60 (distribution); Vinokurov et al. (2010): 151 (check-list: eastern Russia); Yamada & Tomokuni (2012): 187 (monograph); Aukema et al. (2013): 59 (check-list: Palaearctic); Yamada & Ishikawa (2016): 429 (check-list: Japan); Cho et al. (2020): 738 (check-list: Korea).

Material examined. Non-types (1 macropterous ♂ 4 macropterous ♀♀ 118 submacropterous \circlearrowleft 3 138 submacropterous \circlearrowleft 8 N5 4 N4), **JAPAN**: Ноккато: Sapporo-shi, Toyohira-ku, Hitsujigaoka, 18.vi.2007, leg. М. Hayashi (7 submacropterous ♂♂ 12 submacropterous ♀♀, TUA); Nemuro City, Habomai Marsh, 7.vii.2017, leg. M. Hayashi (1 submacropterous ♂ 7 submacropterous ♀♀, TUA); Iwanai-gun, Kyowa-cho, Kunitomi, Inaho Mountain Pass, 43°03′28.1″N 140°41′05.2″E, 1.x.2017, leg. T. Ban (1 submacropterous ♂ 2 submacropterous ♀♀, TUA); Kamikawagun, Shimizu-cho, Kitashimizu For. Rd., 43°00′17.4″N 142°50′35.9″E, 5.viii.2019, leg. J. Souma (6 submacropterous 33 2 submacropterous ♀♀ 6 N5 4 N4, TUA); Kamikawa-gun, Shimizu-cho, Route 274, 42°58'45.3"N 142°49'44.8"E, 6.viii.2019, leg. J. Souma (1 macropterous 3 2 macropterous 2 11 submacropterous 3 12 submacropterous 2,TUA); Kamikawa-gun, Shimizu-cho, Shimizu Baseline, 43°01′18.3″N 142°53′29.2″E, 7.viii.2019, leg. J. Souma (2 submacropterous 33 1 submacropterous 2, TUA); Kamikawa-gun, Shimizu-cho, Shimizu east line 1, 43°01'16.7"N 142°53'47.4"E, 30.vii.2020, leg. J. Souma (2 submacropterous \circlearrowleft 2 submacropterous \circlearrowleft , NMPC). **Honshu:** Aomori-ken, Tsugaru-shi, Kidukuritateoka, Hiratakinuma, 28.ix.1992, leg. M. Hayashi (1 submacropterous 2, TUA); Akita Pref., Kazuno, Hachimantai, Fukenoyu, 1,120 m, 25.viii.2000, leg. M. Hayashi et al. (3 submacropterous ♂♂ 4 submacropterous ♀♀, TUA); as above but 13.ix.2000 (36 submacropterous ♂♂ 27 submacropterous ♀♀, TUA); as above but 10.ix.2001 (2 submacropterous \$\oint_{\infty}\$, TUA); Tochigi-ken, Haga-gun, Motegi-machi, Mt. Kamakura, 36°34′17.8″N 140°11′14.4″E, 11.vii.2019, leg. J. Souma (1 submacropterous 2, TUA); Gunma-Pref, Katashina-Vil, Mt. Hotaka, 10.viii.1999, leg. S. Nagashima (1 macropterous ♀ 1 submacropterous ♂, TUA); Saitama-ken, Chichibu-shi, Shimoyoshida, Torikata, 26.iv.1996, leg. M. Hayashi (2 submacropterous 33 3 Shimotano, 36°05'23.8"N 139°07'00.1"E, 29.v.2019, leg. J. Souma (1 submacropterous ♂ 1 submacropterous ♀, TUA); Kanagawa-ken, Ashigarakami-gun, Yamakita-machi, Nakagawa, 35°26'45.5"N 139°02'52.4"E, 30.vi.2018, leg. J. Souma (1 submacropterous ♀, TUA); Nîgata-ken, Nagaoka-shi, Kuriyamazawa, alt. 373 m, 37.395468 N 139.020894 E, 15.v.2016, leg. Gô Mashima (1 submacropterous 3 1 submacropterous Ç, TUA); Nagano Pref., Suwa-gun, Hara-mura, 4.vii.1998, leg. J. Narukawa (1 submacropterous [♀], TUA); Shinano, Kamisuwa, 18.vii.1951, leg. M. Takahashi (1 submacropterous ♀, ELKU); Shinano, Kirigamine, 10.viii.1959, leg. S. Miyamoto (2 N5, ELKU); Toyama, Ikuji, 4.viii.1960, leg. T. Hidaka (1 macropterous ♀ 1 submacropterous ♀, ELKU); Mie Pref., Inabe-shi, Fujiwara-chô, Kurakake-tôge Pass, 30.vi.2012, leg. N. Tsuji (1 submacropterous ♂ 1 submacropterous ♀, ELKU); Aki, Sandankyô, 10–11.vi.1939, leg. Teiso Esaki (2 submacropterous ♀♀, ELKU). Sнікоки: Iyo, W. Kuma, Kawasemura, 22.v.1949, leg. M. Miyatake (1 submacropterous ♀, ELKU). KYUSHU: Fukuoka, Fukuchi, 29.iv.1956, leg. T. Hidaka (1 submacropterous ♀, ELKU); Ôita Pref., Kokonoe-machi, Yutsubo, Jizôbaru Marshland, 17.viii.2019, leg. R. Ito (43 submacropterous 3351 submacropterous 99, ELKU) (Fig. 5).

Note. The label data of two specimens collected by Teiso Esaki corresponds to a single paratype of *Agramma nexile* from Honshu described by Drake (1948). Six specimens from Honshu and Shikoku collected in the 1930s–1950s, which are deposited at ELKU, had been recorded as *A. nexile* by Takeya (1951, 1953, 1962). The collection site of 19 specimens from Sapporo, Hokkaido provided by M. Hayashi corresponds to type locality of *A. japonicum* and one of paratype localities of *A. nexile* described by Drake (1948).

Diagnosis. Recognized among other species of Agramma by a combination of the following characters: frons convex, descending to base of clypeus; a pair of frontal spines obliquely protruding downward, touching clypeus at apices, separated from each other at apices; distance between apices of frontal spines as long as their length; pubescence on body less than 0.5 times as long as diameter of compound eye; rostrum reaching middle part of mesosternum; median carina of pronotum distinct throughout its length (Fig. 3D); costal area with a single row of areolae throughout its length, wider than tibia; areolae of costal area less than 2 times as long as its maximum width at middle of hemelytron; subcostal-discoidal boundary vein present throughout its length; subcostal area with 4 rows of areolae at widest part; discoidal-sutural boundary vein absent; discoidal-sutural area with 8 rows of areolae at widest part; outer and inner margins of paramere angularly curved in middle part (Figs 3E, F); female terminalia hexagonal in ventral view (Fig. 2H); and posterior margin of female terminalia protruding posteriad in middle part.

Redescription. Coloration. Head, calli, pronotal disc, basal part of posterior process, thoracic pleura, sternal laminae, apical part of tarsi and abdomen black; antenna, bucculae, rostrum, collar, apical part of posterior process, hemelytron, legs except apical part of tarsi brown; compound eyes dark red; pubescence on body yellowish (Figs 1F–J, 2B, D, E, H).

Macropterous morph. Body (Figs 1F, G) approximately 2.8 times as long as maximum width across hemelytra. Ratios of lengths from antennal segments I to IV as 1.4: 1.0: 2.7: 1.7. Bucculae 2.8 times as long as its maximum height, with 2 rows of areolae throughout its length. Rostrum (Fig. 2B) 0.6 times as long as antennae.

Pronotum (Figs 1F, G, 3D) 1.3 times as long as maximum width across humeri, without paranota. Pronotal disc higher than hemelytron at highest part of each. Collar

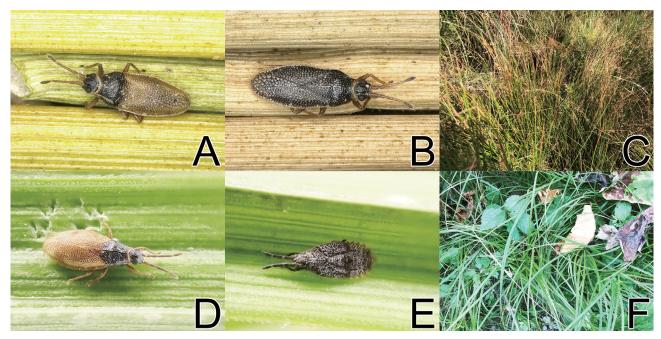


Fig 4. A, B – habitus images of living adults (photographs taken indoor) for *A. abruptifrons* Golub, 1990 from Mie, Honshu, Japan. C – host plant (*Juncus* sp.) for *A. abruptifrons* at Mie, Honshu, Japan. D, E – habitus images of a living adult and a living fifth instar nymph (photographs taken indoors) for *A. japonicum* (Drake, 1948) from Hokkaido, Japan. F – host plant (*Carex* sp.) for *A. japonicum* from Hokkaido, Japan.

lower than pronotal disc at highest part of each; anterior margin gently curved inward. Median carina of pronotum distinct throughout its length. Posterior process 0.8 time as long as its maximum width.

Hemelytron (Figs 1F, G) 3.3 times as long as its maximum width; maximum width across hemelytra 1.3 times as wide as maximum width across humeri; apices of hemelytra overlapping each other in rest.

Abdomen 1.7 times as long as its maximum width. Pygophore (Figs 2D, 3F) compressed dorsoventrally, semicircular in ventral view, reaching level far remote from apex of discoidal-sutural area of hemelytron; anterior margin of dorsum gently curved inward. Paramere (Fig. 3E) expanded in middle part. Female terminalia (Fig. 2H) reaching level far remote from apex of discoidal-sutural area of hemelytron.

Submacropterous morph. General appearance is very similar to that of macropterous morph except for the following characters: body (Figs 1H–J) approximately 2.6 times as long as maximum width across hemelytra; pronotal disc as high as hemelytron at highest part of each; hemelytron 3 times as long as its maximum width; pygophore (Fig. 2E) reaching apex of discoidal-sutural area of hemelytron.

Measurements (5 macropterous and 256 submacropterous morphs). Body length with hemelytra 1.8–2.3 mm; maximum width across hemelytra 0.7–0.9 mm; pronotal width across paranota 0.5–0.6 mm.

Remarks. The above-recorded specimens well match the photographs of the holotype (Henry 2020b) and the original description (Drake 1948) of *A. japonicum* described from "Sapporo, Japan" [= Japan: Hokkaido, Sapporo-shi] in terms of general appearance.

Agramma japonicum strongly resembles A. nexile in general appearance, and the identification of these two species in Japan has long been challenging (e.g. Drake 1948; Takeya 1962; Yamada & Tomokuni 2012). However, based on a comparison between hundreds of specimens together with the photographs of the holotype (Henry 2020b) of A. japonicum and the photographs of the holotype (Henry 2020a) of A. nexile, a single main characteristic was recognized that permits easy differentiation between A. japonicum and A. nexile, i.e., the areolae of the costal area are less than 2 times as long as its maximum width at middle of hemelytron. In contrast, A. nexile has the areolae of costal area more than 3 times as long as its maximum width at middle of hemelytron.

Host plants. Carex spp. (Cyperaceae) (Fig. 4F) have been confirmed as host plants for A. japonicum (MIYAMOTO 1965, 2008; YAMADA & TOMOKUNI 2012; MAEHARA 2014; TOMOKUNI 2014; OKOCHI 2019; present study). They have also been collected from the following monocotyledonous herbs of four families but without any data on its development: Ophiopogon japonicus (Thunb.) Ker Gawl. (Asparagaceae) (TOMOKUNI 1979); Liriope sp. (Asparagaceae) (TOMOKUNI 1979); Cyperus sp. (Cyperaceae) (YAMADA & TOMOKUNI 2012); Scirpus wichurae Boeck. f. wichurae (Cyperaceae) (TOMOKUNI 1979); Miscanthus sp. (Poaceae) (TAKEYA 1962; YAMADA & TOMOKUNI 2012); poaceous herb (TOMOKUNI 1987).

Biology. A number of individuals of *A. japonicum* were collected from the leaves of *Carex* sp. (Fig. 4F) in Japan proper, suggesting that this lace bug appears to feed on the leaves as do many tingids (SCHUH & SLATER 1995). This lace bug is often collected in dimly lit environments and it has rarely been found in sunny environments (MAEHARA 2014).

In Japan, adults were collected from April to October (Drake 1948; Takeya 1953; 1962; Kerzhner 1978; Tomokuni 1979, 1987, 2005, 2014; Takahashi 1990; Tomokuni & Ishikawa 2002; Yamada & Tomokuni 2012; Maehara 2014; Okochi 2019; present study); nymphs were observed in July and August (Tomokuni 1987, 2014; Tomokuni & Ishikawa 2002; Yamada & Tomokuni 2012; present study); the overwintering form is unknown.

Distribution. Japan (Kunashiri Island, Hokkaido, Honshu, Hachijo Island, Sado Island, Shikoku, Kyushu) (Kerzhner 1978; Yamada & Ishikawa 2016; new record from Kyushu); China: Fujian ((Drake & Maa 1953); Korea (Lee 1967); Russia: Far East (Vinokurov et al. 2010); Taiwan (Tomokuni 2006).

In Japan, *A. japonicum* inhabits the wetland and forest floor with cool- and warm-temperate climates.

A total of 273 specimens from Japan including "A. nexile" recorded by the previous authors (Drake 1948; Takeya 1951, 1953, 1962) were examined, and all of these are A. japonicum. In addition, the illustrations and photographs of A. nexile from Japan provided by the previous authors (ESAKI 1952; MIYAMOTO 1965, 2008; Lee 1969; YAMADA & TOMOKUNI 2012; TOMOKUNI 2014) in fact represent A. japonicum. Therefore, at least most of, possibly all previous distributional records of A. nexile from Japan (e.g. Drake 1948; Takeya 1962; Yamada & Tomokuni 2012) probably correspond to A. japonicum, and "true" A. nexile described from Taiwan appears not to be present in Japan.

Key to species of Agramma from Japan

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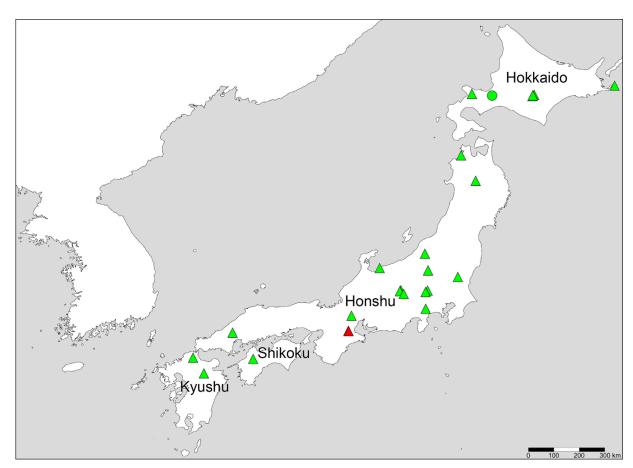


Fig. 5. Collection sites of two species of *Agramma* from Japan used for present study. Red icon = *A. abruptifrons* Golub, 1990; green icons = *A. japonicum*. Circle = type locality; triangles = other localities.

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