



Clarifying the identity of two resembling hoverfly species, *Betasyrphus serarius* and *B. nipponensis* (Diptera: Syrphidae: Syrphini), based on morphology and DNA barcoding

Chan-Ouk Kim, Ho-Yeon Han *

Division of Biological Science and Technology, Yonsei University, 1 Yonseidae-gil, Wonju-si, Gangwon-do 26493, Republic of Korea

ARTICLE INFO

Keywords:

Syrphini
Betasyrphus
 DNA barcoding
 Male genitalia
 Wing interference patterns
 Wing microtrichia distributions

ABSTRACT

The two Palaearctic members of the hoverfly genus *Betasyrphus*, *B. serarius* (Wiedemann, 1830) and *B. nipponensis* (Goot, 1964), closely resemble each other, except for their male genitalic characters. For this reason, these two species have been often mistaken for each other. In Korea, only *B. serarius* has been recognized as a sole species based on mixed specimens from these two species. In the present study, we attempted to define *B. serarius* and *B. nipponensis* more precisely and identify additional diagnostic characteristics to distinguish these species. We examined external morphological characters including the genitalic structures, the wing microtrichia distributions (WMDs), as well as the wing interference patterns (WIPs). In addition, we analyzed the DNA barcode sequences of individuals, covering as many morphological variants as possible, to distinguish the females of these two species. As a result, we found some additional diagnostic male genitalic and WMD characters. Unfortunately, despite our efforts, females of these two species remain undistinguishable. DNA barcoding analysis did not reveal any significant differences between *B. serarius* and *B. nipponensis*. Our analysis based on 20 Korean samples and 486 Syrphidae sequences retrieved from BOLD Systems (ver. 4) and GenBank showed that the nine available *Betasyrphus* species including the type species formed a robust barcode cluster. *Betasyrphus serarius* and *B. nipponensis* together with three unidentified species from Pakistan, Australia and Malaysia also formed a strong sub-cluster. In addition, we provide an identification key, diagnoses, and descriptions with color photographs.

Introduction

The hoverfly genus *Betasyrphus* Matsumura, 1917 (Diptera: Syrphidae) currently includes 19 valid species from four zoogeographical regions: 13 Afrotropical, two Palaearctic, six Oriental and one Australasian (Catalogue of Life as of September 2021; <https://www.catalogueoflife.org>). Although the distributions of 18 species are each limited to a single zoogeographical region, the type species *B. serarius* (Wiedemann, 1830) is known to be widely distributed in the Palaearctic, Oriental, Afrotropical, and Australasian regions.

There are two similar *Betasyrphus* species in the Palaearctic, namely *B. serarius* (type locality: Macau, China) and *B. nipponensis* (Goot, 1964; type locality: Shikoku, Japan). Ôhara (1984) compared the holotype male of *B. nipponensis* with Japanese specimens identified as *B. serarius*. He concluded that these two species could only be distinguished by examining their male genitalia. Therefore, the females could not be discerned. On the other hand, Mutin and Barkalov (1999), in their

Russian Far East Syrphidae key, provided a couplet to distinguish them based on the presence or absence of yellow hairs on the scutellum.

In Korea, *B. serarius* has been the only reported *Betasyrphus* species, as recorded by Matsumura and Adachi (1917). In the present study, the examination of male genitalia revealed that approximately 10% of the Korean males previously identified as *B. serarius* (about 200 specimens of both species examined) actually belong to *B. nipponensis*. Except for their differing male genitalic characters, these two species are not distinguishable, even based on Mutin and Barkalov's key (1999). Both species are the only known Palaearctic *Betasyrphus* species so far, but there is a problem about the identity of *B. serarius*; i.e., male genitalia of *B. nipponensis* is known but from the original description it seems that Wiedemann had only females for the *B. serarius* description. In other words, based on currently available information, what is not clear is if the name *serarius* applies to the taxon *B. nipponensis* or *B. serarius* sensu Ôhara (1984) (see Remarks of *B. serarius* for further discussion).

Here we provide diagnoses and descriptions of these two Palaearctic

* Corresponding author.

E-mail address: hyhan@yonsei.ac.kr (H.-Y. Han).

<https://doi.org/10.1016/j.jape.2022.101914>

Received 16 November 2021; Received in revised form 1 April 2022; Accepted 5 April 2022

Available online 9 April 2022

1226-8615/© 2022 Published by Elsevier B.V. on behalf of Korean Society of Applied Entomology.

Betasyrphus species and discuss their variability, including male genital characters and wing microtrichia distributions (WMDs). We also examined their wing interference patterns (WIPs) to acquire additional characters for distinguishing these species. We conducted a DNA barcoding analysis based on 20 Korean *Betasyrphus* sequences as well as other sequences from *Betasyrphus* and related syrphid species retrieved from the Barcode of Life Data (BOLD) Systems (<https://www.boldsystems.org>; as of March 2022) and GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; as of March 2022). Based on the morphological and DNA barcoding analyses, we discuss the problems and solutions relative to discriminating this cryptic species pair (*B. serarius* and *B. nipponensis*).

Material and methods

The morphological terminology and interpretations mainly follows Cumming and Wood (2017), but we also follows Dušek and Láška (1976), Thompson (1999), and Vujić et al. (2008) for some genitalic and wing terminology that were not described by Cumming and Wood. In addition, two lengths and eleven ratios used in the descriptions were modified from Han and Norrbom (2005): body length (anterior margin of head excluding antenna to posterior margin of abdomen); wing length (anterior margin of tegula to apex of vein R_{4+5}); head ratio (head length/head height); face-head ratio (widest width of face in anterior view/width of head); eye ratio (shortest eye diameter/longest eye diameter); gena-eye ratio (genal height/longest eye diameter); antenna-head ratio (length of antenna/length of head); postpedicel-pedicel ratio (length of postpedicel/length of pedicel); arista-antenna ratio (length of arista/length of antenna excluding arista); wing ratio (wing length/wing width); wing-thorax ratio (wing length/thorax length); vein M ratio (distance along vein M between crossveins r-m and dm-cu/distance between crossveins r-m and bm-cu); and vein R_{4+5} ratio (distance along vein R_{4+5} between crossvein r-m and vein R_{4+5} apex/distance between crossvein r-m and basal node of vein R_{4+5}).

Molecular methods generally follows Han and Ro (2016; 2018). For DNA barcoding analysis, 657 bp long fragments of the mitochondrial *COI* gene (the DNA barcode region) were obtained from 20 Korean *Betasyrphus* specimens. The collection and voucher data, BOLD Systems process IDs (KBET001-22–020-22), and GenBank accession numbers (OL333563–333582) are presented in Table 1. The voucher information, photographs, and DNA barcode sequences of the analyzed Korean *Betasyrphus* specimens are accessible through the public dataset “DS-KORBET” (Dataset ID: dx.<https://doi.org/10.5883/DS-KORBET>) on the BOLD Systems.

We also retrieved 486 publicly available sequences from BOLD Systems and GenBank (as of March 2022). The sequences were examined and edited using BioEdit (version 7.1.9, 2012; Hall, 1999). Alignment was not necessary for the *COI* barcode fragments because no indels were found. Neighbor-joining (NJ) analysis (Saitou and Nei, 1987) was performed in MEGA X (Kumar et al., 2018) using the Kimura 2-parameter model of nucleotide substitution (Kimura, 1980). The reliability of clustering patterns in the NJ tree was determined using a bootstrap test (Felsenstein, 1985) with 3000 replications.

For the Korean males of *B. serarius* and *B. nipponensis*, a maximum parsimony network was constructed with TCS 1.21 based on default setting (Clement et al., 2002), implemented in the software package PopART (version 1.7, Leigh and Bryant, 2015). Such network allows the identification of possible haplotype sharing between species as a consequence of recent speciation or on-going hybridization process (Raupach et al., 2020).

Consecutive digital images in different focal planes (usually 50 or more shots per figure) were captured using a Fujifilm X-S1 camera (Tokyo, Japan) equipped with a Raynox DCR-250 macro-conversion lens. Photographs of the genitalia and the wing microtrichia distributions (WMDs) were obtained with a Nikon D90 camera (Tokyo, Japan) mounted on an Olympus CX41 compound microscope (Tokyo, Japan).

Table 1

Collection and voucher information of Korean *Betasyrphus* specimens sequenced in this study. The voucher specimen numbers, BOLD Systems process IDs, and GenBank accession numbers are indicated in parentheses after the locality data.

<i>Betasyrphus serarius</i> (Wiedemann, 1830)	
1♂, Korea: Gangwon-do, Yeongwol-gun, Jundong-myeon, Heungwol-ri, Mt. Taehwasan, N37°07'03.3" E128°29'07.4", 30.VII.2019, S.S. Euo, C.O. Kim, and J.H. Choi (KNA), (voucher no.: YSUW200701016; BOLD ID: KBET001-22; GenBank acc. no.: OL333563).	
1♂, Korea: Gangwon-do, Wonju-si, Panbu-myeon, Seogok-ri, Mt. Baegunsan, N37°14'59" E127°57'46", 19.VIII.2007, H.S. Lee, and S.W. Suk (KNA), (voucher no.: YSUW200701017; BOLD ID: KBET002-22; GenBank acc. no.: OL333564).	
2♂, Korea: Gangwon-do, Jeongseon-gun, Nam-myeon, Yupyeong-ri, Mt. Mindungsan, N37°16'10" E128°46'49", 10.VIII.2019, S.S. Euo, C.O. Kim, and J.H. Choi (KNA), (voucher no.: YSUW200701018, 019; BOLD ID: KBET003-22, 004-22; GenBank acc. no.: OL333565, OL333566).	
1♂, Korea: Gangwon-do, Jeongseon-gun, Jeongseon-eup, Mt. Gariwangsan, N37°27'40" E128°33'48", 27.IX.2011, S.W. Suk, and Y.B. Lee (KNA), (voucher no.: YSUW200701020; BOLD ID: KBET005-22; GenBank acc. no.: OL333567).	
<i>Betasyrphus nipponensis</i> (Goot, 1964)	
1♂, Korea: Gangwon-do, Jeongseon-gun, Nam-myeon, Yupyeong-ri, Mt. Mindungsan, N37°16'10" E128°46'49", 12.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi, (voucher no.: YSUW200701186; BOLD ID: KBET006-22; GenBank acc. no.: OL333568).	
1♂, Korea: Gangwon-do, Hongcheon-gun, Nae-myeon, Gwangwon-ri, Woldoon-gol, N37°50'52" E128°25'24", 16.VI.2018, S.S. Euo, C.O. Kim, and J.H. Choi, (voucher no.: YSUW200701187; BOLD ID: KBET007-22; GenBank acc. no.: OL333569).	
1♂, Korea: Gangwon-do, Hongcheon-gun, Nae-myeon, Bangnae-ri, N37°51'11" E128°16'52", 13.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi, (voucher no.: YSUW200701188; BOLD ID: KBET008-22; GenBank acc. no.: OL333570).	
1♂, Korea: Gangwon-do, Jeongseon-gun, Nam-myeon, Yupyeong-ri, Mt. Mindungsan, N37°16'10" E128°46'49", 13.V.2017, S.S. Euo et al., (voucher no.: YSUW200701189; BOLD ID: KBET009-22; GenBank acc. no.: OL333571).	
1♂, Korea: Gyeonggi-do, Gwangju-si, Docheok-myeon, Sangnim-ri, Mt. Taehwasan, N37°18'44" E127°18'36", 10.VII.2017, H.Y. Han et al., (voucher no.: YSUW200701190; BOLD ID: KBET010-22; GenBank acc. no.: OL333572).	
<i>Betasyrphus</i> sp. (<i>B. serarius</i> or <i>B. nipponensis</i>)	
1♀, Korea: Chungcheongbuk-do, Yeongdong-gun, Sangchon-myeon, Goja-ri, Mt. Sambongsan, N36°05'33.0" E127°50'08.7", 25.VI.2019, S.S. Euo, C.O. Kim, and J. H. Choi, (voucher no.: YSUW200701191; BOLD ID: KBET011-22; GenBank acc. no.: OL333573).	
1♀, Korea: Gangwon-do, Wonju-si, Panbu-myeon, Seogok-ri, Mt. Baegunsan, N37°14'59" E127°57'46", 23.VI.2017, C.O. Kim, and J.H. Choi, (voucher no.: YSUW200701192; BOLD ID: KBET012-22; GenBank acc. no.: OL333574).	
4♀, Korea: Gangwon-do, Jeongseon-gun, Nam-myeon, Yupyeong-ri, Mt. Mindungsan, N37°16'10" E128°46'49", 12.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi, (voucher no.: YSUW200701193, 194, 195, 196; BOLD ID: KBET013-22, 014-22, 015-22, 016-22; GenBank acc. no.: OL333575, OL333576, OL333577, OL333578).	
1♀, Korea: Gangwon-do, Wonju-si, Heungeop-myeon, Maeji-ri, Yonsei Univ. Mirae Campus, N37°17'10" E127°54'01", 10.X.2018, S.S. Euo, (voucher no.: YSUW200701197; BOLD ID: KBET017-22; GenBank acc. no.: OL333579).	
3♀, Korea: Gangwon-do, Hongcheon-gun, Nae-myeon, Bangnae-ri, N37°51'11" E128°16'52", 13.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi, (voucher no.: YSUW200701198, 199, 200; BOLD ID: KBET018-22, 019-22, 020-22; GenBank acc. no.: OL333580, OL333581, OL333582).	

The images were stacked using Helicon Focus software® (version 7.7.4, Helicon Soft, Ltd., Kharkiv, Ukraine).

WIP images were obtained according to the methods of Shevtsova et al. (2011) and Hosseini et al. (2019). Because of the large size of *Betasyrphus* wings, we took five separate images for each wing and stitched them together using Adobe Photoshop® (version 22.5, Adobe Systems Inc., San José, CA, USA). The method for preparing wings can be summarized as follows: (1) each dissected wing was soaked in 95% ethanol for approximately 12 h to remove foreign substances contaminating the wings; (2) each soaked wing was placed on a slide glass, and carefully covered with a cover glass to keep it flat; (3) after approximately 3 h of drying, each slide was carefully placed horizontally against a dark background, which consisted of black square box with a slide holder; (4) photographs were taken using a Fuji X-S1 camera with the setting described above with the only addition of a LED illumination

ring; (5) each wing was tilted by approximately 5° in the four directions, and pictures were captured upon observation of interference colorations; (6) image stacking was performed as described above; and (7) each WIP picture was completed after stitching five independently stacked photographs.

Most of the examined specimens are deposited in the Division of Biological Science and Technology, Yonsei University, Mirae Campus, Korea (YSUW). Some specimens are deposited in the National Institute of Biological Resources, Incheon, Korea (NIBR), and others in the Korea National Arboretum, Pocheon, Korea (KNA) as well. Abbreviations of the other institutions mentioned in the text are as follows: ZMUC: Zoological Museum, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark; NMW: Naturhistorisches Museum Wien, Postfach 417, Burgring 7, 1010 Vienna, Austria; and EUMJ: Entomological Laboratory, Faculty of Agriculture, Ehime University, Tarumi 3-5-7 Matsuyama, Japan.

Genus *Betasyrphus* Matsumura, 1917

Betasyrphus Matsumura in Matsumura and Adachi, 1917: 143 (Type-species: *Syrphus serarius* Wiedemann, 1830); Vockeroth, 1969: 41 (in Syrphini generic revision); Ghorpadé, 1994: 4 (in Indian Syrphini key including five Oriental *Betasyrphus* species); Thompson and Rotheray, 1998: 102 (in Palaearctic syrphid generic key); Rotheray and Gilbert, 1999: 12 (in phylogenetic discussion based on immature morphology); Young et al., 2016: 8 (in Syrphidae molecular phylogenetic analysis); Mengual et al., 2018: 160 (in Syrphini molecular phylogenetic analysis).

Diagnosis. The members of the genus *Betasyrphus* can be distinguished from other syrphid taxa based on the combination of the following characteristics [extracted and modified from Matsumura and Adachi (1917), Vockeroth (1969), and Ssymank (2010)]: (1) anterior anepisternum bare; (2) lower lobe of the calypter with a few hairs on dorsal surface; (3) 3 narrow transverse yellowish bands on abdominal tergites 2–4 extend to lateral margins, with each band partially dusted with yellowish white to greyish pruniosity. Male genitalia: (4) surstylus relatively long (at least as long as epandrial height); (5) in lateral view, superior lobe rather long and upright without any teeth; and (6) aedeagal basiphallus broad with two pairs of long and pointed latero-ventral appendages (Fig. 9E, J; baso- and apico-ventral processes).

Monophyly of *Betasyrphus*. Although this genus seems to be a morphologically cohesive taxon, we were unable to identify any generic characteristics unique to them. Nevertheless, our DNA barcoding analysis showed that all nine available *Betasyrphus* species including the type species were strongly clustered (see “DNA barcoding of *Betasyrphus* and the related taxa”).

Distribution. Palaearctic, Afrotropical, Oriental, Australasian regions.

Biology. To date, aphidophagous habits have been observed in four *Betasyrphus* species: *B. adligatus* (Wiedemann, 1824), *B. isaaci* (Bhatia, 1933), *B. nipponensis*, and *B. serarius*. A total of 42 species of the following 23 aphid genera are recognized as their preys: *Aphis* Linnaeus, 1758; *Aulacorthum* Mordvilko, 1914; *Brachycaudus* Goot, 1913; *Brevicoryne* Goot, 1915; *Capitophorus* Goot, 1913; *Hayhurstia* Guercio, 1917; *Hyadaphis* Kirkaldy, 1904; *Hyalopterus* Koch, 1854; *Hyperomyzus* Börner, 1933; *Lachnus* Burmeister, 1835; *Lipaphis* Mordvilko, 1928; *Macrosiphoniella* Guercio, 1911; *Macrosiphum* Passerini, 1860; *Megoura* Buckton, 1876; *Melanaphis* Goot, 1917; *Myzus* Passerini, 1860; *Neophyllaphis* Takahashi, 1920; *Ovatus* Goot, 1913; *Periphyllus* Hoeven, 1863; *Phorodon* Passerini, 1860; *Rhopalosiphum* Koch, 1854; *Sitobion* Mordvilko, 1914; and *Uroleucon* Mordvilko, 1914 (Brunetti, 1923; Bhatia and Shaffi, 1933; Ninomiya, 1956; Ninomiya, 1957b; Minamikawa and Fukuhara, 1964; Thompson and Simmonds, 1965; Okuno, 1967; Ghosh, 1974; Raychaudhuri et al., 1978; Ghorpadé, 1981; Agarwala et al., 1987; Radhakrishnan and Muraleedharan, 1993; Bijaya et al., 1996; Sivova, 2003; Chaudhary and Singh, 2012; Kumari, 2020). There also are records as unidentified aphids on *Prunus mume* (Siebold) Siebold and Zucc. (family Rosaceae), *Prunus salicina* Lindl., *Magnolia* sp. (family

Manoliaceae), *Rubus* sp. (family Rosaceae), and Mustard plant (Bhatia and Shaffi, 1933; Okuno, 1967; Rai, 1976; Ghorpadé, 1981).

Key to the species of the genus *Betasyrphus* in the Palaearctic region

1. Eyes dichoptic (Fig. 4I–P)..... *Betasyrphus serarius* or *B. nipponensis* (female)
 - Eyes holoptic (Fig. 4A–H)..... (male) 2
2. Apical 1/3 of wing cell br anterior to spurious vein predominantly microtrichose (bare portion no more than half within this region; Fig. 6A, B); male genitalia with surstylus relatively wide in caudal view (middle width about 1/3 of length when oriented to show broadest area; Fig. 9B)..... *B. serarius*
 - Apical 1/3 of wing cell br anterior to spurious vein almost bare (Fig. 6C, D); male genitalia with surstylus relatively narrow in caudal view (middle width about 1/8 of length; Fig. 9G)..... *B. nipponensis*

Betasyrphus serarius (Wiedemann, 1830) (Figs. 1, 3, 4–7, 9, 10)

Syrphus serarius Wiedemann, 1830: 128 (type-locality: China, Macau); Denner, 2017: 79 (syntypes 1♀, NMW; 2♀, ZMUC); Schiner, 1868: 352 (in Sri Lanka syrphid collection list); Coquillett, 1898: 321 (Japanese specimens); Meijere, 1908: 296 (redescription of Sri Lankan specimens); Brunetti, 1923: 73 (India, Pakistan and Nepal distribution with redescription); Shiraki, 1930: 360 (East Asian distribution with redescription); Bhatia and Shaffi, 1933: 559 (morphology and biology of immature stages – India); Hull, 1936: 195 (in Australian checklist); Doi, 1938: 10 (in Korean checklist); Shiraki and Edashige, 1953: 102 (Japanese and Korean records); Ninomiya, 1956: 225 (prey and host plant records); Ninomiya, 1957a: 124 (immature biology); Ninomiya, 1957b: 189 (immature biology); Ninomiya, 1962: 24 (hymenopterous parasites list); Coe, 1964: 261 (in eastern Nepal checklist); Doesburg, 1966: 63 (in New Guinea and Australian checklist); Okuno, 1967: 125 (in Japanese aphidophagous syrphid third instar larval key); ZSK, 1968: 178 (in Korean checklist); Kim et al., 1971: 848 (Korean distribution); Kim, 1972: 42 (in Korean checklist); Kim, 1975: 40 (in Korean checklist).

Syrphus serarius [misspelling of *Syrphus*]: Ninomiya, 1959: 23 (description of immature stages).

Metasyrphus serarius [misidentification of *B. keiseri* Ssymank (2010)]: Keiser, 1971: 228 (new Madagascar record).

Betasyrphus serarius: Matsumura and Adachi, 1917: 144 (description of Japanese specimens); Hippa, 1968: 48 (redescription); Vockeroth, 1969: 69 (redescription and distribution); Yano et al., 1979: 16 (biology of immature stages in Japan); Smith and Vockeroth, 1980: 490 (in Afrotropical Syrphidae list); Ghorpadé, 1981: 68 (prey and host plants lists in India and neighboring countries); Agarwala et al., 1987: 20 (prey records in North East India); Agarwala et al., 1989: 268 (prey and host plant record, and biology in India); Peck, 1988: 13 (in Palaearctic catalog); Radhakrishnan and Muraleedharan, 1993: 175 (prey record in Southern India); ESK and KSAE, 1994: 288 (in Korean checklist); Bijaya et al., 1996: 114 (prey record in India); Dirickx, 1998: 23 (in Afrotropical catalog); Mutin and Barkalov, 1999: 376 (in Russian Far East Syrphidae key); Han and Choi, 2001: 21 (in Korean catalog); Whittington, 2003: 588 (in Afrotropical checklist); Huo et al., 2007: 108 (in identification manual of Syrphidae in Mt. Qinling-Bashan, China); Paek et al., 2010: 229 (in Korean checklist); Han, 2012: 304 (in Korean illustrated handbook); Huang and Cheng, 2012: 157 (redescription in Chinese catalog); Han et al., 2014: 38 (in Korean catalog); Ôhara et al., 2014: 466 (in Japanese catalog); Choi et al., 2018: 50 (in Korean catalog); NIBR, 2019: 450 (in Korean catalog); Kumari, 2020: 572 (prey record in India); Ichige and Sakai, 2020: 51 (in Tsushima Island and Nagasaki record); Robertson et al., 2020: 567 (in list of flower visitors – *Ozothamnus diosmifolius* (Asteraceae), *Bidens pilosa* (Asteraceae) in

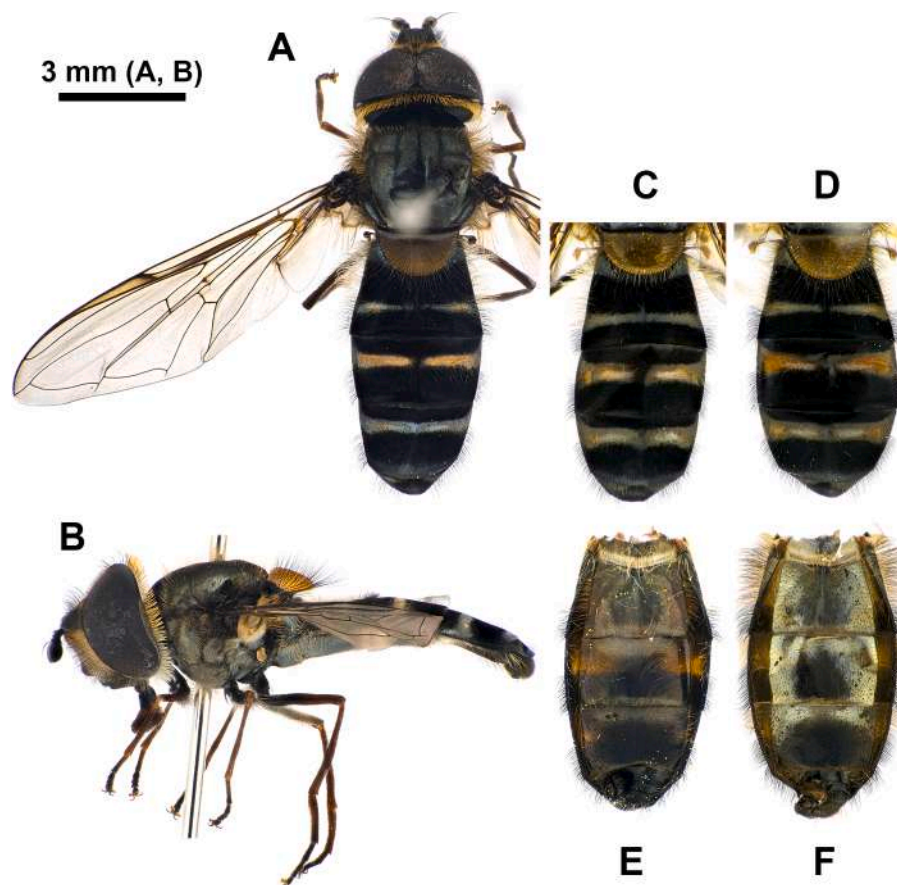


Fig. 1. *Betasyrphus serarius* males. (A, B) Body, dorsal and lateral view. (C–F) Abdomen, dorsal (C, D) and ventral view (E, F), showing a range of variation. Voucher specimen codes: A, B - BetSer_M2; C - BetSer_M5; D - BetSer_M9; E - BetSer_M3; F - BetSer_M4.

Australia); Huo, 2020: 139 (in Chinese catalog).

Diagnosis. Palaearctic *B. serarius* and *B. nipponensis* are closely related species showing almost identical appearance. They can be together distinguished from the remaining *Betasyrphus* species by the combination of the following characteristics: (1) compound eye densely covered with tiny yellowish hairs (Fig. 4); (2) postpedicel about twice as long as pedicel and scape together (Fig. 4); (3) arista dark brown to brownish black (Fig. 4); (4) face covered with black and brownish yellow hairs mixed (more black hairs in males – Fig. 4A–D, but variably mixed in females – Fig. 4I–L); (5) black facial stripe not reaching antennal base (Fig. 4A–D, I–L); (6) scutellum covered with variably mixed black and brownish yellow hairs (Fig. 5); (7) femora basally brownish black, and apically brown to dark brown (Fig. 1B); (8) pterostigma brownish yellow, basally with narrow inwardly slanted (about 45° angle) dark brown vitta (Fig. 6A, C); (9) halter brownish yellow to dark brown (Fig. 1A, C, D); (10) abdomen brownish black with 3 light grey to brownish yellow transverse bands on tergites 2–4, with each band reaching lateral margins and often interrupted in middle (Fig. 1A, C, D); and (11) surstyli more or less symmetrical (Fig. 9B, G).

Ōhara (1984) initially distinguished *B. serarius* from *B. nipponensis* only based on its male genitalic characters. In the present study, we found one additional non-genitalic male character supporting such distinctions. However, both Ōhara (1984) and our study failed to distinguish between females of these two species (see “Wing microtrichia distributions (WMDs)” and “DNA barcoding of *Betasyrphus* and the related taxa” for further details). *Betasyrphus serarius* males can be distinguished from *B. nipponensis* as follows: (1) apical 1/3 of cell br anterior to spurious vein predominantly microtrichose (bare portion no more than half within this region) vs. almost bare except for marginal area (Fig. 6A, B vs. C, D); (2) surstylus relatively wide in caudal view

(middle width about 1/3 of length when oriented to show broadest area) vs. narrow (middle width about 1/8 of length) (Fig. 9B vs. G); (3) in lateral view, surstyler apodeme strongly concave (almost U-shape) vs. slightly concave (Fig. 9A vs. F); (4) in ventral view, surstyler apodeme about as long as wide vs. at least 1.5x longer than wide (Fig. 9D vs. I); (5) lateral protuberance of hypandrium about as long as lingula vs. distinctly longer than lingula (Fig. 9C vs. H); (6) in lateral view, distiphallus relatively long, about 9x as long as middle width vs. relatively short, about 7x as long as middle width (Fig. 9E vs. J); (7) in lateral view, two ventral processes of basiphallus convergent but not touching each other vs. more or less parallel (Fig. 9E vs. J); and (8) in lateral view, apico-ventral process relatively long vs. relatively short (appears associated with distiphallus length; Fig. 9E vs. J).

Mutin and Barkalov (1999), in their Russian Far East Syrphidae key, provided a couplet that distinguished *B. serarius* from *B. nipponensis* based on the presence or absence of yellow hairs on the scutellum. However, we found that this character is highly variable in the two species (Fig. 5), and thus should not be used as such. Ichige and Noshita (2008) and Takeuchi (2017) reached the same conclusion after examining Japanese specimens. In fact, the brownish yellow haired area of *B. serarius* males tended to be smaller than that of *B. nipponensis* males (Fig. 5A, B vs. C, D), but the variation is continuous and overlapped between the two species. The only conclusion from the analysis of this character is that males displaying a brownish yellow haired area larger than as depicted in Fig. 5B can be safely regarded as *B. nipponensis* (about 30% of *B. nipponensis* males but none of *B. serarius* males). This rule may be helpful in initially sorting out at least 30% of *B. nipponensis* males. This character is even more variable in females (Fig. 5E–H), we can only speculate that females with a brownish yellow haired area larger than those depicted in Fig. 5G and H (about 10% of all females) are more

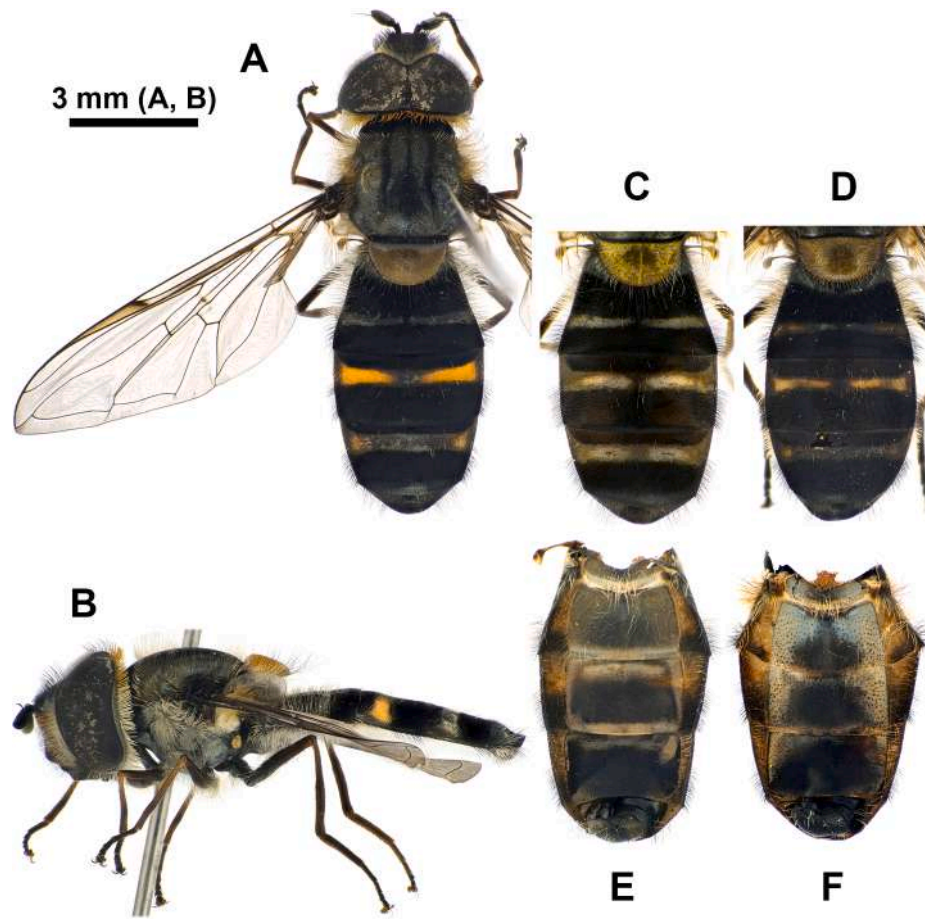


Fig. 2. *Betasyrphus nipponensis* males. (A, B) Body, dorsal and lateral view. (C–F) Abdomen, dorsal (C, D) and ventral view (E, F), showing a range of variation. Voucher specimen codes: A, B - BetNip_M2; C - BetNip_M10; D - BetNip_M7; E - BetNip_M6; F - BetNip_M4.

likely to belong to *B. nipponensis*.

Description of Korean material. Male. Predominantly blackish with 3 light grey to brownish yellow transverse bands on abdomen. Length and ratios: body length 8.90–12.00 mm; wing length 7.13–9.87 mm; head ratio 0.66–0.76; face ratio 0.43–0.45; eye ratio 0.47–0.54; gena-eye ratio 0.03–0.05; antenna-head ratio 0.46–0.52; postpedicel-pedicel ratio 3.50–4.60; arista-antenna ratio 0.81–0.90; wing ratio 3.29–3.34; wing-thorax ratio 2.22–2.37; vein M ratio 2.37–2.92; vein R_{4+5} ratio 3.27–3.53. Head (Fig. 4A, B, E, F) holoptic with eye contiguity about as long as vertical triangle; compound eye dark brown with slight purplish tinge, densely covered with relatively long yellowish hairs; vertex brownish black with black hairs; ocellar triangle brownish black with black hairs; occiput brownish black ground color with pale yellow to yellowish white pruinosity (pruinosity stronger in lower area), marginally covered with long erect orange to pale yellow hairs, shorter black hairs mixed in upper half (Fig. 1B); frons brownish black with black hairs, about posterior 1/3 dusted with yellow to pale yellow pruinosity (Fig. 4E, F); lunule bare, brownish black with brown medio-ventral and latero-ventral margins (Fig. 4A, B); antenna almost entirely brownish black (Fig. 4A, B, E, F); scape brownish black with short and stout black hairs on apical margin; pedicel brownish black with short and stout black hairs on apical margin; postpedicel almost entirely brownish black with ventro-basal brownish area (some specimens entirely brownish black); arista dark brown to brownish black, but often with brighter basal margin; face brownish yellow ground color, largely with black hairs mixed with brownish yellow hairs around the mouth and near the eyes (Fig. 4A, B); face with pale yellow to pale grey pruinosity (Fig. 4A, B); black longitudinal facial stripe from lower facial margin to about 2/3 position toward antennal sockets, about 0.3x as

wide as facial width, with rounded knob in middle, and almost bare (Fig. 1B, Fig. 4A, B); gena narrow, brownish black with moderate yellowish white pruinosity, with pale yellow hairs (black hairs sparse mixed in a few specimens). Thorax largely black ground color with bluish tinge and greyish pruinosity, with long wavy brownish yellow hairs (Fig. 1A, B); postpronotal lobe black, bare; notopleuron shiny black with wavy brownish yellow hairs (Fig. 1A, B); scutum subshiny black with 2 pairs of wide longitudinal greyish pruinosity bands (Fig. 1A; can be observed under appropriate lighting – Ssymank, 2010), median bands interrupted widely in middle; scutum mostly covered with wavy brownish yellow hairs but laterally mixed with some wavy black hairs; postalar callus shiny brownish black with wavy yellowish brown hairs but anteriorly mixed with some black hairs in most specimens; scutellum largely brownish yellow but baso-ventral corners narrowly brownish black (Fig. 5A, B); scutellum largely covered with wavy black hairs, but basal margin variably mixed with wavy brownish yellow hairs (Fig. 5A, B); proepimeron shiny black with pale yellow pruinosity, sparsely covered with short pale yellow hairs; anterior anepisternum black with pale yellow pruinosity, bare; posterior anepisternum black with pale yellow pruinosity, anterior 1/5 bare and posterior 4/5 covered with wavy pale yellow hairs (postero-dorsally mixed with wavy brownish hairs in some specimens); katapisternum black with upper and lower wavy brownish yellow hair patches; anterior anepimeron black with pale yellow pruinosity, covered with wavy pale yellow hairs (some specimens wavy brownish hairs mixed dorsally); dorsomedial and posterior anepimeron black with pale yellow pruinosity, bare; katepimeron subshiny black with pale yellow pruinosity, covered with wavy pale yellow hairs; meron subshiny black, dorsally slightly dusted with pale yellow pruinosity, bare; katatergite shiny black with pale yellow

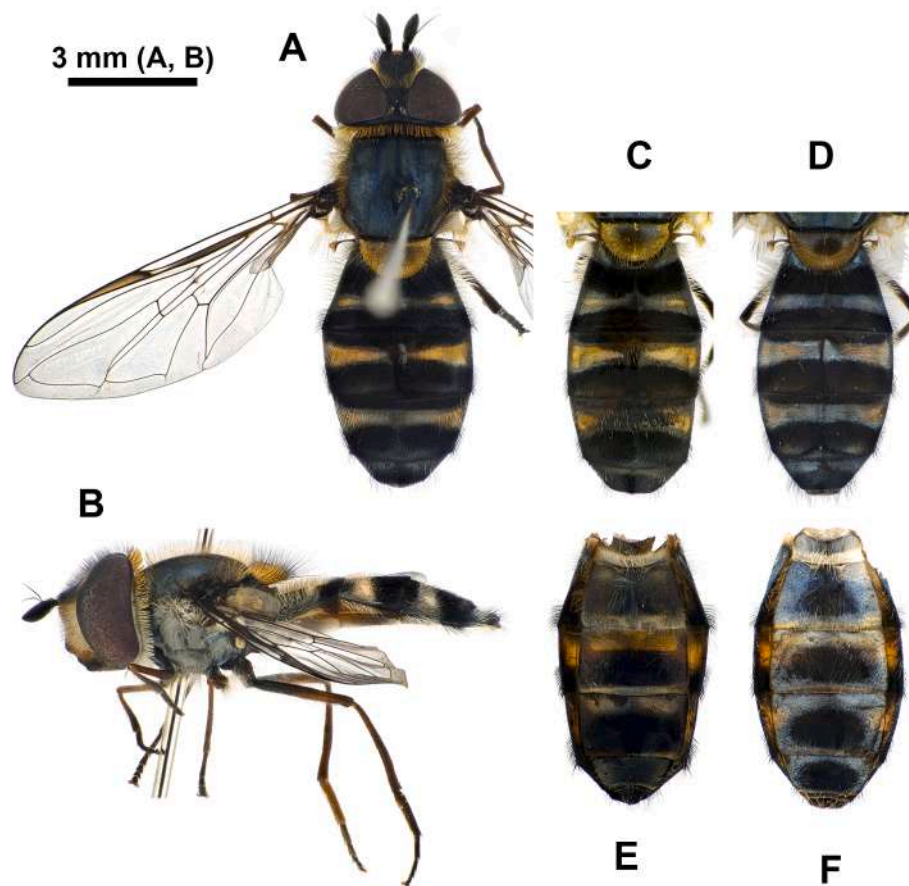


Fig. 3. *Betasyrphus serarius* or *B. nipponensis* females. (A, B) Body, dorsal and lateral view. (C–F) Abdomen, dorsal (C, D) and ventral view (E, F), showing a range of variation Voucher specimen codes: A, B -BetSp_F13; C - BetSp_F14; D - BetSp_F6; E - BetSp_F3; F - BetSp_F6.

pruinosity, densely covered with short pale yellow hairs; anatergite shiny black, bare; metasternum brownish black, bare; halter with stem brownish yellow to dark brown, knob variably mixed with light and dark brown coloration (Fig. 1A, C, D). Wing (Fig. 1A, B, Fig. 6A, B) largely hyaline with slight brownish tinge; veins yellowish brown to dark brown; tegula brownish black with short black hairs; basicosta brownish black, mostly with short brownish yellow hairs except short black hairs on baso-ventral side; vein C almost entirely covered with short black hairs except short brownish yellow hairs mixed on baso-ventral margin; pterostigma brownish yellow, basally with narrow 45° inwardly slanted dark brown longitudinal vitta (Fig. 6A); cell sc before pterostigma largely brownish yellow with about apical 1/8 hyaline; some areas basal to anterior branch of media and alular incision brownish yellow; distinct spurious vein shortly interrupted at about basal 1/3, with distinct knob at base of apical vein right after interruption; wing membrane largely covered with microtrichiae with basal bare areas as in Fig. 6B with some variation; apical 1/3 of cell br anterior to spurious vein predominantly microtrichose (bare portion no more than half within this region – Fig. 6B); upper and lower calypters pale yellow with darker margin, covered with long pale yellow to brownish marginal hairs; lower calypter with short sparse dorsal hairs. Legs: coxae and trochanters brownish black, with fore and mid coxae, and mid and hind trochanters mainly with black hairs mixed with some yellowish brown hairs; hind coxa and fore trochanter mainly with yellowish brown hairs mixed with some black hairs; femora basally brownish black and apically brown to dark brown; fore and mid femora postero-basally with long wavy brownish yellow hairs, postero-apically with shorter wavy black hairs (wave getting weaker towards apex); hind femora antero-basally with long wavy brownish yellow and black hairs mixed; tibiae brown with short black hairs; tarsomeres brownish black with fore and mid

tarsomeres entirely covered with short black hairs, with hind tarsomere covered with short black hairs dorsally and short brownish yellow hairs ventrally. Abdominal tergites (Fig. 1A, C, D) brownish black with wavy brownish yellow and black hairs (wave getting weaker towards apex); 3 light grey to brownish yellow transverse bands on tergites 2–4, with each band partially dusted with yellowish white pruinosity, reaching lateral margins, often interrupted in middle; tergite 1 subshiny with brownish yellow hairs; tergites 2–4 each with brownish yellow hairs anteriorly, black hairs posteriorly; tergite 5 brownish black with pair of antero-lateral yellowish grey pruinose specks, largely with black hairs but laterally mixed with few yellowish brown hairs; sternites 1–8 brownish black to dark brown ground color with 1–4 with pale yellowish pruinosity in various intensity (Fig. 1E vs. F show rough range of variation); sternite 1 with wavy pale yellow hairs; sternite 2 largely with pale yellow hairs, sometimes mixed sparsely with shorter black hairs; sternites 3–4 largely with short black hairs mixed sparsely with longer (at least 2x) pale yellow hairs; sternites 5–7 largely with black hairs; sternite 8 largely with brownish yellow hairs. Male genitalia (Fig. 9A–E): epandrium about as long as high in lateral view, densely with tiny hairs; cerci short, slightly seen in lateral view (Fig. 9A), narrow kidney shape in caudal view (Fig. 9B), with long brownish yellow hairs; surstylus relatively wide in caudal view (middle width about 1/3 of length when oriented to show broadest area), slightly curved anteriorly with rounded apex in lateral view, basally covered with long brownish yellow hairs, apically with short hairs; surstyler apodeme about as long as wide in ventral view (Fig. 9D); hypandrium (Fig. 9A, C) with finger-shaped lingula with pointed apex in lateral view, lateral protuberance about as long as lingula; superior lobe twice as high as long, sparsely covered with short brownish yellow hairs laterally, with strong upward hook subapically (Fig. 9B, C); distiphallus laterally flattened, down-curved

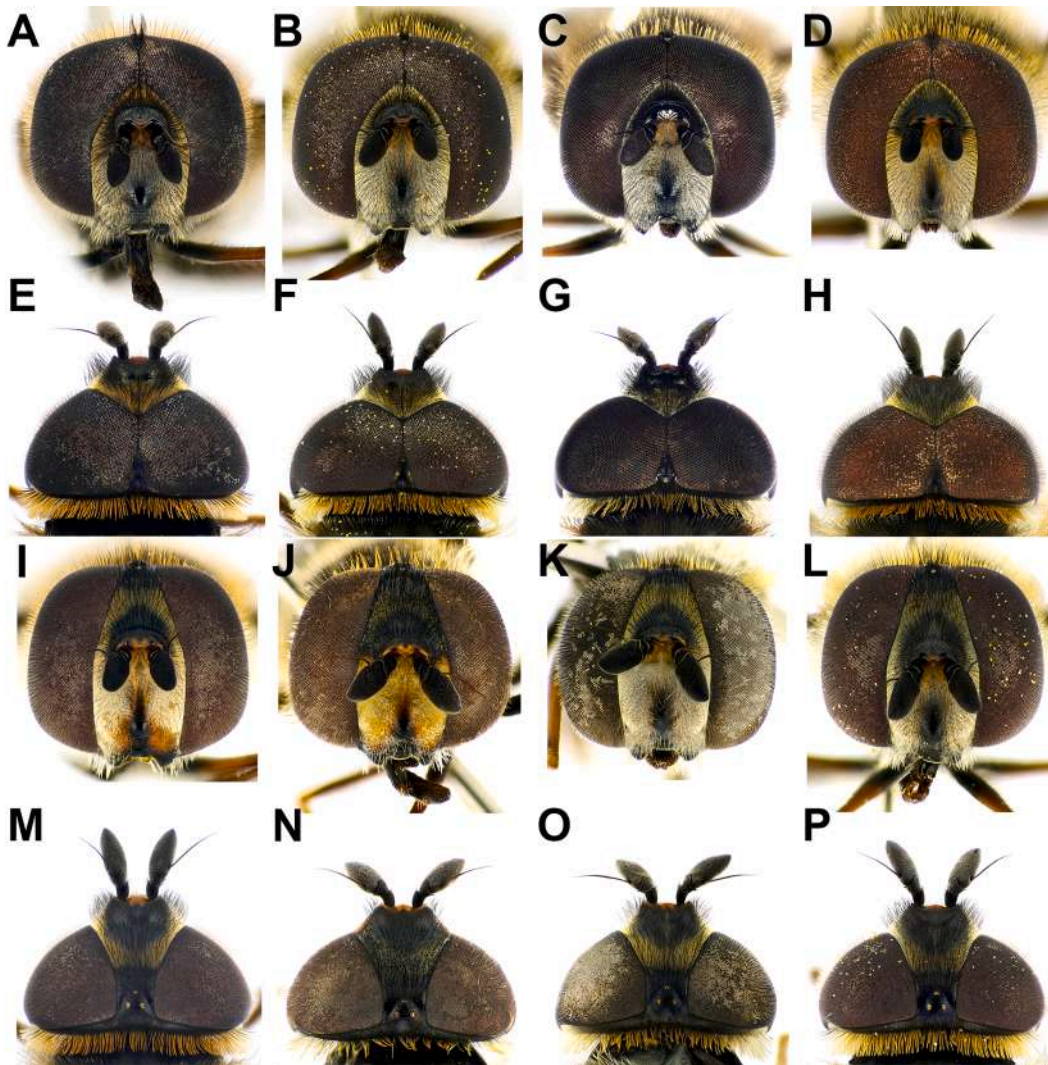


Fig. 4. Heads, frontal view and dorsal view, showing a range of variation. (A, B, E, F) *Betasyrphus serarius* males. (C, D, G, H) *B. nipponensis* males. (I–P) *B. serarius* or *B. nipponensis* females. Voucher specimen codes: A, E - BetSer_M2; B, F - Bet Ser_M3; C, G - BetNip_M1; D, H - BetNip_M11; I, M - BetSp_F13; J, N - BetSp_F15; K, O - BetSp_F2; L, P - BetSp_F8.

with apical 1/3 gradually pointed, about 9x as long as middle width in lateral view (Fig. 9E); 2 ventral processes of basiphallus convergent but not touching each other in lateral view, apico-ventral process about half as long as distiphallus; aedeagal apodeme with basal half ventrally swollen; sperm duct about 2/3 as long as aedeagal apodeme; ejaculatory apodeme rod-shape, about 1/3 as long as aedeagal apodeme.

Female. Since we were not able to distinguish females of *B. serarius* and *B. nipponensis*, the following female characteristics are presumably those of both species different from males. Length and ratios: body length 9.20–11.70 mm; wing length 7.67–9.47 mm; head ratio 0.67–0.71; face ratio 0.42–0.45; eye ratio 0.49–0.55; gena-eye ratio 0.01–0.03; antenna-head ratio 0.58–0.62; postpedicel-pedicel ratio 4.67–5.67; arista-antenna ratio 0.77–0.83; wing ratio 2.67–3.38; wing-thorax ratio 2.33–2.82; vein M ratio 2.33–2.82; vein R_{4+5} ratio 3.06–3.50. Head (Fig. 4I–P) dichoptic with vertex about 0.15x as wide as head in dorsal view; frons brownish black in ground color with black hairs, variably dusted with yellow to pale yellow pruinosity except for semicircular area posterior to lunule and about 1/3 area anterior to ocellar triangle; face brownish yellow ground color with black and bare longitudinal stripe from facial margin (about 0.14–0.29x as wide as facial width), brownish yellow area slightly to heavily covered with pale yellow to pale grey pruinosity, covered also with variably mixed black and brownish yellow to pale yellow hairs. Thorax: scutellum covered

with variably mixed wavy black and brownish yellow hairs (Fig. 5E–H). Wing (Fig. 7): wing largely covered with microtrichiae with wider and more variable basal bare areas than those of males; cell br largely bare. Abdomen: abdominal bands often slightly thicker than those of males (Fig. 3A, C, D); sternite 5 sometimes with pruinose area along anterior and lateral margin (Fig. 3F). Female postabdomen (Fig. 10) largely microtrichose; tergites 6 and 7, and sternites 6 and 7 sparsely with short black hairs apically; tergite 8 sparsely covered with short black hairs on posterior 1/2–1/4, anteriorly with 3 apically peaked brownish sclerite (large middle one plus short lateral ones) plus more or less translucent posterior membranous area (Fig. 10B); epiproct with pair of sclerotized plates; cercus short, brown, covered with short brownish hairs; sternite 8 covered with short black hairs except for basal 1/5–2/5 area, more or less rectangular shape with anterior 2/3 sclerotized and posteriorly membranous; sternite 9 shallowly triangular, with short and stout hairs (Fig. 10D).

Material examined (males only). Korea: Majority of the following specimens are deposited in YSUW, other depositories indicated in parentheses. Chungcheongbuk-do: 10♂, Jecheon-si, Songhak-myeon, Mt. Songhaksan, N37°12'29" E128°16'7", 3.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 3♂, Yeongdon-gun, Sangchon-myeon, Goja-ri, Mt. Sambongsan, N36°05'33.0" E127°50'08.7", 25.VI.2019, S.S. Euo, C.O. Kim, and J.H. Choi; Gangwon-do: 5♂, Hongcheon-gun, Nae-myeon,

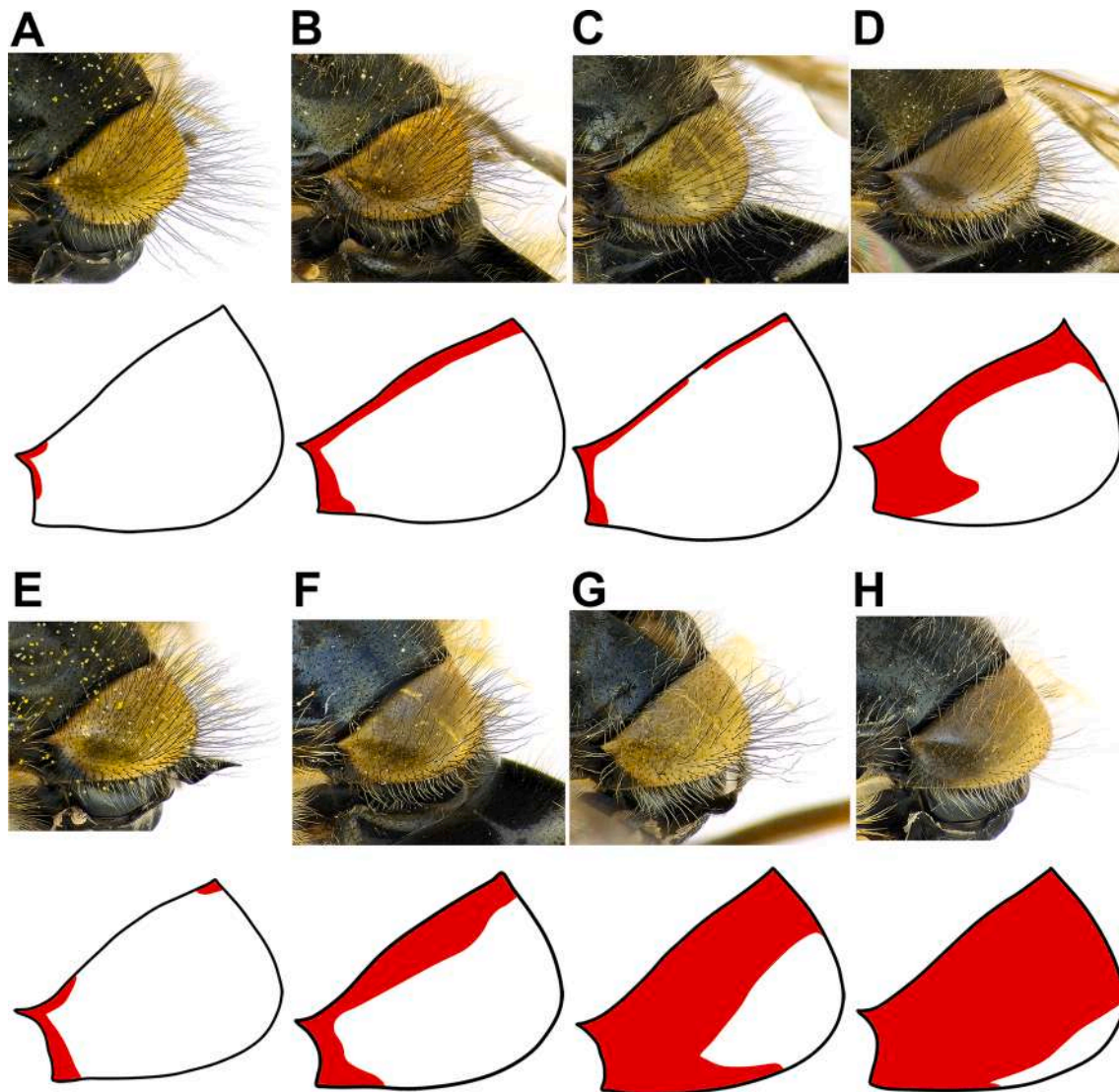


Fig. 5. Scutella in dorso-lateral view, showing a range of variation. (A, B) *Betasyrphus serarius* males. (C, D) *B. nipponensis* males. (E–H) *B. serarius* or *B. nipponensis* females. The simplified diagrams below each photograph show the distribution of brownish yellow hairs (red areas). Voucher specimen codes: A - BetSer_M3; B - BetSer_M1; C - BetNip_M10; D - BetNip_M9; E - BetSp_F8; F - BetSp_F14; G - BetSp_F2; H - BetSp_F4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Bangnae-ri, N37°51'11" E128°16'52", 29.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 2♂, ditto, 13.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Hongcheon-gun, Nae-myeon, Gwangwon-ri, Woldoon-gol, N37°50'52" E128°25'24", 26.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 5♂, Hongcheon-gun, Nae-myeon, Mt. Gyeongsan, N37°43'41" E128°27'55", 18.VIII.2020, S.S. Euo, and C.O. Kim (NIBR); 1♂, Jeongseon-gun, Gohan-eup, Mt. Hambaeksan, Manhang-jae, N37°8'53" E128°54'14", 23.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 2♂, ditto, 2.VIII.2017, C.O. Kim, W.R. Ha, and J.H. Choi (NIBR); 1♂, Jeongseon-gun, Jeongseon-eup, Mt. Gariwangsan, N37°27'40" E128°33'48", 27.IX.2011, S.W. Suk, and Y.B. Lee (KNA); 2♂, Jeongseon-gun, Nam-myeon, Yupyeong-ri, Mt. Mindungsan, N37°16'10" E128°46'49", 10.VIII.2019, S.S. Euo, C.O. Kim, and J.H. Choi (KNA); 5♂, ditto, 12.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Samcheok-si, Geunsan-dong, Mt. Geunsan, N37°24'48" E129°08'29", 6.V.2017, S.S. Euo et al.; 2♂, ditto, 13.V.2020, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Wonju-si, Heungeop-myeon, Maeji-ri, Yonsei Univ. Mirae Campus, N37°17'10" E127°54'01", 7.X.2016, S.S. Euo, and C.O. Kim; 5♂, ditto, 28.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 5♂, ditto, 1.X.2017, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 5♂, ditto, 13.IX.2018,

S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 1♂, ditto, 17.IX.2018, S.S. Euo; 1♂, ditto, 28.IX.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, ditto, 26.V.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, ditto, 10.X.2018, S.S. Euo; 1♂, Wonju-si, Panbu-myeon, Seogok-ri, Mt. Baegunsan, N37°14'59" E127°57'46", 19.VIII.2007, H.S. Lee, and S.W. Suk (KNA); 14♂ (5♂ in NIBR), 1.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi; 4♂, ditto, 23.VI.2017, C.O. Kim, and J.H. Choi; 5♂, ditto, 27.VI.2017, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 4♂, Yeongwol-gun, Jundong-myeon, Hwawon-ri, N37°09'40.1" E128°38'11.2", 12.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Yeongwol-gun, Jundong-myeon, Heungwol-ri, Mt. Taehwasan, N37°07'03.3" E128°29'07.4", 30.VII.2019, S.S. Euo, C.O. Kim, and J.H. Choi (KNA); 3♂, ditto, 2.VII.2020, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); Gyeongsangnam-do: 5♂, Hamyang-gun, Hamyang-eup, Jungnim-ri, Mt. Sambongsan, N35°26'50" E127°40'10", 16.VII.2020, S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); Jeju-do: 24♂ (5♂ in NIBR), Jeju-si, Aewol-eup, Bongserong-ri, Handae Oreum, N33°21'23" E126°25'29", 19.VI.2017, H.Y. Han, K.E. Ro, and S.S. Euo; 5♂, ditto, 13.VI.2018, H.Y. Han, K.E. Ro, and S.S. Euo (NIBR); Jeollanam-do: 5♂, Gwangyang-si, Ongnyong-myeon, from Baegunsa Temple to Mt. Baegunsan, N35°6'23" E127°37'17", 8.IX.2017,

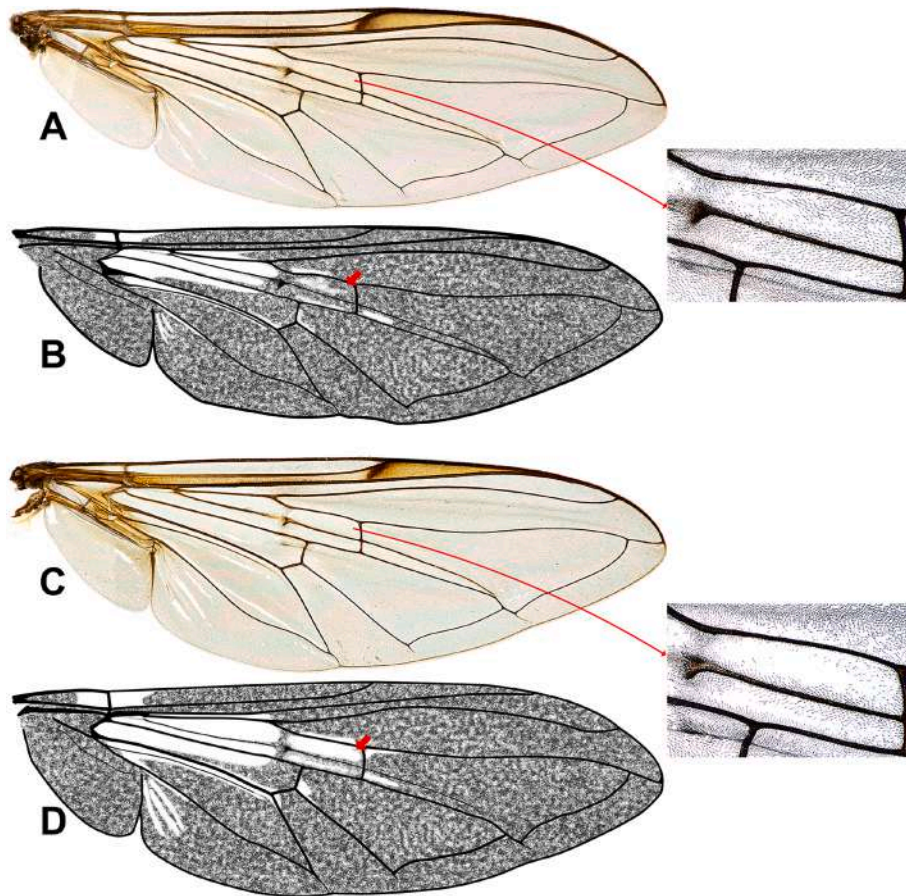


Fig. 6. Wings and wing microtrichia distribution (WMD) diagrams of *Betasyrphus* males. (A, B) *B. serarius* male. (C, D) *B. nipponensis* male. Voucher specimen codes: A, B - BetSer_M7; C, D - BetNip_M2.

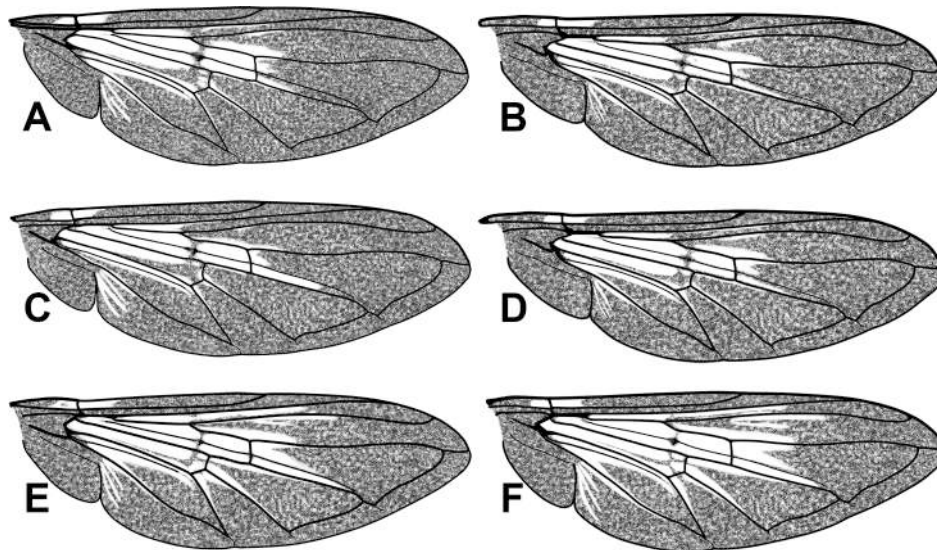


Fig. 7. Wing microtrichia distribution (WMD) diagrams of *Betasyrphus serarius* or *B. nipponensis* females, showing a range of variation. Voucher specimen codes: A - BetSp_F1; B - BetSp_F11; C - BetSp_F8; D - BetSp_F6; E - BetSp_F4; F - BetSp_F2.

S.S. Euo, C.O. Kim, and J.H. Choi (NIBR); 7♂ (5♂ in NIBR), ditto, 27.V.2017, S.S. Euo et al.; 6♂, Gwangyang-si, Ongnyong-myeon, Mt. Baegunsan from Hanjae hill, N35°6'23" E127°37'17", 16.V.2019, S.S. Euo, C.O. Kim, and J.H. Choi; 5♂, Haenam-gun, Haenam-eup, Gugyo-ri, Mt. Geumgangsán, N34°35'28" E126°36'7", 17.V.2019, S.S. Euo, C.O. Kim, and J.H. Choi; 2♂, Wando-gun, Wando-eup, from Sosepo Port to

Sanghwangbong, N34°20'02" E126°40'19", 28.V.2017, S.S. Euo et al.; 5♂, Yeosu-si, Deokchung-dong, Mt. Maraesan from Chungminsá Temple, N34°45'55" E127°44'31", 23.IV.2017, S.S. Euo, C.O. Kim, and W.R. Ha (NIBR).

Additional material examined (presumably mixed females of *B. serarius* and *B. nipponensis*; see the Remarks of *B. serarius*). Korea:

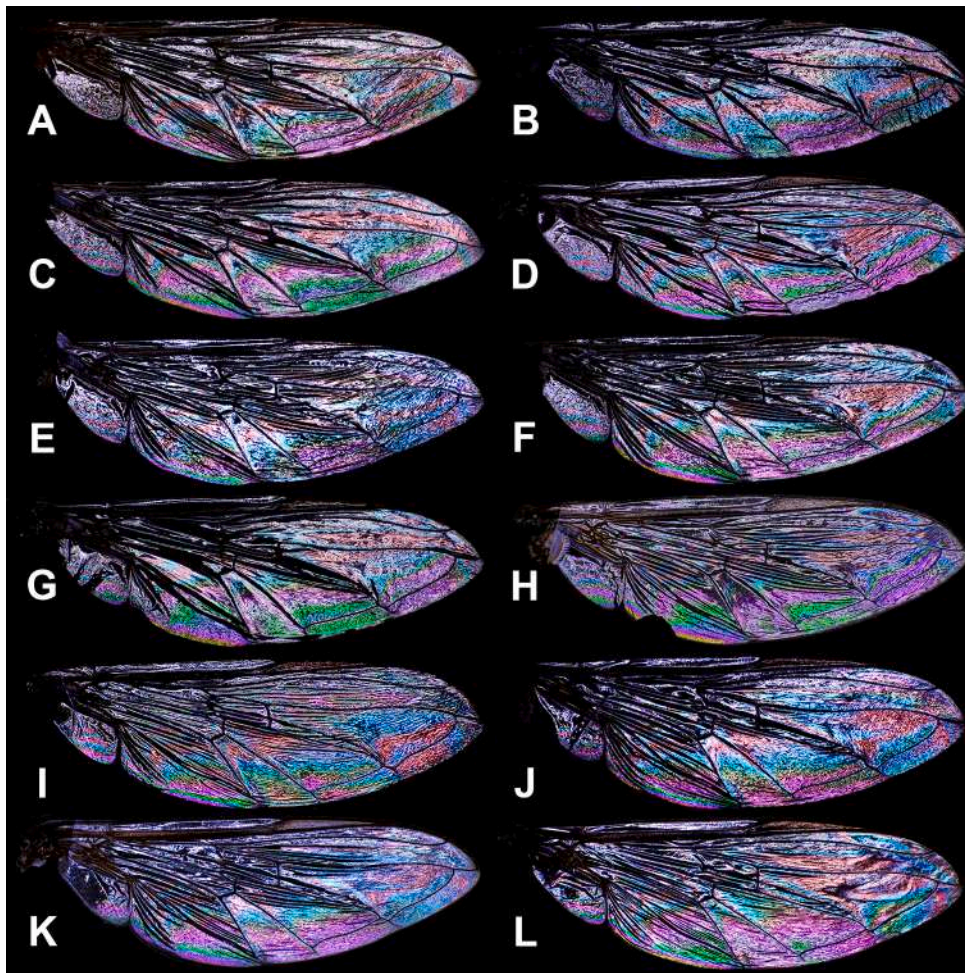


Fig. 8. Wing interference patterns (WIPs), showing a range of variation. (A–D) *Betasyrphus serarius* males. (E–H) *B. nipponensis* males: (G, H) right and left (mirror-reversed) wings of the same individual. (I–L) *B. serarius* or *B. nipponensis* females. Voucher specimen codes: A - BetSer_M8; B - BetSer_M10; C - BetSer_M7; D - BetSer_M9; E - BetNip_M2; F - BetNip_M5; G, H - BetNip_M6; I - BetSp_F8; J - BetSp_F1; K - BetSp_F2; L - BetSp_F6.

following specimens are deposited in YSUW. Chungcheongbuk-do: 1♀, Jecheon-si, Geumseong-myeon, Yanghwa-ri, N37°4'6" E128°12'10", 27.IX.2012, S.W. Suk, and H.S. Lee; 2♀, Yeongdong-gun, Sangchon-myeon, Goja-ri, Mt. Sambongsan, N36°05'33.0" E127°50'08.7", 26.V.2020, S.S. Euo et al.; 2♀, ditto, 25.VI.2019, S.S. Euo, C.O. Kim, and J.H. Choi; Gangwon-do: 1♀, Donghae-si, Samhwa-dong, Mureung valley, N37°28'02" E129°01'53", S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, Hoengseong-gun, Dunnae-myeon, Sapgyo-ri, Mt. Cheongtaesan, N37°30'40" E128°18'01", 7.VII.2001, D.S. Choi, S.K. Kim, and D.S. Kang; 1♀, Hongcheon-gun, Nae-myeon, Bangnae-ri, N37°51'11" E128°16'52", 6.X.2020, S.S. Euo, C.O. Kim, S.P. Han; 4♀, ditto, 13.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 2♀, Hongcheon-gun, Nae-myeon, Gwangwon-ri, Woldoon-gol, N37°50'52" E128°25'24", 26.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 2♀, ditto, 12.VIII.2019, S.S. Euo, and C.O. Kim; 1♀, ditto, 5.X.2017, S.S. Euo, and C.O. Kim; 1♀, Inje-gun, Girin-myeon, Seori, Mt. Maebongsan, N37°56'43.1" E128°13'40", 2.VI.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 2♀, Jeongseon-gun, Nam-myeon, Yupyong-ri, Mt. Mindungsan, N37°16'10" E128°46'49", 8.VI.2020, C.O. Kim et al.; 2♀, ditto, 4.VII.2008, H.Y. Han et al.; 2♀, ditto, 12.VII.2017, S.S. Euo, C.O. Kim, and W.R. Ha; 1♀, ditto, 26.VII.2017, S.S. Euo et al.; 4♀, ditto, 12.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 3♀, ditto, 10.VIII.2019, S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, Pyeongchang-gun, Jinbu-myeon, Jangjeon-ri, Jangjeon valley, N37°27'59.2" E128°32'18.7", 5.VI.2019, S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, ditto, 29.IX.2020, S.S. Euo, and C.O. Kim; 2♀, ditto, 5.VI.2020, S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, Samcheok-si, Dogye-eup, Mugeon-ri, Moss waterfall, N37°15'32.6"

E129°06'34.8", 17.IX.2019, S.S. Euo, and C.O. Kim; 1♀, Samcheok-si, Geunsan-dong, Mt. Geunsan, N37°24'48" E129°08'29", 6.V.2017, S.S. Euo et al.; 1♀, Wonju-si, Gwirae-myeon, Unnam-2ri, Darigol, N37°10'51" E127°56'16.2", 4.V.2017, S.S. Euo, and W.R. Ha; 1♀, Wonju-si, Gwirae-myeon, Unnam-ri, from Inbeolgol to Mt. Sibjabong, N37°12'40" E127°55'50", 23.IX.2016, S.S. Euo, and C.O. Kim; 1♀, Wonju-si, Gwirae-myeon, from Cheoneunsa Temple to Mt. Sibjabong, N37°13'34" E127°54'36", 28.IV.2017, S.S. Euo, C.O. Kim, and W.R. Ha; 2♀, Wonju-si, Heungeop-myeon, Maeji-ri, Yonsei Univ. Mirae Campus, N37°17'10" E127°54'01", 28.VI.2001, D.S. Choi; 1♀, ditto, 7.X.2016, S.S. Euo, and C.O. Kim; 1♀, ditto, 28.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, ditto, 3.X.2017, S.S. Euo, and C.O. Kim; 1♀, ditto, 10.X.2018, S.S. Euo; 1♀, Wonju-si, Panbu-myeon, Seogok-ri, Mt. Baegunsan, N37°14'59" E127°57'46", 16.VI.2002, D.S. Choi et al.; 1♀, ditto, 1.IX.2017, S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, ditto, 23.VI.2017, C.O. Kim, and J.H. Choi; 1♀, Yeongwol-gun, Jungdong-myeon, Hwawon-ri, N37°09'40.1" E128°38'11.2", 12.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♀, Yeongwol-gun, Yeongwol-eup, Heungwol-ri, Mt. Taehwasan, N37°07'03.3" E128°29'07.4", 16.VIII.2018, H.Y. Han et al.; and Jeollabuk-do: 3♀, Sunchang-gun, Bokheung-myeon, Hwayang-ri, Mt. Hwagaesan, N35°27'42" E128°54'8", 17.VII.2020, C.O. Kim, and J.H. Choi.

Distribution. Korea, Japan, China, Russian Far East, Oriental Region, New Guinea, Australia, Madagascar. This distribution data should be revised when conducting a more comprehensive study covering specimens from all these regions in the future. Even though limited by the

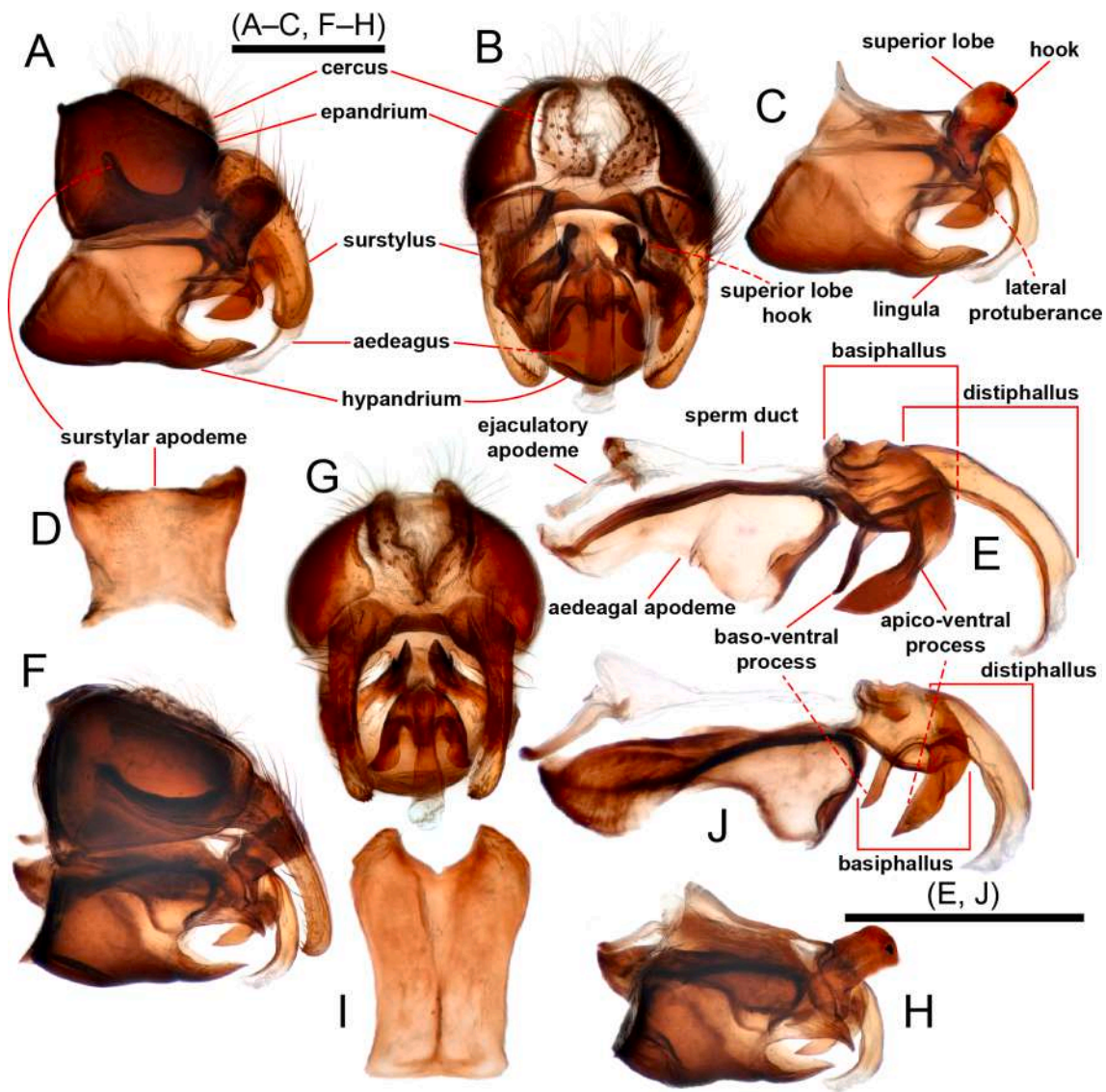


Fig. 9. Male genitalia. (A–E) *Betasyrphus serarius*: (A) lateral view; (B) caudal view; (C) hypandrium, lateral view; (D) surstylar apodeme, ventral view; (E) aedeagus, lateral view. (F–J) *B. nipponensis*: (F) lateral view; (G) caudal view; (H) hypandrium, lateral view; (I) surstylar apodeme, ventral view; (J) aedeagus, lateral view. Scale bars: 0.3 mm. Voucher specimen codes: A–E - BetSer_M3; F–J - BetNip_M11.

sample size, our DNA barcoding analysis of non-East Asian *Betasyrphus* public sequences that were deposited as either *B. serarius* or *B. sp.* appear to be independent species closely related to both *B. serarius* and *B. nipponensis* (see DNA barcoding of *Betasyrphus* and the related taxa).

Biology. *Betasyrphus serarius* is one of the most common syrphid species in Korea. In this country, its flight period spans from April to October with a peak in June. Male flies have often been observed while hovering over mountain tops and ridges. On the other hand, females (either belonging to *B. serarius* or *B. nipponensis*) have been more often observed while feeding on flower nectar. They are also known to prefer laying eggs on small to medium-sized young aphid colonies (Kan, 1988). In India, these insects require 24–26 days to develop from eggs into adults, with a larval period of approximately 13 days (Bijaya et al., 1996). During their larval period, one larva could consume 277–400 individuals of *Brevicoryne brassicae* (cabbage aphid). See Biology of the genus *Betasyrphus* for the prey and host plant records.

Remarks. As mentioned in the Introduction and Diagnosis, only males of the two *Betasyrphus* species in Korea could be distinguished, while females remained inseparable. One of these species could be clearly recognized as *B. nipponensis* due to the known male genitalic characters

of the holotype (Ôhara, 1984). However, it is still unknown whether *B. serarius* is a senior synonym of *B. nipponensis* or *B. serarius* sensu Ôhara (1984), because the only known syntypes of *B. serarius* are female (Ssymank, 2010; Denner, 2017). So we follow Ôhara's species concept for *B. serarius* until new material from its type locality is available.

Betasyrphus nipponensis (Goot, 1964) (Figs. 2, 4–6, 9)

(Korean name: Dalm-Eun-Geom-Jeong-Neop-Jeok-Kkot-Deung-E; new Korean record).

Syrphus fulvicornis Shiraki and Edashige, 1953: 102 (Type-locality: Mt. Ishizuchi, Ehime, Shikoku, Japan; holotype ♂, EUMJ).

Syrphus nipponensis Goot, 1964: 218 (new name for *fulvicornis* Shiraki and Edashige, 1953, nec *fulvicornis* Meigen, 1822; see Remarks).

Epistrophe nipponensis (Goot, 1964): Peck, 1988: 21 (in Palaeartic catalog).

Betasyrphus nipponensis (Goot, 1964): Ôhara, 1984: 534 (comb. nov., and redescription); Mutin and Barkalov, 1997: 184 (new records in Sakhalin and the Kuril Islands); Mutin and Barkalov, 1999: 376 (in FE Russia key); Sivova, 2003: 121 (biology and description of immature

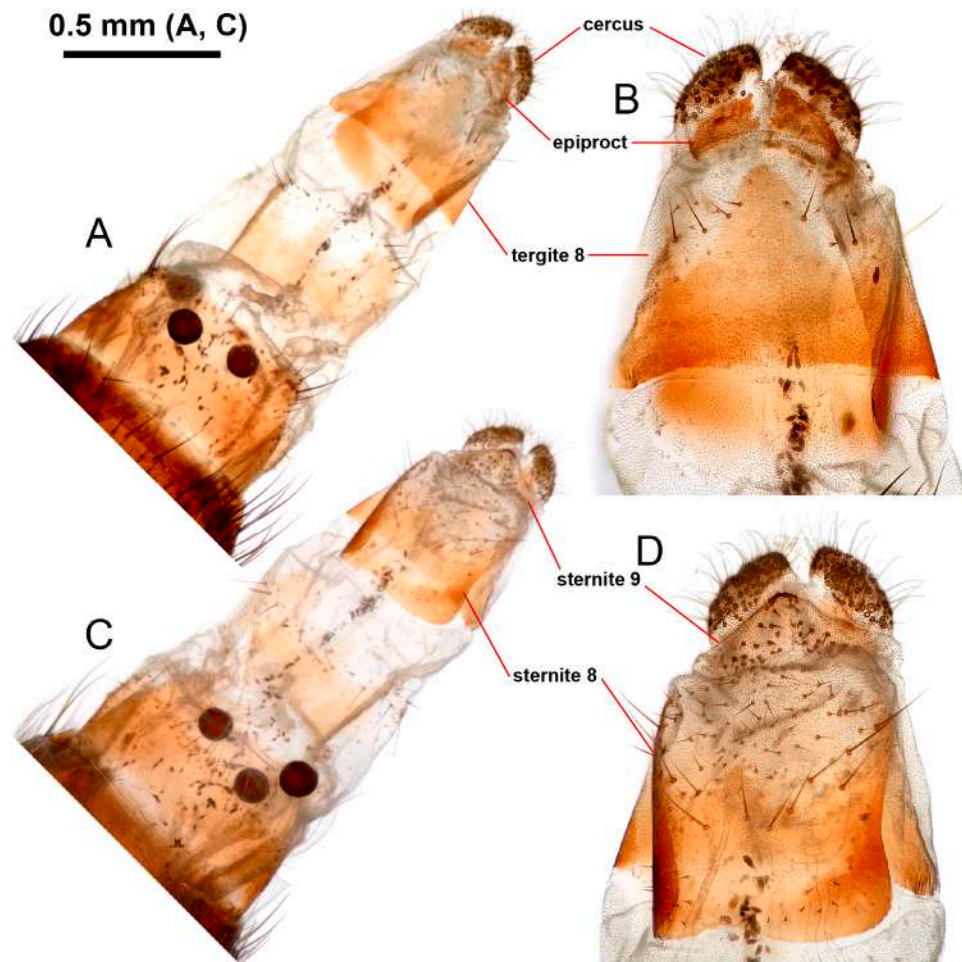


Fig. 10. Postabdomen of *Betasyrphus serarius* or *B. nipponensis* female: (A, B) dorsal view; (C, D) ventral view. Voucher specimen code: A–D - BetSp F2.

stages in FE Russia); Ôhara et al., 2014: 465 (in Japanese catalog).

Diagnosis. See Diagnosis of *B. serarius*.

Description of Korean material. Male. Body length 9.1–11.6 mm; wing length 7.87–9.30 mm; head ratio 0.64–0.71; face ratio 0.44–0.48; eye ratio 0.46–0.51; gena-eye ratio 0.03–0.04; antenna-head ratio 0.50–0.57; postpedicel-pedicel ratio 4.17–4.80; arista-antenna ratio 0.69–0.90; wing ratio 3.07–3.40; wing-thorax ratio 2.39–2.56; vein M ratio 2.38–2.70; vein R_{4+5} ratio 3.16–3.47. Head (Fig. 4C, D, G, H) holoptic, eye contiguity as long as vertical triangle; compound eye dark brown with slight purplish tinge, densely covered with relatively long yellowish hairs; vertex brownish black with black hairs; ocellar triangle brownish black with black hairs; occiput brownish black ground color with pale yellow to yellowish white pruinosity (pruinosity stronger in lower area), marginally covered with long erect orange to pale yellow hairs, shorter black hairs mixed in upper half (Fig. 2B); frons brownish black with black hairs, about posterior 1/3, dusted with yellow to pale yellow pruinosity (dusted area tends to be slightly shorter than in *B. serarius*; Fig. 4C, D, G, H vs. A, B, E, F); lunule bare, brownish black with brown medio-ventral and latero-ventral margins (Fig. 4C, D); antenna almost entirely brownish black (Fig. 4C, D, G, H); scape brownish black with short and stout black hairs on apical margin; pedicel brownish black with short and stout black hairs on apical margin; postpedicel almost entirely brownish black with ventro-basal brownish area (some specimens entirely brownish black); arista dark brown to brownish black, but often with brighter basal margin; face brownish yellow ground color, largely with black hairs mixed with brownish yellow hairs around the mouth and near the eyes (Fig. 4C, D); face with pale yellow to pale grey pruinosity (Fig. 4C, D); black longitudinal facial

stripe from lower facial margin to about 2/3 position toward antennal sockets, 0.26–0.29x as wide as facial width, with rounded knob in middle (Fig. 2B, 4C, D); gena narrow, brownish black with moderate yellowish white pruinosity, with pale yellow hairs (black hairs sparse mixed in a few specimens). Thorax largely black ground color with bluish tinge and greyish pruinosity, with long wavy brownish yellow hairs (Fig. 2A, B); postpronotal lobe black, bare; notopleuron shiny black with wavy brownish yellow hairs (Fig. 2A, B); scutum subshiny black with 2 pairs of wide longitudinal greyish pruinose bands (Fig. 2A; can be observed under appropriate lighting – Ssymank, 2010), median bands interrupted widely in middle; scutum mostly covered with wavy brownish yellow hairs but laterally mixed with some wavy black hairs; postalar callus shiny brownish black with wavy yellowish brown hairs but anteriorly mixed with some black hairs in most specimens; scutellum largely brownish yellow but baso-ventral corners narrowly brownish black (Fig. 5C, D); scutellum largely covered with wavy black hairs, but wavy brownish yellow hairs basally mixed, some specimens with brownish yellow hairs distributed as large as about basal 1/3 (Fig. 5C, D); proepimeron shiny black with pale yellow pruinosity, sparsely covered with short pale yellow hairs; anterior anepisternum black with pale yellow pruinosity, bare; posterior anepisternum black with pale yellow pruinosity, anterior 1/5 bare and posterior 4/5 covered with wavy pale yellow hairs (postero-dorsally mixed with wavy brownish hairs in some specimens); katepisternum black with upper and lower wavy brownish yellow hair patches; anterior anepimeron black with pale yellow pruinosity, covered with wavy pale yellow hairs (some specimens wavy brownish hairs mixed dorsally); dorsomedial and posterior anepimeron black with pale yellow pruinosity, bare; katepimeron

subshiny black with pale yellow pruinosity, covered with wavy pale yellow hairs; meron subshiny black, dorsally slightly dusted with pale yellow pruinosity, bare; katatergite shiny black with pale yellow pruinosity, densely covered with short pale yellow hairs; anatergite shiny black, bare; metasternum brownish black, bare; halter with stem brownish yellow to dark brown, knob variably mixed with light and dark brown coloration (Fig. 2A, C, D). Wing (Fig. 2A, B, Fig. 6C, D) largely hyaline with slight brownish tinge; veins yellowish brown to dark brown; tegula brownish black with short black hairs; basicosta brownish black, mostly with short brownish yellow hairs except short black hairs on baso-ventral side; vein C almost entirely covered with short black hairs except short brownish yellow hairs mixed on baso-ventral margin; pterostigma brownish yellow, basally with narrow 45° inwardly slanted dark brown longitudinal vitta (Fig. 6C); cell sc before pterostigma largely brownish yellow with about apical 1/7–1/6 hyaline; some areas basal to anterior branch of media and alular incision brownish yellow; distinct spurious vein shortly interrupted at about basal 1/3, with distinct knob at base of apical vein right after interruption; wing membrane largely covered with microtrichiae with basal bare areas as in Fig. 6D with some variation; apical 1/3 of cell br anterior to spurious vein almost bare except for marginal area (Fig. 6D); upper and lower calypters pale yellow with darker margin, covered with long pale yellow to brownish marginal hairs; lower calypter with short sparse dorsal hairs. Legs: coxae and trochanters brownish black, with fore and mid coxae, and mid and hind trochanters mainly with black hairs mixed with some yellowish brown hairs; hind coxa and fore trochanter mainly with yellowish brown hairs mixed with some black hairs; femora basally brownish black and apically brown to dark brown; fore and mid femora postero-basally with long wavy brownish yellow hairs, postero-apically with shorter wavy black hairs (wave getting weaker towards apex); hind femora antero-basally with long wavy brownish yellow and black hairs mixed; tibiae brown with short black hairs; tarsomeres brownish black with fore and mid tarsomeres entirely covered with short black hairs, with hind tarsomere covered with short black hairs dorsally and short brownish yellow hairs ventrally. Abdominal tergites (Fig. 2A, C, D) brownish black with wavy brownish yellow and black hairs (wave getting weaker towards apex); 3 light grey to brownish yellow transverse bands on tergites 2–4, with each band partially dusted with yellowish white pruinosity, reaching lateral margins, often interrupted in middle; tergite 1 subshiny with brownish yellow hairs; tergites 2–4 each with brownish yellow hairs anteriorly, black hairs posteriorly; tergite 5 brownish black with pair of antero-lateral yellowish grey pruinose specks, largely with black hairs but laterally mixed with few yellowish brown hairs; sternites 1–8 brownish black to dark brown ground color with 1–4 with pale yellowish pruinosity in various intensity (Fig. 2E vs. F show rough range of variation); sternite 1 with wavy pale yellow hairs; sternite 2 largely with pale yellow hairs, sometimes mixed sparsely with shorter black hairs; sternites 3–4 largely with short black hairs mixed sparsely with longer (at least 2x) pale yellow hairs; sternites 5–7 largely with black hairs; sternite 8 largely with brownish yellow hairs. Male genitalia (Fig. 9F–J): epandrium about 1.3x as long as high in lateral view, densely with tiny hairs; cerci short, slightly seen in lateral view (Fig. 9F), narrow kidney shape in caudal view (Fig. 9G), with long brownish yellow hairs; surstylus narrow in caudal view (middle width about 1/8 of length when oriented to show broadest area), slightly curved anteriorly with anteroapically pointed apex in lateral view, basally covered with long brownish yellow hairs, apically with short hairs; surstylar apodeme at least 1.5x longer than wide in ventral view (Fig. 9I); hypandrium (Fig. 9F, H) with finger-shaped lingula with pointed apex in lateral view (slightly narrower than that of *B. serarius*), lateral protuberance distinctly longer than lingula; superior lobe twice as high as long, sparsely covered with short brownish yellow hairs laterally, with strong upward hook subapically (hook much smaller than that of *B. serarius*; Fig. 9G, H); distiphallus laterally flattened, down-curved with apical 1/3 gradually pointed, about 7x as long as middle width in lateral view (Fig. 9J); 2 ventral processes of basiphallus more or

less parallel in lateral view, apico-ventral process about half as long as distiphallus; aedeagal apodeme with about basal 1/3 ventrally swollen; sperm duct about 3/4 as long as aedeagal apodeme; ejaculatory apodeme rod-shape, about 1/3 as long as aedeagal apodeme.

Female. See Description of Korean material of *B. serarius*.

Material examined (males only). KOREA: Majority of the following specimens are deposited in YSUW, except for the one with other depositories indicated in parentheses. Chungcheongbuk-do: 1♂, Yeongdong-gun, Sangchon-myeon, Goja-ri, Mt. Sambongsan, N35°26'50" E127°40'10", 25.VI.2019, S.S. Euo, C.O. Kim, and J.H. Choi; Gangwon-do: 1♂, Hongcheon-gun, Nae-myeon, Bangnae-ri, N37°51'11" E128°16'52", 13.X.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Hongcheon-gun, Nae-myeon, Gwangwon-ri, Woldoon-gol, N37°50'52" E128°25'24", 16.VI.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 2♂ (1♂ in NIBR), Inje-gun, Girin-myeon, Seo-ri, Mt. Maebongsan, N37°56'43.1" E128°13'40", 6.VII.2017, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Jeongseon-gun, Nam-myeon, Yuyeong-ri, Mt. Mindongsan, N37°16'10" E128°46'49", 13.V.2017, S.S. Euo et al.; 1♂, ditto, 12.VII.2018, S.S. Euo, C.O. Kim, and J.H. Choi; 1♂, Pyeongchang-gun, Jinbu-myeon, Jangjeon-ri, Jangjeon valley, N37°27'59.2" E128°32'18.7", 8.X.2019, S.S. Euo, and C.O. Kim; 2♂, Wonju-si, Heungeop-myeon, Maeji-ri, Yonsei Univ. Mirae Campus, N37°17'10" E127°54'01", 13.VI.2001(em. 17.VI.2001), D.S. Choi; 1♂, ditto, 10.X.2018, S.S. Euo; 1♂, Wonju-si, Panbu-myeon, Seogok-ri, Mt. Baegunsan, N37°14'59" E127°57'46", 23.VI.2017, C.O. Kim, and J.H. Choi; 1♂, ditto, 19.IX.2019, S.S. Euo, and C.O. Kim; Gyeonggi-do: 1♂, Gwangju-si, Docheok-myeon, Sangnim-ri, Mt. Taehwasan, N37°18'44" E127°18'36", 10.VII.2017, H.Y. Han et al.

See Additional material examined of *B. serarius* for females.

Distribution. Korea (new record), Japan, Russian Far East.

Biology. In Korea (present study) and Japan (Öhara, 1984), *B. nipponensis* flies have often been collected together with those of *B. serarius*, showing similar flight behavior. The former species constitute approximately 10% of the Korean *Betasyrphus* males (about 200 specimens of both species examined). See Biology of the genus *Betasyrphus* for prey and host records. Due to the frequent misidentification of *B. nipponensis* as *B. serarius* and the inability to separate females of these two species, the previously known biology of *B. serarius* might partially correspond to *B. nipponensis*.

Remarks. In the past, Shiraki and Edashige (1953) named this species as *Syrphus fulvicornis*. Goot (1964) suggested a new name, *S. nipponensis*, for *S. fulvicornis* Shiraki and Edashige, 1953 due to its homonymy with *S. fulvicornis* Meigen, 1822. This homonymization, however, may turn out to be no longer valid considering the current classification of the family Syrphidae (*S. fulvicornis* Meigen is currently placed under the genus *Cheilisia* Meigen, 1822). This topic needs to be clarified in a more comprehensive study of *Betasyrphus* in the future.

Wing microtrichia distributions (WMDs)

Since only males of *B. serarius* and *B. nipponensis* could be distinguished based on their genitalic characters, we attempted to find additional diagnostic characters that applied to both sexes. Vockeroth (1958) suggested that analyzing wing microtrichia distributions (WMDs) can yield useful characters to discern closely related syrphid taxa. For example, Metz and Thompson (2001) used the WMDs to distinguish between the sister species *Toxomerus intermedius* (Hull, 1949) and *T. teliger* (Fluke, 1953).

By observing *Betasyrphus* males previously identified by genitalic examination, we discovered a single WMD character useful for distinguishing males of *B. serarius* from those of *B. nipponensis*. We found that *Betasyrphus* wings are largely microtrichiose but exhibit some bare areas in the basal half. Such bare areas tended to be larger in *B. nipponensis*, showing discrete interspecific differences in the apical 1/3 of cell br above the spurious vein (bare area less than half within this region – Fig. 6A, B vs. more than half – Fig. 6C, D). Using this non-

genital character, we were able to identify all Korean *Betasyrphus* males correctly.

Unfortunately, we were unable to unravel females based on WMDs. Females tended to display larger basal bare areas than males, thus showing only a single WMD state (i.e., cell br almost completely bare). We failed to find any additional microtrichial characters that showed a similarly discrete character state distribution. Nevertheless, we believe that a combination of two or more microtrichial characters may be used for this purpose in the future, but only by applying more sensitive diagnostic tools, such as microsatellite analysis, and the availability of correctly identified female specimens.

Wing interference patterns (WIPs)

WIPs are structural color patterns that appear in thin and transparent wings due to thin-film interference, and are known to be useful for the classification of small winged insects (Shevtsova et al., 2011; Hawkes et al., 2019). WIPs have also been used to classify various taxa of the order Diptera (e.g., Shevtsova et al., 2011; Katayama et al., 2014; Zhang et al., 2016; Gebru et al., 2018; Hawkes et al., 2019). Although WIP analysis has never been applied to the family Syrphidae, we attempted to do so in our *Betasyrphus* species.

Unfortunately, Korean *Betasyrphus* species showed high inter- and intraspecific variability for WIPs (Fig. 8), with some specimens even

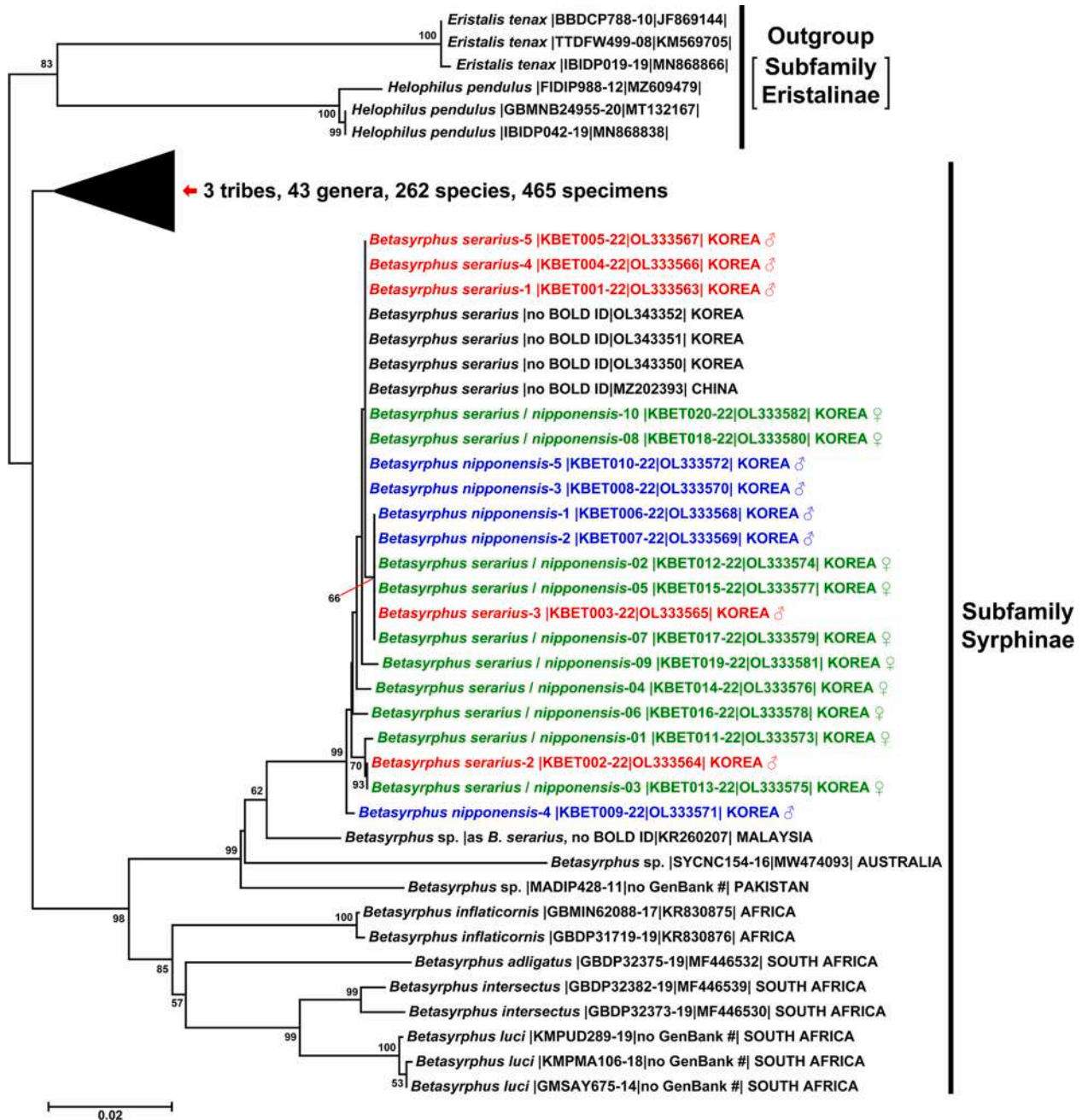


Fig. 11. Neighbor-joining tree based on Kimura 2-parameter distance of 486 Syrphidae DNA barcode sequences mostly retrieved from BOLD Systems (<https://www.boldsystems.org>; as of March 2022) and GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; as of March 2022), including 20 newly obtained Korean *Betasyrphus* sequences (*B. serarius* males are highlighted in red; *B. nipponensis* males are highlighted in blue; *B. serarius* or *B. nipponensis* females are highlighted in green; numbers after the scientific name indicate the voucher specimen numbers). Numbers on each corresponding node indicate the bootstrap values after 3000 replications (only values higher than 50% are shown). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

displaying differences between their right and left wings (Fig. 8G vs. 8H – mirror image). Even after observing males that had been correctly identified by genitalic examination, we failed to find any WIP-based character that could be used to separate the two species. Here, we report some examples of our WIP analyses as information for the readers (Fig. 8).

DNA barcoding of *Betasyrphus* and the related taxa

Taxon sampling

For DNA barcoding analysis, we sampled five genitalia-identified males for each of *B. serarius* and *B. nipponensis*. They were freshly preserved Korean specimens, covering as many variants as possible. Since only males can be identified to species, we sequenced 10 females identified to the genus. We tried to include female specimens from the same lots where *B. nipponensis* males had been collected. This was done in order to include at least some females of *B. nipponensis*, despite the rarity of this species; in fact, *B. nipponensis* represents less than 10% of *Betasyrphus* in Korea, according to male-based data.

In addition, we retrieved 15 DNA barcode sequences of the genus *Betasyrphus*, including five identified and three unidentified species from BOLD Systems and GenBank. We also retrieved 465 selected barcodes of related taxa (262 species, 43 genera and three tribes of the subfamily Syrphinae) to test the monophyly of the genus *Betasyrphus* and unravel any related genera. We tried to include as many sequences as possible from the group 1 of the tribe Syrphini (Young et al., 2016; Mengual et al., 2018; list of Syrphidae genera: https://en.wikipedia.org/wiki/List_of_Syrphidae_genera). The resulting neighbor-joining (NJ) tree was

rooted using the genera *Helophilus* Fabricius, 1805 and *Eristalis* Latreille, 1804 of the subfamily Eristalinae.

Identity of Korean *Betasyrphus* by comparison with available barcodes of other *Betasyrphus* species

Our DNA barcoding analysis was not sensitive enough to separate *B. serarius* and *B. nipponensis* individuals. Indeed, all 23 Korean and single Chinese barcode sequences of these two species were closely clustered together, showing very little sequence divergence (Fig. 11). Similar examples can be found in other insect (e.g., Diptera-Tephritidae: Han and Ro, 2019; Coleoptera-Carabidae: Raupach et al., 2020). Nevertheless, our analysis strongly supports the cluster of the genus *Betasyrphus*, with a 98% bootstrap value. Considering the breadth of our taxon sampling scheme, this genus appears to be a monophyletic group. It is also interesting to notes that three unidentified species from Pakistan, Australian and Malaysian (deposited as *B. serarius*) barcodes closely form a strong cluster (99% bootstrap support) together with both *B. serarius* and *B. nipponensis*. Therefore, the exceptionally wide current distribution of *B. serarius* should be re-evaluated for additional species.

Young et al. (2016) and Mengual et al. (2018) carried out phylogenomic and multigene analyses that showed convincing intergeneric relationships involving the genus *Betasyrphus*. However, our DNA barcoding analysis did not reveal such relationships, obviously due to the lack of phylogenetic signals in deeper branches. Instead, our barcoding analysis seemed effective for species-level analysis within the genus *Betasyrphus*, given the relatively high internal branch supports (Fig. 11).

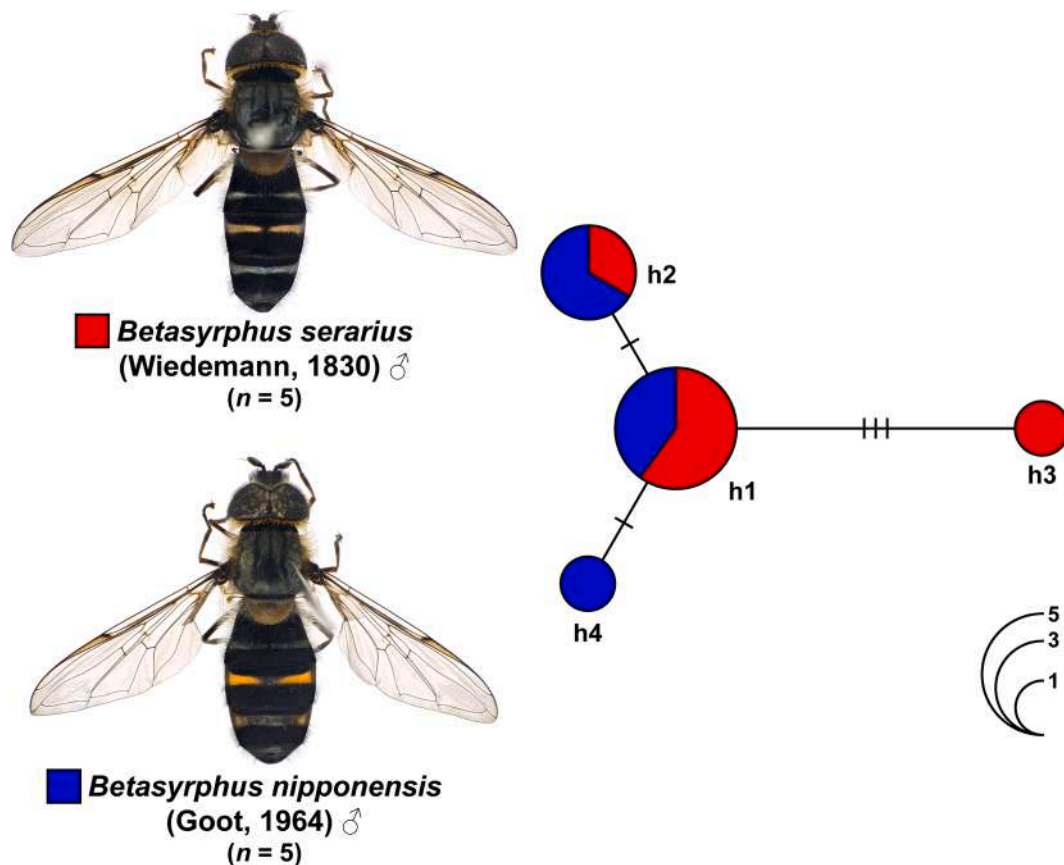


Fig. 12. Maximum statistical parsimony network of the DNA barcode sequences of the *Betasyrphus serarius* (red) and *B. nipponensis* (blue) males. The numbers of analyzed specimens (n) are listed. Big circles represent the haplotype and hatch marks represent mutational steps. The diameter of circles is proportional to the number of haplotypes sampled (see given open circles with numbers). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Haplotype analysis of Korean *Betasyrphus* species

Our maximum parsimony network analysis showed multiple sharing of haplotypes for *Betasyrphus serarius* (n = 5) and *B. nipponensis* (n = 5) (Fig. 12). We only used males, because females could not be identified to the species. As a result, the most dominant haplotype (h1) was shared by three specimens of *B. serarius* and two specimens of *B. nipponensis*. The second dominant haplotype (h2) was shared by one specimen of *B. serarius* and two specimens of *B. nipponensis*. The remaining two haplotypes were revealed only for one specimen (*B. serarius* – h3, *B. nipponensis* – h4). The two haplotypes (h2, h4) were separated by one mutational step from the most dominant haplotype (h1), and h3 indicated by a single specimen of *B. serarius* was separated by three mutational steps. Because these male specimens could be clearly separated by a number of characters in male genitalia (Fig. 9E vs. J), we do not believe that their haplotype sharing is a result of extensive hybridization. Instead, this haplotype sharing pattern appears to be a consequence of recent speciation from a common ancestor.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to Kyung-Eui Ro, Deuk-Soo Choi, Hye-Woo Byun, Sam-Kyu Kim, Hyun-Suk Lee, O-Young Lim, Chan-Hee Park, Sang-Wook Suk, Jong-Su Lim, Dong-Jun Cha, Seul-Ma-Ro Hwang, Yong-Bong Lee, Jong-Mi Jung, Hak-Seon Lee, Dong-Han Kim, Han-Saem Lee, Seung-Su Euo, Soo-Hyun Jeong, Jeong-Hwan Choi, Woon-Ryoung Ha, Seong-Pil Han for collecting and curating Korean syrphid flies in YSUW. We thank art director, Dong-Jin Lee who provided some technical assistance with the Photoshop illustration. We also thank Thomas Pape for kindly searching for syntypes of *B. serarius* in ZMUC, albeit unsuccessfully. We are grateful to three anonymous reviewers for their careful reading and many helpful comments and suggestions. This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202002205). This work was also supported in part by a grant from the Korea National Arboretum, Korea Forest Service (KNA 1-1-20, 16-1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aspen.2022.101914>.

References

- Agarwala, B.K., Das, S., Bhaumik, A.K., 1987. Natural food range and feeding habits of aphidophagous insects in north east India. *J. Aphidol.* 1, 18–22.
- Agarwala, B.K., Bhaumik, A.K., Gilbert, F.S., 1989. Relative development and voracity of six species of Aphidophagous syrphids in cruciferous crops. *Proc.: Anim. Sci.* 98, 267–274.
- Bhatia, H.L., Shaffi, M., 1933. Life-Histories of some Indian Syrphidae. *Indian J. Agri. Sci.* 2, 543–570.
- Bijaya, P., Varatharajan, R., Singh, T.K., 1996. Predatory potential, population density and development of *Betasyrphus serarius* (Weid.), a syrphid predator of *Brevicoryne brassicae* (Linn.) on cabbage. *Uttar Pradesh J. Zool.* 16, 114–116.
- Börner, C., 1933. Kleine Mitteilungen über Blattläuse Self-published. Naumburg (Saale) 1–4.
- Brunetti, E., 1923. The Fauna of British India, including Ceylon and Burma. Diptera. Vol. III. Pipunculidae, Syrphidae, Conopidae, Oestridae. Taylor and Francis, London. pp. 1–424.
- Buckton, G.B., 1876. Monograph of British Aphides. 1, pp. 1–193.
- Burmeister, H.C.C., 1835. *Handbuch der Entomologie: Rhynchota*. Enslin, Berlin, pp. 1–396.
- Chaudhary, H.C., Singh, R., 2012. Records of the predators of aphids (Homoptera: Aphididae) in eastern Uttar Pradesh. *Aphidol. Soc., India* 25&26, 13–30.

- Choi, D.S., Suk, S.W., Lee, S.B., Han, H.Y., 2018. Syrphidae III, Arthropoda: Insecta: Diptera: Brachycera: Syrphidae: Syrphinae. In: *Insect Fauna of Korea*. NIBR, 5, 1–114.
- Clement, M., Snell, Q., Walker, P., Posada, D., Crandall, K., 2002. TCS: Estimating Gene Genealogies. In: *Proceedings of the 16th International Parallel and Distributed Processing Symposium*, p. 184.
- Coe, R.L., 1964. Diptera from Nepal. *Syrphidae*. *Bull. Brit. Mus. Nat. Hist.* 15, 255–290.
- Coquillett, D.W., 1898. Report on a collection of Japanese Diptera, presented to the United States National Museum by the Imperial University of Tokyo. *Proc. U.S. Natl. Mus.* 21, 301–340.
- Cumming, J., Wood, D., 2017. Adult morphology and terminology, in: Kirk-Spriggs, A.H., Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera*. Vol. 1. Introductory chapters and keys to Diptera families. *Suricata* 4. SANBI Graphics & Editing, Pretoria, pp. 89–133.
- Denner, F., 2017. Type specimens of Syrphidae (Insecta: Diptera) in the Natural History Museum in Vienna. *Ann. Naturhist. Mus. Wien*, B. 119, 55–166.
- Dirickx, H.G., 1998. Catalogue of synonyms and geography of the Syrphidae (Diptera) of the Afrotropical region. *Muséum d'histoire naturelle, Ville de Genève*, pp. 1–187.
- Doesburg, P.H. van, 1966. On some Syrphidae from New Guinea and Australia. *Entomol. Ts. Arg.* 87, 60–68.
- Doi, H., 1938. A List of the Diptera of Korea. *Bull. Sci. Mus. Keizyo, Korea*. 72, 8–11 in Japanese.
- Dusek, J., Láška, P., 1976. European species of *Metasyrphus*: key, descriptions and notes (Diptera, Syrphidae). *Acta Entomol. Bohemoslov.* 73, 263–282.
- Entomological Society of Korea (ESK), Korean Society of Applied Entomology (KSAE), 1994. Syrphidae. In *Check list of Insects from Korea*. Kon-kuk University press, Seoul, Korea. pp. 288–292 (in Korean).
- Fabricius, J.C., 1805. *Systema Antliatorum Secundum Ordines, Genera, Species Adiectis Synonymis, Locis, Observationibus, Descriptionibus*. C. Reichard, Brunsvigae, pp. 15–372.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.
- Fluke, C.L., 1953. New Syrphidae from North America. *J. Kans. Entomol. Soc.* 26, 125–129.
- Gebru, A., Jansson, S., Ignell, R., Kirkeby, C., Prangma, J.C., Brydegaard, M., 2018. Multiband modulation spectroscopy for the determination of sex and species of mosquitoes in flight. *J. Biophotonics* 11, 1–13.
- Ghorpadé, K.D., 1981. Insect prey of Syrphidae (Diptera) from India and Neighbouring Countries: a Review and Bibliography. *Prog. Pest Manage.* 27, 62–82.
- Ghorpadé, K.D., 1994. Diagnostic keys to new and known genera and species of Indian subcontinent Syrphini (Diptera: Syrphidae). *Colemania Insect Biosyst.* 3, 1–15.
- Ghosh, A.K., 1974. Aphids (Homoptera: Insecta) of economic importance in India. *Indian Agriculturalist*. 18, 81–214.
- Goot, P. van der, 1913. Zur Systematic der Aphiden. *Tijdschr. Ent.* 56, 69–155.
- Goot, P. van der, 1915. Beitrage zur kenntnis der Hollandschen blattläuse, eine morphologisch-systemaische studie. H.D. Tjeenk Willink & Zoon, Haarlem, pp. 1–600.
- Goot, P. van der, 1917. Zur kenntnis der blattläuse Java's. *Contributions a la faune des Indes Néerlandaises* 1, 1–301.
- Goot, V.S. van der, 1964. Fluke's catalogue of neotropical Syrphidae (Insecta, Diptera), a critical study with an appendix on new names in Syrphidae. *Beaufortia* 10, 212–221.
- Guercio, G. del, 1911. Intorno ad alcuni afididi della Penisola Iberica e di altre località raccolti dal Prof. I. S. Tavares. *Redia* 7, 296–333.
- Guercio, G. del, 1917. Contribuzione alla conoscenza degli afidi. *Redia* 12, 197–277.
- Hall, T., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* 41, 95–98.
- Han, H.Y., 2012. Order Diptera. In: Park, K.T., Kwon, Y.J., Park, J.K., Bae, Y.S., Bae, Y.J., Byun, B.K., Lee, B.W., Lee, S.H., Lee, J.W., Lee, J.E., Han, K.D., Han, H.Y., Korea National Arboretum (KNA) (Eds.), *Insects of Korea*. GeoBook, Seoul. pp. 304–312.
- Han, H.Y., Choi, D.S., 2001. Family Syrphidae. *Economic Insects of Korea*. *Insecta Koreana* 15 (Supple. 22), 1–224 in Korean.
- Han, H.Y., Norrbom, A.L., 2005. A systematic revision of the New World species of *Trypeta* Meigen (Diptera: Tephritidae). *Syst. Entomol.* 30, 208–247.
- Han, H.Y., Ro, K.E., 2016. Molecular phylogeny of the superfamily Tephritoidea (Insecta: Diptera) reanalysed based on expanded taxon sampling and sequence data. *J. Zool. Syst. Evol. Res.* 54, 276–288.
- Han, H.Y., Ro, K.E., 2018. Discovery of a naturally occurring individual of *Acanthiophilus helianthi* (Rossi) (Diptera: Tephritidae) in Korea, a managed quarantine pest by the Korean Animal and Plant Quarantine Agency. *J. Asia Pac. Entomol.* 21, 1262–1267.
- Han, H.Y., Ro, K.E., 2019. DNA barcoding reveals a species group of the genus *Campiglossa* (Diptera, Tephritidae, Tephritinae) with recognition of a new species from East Asia and previously unknown females of *Campiglossa coei* (Hardy). *ZooKeys* 899, 1–36.
- Han, H.Y., Suk, S.W., Lee, Y.B., Lee, H.S., 2014. National List of Species of Korea, Insect (Diptera II). NIBR 1–268 in Korean.
- Hawkes, M.F., Duffy, E., Joag, R., Skeats, A., Radwan, J., Wedell, N., Sharma, M.D., Hosken, D.J., Troscianko, J., 2019. Sexual selection drives the evolution of male wing interference patterns. *Proc. R. Soc. B* 286, 1–8.
- Hippa, H., 1968. A generic revision of the genus *Syrphus* and allied genera (Diptera, Syrphidae) in the palaearctic region, with description of the male genitalia. *Acta Entomol. Fenn.* 25, 1–94.
- Hoeven, J. van der, 1863. Over een klein Hemipterum, dat op de bladen van verschillende soorten van *Acer* gevonden wordt. *Tijdschrift voor Entomologie* 6–17.
- Hosseini, F., Lotfalizadeh, H., Norouzi, M., Dadpour, M., 2019. Wing interference colours in *Eurytoma* (Hymenoptera: Eurytomidae): variation in patterns among populations and sexes of five species. *Syst. Biodivers.* 17, 679–689.

- Huang, C., Cheng, X., 2012. Diptera Syrphidae. In: Fauna Sinica. Insecta, 50. Science Press, Beijing, pp. 1–852 in Chinese.
- Hull, F.M., 1936. A Check list of the described species of Syrphidae from Australia and the Regional Islands. J. Fred. Malay States Mus. 18, 190–212.
- Hull, F.M., 1949. American Syrphid Flies of the subfamilies Cheilosinae and Syrphinae. Bull. Brooklyn ent. Soc. 44, 73–79.
- Huo, K.K., Guodong, R., Zhemin, Z., 2007. Fauna of Syrphidae from Mt. Qinling-Bashan in China (Insecta: Diptera). Science press, Beijing, pp. 1–512.
- Huo, K.K., 2020. Syrphidae. In: Yang, D., Wang, M.Q., Li, W.L., et al., Species Catalogue of China. Vol. 2. Animals, Insecta (VII), Diptera (3): Cyclorrhaphous Brachycera. 2, 30–181.
- Ichige, K., Noshita, H., 2008. Records of Syrphidae (Diptera) from Goto Islands, Nagasaki Pref., Japan Part II. Hana Abu. 50, 5–17.
- Ichige, K., Sakai, Y., 2020. Syrphidae fauna (Diptera, Syrphidae) of Tsushima Island, Nagasaki, Japan. Hana Abu. 50, 51–58.
- Kan, E., 1988. Assessment of aphid colonies by hoverflies. II pea aphids and 3 syrphid species; *Betasyrphus serarius* (Wiedemann), *Metasyrphus frequens* Matsumura and *Syrphus vitripennis* (Meigen) (Diptera: Syrphidae). J. Ethol. 6, 135–142.
- Katayama, N., Abbott, J.K., Kjerandsen, J., Takahashi, Y., Svensson, E.L., 2014. Sexual selection on wing interference patterns in *Drosophila melanogaster*. PNAS 111, 15144–15148.
- Keiser, F., 1971. Syrphidae von Madagaskar (Dipt.). Verhandlungen der Naturforschenden Gesellschaft in Basel. 81, 223–318.
- Kim, C.W., Park, S.H., Lee, K.W., Lee, C.U., Lee, T.J., Cho, B.S., 1971. Illustrated Encyclopedia of Fauna and Flora of Korean Insecta (IV). 12, pp. 827–887 (in Korean).
- Kim, J.I., 1972. Syrphidae in Korea. Korea Univ. Master's thesis. 1–97 (in Korean).
- Kim, J.I., 1975. A list of Syrphidae (Diptera) from Korea. Korean J. Entomol. 5, 38–42 in Korean.
- Kimura, M., 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16, 111–120.
- Kirkaldy, G.W., 1904. Bibliographical and nomenclatural notes on the Hemiptera. No.3. Entomologist. 37, 279–283.
- Koch, C.L., 1854. Die Pflanzenläuse Aphiden getreu nach dem Leben abgebildet und beschrieben vol. 4, 101–134.
- Kumar, S., Stecher, G., Li, M., Knyaz, C., Tamura, K., 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol. Biol. Evol. 35, 1547–1549.
- Kumari, M., 2020. Biology of *Betasyrphus serarius* (Wiedemann)-a syrphid predator of green apple aphid. Indian J. Entomol. 82, 572–573.
- Latreille, P.A., 1804. Tableau méthodique des insectes, in: Société de Naturalistes et d'Agriculteurs, Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, principalement à l'agriculture et à l'économie rurale et domestique. Tome XXIV [Section 3]: Tableaux méthodiques des insectes. Deterville, Paris. pp. 129–200.
- Leigh, J.W., Bryant, D., 2015. POPART: full-feature software for haplotype network construction. Methods Ecol. Evol. 6, 1110–1116.
- Linnaeus, C., 1758. Systema naturae per genera tri naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio Decima, Reformata Laurentii Salvii, Holmiae (Stockholm). pp. 1–824.
- Matsumura, S., Adachi, J., 1917. Synopsis of the Economic Syrphidae of Japan. Part II. Ent. Mag. Kyoto. 2, 133–156.
- Meigen, J.W., 1822. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. Dritter Theil. Schulz-Wundermann, Hamm. 3, 1–416.
- Meijere, J.C.H. de, 1908. Studien über südasiatische Dipteren. III. Tijdschrift voor Entomologie. 51, 191–331.
- Mengual, X., Ståhls, G., Láská, P., Mazánek, L., Rojo, S., 2018. Molecular phylogenetics of the predatory lineage of flower flies *Eupeodes-Scaeva* (Diptera: Syrphidae), with the description of the Neotropical genus *Austroscaeva* gen. nov. J. Zool. Syst. Evol. Res. 56, 148–169.
- Metz, M., Thompson, F.C., 2001. A revision of the larger species of *Toxomerus* (Diptera: Syrphidae) with description of a new species. Stud. Dipt. 8, 225–256.
- Minamikawa, J., Fukuhara, N., 1964. On the Syrphid larvae attacking the aphid, *Myzus persicae* Sulzer. Kontyû, Tokyo. 32, 225.
- Mordvilko, A.K., 1914. Insectes Hémiptères (Insecta, Hémiptera, Aphidoidea). Fauna de la Russie 1, 1–236 in Russian.
- Mordvilko, A.K., 1928. The evolution of cycles and the origin of heteroecy (migrations) in plant lice. Ann. Mag. Nat. Hist. 2, 570–582.
- Mutin, V.A., Barkalov, A.V., 1997. A review of the hoverflies (Diptera: Syrphidae) of Sakhalin and the Kuril Islands, with descriptions of two new species. Species Diversity 2, 179–230.
- Mutin, V.A., Barkalov, A.V., 1999. Key to the insects of Russian Far East. Vol. VI. Diptera and Siphonaptera. Pt 1. Vladivostok. Dal'nauka. pp. 342–500 (in Russian).
- National Institute of Biological Resources (NIBR), 2019. National Species List of Korea. III. Insects (Hexapoda). Disignzip. pp. 1–988.
- Ninomiya, E., 1956. On the food habits of some aphidophagous syrphid larvae. I. Ôyô-Kontyû. 12, 225–229 in Japanese.
- Ninomiya, E., 1957a. On the number of aphids destroyed by syrphid larvae. Jpn. J. Appl. Entomol. Zool. 1, 119–124 in Japanese, English summary.
- Ninomiya, E., 1957b. On the food habits of some aphidophagous syrphid larvae. II. Jpn. J. Appl. Entomol. Zool. 1, 186–192 in Japanese, English summary.
- Ninomiya, E., 1959. Further notes on the immature stages of aphidophagous syrphid flies of Japan. Sci. Bull. Fac. Lib. Arts Educ. Nagasaki Univ. 10, 23–52 in Japanese, English summary.
- Ninomiya, E., 1962. On the rate of parasitism of Hymenopterous parasites of aphidophagous syrphids in Nagasaki. Sci. Bull. Fac. Lib. Arts Educ. Nagasaki Univ. 13, 23–36 in Japanese.
- Ôhara, K., 1984. Taxonomic note on *Syrphus nipponensis* van der Goot (Diptera, Syrphidae). Kontyû, Tokyo. 52, 533–536.
- Ôhara, K., Ohishi, H., Ichige, K., 2014. Catalogue of the insects of Japan Vol. 8, Part 1 Diptera (Nematocera-Brachycera Aschiza). Entomological Society of Japan, Touka Shobo, Fukuoka. 1–539 (in Japanese).
- Okuno, T., 1967. On the syrphid larvae attacking the aphids in Japan (Diptera). Mushi 41, 123–141.
- Paek, M.K., Hwang, J.M., Jung, K.S., Kim, T.W., Kim, M.C., Lee, Y.J., Cho, Y.B., Park S. W., Lee, H.S., Ku, D.S., Jeong, J.C., Kim K.G., Choi, D.S., Shin, E.H., Hwang, J.H., Lee, J.S., Kim, S.S., Bae, Y.S., 2010. Checklist of Korean insects. In: Paek, M.K. and Cho, Y.K. (Eds.) Nature & Ecology Academics. Series 2, Nature & Ecology, Seoul. pp. 1–598.
- Passerini, G., 1860. Gli Afidi con un prospetto dei generi ed alcune specie nuove Italiane. Parma. pp. 1–40.
- Peck, L.V., 1988. Family Syrphidae. In: Soós, Á., Papp, L. (Eds.), Catalogue of Palaearctic Diptera. Akademiai Kiado, Budapest. 8, pp. 11–230.
- Radhakrishnan, B., Muraleedharan, N., 1993. Bio-ecology of six species of syrphid predators of the tea aphid, *Toxoptera aurantii* (Boyer de Fonscolombe) in southern India. Entomol. 18, 175–180.
- Rai, B.K., 1976. Pests of Oilseed Crops in India and Their Control. ICAR, New Delhi, pp. 1–121.
- Raupach, M.J., Hannig, K., Morinière, J., Hendrich, L., 2020. A DNA barcode library for ground beetles of Germany: the genus *Pterostichus* Bonelli, 1810 and allied taxa (Insecta, Coleoptera, Carabidae). ZooKeys 980, 93–117.
- Raychaudhuri, D.N., Dutta, S., Agarwal, B.K., Raychaudhuri, D., Raha, S.K., 1978. Some parasites and predators of aphids from northeast India and Bhutan. Entomol. 3, 91–94.
- Robertson, A.R., Finch, J.T.D., Young, A.D., Spooner-Hart, R.N., Outim, S.K.M., Cook, J. M., 2020. Species diversity in bee flies and hover flies (Diptera: Bombyliidae and Syrphidae) in the horticultural environments of the Blue Mountains, Australia. Austral Entomol. 59, 561–571.
- Rotheray, G., Gilbert, F.S., 1999. Phylogeny of Palaearctic Syrphidae (Diptera): evidence from larval stages. Zool. J. Linn. Soc. 127, 1–112.
- Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4, 406–425.
- Schiner, J.R., 1868. Diptera. In: Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Willerstorff-Urbair. Zoologischer Theil. 2, 1–388.
- Shevtsova, E., Hansson, C., Janzen, D.H., Kjerandsen, J., 2011. Stable structural color patterns displayed on transparent insect wings. PNAS 108, 668–673.
- Shiraki, T., 1930. Die Syrphiden des Japanischen Kaiserreichs, mit Berücksichtigung benachbarter Gebiete. Mem. Fac. Agric. Taihoku Imp. Univ. 1, 1–446.
- Shiraki, T., Edashige, T., 1953. The insect fauna of Mt. Ishizuchi and Omogo Valley, Iyo, Japan. The Syrphidae (Diptera). Trans. Shikoku Ent. Soc. 3, 84–125.
- Sivova, A.V., 2003. Morphology and biology of the preimaginal stages of *Betasyrphus nipponensis* (Van der Goot, 1964) (Diptera, Syrphidae). Chiteniya Pamyati Alekseya Ivanovicha Kurentsova. 13, 121–124 (in Russian, English abstract).
- Smith, K.G.V., Vockeroth, J.R., 1980. 38. Family Syrphidae. In: Crosskey, R.W. et al. (Eds.), Catalogue of the Diptera of the Afrotropical region. British Museum (Natural History). pp. 488–510.
- Ssymank, A., 2010. Review of the species of *Betasyrphus* Matsumura, 1917 (Diptera: Syrphidae) from Madagascar with description of a new species. Zootaxa 2417, 40–50.
- Takahashi, R., 1920. A new genus and species of aphid from Japan (Hem.). Can. Entomol. 52, 19–20.
- Takeuchi, M., 2017. The first record of *Betasyrphus nipponensis* from central Honshu, Japan (Diptera, Syrphidae). Hana Abu. 44, 28.
- Thompson, F.C., 1999. A key to the genera of the flower flies (Diptera: Syrphidae) of the Neotropical region including descriptions of new genera and species and a glossary of taxonomic terms. Contrib. Entomol. Internat. 3, 321–378.
- Thompson, F.C., Rotheray, G., 1998. Family Syrphidae. In: Papp, L., Darvas, B. (Eds.), Manual of Palaearctic Diptera, Vol. 3. Science Herald, Budapest, pp. 81–139.
- Thompson, W.R., Simmonds, F.J., 1965. A catalogue of the parasites and predators of insect pests. Section 4. Host predator catalogue. CAB, England. pp. 1–208.
- Vockeroth, J.R., 1958. Two new Nearctic species of *Spilomyia* (Diptera: Syrphidae), with a note on the taxonomic value of wing microtrichia in the Syrphidae. Can. Entomol. 90, 284–291.
- Vockeroth, J.R., 1969. A revision of the genera of the Syrphini (Diptera: Syrphidae). Mem. Ent. Soc. Can. 62, 5–176.
- Vujić, A., Ståhls, G., Rojo, S., Radenković, S., Simić, S., 2008. Systematics and phylogeny of the tribe Paragini (Diptera: Syrphidae) based on molecular and morphological characters. Zool. J. Linn. Soc. 152, 507–536.
- Whittington, A.E., 2003. The Afrotropical Syrphidae fauna: an assessment. Studia Dipterologica 10, 519–607.
- Wiedemann, C.R.W., 1824. Munus rectoris in Academia Chritiana Albertina aditurus Analecta entomologica ex Museo Regio Havniensi maxime congesta profert iconibusque illustrat. Regio typographo scholarum, Kiliae, pp. 1–60.
- Wiedemann, C.R.W., 1830. Außereuropäische zweiflügelige Insekten. Zweiter Theil. Hamm, Schulzische Buchhandlung, pp. 1–684.
- Yano, K., Omura, K., Okuno, T., 1979. Faunal and biological studies on the insects of paddy fields in Asia. Part III. Syrphidae from Japan (Diptera). Bull. Fac. Agric. Yamaguti Univ. 30, 12–38.

- Young, A.D., Lemmon, A.R., Skevington, J.H., Mengual, X., Ståhls, G., Reemer, M., Jordaens, K., Kelso, S., Lemmon, E.M., Hauser, M., De Meyer, M., Misof, B., Wiegmann, B.M., 2016. Anchored enrichment dataset for true flies (order Diptera) reveals insights into the phylogeny of flower flies (family Syrphidae). *BMC Evol. Biol.* 16, 1–13.
- Zhang, D., Ge, Y.Q., Li, X.Y., Liu, X.H., Zhang, M., Wang, R.R., 2016. Review of the *Lispe caesia*-group (Diptera: Muscidae) from Palaearctic and adjacent regions, with redescrptions and one new synonymy. *Zootaxa* 4098, 43–72.
- Zoological Society of Korea (ZSK), 1968. *Nomina Animalium Koreanorum. Insecta* 2, 172–187 in Korean.