A THESIS

FOR THE DEGREE OF MASTER OF SCIENCE

Systematic Review of genus *Nomada* (Hymenoptera: Apidae) in Korea, with Phylogeny and Evolution of subfamily Nomadinae

알락꽃벌속에 대한 분류 및 알락꽃벌아과의 계통, 진화학적 연구

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Program in Entomology

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August, 2022

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UNDER THE DIRECTION OF ADVISER SEUNGHWAN LEE
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

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APPROVED AS A QUALIFIED DISSERTATION OF KAYUN LIM
FOR THE DEGREE OF MASTER OF SCIENCE
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ABSTRACT

Systematic Review of genus *Nomada* (Hymenoptera: Apidae) in Korea with Phylogeny and Evolution of subfamily Nomadinae

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The systematic studies had three main subjects: i) Taxonomic review of the Genus *Nomada* (Hymenoptera: Apidae) in the Korean Peninsula; ii) Molecular Phylogeny of subfamily Nomadinae and species-group concept reconstruction of genus *Nomada*; iii) Harrison's rule corroborated for the body size of cleptoparasitic cuckoo bees (Hymenoptera: Apidae: Nomadinae) and their hosts.

In the first section, a total of forty-five species of in the genus *Nomada* was reviewed with three new records, *Nomada aswensis* Tsuneki, *Nomada fusca* Schwarz, *Nomada pulawskii* Tsuneki, and three new species. Illustration of the adult external morphology, male genitalia, and the flower association for each species were also given in the present study.

In the second part, Phylogenetic study of the subfamily Nomadinae based on six targeted molecular fragments of mitochondrial DNA (COI), five nuclear protein-

coding genes of elongation factor 1α (EF-1α), sodium potassium adenosine triphosphatase (Nak), long-wavelength rhodopsin (opsin), RNA polymerase II (Pol II), and Wingless supported a monophyly of Nomadinae and they also indicated that hexepeolini is the sister group of the genus *Nomada* with necessity of species-group reclassification. Especially, *Nomada tsunekiana*, *N. emarginata*, *N, flavopicta,* which was designated as *ruficornis* species-group were part of a clade with *basalis* species-group. Also, *N. aswensis, N. kaguya* (previously *ruficornis* species-group), and *N. taicho* (previously *furva* species-group) moved to *armata* species-group. Lastly, *N. lathburiana* (previously *ruficornis* species-group) was part of a clade with *bifasciata* species-group, but further investigation is needed because of the distinct morphological descreapancy with the current *bifasciata* species-group.

In the last chapter, host shift fluctuations and applicability of Harrison's rule for the subfamily Nomadinae were conducted. the results revealed that early in their evolution, parasites used closer relatives, before attacking less related groups later. To be specific, In the clade of Ammobatoidini + Neolarrini + Biastini + Hexepeolini + Nomadini, the host shift occurred from Andrenidae to Halictidae at least three times in this group. Lastly, Harrison's rule in Nomadinae was confirmed, supporting that body size dynamics influence the host shifts of cleptoparasitic bees.

Key words: *Nomada*, Nomadinae, Cuckoo bees, Cleptoparasites, Harrison's rule, Korean Peninsula

Student number: 2020-21301

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PART I. Taxonomic review of Genus *Nomada* (Hymenoptera: Apidae) in the Korean Peninsula

PART I. Taxonomic review of the Genus *Nomada* (Hymenoptera: Apidae) in the Korean Peninsula

Abstract

The genus *Nomada* is reviewed as 45 species of 8 species-group in the Korean Peninsula, including three new records, *Nomada aswensis* Tsuneki, *Nomada fusca* Schwarz, *Nomada pulawskii* Tsuneki, and three new species. Diagnosis and descriptions for all Korean species are redescribed with keys to species-group and species. Illustration of the adult external morphology, male genitalia, and the flower association for each species were also provided.

Keywords: *Nomada*, revision, new records, new species, the Korean Peninsula

1. Introduction

1.1. General introduction of the Genus *Nomada*

Apidae is the largest and most diverse family of bees, with over 5880 species in 205 genera and 34 tribes (Bossert et al., 2019). *Nomada* Scopoli, 1770 is the only genus of Nomadini in Apidae and comprises around 800 described species worldwide (Smit, 2018). The genus is so far the largest genus of brood parasitic bees worldwide, and species of the genus occur on all continents except Antarctica (Alexander, 1994).

This genus can be distinguished by red, yellow marking on tergum, usually red integumental marking on scutum in female, and black marking on scutum in males. Body length is between 3 to 16mm. A fifth of the sternum of the female is emarginate with a tuft of stiff hair on each basal lobe, and a sixth of the tergum has a tuft of bristles on side of the pygidial plate. And the apex of it has blunt spine-like setae, not bifid as in other Nomadinae (Michener, 2007).

Cleptoparasitism refers to a form of stealing items such as food or a nest from the host's possession, and it is one of the common phenomena of exploitation between animals (Iyengar, 2008). Nest-building solitary bees fill enough pollen in their nest to sustain the growth of their progeny (Müller et al., 2006). Cleptoparasitic bees do not collect pollen for their own nest. Instead, they enter the nest which belongs to other bee species and lay their own eggs in pollen. In 1955, Linsley and Macswain observed the life stage of *N. opacella* Timberlake, *N. edwardsii* Cresson, *N. obscurella* Fowler. They found that the *Nomada* larvae destroy the eggs of hosts using long, sharply curved mandibles in the first larval stage, which is less than two days.

The parasitic offspring consume the pollen in the nest of host and keep developing before emerging from the host nest (Cardinal et al., 2010). Nomad bees are reported as all cleptoparasitic bees, mainly parasite the genus *Andrena* (Andrenidae). According to Maeta et al., 1996, Korean *Nomada* species parasite on genus *Eucera*, *Tetralonia*, *Rhopalomelissa*, *Lasioglossum*, and *Andrena* (Table 1). However, cleptoparasitism was also reported on *Agapostemon*, *Halictus*, *Lipotriches* (Halictidae), *Panurgus* (Andrenidae), *Melitta* (Mellitidae), and *Exomalopsis* (Apidae) in Non-Korean species (Michener, 2007).

Table 1. Host information of Korean *Nomada*

No.	Species Name	Host	Reference
1	*Nomada comparata* Cockerell	*Andrena micado* Strand & Yasumatsu, *A richardasi* Hirashima	Maeta et al., 1996
2	*Nomada fervens* Smith	*A. sublevigata* Hirashima	
3	*Nomada flavoguttata* (Kirby)	*A. falsifica* Perkins	Smit, 2018
		A. minutula (Kirby)	
		A. minutuloides Perkins	
		A. semilaevis Pérez	
		A. subopaca Nylander	
4	*Nomada guttulata* Schenck	*A. labiata* Fabricus	
		A. potentillae Panzer	
		A. sphecodimorpha Hedicke	
		A. florivaga Eversmann	
5	*Nomada harimensis* Cockerell	*A. ruficurus rabicurus* Hirashima	Maeta et al., 1996
6	*Nomada japonica* Smith	*Eucera spurcatipes* (Perez)	
		Tetralonia nipponensis (Perez)	
7	*Nomada kaguya* Hirashima	*Lipotriches yasumatsui* (Hirashima)	
8	*Nomada lathburiana* (Kirby)	*A. barbareae* Panzer	Smit, 2018
		A. cineraria (Linnaeus)	
		A. danuvia Stöckhert	
		A. vaga Panzer	
9	*Nomada nipponica* Yasumatsu & Hirashima	*A. knuthi* Alfken	Maeta et al., 1996
10	*Nomada okamotonis* Matsumura	*A. valeriana* Hirashima	
11	*Nomada okubira* Tsuneki	*Lasioglossum sakagamii* Ebmer	
12	*Nomada opaca* Alfken	*A. fulvida* Schenk	Smit, 2018
13	*Nomada shirakii* Yasumatsu & Hirashima	*A. tsukubana* Hirashima	Mitai & Tadauchi, 2007
14	*Nomada striata* Fabricius	*A. wilkella* (Kirby),	Smit, 2018
		A. gelriae van der Vecht,	
		A. similis Smith,	
		A. aberrans Eversmann,	
		A. intermedia Thomson,	
		A. pandellei Pérez	

1.2. Historical review of *Nomada*

After Linnaeus (1758) placed all bees into the genus *Apis*, there have been a lot of attempts to divide this group to elucidate a more comprehensive phylogeny of Anthophila. In 1802, Kirby divided bees into two groups; one was a short-tongued bee group called *Melitta*, and the other was a long-tongued bee group that belonged to *Apis*. From the introduction of Linnaeus nomenclature until the end of the 18th Century, the name of the genus *Nomada* was proposed with other four genera of bees, *Andrena*, *Apis*, *Eucera*, and *Hylaeus*. Ashmead (1899) divided bees into 14 families and placed the genus *Nomada* into Nomadidae. He also suggested that most bees in Nomadidae are descendent of Anthophoridae. On the other hand, Robertson (1904) put *Nomada* into Anthophoroidea. After that, Michener (1944) suggested the tribe Nomadini in Family Apidae, Subfamily Anthophorinae. Then the tribe Nomadini was separated from Anthophorinae into Nomadinae by Warncke (1977). As the molecular phylogenetic and phylogenomic analysis develops, there were a lot of attempts to get a higher resolution of the phylogeny of Nomadinae to understand the evolution of cleptoparasitism in Anthophila (Cardinal et al., 2010; Litman et al., 2013; Bossert et al., 2019). Based on the molecular phylogenetic and phylogenomic study, it was revealed that *Nomada* was placed in the subfamily Nomadinae, family Apidae, and almost all cleptoparasitic bees in Apidae is monophyletic (Cardinal et al., 2010; Litman et al., 2013; Bossert et al., 2019).

There was various effort to set grouping within *Nomada*. Snelling (1986) conducted it using New World *Nomada* and separated it into three genera: *Hypochrotaenia*,

Centrias, and *Nomada*. Moreover, he suggested three subgenera for *Hypochrotaenia*, and six for *Nomada*. After that, Alexander (1994) proposed 16 species groups based on the adult morphology, including genitalia and associated structures, which were *Vegana*, *Gigas*, *Adducta*, *Vincta*, *Odontophora*, *Erigeornis*, *Ruficornis*, *Armata*, *Belfragei*, *Superba*, *Basalis*, *Roberjeotiana*, *Bifasciata*, *Trispinosa*, *Integra*, and *Furva* species group. However, the author commented that the *ruficornis* species group might be paraphyletic.

1.3. History of Korean *Nomada*

Thirty-nine species of *Nomada* have been previously reported in Korea before this study. In 1926, Cockerell firstly reported one species, *Nomada koreana* (Cockerell) from Musan, North Korea. After that, Yasumatsu & Hirashima (1951) reported *N. nipponica* (Yasumatsu & Hirashima) as a new species which inhabits in Korea. Then two years later, they reported *N. orientalis* (Yasumatsu & Hirashima) as a new species from Korea and Japan (Yasumatsu & Hirashima, 1953), but the species was synonymized as *N. harimensis* Cockerell by Tsuneki (1973). Hirashima (1960) reported Korean *N. japonica* Smith in 1960. After that, Kim (1970) described *N. calloptera* (Cockerell), *N. koebelei* (Tsuneki), *N. galloisi* (Yasumatsu & Hirashima) inhabit in Korea for the first time. But *N. koebelei* (Tsuneki) was synonymized later by Mitai et al., (2007) as *Nomada fervens* Smith. After that, Tsuneki (1986) reported *N. esakii* (Yasumatsu & Hirashima), *N. ginran* (Tsuneki), *N. maculifrons* (Smith), *N. sabensis* (Tsuneki), as new records from Korea and reported 3 new species, *N.*

shoyozana (Tsuneki), *N. temmasana* (Tsuneki), *N. koreana* (Tsuneki). But Schwarz (1999) proved that *N. koreana* (Tsuneki) is different species from *N. koreana* (Cockerell). Therefore, he replaced *N. koreana* (Tsuneki), 1986 as a new species, *N. tsunekiana*. Later, Mital et al., (2003) redescribed *N. temmasa* (Tsuneki) to *N. temmasana temmasana* (Tsuneki), since the authors reported the subspecies *N. temmasana akitsushimae* (Mitai, Hirashima and Tadauchi). Thereafter, Mitai et al., (2007) synonymized *N. esakii* (Yasumatsu & Hirashima) to *N. amurensis* (Radoszkowsky). And they described *N. hakonensis* (Cockerell), *N. icazi* (Tsuneki), *N. pacifica* (Tsuneki), and *N. panzeri orientis* (Tsuneki) inhabit in Korea. Sooner After, Won (2005) proposed four new species in his Ph.D. thesis, which are *N. kimi*, *N. mani*, *N. bidentata*, and *N. kuami*, but they are not published as a paper. Won et al., (2008) reported five additional species records, which are *N. comparata* (Cockerell), *N. fulvicornis jezoensis* (Matsumura), *N. kaguya* (Hirashima), and *N. shirakii* (Yasumatsu & Hirashima). In 2013, Insect Fuana of Korea Vol 13, No.5 was released, which describes taxonomic revision of *Nomada* in Korea. Authors reported lots of new records which are *N. okubira* (Tsuneki), *N. taico* (Tsuneki), *N. opaca* (Alfken), *N. okamotonis* (Matsumura), *N. abtana* (Tsuneki), *N. guttulata* (Schenck), *N. lathburiana* (Kirby), *N. leucophtalma* (Kirby), *N. pyrifera* (Cockerell), *N. montvena* (Tsuneki), *N. striata* (Fabricus), *N. hakusana hakusana* (Tsuneki), *N. flavoguttata* (Kirby), *N. esana* (Tsuneki), *N. pacifica* (Tsuneki), *and N. pekingensis* (Tsuneki). However, there was no additional taxonomical research after 2013. Given that *Nomada* is the largest genus of cleptoparasitic bees, a continuous taxonomical

investigation must be conducted. Therefore, the aim of this chapter is to examine the hidden diversity of *Nomada* from Korea.

Table 2. History of Korean records of the genus *Nomada*

No.	Author	Years	Recorded species	Korean name
1	Cockerell	1926	*Nomada koreana* Cockerell, 1926	참알락꽃벌
2	Yasumatsu & Hirashima	1951	*Nomada nipponica* Yasumatsu & Hirashima, 1951	일본알락꽃벌
3	Yasumatsu & Hirashima	1953	*Nomada harimensis* Cockerell, 1914 (=described as *N. orientalis* Yasumatsu & Hirashima, 1953)	동양알락꽃벌
4	Hirashima	1960	*Nomada japonica* Smith, 1873	왜알락꽃벌
5	Kim	1970	*Nomada calloptera* Cockerell, 1918	콜체렐알락꽃벌
6	Kim	1970	*Nomada fervens* Smith, 1873 (=syn. *Nomada koebelei* Yano, 1932)	꼬마알락꽃벌
7	Kim	1970	*Nomada galloisi* Yasumatsu & Hirashima, 1953	갈로이시알락꽃벌
8	Tsuneki	1986	*Nomada amurensis* Radoszkowsky, 1876 (=described as *Nomada esakii* Yasumatsu & Hirashima, 1953)	북방알락꽃벌
9	Tsuneki	1986	*Nomada ginran* Tsuneki, 1973	흰털허리알락꽃벌
10	Tsuneki	1986	*Nomada maculifrons* Smith, 1869	가위털알락꽃벌
11	Tsuneki	1986	*Nomada sabaensis* Tsuneki, 1973	네가시알락꽃벌
12	Tsuneki	1986	*Nomada shoyozana* Tsuneki, 1986	소요알락꽃벌
13	Tsuneki	1986	*Nomada temmasana temmasana* Tsuneki, 1986	천마알락꽃벌
14	Tsuneki	1986	*Nomada tsunekiana* Schwarz, 1999 (=described as *Nomada koreana* Tsuneki, 1986)	황띠알락꽃벌
15	Mitai & Tadauchi	2007	*Nomada flavoguttata* (Kirby, 1802)	배광택알락꽃벌
16	Mitai & Tadauchi	2007	*Nomada hakonensis* Cockerell, 1911	긴더듬이알락꽃벌
17	Mitai & Tadauchi	2007	*Nomada icazti* Tsuneki, 1976	번개무늬알락꽃벌
18	Mitai & Tadauchi	2007	*Nomada pacifica* Tsuneki, 1973	뭉툭턱알락꽃벌
19	Mitai & Tadauchi	2007	*Nomada panzeri orientis* Tsuneki, 1973	날씬알락꽃벌
20	Won et al.	2008	*Nomada comparata* Cockerell, 1911	쌍발톱알락꽃벌
21	Won et al.	2008	*Nomada hakusana hakusana* Tsuneki, 1973	넓은더듬이알락꽃벌
22	Won et al.	2008	*Nomada fulvicornis jezoensis* Matsumura, 1912	마름모점알락꽃벌
23	Won et al.	2008	*Nomada kaguya* Hirashima, 1953	노랑방패알락꽃벌
24	Won et al.	2008	*Nomada shirakii* Yasumatsu & Hirashima, 1951	작은점알락꽃벌
25	Mitai et al.	2008	*Nomada esana* Tsuneki, 1973	노랑뒷가슴알락꽃벌
26	Mitai et al.	2008	*Nomada opaca* Alfken, 1913	쌍니알락꽃벌
27	Mitai et al.	2008	*Nomada sexfasciata* Panzer, 1799	방패입술알락꽃벌
28	Mitai et al.	2008	*Nomada roberjeotiana aino* Tsuneki, 1973	은포알락꽃벌
29	Won & Kim	2013	*Nomada abtana* Tsuneki, 1973	갈색방패알락꽃벌

30	Won & Kim	2013	*Nomada guttulata* Schenck, 1861	민무늬허리알락꽃벌
31	Won & Kim	2013	*Nomada lathburiana* (Kirby, 1802)	붉은털알락꽃벌
32	Won & Kim	2013	*Nomada leucophthalma* (Kirby, 1802)	곰보알락꽃벌
33	Won & Kim	2013	*Nomada montverna* Tsuneki, 1973	작은알락꽃벌
34	Won & Kim	2013	*Nomada okamotonis* Matsumura, 1912	영원알락꽃벌
35	Won & Kim	2013	*Nomada okubira* Tsuneki, 1973	애알락꽃벌
36	Won & Kim	2013	*Nomada pyrifera* Cockerell, 1918	어슷더듬이알락꽃벌
37	Won & Kim	2013	*Nomada striata* Fabricius, 1793	등근입술알락꽃벌
38	Won & Kim	2013	*Nomada taicho* Tsuneki, 1973	넓적머리알락꽃벌
39	Won & Kim	2013	*Nomada pekingensis* Tsuneki, 1986	노랑털알락꽃벌

2. Materials and methods

2.1. Material examined

Collection of bees

Materials for this study were mostly collected from 2020 to 2021. The samples were mainly collected by sweeping, yellow pan trap, and malaise trap installed in the mixed forest. Most specimens examined in this study were stored in the College of Agriculture and Life Sciences, Seoul National University (CALS, SNU). Some specimens were borrowed from the National Academy of Agricultural Science (NAAS, Wanju, Korea), Korea National Arboretum (KNA, Pocheon, Korea), and Geolim Entomological Institute (GE), National Institute of Biological Resources (NIBR, Incheon, Korea), and personal collection from Mr. Jan Smit, Mr. Keiichi Otsui, and Dr. Heung-sik Lee.

Sample preparation

Most of the specimens were preserved in dry for identification after the separation of one mid-leg for molecular work. The legs and remaining specimens were preserved in 99% ethyl alcohol. To examine the sternum, tergum and genitalia, the specimens were relaxed in hot water for 1 min. The apical segment of the abdomen was separated using a hooked pin or forceps or removed entirely. Separated abdomens were cleared by heating in 5ml tubes of 10% potassium hydroxide (KOH) for 1 hour at 70%. After the examination, dissected parts were stored in polyethylene genitalia vials with glycerin.

Examinations

Photographs of dorsal habitus were captured using a Canon digital camera (80d, MP-E 65mm f/2.8 1–5x Macro lens mounted). Multiple layers of photographs were merged using Zerene Stacker 1.04 software (Zerene Systems 2014; http://www.zerenesystems.com/cms/stacker). Mild calibration of images and plates was conducted using software (Photoshop CC 2014, Adobe system, USA). Specimens were examined under the Olympus SZ61 stereomicroscope and photographed using a DMC 5400 digital camera with a Leica Z16 APO motorized macroscope.

2.2 Terminology

Terminology for the adult character of *Nomada* follows Smit (2018), and male genitalia follows Mitai & Tadauchi (2007). The terminology of morphological

structure follows Harris (1979), Alexander (1994), Mitai & Tadauchi (2007), Michener (2007), and Won & Kim (2013). Abbreviations used for the collection data are as follows: GE, Georim Entomological Institute; KNA, Korea National Arboretum; LHSC, the personal collection from Dr. Heung-sik Lee; NAAS, National Academy of Agricultural Science; NIBR, National Institute of Biological Resources; SNU, Seoul National University.

Our taxonomy of flowering plants follows The World Flora Online (http://www.worldfloraonline.org/) and National Species List of Korea (2019). The province abbreviations are as follows: **CB**, Chungcheongbuk-do; **CN**, Chungcheongnam-do; **GB**, Gyeongsangbuk-do; **GG**, Gyeonggi-do; **GW**, Gangwon-do; **GN**, Gyeongsangnam-do; **IN,** Incheon; **JB**, Jeollabuk-do; **JN**, Jeollanam-do; **JJ**, Jeju-do; **PY:** Pyeongyang-si (North Korea). Abbreviations for morphological characters in measurement: **LID**, lower interocular distance; **UID**, upper interocular distance; **FL1**–**FL3**, length of flagellum 1–3; **FW1**–**FW3**, wide of flagellum 1–3; **HTS**, setae on the outer apical margin of the hind tibiae.

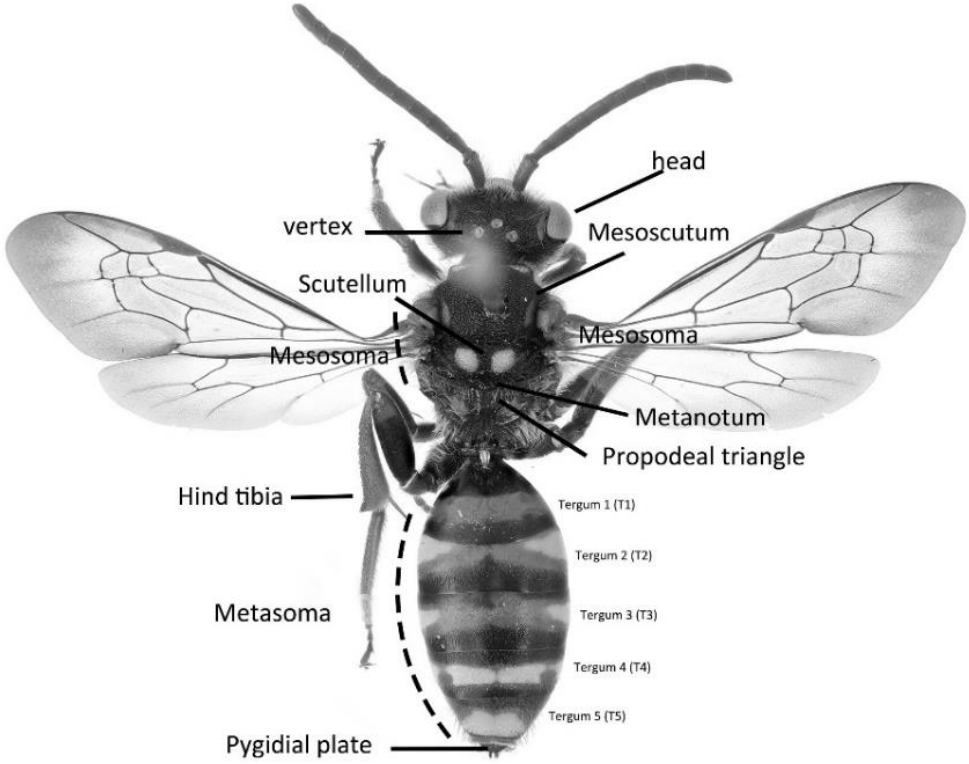

Figure 1. The dorsal habitus of *Nomada fulvicornis jezoensis* Matsumura.

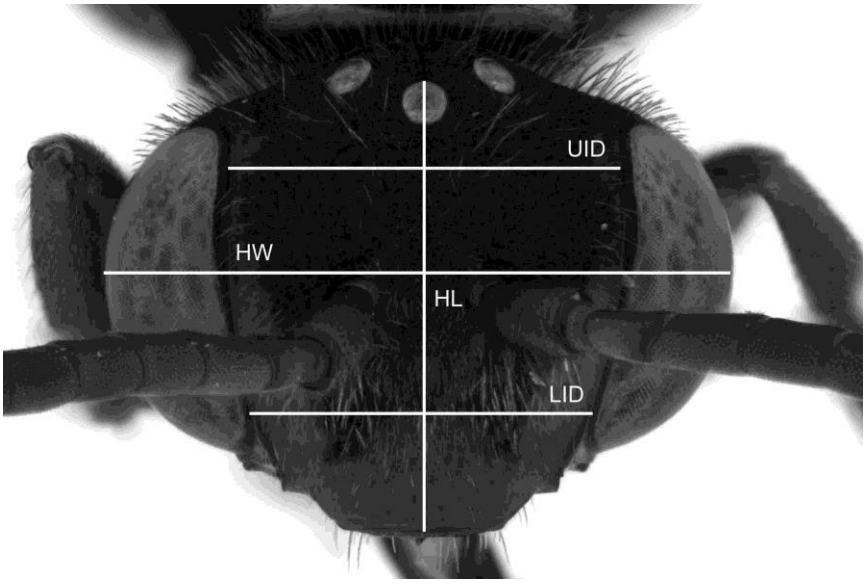

Figure 2. Head in front. (*Nomada fulvicornis jezoensis* Matsumura)

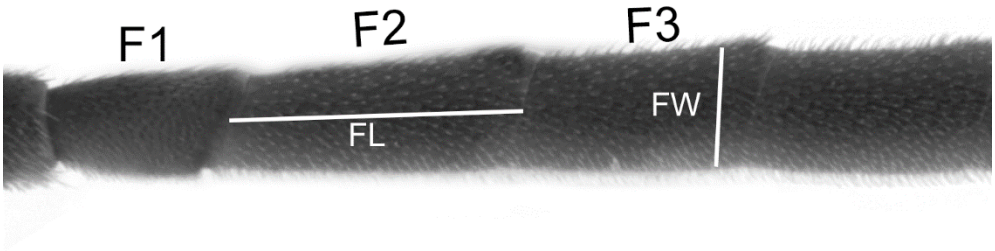

Figure 3. Ventral habitus of antennae. (*Nomada hakonensis* Cockerell)

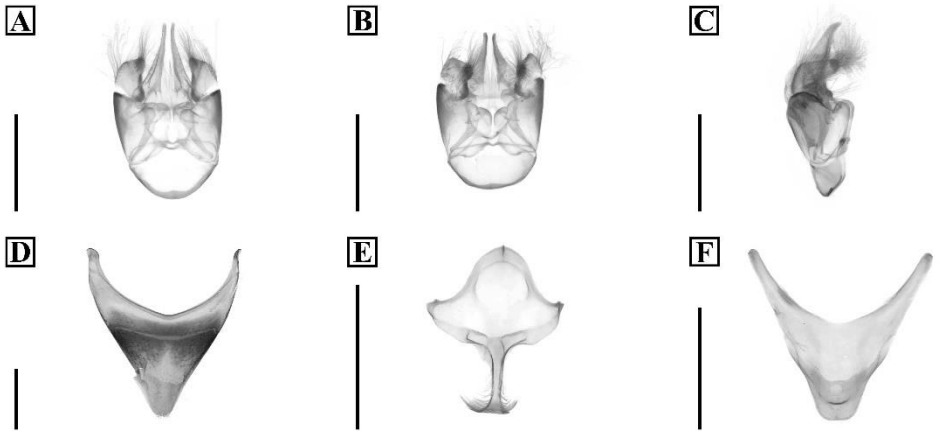

Figure 4. Male terminalia of *Nomada ginran* Tsuneki. A, Genital capsule in ventral view; B, Genital capsule in dorsal view; C, Genital capsule in lateral view; D, 7th tergum in dorsal view; E, 7th sternum in ventral view; F, 8th sternum in ventral view (Scale bar 0.5 mm)

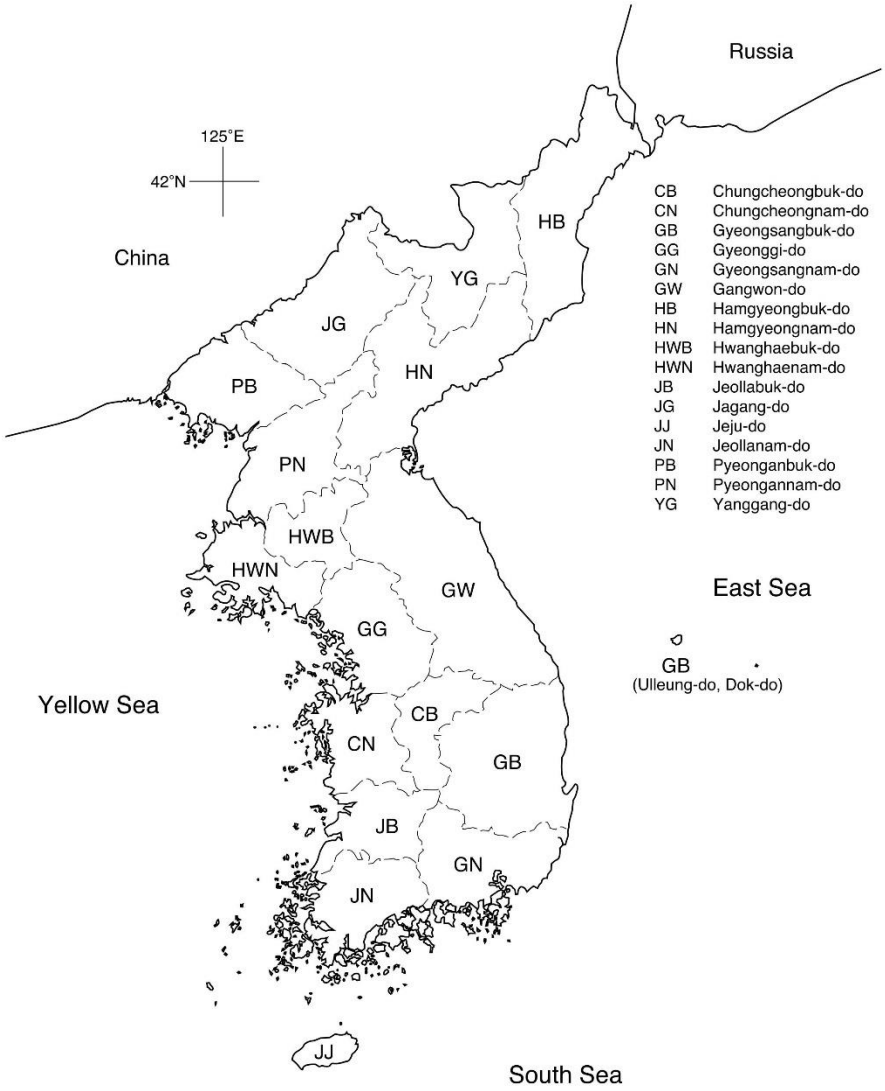

Figure 5. Abbreviation of localities in Korea, from Jeonghaengsa.

3. Result

Systematic Accounts

Order Hymenoptera 벌목

Suborder Apocrita 벌아목

Superfamily Apoidea 꿀벌상과

Family Apidae 꿀벌과

Genus *Nomada* 알락꽃벌속

Type species: *Apis ruficornis* Linnaeus, 1758

Diagnosis. Submarginal cells two to three in number, first submarginal cell distinctly longer than remaining in both sexes. Antennae mostly cylindrical in female, cylindrical to swollen in male. Apical margin or 5th sternum in female laterally with black tuft. 7th sternum in male apically narrow sometimes laterally concave.

Key to Korean species-groups of *Nomada*

Females

1. HTS strongly bent inward..... ***bifasciata* species-group**

– HTS not bent inward, rather absent or with dense hair without space or sparsely with numerous setae..... **2**

2. Head distinctly protuberant ..... ***superba* species-group**

– Head not protuberant **3**

3. Body size small, 4.3–5.54 mm ..... ***furva* species-group**

– Body size moderate to large, 6.84–11.8 mm **4**

4. HTS with a range of digitiform setae ..... ***tripsona* species-group**

– HTS without digitiform setae **5**

5. HTS leaf-like or stout and slightly round at tip ..... ***armata* species-group**

– HTS absent or spine to hair-like setae **6**

6. Propodeal triangle not horizontally rugose ..... ***ruficornis* species-group**

– Propodeal triangle horizontally rugose **7**

7. HTS absent or with apically with a number of short, yellow setae. If absent, metanotum entirely yellow ..... ***basalis* species-group**

– HTS with short stout spines. If absent, metanotum is entirely black or red ..... ***roberjeotiana* species-group**

Males

1. Gonostylus spatulate **2**

– Gonostylus not spatulate **3**

2. T2 black except lateral yellow maculation ..... ***roberjeotiana* species-group**

– T2 tinged with black and brown maculation on middle except lateral yellow maculation ..... ***bifasciata* species-group**

3. 7th sternum sharp at tip ..... ***furva* species-group**

– 7th sternum truncate or convex at tip **4**

4. S8 sharply narrowed and distinctly protruded at tip as in Pl 2-23. ..... ***tripsona* species-group**

– S8 apically round or gradually protrude at tip as in Pl 2-21 ..... **5**

5. Terga tinged with dark black and yellow only ..... ***superba* species-group**

– Terga tinged with brown to dark brown and yellow **6**

6. F2 shorter than F1 ..... ***basalis* species-group**

– F2 about as wide as F1 or F1 distincly shorter than F2 ..... **7**

7. Gonostylus fin-like, basoventral lobe absent or very weelky present as in Pl 2-10, ... ***armata* species-group**

– Gonostylus cylindrical, basoventral lobe mostly present. If absent, FL1: F2 over 1.8 ..... ***ruficornis* species group**

***Nomada armata* species-group**

Nomada armata species-group Alexander, 1994: 224.

Diagnosis. F1 about as wide as F2 or slightly shorter in both sexes. HTS leaf-like or stout and slightly round at tip except posteriormost seta in female, HTS 2 to 3 in number, acute at tip in male. Gonostylus fin-like, basoventral lobe absent or very weelky present.

Key to Korean species of *Nomada armata* species-group

Females

1. Scutellum entirely yellow ..... ***Nomada kaguya***

– Scutellum entirely red **2**

2. F2 about as wide as flagella ..... ***Nomada taicho***

– Scutellum entirely red **3**

3. Propodeal triangle entirely reddish brown ..... ***Nomada aswensis***

– Scutellum entirely red ..... ***Nomada ginran***

Males

1. Scutellum entirely yellow ..... ***Nomada kaguya***

– Scutellum entirely red **2**

2. T1 dark brown ..... ***Nomada aswensis***

– Distinct yellow wavy maculations with black spots on T1 ..... **3**

3. Mandible short and subacute at tip ..... ***Nomada ginran***

– Mandible long and sharp ..... ***Nomada taicho***

***Nomada aswensis* Tsuneki, 1973 굵은두가시알락꽃벌(신칭)**

Nomada aswensis Tsuneki, 1973: 100–103; Alexander & Schwarz, 1994: 245; Ikudome, 1999: 655; Mitai & Tadauchi, 2007: 45–49. Holotype ♀. TD: MNHAH. TL: Japan.

(Plates 1-3, 1-4, 2-2)

Description. Female. Body length 4.54–6.17 mm. *Head*. In frontal view about 1.27–1.34x wider than long; LID:UID=1:1.26–1.28. Head densely foveolate except clypeus foveolate-puncticuiate. Mandible simple, subacute at tip. Labrum tridentate. Vertex and frons intermixed with short golden and dark brown hair. Following area covered with short white plumose: paraocular area, supraclypeal area, and clypeus. Labrum covered with short light brown plumose. Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short golden hair. F1: F2: F3=1:1.26–1.40:1.08–1.12; FW1:FL1=1:1.24–1.46; FW2:FL2=1:1.85–2.05; FW3:FL3=1:1.42–1.68.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Scutellum flat, with shallow furrow. Propodeal triangle basally substrigulate to irregularly rugose, remaining shagreened. Mesoscutum, scutellum, metanotum sparsely with short golden hair. Hind tibiae covered with long light brown hair; HTS amber, three to four in number, posteriormost setae thin and long, the remaining short, leaf-like shaped, mostly stout but subacute at tip.

Metasoma. Smooth. Covered with short and decumbent golden hair.

Colors. Head mostly dark orange. Antennae anteriorly dark orange, posteriorly dark

orange to dark brown. Following area tinged with reddish brown: Vertex, frons, supraclypeal area, side of clypeus, central area of labrum, and tip of mandible. Mesoscutum black with two red lines or dark orange with thick median black line, basally tinged with black. Propodeal triangle entirely reddish brown. Legs mostly dark orange. Terga entirely dark orange.

Male. Body length 4.82–6.05 mm. *Head*. In frontal view about 1.21–1.26x wider than long; UID: LID=1: 1.28–1.29. Head densely foveolate. Mandible simple, subacute at tip. Labrum tridentate. Vertex and frons with long golden plumose. Following area covered with long light brown plumose: supraclypeal area, lower paraocular area, and clypeus. Labrum intermixed with long golden to light brown plumose. Mandible with long golden hair. Antennae with scape swollen, distinctly wider than flagella, covered with short golden plumose. F1:F2:F3=1:1.05–1.54:0.91–1.24; FW1:FL1=1:1.08–1.38; FW2:FL2=1:1.57–1.78; FW3:FL3=1:1.35–1.37.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Propodeal triangle basally substrigulate to irregularly rugose, remaining shagreened. Furrow absent on scutellum. Mesoscutum, scutellum and metanotum covered with long light brown plumose. Hind tibiae covered with long light brown hair; HTS light brown, three in number, posteriormost seta distinctly longer than remaining setae.

Metasoma. Punctate. Covered with short and decumbent golden hair. Pygidial plate distinctly notched.

Coloration. Head mostly black. Flagella anteriorly dark orange, posteriorly dark orange to dark brown. Scape entirely reddish brown. Following area tinged with

bright yellow: apical part of paraocular area, clypeus, labrum and mandible except reddish brown tip. Mesoscutum, metanotum, and propodeum entirely black. Scutellum black, sometimes with two red oval maculations. Legs dark brown. Terga mostly dark brown; T2 laterally with two bright yellow triangular maculations; T3 lateral margin with two bright yellow spots.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-2. Gonostylus cylindrical, narrow at tip, laterally and apically with long plumose; basoventral lobe absent.

Specimen Examined. JJ: 2♂, 3♀, Temple Gwan Eum 17. iv. 1998, coll. Seunghwan Lee (NAAS).

Distribution. Japan, Korea.

Floral records. *Ligustrum japonicum* Thunb. (Oleaceae); *Corydalis incisa* (Thunb.) Pers. (Papaveraceae)

Host. *Lasioglossum allodalum* Ebmer & Sakagami, 1985.

Remarks. This species can be confused with *Nomada flavoguttata* (Kirby, 1802) because of the small body size but can be distinguished by having amber, leaf-like HTS in female. In *N. aswensis* males, HTS is evidently thinner and longer than *N. flavoguttata* males.

***Nomada ginran* Tsuneki, 1973 흰털허리알락꽃벌**

Nomada ginran Tsuneki, 1973: 85–87; Tsuneki, 1986: 35; Alexander & Schwarz, 1994: 256; Ikudome, 1999: 653–654; Won & Kim, 2013: 9–10. Holotype ♀. TD: MNHAH. TL: Japan.

Nomada yasha Tsuneki, 1986: 36–37.

(Plates 1-18, 1-19, 2-10)

Description. **Female.** Body length 6.84–7.24 mm. *Head*. In frontal view about 1.33–1.44x wider than long; LID:UID=1:1.15-1.18. Head densely foveolate. Mandible simple, subacute at tip. Labrum tridentate at apex. Short black hair sparsely on vertex; yellow short hair on frons and upper paraocular area; short white plumose on supraclypeus, clypeus, lower paraocular area, labrum; Mandible with long golden hair. Antennae with scape cylindrical, as wide as flagella. FL1:FL2:FL3=1:1.16–1.30:1.07–1.22; FW1:FL1=1:1.32–1.42; FW2:FL2=1:1.66–1.82; FW3:FL3=1.54–1.58.

Mesosoma. Mesocutum, scutellum, metanotum densely foveolate. Scutellum with shallow furrow. Propodeal triangle predominantly rugose, laterally polished. Mesoscutum, scutellum, metanotum with short red hair; side of propodeal triangle with dense white plumose tuft. Hind tibiae with amber to dark amber hair; HTS amber, 3 in number, posteriormost seta long and thin, remaining relatively short and stout.

Metasoma. Entirely smooth; covered with short red hair.

Colors. Head predominantly red except black vertex and frons. Mesoscutum dark red with median thick black longitudinal maculation. Scutellum, metanotum entirely dark

red. Propodeal triangle black. Most of legs and Metasoma. dark red, tinged with black.

Male. Body length 7.25–7.3 mm. *Head*. In frontal view about 1.24–1.30x wider than long. LID:UID=1:1.18–1.25. Head foveolate, distinctly denser near vertex. Mandible short, subacute at tip. Labral tooth present near apex. Long white plumose predominantly distributed on head except short golden hair near vertex and long golden hair on mandible. Antennae with scape swollen, wider than flagella, with short golden hair. FL1:FL2:FL3=1:1.25–1.51:1.01–1.24; FW1:FL1=1:1.04–1.19; FW2:FL2=1:1.45–1.63; FW3:FL3=1:1.16–1.21.

Mesosoma. Mesoscutum, scutellum, metanotum foveolate, punctures sparser in metanotum. Propodeal triangle predominantly rugose, laterally polished. Mesoscutum, scutellum, metanotum with yellowish white to golden hair. Side of the propodeum with white plumose. Hind tibiae covered with long, transparent white hair; HTS amber, 3 in number, posteriormost seta long and thin, remaining distinctly short and evidently thicker than posteriormost one.

Metasoma. Entirely smooth; covered with short golden hair on the basal part of each tergum.

Male terminalia. 7th Metasomal sternum as in pl 2-10 F. 7th Metasomal tergum as in pl 2-10 D. 8th Metasomal sternum as in pl 2-10 E. Gonostylus short, strongly curved, blunt at the apical portion with long plumose vestiture at the tip and middle section. Gonocoxites with dorsal invagination present.

Colors. Head predominantly black with the following areas yellow: malar area, basal part of the clypeus, upper part of the compound eyes. Labrum black. Mandible yellow

to dark amber. Mesosoma mostly black, two yellow maculae on scutellum of considerable variable size; Most of legs mixed with black and dark brown. Metasoma. mostly yellow and brown; T1 dark brown on apical half and laterally with two dark brown spots on yellow wavy maculation; T2-T5 mostly ivory, and pale brown on intermacular space, background color dark brown.

Specimen Examined. CN: 2♀, Daesan-1ri, Daesan-eub, Seosan-si, 20. v. 2006, coll. Heung-sik Lee (LHSC). **GB:** 2♀, 280, Daehak-ro, Yeungnam University, Gyeongsan-si, 12. iv. ~ 01. v. 2017, coll. J.W. Lee (GE); 1♀, 280, Daehak-ro, Yeungnam University, Gyeongsan-si, 01. ~15. v. 2017, coll. J.W. Lee (GE). **GG:** 1♂, Anyang-si, 25. v. 1986, coll. J.G. Lee (SNU); 1♂, Anyang-si, 19. v. 1987, coll. Y.H. Ko (SNU); 1♀, Suwon-si, 20. v. 1990, coll. Lee Tae Kim (SNU); 1♀, Gwanggyo, 22. v. 1990, coll. S.C.Y. (SNU); 1♀, Gwanggyo, 29. v. 1990, coll. K.H.H. (SNU); 1♀, Cheonma, Namyangju-si, 20. iv. 1992, coll. H.K. (SNU); 1♂, Sangrok-sa, Suwon-si, 2. vi. 1995, coll. Seong-ho Choi (SNU); 1♂, Sangrok-sa, Suwon-si, 30. v. 1995, coll. Seong-ho Choi (SNU); 1♂, Bugjeju, Jocheon-eup, Seonheul-ri, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 1♀, Mt. Taehwa, Gwangju-si, 08. v. 1998, coll. Seunghwan Lee (NAAS); 5♀, 3♂, Mt. Taehwa, Gwangju-si, 08. v. 1998, coll. Heungtae Kim (SNU); 1♂, Gwangju-si, 18. v. 1998, coll. H.S. Lee (SNU); 1♂, Mt. Unilsan, Yeoju-si, 18. iv. 2001, coll. H.S. Lee (SNU); 1♂, Mt. Ungilsan, Yeoju-si, 18. iv. 2001, coll. H.S. Lee (SNU); 1♂, Eun-gol, Yulgeuk-ri, Heungcheon-myeon, Yeoju-si, 07. v. 2003, coll. Youngbo Lee (NAAS); 1♀, Dobong-gu, Mt. Bukhan, 20. ~ 24. iv. 2011, coll. H.S. Lee (LHSC); 1♀, 73, hwanghaksansumogwon-gil, Yeoju-si, 5. v. 2019, coll.

Junseo Hyun (SNU); 1♀, Soheul-eup, Pocheon-si, 25. v. 2020, coll. Kayun Lim (SNU); 2♀, Makgye-dong, Gwacheon-si, GG, 25. iv. 2021 wonwoong Kim (SNU); 2♀, Mt. Hwaya, Cheongpyeong-myeon, Gapyeong-gun, 19. iv. 2021, coll. S.J. Cho, Kayun Lim (SNU). **GN:** 1♂, Temple Tongdo Hapcheon-gun, 10. iv. 1997, coll. Heung-sik Lee (LHSC). **GW:** 1♂, Mt. Odae, Jinbu-myeon, 30. v. 1996, coll. H.S. Lee (SNU); 6♀, 5♂, Mt. Kujeol, Hongcheon-gun, 08. v. 1998, coll. Unknown (SNU); 1♀, Mt. Kujeol, Hongcheon-gun, 29. v. 1998, coll. Heung-sik Lee (SNU); 1♀, Mt. Odae, Hongcheon-gun, 29. iv. 2004, M.K. Paek (LHSC); 2♂, Mt. Cheongtae, Hoengseung-gun, 22. v. 2010, coll. Heung-sik Lee (LHSC); 1♂, Vivaldi-park, Hongcheon-gun, 13. v. 2011. coll. H.S. Lee (LHSC); 9♂, Bukbang-myeon, Hongcheon-gun, 15. v. 2012, coll. S.J. Jang (LHSC); 3♀, Dongchon-ri, Hwacheon-eup, Hwacheon-gun, 16. iv. ~ 14. v. 2017, coll. Min hyeuk Lee (SNU); 20♀, 12♂, Seorim valley, Seorim-ri, Seo myeon, Yangyang-gun, 18. iv. ~10. v. 2018, coll. Sang hyeok Nam (SNU); 1♀, 854, Han-gye-ri, Buk-myeon, Inje-gun, 22. v. 2018, coll. Sang hyeok Nam (SNU); 6♀, Seorim valley, Seorim-ri, Seo myeon, Yangyang-gun, 10. ~ 23. v. 2018, coll. Sang hyeok Nam (SNU); 4♀, Yongdae-ri, Buk-myeon, Inje-gun, 22. v. ~ 04. vi. 2018, coll. Min hyeuk Lee (SNU); 4♀, 854, Han-gye-ri, Buk-myeon, Inje-gun, 03. ~ 19. v. 2018, coll. Park & Nam (SNU); 1♀, 916-70, Punchbowl-ro, Haean-myeon, Yanggu-gun, 21. v. ~05. vi. 2018, coll. Unknown (KNA); 5♀, Seorim valley, Seorim-ri, Seo myeon, Yangyang-gun, 23. v.~05. vi. 2018, coll. Sang hyeok Nam (SNU); 2♀, 854, Han-gye-ri, Buk-myeon, Inje-gun, 27. vi. 2018, coll. Min hyeuk Lee (SNU); 1♀, 854, Han-gye-ri, Bukmyeon, Inje-gun, 04. vi. 2018, coll. Sanghyuk Nam (SNU); 1♂, 43,

Yaksu-gil, Seo-myeon, Yangyang-gun, 28. v. 2020, coll. Jaeseok Oh (SNU); 1♀, 854, Han-gye-ri, Bukmyeon, Inje-gun, 16. iv. ~ 01. v. 2020, coll. KY Lim, JS Oh, and DY Park (SNU); 1♀, 854, Han-gye-ri, Bukmyeon, Inje-gun, 01. v. ~ 13. viii. 2020, coll. KY Lim, JS Oh, and DY Park (SNU); 1♀, Mt. Odae, san 1, Dongsan-ri, Jinbu-myeon, Pyeongchang-gun, GG, 10. v. ~ 03. vi. 2021, coll. Duk-young Park (SNU); 1♀, 65-32, Morangol-gil, Buk-myeon, Inje-gun, 20. iv. 2021, coll. MH Lee, DY Park (SNU); 1♀, Manjong-ri, Hojeo-myeon, Wonju-si, 24. iv. 2021, coll. wonwoong Kim (SNU). **JJ:** 4♀, 10♂, Temple Gwaneum, Jeju-si, 17. vii. 1997, coll. Seunghwan Lee (SNU); 1♂, Jeju-si, 15. iv. 1998, coll. Seunghwan Lee (SNU); 5♀, 13♂, Temple Gwaneum, Jeju-si, 17. iv. 1998, coll. Seunghwan Lee (SNU); 1♀, 2596, 516-ro, Jeju-si, 11. iv. 2021 wonwoong Kim (SNU). **JN:** 1♀, Pia-gol, Mt. Chiri, 24. ~ 25. iv. 1999, coll. K.S. Woo (LHSC); 1♂, Temple Daeheung, Samsan-myeon, Haenam-gun, 12. v. 2005, coll. Youngbo Lee (NAAS); 1♂, Daea Arboretum, Dongsang-myeon, Wangju-gun, 16. iv. 2012, coll. Junmo Park (SNU). **Seoul:** 1♀, Cheonggye, 31. v. 1986, coll. D.G. Lee (SNU); 2♀, Anyang Arboretum, Mt. Gwanak, Anyang-si, 20. ~ 30. iv. 2002, coll. Unknown (LHSC); 1♀, Gugi-dong, Jongno-gu, 08. vi. ~ 22. vii. 2010, coll. Jong-cheol Jeong (LHSC); 1♀, Mt. Gwanak, Daehak-dong, Gwanak-gu, 23. vi. 2013, coll. Geum Seong Ko (LHSC); 5♀, Mt. Gwanak, Gwanak-gu, Seoul. 27. v. 2016, coll. Sanghyuk Nam (SNU); 2♀, Same location and collector, 28. v. 2016 (SNU); 2♀, Same location and collector, 30. v. 2016 (SNU); 2♀, 1♂, Seoul National University, 1, Gwanak-ro, Gwanak-gu, Seoul, 04. v. 2020, coll. Kayun Lim (SNU); 1♂, College of agriculture and life science, 1, Gwanak-gu, Seoul, 15. v. 2020 coll. Kayun Lim &

Duk-young Park (SNU); 1♀, 38, Oryu-ro 8ra-gil, Guro-gu, Seoul, 20. v. 2020, coll. Kayun Lim (SNU).

Distribution. Korea, Japan.

Floral records. *Trigonotis peduncularis* (Trevir.) Steven ex Palib. (Boraginaceae); *Rhododendron schlippenbachii Maxim.*, *Rhododendron mucronulatum* Turcz. (Ericaceae); *Rubus crataegifolius* Bunge, *Stephanandra incisa* (Thunb.) Zabel (Rosaceae); *Acer tataricum* subsp. *ginnala* (Maxim.) (Sapindaceae); *Staphylea bumalda* DC. (Staphyleaceae); *Camellia japonica* L. (Theaceae)

Host. *Andrena halictoides* (presumed, personal commination with Dr. Heung-sik Lee)

Remarks. *Nomada ginran* is one of the most common species in South Korea.

***Nomada kaguya* Hirashima, 1953 노랑방패알락꽃벌**

Nomada kaguya Hirashima, 1953: 135–136; Tsuneki, 1973: 107–109; Alexander & Schwarz, 1994: 249; Mitai & Tadauchi, 2007: 101–105; Won et al., 2008: 49; Won and Kim, 2013: 42–43.

Holotype ♀. TD: ELKU. TL: Japan.

(Plates 1-30, 2-17)

Description. Female. Not examined in this study.

Male. Body length 6.51 mm. *Head*. In frontal view about 1.32x wider than long. LID:UID=1:1.15. Head densely foveolate. Mandible slightly curved on center, subacute at tip. Labral tridentate on center. Short golden hair near vertex. Short golden

plumose densely on paraocular area, supraclypeal area, clypeus. Labrum intermixed with short golden hair and plumose. Mandible with short and long golden hair. Antennae with scape swollen, slightly wider than flagella, covered with short golden hair. FL1:FL2:FL3=1:1.07:1.04; FW1:FL1=1:1.44; FW2:FL2=1:1.49; FW3:FL3=1:1.41.

Mesosoma. Mesoscutum, scutellum, metanotum, side of propodeum foveolate. Scutellum flat, with shallow furrow. 2/3 of propodeal triangle irregularly rugose, remaining shiny. Mesoscutum sparsely covered with short golden hair. Scutellum, metanotum with short, golden, week plumose. Side of propodeum covered with yellow to white short plumose. Hind tibiae covered with short light brown hair; HTS amber to dark brown, 3 in number, slightly thicker than hair on hind tibiae.

Metasoma. Punctate, interspace shiny; covered with short decumbent golden hair. Pygidial plate distinctly notched, round at tip.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-17. Gonostylus short, fin-like, round at tip; apically and laterally with long sinuate plumose; basoventral lobe very weeky present. Gonocoxites with week dorsal invagination.

Colors. Head predominantly black. Antennae mostly dark brown; scape entirely black. Tinged with bright yellow as follows: near vertex, malar area, margin of clypeus, labrum, mandible except dark brown to reddish brown at tip. Mesoscutum and propodeum entirely black. Scutellum entirely bright yellow. Metanotum black with yellow maculation on center. Most legs dark brown, tinged with dark orange. Terga

mostly black; T2–T4 laterally with triangular bright yellow maculation. T5–T6 with bright yellow band.

Specimen Examined. GG: 1♂, Mt. Geumhak, Dongsong-eup, Cherwon-gun, 19. ix. 2020, coll. Kayun Lim (SNU).

Distribution. Korea, Japan.

Floral records. *Aster iinumae* Kitam. ex Hara; *Aster yomena* (Kitam.) Honda; *Picris hieracioides* subsp. *japonica* (Thunb.) Krylov (Mitai & Tadauchi, 2007); *Symphyotrichum pilosum* (Willd.) G.L. Nesom (Compositae).

Host. *Lipotriches yasumatsui* (Suda 1980; Maeta et al., 1996).

Remarks. This species is one of the distinctive species among Korean species in that it has a flat, bright yellow scutellum. Floral use of *S. pilosum* was confirmed in this study for the first time.

***Nomada taicho* Tsuneki, 1973 넓적머리알락꽃벌**

Nomada taicho Tsuneki, 1973: 47; Alexander & Schwarz, 1994: 257; Mitai & Tadauchi, 2006: 243–245; Won & Kim, 2013: 17–18. Holotype ♀. TD: MNHAH. TL: Japan.

(Plates 1-48, 1-49, 2-26, 3-4)

Description. **Female.** Body length 7–7.6 mm. *Head*. In frontal view about 1.47–1.49x wider than long; LID:UID=1:1.13–1.19. Head punctate. Mandible, sharp at tip. Labrum tridentate. Short golden hair sparsely on frons and paraocular area. Long white plumose, golden hair, and labrum sparsely on supraclypeal area and clypeus.

Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short golden hair. F1: F2: F3=1:0.8–1:0.8–0.9; FW1:FL1=1:1.66–2.05; FW2:FL2=1:1.44–1.73; FW3:FL3=1:1.29–1.55.

Mesosoma. Mesoscutum, scutellum punctate, interspace smooth and shiny. Metanotum foveolate. Scutellum flat, with very week furrow. 2/3 of upper propodeal triangle rugose-reticulate, remaining smooth and shiny. Mesoscutum and scutellum sparsely with short golden hair. Metanotum with short plumose. Hind tibiae covered with thick golden hair; HTS amber, 3 to 4 in number, length nearly equal in length, stout but subacute at tip.

Metasoma. Weakly punctate, interspace shiny. Covered with short and decumbent golden hair.

Colors. Head mostly black. Antennae dark orange. Following area dark orange: paraocular area, supraclypeal area, clypeus, labrum, mandible except reddish tip. Side of supraclypeal area and clypeus tinged with reddish brown. Mesoscutum dark orange with median thick black line, laterally with smear black maculation. Scutellum and metanotum entirely orange. Propodeal triangle entirely reddish brown. Legs mostly orange, tinged with dark brown. Terga entirely orange.

Male. Body length 6.6–7.3 mm. *Head*. In frontal view about 1.44–1.48x wider than long; UID: LID=1: 1.20–1.26. Head densely foveolate. Mandible, sharp at tip. Labrum tridentate near apex. Vertex and frons with long golden plumose, remaining area intermixed with long golden or white plumose except mandible with long golden hair. Antennae with scape swollen, covered with short golden plumose.

F1:F2:F3=1:1.1–1.3:1–1.1; FW1:FL1=1:1.04–1.22; FW2:FL2=1:1.33–1.40; FW3:FL3=1:1.11–1.27.

Mesosoma. Mesoscutum, scutellum punctate, interspace smooth and shiny. Metanotum foveolate. 2/3 of upper propodeal triangle rugose-reticulate, remaining smooth and shiny. Mesoscutum, scutellum and metanotum densely covered with long golden hair. Hind tibiae covered with long and thick light brown hair; HTS amber, 4 in number, length nearly equal in length, slightly thicker than hair on hind tibiae.

Metasoma. Punctate. Covered with short and decumbent golden hair.

Coloration. Head mostly black. Flagella anteriorly dark orange, posteriorly dark brown. Scape entirely dark brown. Following area tinged with bright yellow: lateral paraocular area, apical clypeus, labrum and mandible except reddish brown tip. Mesoscutum, metanotum, propodeum entirely black. Scutellum black or with red oval maculations. Legs mostly dark brown, tinged with black. Terga mostly black; T1 laterally with yellow maculations with black spots; T2 laterally tinged with yellow; remaining black.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-26. Gonostylus cylindrical, subacute at tip, laterally and apically with long plumose; basoventral lobe absent.

Specimen Examined. GG: 1♂, Mt. Gamak, Yangju-si, 12. v. 2006, coll. M.K. Baek (LHSC). **GW:** 1♀, Manjong-ri, Hojeo-myeon, Wonju-si, coll. 24. iv. 2021, coll. Wonwoong Kim (SNU); 3♀, Makgye-dong, Gwacheon-si, 25. iv. 2021, coll. Wonwoong Kim (SNU); 2♀, same locality, 13. v. 2021, coll. Wonwoong Kim (SNU);

1♂, Mt. Gariwang, 217-114, Jungwangsan-gil, Daehwa-myeon, Pyeongchang-gun, 11. v. 2021, coll. Kayun Lim, Duk-young Park, Jaeseok Oh, Wonwoong Kim (SNU). **JJ:** 1♂, unknown, 15. v. 1983, coll. Unknown (NAAS); 1♀, 11♂, vi. Gwaneumsa, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 2♀, 12♂, Temple Gwan Eum, 17. iv. 1998, coll. Seunghwan Lee (NAAS).

Distribution. Japan, Korea.

Floral records. *Brassica rapa* L. (Brassicaceae) (Mitai & Tadauchi, 2006); *Sorbus commixta* Hedl. (Rosaceae); *Stellaria alsine* var. alsine (Status uncertain).

Host. Unknown.

Remarks. This species is distinguished from the other Korean species by extraordinary broad heads in both sexes.

***Nomada basalis* species-group**
Nomada basalis species-group Alexander, 1994: 226.

Diagnosis. HTS absent or with apically with a number of short, yellow setae in both sexes. If absent, metanotum entirely yellow in female and F2 is shorter than F1 in male.

Key to Korean species of *Nomada basalis* species-group

1. HTS entirely absent in both sexes..... ***Nomada tsunekiana***

– HTS present in both sexes..... ***Nomada japonica***

***Nomada japonica* Smith 1873, 왜알락꽃벌**

Nomada japonica Smith, 1873: 203; Torre, 1896: 352; Cockerell, 1905: 31: 313; Meade-Waldo, 1913: 12: 98; Yano, 1932: 261; Yano, 1950: 1489; Pittioni, 1953, 59: 241; Hirashima, 1960:60; Hirashima, 1965: 309; Kim, 1970: 674; Tsuneki, 1973: 50; Tsuneki: 1986: 35; Alexander & Schwarz, 1994: 255; Ikudome, 1999: 653; Mitai & Tadauchi, 2005; Won & Kim, 2013: 11–13. Holotype ♀. TD: BNHM. TL: Japan. (Plates 1-28, 1-29, 2-16, 3-3 B)

Description. Female. Body length 11.11–11.78 mm. *Head*. In frontal view about 1.29–1.34x wider than long; LID:UID=1:1.13–1.20. Head densely foveolate. Mandible simple and broad, round at tip. Serrate carina on labrum and the labral tooth located at apical margin. Long golden plumose cover as follows: vertex, frons,

supraclypeal area, clypeus. Same but short hair on paraocular area. Labrum intermix with short golden hair and white plumose. Labrum with long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short golden hair. FL1:FL2:FL3=1:0.74–0.85:0.77–0.79; FW1:FL1=1:1.60–1.89; FW2:FL2=1:1.28–1.49; FW3:FL3=1.14–1.33.

Mesosoma. Mesoscutum, scutellum, metanotum entirely foveolate. Side of propodeum areolate. Scutellum with deep furrow. Propodeal triangle irregularly rugose on basal half, remaining portion shagreened. Mesoscutum, scutellum, metanotum with long golden plumose. Side of propodeum covered with yellowish white long plumose. Hind tibiae covered with short golden hair; HTS intermixed with a number of short yellow setae and long ivory pubescence.

Metasoma. distinctly punctuated and interspaces between punctures not as wide as the puncture; covered with decumbent yellowish hair.

Colors. Head predominantly red with the following areas black: Frons, vertex, and side of the clypeus; reddish yellow spot on frons. Mesoscutum with red, four longitudinal maculation. Scutellum and metanotum entirely dark orange. Propodeum black. Legs mostly dark orange, tinged with black. Terga mostly dark orange; T2 with inverted dark brown triangle maculation; T2, and T3 with yellow maculation; and the other tergum with entire yellow band.

Male. Body length 10.92–12.03mm. *Head*. In frontal view about 1.28–1.37x wider than long; LID:UID=1:1.06–1.10. Head densely foveolate. Labrum and mandible as in female. Long golden plumose present on vertex, frons, paraocular area,

supraclypeal area, clypeus. Antennae with scape cylindrical, slightly swollen and wider than flagella, with dense golden plumose. FL1:FL2:FL3=1:0.67–0.59:0.65–0.67; FW1:FL1=1:1.59–1.76; FW2:FL2=1:1.20–1.31; FW3:FL3=1:1.04–1.16.

Mesosoma. same as in female.

Metasoma. Closely punctuate; entirely covered with short golden hair on each tergum; pygidial plate blunt.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-16. Gonostylus long, cylindrical-like and strongly bent with long plumose vestiture at the tip and middle section. Gonocoxites with dorsal invagination present, longitudinally modified.

Colors. Head predominantly yellow with the following areas black: Frons, vertex, and side of the clypeus. Antennae mostly dark orange; scape anteriorly dark orange and bright yellow, posteriorly black. Mandible reddish brown at tip. Mesoscutum and propodeum entirely black. Scutellum bright yellow to dark orange. Metanotum dark orange to black. Legs tinged with bright yellow, dark orange, and black. T1 upper half black, lower half dark orange; T2 with inverted dark brown triangle maculation, the remaining portion of terga with yellow and dark brown band.

Specimen Examined. CB: 1♀, Mt. Uam, 22. vi. 1991, coll. Y.J.Y. (SNU). **CN:** 1♂, Eoeun-ri Taean-eub, Taean-gun, 20. v. 2006, coll. Heung-sik Lee (LHSC). **GG:** 1♀, Anyang-si, 14. v. 1980, coll. L.S.P. (SNU); 1♂, Suwon-si, 24. v. 1985, coll. J.D.S. (SNU); 1♂, Gwanggyo, 10. v. 1986, coll. J.L. Lee (SNU); 1♂, Anyang-si, 30. v. 1987,

coll. S.W.S. (SNU); 1♀, Anyang Arboretum, 29. iv. 1989, coll. Y.U.M. (SNU); 1♀, Anyang Arboretum, 6. v. 1989, coll. Seo Byung-chang (SNU); 1♂, Gwanggyo, 26. v. 1990, coll. K.H.H. (SNU); 1♂, Mt. Yongmun, 26. v. 1990, coll. Dong-guk Park (SNU); 1♂, Gwanggyo, 26. v. 1990, coll. K.H.H. (SNU); 1♂, Suwon-si, 1. vi. 1990, coll. B.H.W. (SNU); 1♂, Mt. Myongji, Gapyeong-gun, 5. v. 1991, coll. Dong-guk Park (SNU); 1♂, Gwangneung, 18. v. 1991, coll. Hyojeong (SNU); 1♀, Gwanggyo, vi. 1992, coll. J.I.B (SNU); 1♂, Suwon-si, 16. v. 1995, coll. Hak-ro Lee (SNU); 1♂, Mirinae, Ansung-si, 11. v. 1996, coll. J.M. Choi (SNU); 1♀, Hantaek Arboretum, Yongin-si, 30. v. 2001, coll. H.S. Lee (SNU); 1♂, Suwon-si, 2. v. 2002, coll. Heung-sik Lee (LHSC); 1♀, Mulhyanggi Arboretum, Sucheong-dong, Osan-si, 02. vi. 2009, coll. H.S. lee (LHSC); 1♀, Mt. Hoam, Siheung 2-dong, Geumcheon-gu, 21. vi. 2012, coll. Myeongwon Kim (SNU); 1♀, Gwanggyo, Suwon-si, 17. v. 2013, coll. H.S. Lee (LHSC); 1♀, 280, Yesulgongwon-ro, Manan-gu, Anyang-si, 20. iv. 2019, coll. Junseo Hyun (SNU); 1♂, 73, Hwangheksansumogwon-gil, Yeoju-si, 5. v. 2019, coll. Junseo Hyun (SNU); 4♂, Mt. Hwaya, Cheongpyeong-myeon, Gapyeong-gun, 19. iv. 2021, coll. Kayun Lim & Soo Jeong Cho (SNU); 1♀, 472-2, Bupyeong-ri, Gangcheon-myeon, Yeoju-si, 24. v. 2021, coll. Wonwoong Kim (SNU). **GW:** 1♀, Bukdaesa, Mt. Odaesan, Jinbu-myeon, 30. v. 1996, coll. H.S. Lee (SNU); 1♂, Bukbang-myeon, Hongcheon-gun, 22. iv. 1997, coll. H.S. Lee (SNU); 1♀, Mt. Baekam, Hongcheon-

gun, 24. v. 2002, Heung-sik Lee (LHSC); 1♀, Jeolgol, Gangdong-myeon, Gangneung-si, 25. v. 2002, coll. Heung-sik Lee (SNU); 2♀, 142-6, Sinheungdong-gil, Jucheon-myeon, Yeongwol-gun, 02. v. 2021, coll. Wonwoong Kim (SNU). **IN:** 1♂, Songdo-dong, Yeonsu-gu, 21. v. 1987, coll. Sang-moon Park (SNU); 1♀, 3. v. 1992, coll. J.I.B. (SNU); 1♂, Ganghwa-gun, 30. v. 1992, coll. H.K. (SNU). **JB:** 1♀, Mt. Seonun, Gochang-gun, 21. v. 1992, coll. Youn Ha-jeong (LHSC); 1♀, Sindeok-myeon, Imsil-gun, 30. iv. 2017, coll. Hae-cheol Park (NAAS). JJ: 1♂, Gamsan-ri, Andeok-myeon, Seogwipo-si, 03. iv. 1983, coll. Unknown (NIBR); 1♀, Sangumburi, San 38, Gyorae-ri, Jocheon-eup, Jeju-si, 24. iv. 1983, coll. Unknown (LHSC); 1♀, Ara, 27. v. 1984, coll. Unknown (LHSC); 1♀, Nohyeong, 5. v. 1985, coll. Unknown (LHSC); 1♀, Seongsan, 12. iv. 1986, coll. Unknown (LHSC); 1♀, Odeung-dong, Jeju-si, 20. vi. 1988, coll. Unknown (LHSC); 1♀, Hagwi-ri, Aeweol-eub, Jeju-si, 08. iv. 2009, coll. Heung-sik Lee (LHSC); 2♀, Ora-dong, jeju-si, 08. iv. 2009, coll. Unknown (LHSC); 1♀, 555-1, Onpyeong-ri, Seongsan-eup, Seogwipo-si, 07. iv. 2021, coll. Seunghyun Lee (SNU). **JN:** 1♂, Cheoneumsa Mt. Jiri, collection date and collector unknown (LHSC); 1♀, Mt. Baekun, 23. vi. 1992, coll. J.C.H. (SNU); 1♂, U-ui do, Sinan-gun, 17. v. 2006, coll. M.K. Paek (LHSC). **Seoul:** 1♂, Mt. Gwanak, 27. v. 1973, coll. Hyung-moon Kim (SNU); 1♂, Seoul Land, 181 Gwangmyeong-ro, Gwacheon-si, 24. v. 1995, coll. S.K. Son (SNU); 1♂, Mt. bulam, Gongneung-dong, Nowon-gu, 05. ~

11. v. 2008, coll. Sangwook Park (LHSC); 1♀, Mt. Gwanak, 27. v. 2016, coll. Sanghyuk Nam (SNU); 1♀, 38, Oryu-ro 8ra-gil, Guro-gu, 08. v. 2020, coll. Kayun Lim (SNU). **PY:** 1♂, Mt. Ryongak, PyeongYang-si, 09. ~ 14. v. 2012, coll. Han Chang-do (NIBR).

Distribution. Korea, Japan, China.

Floral records. Compositae (*Cirsium japonicum var. maackii (Maxim.)* Matsum*, Taraxacum platycarpum* Dahlst.), Brassicaceae (*Brassica napus* L.), Crassulaceae (*Sedum kamtschaticum* Fisch.), Ericaceae (*Rhododendron schlippenbachii* Maxim.).

Host. *Eucerea spurcatipes* (Masuda, 1940; Maeta et al., 1996*)*, *Tetralonia nipponensis* (Hirashima, 1972; Maeta et al., 1996).

Remarks. *Nomada japonica* is one of the most common species as *N. ginran* in South Korea.

***Nomada tsunekiana* Schwarz, 1999 황띠알락꽃벌**

Nomada koreana Tsuneki, 1986: 33–34; Alexander & Schwarz, 1994: 239, junior synonym of *Nomada koreana* Cockerell 1926. Synonymized by Schwarz, 1999: 260. *Nomada tsunekiana* Schwarz 1999: 260.

Holotype ♀. TD: MNHAH. TL: Korea.

(Plates 1-50, 1-51, 2-27)

Description. Female. Body length 7.88–9.39 mm. *Head*. In frontal view about 1.32–1.35x wider than long; LID:UID=1:1.14–1.18. Head densely foveolate except clypeus foveolate-puncticuiate. Mandible simple, subacute at tip. Labral tooth near

apex with serrate carina. Vertex, frons and upper paraocular area with short golden plumose. Following area covered with short golden hair: lower paraocular area, supraclypeal area, clypeus and mandible. Labrum intermixed with short golden hair and plumose. Antennae with scape cylindrical, about as wide as flagella, covered with long golden plumose. F1: F2: F3=1:1.05–1.19:0.88–1.07; FW1:FL1=1:1.42–1.51; FW2:FL2=1:1.56–1.70; FW3:FL3=1:1.21–1.42.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Interspace between punctures on scutellum substrigulate. Propodeal triangle horizontally rugose at basal area, remaining shagreened. Mesoscutum, scutellum, metanotum sparsely with short golden plumose. Hind tibiae covered with short golden hair; HTS absent.

Metasoma. Punctate. Covered with short and decumbent golden hair.

Colors. Head mostly black. Antennae anteriorly dark orange, posteriorly dark orange to dark brown. Paraocular area tinged with bright yellow, remaining black. Labrum intermixed with bright yellow and dark brown. Mandible basally dark brown, orange on center, reddish brown at tip. Mesoscutum and propodeum entirely black. Scutellum black with two bright yellow oval maculations. Metanotum entirely bright yellow. Hind tibiae predominantly dark orange, tinged with dark brown. Terga mostly black; T1–T2 laterally with two bright yellow lines; T3–T5 with bright yellow band.

Male. Body length 8.22–9.31 mm. *Head*. In frontal view about 1.29–1.32x wider than long; UID: LID=1: 1.18–1.19. Head densely foveolate. Mandible simple, subacute at tip. Labral tooth near apex with serrate carina. Short golden to white plumose densely on anterior head. Labrum intermixed with short golden hair and

white plumose. Mandible with long golden hair. Antennae with scape swollen, distinctly wider than flagella, covered with long golden plumose. F1:F2:F3=1:1.14–1.19:0.94–0.98; FW1:FL1=1:1.20–1.25; FW2:FL2=1:1.33–1.45; FW3:FL3=1:1.08–1.12.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Interspace between punctures on scutellum substrigulate. Propodeal triangle horizontally rugose at basal area, remaining shagreened. Mesoscutum covered with long, week golden plumose. Scutellum and metanotum covered with short golden plumose. Hind tibiae covered with short golden hair; HTS absent.

Metasoma. Punctate. Covered with short and decumbent golden hair. Pygidial plate entirely round.

Coloration. Head mostly bright yellow. Flagella anteriorly dark orange, posteriorly dark brown to dark black. Scape anteriorly bright yellow, posteriorly black. Following area black: vertex, frons, supraclypeal area, side of clypeus, remaining entirely bright yellow except mandible with reddish brown tip. Mesoscutum and propodeum entirely black. Scutellum black with two bright yellow oval maculations. Metanotum entirely bright yellow. Legs intermixed with bright yellow and black. Terga mostly black; T1 laterally with two bright yellow lines; T2 laterally with triangular bright yellow maculations; T3–T6 with bright yellow mands.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-27. Gonostylus cylindrical, subacute at tip, laterally and apically with long sinuate hair; basoventral lobe absent.

Specimen Examined. GG: 4♀, Mt. Taehwa, Gwangju-si, 2. xi. 1998, coll. Seunghwan Lee (NAAS). **GW:** 2♂, Temple Geonbong, 28. viii. 1990, coll. Jin Ill Kim (NAAS); 1♂, National Environment Research Institute, Hongcheon-gun, 14. ix. 2012, coll. S.J. Jang (LHSC).

Distribution. Korea.

Floral records. *Lespedeza bicolor* Turcz. (Fabaceae).

Host. Unknown.

Remarks. Tsuneki (1986) firstly reported this species as *Nomada koreana*, but *N. koreana* was already occupied before Tsuneki (1986) by Cockerell (1926). Thereafter, Schwarz (1999) reexamined these two species and reported this species as the new species, *Nomada tsuneki*. So far, *N. tsuneki* has been reported only in Korea.

***Nomada bifasciata* species-group**

Nomada bifasciata species-group Alexander, 1994: 228.

Diagnosis. HTS 2 in number, strongly bent inward in famle, 3 in number, posteriormost seta thin, remaining two slightly shorter and thicker than posteriormost one in male. Adittionally, head predominantly bright yellow except following are black: vertex, frons, and side of clypeus.

***Nomada comparata* Cockerell, 1911 쌍발톱알락꽃벌**

Nomada maculifrons var. *comparata* Cockerell, 1911: 644–645.

Nomada comparata Yasumatsu & Hirashima, 1952: 80–84; Tsuneki, 1973: 56–58; Alexander & Schwarz, 1994: 255; Mitai & Tadauchi, 2004: 93–97; Won et al., 2008: 48; Won & Kim: 13–15. Holotype ♀. TD: MNHAH. TL: uncertain.

(Plates 1-7, 1-8, 2-4, 3-1)

Description. Female. Body length 10.08–11.57 mm. *Head*. In frontal view about 1.29–1.36x wider than long; LID:UID=1:1.07–1.08. Head densely foveolate. Mandible long, simple, acute apically. Labral tooth at tip. Long golden plumose distributed on frons, vertex, paraocular area. Supraclypeus and clypeus with short golden hair. Labrum intermix with short golden plumose and long dark amber hair. Long golden hair on mandible. Antennae with scape cylindrical, about as wide as flagella, covered with short golden hair. FL1:FL2:FL3=1:1–1.10:0.82–0.90; FW1:FL1=1:1.45–1.68; FW2:FL2=1:1.55–1.78; FW3:FL3=1:1.21–1.38.

Mesosoma. Mesoscutum deeply areolate, sparsely covered with suberect golden hair; Scutellum shallowly furrowed, with punctures areolate, covered with short golden hair; Propodeal triangle deeply rugose on upper half, remaining shagreened. Side of the propodeal triangle distinctly areolate, covered with long yellowish white plumose. Hind tibia covered with thick, dark brown hair; HTS two in number, strongly bent inward.

Metasoma. finely punctuated; covered with short, decumbent pale-yellow hair.

Colors. Head mostly black; Scape predominantly dark orange; Lower paraocular area pale yellow, with the following areas black: frons, vertex, side of the clypeus; dark orange as follows: upper paraocular area and clypeus, labrum, mandible; tip of the

mandible dark red; supraclypeal area with circular dark orange maculation, sometimes tinged with black. Mesoscutum mostly black with four longitudinal dark red maculation; Scutellum black with circular pale-yellow maculation; Metanotum tinged with pale yellow or entirely black. Most of legs dark orange. Terga mostly reddish brown; T2-T3 laterally tinged with pale-yellow triangular maculation. T4–T5 with pale-yellow band.

Male. Body length 10.44–11.08 mm. *Head*. In frontal view about 1.31–1.44x wider than long. LID:UID=1:1.07–1.12. Head densely foveolate. Mandible long, simple, acute apically. Labral tooth absent. Long golden plumose on frons, vertex, paraocular area, supraclypeus, and clypeus. Labrum intermix with short golden plumose and hair. Mandible with long golden hair. Antennae with scape swollen, covered with short yellowish plumose. FL1:FL2:FL3=1:1.17–1.30:0.94–1.10; FW1:FL1=1:1.10–1.24; FW2:FL2=1:1.30–1.57; FW3:FL3=1:03–1.21.

Mesosoma. Mesoscutum densely foveolate. Scutellum and metanotum areolate. Propodeal triangle rugose upper 1/3 area, the remaining wrinkled. Mesoscutum, scutellum, metanotum, side of propodeum with long golden plumose. Hind tibiae covered with short golden hair; HTS amber to dark amber, 3 in number, posteriormost seta thin, remaining two slightly shorter and thicker than posteriormost one.

Metasoma. Punctuation identical as in female; Pygidial plate distinctly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal

tergum as in pl 2-4. Gonostylus long, laterally spatulate, curved posteriorly with long and sinuated hair at tip and lateral section. Basoventral lobe distinctly present, truncated, long hair present at tip. Gonostylus with dorsal invagination, furrow distinctly rounded.

Colors. Head mostly black. Scape anteriorly yellow, posteriorly black. Following areas tinged with bright yellow: paraocular area, clypeus, labrum, and mandible; Supraclypeal area bright yellow or sometimes entirely black. Scutum and propodeal triangle and its side entirely black. Scutellum as in female. T1 upper half black, lower half brown; T1−T6 tinged with black and brown maculation on middle, remaining portion pale yellow.

Specimen Examined. CB: 2♂**,** Jungnyeong rest space, Daegang-myeon, Danyang-gun, 9. v. 1997, coll. H.S. Lee (LHSC). **CN:** 1♂**,** Mt. Sanjesan, Nae3ri, Iwon-myeon, Taean-gun, 20. v. 2006, coll. H.S. Lee. **GB:** 1♂**,** Andong-si, 1. v. 1994, coll. J.Y. Lee; 1♀, Mt. Sobaek, 28. v. 1999, M.H. Kim. **GG:** 1♂**,** Gwanggyo, Suwon-si, 03. vi. 1990, coll. C.S.H. (LSHC); 4♂**,** Mt. Taehwa, 8. v. 1998, coll. H.T. Kim (SNU); 1♀, Jeolgol, Gangdong-myeon, Gangneung-si, 25. v. 2002, coll. H.S. Lee (LHSC). **GW:** 1♂**,** Buk-dae Temple, Mt. Odae, 10. v. 1996, coll, H.S. Lee (LHSC); 1♀, Dowon-ri, Goseoung-gun, 28. iv. 2002, coll. H.S. Lee (LHSC); 2♂, Cheongtae huyangrim, Hoengseong-gun, 22. v. 2010, coll. H.S. Lee (LHSC); 1♂, Yongdae-ri, Bukmyeon, Inje-gun, 8–22. v. 2018, coll. Min Hyeuk Lee (SNU); 2♀, Malaise trap, [38°08'46.5"N 128°15'47.5"E], 854, Hangye-ri, Buk-myeon, Inje-gun, coll. Min Hyeuk Lee (SNU). **JJ:** 1♂, Seonheul-ri, Jocheon-eup, Bugjeju-gun, 17. vii. 1997, coll. Seunghwan Lee

(NAAS); 1♂, Donnaeko, Seoquipo-si, 30.iv.2003, H.S. Lee (LHSC). **JN:** 1♂, Nogodan, Mt. Jiri, Gurye-gun, 26. v. 1997, coll. Heungsik Lee (LHSC); 1♂, Simwon, Mt. Jiri, Gurye-gun, 23. v. 1999, coll. H.T. Kim.

Distribution. Korea, Japan.

Floral records. *Valeriana fauriei* Briq. (Caprifoliaceae); *Trifolium repens* L. (Leguminosae); *Rubus crataegifolius* Bunge, *Rubus pungens* Cambess., *Sorbus commixta* Hedl. (Rosaceae), *Staphylea bumalda* DC. (Staphyleaceae).

Host. In 9th Jun, 2021, patrolling female of *N. comparata* was found near the nesting area of *Halictus tsingtouensis* in Mt. Gariwang but excavating the host nests was failed. Therefore, it is presumed that *H. tsingtouensis* is the host of *N. comparata* but future investigation must be conducted for confirmation. Hosts of *N. comparata* in Japan as follows: *Andrena mikado* (Hirashima, 1962; Maeta et al., 1996) and *Andrena richardsi* (Suda, 1980; Maeta et al., 1996).

Remarks.

N. comparata is distinctly distinguished species among Korean species in that it has stout, strongly curved two setae.

***Nomada furva* species-group**

Nomada furva species-group Alexander, 1994: 230.

Diagnosis. The *Nomada furva* species-group is characterized by male gonostylus which is strongly bent in ventral view and subgenital brush consists of two prominent

lateral tufts (Mitai & Tadauchi, 2006). Additionally, they are small-bodied about 4–6 mm in both sexes.

Key to Korean species of *Nomada furva* species-group

1. Hind tibia with one to three setae on apical margin, posteriormost setae long, the others relatively shorter and thinner than posteriormost one in both sexes; gonostylus without any knob in male.....***Nomada okubira***

– Apical hind tibial setae three in number, posteriormost setae long, the others relatively much shorter and stout, thicker than hair on hind tibiae in both sexes; gonostylus with week knobs just below tip in male.....***Nomada pulawskii***

***Nomada okubira* Tsuneki, 1973 애알락꽃벌**

Nomada dalii okubira Tsuneki, 1973:122. Holotype ♀. TD: TIM. TL: Japan.

Nomada sheppardana okubira Tsuneki, 1975: 463; Alexander and Schwarz, 1994: 257; Ikudome, 1999: 656.

Nomada etigonis Tsuneki, 1986: 57; Alexander and Schwarz, 1994: 243.

Nomada okubira: Mitai & Tadauchi, 2006: 240 stat. nov.; Won and Kim, 2013: 16–17.

(Plates 1-35, 1-36, 2-20)

Description. Female. Body length 4.61–5.54 mm. *Head.* In frontal view about 1.24–

1.26x wider than long; LID:UID=1:1.23–1.29. Head mostly foveolate. Mandible simple, subacute at tip. Labral tooth below center. Short reddish golden hair sparsely near vertex and upper paraocular area. Following area intermixed with short white plumose and golden hair: lower paraocular area, frons, clypeus and labrum. Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short golden plumose. F1: F2: F3=1:0.96–0.98:0.82–0.95; FW1:FL1=1:1.49–1.80; FW2:FL2=1:1.65–1.68; FW3:FL3=1:1.49–1.58.

Mesosoma. Mesoscutum, scutellum, and metanotum densely foveolate. Scutellum flat, with shallow furrow. Propodeal triangle entirely rugose. Mesoscutum and scutellum covered with short reddish golden hair. Metanotum with short golden plumose. Hind tibiae covered with short light brown hair; HTS dark amber, 1 to 2 in number, posteriormost seta distinctly longer and thicker than hair on hind tibiae, remaining slightly shorter and thinner than posteriormost one.

Metasoma. Sparsely punctate, remaining area smooth and shiny. Covered with short and decumbent golden hair.

Colors. Head mostly black. Antennae mostly dark orange. Scape and F2–F6 tinged with dark brown. Following area tinged with dark red: margin of paraocular area, lower half of clypeus, labrum and mandible. Mesoscutum and propodeum entirely black. Scutellum black with red oval maculation. Metanotum entirely dark red. Legs dark brown. Terga mostly dark red; T2 laterally tinged with bright yellow.

Male. Body length 4.75–5.27 mm. *Head*. In frontal view about 1.19–1.24x wider than long; UID: LID=1: 1.31–1.37. Head densely foveolate. Vertex with short red hair. Following area intermixed with short golden or white plumose, and short reddish hair: paraocular area, frons, clypeus, and labrum. Mandible covered with long plumose. Antennae with scape swollen, slightly wider than flagella, covered with short week golden plumose. F1: F2: F3=1:0.8:0.8; FW1:FL1=1:1.44–1.61; FW2:FL2=1: 1.31–1.37; FW3:FL3=1:1.2–1.5.

Mesosoma. Mesoscutum, scutellum, and metanotum entirely foveolate. Propodeal triangle entirely rugose. Mesoscutum with short golden hair. Scutellum and metanotum with golden plumose, plumose on metanotum distinctly shorter than plumose on scutellum. Side of propodeum with short white plumose tuft. Hind tibiae covered with long white hair; HTS 3 in number, posteriormost seta slightly longer than remaining.

Metasoma. Sparsely punctate, remaining area smooth and shiny. Covered with short and decumbent golden hair.

Coloration. Head predominantly black. Malar area, mandible bright yellow except reddish brown tip of mandible. Labrum mixed with black and bright yellow. Mesoscutum, scutellum, metanotum, propodeum entirely black. Legs mostly black, tinged with dark orange. Terga mostly black; T2 laterally tinged with bright yellow.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal

tergum as in pl 2-20. Gonocoxite long, cylindrical, subacute at tip; basoventral lobe present. Gonostylus and basoventral lobe apically with dense tuft. Long sinuate hair present on lateral gonostylus. Gonocoxite with strong invagination.

Specimen Examined.

GG: 1♀, Mt. Yeogi, Suwon-si, 14. vii. 1995, coll. June-Yeol Choi (NAAS); 1♂, same locality, 22. iv. 1998, coll. Seung-Hwan Lee (NAAS); 1♂, Mt. Taehwa, Gwangju, 8. v. 1998, coll. Seung-Hwan Lee (NAAS); 1♂, same locality, 22. vii. 1998, coll. Seung-Hwan Lee (NAAS). **GW:** 1♂, Sangweonsa, Mt. Chiak, Seongnam-ri, Sinlim-myeon, Wonju-si, 26. v. 2009, coll. Heung-sik Lee (LHSC); 2♀, Soheul-eup, Pocheon-si, 25. v. 2020, Kayun Lim leg. (SNU); 1♂, [38°04'40.9"N 128°26'49.3"E], 460-2, Osaek-ri, Seo-myeon, Yangyang-gun, 29. v. 2020, coll. Duk-Young Park (SNU). **JJ:** 3♀, 226, Yeongsil-ro, Seogwipo-si, 11. vi. 1998, coll. Jae-Seon Lee (NAAS); 1♂, Seonheul, Jocheon-eup, Bugjeju-gun, 17. iv. 1998, coll. Seung-Hwan Lee (NAAS); 1♂, Jeju College of Technology, Jeju-si, 6. viii. 2003, coll. Heung-sik Lee (LHSC); 1♀, 1♂, [33°17'46.9"N 126°20'48.6"E], San 3-89, Donggwang-ri, Andeok-myeon, Seogwipo-si, 23. vii. 2020, coll. Duk-Young Park (SNU); 1♂, [33°27'51.5"N 126°47'24.1"E], San 209, Songdang-ri, Gujwa-eup, Jeju-si, 24. vii. 2020, coll. Duk-Young Park (SNU); 1♀, [33°27'40.7"N 126°40'50.5"E], Daeheul-ri, Jochen-eup, Jeju-si, San 33, 24. vii. 2020, coll. Duk-Young Park (SNU).

Distribution. Japan, Korea.

Floral records. *Ranunculus japonicus* Thunb. (Ranunculaceae); *Brassica sp., Cardamine leucantha* (Tausch) O.E.Schulz (Brassicaceae); *Duchesnea chrysantha*

(Zoll. & Moritzi) Miq., *Potentilla sundaica var. robusta* (Franch. & Savatier) Kitag. (Rosaceae); *Trifolium pratense* L. (Leguminosae); *Chrysanthemum leucanthemum* L., Erigeron *philadelphicus L., Miyamayomena savatieri* (Makino) Kitam., *Stenactis annua Cass. Taraxacum campylodes* G.E.Haglund, (Asteraceae) (Mitai & Tadauchi 2006).

Host. *Lasioglossum sakagamii* Ebmer,1978 (Sakagami et al., 1982; Maeta et al., 1996).

Remarks. This species was described as *Nomada dalii okubira* Tsuneki, 1973, a subspecies of *N. dalii* Curtis by Tsuneki (1973), and recombined as *Nomada sheppardana okubira* in Tsuneki 1975, which is recently accepted as a valid species, *Nomada okubira* (Tsuneki, 1973) by Mitai & Tadauchi (2006).

***Nomada pulawskii* Tsuneki, 1973 작은두가시알락꽃벌(신칭)**

Nomada pulawskii Tsuneki, 1973: 125; Alexander & Schwarz, 1994: 257; Mitai & Tadauchi, 2006: 243. Holotype ♀. TD: MNHAH. TL: Japan.

(Plates 1-43, 1-44, 2-24)

Description. Female. Body length 4.30–5.17 mm. *Head*. In frontal view about 1.27–1.28x wider than long; LID:UID=1:1.27–1.28. Head densely foveolate except clypeus foveolate above, punctate below. Mandible simple, subacute at tip. Labrum tridentate. Vertex and frons with long reddish hair. Following area intermixed with long golden and white plumose: paraocular area, supraclypeal area, clypeus. Labrum

with short golden plumose. Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short golden hair. FL1:FL2:FL3=1:0.85–0.95:0.80–0.91; FW1:FL1=1:1.58–2.13; FW2:FL2=1:1.69–1.74; FW3:FL3=1:1.42–1.58.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Scutellum with deep furrow. Propodeal triangle entirely rugose. Mesoscutum and scutellum with short reddish golden hair. Metanotum with short golden plumose. Hind tibiae covered with short light brown hair; HTS dark reddish brown, three in number, posteriormost seta longer than hair on hind tibiae, remaining distinctly shorter and thicker than posteriormost one.

Metasoma. Punctate, interspace smooth and shiny. Covered with short and decumbent dark brown hair.

Colors. Head mostly black. Antennae anteriorly dark orange, posteriorly dark brown. Following area tinged with dark red: margin of paraocular area, apical area of clypeus, labrum and mandible except reddish brown tip. Mesoscutum, propodeum, and metanotum entirely black. Scutellum black with red oval maculation. Legs black, tinged with dark brown. Terga mostly black; T2 laterally with two smear dark red maculations.

Male. Body length 4.97–5.35 mm. *Head*. In frontal view about 1.25–1.26x wider than long; UID: LID=1: 1.31–1.33. Head densely foveolate, except clypeus punctate.

Mandible simple, subacute at tip. Labrum tridentate. Vertex and frons with short golden to white hair. Following area intermixed with short golden hair and white plumose: supraclypeal area, paraocular area, and clypeus. Labrum intermixed with short golden hair and white plumose. Mandible with long golden hair. Antennae with scape swollen, slightly wider than flagella, covered with short light brown week plumose. FL1:FL2:FL3=1:0.86–1.03:0.81–0.99; FW1:FL1=1:1.29–1.67; FW2:FL2=1:1.31–1.47; FW3:FL3=1:1.20–1.25.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Propodeal triangle entirely rugose. Furrow absent on scutellum. Mesoscutum and scutellum covered with golden to white hair. Hind tibiae covered with short white brown hair; HTS light brown, 3 in number, posteriormost seta as long as hair on hind tibiae, remaining distinctly shorter than posteriormost seta, acute at tip.

Metasoma. Punctate. Covered with short and decumbent golden hair. Pygidial plate distinctly notched.

Coloration. Head mostly black. Antennae anteriorly dark orange, posteriorly dark brown. Following area tinged with bright yellow: near vertex, malar area, apical margin of clypeus but median area black, mandible except reddish brown tip. Labrum intermixed with bright yellow and black. Mesoscutum, scutellum, metanotum, propodeum entirely black. Legs mostly dark brown, tinged with dark orange. Terga entirely dark brown.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal

tergum as in pl 2-24. Gonostylus cylindrical, acute at tip, week knobs laterally present, basoventral lobe present. Gonostylus and basoventral lobe apically with dense tuft. Long sinuate hair present on lateral gonostylus. Gonocoxite with strong invagination.

Specimen Examined.

GG: 3♀, 2♂, [37°22'53.6"N 126°54'42.1"E], Mt. Suri, Byeongmogan-ro 37, 247 beon-gil, Manan-gu, Anyang-si, 20. vi. 2020, coll. Kayun Lim (SNU); 1♀, Bukhansan National Park, Songchugyegok, Jangheung-myeon, Yangju-si, 08. iv. ~ 21. vii. 2010, coll. Heung-sik Lee (LHSC). **GW:** 1♂, Mt. Gujeol, Hongcheon-gun, 29. v. 1998, coll. Heung-sik Lee (LHSC); 1♂, 271, Osaek-ri, Seo-myeon, Yangyang-gun, on *Stephainandra incisa* (Thunb.) Zabel, 29. v. 2020, coll. Seunghyun Lee (SNU). **Seoul:** 1♀, [37°26'27.4"N 127°03'10.1"E], Mt. Cheonggye, 429-2, Wonji-dong, Seocho-gu, 27. vi. 2020, coll. Kayun Lim (SNU); 1♀, 205-5, Sillim-dong, Gwanak-gu, 16. vi. 2020, coll. Kayun Lim (SNU).

Distribution. Japan, Korea.

Floral records. *Geranium krameri* Franch. & Sav. (Geraniaceae); *Petasites japonicus* (Siebold & Zucc.) Maxim. (Asteraceae) (Mitai & Tadauchi 2006); *Stephanandra incisa* (Thunb.) Zabel (Rosaceae); *Erigeron annuus* (L.) Pers. (Compositae).

Host. Unknown.

Remarks. This species is very similar in general appearance to *Nomada okubira* Tsuneki but distinguished by two thick and short setae on the hind tibiae. The setae are significantly thinner in *N. okubira* in both sexes. The male of *N. pulawskii* differs

from *N. okubira* in that week knobs are presented in gonostylus in *N. pulawskii*, while it is absent in *N. okubira*.

***Nomada roberjeotiana* species-group**
Nomada roberjeotiana species-group Alexander, 1994: 218.

Diagnosis. Mesoscutum and propodeal entirely black without any reddish maculations in both sexes. HTS with short stout spines in both sexes. If absent, metanotum is entirely black or red in female, bright yellow in male. Gonostylus spatulate in male. Mostly active from late summer to fall.

Key to Korean species of *Nomada roberjeotiana* species-group

Females

1. HTS absent.....***Nomada esana***

– HTS present **2**

2. Scutellum entirely red.....***Nomada roberjeotiana aino***

– Scutellum tinged with yellow **3**

3. Clypeus apically and widely tinged with dark orange **4**

– Clypeus black, apically with thin dark orange line..... **5**

4. Scutellum yellow, terga mostly dark brown. HTS distinctly thicker than hair on hind tibiae ..... ***Nomada okamotonis***

– Scutellum ivory, terga mostly black. HTS as thin as hair in hind tibiae .....

.....***Nomada temmasana temmasana***

5. Paraocular area laterally with yellow triangular maculations .....

.....***Nomada shoyozana***

– Paraocular area black or dark orange at lateral margin..... **6**

6. Labrum black ..... ***Nomada galloisi***

– Labrum dark orange.....***Nomada hakusana hakusana***

Males

1. HTS absent.....***Nomada esana***

– HTS present **2**

2. Supraclypeal area tinged bright yellow..... **3**

– Supraclypeal area entirely black **5**

3. Supraclypeal area with yellow rectangular maculation .....

.....***Nomada shoyozana***

– Supraclypeal area entirely yellow or with yellow round spot..... **4**

4. HTS shorter than hair on hind tibiae.....***Nomada roberjeotiana aino***

– HTS as long as hair on hind tibiae ..... ***Nomada okamotonis***

5. Clypeus entirely yellow .....***Nomada temmasana temmasana***

– Clypeus intermix with black and yellow..... **6**

6. T3 laterally with yellow round maculation .....

..... ***Nomada galloisi***

– T3 with interrupted yellow band.....***Nomada hakusana hakusana***

***Nomada esana* Tsuneki 1973, 노랑뒷가슴알락꽃벌**

Nomada esana Tsuneki, 1973: 36–37; Alexander & Schwarz, 1994: 261; Mitai & Tadauchi, 2007: 156, 159; Won & Kim, 2013: 32–33. Holotype ♀. TD: MNHAH. TL: Japan.

(Plates 1-9, 2-5)

Description. Female. Not examined.

Male. Body length 9.72 mm. *Head.* In frontal view about 1.24x wider than long; LID:UID=1:1.07. Head densely Foveolate. Mandible simple and subacute at tip. Labrum with median carina; labral tooth above the apical margin. Short yellow hair and white plumose sparsely on vertex. Same hair densely on the following area: frons, paraocular area, supraclypeus, clypeus and labrum. Mandible with short golden hair. Antennae with scape cylindrical, slightly wider than flagella, covered with evidently short golden hair. FL1:FL2:FL3=1:1.01:0.87; FW1:FL1=1:1.37; FW2:FL2=1:1.38; FW3:FL3=1:1.18.

Mesosoma. Mesocutum, scutellum, metanotum densely foveolate. Scutellum with shallow furrow. Propodeal triangle horizontally rugose at basal area, the remaining alveolate. Mesoscutum, scutellum, metanotum with short suberect golden hair; side of propodeum covered with short yellowish white plumose. Hind tibiae covered with short amber hair; HTS absent.

Metasoma. Punctate; covered with decumbent amber hair.

Colors. Head predominantly black. Antennae tinged with black and dark orang.

Paraocular area and labrum entirely bright yellow. Clypeus tinged with bright yellow and black. Mandible basally bright yellow, apically reddish dark brown. Mesoscutum black except bright yellow metanotum. Legs tinged with black and dark orange. Terga predominantly black; T1–T3 with bright yellow triangular maculation; T4–T6 with bright yellow band.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-5. Gonostylus long, spatulate, laterally and apically with long hair. Basoventral lobe absent. Gonocoxites with dorsal, small invagination.

Specimen Examined. GG: 1♂, Mt. Taehwa, Gwangju-si, 19. viii. 1998, coll. Seunghwan Lee (NAAS).

Distribution. Japan, Korea, Russia.

Floral records. Unknown.

Host. Unknown.

Remarks. Alexander (1994) noted that *N. esana* may belong to *roberjeotiana* species-group, as well as Proshchalykin & Lelej (2010). On the other hand, Won & Kim (2013) designated the species into the *ruficornis* species-group. Because its first two flagella are equal in length in males and its distinct gonostylus habitus as in Pl 2-5, this species must be moved into the *roberjeotiana* species-group.

Nomada galloisi Yasumatsu & Hirashima, 1953 갈로이시알락꽃벌

Nomada galloisi Yasumatsu & Hirashima, 1953: 34–36; Hirashima, 1965: 309; Tsuneki, 1973: 42–44; Alexander & Schwarz, 1994: 243; Mitai & Tadauchi, 2003:

314–315; Won & Kim, 2013: 19–20. Holotype ♂. TD: MNHAH. TL: Japan

(Plates 1-17, 2-9)

Description. Female. Not examined in this study.

Male. Body length 7.97 mm. *Head*. In frontal view about 1.31x wider than long. LID:UID=1:1.17. Head densely foveolate. Mandible apically narrow, about as half as width of malar area, acute at tip. Labral tooth centrally, a range of projections below to tooth. White long plumose densely cover as follows: vertex, frons, paraocular area, supraclypeal area, clypeus. Labrum intermixed with short golden hair and white plumose. Mandible with short golden and white hair. Antennae with scape swollen, narrow near antennal sockets, short golden plumose. FL1:FL2:FL3=1:1.32:1.16; FW1:FL1=1:1.11; FW2:FL2=1:1.48; FW3:FL3=1:1.31.

Mesosoma. Mesoscutum, scutellum, metanotum, side of propodeum punctate, interspace shiny. Scutellum flat. Propodeal triangle entirely shagreened. Mesoscutum and scutellum with short golden hair. Metanotum and side of propodeum with short white plumose. Hind tibiae covered with yellow to white long hair; HTS amber, one stout seta present.

Metasoma. Punctate, interspace shiny; covered with short decumbent golden hair. Pygidial plate slightly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-9. Gonostylus long, spatulate, round at tip; apically and laterally with long straight vestiture. Basoventral lobe entirely absent. Gonocoxites with week dorsal invagination.

Colors. Head predominantly black. Antennae mostly dark brown; scape anteriorly bright yellow, posteriorly black. Tinged with bright yellow as follows: lower paraocular area, clypeus, labrum, mandible except reddish brown at tip. Mesoscutum and metanotum entirely black. Scutellum black with yellow oval maculation. Propodeum reddish brown. Legs mostly dark orange to amber. Terga predominantly reddish brown; T2–T3 laterally with oval ivory maculation.

Specimen Examined. GG: 1♂, Mt. Gamak, 24. viii. 1967, coll. Jin-Guk Oh (GE).

Distribution. Korea, Japan.

Floral records. *Geranium thunbergii* Siebold ex Lindl. & Paxton (Geraniaceae) (Mitai & Tadauchi, 2003).

Host. Unknown.

Remarks. This species was recorded in South Korea for the first time by Kim (1970), but the position of a voucher specimen of the record was dubious. Therefore, it was controversial if the record was valid (Won and Kim, 2013). In this study, one male specimen was found in GE, and therefore, the validity of this species is confirmed.

***Nomada hakusana hakusana* Tsuneki, 1973 넓은더듬이알락꽃벌**

Nomada melanura hakusana Tsuneki, 1973: 32–33 (*Nomada melanura* Tsuneki is preoccupied by Mocsáry, 1883). Holotype ♀. TD: MNHAH. TL: Japan.*Nomada momoglonis hakusana* Tsuneki, 1975: 463.

Nomada hakusana hakusana: Alexander & Schwarz, 1994: 243; Mitai & Tadauchi, 2003: 309–310.

(Plates 1-23, 2-13)

Description. **Female.** Not examined in this study.

Male. 9.97 mm. *Head*. In frontal view about 1.33x wider than long; LID:UID=1:1.05. Head densely foveolate. Mandible simple, subacute at tip. Labral tooth at apex with serrate carina. Short white plumose densely cover anterior head. Labrum covered with short yellowish white plumose. Mandible with long golden hair. Antennae cylindrical, narrow apically, basally slightly wider than flagella, covered with short golden plumose. F1: F2: F3=1:0.76:0.71; FW1:FL1=1:1.49; FW2:FL2=1:1.09; FW3:FL3=1:1.03.

Mesosoma. Mesoscutum foveolate, scutellum and metanotum punctate. Propodeal triangle horizontally rugose at basal area, remaining shagreened. Mesoscutum densely covered with short golden hair. Scutellum, metanotum sparsely with short golden plumose. Hind tibiae covered with short light brown hair; HTS 4 in number, posteriormost seta as thin as hair on hind tibiae, remaining stout but acute at tip.

Metasoma. Deeply punctate. Covered with short and decumbent golden hair.

Colors. Head mostly black. Antennae anteriorly dark orange, posteriorly dark brown. Scape intermixed with bright yellow and black. Following area tinged with bright yellow: lower part of paraocular area, clypeus, labrum, mandible except reddish brown at tip. Mesoscutum, metanotum, propodeum entirely black. Scutellum black with two bright yellow oval maculations. Legs mostly dark orange; hind coxa

intermixed with bright yellow and black; hind tibiae dark orange, black on center. Terga mostly black; T1−T2 laterally tinged with bright yellow; T3−T6 with bright yellow bands.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-13. Gonostylus spatulate, blunt at tip, laterally and apically with long hair; basoventral lobe absent.

Specimen Examined. GG: 1♂, Sinwon-ri, Pogok-eup, Cheoin-gu, Yongin-si, 10. x. 2014, coll. Lee, Lee, & Choi (SNU).

Distribution. Japan, Korea.

Floral records. Unknown.

Host. Unknown.

Remarks. In 1973, Tsuneki reported *Nomada melanura* as a new species, and additionally, he proposed *Nomada melanura hakusana* as its subspecies. However, since the name, *Nomada melanura,* was already occupied by Mocsáry, 1883, Alexander (1994) reproposed the species name as *Nomada hakusana hakusana,* and separated the species from *Nomada hakusana momoglonis* Tsuneki, 1975.

Nomada okamotonis Matsumura, 1912 영원방패알락꽃벌

Nomada okamotonis Matsumura, 1912: 198–199; Matsumura, 1930: 170–171; Matsumura, 1931: 8; Hirashima, 1965: 309; Alexander & Schwarz, 1994: 243; Mitai & Tadauchi, 2003: 307–309; Won & Kim, 2013: 21–22. Holotype ♀, in reality ♂. TD:

Uncertain. TL: Japan.

Nomada okamotonis kaiensis Tsuneki, 1976: 157–158.

Diagnosis. Body length 7.80–10.50 mm in female, 8.00–9.50 mm in male (Mitai & Tadauchi, 2003). Terga mostly dark brown to black; T2–T3 laterally tinged with yellow; T4–T5 with bright yellow bands in female. T2–T3 as in female, T4–T6 with bright yellow bands in male. HTS 5 in number, short and robust in both sexes (Won & Kim, 2013).

Distribution. Japan, Korea (Including North Korea), Russia

Remarks. Tsuneki (1976) suggested that *Nomada okamotonis kaiensis* differs from *Nomada okamotonis* in that the subspecies has better developed carinae at clypeus, finer and closer punctures, and the brown tip of antennae. However, since these characters are variable individually, it was synonymized with *N. okamotonis* by Mitai et al., 2003.

***Nomada roberjeotiana aino* Tsuneki, 1973 은포알락꽃벌**

Nomada aino Tsuneki, 1973: 40–42. Holotype ♂. TD: MNHAH. TL: Japan.

Nomada roberjeotiana aino: Tsuneki, 1975: 464–466; Mitai et al., 2003: 312–314; Mitai et al., 2008: 20; Won & Kim, 2013: 22–23.

Diagnosis. Body length 7.50–10.50 mm in female, 7.00–10.50 mm in male (Tadauchi & Murao, 2014). Terga mostly black; T1 reddish brown; T2–T3 laterally with two pale yellow spots; T5 with pale yellow rectangular maculation in female. Terga mostly black; T1 as in female. T2–T4 laterally with two bright yellow triangular

maculations; T5–T6 with median bright yellow band in male. HTS dark amber, 7 in number, posteriormost seta as thin as hair on hind tibiae, remaining distinctly shorter than posteriormost seta, stout, and subacute at tip in female. HTS 5 in number, as in female.

Distribution. Europe, Russia, Korea (North Korea only), Japan.

Remarks. *Nomada roberjeotiana aino* Tsuneki belongs to subspecies of the Palearctic species, *Nomada roberjeotiana,* and the major difference is based on the tergum coloration. *N. roberjeotiana aino* has pale yellow maculation on tergum, while it is white Palearctic species (Mitai et al., 2008). Any specimens of this species were not examined in this study. The diagnosis of this species was taken from Mitai *et al.* (2008).

***Nomada shoyozana* Tsuneki, 1986 소요알락꽃벌**

Nomada shoyozana Tsuneki, 1986: 34; Alexander & Schwarz, 1994: 252; Mitai *et al*., 2008: 20–23; Won & Kim, 2013: 23–24. Holotype ♂. TD: MNHAH. TL: Korea.

Diagnosis. Body length 7.50 mm in female, 7.50–8.00 mm in male (Mitai *et al.*, 2008). Terga mostly black; Lateral side of T1 with yellow spots; T2–T4 laterally with yellow maculation; T5 with yellow band in female. T1–T4 laterally with yellow maculations; T6 with yellow band in male. HTS light brown to dark brown, 4 in number, posteriormost seta thin and straight, remaining stout, sharp at tip, bent inward in female. HTS transparent or light brown, 2 to 3 in number, as thin as hair on hind

tibiae, distribute with space in male.

Distribution. Korea (including North Korea).

Remarks. *Nomada shoyozana* Tsuneki is similar to *N. hakusana hakusana* Tsuneki, but differ in having 2 thin HTS, while it is 4 in number, distinctly shorter and stout in *N. hakusana hakusana*. Any specimens of this species were not examined in this study. The diagnosis of this species was taken from Mitai *et al.* (2008).

***Nomada temmasana temmasana* Tsuneki, 1986 천마알락꽃벌**

Nomada temmasana Tsuneki, 1986: 34; Alexander & Schwarz, 1994: 243; Won & Kim, 2013: 24. Holotype ♀. TD: MNHAH. TL: Korea.

Nomada temmasana temmasana: Mitai *et al.*, 2003: 299–302.

Diagnosis. Female. Body length 6.50 mm (Tsuneki, 1986). T2 laterally tinged with bright yellow; T3–T5 with short yellow bands. HTS dark brown, about 20 in number, short, acute at tip. Male is unknown.

Distribution. Korea.

Remarks.

The holotype of this species was collected in South Korea and reported as a new species by Tsuneki (1986). It resembles with Japanese subspecies, *Nomada temmasana akitsushimae* Mitai, but has different coloration. Korean subspecies has black clypeus and mandible, while they are brownish-yellow in the Japanese subspecies (Mitai et al., 2008). Since any specimens of this species were not

examined in this study, the diagnosis of this species was taken from Mitai et al. (2008).

***Nomada ruficornis* species-group**

Nomada ruficornis species-group Alexander, 1994: 218.

Diagnosis. Body size small to moderate, about 5–10 mm. Scape mostly cylindrical but width of scape in comparison with flagella significantly variable in male. F1 distinctly shorter than F2 in both sexes. Gonostylus cylindrical, rounded apically, and slightly bent posteriorly but not strongly as in *furva* species-group.

Key to Korean species of *Nomada ruficornis* species-group

Females

1. HTS long and as thin as hair on hind tibiae **2**

– HTS length variable and thicker than hair on hind tibiae except long and thin posteriormost seta **5**

2. HTS 4 in number, evenly distributed with space **3**

– HTS more than 10 in number without distinct space **4**

3. Propodeal triangle dark orange with median thick black line....***Nomada sabaensis***

– Propodeal triangle entirely black, laterally with two red dots.....***Nomada shirakii***

4. HTS curved, equal in length ..... ***Nomada harimensis***

– HTS straight, short gradually ..... ***Nomada pacifica***

5. Scutellum black.....*Nomada* **sp.nov. 2**

– Scutellum reddish or bright yellow..... **6**

6. Scutellum tinged with bright yellow..... **7**

– Scutellum dark orange to red **8**

7. Propodeum laterally with two dark orange dots .....

.....***Nomada fulvicornis jeizoensis***

– Propodeum entirely black without any dots.....***Nomada lathburiana***

8. Propodeal triangle with two yellow zigzag patterns .....***Nomada icazti***

– Propodeal triangle without two yellow zigzag patterns **9**

9. HTS distinctly black **10**

– HTS light brown to dark brown..... **14**

10. HTS stout, round at tip.....***Nomada guttulata***

– HTS subacute to acute at tip **11**

11. Paraocular area dark orange, sometimes tinged with bright yellow **12**

– Paraocular area mostly black, lateral margin weekly tinged with dark red **13**

12. Labral tooth on apical one-third, laterally with serrate carina .....

.....***Nomada calloptera***

– Labral tooth at apex .....***Nomada maculifrons***

13. Propodeal triangle red with median black line.....***Nomada leucophthalma***

– Propodeal triangle black .....***Nomada fusca***

14. Mandible bidentate..... **15**

– Mandible simple or truncate **16**

15. Scutellum covered with golden plumose .....***Nomada opaca***

– Scutellum covered with white hair.....***Nomada* sp.nov. 3**

16. T5 entirely red..... **17**

– T5 with bright yellow band..... **19**

17. HTS dark brown, round at tip .....***Nomada flavoguttata***

– HTS light brown, sharp at tip..... **18**

18. Paraocular area and supraclypeal area dark orange. Propodeal triangle red with median black line .....***Nomada hakonensis***

– Paraocular area and supraclypeal area black, lateral margin of paraocular area weekly tinged with dark red. Propodeal triangle entirely black.....

.....***Nomada montverna***

19. HTS stout, truncate at tip, distributed without space ..... ***Nomada pyrifera***

– HTS subacute, distributed with space **20**

20. T4 entirely dark brown.....***Nomada* sp.nov. 1**

– T4 tinged with yellow **21**

21. Scutellum foveolate, the biggest interspace as wide as puncture.....

.....***Nomada abtana***

– Densely foveolate without wide interspace **22**

22. Mandible truncate .....***Nomada striata***

– Mandible simple..... **23**

23. Antennae entirely dark orange .....***Nomada panzeri orientis***

– Antennae posteriorly tinged with black **24**

24. Propodeal triangle black; HTS irregularly distributed.....

..... ***Nomada amurensis***

– Propodeal triangle black laterally tinged with dark red; HTS evenly distributed

..... ***Nomada fervens***

Males

1. Clypeus entirely black..... ***Nomada harimensis***

– Clypeus tinged with yellow..... **2**

2. Gonostylus distinctly long and slender, acute apically .....***Nomada maculifrons***

– Gonostylus blunt and thick **3**

3. Supraclypeal area fully bright yellow ..... ***Nomada pyrifera***

–Supraclypeal area fully black or tinged with quadrate yellow maculation **4**

4. Mandible truncate **5**

– Mandible simple or dentate..... **7**

5. Clypeus with yellow triangular maculation, somewhat laterally tinged with black

..... ***Nomada pacifica***

– Clypeus mostly black; apical margin with yellow band **6**

6. T2 basally tinged with dark brown, adults active in summer.....

.....***Nomada abtana***

– T2 dark orange, adults active in spring ..... ***Nomada striata***

7. Pygidial plate triangularly notched **8**

– Pygidial plate not triangularly notched **9**

8. T1 entirely dark brown..... ***Nomada amurensis***

– T1 entirely pale brown, laterally with two dark brown oval maculation .....

..... ***Nomada calloptera***

9. Pygidial plate shallowly and roundly notched **10**

– Pygidial plate distinctly notched **13**

10. T2–T6 with distinct wide yellow band..... ***Nomada lathburiana***

– Partly with yellow band or widely darkened, but at least T2–T3 without yellow band

..... **11**

11. HTS slender, difficult to differentiate among surrounding hair

..... ***Nomada montverna***

– HTS thickness variable, evidently distinguished from surrounding hair **12**

12. Basoventral lobe distinctly present ..... ***Nomada guttulata***

– Basoventral lobe absent ..... ***Nomada flavoguttata***

13. T2 laterally with distinct yellow maculation, T3 laterally with small yellow spots, remaining entirely dark brown..... ***Nomada hakonensis***

– Yellow maculation present on T3–T5 ..... **14**

14. Mandible bidentate..... ***Nomada opaca***

– Mandible simple..... **15**

15. HTS thick, cylindrical ..... ***Nomada fulvicornis jeizoensis***

– HTS thin, hair-like **16**

16. Abdomen entirely black with inverted triangle maculation .....

.....***Nomada leucophthalma***

– Abdomen without inverted triangle maculation..... **17**

17. T2 dark brown with semicircle maculation on middle.....

.....***Nomada shirakii***

– T2 laterally with yellow maculation **18**

18. Abdomen tinged with pale brown..... **19**

– Abdomen tinged with only dark brown and yellow..... **20**

19. Gonostylus sharp, crescent-like ..... ***Nomada fervens***

– Gonostylus thick, triangular.....***Nomada icazti***

20. Clypeus with yellow triangular maculation, somewhat laterally

.....

tinged with black.....***Nomada panzeri orientis***

– Clypeus mostly black, apical margin with yellow band..... **21**

21. F1 about half as long as F2, scutellum with two red oval maculation .....

.....***Nomada fusca***

– F1 one third of F2, scutellum entirely black .....

.....***Nomada* sp. nov. 1**

***Nomada abtana* Tsuneki 1973, 갈색방패알락꽃벌**

Nomada abtana Tsuneki, 1973: 126–128; Alexander & Schwarz, 1994: 244; Mitai & Tadauchi, 2007: 28–32; Won & Kim, 2013: 28–29. Holotype ♂. TD: MNHAH. TL: Japan.

(Plate 1-1)

Description. Female. Body length 8.03 mm. *Head*. In frontal view about 1.26x wider than long; LID:UID=1:1.09. Head densely foveolate. Mandible long, simple, acute and round apically. Labral tooth below the center. Short golden hair sparsely on frons and vertex, densely cover following area: paraocular area, supraclypeus, clypeus and mandible; Labrum intermix with short golden or dark brown hair. Antennae with scape cylindrical, about as wide as flagella, covered with yellowish hair. FL1:FL2:FL3=1:1.38:1.17; FW1:FL1=1:1.19; FW2:FL2=1:1.63; FW3:FL3=1:1.32.

Mesosoma. Mesocutum foveate-reticulate. Scutellum distinctly furrowed, densely foveolate, punctures smaller in basal area. Propodeal triangle irregularly rugose upper area, the remaining shagreened. Mesoscutum and scutellum with short decumbent golden hair; side of propodeum covered with short white plumose. Hind tibiae covered with dark amber hair; HTS dark amber, 4 in number, posteriormost seta long and thin, the remaining short, stout, slightly blunt at the tip.

Metasoma. Distinctly punctuated and interspaces between punctures not as wide as the puncture; covered with decumbent dark amber hair.

Colors. Head predominantly black. Antennae posteriorly dark brown and anteriorly dark orange. Following area tinged with reddish orange; vertex, side of the paraocular

area, clypeus, malar area, and mandible. Labrum tinged with reddish orange and dark brown. Mandible reddish brown at tip. Mesoscutum mostly black with two red longitudinal maculation; scutellum tinged black with two dark orange oval maculation. Propodeal triangle and its side entirely black. Leg mostly dark amber. Terga mostly dark brown; T2 and T4 laterally with ivory spots; T3 entirely dark brown; T5 with ivory band.

Male. Not examined.

Specimen Examined. GB: 1♀, Gyeongju-si, Mt. Namsan, 6. vi. 1992, coll. G.Y. Lee (GE).

Distribution. Korea, Japan.

Floral records. *Rorippa sylvestris* (L.) Besser (Brassicaceae); *Picris hieracioides* Sibth. & Sm. (Compositae); *Trifolium repens* L. (Leguminosae) (Mital and Tadauchi 2007).

Host. Unknown.

Remarks. *N. abtana* is closely resembled *N. striata* Fabricius but differs in having weakly convergent inner eye margins. Additionally, they have a phenological asynchrony. *N. abtana* is active in summer, while *N. striata* is active in spring (Mitai & Tadauchi, 2007).

***Nomada* sp. nov. 1**

(Plates 1-52, 1-53, 2-28, 3-5)

Description. Female. Body length 7.55–8.75mm. *Head*. In frontal view about 1.29–1.40x wider than long; LID:UID=1:1.06–1.11. Head entirely imbricate-punctate except for vertex foveolate. Mandible long, simple, acute apically. Labral tooth centrally. Short golden plumose and long black hair sparsely cover following area: frons, vertex, paraocular area, clypeus, mandible and labrum. Antennae with scape cylindrical, about as wide as flagella, with short dark brown hair. F1: F2: F3=1:1.12–1.20:0.96–1.06; FW1:FL1=1:1.34–64; FW2:FL2=1:1.60–70; FW3:FL3=1:1.36–1.48.

Mesosoma. Mesoscutum, scutellum, metanotum entirely imbricate-punctate. Propodeal triangle entirely rugose, its side weekly alveolate. Mesoscutum and scutellum with erect, long golden hair; side of propodeum covered with yellowish white plumose. Hind tibiae intermixed with long dark brown hair and relatively short light brown hair; HTS dark brown, 5 to 6 in number, posteriormost seta long, the remaining distinctly shorter and thicker than posteriormost one, irregularly distributed.

Metasoma. Finely imbricate-punctate. Covered with short and decumbent dark brown hair.

Colors. Head mostly black. antennae anteriorly dark orange, posteriorly dark brown.

Side of vertex, margin of clypeus tinged with dark orange. Labrum tinged with bright yellow and dark orange. Mandible dark orange. Mesoscutum mostly black, with two longitudinal blurry red lines; scutellum tinged with red, metanotum black or red. propodeal triangle black, with two oval red maculation; side of propodeum entirely black; Leg mostly dark brown. Terga mostly dark brown; T2 laterally with two bright yellow triangular maculation, centrally with inverted black triangular maculation; T3–T4 dark brown; T5 with bright yellow square maculation.

Male. Body length 7.87–8.6mm. *Head*. In frontal view about 1.29–1.35x wider than long; UID: LID=1: 1.17–1.20. Following area densely foveolate: vertex, frons, paraocular area, clypeus. Labrum very finely punctate or foveolate. Mandible simple, acute apically. Labral tooth just below the center. Yellowish white plumose densely cover as follows: vertex, frons, paraocular area, clypeus, mandible. Labrum intermixed with long, white plumose and golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with long golden plumose; F1: F2: F3=1:1.15–1.25:0.99–1.12; FW1:FL1=1:1.10–1.48; FW2:FL2=1: 1.46–1.61; FW3:FL3=1:1.29–31.

Mesosoma. Mesoscutum, scutellum, metanotum deeply foveolate. Scutellum weekly furrowed. Propodeal triangle entirely rugose, its side distinctly areolate. Yellowish white plumose on mesoscutum, scutellum, metanotum, side of propodeum. Hind tibiae covered with yellowish white hair; HTS light brown, 4 to 5 in number, posteriormost seta slightly longer than the remaining, intermixed with white, straight hair.

Metasoma. imbricate-punctate. Covered with short and decumbent golden hair.

Coloration. Head mostly black. antennae predominantly dark brown, scape anteriorly tinged with dark orange; the following area tinged with bright yellow: malar area, basal area of clypeus, labrum. Mandible mixed with bright yellow and dark orange. Mesoscutum, scutellum, metanotum, propodeal triangle and its side wholly black. Legs tinged with dark orange and dark brown. Terga mostly black; T2−T3 laterally with two bright yellow triangular maculation; T2 centrally with inverted black triangular maculation; T4–6 with bright yellow band.

Male terminalia. 7th tergum narrow and blunt apically; 7th sternum concave below the center; 8th sternum as in Fig 2-28. Gonocoxite acute; Gonostylus short; blunt apically; bent posteriorly; basoventral lobe present. Gonostylus and basoventral lobe laterally with long vestiture.

Specimen Examined. GW: Holotype ♀**,** pantrap, [N38°08'46.7", E128°15'50.0"], 854, Hangye-ri, Buk-myeon, Inje-gun, 14.iii.2021, coll. Kayun Lim, Duk-Young Park, Jae Seok Oh, Ji Won Son (SNU); ♂: same locality, date and collector. Paratypes 6♂, same data as for holotype (SNU). 1♀, 9♂, congruent locality for holotype, 13.iii.2021, coll. Seunghwan Lee (SNU); 7♀, same locality and collector as for holotype, 21.iii.2021, coll. Seunghwan Lee (SNU).

Distribution. Korea.

Floral records. Unknown.

Host. Unknown.

Remarks. This new species can be confused with *Nomada shirakii* Yasumatsu and

Hirashima, 1951, but can be distinguished by rather irregular dispersion and length of HTS in female. The irregularly distributed HTS is 5 to 6 in number, and length is extremely variable in the new species, while HTS is 4 in number, and evenly distributed in *N. sabaensis.* In the male of the new species, scape is comparatively cylindrical.

***Nomada* sp. nov. 2**

(Plate 1-54)

Description. Female. Body length 9.6 mm. *Head*. In frontal view about 1.34x wider than long; LID:UID=1.12. Frons, paraocular area, clypeus, labrum entirely imbricate-punctate. Mandible long, simple, acute apically. Labrum with triangular-shaped tooth on center, above the serrate carina. Appressed golden plumose sparsely on the following area: vertex, frons, paraocular area, clypeus, labrum. Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, with appressed golden hair. Appressed yellowish white plumose sparsely on frons. F1: F2: F3=1:1.60:1.33; FW1:FL1=1:1.08; FW2:FL2=1:1.83; FW3:FL3=1:1.52.

Mesosoma. Mesoscutum and scutellum deeply areolate, metanotum minutely areolate. Propodeal triangle irregularly rugose on upper 1/3 area, remaining portion finely reticulate, its side weekly alveolate. Mesoscutum, scutellum, metanotum with decumbent golden hair; side of propodeum sparsely covered with short yellowish white hair. Hind tibiae covered with short dark brown hair; HTS eight in number, posteriormost two setae long and sharp, remaining short, stout and blunt apically.

Metasoma. Densely foveolate; covered with short and decumbent golden hair.

Colors. Head predominantly black. Antennae dark brown anteriorly and black posteriorly. Side of the vertex and margin of the clypeus faintly tinged with dark red. Labrum and mandible tinged with dark red and brown. Mesoscutum, scutellum, metanotum, propodeal triangle entirely black. Legs mostly dark brown, tinged with dark red. Terga mostly black; T2 laterally with two yellow triangular maculation; T3 slightly tinged with yellow; T4–T5 with thick yellow band.

Male. Not examined.

Specimen Examined. GW: Holotype ♀, Dumun Dongjae, Gohan-ri, Gohan-eup, Jeongseon-gun, 28. viii. 2021, coll. Soo Jeong Cho (SNU).

Distribution. Korea.

Floral records. *Miyamayomena koraiensis* (Nakai) Kitam. (Compositae).

Host. Unknown.

Remarks. Most closely related to *Nomada fusca* Schwarz, 1986, but can be distinguished by HTS. In *N. fusca*, HTS are 4 to 6 in number, evenly distributed and long evenly.

***Nomada amurensis* Radoszkowsky, 1876 북방알락꽃벌**

Nomada amurensis Radoszkowsky, 1876: 91–93; Alexander & Schwarz, 1994: 244; Mitai & Tadauchi, 2007: 36–42; Won & Kim, 2013: 29–30. Holotype ♀. TD: ZIRAS. TL: Russia.

Nomada esakii Yasumatsu et Hirashima, 1953: 31–34; Tsuneki, 1973: 92–95;

Alexander & Schwarz, 1994: 246.

Nomada sudai Tsuneki, 1976: 152–154; Alexander & Schwarz, 1994: 252.

(Plates 1-2, 2-1)

Description. Female. Not examined.

Male. Body length 6.65–7.87 mm. *Head*. In frontal view about 1.24–1.27x wider than long; LID:UID=1:1.16–1.18. Head entirely areolate. Mandible long, simple acute apically. Labrum with tooth on just below center. Yellow plumose sparsely on vertex; white plumose densely on clypeus, supraclypeus, and labrum. Mandible mixed with short white hair and long golden hair. Antennae with scape swollen, wider than flagella, with yellow plumose. FL1:FL2:FL3=1:1.45–2.05:1.15–1.60; FW1:FL1=1:0.98–1.15; FW2:FL2=1:1.65–1.82; FW3:FL3=1:1.31–1.37.

Mesosoma. Mesocutum and scutellum densely foveolate. Scutellum with shallow furrow. Propodeal triangle irregularly rugose about upper 1/2 area, the remaining shagreened. Mesoscutum with long golden hair; scutellum and metanotum with long yellow plumose; side of the propodeal triangle with long white plumose. Hind tibiae covered with long golden hair; HTS 7 to 10 in number, long and thin, length nearly equal each other.

Metasoma. distinctly punctuated and interspace wider than the punctures; covered with decumbent golden hair.

Colors. Head predominantly black. Flagella anteriorly dark orange, posteriorly dark brown. Scape entirely black. Tinged as bright yellow as follows: paraocular area, malar area, apical clypeus, labrum and mandible except reddish brown at tip.

Mesoscutum, scutellum, metanotum, propodeal triangle entirely black. Legs mostly dark brown, tinged with dark orange. Terga mostly black, T1 laterally with small yellow spots; T2–T4 laterally with two yellow oval maculation; T5–T6 with yellow band.

Male terminalia. 7th tergum, 7th sternum, and 8th sternum as in Fig 2-1. Gonostylus short; blunt apically; basoventral lobe present. Gonostylus and basoventral lobe with long vestiture.

Specimen Examined. GG: 2♂, Yellow pan trap, Mt. Yeogi, Suwon-si, 3. iv. 1998, coll. Seunghwan Lee (NAAS); 4♂, Same locality and collector (NAAS).

Distribution. Japan, Kazakhstan, Korea, Russia.

Floral records. *Angelica pubescens* Maxim., *Heracleum sphondylium var. nipponicum* (Kitag.) H. Ohba (Apiaceae); *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae); *Patrinia villosa* Juss. (Caprifoliaceae); *Erigeron philadelphicus* L., *Erigeron annuus* (L.) Pers., *Petasites japonicus* (Siebold & Zucc.) Maxim. (Compositae); *Salix caprea* L., *Pieris japonica* (Thunb.) D. Don ex G. Don (Ericaceae) (Mital and Tadauchi 2007).

Host. Unknown.

Remarks. *N. amurensis* is close to *N. fervens* in that both species have crescent-like gonostylus in males. However, this species can be distinguished by the wider basal area of the 7th sternum.

***Nomada* sp. nov. 3**

(Plates 1-55)

Description. Female. Body length 8.95 mm. *Head.* In frontal view about 1.32x wider than long; LID:UID=1:1.15. Vertex, frons, paraocular area foveolate; clypeus imbricate-punctate; labrum finely foveolate. Mandible long, bidentate. Labral tooth centrally. Short yellowish white hair on vertex and frons; short golden hair on mandible and labrum. Antennae with scape cylindrical, about as wide as flagella, with short light brown hair. F1:F2: F3=1:1.06:0.91; FW1:FL1=1:1.82; FW2:FL2=1:1.71; FW3:FL3=1:1.45.

Mesosoma. Mesoscutum, scutellum, metanotum deeply foveolate. Propodeal triangle irregularly rugose on upper 1/3 area, remaining portion shagreened; its side areolate. Scutellum distinctly uplifted and weekly furrowed. Hair absent on mesoscutum; scutellum and side of propodeal triangle with yellowish white hair. Hind tibiae covered with light brown, short hair; HTS dark brown, 2 in number, stout, blunt apically.

Metasoma. Punctate; covered with short and decumbent golden hair.

Colors. Head mostly black. Antennae predominantly dark orange; F1–F2 posteriorly dark brown. Side of vertex, margin of clypeus, paraocular area tinged with dark orange. Labrum and mandible dark red. Mesoscutum dark red, with three thick black longitudinal maculation. Scutellum and metanotum tinged with dark red. Propodeal triangle black with two red oval maculation; same but wider maculation on its side. Legs mostly dark orange, tinged with dark brown. Terga mostly dark orange; T1 upper

half black and lower half dark orange with two oval dark brown spots; T2 laterally with two ivory triangular maculation; T3 entirely tinged with dark orange and black; T4 with two rectangular ivory bands; T5 mostly dark brown with ivory, square maculation.

Male. Not examined.

Specimen Examined. GW: Holotype 1♀, 5481, Gyeonggang-ro, Daegwallyeoung-myeon, Pyeongchan-gun, 18. v. 2017, coll. Sang Hyeok Nam (SNU).

Distribution. Korea

Floral records. Unknown.

Host. Unknown.

Remarks. This new species can be confused with *Nomada moeschleri* Alfken, 1913, but *N. moeschleri* has only one seta on the hind tibiae. This species is also similar to *Nomada opaca* Alfken, 1913, but F1 is about a quarter shorter than F2, while F1 is evidently about half as long as shorter in *N. opaca*.

***Nomada calloptera* Cockerell, 1918 콕케렐알락꽃벌**

Nomada calloptera Cockerell, 1918: 479–480; Kim, 1970: 674; Tsuneki, 1986: 35; Mitai & Tadauchi, 2007:54; Won & Kim, 2013: 30. Holotype ♂. TD: USNM. TL: Japan.

Nomada rengnio Tsuneki, 1973: 91–92; Alexander & Schwarz, 1994: 251; Ikudome, 1999: 654–655.

Nomada sakura Tsuneki, 1976: 150–152.

(Plates 1-5, 1-6, 2-3)

Description. **Female.** Body length 9.4 mm.

Head. In frontal view about 1.25x wider than long; LID:UID=1:1.12. Frons, paraocular area foveolate; clypeus foveolate-fovealate; labrum punctate. Labral tooth below the center. Mandible long, acute at tip. Short and white, week plumose sparsely on vertex and frons; labrum intermix with short orange hair and long dark orange hair; Mandible with long dark orange hair. Antennae with scape cylindrical, about as wide as flagella, covered with short, red thin hair. FL1:FL2:FL3=1:1.19:1.09; FW1:FL1=1:1.27; FW2:FL2=1:1.57; FW3:FL3=1.1.36.

Mesosoma. Mesoscutum and metanotum deeply areolate, scutellum foveolate. Propodeal triangle irregularly rugose on basal half, remaining portion finely reticulate. Mesoscutum, scutellum, metanotum with decumbent short white hair. Side of propodeum covered with white plumose. Hind tibiae covered with dark brown hair; HTS dark brown, six in number, two posteriormost seta evidently longer, the others much shorter and thicker.

Metasoma. densely punctuated. Covered with short, decumbent ivory-colored hair.

Colors. Head predominantly dark red, basal of the paraocular area brighter than the others; Tinged black as follows: near ocelli, frons except dark red circular maculation, longitudinal maculation on the side of the clypeus. Mesoscutum predominantly dark red, marked with three longitudinal lines; Scutellum dark red, basal area tinged with black; propodeal triangle and side of the propodeal triangle dark red, with black longitudinal line on the middle. Most of the legs dark red. Terga mostly orange; T2

with two ivory circular maculation on the side; T3 slightly tinged with ivory maculation; remaining tergum with distinct two ivory band.

Male. Body length 7.16–10.14 mm. *Head*. In frontal view about 1.25–1.38x wider than long. LID:UID=1:1.15–1.18. Head entirely foveolate. Labral tooth below the center. Mandible long, acute at tip. Yellowish white plumose on clypeus, paraocular area, vertex, and labrum; mandible with long golden hair. Antennae with Scape swollen, about as wide as flagella, with plumose hair. FL1:FL2:FL3=1:1.42–1.95:1.14–1.53; FW1:FL1=1:0.96–1.29; FW2:FL2=1:1.84–2.00; FW3:FL3=1:1.39–1.42.

Mesosoma. Mesoscutum, scutellum, metanotum entirely areolate. Propodeal triangle as in female. Mesoscutum, scutellum, metanotum with long golden plumose. Side of the propodeum covered with yellowish white plumose. Hind tibia covered with long, yellowish white hair; HTS amber to dark amber, 3 to 5 in number, posteriormost seta long and thin, remaining thick and shorter than posteriormost seta.

Metasoma. Punctuation identical as in female; Pygidial plate distinctly notched.

Colors Head predominantly black, anterior scape, malar area, and the lowermost clypeus, labrum and mandible bright yellow; tip of the mandible dark brown. Mesosoma and scutellum entirely black. Legs tinged with black and dark red. Tergum mostly brown; T1 with two black circular maculation; T2 tinged with ivory-color on side, bright brown tinged on the middle; T3–T6 tinged with bright brown upper half, ivory lower half; T2–T5 with two circular, dark brown maculation on side.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal

tergum as in pl 2-3. Gonostylus long, cylindrical-like and slightly curved with long, laterally and apically with dense plumose vestiture. Basoventral lobe strongly produced, posteriorly decumbent. Gonocoxites with dorsal invagination, furrow somewhat reticular.

Specimen Examined. CB: 1♂, Cheongpung-myeon, Jecheon-si, 9.v.2008, coll. H.S. Lee (LHSC). **GN:** 1♂, Pyochungsa Temple, 26.iv.2003, coll. H.S. Lee (LHSC). **GW:** 1♂, Kwangreung, 6.v.1994, coll. H.S. Lee (LHSC); 4♂, [37°48'35"N 128°49'31"E], 1115, Nodong-ri, Sacheon-myeon, Gangneung-si, coll. H.S. Lee (LHSC); 1♂, [37°48'29.0"N 128°34'28.0"E], Bukdae Temple, Mt. Odae, Pyeongchang-gun, 27.v.2008, coll. H.S. Lee (LHSC); 1♂, Sangchangbong-ri, Gonggeun-myeon, Hoengseong-gun, 25.v.2009, coll. H.S. Lee (LHSC). 1♀, Yellow pan trap, 5481, Gyeonggang-ro, Daegwallyeong-myeon, Pyeongchang-gun, 06.vi.2018, coll. Unknown (SNU). **JJ:** 1♂, Ilchulbong, Seogwipo-si, 15.v.1983, coll. Unknown (NIBR).

Distribution. Korea, Japan.

Floral records. *Cardamine leucantha* (Tausch) O.E. Schulz (Brassicaceae); *Malus pumila* Mill., *Prunus armeniaca* var. ansu Maxim. (Rosaceae).

Host. *Andrena japonica* Hirashima (Murota and Kurokawa, 2002; Maeta et al., 2004).

Remarks. *Nomada calloptera* Cockerell can be confused with *Nomada shirakii* Yasumatsu & Hirashima but can be differed by S8. Its tip is convex in *N. calloptera*, while it is nearly flat in *N. shirakii*.

***Nomada fervens* Smith 1873, 꼬마알락꽃벌**

***Nomada fervens* Smith 1873:** 203; Kim, 1970: 674; Alexander & Schwarz, 1994: 262; Mitai & Tadauchi, 2007: 61; Won & Kim, 2013: 33–34. Holotype ♀. TD: USNM. TL: Japan.

(Plates 1-10, 1-11, 2-6)

Description. Female. Body length 10.5–11.6 mm. *Head.* In frontal view about 1.17–1.28x wider than long; LID:UID=1:1.03–1.18. Head densely Foveolate. Mandible long, simple, subacute apically. Labral tooth below the center. Short golden and dark brown hair sparsely on vertex; white plumose cover on supraclypeal and clypeus; dark brown hair on paraocular area and clypeus; labrum intermix with short golden hair and white plumose; Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with dark brown hair. FL1:FL2:FL3=1:1.12–1.30:0.93–1.14; FW1:FL1=1:1.42–1.92; FW2:FL2=1:1.74–1.77; FW3:FL3=1:1.46–1.60.

Mesosoma. Mesocutum, scutellum, and metanotum densely foveolate. Scutellum with shallow furrow. Propodeal triangle rugose basally, the remaining shagreened. Mesoscutum and scutellum with short golden hair; metanotum with short yellowish white plumose. Side of the propodeum with very short plumose; Hind tibiae covered with long golden hair; HTS 5 in number, first two posteriormost seta slightly longer and hair like, the remaining short and stout, sometimes hooked inward.

Metasoma. Distinctly punctuated, covered with decumbent golden hair.

Colors. Head mostly dark orange. Antennae anteriorly dark orange, posteriorly dark

orange to black. Vertex and frons black except red supraclypeal area. Mandible reddish brown apically. Mesoscutum mostly dark red with three black longitudinal maculation; scutellum and metanotum entirely dark red. Propodeal triangle black, with two oval dark red maculation. Side of propodeum predominantly black with four oval dark red maculation. Legs are tinged with dark brown and reddish orange. Terga dark orange to black; T1 laterally with two black spots; T2–T3 laterally with ivory maculation, maculation on T3 evidently smaller than T2; T4–T5 with ivory bands.

Male. Body length 9.59–10.30 mm. *Head.* In frontal view about 1.25–1.28x wider than long; LID:UID=1:1.10–1.15. Head densely Foveolate. Mandible long, simple, subacute apically. Labral tooth below the center. Golden plumose cover following area: vertex, paraocular area, clypeus, labrum. Mandible with long golden hair and short white hair. Antennae with scape cylindrical, wider than flagella, covered with golden plumose. FL1:FL2:FL3=1:1.77–1.89:1.26–1.43; FW1:FL1=1:0.87–0.92; FW2:FL2=1:1.62–1.72; FW3:FL3=1:1.22–1.29.

Mesosoma. Mesocutum, scutellum, metanotum densely foveolate. Scutellum with shallow furrow. Propodeal triangle rugose on 1/3 of basal area, the remaining shagreened. Mesoscutum, scutellum, metanotum with long golden plumose; side of the propodeum with long ivory plumose. Hind tibiae covered with long golden hair or transparent white hair; HTS 3 to N in number, posteriormost seta distantly longer than remaining.

Metasoma. Distinctly punctuate, covered with decumbent golden hair.

Colors. Head mostly black. Antennae anteriorly dark orange except bright yellow

scape, posteriorly black. Paraocular area and lower half of clypeus, labrum, mandible basally bright yellow. Mandible apically reddish brown. Mesoscutum, metanotum, propodeum entirely black. Scutellum with two oval dark orange maculation. Legs are tinged with dark brown and dark orange. Terga mostly dark orange; T2–T3 laterally with triangular yellow maculation; T4–T6 with yellow band.

Male terminalia. 7th tergum, 7th sternum, and 8th sternum as in Fig 2-6. Gonostylus long, cylindrical; basoventral lobe present. Gonostylus with long, sinuate hair; Basoventral lobe with short plumose.

Specimen Examined. GB: 1♀, Andong University, Gyeongdong-ro, Andong-si, 12. v. 1996, coll. J.E. Jung (LHSC); 1♂, Waegwan-eup, Chilgok-gun, locality and collection date unknown (SNU). **GG**: 1♂, National Institute of Agricultural Sciences, Seodun-dong, Gwonseon-gu, 21. iv. 1989, coll. Ki-Jeong Hong (NAAS); 1♀, Mt. Yeogi, Suwon-si, 25. iv. 1994, Seunghwan Lee (NAAS); 1♂, same locality and collector, 31. iii. 1998 (NAAS); 1♀, same locality, 22. iv. 1998, coll. Seunghwan Lee (NAAS); 1♂, Anyang-si, 7.v. 1995, coll. H.S. Lee (SNU); 1♀, Seoul National University Arboretum, Seodun-dong, Gwonseon-gu, 1. v. 2002, coll. Won Mok Kim (NAAS); 1♀, 51-7, Korea National Arboretum, Jikdong-ri, Soheul-eup, Pochen-si, 31. v. 2013, coll. I.G. Kim (GE); 1♀, 280, Yesulgongwon-ro, Manan-gu, Anyang-si, 20. iv. 2019, coll. Junseo Hyun (SNU). **GW**: 1♂, Mt. Odae, 24. v. 2002, coll. H.S. Lee (LHSC); 1♀, Yongdae-ri, Bukmyeon, Inje-gun, 22. v. ~ 04. vi. 2018, coll. Minhyeuk Lee (SNU). **JJ**: 1♂, Nogodan, 25. vi. 1993, coll. W.K. (NAAS)

Distribution. Korea, Japan

Floral records. *Brassica rapa* L. (Brassicaceae); *Pilosella caespitosa* (Dumort.) P.D. Sell & C. West (Compositae); *Calystegia soldanella* (L.) Roem. & Schult. (Convolvulaceae); (Mitai & Tadauchi, 2007); *Chaenomeles speciosa* (Sweet) Nakai, *Prunus armeniaca* var. ansu Maxim., *Prunus persica* (L.) Batsch, *Sorbus commixta* Hedl. (Rosaceae)

Host. *Andrena sublevigata* Hirashima, 1966 (Maeta et al., 1996)

Remarks. *N. fervens* is closely resembled *N. maculifrons* but differs in having short and stout setae while they are long, slightly curved setae in *N. maculifrons* female. In males, two oval ferruginous spots in 7th tergum, but they are absent in *N. fervens*.

***Nomada flavoguttata* (Kirby, 1802) 배광택알락꽃벌**

Apis flavoguttata Kirby, 1802: 215–216. Holotype ♂. TD: BNHM. TL: UK.

Nomada rufocincta Kirby, 1802: 216.

Nomada minuta Fabricus, 1805: 394.

Nomada nana Schenck, 1874: 343.

Nomada pygmaea Schenck, 1874: 342.

Nomada flavoguttata var. *hoeppneri* Alfken, 1898: 158.

Nomada flavoguttata var. *serotina* Schmiedeknecht, 1882: 190.

Nomada alfkeni Cockerell, 1907: 131

Nomada kurilensis Yasumatsu, 1939: 6–7.

Nomada flavoguttata japonensis Tsuneki, 1973: 115–119.

Nomada tridentata Tsuneki, 1986: 49–50.

(Plates 1-12, 1-13, 2-7)

Description. Female. Body length 6.14–6.18 mm. *Head.* In frontal view about 1.29–1.31x wider than long; LID:UID=1:1.15–1.23. Head mostly foveolate; paraocular area punctate; clypeus foveolate to punctate. Mandible simple, subacute at tip. Labral tooth centrally. Short golden hair near vertex. Short white plumose on supraclypeal area, clypeus, side of clypeus. Labrum intermixed with short golden hair and white plumose. Mandible with short or long yellowish white hair. Antennae with scape slightly swollen, about as wide as flagella, short golden hair. FL1:FL2:FL3=1:1.40–1.67:1.15–1.40; FW1:FL1=1:1.14–1.44; FW2:FL2=1:1.87–1.97; FW3:FL3=1: 1.44–1.63.

Mesosoma. Mesoscutum scutellum, metanotum densely foveolate. Scutellum with shallow furrow. 2/3 of propodeal triangle rugose-reticulate, remaining weekly strigulate. Mesoscutum and scutellum covered with short red hair. Metanotum with short red plumose. Side of propodeum with short yellowish white plumose. Hind tibiae covered with yellowish white hair; HTS 4 in number, posteriormost seta longer than hair on hind tibiae, remaining distinct short and stout.

Metasoma. weekly punctuated interspace smooth and shiny; covered with short, decumbent pale-yellow hair.

Colors. Head mostly reddish orange. Following area tinged with black: vertex, frons, side of clypeus. Tip of mandible reddish brown. Mesoscutum red with three longitudinal black lines. Scutellum black with red rectangular maculation. Metanotum red. Propodeal triangle tinged with dark orange and black, median black

line presented. Legs mostly dark orange. Terga mostly red; T1 upper half black, lower half red; T2 laterally with bright yellow maculation.

Male. Body length 5.4–6.3 mm. *Head*. In frontal view about 1.26–1.29x wider than long; LID:UID=1:1.19–1.21. Head foveolate. Mandible simple, subacute at tip. Labral tooth centrally. Yellow to white long plumose distributed on head. Labrum intermixed with long golden hair and white plumose. Mandible with yellow to white short hair. Antennae with scape swollen, wider than flagella, covered with long golden hair. FL1:FL2:FL3=1:1.8–2.4:1.5–1.7; FW1:FL1=1:0.77–1; FW2:FL2=1:81–2.01; FW3:FL3=1:37–1.46.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Scutellum with shallow furrow. 2/3 of propodeal triangle rugose, remaining shagreened. Mesoscutum, scutellum, metanotum with golden plumose. Side of propodeum covered with long white plumose. Hind tibiae covered with yellowish white short hair; HTS amber to dark amber, 3 to 4 in number, posteriormost seta slightly long, remaining distinctly shorter and stout, subacute at tip.

Metasoma. Sparsely punctate; interspace wider than puncture and shiny. Pygidial plate nearly round.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-7. Gonostylus short and stout, fin-like, round at tip, apically and laterally with long, sinuate hair. Basoventral lobe absent. Gonocoxite with dorsal invagination, furrow distinctly rounded.

Colors Head dominantly black. Antennae anteriorly dark orange, posteriorly dark

brown; scape anteriorly bright yellow, posteriorly black. Following area bright yellow: side of vertex, paraocular area, more than 2/3 of clypeus, labrum, mandible. Mesoscutum, metanotum, propodeum entirely black. Scutellum with two red oval maculation. Leg mostly dark orange, tinged with dark brown. T1 upper half black, lower half dark brown, laterally with two black dots; T2–T3 laterally with yellow maculation; T4–T6 tinged with dark brown and dark yellow.

Specimen Examined. GG: 12♀, 8♂, Mt. Yeogi, Suwon-si, 3. iv. 1998, coll. Seunghwan Lee (NAAS); 1♀, same locality, 22. iv. 1998, coll. Seunghwan Lee (NAAS). **JJ:** 11♀, Temple Gwan eum, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 3♂, Jocheon-eup, Seonheul-ri, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 1♂, Jeju-si, 15. iv. 1998, coll. Seunghwan Lee (NAAS); 5♀, 3♂, Temple Gwan eum, 17. iv. 1998, coll. Seunghwan Lee (NAAS).

Distribution. Algeria, Europe, Japan, Korea, Morocco, Tunisia, Turkey.

Floral records. *Salix caprea* L. (Salicaceae); *Ranunculus japonicus* Thunb. (Ranunculaceae); *Corydalis heterocarpa* var. *japonica* (Franch. & Sav.) Ohwi, *Corydalis incisa* (Thunb.) Pers. (Papaveraceae); *Duchesnea chrysantha* (Zoll. & Moritzi) Miq., Potentilla discolor Bellardi ex Colla, *Potentilla recta* Jacq., *Rubus pannosus* P.J. Müll. & Wirtg. (Rosaceae); *Veronica persica* Poir., *Leucanthemum vulgare* (Vaill.) Lam., *Petasites japonicus* (Siebold & Zucc.) Maxim., *Petasites japonicus* subsp. *giganteus* F. Schmidt ex Kitam., *Taraxacum campylodes* G.E. Haglund (Compositae) (Mitai & Tadauchi, 2007)

Host. *Andrena falsifica*, *A. minutula*, *A. minutuloides*, *A. semilaevis*, *A. subopaca*

(Perkins, 1919; Stoeckhert, 1933; Kocourek, 1966, Westrich, 1989).

Remarks. Female of this species can be confused with *Nomada hakonensis* Cockerell, 1911 but can be distinguished by length of F2. F2 is at least two times longer than F1 in *N. hakonensis*, while it is relatively shorter (1.4–1.7) in *N. flavoguttata*.

Nomada fulvicornis jezoensis Matsumura, 1912 마름모점알락꽃벌

Nomada jezoensis Matsumura, 1912: 196–197. Holotype ♀. TD: Uncertain. TL: Japan.

Nomada lineola jezoensis: Tsuneki, 1973: 58–60.

Nomada fulvicornis jezoensis: Alexander & Schwarz, 1994: 248; Won *et al*., 2008:48. (Plates 1-14, 1-15, 2-8)

Description. **Female.** Body length 9.31–11.2 mm. *Head.* In frontal view about 1.17–1.39x wider than long; LID:UID=1:1.17–1.23. Clypeus foveolate-puncticulate, remaining head densely foveolate. Mandible simple, narrow and acute at tip. Labral tooth near apex. Short golden hair sparsely near vertex, paraocular area, frons and clypeus. Short white plumose near clypeus. Antennae with scape cylindrical, wider than flagella, with short light brown hair. F1: F2: F3=1:1.31–1.42:1.03–1.10; FW1:FL1=1:1.24–1.49; FW2:FL2=1:1.67–1.90; FW3:FL3=1:1.37–1.47.

Mesosoma. Mesoscutum, scutellum, metanotum entirely foveolate. 1/3 of propodeal triangle rugose-reticulate, remaining shagreened. Mesoscutum and scutellum sparsely with long golden hair; metanotum with short golden plumose. Side of propodeum covered with long golden plumose. Hind tibiae with short transparent

white hair; HTS short, 5 to 6 in number, posteriormost seta light brown and thin, remaining dark amber and stout, subacute at tip.

Metasoma. Punctate. Covered with short and decumbent golden hair.

Colors. Head mostly black. Tinged with red as follows: paraocular area, frons, clypeus, labrum, and mandible except reddish brown tip. Antennae entirely orange. Mesoscutum mostly black, laterally with red longitudinal maculation. Scutellum black with bright yellow oval maculation. Metanotum entirely black. Propodeal triangle black and its side with red oval maculation. Legs mostly dark orange and tinged with black. Terga mostly red and basally with black bands; T2–T3 laterally with ivory, triangular maculation; T4–T5 with ivory, squared maculation.

Male. Body length 9.5–10 mm. *Head.* In frontal view about 1.33–1.37x wider than long; UID: LID=1: 1.13–1.17. Clypeus punctate, remaining head mostly foveolate. While plumose densely cover as follows: vertex, frons, paraocular area, clypeus. Labrum intermixed with short white plumose and golden hair. Mandible with long golden hair and short white hair. Antennae with scape swollen, distinctly wider than flagella, covered with golden plumose. F1: F2: F3=1:1.55–2.04:1.20–1.54; FW1:FL1=1:0.88–1.19; FW2:FL2=1: 1.75–1.97; FW3:FL3=1:1.27–1.53.

Mesosoma. Mesoscutum and side of propodeum densely foveolate. Scutellum and metanotum areolate. 2/3 of propodeal triangle rugose-reticulate, remaining shagreened. Mesoscutum, scutellum, metanotum and side of propodeum with long white plumose. Hind tibiae covered with short white hair; HTS amber, three to five in number, slightly longer and thicker than hair on hind tibiae.

Metasoma. Punctated. Covered with short and decumbent white hair.

Coloration: Head mostly black. Flagella mostly dark brown, posteriorly tinged with back at F1–F4. Scape anteriorly bright yellow, posteriorly black. Following area tinged with bright yellow: paraocular area, basal clypeus, labrum, mandible except reddish brown tip. Mesoscutum, metanotum, propodeum entirely black. Scutellum black with two bright yellow oval maculation. T1 black, laterally with two black dot and tinged with bright yellow; T2–T3 mostly dark brown to black, laterally with triangular bright yellow maculation. T4–T6 mostly black with bright yellow band.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-8. Gonocoxite stout, blunt at tip; bent posteriorly; basoventral lobe present. Gonostylus and basoventral lobe apically and laterally with long and sinuate hair.

Specimen Examined. GG: 1♀, Mt. Myeongji, Buk-myeon, Gapyeong-gun, 20. vi. 1992, coll. J.I.B (SNU); 1♂, [37°32'58"N 127°27'20"E], Yangseo-myeon, Yangpyeong-gun, 2. vi. 2007, coll. S.W. Park (LHSC). **GW:** 1♂, Woljeong Temple, Mt. Odae, 10. v. 1996, coll. H.S. Lee (LHSC); 1♂, Pan trap, Mt. Kujeol, Hongcheon-gun, 8. v. 1998, coll. Unknown (LHSC); 1♀, Baekdamsanjang, Mt. Seorak, 27. vi. 2002, coll. HS. Lee (LHSC); 1♂, Myeonggye-ri, Nae-myeon, Hongcheon-gun, 29. iv. 2007, coll. H.S. Lee (LHSC); 1♂, Mt. Sukbyeong, Imgye-myeon, Imgye-ri, Jeongsun-gun, 22. v. 2002, coll. Y.B. Lee (NAAS); 1♀, Seorim vally, Seorim-ri, Seo-myeon, Yangyang-gun, 10. ~ 23. v. 2018, coll. Sanghyeok Nam (SNU); 1♂, [38°08'46.5"N 128°15'47.5"E], Malaise trap, 854, Hangye-ri, Buk-myeon, Inje-gun,

15. iv. ~ 03. v. 2019, coll. Park and Nam (SNU); 1♂, same locality, 01. v. 2020, coll. K.Y. Lim, J.Y. Choi, M.S. Oh (SNU); 1♂, same locality, 29. v. 2020, coll. J.Y. Choi and M.S. Oh (SNU); 1♀, Mt. Seorak, 1125, Baekdam-ro, Buk-myeon, Inje-gun, 05. vi. 2020, coll. DY Park (SNU). **JN:** 1♂, Gwangyang, Chusan, 28. iv. 1995, coll. H.S. Lee (LHSC); 2♂, Simwon, Mt. Jiri, coll. 5. vi. 1996, coll. H.S. Lee (SNU).

Distribution. Japan, Korea

Floral records. *Taraxacum campylodes* G.E. Haglund (Compositae) (Mitai & Tadauchi, 2007); *Pyrus ussuriensis* Maxim. ex Rupr. (Rosaceae)

Host. Unknown.

Remarks. This species is a subspecies of *Nomada fulvicornis* Fabricus, 1793. The difference of this species from *N. fulvicornis* is the length of the flagellar segment (see Mitai & Tadauchi, 2007 for detailed description).

***Nomada fusca* Schwarz, 1986 적색두점알락꽃벌 (미기록)**

Nomada fusca Schwarz, 1986: 434; Mitai & Tadauchi, 2007; 75–77; Smit, 2018: 157.

Holotype ♀. TD: Unavailable. TL: Finland.

(Plate 1-16)

Description. **Female.** Body length 7.79 mm. *Head.* In frontal view about 1.30x wider than long; LID:UID =1: 1.20. Head densely foveolate. Mandible simple, subacute at tip. Labral tooth near apex. Golden or black short hair sparsely distributed on frontal head, labrum and mandible. Antennae with scape cylindrical, about as wide as flagella, covered with short black hair.

F1: F2: F3=1:1.11:0.92; FW1:FL1=1:1.49; FW2:FL2=1:1.65; FW3:FL3=1:1.42.

Mesosoma. Mesoscutum, scutellum, metanotum densely foveolate. Side of propodeum areolate. 1/3 of propodeal triangle rugose, remaining shagreened. Mesoscutum, scutellum, metanotum sparsely covered with golden or dark brown hair. Hind tibiae covered with short, light brown to dark brown hair; HTS dark brown, 1 to 4 in number, evidently thicker than hair on hind tibiae.

Metasoma. Densely punctate; covered with short and dark brown hair.

Colors. Head predominantly black. Antennae mostly dark brown, tinged orange at tip. Scape black, dark orange near antennal sockets. Margin of paraocular area tinged dark red, clypeus tinged with black and jagged dark red. Labrum and mandible dark red, reddish brown at tip on mandible. Mesoscutum and metanotum, propodeal triangle black. Scutellum black with two oval dark red maculation. Legs tinged with black with dark red. Terga mostly black; T2–T3 laterally with bright yellow maculation; T4–T5 with bright yellow band.

Male. Not examined in this study.

Specimen Examined. GW: 1♀, 164, Baramkkonmaeul-gil, Sokcho-si, 02. vii. 2020, coll. Kayun Lim (SNU).

Distribution. Estonia, Europe, Japan, Korea (new record), Russia.

Floral records. *Cosmos sulphureus* Cav. (Compositae) (new record).

Host. Unknown.

Remarks. HTS of this species is usually known as 4 to 6 in number (Smit, 2018), but rarely only one HTS presented as in Pl. 1-16 G.

***Nomada guttulata* Schenck, 1861 민무늬허리알락꽃벌**

Nomada guttulata Schenck, 1861: 391; Tsuneki, 1973: 109–110; Alexander & Schwarz, 1994: 248; Mitai & Tadauchi, 2007: 77–81; Won & Kim, 2013:37–38. Type information unavailable.

Nomada mishimana Tsuneki, 1976

(Plates 1-20, 2-11)

***Description.* Female.** Not examined in this study.

Male. Body length 5.68 mm. *Head* (Pl. N) In frontal view about 1.28x wider than long. LID:UID=1:1.19. Head densely foveolate. Mandible broad, subacute at tip. Labral tooth centrally. Golden plumose as follows: vertex, upper paraocular area. White plumose distributed on frons, supraclypeal area, clypeus, lower paraocular area. Labrum with long golden hair and white plumose. Mandible with short golden hair. Antennae with scape swollen, slightly wider than flagella, covered with short golden hair. FL1:FL2:FL3=1:1.18:0.95; FW1:FL1=1:1.44; FW2:FL2=1:1.58; FW3:FL3=1:1.24.

Mesosoma. Mesoscutum and scutellum densely foveolate. Metanotum areolate. Propodeal triangle confused-rugulose, laterally shagreened. Mesoscutum and scutellum sparsely with long golden hair. Metanotum with short, week white plumose. Side of propodeum covered with long white plumose. Hind tibiae covered with short transparent white hair; HTS 4 in number, two posteriormost setae amber and thin, slightly shorter than hair on hind tibiae, remaining dark amber, distinctly short and stout.

Metasoma. Punctate; covered with short decumbent golden hair. Pygidial plate slightly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-11. Gonostylus extremely short, stout and ovate apically and laterally with long sinuate vestiture; basoventral love present.

Colors. Head predominantly black. Antennae mostly dark orange; scape anteriorly orange, posteriorly black. Malar area, labrum, mandible bright yellow except reddish brown tip of mandible. Mesoscutum, metanotum, propodeal triangle entirely black. Scutellum black with two dark red spots. Legs dark orange. Terga predominantly dark orange, T2 laterally with smear yellow maculation.

Specimen Examined GN: 1♂, Mt. Mui, Museon-ri, Sangni-myeon, Goseong-gun, 12. iv. 1997, coll. J.S. Kim (NIBR).

Distribution. Europe, Japan, Kazakhstan, Korea, Israel, Russia, Turkey, Kyrgyzstan.

Floral records. *Ranunculus japonicus* Thunb. (Ranunculaceae); *Potentilla fragarioides* L. (Rosaceae); *Taraxacum albidum* Dahlst. (Compositae) (Mitai & Tadauchi, 2007).

Host. *Andrena labiata* Fabricius, *A. potentillae* Panzer, *A. sphecodimorpha* Hedike, *A. florivaga* Eversmann (Smit, 2018; citation therein).

Remarks. This species can be confused with *Nomada montverna* Tsuneki, but can be distinguished by distinct red spots on scutellum and stout HTS.

***Nomada hakonensis* Cockerell, 1911 긴더듬이알락꽃벌**

Nomada hakonensis Cockerell, 1911:647; Hirashima, 1965: 309; Tsuneki, 1973: 104–106; Alexander & Schwarz, 1994: 248; Mitai & Tadauchi, 2007: 86–91; Won & Kim, 2013: 36–37. Holotype ♀. TD: Uncertain. TL: Japan.

(Plates 1-21, 1-22, 2-12, 3-3)

Description. **Female.** Body length 4.84–6.02 mm. *Head.* In frontal view about 1.26–1.31x wider than long; LID:UID=1:1.11–1.16. Vertex and clypeus punctate, remaining head densely foveolate. Mandible simple, narrow acute at tip. Labrum tridentate. Short reddish golden hair sparsely near vertex and upper paraocular area. Short white plumose on frons, lower paraocular area. Clypeus and labrum intermix with short golden hair and white plumose. Antennae with scape cylindrical, about as wide as flagella, covered with short red golden hair. F1: F2: F3=1:1.92–2.02:1.48–1.70; FW1:FL1=1:1.18–1.31; FW2:FL2=1:2.43–2.56; FW3:FL3=1:1.89–1.94.

Mesosoma. Mesoscutum, scutellum densely foveolate. Metanotum areolate. Upper 2/3 of propodeal triangle irregularly rugose, remaining shagreened. Mesoscutum, scutellum, and metanotum sparsely with short red golden hair. Side of propodeal covered with short white plumose. Hind tibiae covered with long light brown hair; HTS light brown, 3 in number, acute at tip, posteriormost seta evidently longer and thicker than hair on hind tibiae, remaining setae shorter and thicker than hair on hind tibiae.

Metasoma. Smooth and shiny. Covered with short and decumbent golden hair.

Colors. Head mostly red to dark orange. Antennae mostly dark orange. Scape

posteriorly tinged with back. Vertex and frons black. Mesoscutum red with three black lines. Scutellum and metanotum red. Propodeal triangle red with inverted black triangle and its side entirely red. Legs mostly dark orange, tinged with dark brown. Terga mostly red; T2 laterally with ivory to bright yellow triangular maculation.

Male. Body length 4.84–6.02 mm. *Head.* In frontal view about 1.24x wider than long; UID: LID=1: 1.10–1.13. Head densely foveolate. Long yellow plumose sparsely near vertex and frons. Clypeus and labrum intermix with long white plumose and golden hair. Mandible with long golden hair. Antennae with scape roughly cylindrical, slightly wider than flagella, covered with short golden plumose. F1: F2: F3=1:2.75–3.35:2.04–2.38; FW1:FL1=1:0.78–1.01; FW2:FL2=1: 2.52–2.72; FW3:FL3=1:1.73–1.83.

Mesosoma. Mesoscutum, scutellum, and metanotum entirely areolate. Upper 2/3 of propodeal triangle irregularly rugose, remaining shagreened. Mesoscutum, scutellum, and metanotum with long golden plumose. Hind tibiae covered with long light brown hair; HTS amber, 3 in number, posteriormost seta thin and long, as wide as hair on hind tibiae, remaining distinctly shorter and thicker than posteriormost seta.

Metasoma. Punctate. Covered with short and decumbent golden hair.

Coloration. Head mostly black. Antennae anteriorly dark brown, posteriorly black. Following area tinged with bright yellow: near vertex, lateral margin of paraocular area, malar area, basal clypeus, labrum and mandible except reddish brown tip. Mesoscutum, scutellum, metanotum, propodeum entirely black. Legs mostly dark brown, tinged with black. Terga mostly dark brown, T1 laterally with two black dots;

T2–T3 laterally with bright yellow triangular maculation.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-12. Gonocoxite cylindrical, blunt at tip; basoventral lobe absent. Gonostylus and basoventral lobe apically and laterally with long and sinuate hair.

Specimen Examined. GB: 1♀, Chunyang-Myeon, Bonghwa-gun, 29. v. 2010, coll. H.S. Lee (LHSC). **GG:** 1♀, Mt. Yeogi, Suwon-si, 16. iv. 1994, coll. J.Y. Choi (NAAS); 2♀, Mt. Taehwa, Gwangju-si, 8. v. 1998, coll. Seunghwan Lee (NAAS); 2♀, Mt. Cheonma, Maseok, Namyangju-si, 13. v. 2004, coll. Taehwa Kang (NAAS). 1♀, Soheul-eup, Pocheon-si, 14. ~ 28. iv. 2018, coll. Unknown (KNA); 1♀, Jikdong-ri, Soheul-eup, Pocheon-si, 06. iv. ~ 04. v. 2018, coll. Unknown (KNA). **GN:** 1♀, Gyeongnam Arboteum, Jinju-si, 30. iv. 2012, coll. Jin Hyeong Hwang (LHSC). **GW:** 1♀, Sangweonsa, Mt. Chiak, Seongnam-ri, Sinlim-myeon, Wonju-si, 26. v. 2009, coll. Heung-sik Lee (LHSC); 1♀, Environment research park, Hongcheon-gun,15. v. 2012, coll. S.J. Jang (LHSC); 1♀, 5481, Gyeonggang-ro, Daegwallyeong-myeon, Pyeongchang-gun, 18. v. 2017, coll. Sang Hyeok Nam (SNU); 1♂, 854, Hangye-ri, Buk-myeon, Inje-gun, 17. iv. ~ 08. v. 2018, coll. Min Hyeuk Lee (SNU); 1♂, Seorim valley, Seorim-ri, Seo-myeon, Yangyang-gun, 18. iv. ~ 10. v. 2018, coll. Sang Hyeok Nam (SNU); 2♀, 854, Hangye-ri, Buk-myeon, Inje-gun, 27. vi. 2018, coll. Min Hyeuk Lee (SNU); 1♀, 746, Temple Baekdam, Baekdam-ro, Buk-myeon, Inje-gun, 04. ~ 05. vi. 2020, coll. Duk-Yeong Park (SNU). **JJ:** 5♀, 1♂, Temple Gwan Eum, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 12♀, Temple Gwan Eum, 17. iv. 1998, coll. Seunghwan Lee (SNU). **JN:** 1♂, Yeonju-ri, Uisin-myeon, Jindo-gun, 13. v. 2005, coll.

Youngbo Lee (NAAS).

Distribution. Japan, Korea.

Floral records. *Ranunculus japonicus* Thunb. (Ranunculaceae); *Brassica rapa* L., *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae); *Potentilla fragarioides* L. (Rosaceae) *Acer macrophyllum* Pursh (Sapindaceae) *Viola grypoceras* A. Gray (Violaceae); *Shortia uniflora* var. *kantoensis* (Diapensiaceae); *Taraxacum campylodes* G.E. Haglund, *Taraxacum platycarpum* Dahlst. (Compositae) (Mitai & Tadauchi, 2007); *Stellaria alsine* var. alsine (Caryophyllaceae)

Host. Unknown.

Remarks. This species is similar to *N. flavoguttata* but easily distinguished by flagellar length. See remarks on *N. flavoguttata* for further description.

***Nomada harimensis* Cockerell, 1914 동양알락꽃벌**

Nomada harimensis Cockerell, 1914: 425; Tsuneki, 1973: 80–83; Alexander & Schwarz, 1994: 248; Mitai & Tadauchi, 2007: 91–96; Won & Kim, 2013: 39–40. Holotype ♂. TD: USNM. TL: Japan.

Nomada orientalis Yasumatsu & Hirashima, 1953: 29–31.

(Plates 1-24, 1-25, 2-14)

Description. **Female.** Body length 7.61–9.07 mm. *Head.* In frontal view about 1.25–1.27x wider than long; LID:UID=1:1.10–1.13. Head mostly foveolate except punctate basal clypeus. Mandible simple, narrowed apically and acute at tip. Labral tooth below center. Short golden hair sparsely cover vertex and frons. Short white

plumose present on frons and lateral clypeus. Labrum intermix long dark brown hair and short golden plumose. Antennae with scape cylindrical, about as wide as flagella, covered with short golden plumose. F1: F2: F3=1:1.41–1.69:1.13–1.35; FW1:FL1=1:1.11–1.36; FW2:FL2=1:1.78–1.97; FW3:FL3=1:1.40–1.58.

Mesosoma. Mesoscutum, scutellum, and metanotum densely foveolate. Scutellum with deep furrow. 1/2 of upper propodeal triangle vertically rugose, remaining substrigulate. Mesoscutum, scutellum, and metanotum with short, week golden plumose. Hind tibiae covered with golden to brown hair; HTS with a range of curved amber hair.

Metasoma. Weakly punctate. Covered with short and decumbent golden hair.

Colors. Head mostly dark orange. Antennae entirely dark orange. Tinged as black as follows: Vertex, frons, side of clypeus. Mesoscutum dark orange with three black lines. Scutellum mostly dark orange, uppermost and lowermost margin black. Metanotum orange, tinged with black centrally. Propodeal triangle dark orange, median area tined with reddish brown to black. Legs dark orange. Terga mostly dark orange: T2–T4 laterally with bright yellow triangular maculation. T5 with rectangular bright yellow maculation.

Male. Body length 7.7–7.8 mm. *Head.* In frontal view about 1.29–1.31x wider than long; UID: LID=1: 1.17–1.18. Head densely foveolate. Vertex and frons with Long yellow plumose. Clypeus and labrum intermix with long golden plumose and hair. Antennae with scape swollen, distinctly wider than flagella, covered with long golden plumose. F1: F2: F3=1:1.6–1.7:1.3–1.4; FW1:FL1=1:0.90–95; FW2:FL2=1: 1.57–

1.73; FW3:FL3=1:1.29–1.36.

Mesosoma. Mesoscutum, scutellum, and metanotum entirely areolate. 2/3 of upper propodeal triangle vertically rugose, remaining substrigulate. Mesoscutum, scutellum, metanotum and side of propodeum with long golden plumose. Hind tibiae covered with long golden hair; HTS with a range of curved amber hair.

Metasoma. Punctate. Covered with short and decumbent golden hair.

Coloration. Head mostly black. Antennae mostly dark brown, scape tinged with smear dark orange. Tinged as bright yellow as follows: lateral margin of paraocular area, malar area, basal clypeus, labrum, and mandible except reddish brown tip. Mesoscutum, scutellum, metanotum, propodeum entirely black. Legs mostly dark orange, tinged with black. Terga mostly dark brown; T2–T5 laterally with bright yellow triangular maculation; T6 with bright yellow rectangular maculation.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-14. Gonocoxite cylindrical, blunt at tip; basoventral lobe present. Gonostylus and basoventral lobe apically and laterally with long and sinuate hair.

Specimen Examined. GG: 1♀, 1♂, Mt. Yeogi, Suwon-si, 3. iv. 1998, coll. Seunghwan Lee (NAAS); 2♀, same locality, 22. iv. 1998, same collector (NAAS); 1♀, Eco-bridge, Uiwang-ri, 22. v. 2000, coll. Kim & Kim (LHSC). **GW:** 1♀, Inje, 25. iv. 1994, coll. S.H. Lee (NAAS).

Distribution. Japan, Korea.

Floral records. *Salix gracilistyla* Miq. (Salicaceae); *Brassica rapa* L. (Brassicaceae); *Potentilla fragarioides* L., *Potentilla freyniana* Bornm., *Rubus pannosus* P.J.Müll. &

Wirtg. (Rosaceae); *Acer sieboldianum* Miq. (Sapindaceae); *Veronica persica* Poir. (Plantaginaceae); *Petasites japonicus* (Siebold & Zucc.) Maxim., *Petasites japonicus* subsp. *giganteus* F. Schmidt ex Kitam. (Compositae) (Mitai & Tadauchi, 2007).

Host. *Andrena ruficurus rabicurus* Hirashima, 1957 (Maeta et al., 1996).

Remarks. Main body coloration of this species is variable. Mostly it is dark orange, but also majority of this species is red-bodied.

Nomada koreana **Cockerell, 1926 참알락꽃벌**

Nomada koreana Cockerell, 1926: 43–44. Holotype ♀. TD: CAS. TL: North Korea.

Nomada koreana Alexander & Schwarz, 1994: 249.

Diagnosis. Female. Body length 7.00 mm (Cockerell, 1926). Mesoscutum red with three black lines. Scutellum entirely red. Terga mostly reddish brown; T2–T3 laterally with lemon-yellow maculations; T4 with transverse maculations; T5 with rectangular yellow maculation. Male is unknown.

Distribution. Korea (North Korea only).

Remarks. *Nomada koreana* Cockerell, 1926 was reported from Musan, North Korea, and any specimens of this species were not examined from South Korea. The diagnosis of this species was taken from its original description, by Cockerell (1926).

Nomada icazti **Tsuneki, 1976 번개무늬알락꽃벌**

Nomada icazti Tsuneki, 1976: 59–61; Alexander & Schwarz, 1994: 248; Mitai & Tadauchi, 2007: 96–100; Won & Kim, 2013: 41–42. Holotype ♀. TD: MNHAH. TL:

Japan.

Nomada wakasana Tsuneki, 1976: 56–58.

(Plates 1-26, 1-27, 2-15)

Description. Female. Body length 9.03–10.26 mm *Head.* In frontal view about 1.28–1.34x wider than long; LID:UID=1:03–1.06. Head densely foveolate. Mandible long, simple, subacute at tip. Labral tooth centrally. short golden hair sparsely on vertex and upper part of paraocular area. Short white plumose sparsely on supraclypeal area, clypeus, lower part of paraocular area. Labrum intermix with short golden hair and long white plumose. Mandible with amber to golden amber long hair. Antennae with scape cylindrical but slightly swollen with short dark brown hair. FL1:FL2:FL3=1:1.47–1.50:1.14–1.33; FW1:FL1=1:1.37–1.64; FW2:FL2=1:2.06–2.35; FW3:FL3=1:1.64–1.96.

Mesosoma. Mesoscutum, scutellum, metanotum deeply foveolate. Side of propodeum areolate. Scutellum with deep furrow. 2/3 of propodeal triangle rugose and sinuate, remaining shagreened. Mesoscutum, scutellum, metanotum with long golden hair. Side of propodeum with short white plumose. Hind tibiae covered with long light brown hair; HTS amber to dark amber, 4 to 5 in number, posteriormost seta long and thin, the others slightly shorter and evidently thicker than posteriormost one.

Metasoma. distinctly punctate; covered with short, decumbent yellow hair.

Colors. Head predominantly dark orange. Tinged with black as follows: vertex, frons except supraclypeal area, side of clypeus. Lateral part of paraocular area and basal of labrum tinged with bright yellow. Mesoscutum mostly dark red with three thick black

lines. Scutellum mostly dark red except upper and lower black margin. Metanotum entirely black. Propodeum mostly dark orange with two bright yellow zigzag patterns, centrally with thick black line. Legs mostly orange. Terga mostly dark red; T1 upper half black, lower half dark red; T2–T4 upper half dark red and lower half dark brown, laterally with ivory and triangular maculation; T5 with ivory band.

Male. Body length 8.88–10.28 mm. *Head*. In frontal view about 1.29-1.37x wider than long. LID:UID=1:1.11–1.19. Head densely foveolate. Mandible simple, acute at tip. Labral tooth centrally. Yellow and white long plumose densely on head. Labrum intermix with short golden hair and long white plumose. Mandible with long golden hair and week yellow to white plumose. Antennae with scape swollen, wider than flagella, with golden plumose. FL1:FL2:FL3=1:1.73–2.45:1.42–1.90; FW1:FL1=1:0.80–0.92; FW2:FL2=1:73–1.96; FW3:FL3=1:1.42–1.46.

Mesosoma. Mesoscutum densely foveolate. Scutellum and metanotum foveolate to areolate. Propodeal triangle areolate-rugose on basal 1/3 area, remaining shagreened. Mesoscutum, scutellum, metanotum sparsely with long golden plumose. Side of propodeum with long white plumose. Hind tibiae covered with long amber hair, HTS amber, 3 to 4 in number, posteriormost seta long and thin, remaining slightly shorter and thicker than posteriormost one.

Metasoma. distinctly punctate; pygidial plate distinctly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-15. Gonostylus short and swollen, curved posteriorly with sinuated hair at the tip and lateral section. Basoventral lobe slightly produced. Gonocoxite with

dorsal invagination, furrow distinctly presented, somewhat rounded.

Colors. Head predominantly black; Scape anteriorly yellow, posteriorly black. The following area bright yellow: paraocular area, basal of the clypeus, labrum. Mandible mostly bright yellow, except its dark red tip. The following area black: mesoscutum, scutellum, propodeal triangle, side of propodeum. Terga mostly dark brown; T1 upper half black, lower half brown with two oval black maculation; T2–T5 upper half dark brown, lower half brown, laterally with triangular pale-yellow maculation; T6 with pale yellow band.

Specimen Examined. GB: 1♀, Kyungpook National University, Gajangdong, Sangju-si, 01. ~ 08. v. 2009, coll. H.S. Lee (LHSC). **GG:** 3♀, 1♂, Exotic Trees Garden, Kwangnung, 16. v. 2013, coll. S.Y. Park (LHSC); 1♀, Jikdong-ri, Soheul-eup, Pocheon-si, 16. ~ 31. v. 2016, coll. Unknown (KNA); 2♀, Soheul-eup, Pocheon-si, 14. ~ 28. iv. 2017, coll. Unknown (KNA); 1♀, 1♂, Jikdong-ri, Soheul-eup, Pocheon-si, 06. iv. ~ 04. v. 2018, coll. Unknown (KNA). **GW:** 8♂, [38°08'46.5"N 128°15'47.5"E], Seorim valley, Seorim-ri, Seo-myeon, Yangyang-gun, 18. iv. ~ 10. v. 2018, coll. Sanghyuk Nam (SNU); 2♂, Malaise trap, 854, Han-gye-ri, Bukmyeon, Inje-gun, 18. iv. ~ 10.v.2018, same collector (SNU); 1♀, 1♂, same locality, coll. Lim, Oh, and Park (SNU). **Seoul:** 1♂, Mt. Gwanak, Gwanak-gu, 28.v.2016, coll. Sanghyuk Nam (SNU).

Distribution. Korea, Japan.

Floral records. *Capsella bursa-pastoris* (L.) Medik (Brassicaceae)

Host. Unknown.

Remarks. This species is the only species which possess bright yellow zigzag patterns in female among Korean species, and therefore it is one of the most distinctive species.

***Nomada leucophthalma* (Kirby, 1802) 곰보알락꽃벌**

Apis leucophthalma Kirby, 1802: 197. Holotype ♂. TD: BNHM. TL: UK.

Nomada leucophthalma: Alexander & Schwarz, 1994: 249; Mitai & Tadauchi, 2007: 109–111; Won & Kim, 2013: 45–46.

Nomada kuro Tsuneki, 1986: 52; Alexander & Schwarz, 1994: 249.

Nomada muinensis Tsuneki, 1986: 53–54; Alexander & Schwarz, 1994: 250.

Diagnosis. Body length 8.00–12.00 mm in female, 8.00–11.00 in male (Smit, 2018). T1–T3 mostly red; T2–T3 laterally with yellow maculation; T4 with interrupted yellow line; T5 tinged with yellow in female. T2–T6 with yellow bands, interrupted on T2–T4 in male. HTS brown to black, 3 to 5 in number in female. HTS 5 in number, sharp at tip.

Distribution. Europe, Japan, Korea Russia.

Remarks. *Nomada leucophthalma* (Kirby) is similar to *N. fusca* Schwarz regarding coloration in female but differs in HTS. HTS is clearly thicker than hair on hind tibiae in *N. fusca*, but it is similar with hair on hind tibiae in *N. leucophthalma*. Since any specimens of this species were not examined in this study, the diagnosis of this species was taken from Smit (2018), and Amiet et al. (2007).

***Nomada maculifrons* Smith, 1869 가위털알락꽃벌**

Nomada maculifrons Smith, 1869: 206; Hirashima, 1965: 309; Tsuneki, 1973: 52–56; Alexander & Schwarz, 1994: 249; Mitai & Tadauchi, 2007: 111–117; Won & Kim, 2013: 46–48. Holotype ♀. TD: BNHM. TL: Japan.

(Plates 1-32, 1-33, 2-19)

Description. **Female.** Body length 8.05–9.96 mm. *Head.* In frontal view about 1.25–1.32x wider than long; LID:UID=1:0.99–1.05. Head mostly foveolate, clypeus foveolate to punctate. Mandible acute at tip, wide about half as long as width of malar area. Labral tooth apically. Long, thick black hair covering as follows: lower portion of paraocular area, side of vertex, basal area of clypeus; Golden plumose covering as following: frons, vertex, upper area of paraocular area. Labrum intermixed with short golden hair and long, dark brown, week plumose. Mandible with long golden hair. Antennae with scape cylindrical, about as wide as flagella, with appressed thick black hair. FL1:FL2:FL3=1:1.39–1.50:1.14–1.76; FW1:FL1=1:1.18–1.31; FW2:FL2=1:1.62–1.90; FW3:FL3=1.1.32–1.50.

Mesosoma. Mesoscutum and scutellum deeply foveolate, with shiny interspace. Side of propodeum foveolate. Metanotum areolate. Propodeal triangle mostly rugose, lower part about 1/3 shagreened. Mesoscutum and metanotum with short golden hair. Scutellum intermixed with short dark brown, golden hair, and long plumose. Side of propodeum covered with white plumose. Hind tibiae mixed with thick black hair and relatively thin brownish hair: HTS black, 5 to 7 in number, posteriormost seta slightly thicker than hair in hind tibiae, remaining shorter and thicker than posteriormost one.

Metasoma. finely punctuated; covered with short, decumbent yellowish hair.

Colors. Head predominantly dark orange, side of the paraocular area and basal of clypeus yellow. Tinged black as follows: vertex, frons except dark orange oval maculation, longitudinal maculation on side of clypeus. Mesoscutum predominantly dark red, marked with three longitudinal lines. Scutellum dark red. Propodeal triangle black with two red oval maculation; Side of the propodeal triangle with black and dark red. Most of the legs dark red. Terga mostly reddish brown; T2 laterally with large pale-yellow spots; T4 and T5 with pale-yellow bands.

Male. Body length 8.35–10.4 mm. *Head*. In frontal view about 1.29x wider than long. LID:UID=1:1.11–1.14. Head mostly foveolate, clypeus foveolate to punctate. Mandible as in female. labral tooth apically. Yellow to white long plumose distributed on frontal area of head. Labrum intermixed with short golden hair and long white plumose. Antennae with scape swollen, wider than flagella, covered with long golden plumose. FL1:FL2:FL3=1:1.75–1.90:1.45–1.76; FW1:FL1=1:0.96–1.00; FW2:FL2=1:1.57–1.84; FW3:FL3=1:1.36–1.47.

Mesosoma. Mesoscutum and scutellum densely foveolate. Metanotum areolate. Side of propodeum foveolate. 2/3 of propodeal triangle rugose, remaining portion shagreened. Mesoscutum, scutellum, metanotum and side of propodeum covered with yellow to white plumose. Hind tibiae covered with long, transparent white hair; HTS amber, 4 to 5 in number, posteriormost seta long and thin, the others slightly shorter and thicker than posteriormost one.

Metasoma. Punctuation identical as in female; Pygidial plate distinctly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-19. Gonostylus slender, long and acute; tip of the gonostylus with plumose; lateral side with long vestiture. Basoventral lobe strongly modified with plumose. Gonocoxites with dorsal invagination.

Colors. Head predominantly black. Antennae mostly dark orange; scape anteriorly yellow, posteriorly black. Following area tinged with bright yellow: paraocular area, supraclypeal area, clypeus, labrum, mandible except reddish brown tip. Mesoscutum, metanotum, propodeal triangle entirely black. Most legs dark orange, tinged with black. Terga mostly brown; T1 with two oval dark brown maculation on pale yellow band; T2–T3 laterally with large pale-yellow spots; T4–T6 with pale yellow band.

Specimen Examined. CN: 1♀, Mt. Heugseong, Cheonan-si, 11. iv. 1998, coll. June Yeol Choi (NAAS). **GG:** 1♀, Anyang-si, 28. v. 1986, coll. P.L. (SNU); 1♀, Uijeongbu-si, 23. v. 1988, coll. H.K.S. (SNU); 1♀, Mt. Gwanggyo, Suwon-si, 28. v. 1990, coll. S.C.Y. (SNU); 1♀, Suwon-si, 30. v. 1994, coll. H.S. Lee (SNU); 1♂, Suwon-si, 10. v. 1996, coll. Chin-Sung Chang (SNU); 15♂, Mt. Yeogi, Suwon-si, 3. iv. 1998, coll. Seunghwan Lee (NAAS); 1♀, Mt. Yumyeong, Yangpyeong-gun, 18. iv. 1998, coll. Eun-kyung Park (LHSC); 1♀, Mt. Taehwa, Chugok-ri, Docheok-myeon, Gwangju-si, 8. v. 1998, coll. H.T. Kim (SNU); 1♀, Mt. Taehwa, Gwangju-si, 8. v. 1998, coll. Seunghwan Lee (NAAS); 1♀, Mt. Gwanggyo, Suwon-si, 24. iv. 1998, coll. H.T. Kim (SNU); 2♂, Anyang-si, 4. v. 1999, coll. Heungtae Kim (SNU); 1♂, Mt. Taehwa, Chugok-ri, Docheok-myeon, Gwangju-si, 6. v. 1999, coll. Heungtae Kim (SNU); 1♀, Hantaek Arboretum Jangpyeong-ri, Baegam-myeon, Cheoin-gu, Yongin-

si, 14. v. 2001, coll. Youngbo Lee (NAAS); 1♀, Gwangneung, Namyangju-si, 16. v. 2004, coll. M.K. Paek (LHSC); 4♂, Yulgeuk-ri, Heungcheon-myeon, Yeoju-si, 7. v. 2003, coll. Youngbo Lee (NAAS); 3♀, 227-26, Myeokgol-ro, Bukmyeon, Gapyeong-gun, 08. v. 2020, coll. K.Y. Lim, J.Y. Choi, M.S. Oh (SNU); 2♀, Soheul-eup, Pocheon-si, 25. v. 2020, coll. Kayun Lim (SNU); 1♂, Mt. Hwaya, Cheongpyeong-myeon, Gapyeong-gun, 19. iv. 2021, coll. K.Y. Lim & S.J. Choi (SNU); 6♂, 35 Gail-ri, Seorak-myeon, Gapyeong-gun, 16. vi. 2021, coll. Kayun Lim; 2♂, Mt. Yumyeoungsan, Seorak-myeon, Gapyeong-gun, 15. iv. 2022, coll. K.Y. Lim, S.H. Jung (SNU). **GW:** 1♀, Taebaeksan, Taebaek-si, 30. v. 1999, coll. Suhyeon Woo (LHSC); 1♀, Mt. Baekam, Hongcheon-gun, 24. v. 2002, coll. Heung-sik Lee (LHSC); 1♂, Mt. Odae, Dongsan-ri, Jinbu-myeon, Pyeongchang-gun, 27. v. 2008, coll. H.S. Lee (LHSC); 1♀, 1♂, vivaldi-park, Hongcheon-gun, 13. v. 2011, coll. H.S. Lee (LHSC); 1♂, Dongchon-ri, Hwacheon-eup, Hwacheon-gun, 16. iv. ~ 14. v. 2018, coll. Minhyuk Lee (SNU); 1♀, 1♂, 142-6, Sinheungdong-gil, Jucheon-myeon, Yeongwol-gun, 2. v. 2021, coll. Wongwoong Kim (SNU); 7♂, Jangjeon-gil, Jinbu-myeon, Pyeongchang-gun, 11. v. 2021, coll. K.Y. Lim, D.Y. Park, W.W. Kim (SNU). **JB:** 1♀, Daebul-ri, Seolcheon-myeon, Muju-gun, 26. v. 1993, coll. Hwa-il Shim (LHSC). **JJ:** 2♀, Jocheon-eup, Seonheul-ri, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 1♀, Temple Gwaneum, Jeju-si, 17. iv. 1998, coll. Seunghwan Lee (NAAS); 2♀, 1555, 1100-ro, Seogwipo-si, 11. vi. 1998, coll. Seunghwan Lee (NAAS); 1♂, 584, Myeongnim-ro, Jeju-si, 11. iv. 2021, coll. Wonwoong Kim (SNU). **JN:** 2♀, Mt. Jiri, Nogodan, Gurye-gun, 27. v. 1994, coll. Ahn song-pog (NAAS); 3♀, same location

and date, coll. D.S. Gu (NAAS); 4♀, same location and date, coll. J.Y. Choi (NAAS); 8♀, same location and date, coll. M.J. Han (NAAS); 2♀, same location and date, S.B. Ahn (NAAS); 6♂, Mt. Jiri, Piagol, Gurye-gun, 25. iv. 1999, coll. Heungtae Kim (SNU); 1♀, Jwasa-ri, Sandong-myeon, Gurye-gun, 5. vi. 1996, coll. H.S. Lee (SNU); 12♀, Mt. Jiri, Nogodan, Gurye-gun, 26. v. 1997, coll. Heung-sik Lee (LHSC); 1♀, Jwasa-ri, Sandong-myeon, Gurye-gun, 23. v. 1999, coll. H.T. Kim (SNU).

Distribution. Japan, Korea.

Floral records. *Weigela florida* (Bunge) A. DC., *Weigela subsessilis* (Nakai) L.H. Bailey, *Weigela praecox* (Lemoine) Bailey, *Valeriana fauriei* Briq. (Caprifoliaceae); *Rhododendron schlippenbachii* Maxim. (Ericaceae); *Staphylea bumalda* DC. (Staphyleaceae); *Corydalis speciosa* Maxim. ex Regel (Papaveraceae); *Chaenomeles sinensis* (Dum.Cours.) Koehne (Rosaceae); *Staphylea bumalda* DC. (Staphyleaceae).

Host. unknown

Remarks. This species can be confused with *Nomada sabaensis* Tsuneki, 1973 female, but can be differentiated by distinct thick HTS while HTS is as thin as hair on hind tibiae in *N. sabaensis*.

Nomada montverna Tsuneki, 1973 작은알락꽃벌

Nomada montverna Tsuneki, 1973: 97–100; Alexander & Schwarz, 1994: 250; Mitai & Tadauchi, 2007: 117–121; Won & Kim, 2013: 48–49. Holotype ♂. TD: MNHAH. TL: Japan.

Diagnosis. Body length 5.00–6.50 mm in female, 4.50–6.00 mm in male (Mitai &

Tadauchi, 2007). Mandible more greatly curved than *N. flavoguttata*.

Supraclypeal area black in female and scutellum entirely black in male, remaining mostly as in *N. flavoguttata*.

Distribution. Japan, Korea.

Remarks. *Nomada montverna* Tsuneki, 1973 is similar to *N. flavoguttata*. The Mandible is more curved than *N. flavoguttata*, but the remaining difference illustrated in Mitai & Tadauchi (2007) is very mild, which indicates the importance of the further detailed investigation. Any specimens of this species were not examined in this study. The diagnosis of this species was taken from Mitai & Tadauchi (2007) and Won & Kim (2013).

***Nomada opaca* Tsuneki 1973, 쌍니알락꽃벌**

Nomada opaca Alfken, 1913: 105; Mitai et al., 2008: 20; Won and Kim, 2013: 49–50; Smit, 2018: 200. Holotype ♀. TD: Uncertain. TL: Germany.

Nomada bifida var. *opaca* Alfken, 1913: 105.

(Plate 1-37)

Description. Female. Body length 9.94 mm. *Head.* In frontal view about 1.26x wider than long; LID:UID=1:1.13. Head densely foveolate. Mandible bidentate. Short golden hair sparsely near vertex. Paraocular area with golden plumose. Supraclypeus, clypeus, labrum intermixed with short golden plumose and long dark brown hair. Mandible with long dark brown hair. Antennae with scape cylindrical, about as wide as flagella, covered with short golden plumose and dark brown hair.

FL1:FL2:FL3=1:1.79:1.43; FW1:FL1=1:0.93; FW2:FL2=1:1.64; FW3:FL3=1:1.35.

Mesosoma. Mesocutum, scutellum, metanotum entirely foveolate. Scutellum with deep furrow. 2/3 of propodeal triangle rugose-reticulate, its side foveolate. Mesoscutum with short golden hair. Scutellum and metanotum with short golden hair. Apex of propodeum laterally with short white plumose. Hind tibiae covered with short light brown to dark brown hair; HTS 4 in number, posteriormost seta long and thin, remaining setae shorter and thicker than posteriormost one.

Metasoma. Densely punctuate. Covered with short decumbent golden hair.

Colors. Head predominantly black. Following area tinged with dark red: margin of paraocular area, basal area of clypeus, labrum, mandible except reddish brown at tip. Mesoscutum mostly black, with 4 longitudinal red lines. Scutellum mostly red, upper and lower margin tinged with black. Metanotum red, centrally tinged with black. Propodeal triangle laterally with two red dots, remaining black. Terga mostly dark red; T1 upper half black, lower half dark red; T2 laterally tinged with bright yellow, upper margin with inverted black triangle; T4–T5 with bright yellow band.

Male. Not examined in this study.

Specimen Examined. GG: 1♀, Eocheon-ri, Maesong-myeon, Hwaseong-si, 11. v. 2016, coll. J.Y. Choi (SNU).

Distribution. Europe, Japan, Korea, Russia.

Floral records. *Rubus crataegifolius* Bunge (Rosaceae).

Host. *Andrena fulvida* Schenk, 1853 (Kocourek, 1966; Stoeckhert, 1933).

Remarks. This species is similar superficially to *N. maculifrons* Smith, 1869 but

easily distinguished by bidentate mandible, while it is simple in *N. maculifrons*.

***Nomada pacifica* Tsuneki, 1973 뭉툭턱알락꽃벌**

Nomada pacifica Tsuneki, 1973: 97–100; Alexander & Schwarz, 1994: 250; Mitai & Tadauchi, 2007: 121–125; Won & Kim, 2013: 50–51. Holotype ♀. TD: MNHAH. TL: Japan.

(Plates 1-38, 1-39, 2-21)

Description. Female. Body length 7.44–8.38 mm. *Head.* In frontal view about 1.29–1.37x wider than long; LID:UID=1:1.13–1.14. Head densely foveolate. Mandible truncate. Labral tooth on center. Short golden hair near vertex. Following area sparsely intermixed with short golden and white plumose: paraocular area, supraclypeus, and clypeus. Short dark brown hair present lower half of paraocular area and lateral area of clypeus. Labrum intermixed with short golden plumose and long dark brown hair. Mandible with long dark brown hair and short golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short dark golden hair. F1: F2: F3=1:1.27–1.72:0.99–1.31; FW1:FL1=1:1.08–1.50; FW2:FL2=1:1.70–1.83; FW3:FL3=1:1.21–1.46.

Mesosoma. Mesoscutum, scutellum, metanotum, and side of propodeum densely foveolate. 2/3 of propodeal triangle rugose, remaining shagreened. Mesoscutum, scutellum, and metanotum sparsely covered with short golden hair. Side of propodeum with golden or white plumose. Hind tibiae covered with short light brown hair; HTS dark amber, 5 in number, intermixed with numerous dark brown setae and

light brown hair.

Metasoma. Punctate. Covered with short and decumbent dark brown hair.

Colors. Head mostly red. Lateral paraocular area tinged with bright yellow. Following area tinged with black: Vertex, frons, side of clypeus. Labrum intermixed with bright yellow and dark red. Mandible dark red with reddish brown tip. Mesoscutum mostly red with three black longitudinal maculation. Scutellum red. Metanotum red but black on median area. Propodeal triangle black, laterally tinged with red. Legs dark orange to dark red. Terga mostly dark red; T2–T3 laterally with bright yellow maculation. T4–T5 with bright yellow band.

Male. Body length 8.1–10 mm. *Head.* In frontal view about 1.24–1.28x wider than long; UID: LID=1: 1.17–1.18. Head densely foveolate. Labral tooth on center. Mandible truncate. Long golden plumose near vertex, paraocular area, and frons. Following area covered with white plumose: supraclypeal area, clypeus, and labrum. Mandible with long golden hair. Antennae with scape swollen, covered with short yellowish golden plumose. F1: F2: F3=1:1.3–2.1:1–1.5; FW1:FL1=1:0.72–1.17; FW2:FL2=1: 1.62–1.76; FW3:FL3=1:1.14–1.3.

Mesosoma. Mesoscutum and scutellum foveolate. Metanotum areolate to areolate-rugose. Upper half of propodeal triangle irregularly rugose, remaining shagreened. Long yellow plumose densely on Mesoscutum, scutellum, and metanotum. Hind tibiae covered with short yellowish white hair; HTS amber, 4 in number, intermixed with numerous white hairs.

Metasoma. Punctate. Densely covered with short and decumbent dark brown hair.

Coloration. Head mostly black. Antennae anteriorly dark orange, posteriorly dark brown to black. Following area tinged as bright yellow follows: lower half of paraocular area, clypeus, and mandible except reddish brown at tip. Labrum mixed with bright yellow and dark brown. Mesoscutum, metanotum, and propodeum entirely black. Scutellum black with two red oval maculation. Legs predominantly dark orange, tinged with black. Terga mostly dark orange; T1 upper half black, lower half dark orange; T2–T3 bright yellow with inverted dark orange triangle. T4–T6 with smear bright yellow band.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-21. Gonostylus short, blunt at tip; basoventral lobe present. Gonostylus and basoventral lobe apically and laterally with long sinuate hair.

Specimen Examined. Seoul: 1♀, Silim-dong, Gwanak-gu, 16. iv. 2004, coll. Unknown (SNU); 2♀, Mt. Gwanak, Gwanak-gu, 27. v. 2016, coll. Sanghyeok Nam (SNU); 1♂, Colleage of agriculture and life sciences, 1, Gwankak-ro, Gwanak-gu, 24. ~ 25. iv. 2020, coll. K.Y. Lim & D.Y. Park (SNU). **GG:** 1♂, National Institute of Agricultural Sciences, Suwon-si, 21. iv. 1989, coll. Ki-Jeong Hong (NAAS); 1♂, Mt. Yeogi, Suwon-si, 11. iv. 1994, coll. Seunghwan Lee (NAAS); same locality, 21. iv. 1989, coll. S.B. Ann (NAAS); 4♂, same locality and collector, 17. iv. 1995, coll. Seunghwan Lee (NAAS).

Distribution. Japan, Korea, Russia.

Floral records. *Prunus persica* (L.) Batsch (Rosaceae).

Host. Unknown.

Remarks. Female of this species can be confused with *N. sabaensis* Tsuneki, 1973, but can be easily separated by HTS. HTS dense and intermixed with five dark brown setae and numerous white hairs, while it is 4 in number, evenly distributed in *N. sabaensis*.

***Nomada panzeri orientis* Tsuneki, 1973 날씬알락꽃벌**

Nomada panzeri orientis Tsuneki, 1973: 68–72; Alexander & Schwarz, 1994: 251; Mitai & Tadauchi, 2007: 125–130; Won & Kim, 2013: 52–52. Holotype ♀. TD: MNHAH. TL: Japan.

Nomada sabanensis Tsuneki, 1973: 60–62.

Nomada floricola Tsuneki, 1973: 78–79.

Nomada yagensis Tsuneki, 1973: 95–96.

Nomada nunobensis Tsuneki, 1986.

(Plates 1-40, 2-22)

Description. **Female.** Not examined in this study.

Male. Body length 7.31–7.98 mm. *Head*. In frontal view about 1.27–1.32x wider than long. LID:UID=1:1.15–1.16. Head densely foveolate. Mandible simple, acute at tip. Labral tooth on center. Following area with long yellowish white plumose: vertex, paraocular area, frons, supraclypeal area. Clypeus and Labrum intermixed with long yellowish white plumose and golden hair. Mandible with long golden hair. Antennae with scape cylindrical, covered with dark brown to golden plumose. FL1:FL2:FL3=1:0.98–1.18:1.03–1.18; FW1:FL1=1:1.20–1.41; FW2:FL2=1:1.45–

1.63; FW3:FL3=1:1.27–1.67.

Mesosoma. Mesoscutum and scutellum densely foveolate. Metanotum areolate to foveolate. Metanotum areolate. 2/3 of paraocular area irregularly rugose, remaining shagreened. Hind tibiae covered with long golden hair; HTS light brown to dark brown, 5 in number, posteriormost setae as thick as hair on hind tibiae, remaining distinctly thicker and shorter than posteriormost setae.

Metasoma. Punctate; covered with short decumbent golden hair. Pygidial plate notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-22. Gonostylus cylindrical, subacute at tip; basoventral lobe weekly present; Gonostylus and basoventral lobe laterally and apically with long sinuate hair.

Colors. Head predominantly black except following area bright yellow: lateral margin of paraocular area, lower 2/3 of clypeus, labrum and mandible except reddish brown tip. Mesoscutum, scutellum, metanotum, and propodeum entirely black. Legs intermixed with dark orange and black. Terga mostly dark brown; T1 upper half black, lower half dark orange to yellow; T2 dark brown with yellow band, basally with inverted dark brown triangle; T3–T4 with smear bright yellow band; T5 with rectangular bright yellow maculation.

Specimen Examined. GG: 1♂, Sori-bong, Jinjeop-eup, Namyangju-si, 15. iii. ~ 14. iv. 2017, coll. Unknown (KNA). **GN:** 1♂, Daegu Arboretum, Dalseo-gu, 03. ~16. v. 2012, coll. Unknown (KNA). **GW:** 1♂, Mt. Chiak, Socho-myeon, Wonju-si, 10. iv. 2015, coll. Unknown (KNA).

Distribution. Japan, Korea, Russia.

Floral records. *Salix futura* Seemen (Salicaceae); *Rorippa indica* (L.) Hiern (Scientific name uncertain) (Brassicaceae) *Corylopsis sinensis* Hemsl. (Hamamelidaceae) *Potentilla fragarioides* var. major Maxim., *Rubus pungens* Cambess. (Rosaceae) *Petasites japonicus* (Siebold & Zucc.) Maxim. *Taraxacum campylodes* G.E. Haglund (Compositae) *Gagea lutea* (L.) Ker Gawl. (Liliaceae) (Mitai & Tadauchi, 2007).

Host. Unknown.

Remarks. Male of this species can be confused with *N. fervens* but can be distinguished by Gonostylus. In *N. panzeri orientis*, basoventral lobe weekly present, while it is distinctly developed. Also, gonostylus of *N. fervens* is slightly longer and thinner than *N. panzeri orientis*.

***Nomada pyrifera* Cockerell, 1918 어슷더듬이알락꽃벌**

Nomada pyrifera Cockerell, 1918: 480–481, Tsuneki, 1973: 60–62; Alexander & Schwarz, 1994: 251; Won & Kim, 2013: 53–54. Holotype ♀. TD: USNM. TL: Japan.

Diagnosis. Body length 9.00–11.00 mm in both sexes (Mitai & Tadauchi, 2003). Terga mostly reddish brown; T1 upper half black; T2 laterally with bright yellow triangular maculations; T4–T5 with bright yellow band in female. T1 upper half black, lower half dark orange; T2 bright yellow, inverted black triangle on center, apically tinged with dark brown; remaining with yellow bands. HTS dark brown, 9 to 11 in

number, stout, truncate at tip, distributed without space except posteriormost seta in female. HTS 5 in number, posteriormost seta long, remaining setae distantly shorter and thicker than posteriormost one, closely distributed.

Distribution. Japan, Korea.

Remarks. Male of *Nomada pyrifera* Cockerell, 1918 is distinctive from the other Korean *Nomada* males in that it has a clear inverted black triangular maculation on T2. Any specimens of this species were not examined in this study. The diagnosis of this species was taken from Mitai & Tadauchi (2007) and Won & Kim (2013).

***Nomada sabaensis* Tsuneki, 1973 네가시알락꽃벌**

Nomada sabaensis Tsuneki, 1973: 112–115; Tsuneki, 1986: 35; Alexander & 1994: 251; Won et al., 2008: 49; Mitai & Tadauchi, 2007: 135–137; Won & Kim, 2013: 54–55. Holotype ♀. TD: MNHAH. TL: Japan.

(Plate 1-45)

Description. **Female.** Body length 8.09–8.39 mm. *Head*. In frontal view about 1.30–1.33x wider than long. LID:UID=1:1.04–1.09. Head mostly foveolate. Mandible simple, acute at tip. Labral tooth on center. Short golden hair near vertex and upper part of paraocular area. Short white plumose sparsely on supraclypeal area, clypeus, lower part of paraocular area. Long dark brown hair sparsely on clypeus and paraocular area. Labrum intermixed with long golden or dark brown hair, and golden plumose. Mandible with long golden hair. Antennae with scape, as wide as flagella, covered with short dark brown hair. FL1:FL2:FL3=1:1.16–1.35:0.94–1.06;

FW1:FL1=1:1.34–1.66; FW2:FL2=1:1.60–1.74; FW3:FL3=1:1.19–1.34.

Mesosoma. Mesoscutum, scutellum, metanotum, side of propodeum foveolate. Scutellum flat, with shallow furrow. 1/3 of propodeal triangle rugose, remaining shagreened. Mesoscutum, scutellum, metanotum sparsely covered with short golden hair. Side of propodeum with yellow to white short plumose. Hind tibiae covered with light brown to dark brown hair; HTS 4 in number, nearly equal in length, evenly distributed, as thin as hair on hind tibiae.

Metasoma. Punctate; covered with short decumbent golden hair.

Colors. Head mostly dark orange. Antennae tinged with dark orange and dark brown. Frons and side of clypeus black. Supraclypeus dark orange. Mandible reddish brown at tip. Mesoscutum predominantly red with three longitudinal black lines. Scutellum entirely red. Metanotum dark orange. Propodeal triangle dark orange, basally tinged with black, black median black line presented. Side of propodeal triangle tinged with dark orange and black. Most of legs dark orange. Terga predominantly dark orange; T2–T4 laterally with ivory maculation, relatively smear in T3; T5 with ivory band.

Male. Unknown.

Specimen Examined. Seoul: 1♀, [37°27'20.8"N 126°56'57.7"E], Seoul National University, Daehak-dong, Gwanak-gu, 6. v. 2015, coll. Minho Jeon (SNU); 1♀, College of agriculture and life sciences, 1, Gwanak-ro, Gwanak-gu, 16. ~ 17. v. 2020, coll. KY Lim, DY Park (SNU). **CN:** 1♀, Mt. Heugseong, Cheonan-si, 11. iv. 1998, coll. June-Yeol Choi (NAAS). **GB:** 1♀, Pohang-si, collection date and collector unknown (SNU). **GG:** 1♀, [37°25 12.7 N 126°56'21.0 E], Seoul National University

arboretum, 280, Yesulgongwon-ro, Manan-gu, Anyang-si, 25. iv. 2020, coll. Kayun Lim (SNU); 1♀, Mulhyanggi Arboretum, Sucheong-dong, Osan-si, 21. iii. 2009, coll. H.S. Lee (LHSC); SEI, 1♀, Suwon-si, 2. v. 2002, coll. H.S. Lee (LHSC); 1♀, Eocheon-ri, Maesong-myeon, Hwaseong-si, 11. v. 2016, coll. J.Y. Choi (SNU); 1♀, National Institute of Agriculture Sciences, 21. iv. 1989, coll. Ki-Jeong Hong (NAAS); 1♀, Yongin-si, 21. v. 1989, coll. G.M. Choi (NAAS); 1♀, Yellow pan trap, Mt. Taehwa, Gwangju-si, 8. v. 1998, coll. Seunghwan Lee (NAAS). **GW:** 1♀, 5481, Gyeonggang-ro, Daegwallyeoung-myeon, Pyeongchang-gun, 18. v. 2017, coll. Sang Hyeok Nam; 1♀, Seorim velly, Seorim-ri, Seo-myeon, Yangyang-gun, 18. iv. ~ 10. v. 2018, coll. Min Hyeuk Lee (SNU); 1♀, Malaise trap, 854, Hangye-ri, Buk-myeon, Inje-gun, 27. vi. 2018, coll. Min Hyeuk Lee (SNU). **JJ:** 1♀, Seongsan, 12. iv. 1986, collector unknown (LHSC); 1♀, Temple Gwaneumsa, 17. vii. 1997, coll. Seunghwan Lee (NAAS).

Distribution. Korea, Japan.

Floral records. *Taraxacum platycarpum* Dahlst. (Compositae); *Prunus persica* (L.) Batsch; *Rubus crataegifolius* Bunge (Rosaceae)

Host. Unknown.

Remarks. Male of this species is still unknown. Floral preference of this species was not discovered in previous studies, but three records are newly reported in this study.

***Nomada shirakii* Yasumatsu & Hirashima, 1951 작은점알락꽃벌**

Nomada shirakii Yasumatsu & Hirashima, 1951: 55–56; Tsuneki, 1973: 51–52; Alexander & Schwarz, 1994: 244; Mitai & Tadauchi, 2007: 137–142; Won et al., 2008: 49; Won & Kim, 2013: 56–57.

Nomada iwakiyamana Tsuneki, 1986: 50–51.

Nomada kotomaria Tsuneki, 1986: 51–52.

Nomada uzenis Tsuneki, 1986: 49.

(Plates 1-47, 2-25)

***Description.* Female.** Not examined in this study.

Male. Body length 9.23–9.31 mm. *Head*. In frontal view about 1.32x wider than long.

LID:UID=1:1.10. Head densely foveolate. Mandible shallow, sharp at tip. Labral tooth centrally. Short golden plumose covered with near vertex and upper paraocular area. Supraclypeal area and clypeus covered with short white plumose. Labrum intermixed with short golden hair and white plumose. Mandible covered with long golden hair and short white hair. Antennae with scape stout and swollen, covered with short golden hair. FL1:FL2:FL3=1:1.63:1.31; FW1:FL1=1:0.84; FW2:FL2=1:1.50; FW3:FL3=1:1.21.

Mesosoma. Mesoscutum and scutellum densely foveolate, without any interspace. Metanotum areolate. Half of propodeal triangle confused-rugulose, remaining shagreened. Mesoscutum, scutellum, metanotum covered with long golden plumose. Side of propodeum long white plumose. Hind tibiae covered with light brown hair;

HTS dark brown to light brown, 4 to 7 in number, stiff and straight.

Metasoma. Punctate; covered with short decumbent golden hair. Pygidial plate distinctly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-25. Gonostylus short, stout, round at tip, laterally and apically with long sinuate vestiture; basoventral lobe present.

Colors. Head predominantly black. Antennae anteriorly dark orange, posteriorly dark brown; scape anteriorly bright yellow, posteriorly black. Tinged with bright yellow as follows: paraocular area, apex of clypeus, labrum, mandible except reddish brown tip. Mesoscutum, metanotum, propodeum entirely black. Scutellum with two red oval maculation. Terga mostly black; T1 black and dark brown at apex; T2 upper half black, lower half dark brown, laterally with bright yellow maculation. T3–T6 black, tinged with dark brown at apex.

Specimen Examined. CN: 1♂, Cheongyang-gun, 12. v. 1987, coll. S.B. Ahn (NAAS), 1♀, same date and locality, coll. W.S. Choi (NAAS); 1♂, Mt. Chilgap, Daechi-ri, Daechi-myeon, Cheongyang-gun, 5. v. 2005, coll. H.S. Won (NIBR); **GG:** 2♀, Mt. Taehwa, 8. v. 1998, coll. Seunghwan Lee (NAAS); 18♂, Mt. Jugeum, Eumhyeon-ri, Naechon-myeon, Pocheon-si, 20. v. 2001, coll. H.S. Won (NIBR); **GN:** 1♂, Cheonggoksa, Geumsan-myeon, Jinju-si, 29. iii. 1986, coll. J.I. Yun (NIBR).

Distribution. Japan, Korea.

Floral records. *Omphalodes japonica* Maxim. (Boraginaceae); *Brassica rapa* L., *Rorippa indica* (L.) Hiern (Brassicaceae); *Spiraea cantoniensis* Lour., *Stephanandra*

incisa (Thunb.) Zabel (Rosaceae); *Acer buergerianum* Miq., *Acer palmatum* Raf., *Acer sieboldianum* Miq. (Sapindaceae) (Mitai & Tadauchi, 2007).

Host. *Andrena tsukubana* Hirashima (Personal communication, Mitai & Tadauchi, 2007).

Remarks. This species can be confused with *Nomada maculifrons* Smith, 1869, but can be distinguished by black clypeus with yellow band at apex, while it is entirely bright yellow in *N. maculifrons*.

Nomada striata Fabricius, 1793 등근입술알락꽃벌

Nomada striata Fabricius, 1793: 348; Alexander & Schwarz, 1994: 252; Won & Kim, 2013: 57–58; Smit, 2018: 232–233. Holotype ♀. TD: Uncertain. TL: Europe.

Diagnosis. Body length 7.00–11.00 mm in female, 9.00–11.00 mm in male (Smit, 2018). Mandible truncated in both sexes. Terga mostly red; T2 laterally with two large yellow spots; T3 laterally with small yellow spots; T4 with interrupted yellow band; T5 with yellow square maculation in female. Terga mostly red; T2–T3 as in female; T4–T5 with yellow interrupted bands; T6 tinged with yellow.

Distribution. Europe, Korea, Russia.

Remarks. *Nomada striata* Fabricius, 1793 is similar to *N. abtana*. See the description for *N. abtana* for a detailed discussion. Any specimens of this species were not examined in this study. The diagnosis of this species was taken from Smit (2018).

***Nomada superba* species-group**

Nomada superba species-group Alexander, 1994: 225.

Diagnosis. HTS with a number of short, light yellow plumose in both sexes. This group may be confused with *basalis* species-group, but can be differed by distinctly protuberant head.

***Nomada sexfasciata* Panzer 1799, 방패입술알락꽃벌**

Nomada sexfasciata Panzer 1799: 18; Mitai & Tadauchi, 2008: 20; Won & Kim, 2013: 60–61; Smit, 2018: 224–225. Holotype ♂. TD: Uncertain. TL: German.

Nomada connexa Kirby, 1802: 199.

Nomada schaefferella Kirby, 1802: 199.

? *vespoides* Schrank, 1802: 408. Nomen dubium.

(Plate 1-46)

Description. Female. Body length 10.26 mm. *Head.* In frontal view about 1.20x wider than long; LID:UID=1:1.12. Clypeus imbricate-punctate, remaining head densely foveolate. Head distinctly protuberant. Mandible broad but sharp at tip. Labral tooth near apex. Short golden plumose sparsely near vertex and clypeus; Slightly longer golden plumose distributed laterally on supraclypeal area. Labrum intermixed with short golden hair and plumose. Antennae with scape cylindrical, about as wide as flagella, covered with short golden hair. FL1:FL2:FL3=1:0.93:0.83; FW1:FL1=1:1.35; FW2:FL2=1:1.29; FW3:FL3=1:1.08.

Mesosoma. Mesocutum, scutellum, metanotum densely foveolate. Propodeal triangle basally substrigulate and rugose, remaining tessellate. Mesoscutum, scutellum, metanotum, side of propodeum covered with long golden plumose. Hind tibiae with long golden hair; HTS with a number of short, light yellow plumose.

Metasoma. Distinctly punctuated; covered with decumbent short golden hair.

Colors. Head predominantly black. Flagella entirely orange; scape anteriorly orange, posteriorly tinged with black and orange. Paraocular area bright yellow, clypeus with black inverted triangle maculation, remaining bright yellow. Labrum and mandible bright yellow except reddish brown tip of mandible. Mesoscutum, metanotum, propodeum entirely black. Scutellum black with two ivory oval maculation. Leg mostly dark orange, tinged with black. Terga mostly black; T1 laterally with two, small ivory oval maculation; T2–T3 laterally with ivory maculation; T4–T5 with ivory band.

Male. Not examined in this study.

Specimen Examined. GW: 1♀, 297, Dutayeon-ro, Bangsan-myeon, Yanggu-gun, 12. vi. 1990, coll. Jin Ill Kim (LHSC).

Distribution. Algeria, Europe, Iran, Israel, Kazakhstan, Korea, Morocco, Russia, Tunisia, Turkey.

Floral records. Unknown.

Host. *Eucera longicornis* Linnaeus (Westrich, 1989), *E. nigrescens* Pérez (Alfken, 1913; Westrich, 1989), *E. interrupta* Bär (Westrich, 1989).

Remarks. *N. sexfasciata* can be confused with *N. tsunekiana* due to its coloration but

can be distinguished by its protuberant head.

***Nomada tripsona* species-group**

Nomada tripsona species-group Alexander, 1994: 229.

Diagnosis. HTS with digitiform setae in female, S8 sharply narrowed and distinctly protruded at tip in male.

Key to Korean species of *Nomada tripsona* species-group

Females

1. Scutellum with two yellow oval dots, metanotum black, tinged with yellow ..... ***Nomada pekingensis***

– Scutellum red, tined with black on center, metanotum red .....

..... ***Nomada nipponica***

Males

1. Margin of paraocular area with dark orange to yellow line .....

..... ***Nomada pekingensis***

– lower part of paraocular area tinged with bright yellow .....

..... ***Nomada nipponica***

***Nomada nipponica* Yasumatsu & Hirashima 1951, 일본알락꽃벌**

Nomada nipponica Yasumatsu & Hirashima 1951: 53; Tsuneki, 1973: 79; Alexander & Schwarz, 1994: 256; Ikudome, 1999: 655; Mitai & Tadauchi, 2005: 6–9; Won & Kim, 2013: 61–62. Holotype ♂. TD: ELKU. TL: Japan.

Nomada babai Tsuneki, 1986: 36; Alexander & Schwarz, 1994: 256.

(Plate 1-34)

***Description.* Female.** Body length 7.68 mm. *Head.* In frontal view about 1.29x wider than long; LID:UID=1:1.14. Head densely foveolate. Mandible shallow, round at tip. Labral tooth near apex. Short golden hair near vertex. Short golden plumose on paraocular area, supraclypeal area, clypeus. Labrum intermixed with short golden hair and plumose. Mandible with short or long golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with short dark brown hair. FL1:FL2:FL3=1:1.19:1.00; FW1:FL1=1:1.47; FW2:FL2=1:1.84; FW3:FL3=1:1.52.

Mesosoma. Mesocutum, scutellum, metanotum densely foveolate. Scutellum flat with very week furrow. 2/3 of propodeal triangle rugose-reticulate, remaining weekly substrigulate. Mesoscutum sparsely covered with short red hair. Scutellum and metanotum with short red plumose. Side of propodeum with long golden plumose. Hind tibiae covered with amber hair; HTS with a range of digitiform setae.

Metasoma. Distinctly punctuated and interspaces between punctures wider than puncture and shiny; covered with decumbent golden hair.

Colors. Head predominantly black. Antennae tinged with orange and dark brown. Following area tinged with reddish yellow: side of vertex, lower part of paraocular

area, 2/3 of clypeus, labrum, mandible except reddish brown tip. Mesoscutum and propodeum entirely black. Scutellum red, tinged with black on center. Metanotum entirely red. Legs mostly orange, tinged with dark brown. Terga mostly reddish orange; T1 upper half black, lower half red; T2–T3 laterally with bright yellow maculation; T4–T5 with bright yellow band.

Male. Not examined.

Specimen Examined. GN: 1♀, [N35°45'15.6" E127°51'1.7"], Gyeongnam Arboretum, Daecheon-ri, Ibanseong-myeon, Jinju-si, 15. iii. ~ 1. vi. 2011, coll. Jin-Hyeong-Hwang (KNA).

Distribution. Korea, Japan.

Floral records. *Brassica* L. (Brassicaceae); *Althaea rosea* (L.) Cav. (Malvaceae) *Ranunculus japonicus* Thunb. (Ranunculaceae) (Mital and Tadauchi 2005).

Host. *Andrena knuthi* Alfken (Suda, 1980).

Remarks. *N. nipponica* can be easily distinguished from the remaining Korean species by distinct digitiform setae.

Nomada pekingensis Tsuneki, 1986 노랑털알락꽃벌

Nomada pekingensis Tsuneki, 1986: 32; Alexander & Schwarz, 1994; 256; Won & Kim, 2013: 63–64. Holotype ♀. TD: MNHAH. TL: China.

(Plate 1-41, 1-42, 2-23)

Description. **Female.** Body length 8.12–9.22 mm. *Head.* In frontal view about 1.32–1.34x wider than long; LID:UID=1:24–1.26. Head densely foveolate. Mandible

round at tip. Labrum with transverse carina. Long reddish yellow plumose regularly distributed on frontal area of head. Labrum intermixed with short and long reddish golden plumose. Mandible with short golden hair. Antennae with scape cylindrical, about as wide as flagella, covered with reddish yellow plumose. FL1:FL2:FL3=1:0.79–0.90:0.75–0.86; FW1:FL1=1:1.43–1.98; FW2:FL2=1:1.43–1.55; FW3:FL3=1.26–1.41.

Mesosoma. Mesoscutum and scutellum densely foveolate. Metanotum densely areolate. 2/3 of propodeal triangle rugose and sinuate, re maining substrigulate. Mesoscutum, scutellum, metanotum and lateral propodeum with reddish golden long plumose. Hind tibiae covered with short white hair, HTS dark orange and reddish brown at tip, three to four in number, short and digitiform.

Metasoma. sparsely punctuated; covered with short, decumbent pale-yellow hair.

Colors. Head predominantly black; Scape tinged with dark orange and brown; The following parts dark orange: side of paraocular area, malar area, apical third of clypeus, and labrum. Tip of the mandible dark red. Mesoscutum and propodeum entirely black. Scutellum mostly black with yellow oval maculation. Metanotum entirely black or tinged with yellow on the middle. Most legs orange, tinged with dark brown. Terga mostly dark orange; T1 basally black, remains dark orange; T2–T3 upper half dark orange and lower half black, laterally tinged with pale-yellow triangular maculation. T4–T5 basally black with pale-yellow band.

Male. Body length 7.94–10.13 mm. *Head*. In frontal view about 1.31–1.38x wider than long; LID:UID=1:1.22–1.28. Head predominantly foveolate except clypeus

foveolate to punctate. Mandible acute at tip. Labrum with transverse carina. Long white plumose on vertex, frons, supraclypeal area, paraocular area, side of clypeus. Labrum covered with short golden hair and white plumose. Mandible with long golden hair. Antennae with scape cylindrical and posteriorly curved, wider than flagella, covered with white plumose hair. FL1:FL2:FL3=1:0.75–0.90:0.63–0.88; FW1:FL1=1:1.30–1.92; FW2:FL2=1:18–1.28; FW3:FL3=1:0.99–1.12.

Mesosoma. Mesoscutum and scutellum densely foveolate. Metanotum densely areolate. Scutellum flat. 2/3 of propodeal triangle rugose and sinuate, re maining substrigulate. Mesoscutum, scutellum, metanotum with long white hair. Side of propodeum covered with long white plumose. Hind tibiae covered with transparent white long hair; HTS amber, 3 in number, distinctly shorter and thicker than hair on hind tibiae.

Metasoma. Punctuation identical as in female; Pygidial plate distinctly notched.

Male terminalia. 7th Metasomal sternum, 7th Metasomal tergum, 8th Metasomal tergum as in pl 2-23. Gonostylus long, strongly bent with long plumose at the tip and middle section. Basoventral lobe strongly produced, posteriorly decumbent with short plumose. Gonocoxites with dorsal invagination, furrow distinctly rounded.

Colors. Head as in female except scape: scape anteriorly yellow, posteriorly black. The following area black: Mesosucutum, Propodeal triangle, side of the propodeal triangle. Scutellum and metanotum as in female. T1 upper half black, lower half brown with two oval pale-yellow maculation; basal 2/3 of T2–T3 dark brown, 1/3 transparent yellow, laterally with triangular pale-yellow maculation. T3–T6 basal 2/3

of T2–T3 dark brown, 1/3 transparent yellow with yellow band.

Specimen Examined.

GG: 1♀, Seoul National University Arboretum, Gwonseon-gu, Suwon-si, 1. v. 2002, coll. W.M. Kim (NAAS); 1♀, Gwonseon-gu, Suwon-si, 8. v. 2001, coll. T.W. Kim (NAAS); 1♂, Pocheon-si, 25. v. 2020, coll. Kayun Lim (SNU). **GW:** 1♂, [N37°55'23.7", E127°43'31.7"], Gangwon Prow Arboretum, Sanong-dong, Chuncheon-si, 16. v. 2012, coll. Gi-Yeong Lee (LHSC). **JJ:** 1♀, 2♂, Seonheul-ri, Jocheon-eup, Bukjeju-gun, 17. vii. 1997, coll. Seunghwan Lee (NAAS); 1♀, Seonheul-ri, Jocheon-eup, Bukjeju-gun, 17. iv. 1998, coll. Seunghwan Lee (NAAS).

Distribution. Korea, China.

Floral records. Unknown.

Host. Unknown.

Remarks. This species can be confused with *Nomada tsunekiana* Schwarz, 1999 but can be distinguished by reddish or dark brown abdominal coloration while abdomen is mostly black with yellow stripes in *N. tsunekiana.*

4. Discussion

In this study, genus *Nomada* was reviewed as 45 species of 8 species-group from Korea, including three species new to Korea, *Nomada aswensis* Tsuneki, *Nomada fusca* Schwarz, *Nomada pulawskii* Tsuneki, and three new species.

Taxonomic study of the genus *Nomada* in Northeast Asia has been problematic because of the split into subspecies between European and Northeast Asian species

with very subtle morphological differences such as coloration and length of flagella. Most of the split subspecies, especially in the *ruficornis* species-group, were concatenated by Mitai & Tadauchi (2007). However, some subspecies still have contentious status, such as *Nomada fulvicornis jezoensis* Matsumura, *N. roberjeotiana aino* Tsuneki. Therefore, further investigation must be conducted by examining the type species of these subspecies to confirm their status.

All of the host records of Northeast Asian species of *Nomada* rely on the Japanese records. Given that generalist cleptoparasites may use novel hosts under the different geographic conditions (Vivallo et al., 2019), the host use of Korean species may be different in comparison with Japanese records. However, new host-cleptoparasites interaction was not found in this study, indicating the necessity of further ecological study.

PART II. Molecular Phylogeny of subfamily Nomadinae and species-group concept reconstruction of genus *Nomada*

Abstract

Genus *Nomada* is the largest genus in Subfamily Nomadinae and the sole genus in the tribe Nomadini, which comprises approximately 800 species. Due to the high morphological variations, the genus is notorious for its taxonomic difficulty, making it one of the controversial groups in the subfamily. Moreover, the position of the tribe in the subfamily is not explicit. To elucidate the complex of its species-group classification and the tribal position, multi-locus phylogeny was conducted with one mitochondrial gene (COI) and five nuclear protein-coding genes (EF1α, Nak, Opsin, Pol II, Wingless). The results suggest that the tribe Hexepeolini is the sister group of the tribe Nomadini and indicate the necessity of species-group reclassification.

Keywords: Nomadinae, *Nomada*, Molecular phylogeny, Multi-locus, Speices-group

1. Introduction

The genus *Nomada* is the largest genus in Subfamily Nomadinae and the only genus in the tribe Nomadini, comprising about 800 species (Smit, 2018). It has mostly Holarctic distribution in that it occurs on all continents except Antarctica (Alexander, 1994; Michener 2007; Droege et al., 2010). Partitioning the genus into subgroups has been controversial due to its morphological diversity, making identification difficult at the species level (Alexander, 1994). For example, Nearctic taxonomists have split the genus into various subgenera or designated as new genera, while most of the Palearctic taxonomists have insisted the species-group concept (Alexander, 1989; Alexander, 1994). Thereafter, Alexander (1989) reconstructed the genus using species-group concept in his phD thesis. Later he incorporated some species-groups and concluded as 16 species-groups in the genus *Nomada* which are *adducta*, *armata*, *basalis*, *belfragei*, *bifasciata*, *erigeronis*, *furva*, *gigas*, *integra*, *odontophora*, *roberjeotiana*, *ruficornis*, *superba*, *tripsona*, *vegana*, and *vincta* (Alexander, 1994). In his thesis, He highlighted that the *ruficornis* species-group, which is the largest among the 16 established species-group, may be paraphyletic group due to the lack of apomorphic characters. Moreover, he designated *Nomada ruficornis* Linnaeus as the type species of the *ruficornis* species-group, but *N. ruficornis* has an apomorphic character that cannot be common trait to the species-group. For instance, the type species has a bifurcated mandible, while most species in the species-group have a simple one. As such, the species which belong to the *ruficornis* species-group are more like the remnants of the species which cannot be merged into the other

subspecies group (Mital & Tadauchi, 2007).

As time goes by, molecular phylogenetics using multi-gene as well as the phylogenomics using ultraconserved elements (UCE) got a higher resolution in bee phylogeny. However, most of the application of molecular data from genus *Nomada* has been focused on obtaining clear tribal relationships in the subfamily Nomadinae, which is still dubious in terms of the position of the genus *Nomada* in the subfamily (Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018; Bossert et al., 2019; Sless et al., 2022). For instance, the tribe Ammobatoidini is inferred to be closest to the Nomadini using multi-gene dataset (Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018), while the tribe Ammobatini and the tribe Neolarrini are presumed to be sister group of the genus *Nomada* using phylogenomics approaches (Bossert et al., 2019; Sless et al., 2022). As the purpose of the previous investigations was to update the current understanding of tribal resolution, only a few species of the genus *Nomada* were used, which indicates a low conviction of its sister group position.

The initial attempt of the molecular phylogenetics of genus *Nomada* to resolve species-group complex was conducted using COI marker by Won (2006) in his phD thesis and paraphyletic of *ruficornis* species-group was confirmed. However, only a single marker was used for the analysis and only 12 species of the genus were used in the study. Recently, Odanaka et al., (2022) provided new classification of subfamily Nomadinae using UCE and showed paraphyly of *ruficornis* species-group, Yet, given its high species diversity in this tribe, it is crucial to reveal the hidden

patterns of the phylogenetic relationships.

In this study, the species-group concept validity of the genus *Nomada* proposed by Alexander (1994) was tested using the molecular phylogenetic approach with an increased sampling of the *ruficornis* species-group whose systematics remains incomplete and controversial. Additionally, the tribal position of Nomadini within the subfamily was evaluated.

2. Materials and Methods

2.1. Taxon sampling

A total of 163 species as ingroup with 2 species as outgroup were used in this analysis and 85 species of the genus *Nomada* belong to the ingroup among 163 species. To be specific, more than half of the entire selected species for this study in the genus *Nomada* comprise *ruficornis* species-group, which is one of the problematic species-groups in the genus. To clarify the validity of the species-group concept by Alexander (1994), *Nomada ruficornis*, *N. roberjeotiana*, *N. bifasciata*, *N. armata*, *N. furva*, which are type species of species-groups were used for this study. In total, sampling in this study in terms of the genus *Nomada* represents 10 species-groups of the 16 species-groups. The sequences of 44 species were newly added by this study, some sequences were downloaded from NCBI, and some species were loaned from Mr. Keiichi Otsui and Finnish Museum of Natural History Zoological Museum (MZH) (Table 3).

2.2. DNA extraction, PCR amplification, and sequencing

Total genomic DNA was extracted by grinding up detached midleg or head of alcohol vouchers or dried specimens, which was removed with forceps that were sanitized before by flame and rinsed in 99% EtOH. DNeasy Blood and Tissue kit (QIAGEN, Inc.) was used for the DNA extraction according to the manufacturer's protocols and stored in –20°C. DNA vouchers were deposited in the Insect Biosystematics Laboratory, Seoul National University.

Genes previously used in Nomadinae phylogeny systematics were selected. One mitochondrial protein coding gene, cytochrome oxidase subunit I gene (COI) (Hebert et. al., 2003, Onuferko et. al., 2019), and five nuclear protein-coding genes (EF-1α, long-wavelength rhodopsin (opsin), NaK, pol II, and wingless) that were used in (Cardinal et al., 2010) were chosen for this study.

PCR products were amplified using Accupowder PCR Premix (Bioneer, Daejeon, Korea) in 20 μl reaction mixture. In case DNA extraction was needed from bad quality specimens, we redesigned the partial primers in threefold. The primers used in this study and specific PCR conditions were listed in Table 4. After the PCR product amplification process, PCR products were purified and sequenced at Bionics CO. (Seoul, Korea).

Table 3. Taxa used in this study with GeneBank accession numbers

Tribe	Species	GeneBank accession number						Specimen Reference
		COI	EF1α	Nak	Opsin	PolII	Wingless	
Outgroup	*Colletes compactus*	DQ872684	DQ884642	MN367513	DQ884542	MN367595	DQ884794	1
	Apis cerana	KM242593	EU184774	EU184750	AB355818	EU184733	EU184716	1
Melectini	*Zacosmia maculata*	MN344989	AY585117	GU245117	AF344637	AY945176	GU245570	1
	Thyreus decorus	OM722174	-	-	-	-	-	2
	Thyreus himalayensis	X	X	X	-	-	-	2
	Xeromelecta californica	MK919652	GU244955	GU245116	AF344613	GU245407	GU245569	1
	Melecta albifrons	MK919610	GU244998	GU245120	HM211837	GU245409	GU245573	1
	Melecta chinensis	OM722175	-	-	-	-	-	2
Caenoprosopidini	*Caenoprosopina holmbergi*	MK919570	GU244983	GU245194	GU245325	GU245476	GU245650	1
	Caenoprosopis crabronina	MK919571	GU245020	GU245195	GU245326	GU245477	GU245651	1
Isepeolini	*Melectoides bellus*	MK919611	GU244999	GU245115	HM211836	GU245406	GU245568	1
	Isepeolus luctuosus	KX821019	GU244953	GU245113	GU245277	GU245404	GU245566	1
	Isepeolus wagenknechti	KX821183	GU244954	GU245114	GU245278	GU245405	GU245567	1
Epeoloidini	*Epeoloides coecutiens*	MK919586	GU244987	GU245131	HM211838	GU245418	GU245584	1
	Epeoloides pilosula	JN293445	GU244966	GU245129	GU245287	GU245416	GU245582	1
Protepeolini	*Leiopodus trochantericus*	MK919603	GU244970	GU245136	GU245291	GU245422	GU245589	1
	Leiopodus abnormis	X	GU244969	GU245135	GU245290	GU245421	GU245588	1
	Leiopodus singularis	X	AY585113	GU245133	AF344624	AY945137	GU245586	1
Rhathymini	*Rhathymus unicolor*	X	GU244973	GU245139	GU245294	GU245425	GU245592	1
Ericrocidini	*Hopliphora velutina*	MK919599	GU244939	GU245086	GU245258	GU245379	GU245539	1
	Hopliphora diabolica	KY084893	KY084881	X	KY084866	KY084853	X	1
	Acanthopus excellens	KY084889	KY084876	X	KY084863	KY084849	X	1
	Mesoplia regalis	KY084901	KY084887	X	KY084871	KY084859	X	1
	Mesoplia rufipes	MK919618	GU244938	GU245085	GU245257	GU245378	GU245538	1
	Ericrocis lata	MN345705	GU244936	GU245083	GU245255	GU245376	GU245536	1
	Ctenioschelus goryi	KY084892	GU244941	GU245088	GU245260	GU245381	GU245541	1
	Mesocheira bicolor	MK919616	GU244940	GU245087	GU245259	GU245380	GU245540	1
	Epiclopus gayi	MK919589	GU244935	GU245082	GU245254	GU245375	GU245535	1
	Mesonychium asteria	KY084898	GU244937	GU245084	GU245256	GU245377	GU245537	1
Ammobatini	*Ammobates punctatus*	KJ838996	GU245011	GU245179	HM211841	GU245463	GU245635	1
	Oreopasites barbarae	MK919624	GU245008	GU245176	AF344626	GU245460	GU245632	1
	Pasites maculatus	MN344150	GU245035	GU245180	HM211842	GU245464	GU245636	1
	Sphecodopsis capensis	MK919639	GU245009	GU245177	GU245317	GU245461	GU245633	1
Brachynomadini	*Paranomada velutina*	MK919627	AY585115	GU245190	AF344627	AY945154	GU245646	1
	Triopasites penniger	MK919650	GU245018	GU245191	AF344633	GU245473	GU245647	1
Epeolini	*Rhinepeolus rufiventris*	MK919638	GU245027	GU245202	GU245331	GU245483	GU245658	1

	Thalestria spinosa	MN342317	GU245024	GU245199	GU245328	GU245480	GU245655	1
	Triepeolus tristis	MN342316	MN367540	MN367496	MN367458	MN367574	MN367661	1
	Triepeolus pectoralis	MN343742	MN367539	MN367495	MN367446	MN367581	MN367659	1
	Triepeolus robustus	MK919585	GU245023	GU245198	AF344634	AY945170	GU245654	1
	Epeolus chamaesarachae	MH089974	MN367522	MN367484	MN367461	MN367573	MN367638	1
	Epeolus interruptus	MH089961	MN367536	MN367494	MN367457	MN367571	MN367654	1
	Epeolus flavociliatus	MN342311	MN367528	MN367482	X	MN367580	MN367658	1
	Epeolus cruciger	MN342321	MN367525	MN367479	MN367459	MN367579	MN367652	1
	Epeolus alpinus	HM375429	X	X	X	X	X	1
	Epeolus schummeli	MN342314	MN367526	MN367480	KC798351	MN367577	MN367653	1
	Epeolus fallax	MN342318	X	X	X	X	X	1
	Epeolus tarsalis	MN342315	MN367527	MN367481	MN367460	MN367578	MN367655	1
	Epeolus variegatus	MK919587	GU244988	GU245203	HM211846	GU245484	GU245659	1
	Epeolus bifasciatus	MH089986	MN367535	MN367500	MN367462	MN367575	MN367649	1
	Epeolus variolosus	MN135626	X	X	X	X	X	1
	Epeolus brumleyi	MH089901	MN367538	MN367493	MN367456	MN367576	MN367657	1
	Epeolus scutellaris	HQ552250	GU245022	GU245197	AF344596	GU245479	GU245653	1
	Epeolus basili	MH090001	MN367532	MN367497	MN367444	MN367557	MN367636	1
	Epeolus pusillus	MH089868	MN367533	MN367498	MN367445	MN367558	MN367637	1
	Epeolus autumnalis	MH089931	MN367534	MN367499	MN367441	MN367562	MN367640	1
	Epeolus ainsliei	MH089843	MN367531	MN367478	MN367440	MN367561	MN367639	1
	Epeolus ilicis	MH090014	X	X	X	X	X	1
	Epeolus lectoides	MH090009	MN367529	MN367476	MN367442	MN367560	MN367641	1
	Epeolus lectus	MH089993	MN367530	MN367477	MN367443	MN367559	MN367642	1
	Epeolus transitorius	MN342320	MN367537	MN367483	MN367463	MN367572	MN367656	1
	Epeolus americanus	GU708026	X	X	X	X	X	1
	Epeolus asperatus	MH090008	MN367514	MN367491	MN367454	MN367570	MN367660	1
	Epeolus mesillae	MH089889	MN367515	MN367490	MN367455	MN367569	MN367651	1
	Epeolus minimus	MH090003	MN367518	MN367492	MN367452	MN367568	MN367646	1
	Epeolus olympiellus	MH089905	MN367517	MN367489	MN367453	MN367566	MN367647	1
	Epeolus canadensis	MH089848	MN367516	MN367485	MN367451	MN367567	MN367643	1
	Epeolus compactus	MH089882	MN367521	MN367487	MN367450	MN367565	MN367645	1
	Epeolus ferrarii	MH089922	MN367519	MN367486	MN367448	MN367563	MN367644	1
	Epeolus splendidus	MH089954	MN367520	MN367488	MN367449	MN367564	MN367648	1
Ammobatoidini	*Holcopasites insoletus*	X	GU245014	GU245184	GU245320	GU245467	GU245640	1
	Holcopasites minimus	X	GU245016	GU245187	GU245322	GU245470	GU245643	1
	Holcopasites stevensi	X	GU245015	GU245186	GU245321	GU245469	GU245642	1
	Holcopasites calliopsidis	MK919598	GU245012	GU245182	AF344600	GU245465	GU245638	1
	Holcopasites arizonicus	X	GU245013	GU245183	GU245319	GU245466	GU245639	1
	Holcopasites ruthae	X	AY585112	GU245181	AF344602	AY945124	GU245637	1
Neolarrini	*Neolarra orbiculata*	MK919620	GU245029	GU245205	GU245333	GU245486	GU245661	1

	Biastes truncatus	MK919567	GU244981	GU245189	HM211844	GU245472	GU245645	1
	Neopasites cressoni	MK919621	GU245017	GU245188	GU245323	GU245471	GU245644	1
Hexepeolini	*Hexepeolus rhodogyne*	MK919597	GU245028	GU245204	GU245332	GU245485	GU245660	1
Nomadini	*Nomada stigma*	KJ839803	X	X	X	X	X	1
	Nomada facilis	HM401068	X	X	X	X	X	1
	Nomada integra	KJ837492	X	X	X	X	X	1
	Nomada pleurosticta	KJ836589	X	X	X	X	X	1
	Nomada argentata	KJ838360	X	X	X	X	X	1
	Nomada obtusifrons	KJ838689	X	X	X	X	X	1
	Nomada roberjeotiana	OM722171	-	-	-	-	-	3
	Nomada rufipes	KJ839802	X	X	KC798374	X	X	1
	Nomada sexfasciata	KJ838028	X	X	KC798376	X	X	1
	Nomada articulata	FJ582337	X	X	X	X	X	
	Nomada japonica	OM722164	-	-	-	-	-	2
	Nomada tsunekiana	-	-	-	-	-	-	2
	Nomada emarginata	KJ836575	X	X	X	X	X	1
	Nomada flavopicta	HM401073	X	X	X	X	X	1
	Nomada imbricata	FJ582365	X	X	X	X	X	1
	Nomada lathburiana	OM722166	-	-	-	-	-	3
	Nomada bifasciata	HM401039	X	X	X	X	X	1
	Nomada fucata	KJ838363	X	X	X	X	X	1
	Nomada succincta	EU678368	X	X	KC798375	-	-	2
	Nomada comparata	OM722155	-	-	-	-	-	2
	Nomada goodeniana	OM722161	-	-	-	-	-	2
	Nomada distinguenda	OM722156	-	X	-	-	-	2
	Nomada similis	KJ838899	X	X	X	X	X	1
	Nomada furva	KJ837852	X	X	X	X	X	1
	Nomada bluethgeni	HQ948021	X	X	X	X	X	1
	Nomada kohli	HQ948035	X	X	X	X	X	1
	Nomada discedens	-	-	-	X	-	X	4
	Nomada sheppardana	-	X	X	X	X	X	4
	Nomada furva group sp2	-	-	-	-	-	X	2
	Nomada furva group sp3	-	-	-	X	-	-	2
	Nomada furva group sp4	-	-	-	X	-	-	2
	Nomada furva group sp5	-	-	-	X	-	-	2
	Nomada okubira	OM722170	-	-	-	-	-	2
	Nomada posthuma	KJ837409	X	X	X	X	X	1
	Nomada nipponica	OM722168	-	-	-	-	-	2
	Nomada armata	OM722152	-	-	-	-	-	3
	Nomada femoralis	HM401070	X	X	X	X	X	1
	Nomada mutabilis	KJ837610	X	X	X	X	X	1

Nomada fuscicornis	HM401074	X	X	X	X	X	1
Nomada ginran	OM722160	-	-	-	-	-	2
Nomada aswensis	OM722153	-	-	-	-	-	5
Nomada taicho	-	-	-	-	-	-	2
Nomada kaguya	OM722165	-	-	-	-	-	2
Nomada atroscutellaris	KJ838079	X	X	X	X	X	1
Nomada hakonensis	-		-	X	-	X	2
Nomada flavoguttata	OM722158	-	-	-	-	-	3
Nomada castellana	KJ838402	X	X	X	X	X	1
Nomada conjungens	KJ837916	X	X	KC798366	X	X	1
Nomada nobilis	KJ836654	X	X	X	X	X	1
Nomada fabriciana	GU706016	X	X	KC798368	X	X	1
Nomada opaca	KJ837130	X	X	X	X	X	1
Nomada maculata	FJ582396	GU245030	GU245206	AF344609	GU245487	GU245662	1
Nomada hirtipes	GU706039	X	X	X	X	X	1
Nomada signata	KJ839435	KF512695	GU245207	KC798377	KF512704	KF512709	1
Nomada panzeri orientis	-	-	-	-	-	-	2
Nomada ferruginata	KJ839795	KF512693	KF512698	KC798369	KF512702	KF512707	1
Nomada panzeri	KJ839787	KF512696	KF512700	KC812731	KF512705	KF512710	1
Nomada merceti	MN938949	MN929005	X	MN917448	X	X	1
Nomada flava	KT074067	KF512692	KF512697	KC798367	KF512701	KF512706	1
Nomada leucophthalma	HQ948036	KF512694	KF512699	KC798372	KF512703	KF512708	1
Nomada vicina	FJ582409	-	-	-	-	-	1
Nomada alboguttata	OM722151	-	-	-	-	-	3
Nomada melathoracica	HQ948037	X	X	X	X	X	1
Nomada fulvicornis	KJ839458	X	X	KC798370	X	X	1
Nomada fulvicornis jezoensis	OM722159	-	-	-	-	-	2
Nomada guttulata	KJ837259	X	X	X	X	X	2
Nomada fervens	OM722157	-	-	-	-	-	2
Nomada mutica	KJ838713	X	X	X	X	X	1
Nomada rhenana	KJ838920	X	X	X	X	X	1
Nomada zonata	HM401090	X	X	X	X	X	1
Nomada marshamella	OM722167	-	-	-	-	-	3
Nomada striata	OM722173	-	-	-	-	-	3
Nomada ruficornis	OM722172	-	-	-	-	-	3
Nomada fusca	-	X	-	-	-	-	2
Nomada symphyti	KJ839448	X	X	X	X	X	1
Nomada villosa	KJ836696	X	X	X	X	X	1
Nomada obscura	OM722169	-	-	-	-	-	3
Nomada icazti	OM722163	-	-	-	-	-	2
Nomada harimensis	OM722162	-	-	-	-	-	5

Nomada sabensis	-	-	-	-	-	-	2
Nomada calloptera	OM722154	-	-	-	-	-	2
Nomada shirakii	X	-	-	-	-	-	5
Nomada abtana	-	X	-	X	X	-	5
Nomada maculifrons	-	-	-	-	-	-	2
Nomada pacifica	X	-	-	-	-	-	2

1: downloaded from NCBI; 2: This study; 3: Finnish Museum of Natural History, (*N. alboguttata*: http://id.luomus.fi/GJAA.549#1; *N. armata*: http://id.luomus.fi/GJAA.551#1; *N. flavoguttata*: http://id.luomus.fi/GJAA.504#1; *N. goodeniana*: http://id.luomus.fi/GJAA.377#1; *N. lathburiana*: http://id.luomus.fi/GJAA.393#1; *N. marshamella*: http://id.luomus.fi/GJAA.366#1; *N. obscura*: http://id.luomus.fi/GJAA.509#1; *N. roberjeotiana*: http://id.luomus.fi/GJAA.572#1; *N. ruficornis*: http://id.luomus.fi/GJAA.492#1; *N. striata*: http://id.luomus.fi/GJAA.588#1); 4: Jan Smit, personal collection; 5: Keiichi Otsui, personal collection.

Table 4. Primer used in this study

Gene	Direction	Primer	Sequences (5' – 3')	Reference
COI	F	LCO1490	GGT CAA CAA ATC ATA AAG ATA TTG G	Hebert et al., 2003
	R	HCO2198	TAA ACT TCA GGG TGA CCA AAA AAT CA	Hebert et al., 2003
EF-1α	F	EmphF2For	GCC TGG GTA TTG GAT AAG CTG AA	Sipes and Wolf, 2001
	R	EmphF2Rev	TGG ATT GTT YTT RGA GTC ACC AG	Sipes and Wolf, 2001
Nak	F	NaKfor2	GCS TTC TTC TCB ACS AAC GCC GTY GAR GG	Cardinal et al., 2010
	R	NaKrev2	ACC TTG ATR CCG GCY GAW CGG CAC TTG GC	Cardinal et al., 2010
Opsin	F	Opsin-For3(mod)	TTC GAY AGA TAC AAC GTR ATC GTN AAR GG	Almeida and Danforth, 2009
	R	Opsin-Rev(mod)	ATA NGG NGT CCA NGC CAT GAA CCA	Almeida and Danforth, 2009
Pol II	F	polfor2a	AAY AAR CCV GTY ATG GGT ATT GTR CA	Danforth et al., 2006
	R	polrev2a	AGR TAN GAR TTC TCR ACG AAT CCT CT	Danforth et al., 2006
Wingless	F	Wg-Collet-For	CAC GTG TCB TCB GRG ATG MGR SAG GA	Almeida and Danforth, 2009
	R	Lep-Wg2a-Rev	ACT ICG CAR CAC CAR TGG AAT GTR CA	Almeida and Danforth, 2009
COI 1	F	COI1F	TAT ATT ATT TTT GCT TTA TG	This study
(mod)	R	COI1R	AAT CAA AAW CTA ATA TTA TTY ATW C	This study
COI 2	F	COI2F	ATA GTD ATA CCW TTT ATA ATT G	This study
(mod)	R	COI2R	GAT AAT ART AAT AAA AYW GC	This study
COI 3	F	COI3F	GTW GAT TTD GCW ATT TTT TC	This study
(mod)	R	COI3R	TAA ATG TTG RTA TAA AAT WGG RTC	This study
EF-1α 1	F	EF1F	TAC GTT ACY ATC ATT GAT GC	This study
(mod)	R	EF1R	ATT TCT TCG AAT CGG CTT TC	This study
EF-1α 2	F	EF2F	TGG TAT TTC GAA AAA TGG ACA AAC C	This study

(mod)	R	EF2R	CAT TTT CCT TCA GTT TTG CC	This study
EF-1α 3	F	EF3F	AAA ATT GGT GGT ATC GGA ACG G	This study
(mod)	R	EF3R	AAC CAA CGT TGT CRC CGG GAA CAG C	This study
Nak 1	F	Nak1F	AAG GAG ATA CAC CAT TTC ATT CAC	This study
(mod)	R	Nak1R	GTC GGC TTC GAT GAT CTG ATT G	This study
Nak 2	F	Nak2F	CGG ATG GCS GCG AAG AAT TGT TTA G	This study
(mod)	R	Nak2R	CTC TCG GGT GCG CCC TTC ATC	This study
Nak 3	F	Nak3F	AGA TCG CCA CGY TGT GCA ACC GTG C	This study
(mod)	R	Nak3R	TCG GGT GCG CCC TTC ATC ACC	This study
Wng 1	F	Wng1F	ATG GTG AGC AAC ACG GAC CG	This study
(mod)	R	Wng1R	TAC CGT GAG TGC CGA GAA TGC	This study
Wng 2	F	Wng2F	TCT ACC TGG AGC CCT CGC CAC	This study
(mod)	R	Wng2R	TCG TCA CCT CCT GCG TCT TGT AG	This study
Opsin 1	F	Opsin1F	GTT TAG CTG GTA AGC CAT TG	This study
(mod)	R	Opsin1R	AAG TAT ACC CAC AAG CTG TAC	This study
Opsin 2	F	Opsin2F	CAA CGA ACT CCT TTT AGA TAT GTA C	This study
(mod)	R	Opsin2R	CAT GAG AGC AAC CTG GAA TKA TCG C	This study
Pol II 1	F	Pol1F	GTA AGA AAA ATG ACG AAG AGG	This study
(mod)	R	Pol1R	ACA AAG TAT ACC CAT GAC AAG	This study
Pol II 2	F	Pol2F	ACA TGA TAA GAA CTC ACA GTA CG	This study
(mod)	R	Pol2R	ATC GTT CAA AAT TCT GTT TAC TTG	This study
Pol II 3	F	Pol3F	ATT GGT ATC GGR GAC ACC ATT GC	This study
(mod)	R	Pol3R	AAT CGT CCT TGA TGA AAT GTG GCA G	This study

2.3. sequencing alignments

Using the SeqMan Pro version 7.1.0., raw sequence data were assembled, checked, and trimmed. All the sequences alignment of 6 genes was performed in MAFFT (Katoh et. al., 2013) version 7 (https://mafft.cbrc.jp/alignment/server/). All the sequences were adjusted in Mega 7 with amino acid translation option. Since the sequence of certain gene differed in length between NCBI data and newly obtained from this study, longer sequences were eliminated. The aligned sequences were combined using SequenceMatrix Windows ver. 1.8 (Vaidya et al., 2011).

2.4. Phylogenetic analyses

Phylogenetic analyses were performed using both Bayesian inference (BI) and Maximum likelihood (ML). Bayesian inference analysis was conducted with Mrbayes 3.2.7a (Ronquist et al., 2012). The best substitution model was selected for each partition under the Bayesian Information Criterion (BIC) using IQTREE (Trifinopoulos et. al., 2016). GTR+F+I+G4 for COI and Nak, TIM+F+I+G4 for ef1a and Wng, TIM3e+I+G4 for opsin, TIM2+F+I+G4 for Pol II were selected as the best fitting model. However, since TIM models were not able to use in MrBayes, GTR+I+G was used to run BI analysis except COI and Nak.

For Mrbayes analysis, we ran 20 million Markov chain Monte Carlo (MCMC) generations and trees were sampled every 100 generations. We ran one cold chain and three heated chains for each MCMC analysis. The first 2,000,000 sampled trees were discarded as burned in. The maximum likelihood analysis was performed using IQTREE (http://iqtree.cibiv.univie.ac.at/) (Trifinopoulos et. al., 2016). The best-fit

substitution model was automatically detected as GTR+F+I+G4 according to the Bayesian Information Criterion (BIC). Branch support was computed using the the UltraFast bootstrap approximation (UBS; Minh et al. 2013) with 1,000 replicates.

3. Results

The dataset used for the phylogenetic reconstruction contained 657 bp of COI, 709 bp of Ef1a, 1466 bp of Nak, 462 bp of Opsin, 843 bp of Pol2, 459 bp of Wng, for a total of 4596 bp of the nucleotide sequence. Phylogenies obtained through Bayesian inference from Mrbayes and Maximum Likelihood from iQtree indicate strong support for the monophyly of Nomadinae (BS=99, PP=100) as in the other analysis (Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018; Bossert et al., 2019). And the two trees showed largely congruent topologies except for a few nodes.

Melectini is sister to the remaining cleptoparasitic lineage with high resolution (BS=99, PP=100), and Each of the tribes Caenoprosopidini, Ammobatini, Ammobatoidini, Hexepeolini construct independent clades. We found support for the relationship among the tribes Isepeolini + Epeoloidini (sensu Sless et al., 2022) + Protepeolini (BS=100, PP=100) + Rhathymini + Ericrocidini (BS=100, PP=100), Brachynomadini + Epeolini (BS=93, PP=100), and Neolarrini + Hexepeolini + Nomadini (BS=97, PP=100).

The only different topology was found between BI and ML analyses which showed the slight tribal difference. In Bayesian inference (BI), *E. ainsliei* and *E. ilicis* constructed the subclade, while it is nested with *E. scutellaris*, *E. basili*, and *E.*

pusillus in Maximum Likelihood (ML).

The tribe Nomadini is strongly supported as monophyletic (BS=99, PP=100), and the tribe Hexepeolini is shown as its sister group. Although the monophyly of the tribe Nomadini is significantly conservative, there is an inaccuracy of previous designation of individual species into each species-group. According to this investigation, the *integra* species-group is showed as sister to the remaining species-groups and it formed an independent clade, as well as *sexfasciata* species-group, while most of other species-groups showed the paraphyly when classifications of Alexander (1994) and Mitai & Tadauchi (2007) were employed. The *erigeronis* species-group formed a subclade with *basalis* species-group, in addition with *N. tsunekiana*, *N. emarginata*, *N. flavopicta* that belonged to *ruficornis* species-group, and *sexfasciata* species-group was revealed as their sister group. With high supporting value (BS=94, PP=100), *Bifasciata* species-group formed subclade with *Nomada lathburiana* (Kirby, 1802) and *Nomada imbricata*, Smith 1854, which is described as *ruficornis* species-group. When it comes to the *armata* species-group, it is also revealed as paraphyletic due to the *Nomada kaguya* Hirashima, 1953 and *Nomada aswensis* Tsuneki, 1973 which is previously treated as *ruficornis* species-group and *Nomada taicho* Tsuneki, 1973, which belongs to the *furva* species-group according to the Alexander and Schwarz (1994). As a range of species which were arranged to *ruficornis* species-group radiated into multiple species-groups, a polyphyly of this species-group was confirmed in this study.

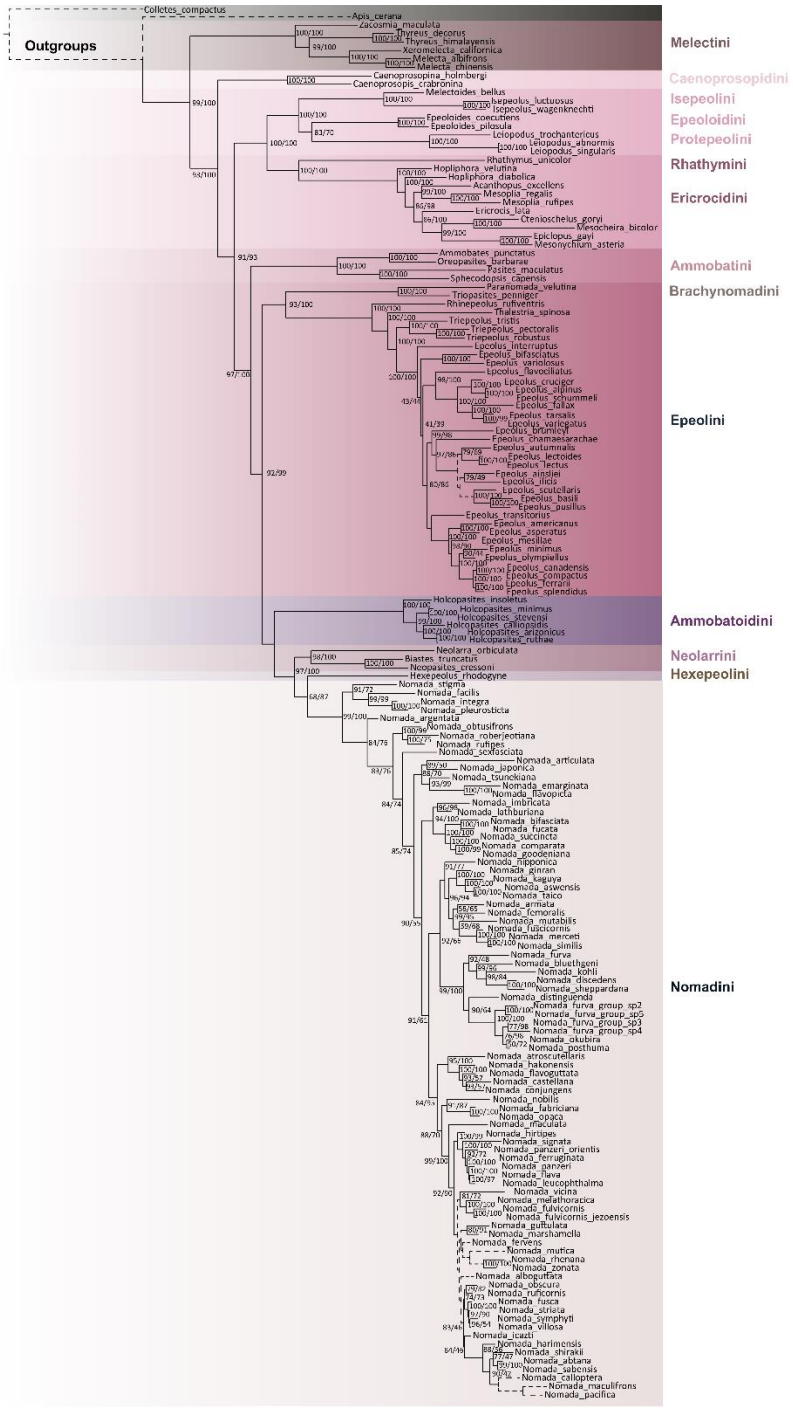

Fig 6. Phylogenetic trees (ML/ BI) of Nomadinae

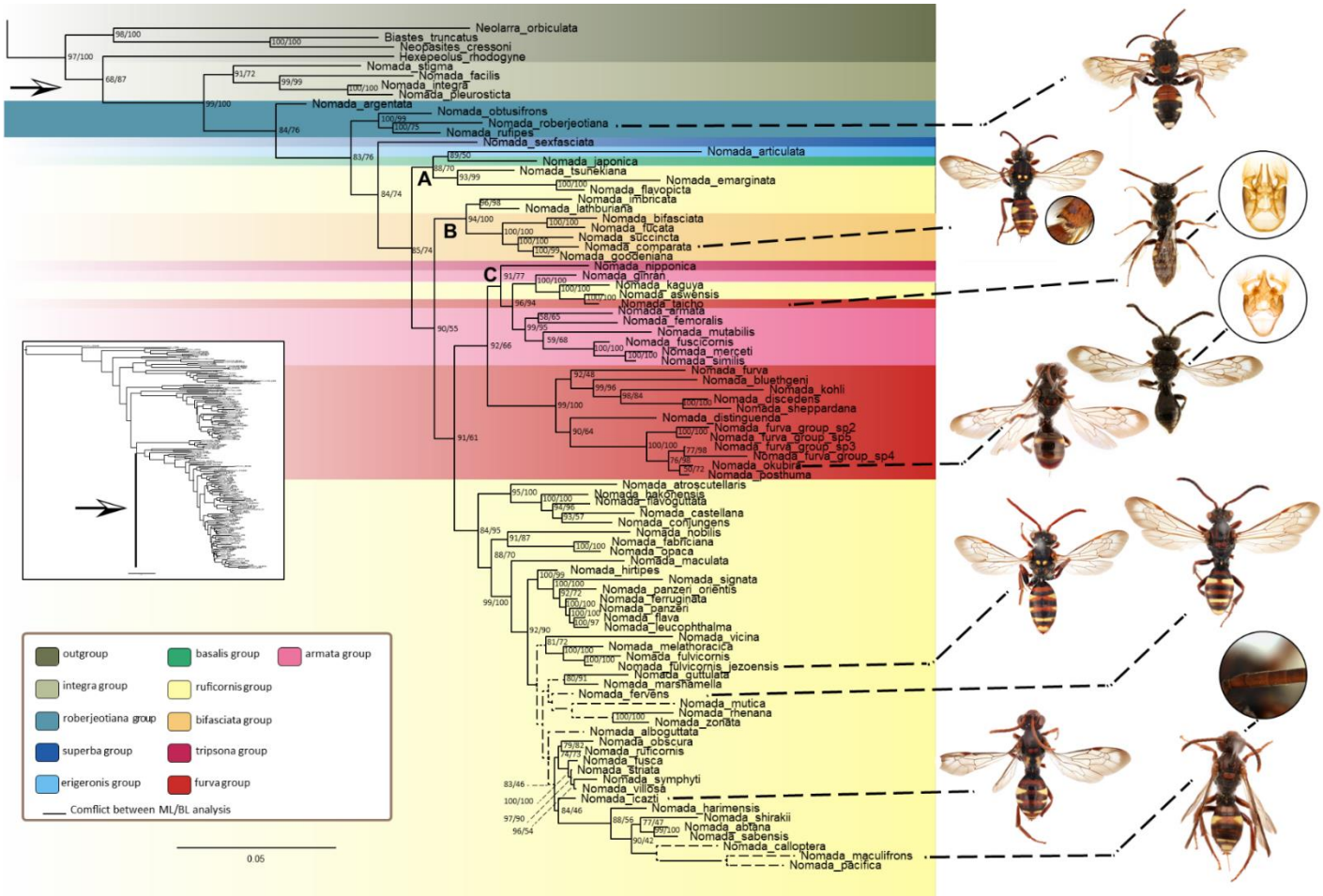

Fig 7. Phylogenetic trees (ML/ BI) of genus *Nomada*

4. Discussion

Phylogeny of Subfamily Nomadinae

Most of the tribal topologies from this study corresponds with the previous investigations (Sless et al., 2022, and the citations therein). The most difference from the preceded studies was the positioning of the tribe Caenoprosopidini, Ammobatoidini, and the positioning of the sister group in the tribe Nomadini and the clades construction of the species-group in genus *Nomada*. Firstly, the tribe Caenoprosopidini is located as sister to the tribes Isepeolini + Epeoloidini + Protepeolini in our study, while it belongs to the 'Nomadinae line' which are the combination of Caenoprosopidini, Ammobatini, Ammobatoidini, Brachynomadini, Epeolini, Hexepeolini, Neolarrini, and Nomadini by Sless et al (2022). Second, the tribe Ammobatoidini constructed a subclade with the tribe Neolarrini, Biastini, Hexepeolini, and Nomadini. However, it is located closest to the tribe Brachnomadini and Epeolini in Sless et al (2022). Also, the tribe Hexepeolini was inferred as the sister group of the tribe Nomadini. However, the possibility of which the tribe Ammobatoidini, Ammobatini, and Neolarrini to be the sister group of the tribe was also proposed in the previous investigation (Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018; Bossert et al., 2019; Sless et al., 2022). The discrepancy between our results and previous studies is likely due to the increased taxon sampling since the most prior studies on *Nomada* have not sampled sufficiently, making it difficult to infer the solid subclades.

Alexander firstly conducted species group classification in the genus *Nomada* in 1994. There has been a range of prior attempts to proceed with the comprehensive

reconstruction of the entire genus *Nomada*, but after he reconstructed the genus into 16 species groups via cladistic analysis, this classification has been commonly used in its morphological taxonomy (Alexander, 1994; Mitai & Tadauchi, 2007; Proshchalykin & Lelej, 2010; Smit, 2018). However, he mentioned that one of the species groups, the *ruficornis* species-group, maybe a paraphyletic group that belongs to a remnant of a more comprehensive clade without relatively distinct apomorphic subunits such as in *armata* and *basalis* group (Alexander, 1994; Mitai & Tadauchi, 2007). Because of this uncertainty, there was confusion about which species was included in which groups. For example, *Nomada ginran* Tsuneki, 1973 was treated as a *bifasciata* species group (Mitai & Tadauchi, 2004). However, it was reconstructed as a member of the *armata* species group later (Mitai & Tadauchi, 2007). Won also indicated in his PhD thesis that the *bifasciata* species group, *tripsona* species group, and partial *ruficornis* species group were not clearly congruent with the classification by Alexander (1994) using mitochondrial COI gene (Won, 2006). Nevertheless, he did not propose a newly modified classification. In Sless (2021), the largest number of *Nomada* was exploited to the phylogenetic analysis compared to the previous investigations but insufficient to resolve the species-group complexity. Species which belong to the six species-groups (*odontophora*, *roberjeotiana*, *armata*, *furva*, *panurgina* and *ruficornis*) were used in the investigation and *odontophora* species-groups located as basal group. In this study, the expanded multi-gene phylogeny confirmed discrepancy of previous classification and redesignation, or discussion will be discussed below.

4.1. Node A (Fig. 7)

Nomada tsunekiana Schwarz, 1999, which distributes only in Korea has been considered as *ruficornis* species-group. However, it formed a subclade with *basalis* and *erigeronis* species-group in this study. According to Alexander (1994), the diagnostic characters of *basalis* species-group were as followed: 1) mandible simple and round at tip; 2) first flagellum evidently longer than second or the first two flagella equal in length; 3) malar space closed posteriorly; 4) pygidial plate rounded; 5) margin of the hind tibia with dense straight hair. Among these characters, 2nd characteristic is the most distinctive character to distinguish the species group from the *ruficornis* species-group. In *N. tsunekiana*, most of the mentioned characters can be applied to its description except the 5th character because the setae are absent on its hind tibial setae. However, the species is more likely to be placed in the *basalis* species-group rather than the *ruficornis* species-group since it should have distinctly shorter first flagella to belong to the *ruficornis* species-group. Therefore, *N. tsunekiana*, *N. emarginata*, *N, flavopicta* should be moved to *basalis* species-group and the absent of hind tibial setae should be accepted as an exception because *N. emarginata* is also historically placed in *ruficornis* species-group and posses no setae on the hind tibiae (Smit, 2018). The complex of *basalis* and *erigeronis* species-group might be arisen due to the sampling limitation because only one species was used to each group for this study. Therefore, merging two groups into one species-group may be unnessecary.

Figure 8. *N. tsunekiana* female. left, antennae in ventral view; right, hind tibiae

4.2. Node B (Fig. 7)

The *bifasciata* species-group comprises 21 species worldwide and one of the well-known apomorphic characters is distinctly produced and backwardly curved setae, which is two to three in number on the margin of hind tibiae in female (Alexander, 1994). However, the species-group formed the subclade with *N. lathburiana*, and *N. imbricata*, which were placed in *ruficornis* species-group (Alexander, 1994), indicating the classification of *bifasciata* species-group may be modified because the apomorphic character for it can not be applied to these two species. For example, female of *N. lathburiana* possess three or four stout and straight setae (Smit, 2018), and female of *N. imbricata* have about three, posteriorly curved setae on their hind tibiae (Copyright Laurence Packer 2014 / Discover Life). Consequently, further investigation with the increased taxon sampling must be conducted to resolve these species-group complexes.

4.3. Node C (Fig. 7)

Expanded multi-gene phylogeny of this study supports the designation of *N. ginran* to *armata* species-group reconstructed by Mitai & Tadauchi, 2007 because the *N. ginran* forms the same clade with *Nomada armata* Herrich-Schäffer, 1839, which is the type species of the *armata* species-group. On the other hand, *N. aswensis* and *N. kaguya* have previously been treated as *ruficornis* species-group, and *N. nipponica*, which was previously treated as *tripsona* species-group, also formed the same clade with *N. armata*. Moreover, *N. taicho*, which has been considered as *furva* species-group by Alexander and Schwarz (1994), is nested in *armata* species-group (Fig. 7, node C). Therefore, it may be plausible to move *N. aswensis* and *N. kaguya* to *armata* species-group. Traditional *ruficornis* species-group has been considered to have evidently shorter first flagellum than second flagellum while it is nearly equal in length in *N. aswensis* female (Mitai & Tadauchi, 2007). Also, *N. kaguya* has similar morphological character with *N. aswensis* and *N. ginran* in that *N. kaguya* has stout setae and generally small-bodied which is less than 8mm (Won and Kim, 2013). However, its first flagellum evidently shorter than second one which indicates the flagellum length can not perfectly work as apomorphic character for *ruficornis* species-group and the redesignation of *ruficornis* species-group with vast samling of the East Palearctic species must be conducted. When it comes to the *N. taicho*, it should be moved into the *armata* species-group because of both morphological and molecular evidence. To be specific, it does not have strongly curved gonostylus with sinuate hair to be *furva* species-group according to the classification by Alexander (1994) and does not form the same subclade with the other species of *furva* species-

group.

5. Conclusion

In this study, the revision of of species-group in genus *Nomada* which is especially focused on the East Palearctic species was conducted. Most of the species-groups from the traditional classification by Alexander (1994) did not form monophyletic clade except the *integra* species-group. However, the discrepancy may be arisen not because the traditional classification is inaccurate, but because there are some exceptions in East paleartic species, particularly in Northeast Asian species since he examined limited collections of Tsuneki, the *Nomada* taxonomist from Japan. Therefore, the current classification must be expanded with those exceptions as it is described in discussion and some species should be moved to the appropriate species-group as follows: *N. tsunekiana, N. emarginata*, and *N, flavopicta* to *basalis* species-group; *N. aswensis*, *N. kaguya,* and *N. taicho* to *armata* species-group. When it comes to the *bifasciata* species-group complex, future study must be proceeded with a broad array of taxa to confirm if the two species, *N. lathburiana* and *N. imbricata* manifestly form an independent subclade with *basalis* species-group, or they are still nested in the group.

PART III. Harrison's rule corroborated for the body size of cleptoparasitic cuckoo bees (Hymenoptera: Apidae: Nomadinae) and their hosts

Abstract

Harrison's rule, that body size is positively correlated between parasites and hosts, has been reported in a range of taxa, but whether the rule is applicable to cleptoparasitic insects is poorly understood. Subfamily Nomadinae, the largest group of cleptoparasitic bees, usurp the nests of a variety of host bees. Within the subfamily, Nomada exploits the most diverse hosts, using at least ten genera from five families. Here, we reassess the phylogeny of Nomadinae, including the expanded sampling of the genus Nomada, to explore host shift fluctuations throughout their evolutionary history and test the applicability of Harrison's rule for the subfamily. Our phylogenetic results are mostly congruent with previous investigations, but we infer the tribe Hexepeolini as a sister taxon to the tribe Nomadini. Additionally, the results reveal discrepancies with the traditional classifications of Nomada. Ancestral state reconstruction of host use indicates that, early in their evolution, parasites used closer relatives, before attacking less related groups later. Lastly, we confirm Harrison's rule in Nomadinae, supporting that body size dynamics influence the host shifts of cleptoparasitic bees.

Keywords: *Nomada*, revision, new records, new species, the Korean Peninsula

1. Introduction

Most wild bees normally visit flowers to collect pollen, nectar, or floral oils to feed their offspring during development and they provide a critical ecosystem service through crops and wild plant pollination (Koh et al., 2016; Danforth et al., 2019). However, throughout their evolutional history, other solitary bees have lost this behavior and choose an easier strategy called 'Cleptoparasitism' (Michener, 2007). Subfamily Nomadinae s.l. (Bossert et al., 2019) (Hymenoptera: Apidae), which comprises the largest and the most diverse taxon in cleptoparasitic bees, do not build their nest. Instead, they usurp the nests of their host bees and lay their eggs in the collected pollen balls that the hosts provisioned for their offspring (Rozen, 2003). Thereafter, either the adult parasitic females or larvae with specialized mandible destroy the eggs of the hosts. Then the larvae consume the pollen until they become adults (Alexander, 1990).

How the entire Nomadinae bees select their hosts remains a question. Even though Tengö and Bergström (1977) documented that the chemical from Dufour's gland has considerable similarity between the genus *Nomada* male and its host female Andrena, if other chemical similarities exist within the cleptoparasitic bees has been poorly studied (Danforth et al., 2019). Not only the physiological factors but also other factors such as phenology and geographical restriction may contribute to the host specificity. For instance, *Nomada galloisi* which only inhabits Japan and South Korea is most active between late August and September (Won & Kim, 2013). Therefore, it cannot take *Andrena sublevigata* as a host, which is the host of *Nomada fervens* (Maeta et al., 1996), due to phenological mismatch since it emerges between late

March to May (Lee et al., 2015). Another example of host selection factor was provided by Vivallo and his colleagues (2019). Using the multivariate analysis, they inferred that new host-cleptoparasite interaction can be created once the geographical or biotic barriers are disappeared (Vivallo et al., 2019).

The host taxon spectrum of Nomadinae is considerably diverse. So far, myriad lineages such as family Andrenidae, Apidae, Colletidae, Halictidae, and Melittidae were recorded as its host (Danforth et al., 2019). Also, Nomadinae has various brood parasitism patterns. For instance, genera in the same tribe might infiltrate hosts in different families, while genera in different tribes might utilize the same host genera (Alexander, 1990). One of the examples of this phenomenon would be the tribe Nomadini, which is the largest genus of cleptoparasitic bees worldwide (Smit, 2018). The tribe has the vast host range in that it utilizes 10 genera of 5 families as hosts (Danforth et al., 2019). On the other hand, all the species which are belonged to the genus *Epeolus* are host-specific on the genus Colletes (Michener, 2007). The majority of the cleptoparasitic bees are single-species specialists, but some other species have 2 to 5 species as their hosts, which normally belong to the same genus (with an exception in the genus Sphecodes), and therefore they have resembled appearance, behavior, and ecology (Westrich, 1989; Maeta et al., 1996; Bogusch, 2003; Bogusch et al., 2006). Intriguingly, the case of different species using only one species as their host is hard to be seen. We can extrapolate it has been mediated from a niche overlap. Even though creating interaction with a new host species is challenging to parasites (Engelstädter and Fortuna, 2019), they may have needed to change hosts into different species to avoid competition which arouses from the niche overlap.

Indeed, host switching has occurred frequently within insects (Habermannová et al., 2013; Hovestadt et al., 2019). For many insects, a switch to a new host indicates that they might face different ecological conditions and biotic interaction, such as competition, from the ancestral hosts (Messina, 2004). And during this parasitic lifestyle, the different conditions may contribute to structural alterations of insects (Wcislo, 1999; Messina, 2004). Those phenomena have been actively reported in insects such as morphological alteration of rostra which acts as a crucial role for oviposition in weevil (Wilhelm et al., 2011), showing various body forms according to different plants feeding in *Nemoria arizonaria* Grote (Greene, 1989), and remarkable structural difference in antennae and labial sensilla between phytophagous and predatory stink bugs (Li et al., 2021).

In female parasitic bees, they have converged on a morphological structure that are enlarged heads, elongated mandible in larvae, and lacking pollen-collecting structure (Wcislo, 1999). Another trait that can be influenced during this alteration would be body size. Interestingly, the body size range within Nomadinae is remarkable, from 2.2mm in *Oreopasites barbarae* to 23mm in *Acanthopus excellens* and larger in others (Schrottky, 1902; Rozen, 1992). This variation may be arisen by the host solitary bee parasitized by Nomadinae because the body size of offspring in solitary bees correlates with the size of pollen balls made by the mothers (Radmacher and Strohm, 2010). This hypothesis is previously proposed in Nomadinae by Rozen (1965). He suggested that the size of an adult parasitic bee depends on the size of the host (Rozen, 1965) and Michener also insisted that the parasitic habit may be associated with rapid morphological divergence (Michener, 2007). However, whether

the morphological structure of the host indeed affects the morphological alteration in cleptoparasitic bees remains still speculative.

This study addresses mainly on Nomadinae and its host body size fluctuation, with expecting that there is an evolutionary trend between body size transition in host-cleptoparasite interaction. To elucidate previously mentioned hypothesis, phylogenetic analysis is a prerequisite process because how body size increases or decreases in Nomadinae can only be differentiated when the phylogenetic investigation of the clade is established (Gould et al., 2004). Therefore, actual allometric measurement and multi-gene phylogenetic investment were conducted in this study, especially with expanding taxon of genus *Nomada*, which has the vast host diversity and is the largest genus of cleptoparasitic bees (Smit, 2018; Danforth et al., 2019).

2. Materials and Methods

2.1. Taxon sampling

In total, we used 104 species for the ingroup. For the outgroup, *Apis cerana* and *Colletes compactus* were selected to represent a range of relatedness and performed well in pilot analyses, compared to the relationships recovered in a recent phylogenomic analysis (Sless et al., 2022). Sequences for 71 species from published papers were taken from NCBI, and we newly added 35 species that have not been analyzed in previous phylogenetic investigations. To minimize missing data and ensure better resolution in the phylogenetic tree, we used sequence data only if the number of available genes was greater than or equal to three. The aim of the sampling

was to use species that have both host and body size information without bias. When species did not fulfill this condition, they were excluded from this study. However, we made exceptions where necessary to ensure that the resultant phylogenetic reconstructions were reliable, with reference to prior works informing our choices (Branstetter et al., 2017; Sless et al., 2022).

We placed special focus on sampling the genus *Nomada* as it has highly-diverse host records (Sless et al., 2022). Specifically, we expanded the sampling of the *furva* species-group because they are distinctly small-bodied and the parasite of genus *Lasioglossum* (Hymenoptera: Halictidae). Two species, *N. aswensis*, and *N. kaguya*, which belong to the *ruficornis* species-group but show similar biology with the *furva* species-group, were also included in this study. We included two type species, *N. ruficornis* from *ruficornis* species-group and *Nomada armata* from *armata* species-group, to fully investigate the composition of these species-group concepts by Alexander (1994), although greater sampling is necessary to fully define the species-groups (Odanaka et al., 2022). The study used DNA samples of Finnish *Nomada* species from the Genomic Resources collection (https://laji.fi/en/theme/luomusgrc/instructions) of the Finnish Museum of Natural History Luomus (https://www.luomus.fi/en), and the HTTP-URIs of the DNA samples are listed in Table 5. In total, our sampling of the genus *Nomada* represents seven of the 16 species-groups, including a range of host information in three families representing Apidae, Andrenidae, and Halictidae. We could not represent all family-level hosts for this group because there are few species attacking some groups, such as Melittidae, and they were more difficult to sample. DNA extraction, PCR

amplification, and sequencing alignment process is entirely congruent with Part II.

Table 5. List of the Subfamily Nomdinae for this study.

Tribe	Species	Host	GeneBank accession number						Specimen Reference
			COI	EF1α	Nak	Opsin	PolII	Wingless	
Outgroup	*Colletes compactus*	N.A.	DQ872684	DQ884642	MN367513	DQ884542	MN367595	DQ884794	1
	Apis cerana	N.A.	KM242593	EU184774	EU184750	AB355818	EU184733	EU184716	1
Melectini	*Zacosmia maculata*	B	MN344989	AY585117	GU245117	AF344637	AY945176	GU245570	1
	Thyreus decorus	B	OM722174	OM906191	OM906168	OM906113	OM906140	OM850366	2
	Xeromelecta californica	B	MK919652	GU244955	GU245116	AF344613	GU245407	GU245569	1
	Melecta albifrons	B	MK919610	GU244998	GU245120	HM211837	GU245409	GU245573	1
	Melecta chinensis	B	OM722175	-	OM906169	OM906114	OM906141	OM850367	2
Caenoprosopidini	*Caenoprosopina holmbergi*	D	MK919570	GU244983	GU245194	GU245325	GU245476	GU245650	1
	Caenoprosopis crabronina	A	MK919571	GU245020	GU245195	GU245326	GU245477	GU245651	1
Isepeolini	*Melectoides bellus*	B	MK919611	GU244999	GU245115	HM211836	GU245406	GU245568	1
	Isepeolus luctuosus	C	KX821019	GU244953	GU245113	GU245277	GU245404	GU245566	1
	Isepeolus wagenknechti	N.A.	KX821183	GU244954	GU245114	GU245278	GU245405	GU245567	1
Epeoloidini	*Epeoloides coecutiens*	E	MK919586	GU244987	GU245131	HM211838	GU245418	GU245584	1
	Epeoloides pilosula	E	JN293445	GU244966	GU245129	GU245287	GU245416	GU245582	1
Protepeolini	*Leiopodus trochantericus*	B	MK919603	GU244970	GU245136	GU245291	GU245422	GU245589	1
	Leiopodus abnormis	B	X	GU244969	GU245135	GU245290	GU245421	GU245588	1
	Leiopodus singularis	B	X	AY585113	GU245133	AF344624	AY945137	GU245586	1
Rhathymini	*Rhathymus unicolor*	B	X	GU244973	GU245139	GU245294	GU245425	GU245592	1
Ericrocidini	*Hopliphora velutina*	N.A.	MK919599	GU244939	GU245086	GU245258	GU245379	GU245539	1
	Hopliphora diabolica	B	KY084893	KY084881	X	KY084866	KY084853	X	1
	Acanthopus excellens	A	KY084889	KY084876	X	KY084863	KY084849	X	1
	Mesoplia regalis	B	KY084901	KY084887	X	KY084871	KY084859	X	1
	Mesoplia rufipes	B	MK919618	GU244938	GU245085	GU245257	GU245378	GU245538	1
	Ericrocis lata	B	MN345705	GU244936	GU245083	GU245255	GU245376	GU245536	1
	Ctenioschelus goryi	N.A.	KY084892	GU244941	GU245088	GU245260	GU245381	GU245541	1
	Mesocheira bicolor	B	MK919616	GU244940	GU245087	GU245259	GU245380	GU245540	1
	Epiclopus gayi	B	MK919589	GU244935	GU245082	GU245254	GU245375	GU245535	1
	Mesonychium asteria	B	KY084898	GU244937	GU245084	GU245256	GU245377	GU245537	1
Ammobatini	*Ammobates punctatus*	B	KJ838996	GU245011	GU245179	HM211841	GU245463	GU245635	1
	Oreopasites barbarae	A	MK919624	GU245008	GU245176	AF344626	GU245460	GU245632	1
	Pasites maculatus	D	MN344150	GU245035	GU245180	HM211842	GU245464	GU245636	1
	Sphecodopsis capensis	C	MK919639	GU245009	GU245177	GU245317	GU245461	GU245633	1
Brachynomadini	*Paranomada velutina*	B	MK919627	AY585115	GU245190	AF344627	AY945154	GU245646	1
	Triopasites penniger	B	MK919650	GU245018	GU245191	AF344633	GU245473	GU245647	1
Epeolini	*Rhinepeolus rufiventris*	N.A.	MK919638	GU245027	GU245202	GU245331	GU245483	GU245658	1
	Thalestria spinosa	A	MN342317	GU245024	GU245199	GU245328	GU245480	GU245655	1
	Triepeolus tristis	B	MN342316	MN367540	MN367496	MN367458	MN367574	MN367661	1

	Triepeolus pectoralis	B	MN343742	MN367539	MN367495	MN367446	MN367581	MN367659	1
	Triepeolus robustus	N.A.	MK919585	GU245023	GU245198	AF344634	AY945170	GU245654	1
	Epeolus chamaesarachae	C	MH089974	MN367522	MN367484	MN367461	MN367573	MN367638	1
	Epeolus interruptus	C	MH089961	MN367536	MN367494	MN367457	MN367571	MN367654	1
	Epeolus flavociliatus	C	MN342311	MN367528	MN367482	X	MN367580	MN367658	1
	Epeolus cruciger	C	MN342321	MN367525	MN367479	MN367459	MN367579	MN367652	1
	Epeolus schummeli	C	MN342314	MN367526	MN367480	KC798351	MN367577	MN367653	1
	Epeolus tarsalis	C	MN342315	MN367527	MN367481	MN367460	MN367578	MN367655	1
	Epeolus variegatus	C	MK919587	GU244988	GU245203	HM211846	GU245484	GU245659	1
	Epeolus bifasciatus	C	MH089986	MN367535	MN367500	MN367462	MN367575	MN367649	1
	Epeolus brumleyi	C	MH089901	MN367538	MN367493	MN367456	MN367576	MN367657	1
	Epeolus scutellaris	C	HQ552250	GU245022	GU245197	AF344596	GU245479	GU245653	1
	Epeolus basili	C	MH090001	MN367532	MN367497	MN367444	MN367557	MN367636	1
	Epeolus pusillus	C	MH089868	MN367533	MN367498	MN367445	MN367558	MN367637	1
	Epeolus autumnalis	C	MH089931	MN367534	MN367499	MN367441	MN367562	MN367640	1
	Epeolus ainsliei	C	MH089843	MN367531	MN367478	MN367440	MN367561	MN367639	1
	Epeolus lectoides	C	MH090009	MN367529	MN367476	MN367442	MN367560	MN367641	1
	Epeolus lectus	C	MH089993	MN367530	MN367477	MN367443	MN367559	MN367642	1
	Epeolus transitorius	C	MN342320	MN367537	MN367483	MN367463	MN367572	MN367656	1
	Epeolus asperatus	C	MH090008	MN367514	MN367491	MN367454	MN367570	MN367660	1
	Epeolus mesillae	C	MH089889	MN367515	MN367490	MN367455	MN367569	MN367651	1
	Epeolus minimus	C	MH090003	MN367518	MN367492	MN367452	MN367568	MN367646	1
	Epeolus olympiellus	C	MH089905	MN367517	MN367489	MN367453	MN367566	MN367647	1
	Epeolus canadensis	C	MH089848	MN367516	MN367485	MN367451	MN367567	MN367643	1
	Epeolus compactus	C	MH089882	MN367521	MN367487	MN367450	MN367565	MN367645	1
	Epeolus ferrarii	C	MH089922	MN367519	MN367486	MN367448	MN367563	MN367644	1
	Epeolus splendidus	C	MH089954	MN367520	MN367488	MN367449	MN367564	MN367648	1
Ammobatoidini	*Holcopasites insoletus*	A	X	GU245014	GU245184	GU245320	GU245467	GU245640	1
	Holcopasites minimus	A	X	GU245016	GU245187	GU245322	GU245470	GU245643	1
	Holcopasites stevensi	A	X	GU245015	GU245186	GU245321	GU245469	GU245642	1
	Holcopasites calliopsidis	A	MK919598	GU245012	GU245182	AF344600	GU245465	GU245638	1
	Holcopasites arizonicus	A	X	GU245013	GU245183	GU245319	GU245466	GU245639	1
	Holcopasites ruthae	A	X	AY585112	GU245181	AF344602	AY945124	GU245637	1
Neolarrini	*Neolarra orbiculata*	N.A.	MK919620	GU245029	GU245205	GU245333	GU245486	GU245661	1
	Biastes truncatus	D	MK919567	GU244981	GU245189	HM211844	GU245472	GU245645	1
	Neopasites cressoni	D	MK919621	GU245017	GU245188	GU245323	GU245471	GU245644	1
Hexepeolini	*Hexepeolus rhodogyne*	A	MK919597	GU245028	GU245204	GU245332	GU245485	GU245660	1
Nomadini	*Nomada roberjeotiana*	A	OM722171	OM906187	OM906164	OM906109	OM906136	OM850362	3
	Nomada japonica	A	OM722164	OM906181	OM906157	OM906103	OM906129	OM850356	2
	Nomada lathburiana	A	OM722166	OM906183	OM906159	OM906105	OM906131	OM850358	3
	Nomada succincta	A	EU678368	X	X	KC798375	OM906142	OM850368	2
	Nomada comparata	A	OM722155	OM906173	OM906148	OM906094	OM906120	OM850348	2
	Nomada goodeniana	A	OM722161	OM906179	OM906154	OM906100	OM906126	OM850353	2

Nomada distinguenda	D	OM722156	OM906174	X	OM906095	OM906121	-	2
Nomada discedens	D	-	-	OM906149	X	OM906143	X	4
Nomada okubira	D	OM722170	OM906186	OM906163	-	OM906135	OM850361	2
Nomada nipponica	A	OM722168	-	OM906161	OM906107	OM906133	-	2
Nomada armata	A	OM722152	OM906171	OM906145	-	OM906117	-	3
Nomada ginran	A	OM722160	OM906178	OM906153	OM906099	OM906125	OM850352	2
Nomada aswensis	D	OM722153	OM906172	OM906146	OM906092	OM906118	-	5
Nomada kaguya	D	OM722165	OM906182	OM906158	OM906104	OM906130	OM850357	2
Nomada flavoguttata	A	OM722158	OM906176	OM906151	OM906097	OM906123	OM850350	3
Nomada maculata	A	FJ582396	GU245030	GU245206	AF344609	GU245487	GU245662	1
Nomada signata	A	KJ839435	KF512695	GU245207	KC798377	KF512704	KF512709	1
Nomada ferruginata	A	KJ839795	KF512693	KF512698	KC798369	KF512702	KF512707	1
Nomada panzeri	A	KJ839787	KF512696	KF512700	KC812731	KF512705	KF512710	1
Nomada flava	A	KT074067	KF512692	KF512697	KC798367	KF512701	KF512706	1
Nomada leucophthalma	A	HQ948036	KF512694	KF512699	KC798372	KF512703	KF512708	1
Nomada alboguttata	A	OM722151	OM906170	OM906144	OM906091	OM906116	OM850346	3
Nomada fulvicornis jezoensis	N.A.	OM722159	OM906177	OM906152	OM906098	OM906124	OM850351	2
Nomada fervens	A	OM722157	OM906175	OM906150	OM906096	OM906122	OM850349	2
Nomada marshamella	A	OM722167	OM906184	OM906160	OM906106	OM906132	OM850359	3
Nomada striata	A	OM722173	OM906190	OM906167	OM906112	OM906139	OM850365	3
Nomada ruficornis	A	OM722172	OM906188	OM906165	OM906110	OM906137	OM850363	3
Nomada obscura	A	OM722169	OM906185	OM906162	OM906108	OM906134	OM850360	3
Nomada icazti	N.A.	OM722163	-	OM906156	OM906102	OM906128	OM850355	2
Nomada harimensis	N.A.	OM722162	OM906180	OM906155	OM906101	OM906127	OM850354	5
Nomada calloptera	A	OM722154	-	OM906147	OM906093	OM906119	OM850347	2
Nomada shirakii	A	x	OM906189	OM906166	OM906111	OM906138	OM850364	5

* -, unpublished; x, unavailable.

A: Andrenidae; B: Apidae; C: Colletidae; D: Halictidae; E: Melittidae.

1: downloaded from NCBI; 2: This study; 3: Finnish Museum of Natural History, (*N. alboguttata*: http://id.luomus.fi/GJAA.549#1; *N. armata*: http://id.luomus.fi/GJAA.551#1; *N. flavoguttata*: http://id.luomus.fi/GJAA.504#1; *N. goodeniana*: http://id.luomus.fi/GJAA.377#1; *N. lathburiana*: http://id.luomus.fi/GJAA.393#1; *N. marshamella*: http://id.luomus.fi/GJAA.366#1; *N. obscura*: http://id.luomus.fi/GJAA.509#1; *N. roberjeotiana*: http://id.luomus.fi/GJAA.572#1; *N. ruficornis*: http://id.luomus.fi/GJAA.492#1; *N. striata*: http://id.luomus.fi/GJAA.588#1); 4:

Jan Smit, personal collection; 5: Keiichi Otsui, personal collection.

2.2. Phylogenetic analyses

Phylogenetic analyses were performed using both Bayesian inference (BI) and Maximum likelihood (ML). The Bayesian inference analysis was conducted with MrBayes 3.2.7a (Ronquist et al., 2012). The best substitution model for BI was selected for each partition under the Bayesian Information Criterion (BIC) using ModelFinder in IQTREE and the same protocol was used in searching for the best substitution model for ML (Nguyen et al., 2015; Kalyaanamoorthy et al., 2017). GTR+F+I+G4 for COI, TIMe+I+G4 for ef1α, TIM3+F+I+G4 for Nak, TIM3e+I+G4 for Opsin, TIM2+F+I+G4 for PolII, and TIM+F+I+G4 for Wng were selected as the best fitting models for BI. For ML, GTR+F+I+G4 for COI, TIM+F+I+G4 for ef1α, TIM3+F+I+G4 for Nak, TIM3e+I+G4 for Opsin, TIM2+F+I+G4 for PolII, TIM+F+I+G4 for Wng were selected (Chernomor et al., 2016). However, since TIM models cannot be used in MrBayes, GTR+I+G was used to run the BI analysis except COI. For the MrBayes analysis, we ran 20 million Markov chain Monte Carlo (MCMC) generations and trees were sampled every 100 generations. We ran one cold chain and three heated chains for each MCMC analysis. The first two million sampled trees were discarded as burn-in. Branch support for the maximum likelihood analysis was computed using the UltraFast bootstrap approximation (UBS; Hoang et al., 2017) with 1,000 replicates.

2.3. Size allometry

We measured two traits of the Nomadinae and their hosts. One is the intertegular distance (minimum distance between the tegulae), which is a useful estimator for the size of bees (Cane et al., 1987). The other is total body length, which was measured

as the maximum length distance from the head to end of the final tergite exclusive of exserted stingers or genitalia. (if curled, this was accounted for using a multi-stage measurement). In total, we obtained about 1,300 body size data from Nomadinae and their hosts (Body length: 73; ITD: 65 out of 106 species of Nomadinae and their corresponding hosts). Among them, we used specimens of 24 species (host: 7, Nomadinae: 17) and prepared photographs using the Microscope (DM 4000B, Leica Microsystem, Wetzlar, Germany) with a USB digital camera (Infinity3, Lumenera Corporation, Ottawa, Ontario) and measured the value of the traits using the measurement option. Since there can be a size difference between male and female bees, measurements were only taken from females. We also collected data from literature such as taxonomic papers, online-accessible specimen photographs in museums, or from taxonomists. The number of measured individuals was different per species because we gathered the data from various sources. Therefore, we used the average value of measurements for the data analysis. Linear regressions were conducted using SPSS Statistics 25 (IBM, Armonk, NY, USA) to gauge the dependence of nomadine body length on host body length, as well as nomadine ITD on host ITD.

2.4. Ancestral character state reconstruction

The host information of each species in Nomadinae was extracted from various literature. In case the multiple species were reported as hosts, the data was prioritized when the parasitic larvae were found in their nest or direct intrude of the parasite to the host nests were recorded in observation. However, when the confirmation was absent, data arose from phenological synchrony between parasites and hosts, or

discussion from taxonomists was used.

The host of Nomadinae was coded as five discrete states by families: (A) Andrenidae, (B) Apidae, (C) Colletidae, (D) Halticidae, and (E) Melittidae. The evolutionary history of host use was mapped on a single tree with a parsimony approach. Trace character history option in Mesquite 3.31 (Maddison & Maddison, 2017) was adopted. The probability of the ancestral state of each node was calculated by Bayestraits v3.0 (Meade & Pagel, 2017) using reversible jump Markov Chain Monte Carlo (RJ-MCMC). An exponential distribution was implemented, seeding from a uniform prior in an interval of 0 - 100. We ran 50 million iterations, sampling every 1,000th iterations. The first million iterations were discarded as burn-in. Acceptance rates were automatically adjusted and achieved in the preferred range of near 35% (Pagel et al., 2016). Parsimony ancestral state reconstruction were performed using the Mesquite v3.70 (Maddison & Maddison, 2021) to trace fluctuation of intertegular distance and body size between hosts and parasites.

3. Results

3.1. Phylogenetic analysis

Regarding taxon sampling, we targeted species that have both host and body size information without bias. In total, 106 species including 2 species for the outgroup and 104 species for the ingroup were used. We extracted novel sequences from 35 species, and 71 species were obtained from NCBI (Table 5). About 30% of ingroup taxa belong to *Nomada*, which has an relatively unstable phylogenetic position and possesses the most host information in the subfamily. The dataset used for

phylogenetic reconstruction contained a total of 4590 bp (657 bp of COI, 709 bp of Ef1α, 1463 bp of Nak, 459 bp of Opsin, 843 bp of PolII, 459 bp of Wng). Phylogenies obtained through Bayesian inference (BI) from MrBayes and maximum likelihood (ML) from IQtree indicate strong support for the monophyly of Nomadinae (Bayesian posterior probability, PP=100, Maximum likelihood bootstrap values, BS=99) (Fig. 9).

Melectini was recovered sister to the remaining cleptoparasitic lineages with high support (PP=100, BS=98) (Fig. 9). Each of the tribes Caenoprosopidini, Ammobatini, Ammobatoidini, Hexepeolini represented independent clades. We found support for the relationship among the tribes Isepeolini + Epeoloidini (sensu Sless et al., 2022) + Protepeolini (PP=100, BS=100,) + Rhathymini + Ericrocidini (PP=100, BS=100), and Brachynomadini + Epeolini (PP=100, BS=94). The BI and ML trees showed largely congruent topologies except for a few nodes (Fig. 9). Topological differences between BI and ML analyses were found in the tribes Caenoprosopidini, Epeolini, and Nomadini. The tribe Caenoprosopidini was placed sister to Isepeolini + Epeoloidini + Protepeolini in BI, while it was sister to Ammobatini in ML.

The tribe Epeolini formed a distinct monophyletic clade (PP=100, BS=100), but some differences between analyses existed within the group. For example, in BI, *Epeolus bifasciatus* formed a subclade with *E. brumleyi*, *E. scutellaris*, *E. basili*, *E. pusillus*, *E. autumnalis*, *E. ainsliei*, *E. lectoides*, and *E. lectus*. However, *E. bifasciatus* grouped with *E. interruptus* in ML. *Epeolus transitorius* was sister to a subclade including *E. asperatus* in BI, but the species was recovered closer to *E. flavociliatus* in ML. *Epeolus chamaesarachae* was recovered as sister to remaining subclades in the tribe

with high support in BL (PP=100), but the species was adjacent to the *E. autumnalis* subclade in ML (BS=88). The remainings are largely congruent with the result in Part II.

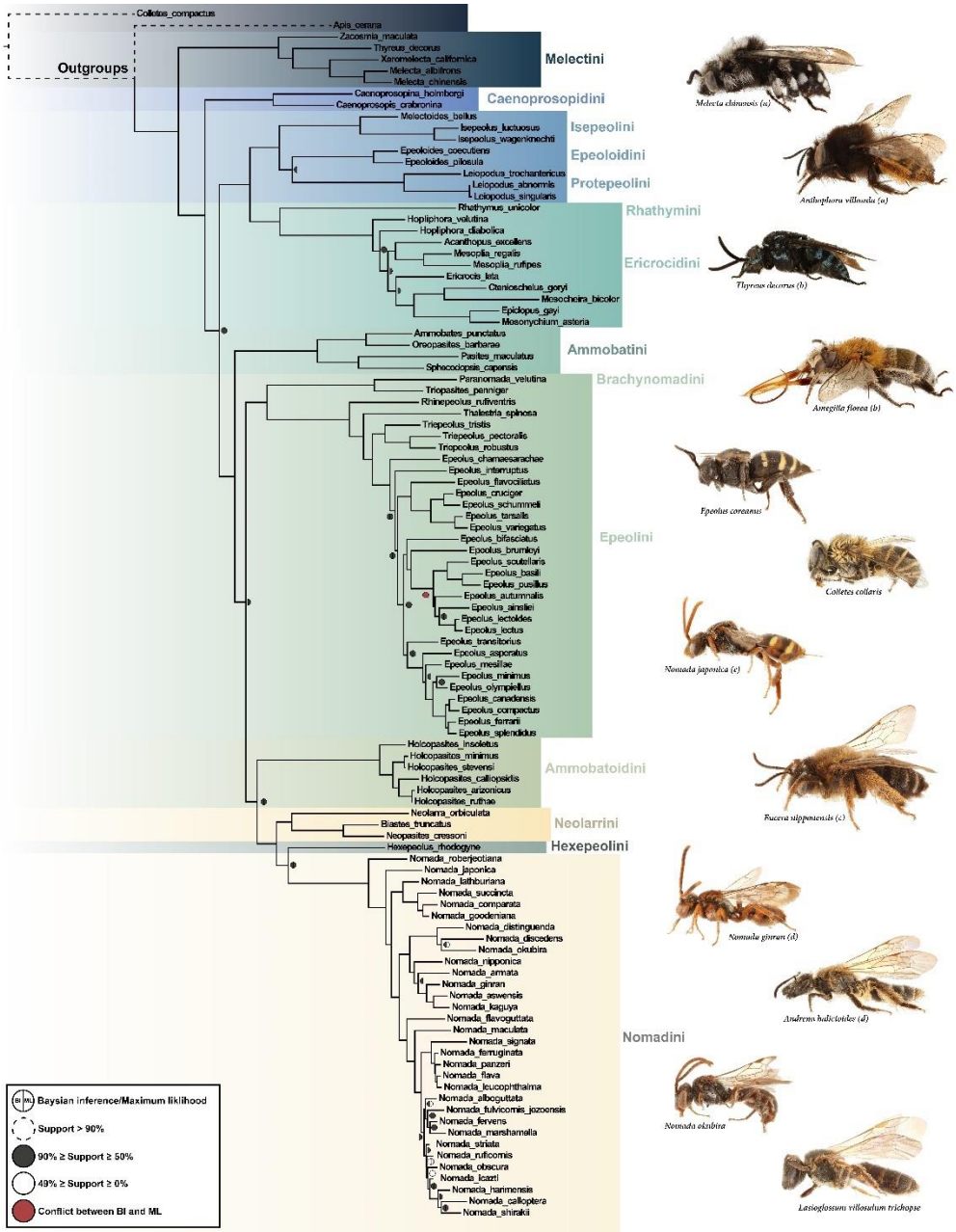

Figure 9. Combined Phylogenetic tree of Nomadinae. Produced with MrBayes. Colors of circles on the node indicate bootstrap supporting values, and the one topological difference between BI and ML trees is presented as a red circle. The tribal classification followed (Sless et al., 2022). Habitus images of cuckoo bees was conducted by Kayun Lim.

3.2. Ancestral state reconstruction and host shift

The ancestral states of host use in Nomadinae were analyzed at the family level to enable easier interpretation of the results, avoid an overestimation of shifts, and accommodate program analytical limits. Except for a few nodes, parsimony and RJ-MCMC analyses were largely congruent. According to the Bayestraits analysis, the common ancestral host of subfamily Nomadinae was the family Apidae, with a probability of ~63% (Fig. 10). This host family is also inferred as the ancestral host for multiple lineages in Nomadinae. Additionally, we found that the host use of Apidae by Melectini, Ericrocidini, Ammobatoidini was conserved. On the other hand, frequent reversal host shifts between Apidae and Andrenidae were detected. After the first reversal host transition from Andrenidae to Apidae happened in the tribal combination of Isepeolini + Parepeolini + Protepeolini + Rathymini + Ericrocidini, host switching also occurred from Apidae to Colletidae and Melittidae (Fig. 10). The common ancestral host of Epeolini was reconstructed as Family Apidae with a probability of ~62%. However, a host switch to the family Colletidae in the genus *Epeolus* was observed with a probability of >99%.

In the clade of Ammobatoidini + Neolarrini + Hexepeolini + Nomadini, their common ancestral host use was yielded as Family Andrenidae with a probability of

>96% (Fig. 10). Thereafter, a host shift occurred from Andrenidae to Halictidae at least three times in this group. To be specific, the first transition happened in the tribe Biasitini, and the remaining two transitions in different clades of the tribe Nomadini. In the tribe Nomadini, there was one switch from Andrenidae to Apidae within our sampling.

The most frequent host switches were observed in the tribe Ammobatini (Fig. 10), and the tribe showed a tendency of reversal host shifts from Andrenidae to Apidae. However, the ancestral host family reconstruction for the tribe was ambiguous and recovered associations with multiple families.

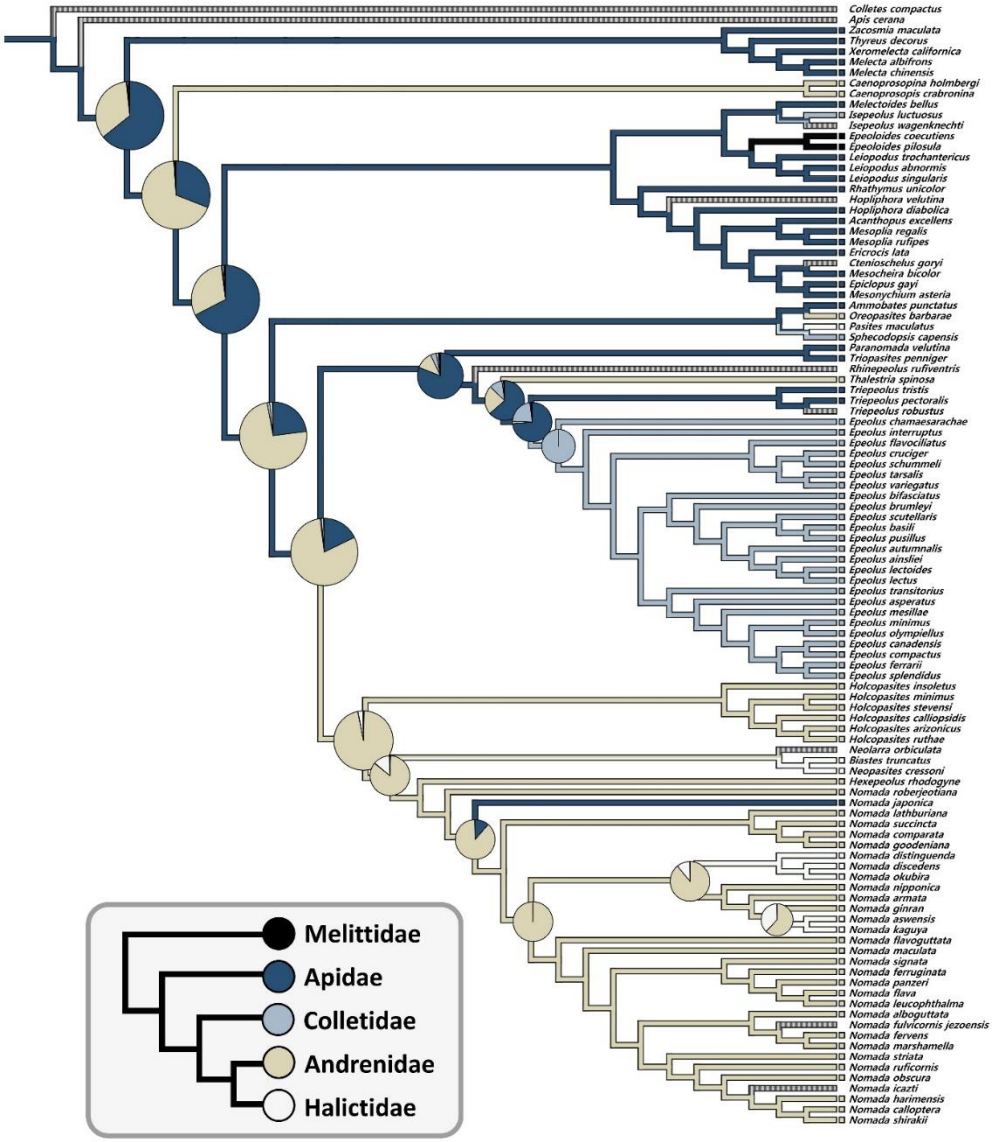

Figure 10. Ancestral state reconstruction of nomadine host associations at the family-level. Produced using the Bayesian analysis. The pie charts represent mean posterior probabilities assessed under RJ-MCMC analysis using Bayestraits. Branch colors indicate the result of parsimony ancestral state reconstruction performed by Mesquite

(Black: Melittidae; Navy: Apidae; Sky blue: Colletidae; Ivory: Andrenidae; White: Halictidae; Mixed black/white lines: outgroups or unknown hosts).

3.3. Allometry and ancestral state reconstruction of body size

The body length of the Nomadinae was on average 9.08 ± 0.36 (mean ± S.E.), widely ranging from 2.5 to 23mm, and the intertegular distance (ITD) was 2.06 ± 0.11, ranging from 0.48 to 6.82mm. The mean body length of the hosts was 10.66 ± 0.38, ranging from 3.6 to 23.28mm and host ITD was 2.84 ± 0.17, ranging from 0.73 to 8.15mm. Our linear regression analysis strongly suggests that the size between Nomadinae and its hosts is highly related in terms of both body length (R^2=0.6879, P <0.05) and ITD (R2=0.7620, P <0.05).

The ancestral state of ITD and body length was of moderate length (mean of full body length of Melectini: 11.06 mm, median ITD of Melectini: 3 mm; mean full body length of hosts: 13.43 mm; mean ITD of Melectini: 3.59 mm), and the length and width of body forms have evolved from medium to extremes (Fig. 11). It was observed in the tribe Ericrocidini that the body evolved to become longer and wider, but this phenomenon was found only in the tribe Ericrocidini. On the other hand, becoming shorter and narrower was observed in multiple lineages. This distinctly recognizable pattern of shrinking was detected in the tribes Ammobatini, Brachynomadini, Ammobatoidini, Neolarrini, and Nomadini.

Intriguingly, we found potential indicators that changing size is related to host shifting across the phylogeny. To be specific, a considerable body size increase was

detected in the tribe Ericrocidini as the host changes from Andrenidae to Apidae. In contrast, both body length and width remained relatively similar within the genus *Epeolus*, which is parasitic on just the genus *Colletes*. This was not always the case, however, as seen among the species-groups of *Nomada*. For example, *N. flavoguttata*, which belongs to the *Nomada ruficornis* species-group and parasitizes the genus *Andrena*, showed a similar body size with species of the *Nomada furva* species-group even though that species-group specializes on a different genus, *Lasioglossum*.

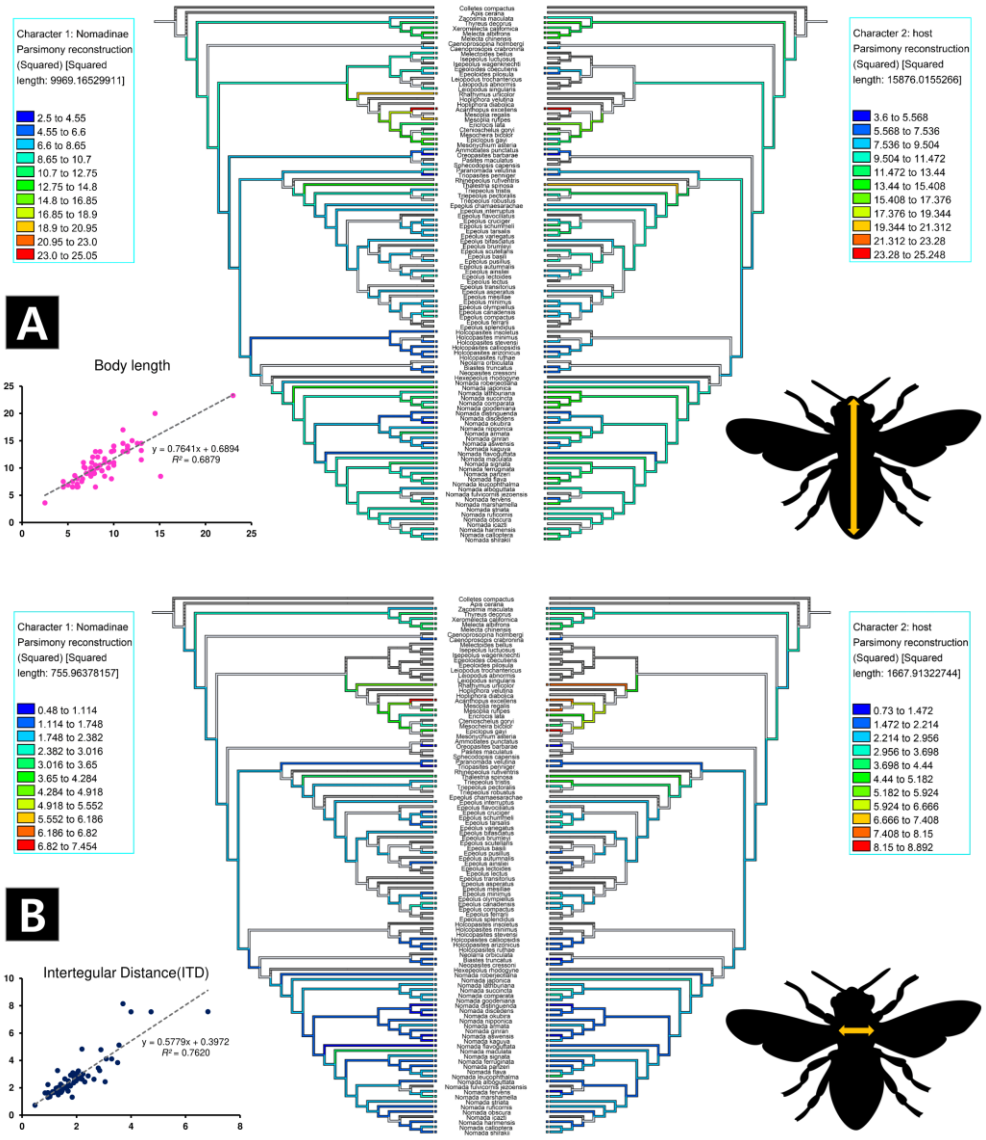

Figure 11. Size correlation between cuckoo bees and hosts. (**A**) Linear regression analysis of entire body length (R^2=0.6879, P <0.05), and Ancestral character estimation of body length of cuckoo bees (left) in accordance with size of the hosts (right). (**B**) Linear regression analysis of ITD (R^2=0.7620, P <0.05).

4. Discussion

4.1. Evolution of the host shift

Our results largely agree with prior studies, with the family Apidae as an original host and multiple switches to other groups and sometimes back to Apidae. In this way, nomadines appear to initially follow Emery's rule, with parasites only attacking close relatives as seen with Melectini attacking Anthophorinae, but later with many groups attacking entirely different families very successfully (Sless et al., 2022).

In comparision to the most recent reconstruction of Nomadinae (Sless et al., 2022), our study determined that host shifting from Apidae to Andrenidae in Nomadinae occurs much earlier. This is because the tribe Caenoprosopidini is shown as sister to the Isepeolini + Epeoloidini + Protepeolini + Rhathymini + Ericrocidini subclade which belongs to the Ericrocidini line (sensu Sless et al., 2022) in our investigation. Conversely, in the previous study, Caenoprosopidini was placed within the Nomadinae line (Sless et al., 2022). Denser sampling of these groups will help resolve these and other disagreements.

Host specificity to certain groups has been frequently used to define taxonomic units, including in cuckoo wasps, fig wasps, and some mites (Costa, 1979; Alexander, 1990; Kimsey, 1992; Chen et al., 2021). Some similar examples exist in Nomadinae. For example, the host genus of *Epeolus* is well known to be limited to the genus *Colletes* (Onuferko et al., 2019), and Ericrocidini is limited to Centridini (Michener, 2007). The common feature of these two examples is that their hosts have specialized nesting strategies, and this may explain some instances of conservatism. Most colletid females apply a cellophane-like layer with their short, bilobed glossa in brood cells

(Michener, 2007; Almeida, 2008). Conversely, many hosts of the tribe Ericrocidini collect floral oil for their brood-cell construction (Danforth et al., 2019). Applying floral oil and other secretions may make it difficult for parasites to access these nests (Almeida, 2008). Both of these specialized nesting behaviors, especially oils which may be hard to digest, could physically inhibit the offspring of parasites (Policarová et al., 2019). It may be that the adaptations for using these nests, in turn, make it harder for them to switch to other host groups with less specialized behaviors, further enforcing patterns of conservatism (Bush, 2009).

Of course, exceptions to conservatism of host use exist, such as the use of many different hosts by *Nomada*. Coincidently, this group also represents another inconsistency with the most recent study (Sless et al., 2022). We found three host shifts in the tribe, while they found one. There are over 800 species of *Nomada* (Smit, 2018) and many of them have unknown hosts, so this result depends heavily on taxon sampling. With greater sampling, we would expect additional host shifts. For instance, the host of the *Nomada emarginata* Morawitz (*ruficornis* species-group) is recorded as *Melitta haemorrhoidalis* Fabricus (Westrich, 1989), which belongs to the family Melittidae, but it was not included in our analysis. Similarly, the unused *Nomada articulata* Smith (*erigeronis* species-group) takes *Agapostemon sericeus* Foster and *A. virescens* Fabricius as their hosts (Snelling, 1986), and this could add another shift. As there are numerous species with unknown or unconfirmed hosts, many of which might invoke additional host shifts when added to the phylogeny, it is difficult to estimate the expected total number of host shifts for this group at this time.

4.2. Host and Body size evolution

Our size allometry analysis strongly supports the positive correlation between parasites and hosts, commonly referred to as Harrison's rule (HR; Harrison, 1915). Further, we found multiple instances where host shifts were linked with body size changes. It is likely that denser taxon sampling will reveal more such linkages between shifts in host use and body size, and it may be that this is a broader co-evolutionary pattern in Nomadinae.

Similar to prior studies on other taxa (Price, 1980; Hanken & Wake, 1993; Tsai et al., 2001; Lafferty & Kuris, 2002), the body size of cleptoparasitic bees was typically smaller than their hosts in this study. We postulate that there is a "lock-and-key" relationship between the Nomadinae and their hosts (referred to in lice prior, based on the need to fit well on hair; (Morand et al., 2000). Most of the hosts of Nomadinae are soil-nesting, solitary bees. Females make their nests underground by digging, and their nest tunnels are typically just large enough to allow them passage. Because cleptoparasitic bees must enter nests to lay their eggs, they are constrained by the size of these tunnels, nest cells, and even the amount of food provisioned for offspring (Roulston & Cane, 2000; Radmacher & Strohm, 2010; Habermannová et al., 2013). Our investigation supports this idea, with host shifts or stability seemingly influencing body size. For example, as shown in Fig. 11, there is relatively little size fluctuation in the genus *Epeolus*, all of which attack *Colletes* (Onuferko et al., 2019). On the other hand, *Nomada*, which parasitizes a vast array of groups, shows scattered size-shifting corresponding with host switches. The ability of cleptoparasitic bees to

modulate their size in response to hosts may contribute to the ability of these bees to switch hosts more readily, which could in turn enable adaptive radiations generated from switching to many new hosts (a possible component of the success of the huge group *Nomada*). Of course, plasticity in host recognition via visual and chemical pathways, as well as adaptability to different nectar and pollen resources, would also be important components.

Another example that highlights the relationship between host switching and body size modulation is found in the tribe Ammobatini. Even though the genus *Melanempis* was excluded from our study because its host is unknown, it is one of the largest nomadines and warrants discussion. According to the most recent study (Sless et al., 2022), Ammobatini includes the small-sized *Oreopasites* (as small as 2.2mm) and *Melanempis* (up to 22mm), demonstrating huge size variation in the group (Rozen, 1992; Lafferty & Kuris, 2002). Alongside this wide range of body sizes, they also parasitize many families: Apidae, Andrenidae, Colletidae, and Halictidae (See supplementary data in Sless et al., 2022). With further data from this group on host associations and body size, and greater taxon sampling, it could be an ideal finer-scale study for looking at the influence of host switching on body size.

Body size is thought to be one of the factors that could contribute to cophylogenetic patterns between hosts and parasites (Sweet et al., 2020). Food resource requirements being similar among close relatives can help explain such patterns, as they should be relatively similar (Morand et al., 2000). Indeed, the ancestral host of Nomadinae was revealed as Apidae in this study (specifically Anthophorinae, Sless et al., 2022), so

co-evolution may have taken place more closely early in the evolution of the nomadines. However, behavioral flexibility can empower parasites to invade novel hosts (Bush, 2009; Westrich, 1989). Such potentials are enhanced when alternative hosts have similar-sized nests (Habermannová et al., 2013), or when their increased abundance makes it more likely for them to be encountered, especially if in the same microhabitat (Parker, 2020). Host chemical cues also likely play an important role but are relatively poorly understood (Tengö & Bergström, 1977). Such factors may help explain how single species can exploit many varied hosts (Packard, 1868). For example, *Nomada flavoguttata* parasites various *Andrena* species such as *Andrena falsifica*, *A. minutula*, *A. minutuloides*, *A. semilaevis*, and *A. subopaca* (Smit, 2018). Notably, all these host species belong to the same subgenus, *Micrandrena*, which is well-known to have diminutive body size, and may also have similar chemical cues and metabolic requirements (Dardón & Ornosa, 2014). However, occasionally, a single *Nomada* species exploits multiple genera or even families as hosts, such as in *N. imbricata*, parasitizing *Andrena* and *Halictus* (Packard, 1868). With greater emphasis on natural history studies to make more host-parasite associations, even more disparate host uses might be discovered.

With the combination of our multi-locus phylogeny and allometric data, our understanding of the evolutionary relationship of size fluctuation between cleptoparasitic bees and their hosts has greatly improved. Based on the scenarios and examples discussed above, host switches appear closely related to changes in body size. The ability to adapt to new hosts more quickly in this way could increase

speciation rate in the presence of potential new hosts, explaining highly diverse groups like *Nomada*. Ultimately, we confirm Harrison's rule, the positive correlation of body size between cleptoparasitic bees and hosts, and with further sampling we expect to find an even stronger impact of body size on the evolution of this group.

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Plates 1.

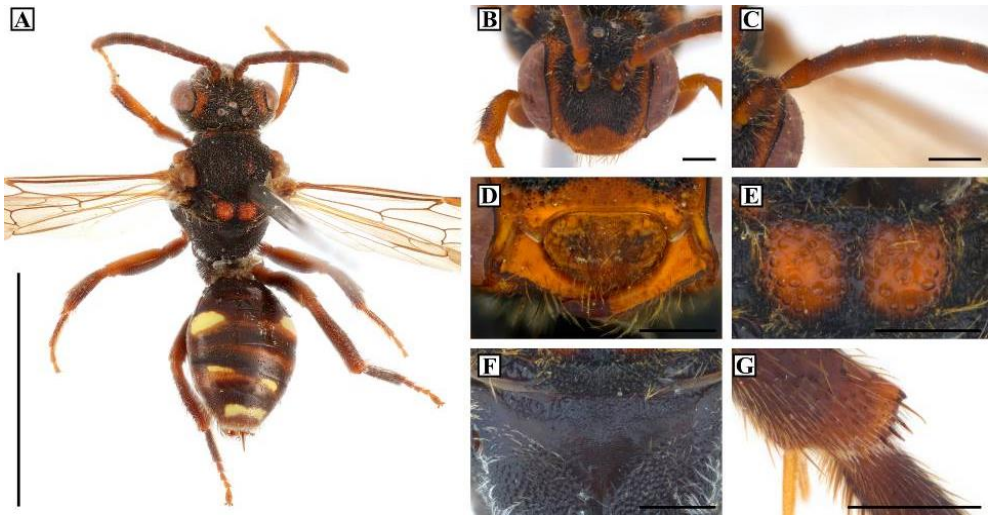

Plate 1-1. *Nomada abtana* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

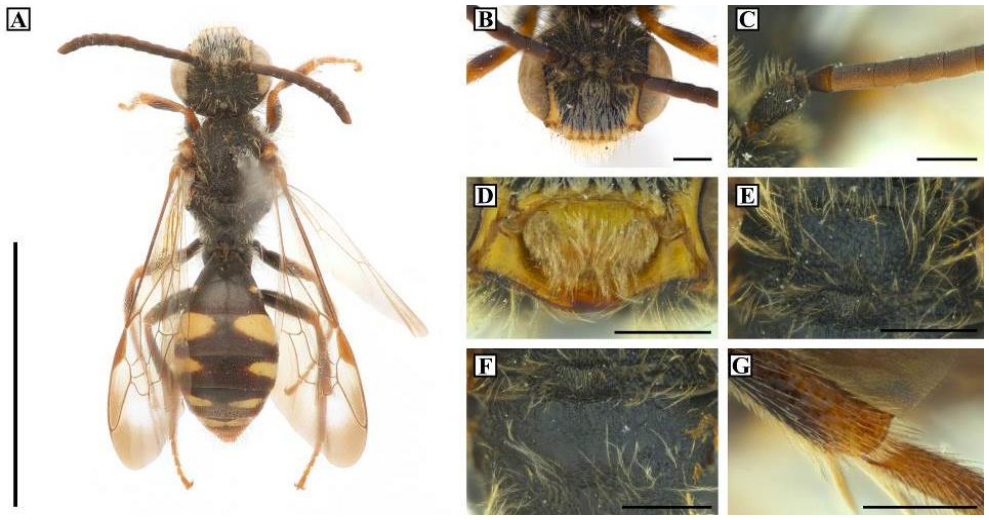

Plate 1-2. *Nomada amurensis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

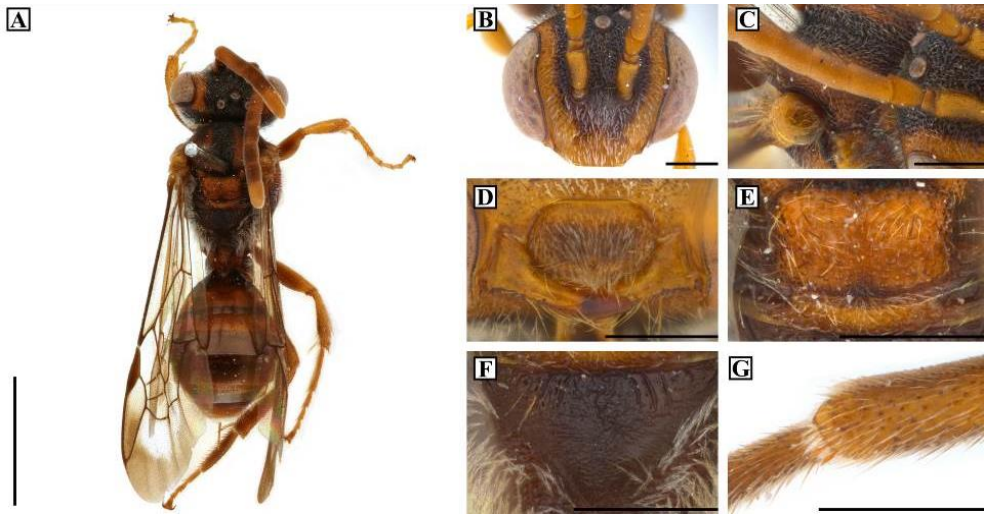

Plate 1-3. *Nomada aswensis* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

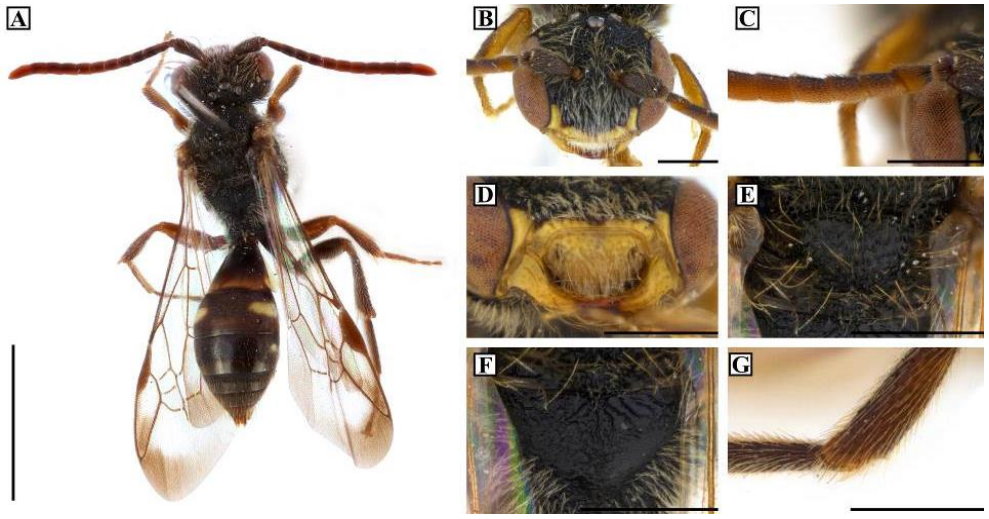

Plate 1-4. *Nomada aswensis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

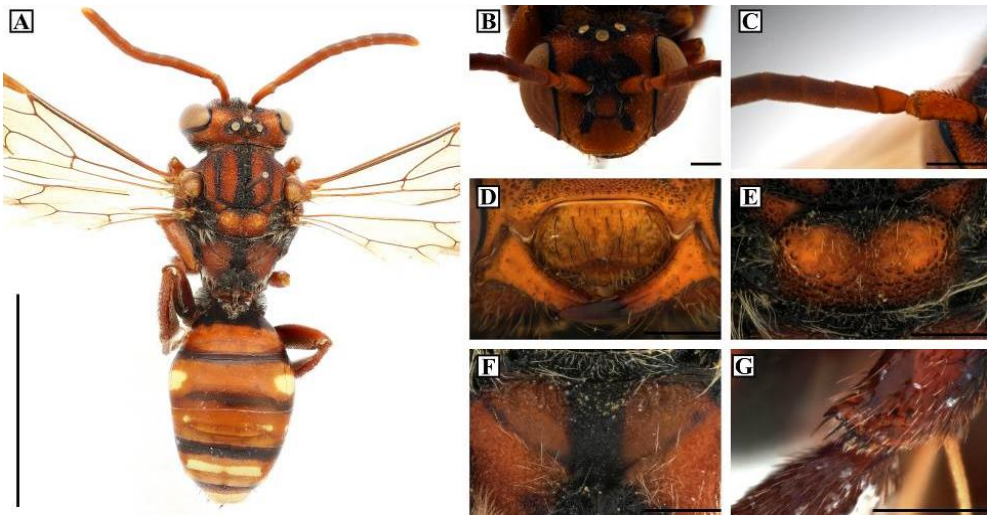

Plate 1-5. *Nomada calloptera* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

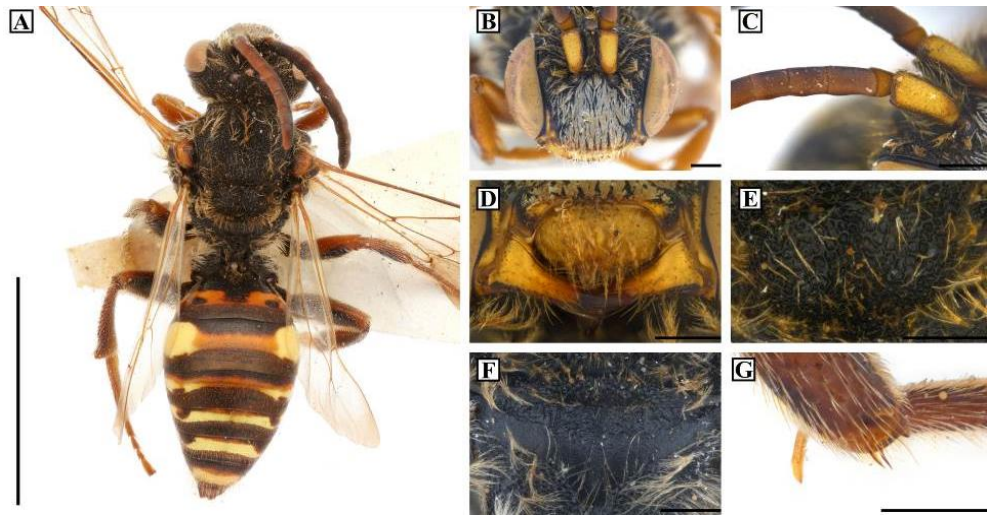

Plate 1-6. *Nomada calloptera* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

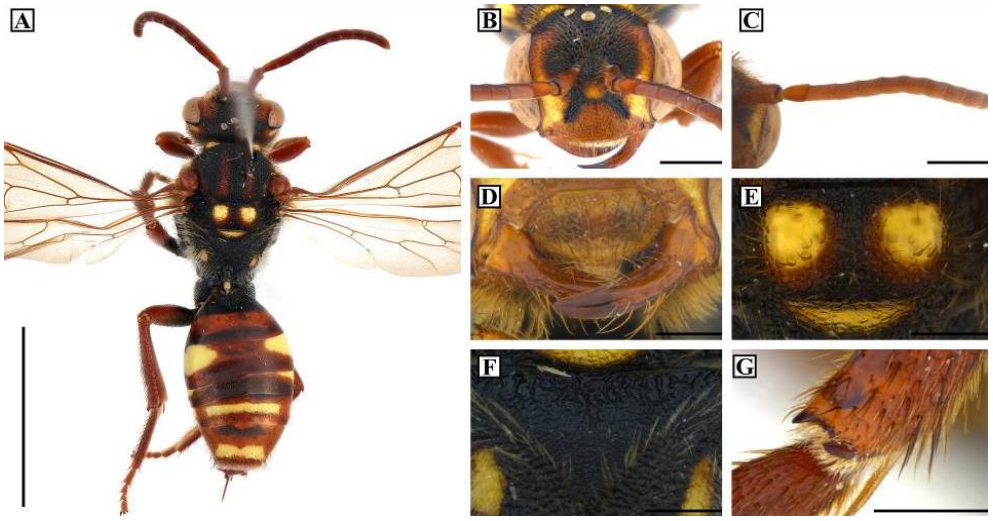

Plate 1-7. *Nomada comparata* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

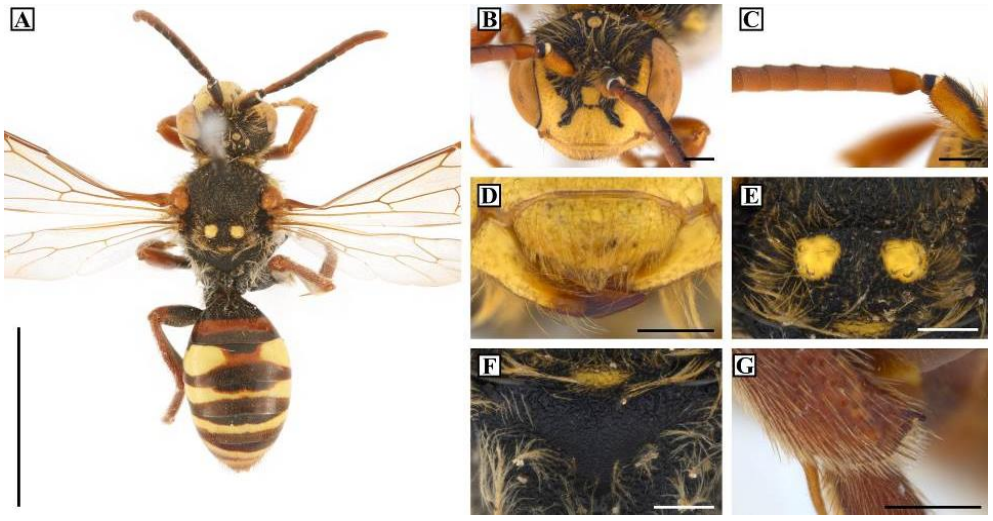

Plate 1-8. *Nomada comparata* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

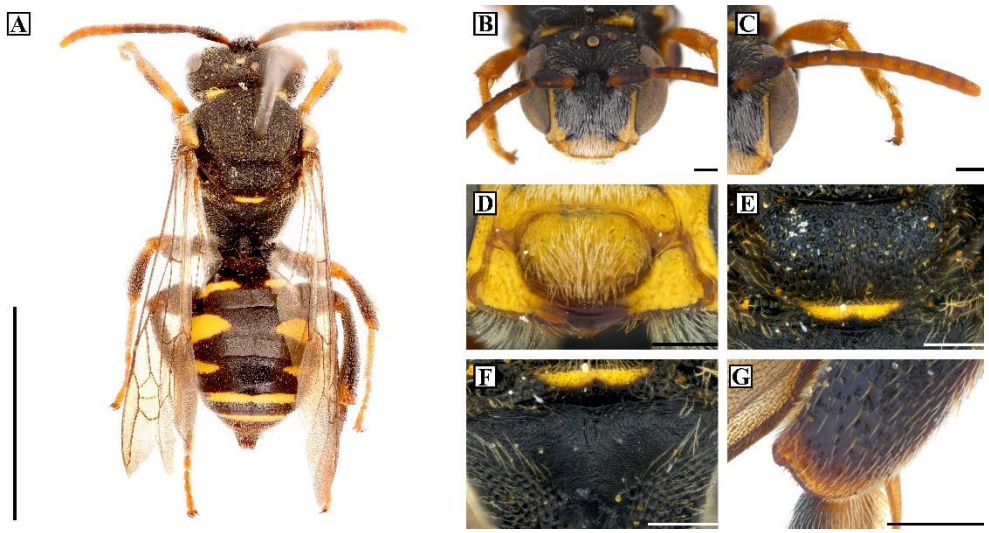

Plate 1-9. *Nomada esana* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

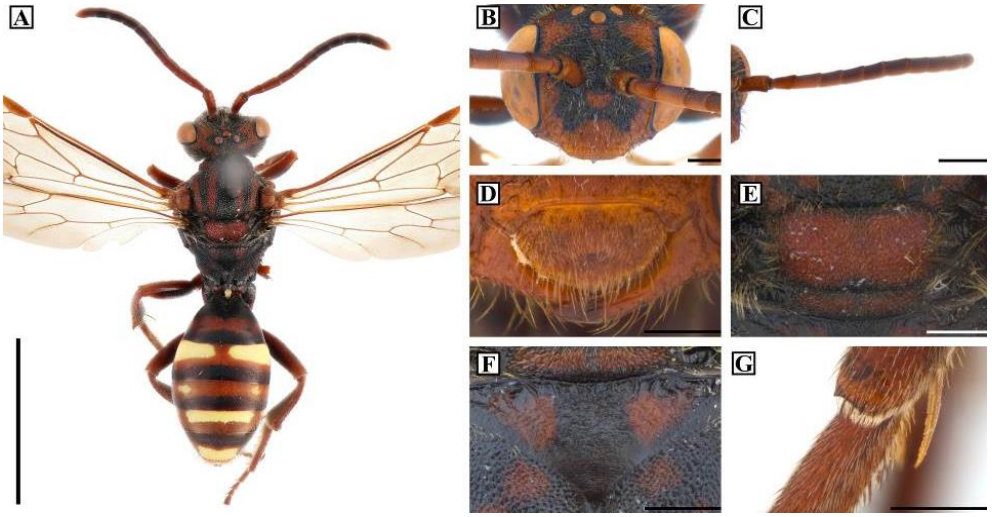

Plate 1-10. *Nomada fervens* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

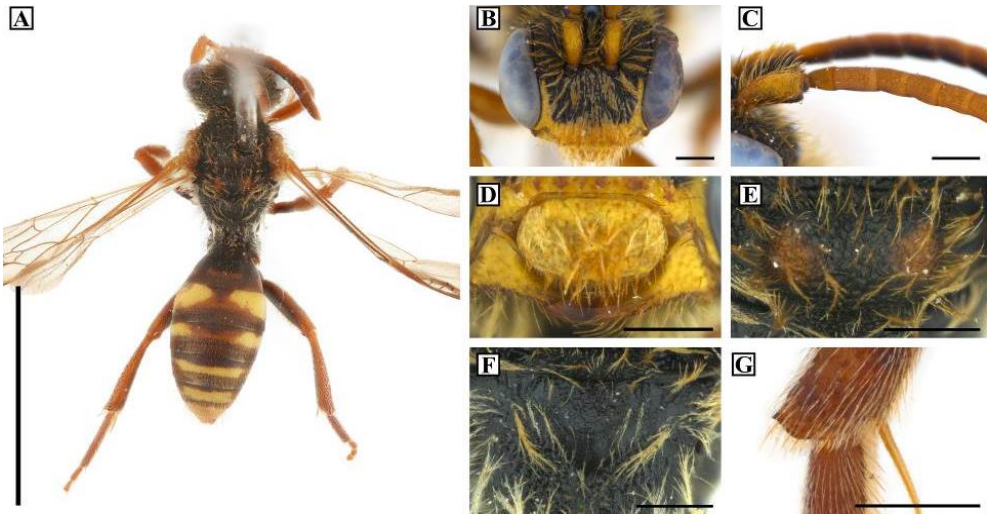

Plate 1-11. *Nomada fervens* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

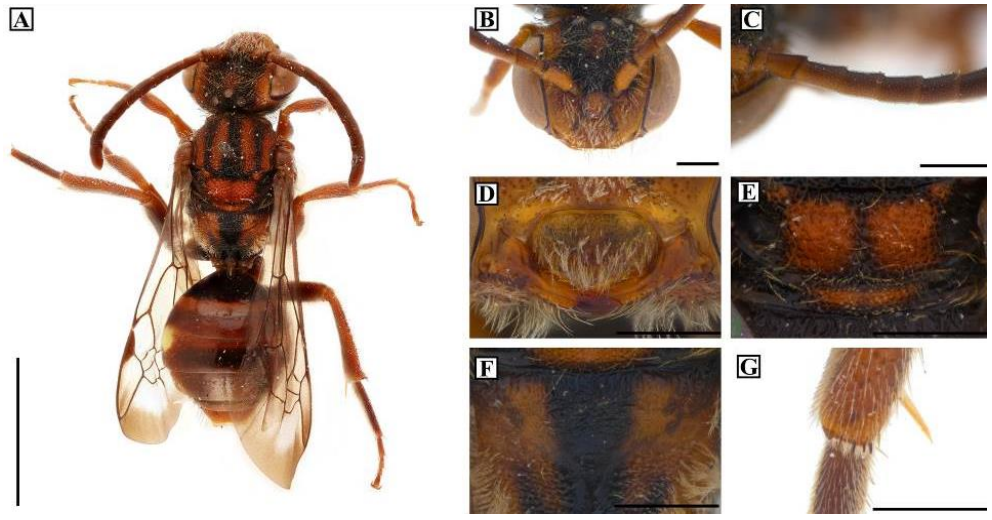

Plate 1-12. *Nomada flavoguttata* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

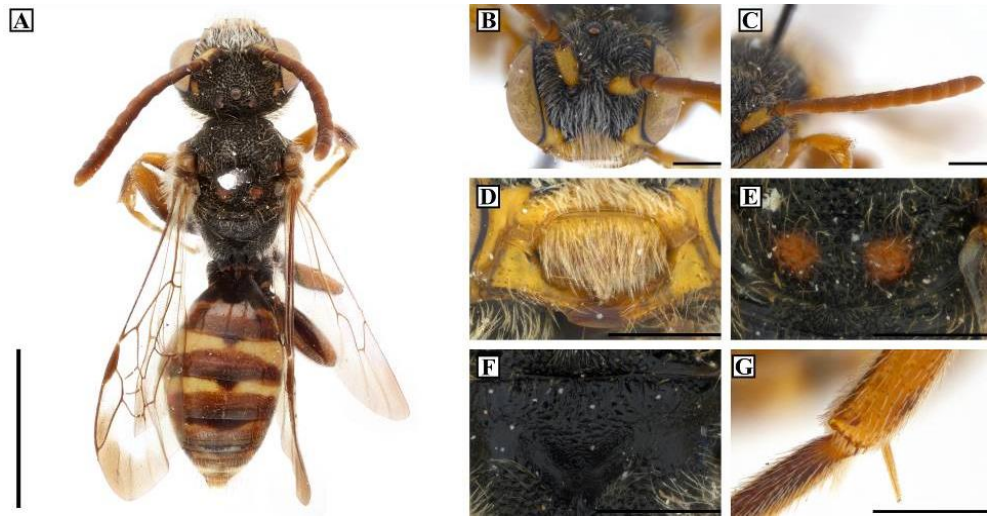

Plate 1-13. *Nomada flavoguttata* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

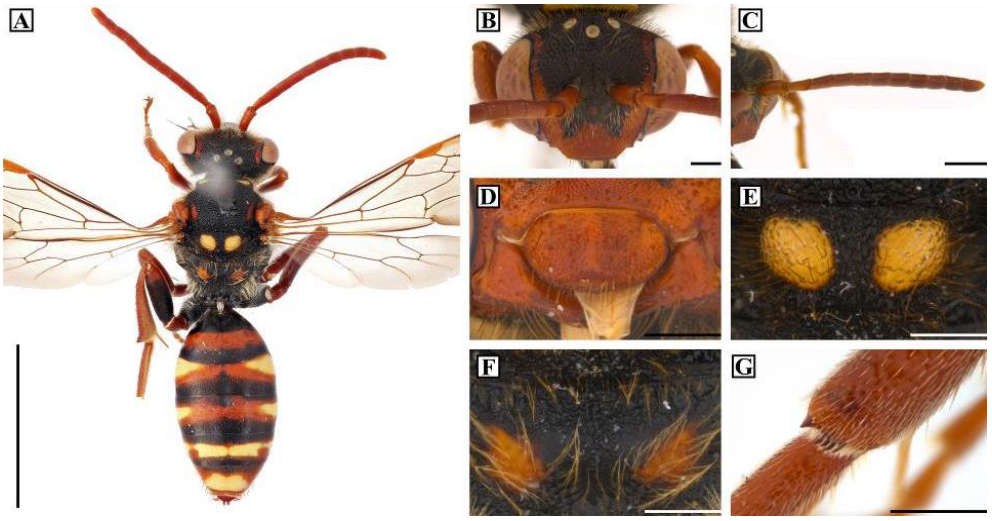

Plate 1-14. *Nomada fulvicornis jezoensis* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

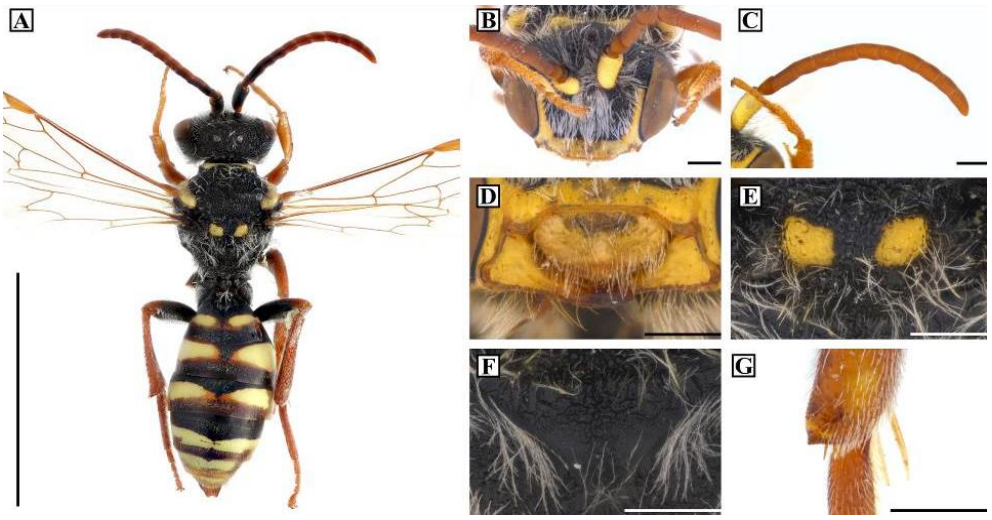

Plate 1-15. *Nomada fulvicornis jezoensis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

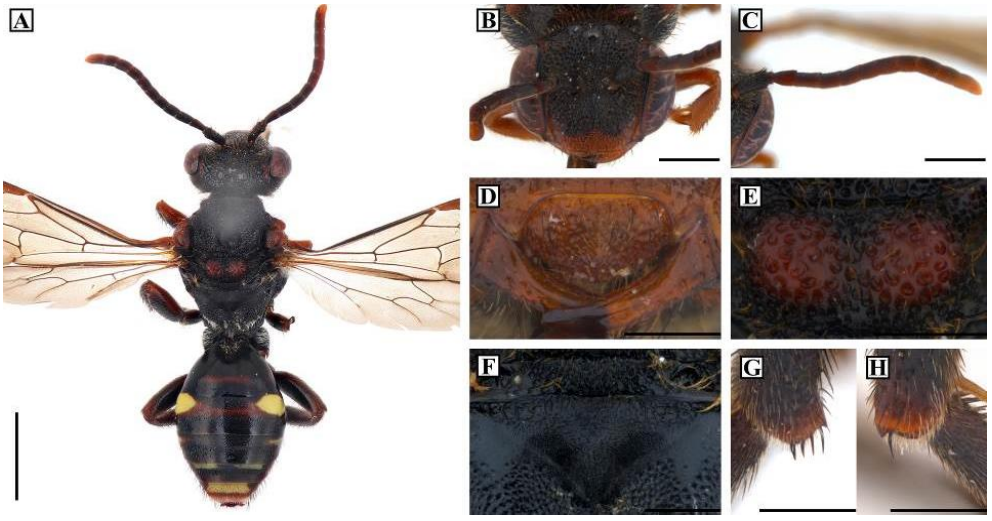

Plate 1-16. *Nomada fusca* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

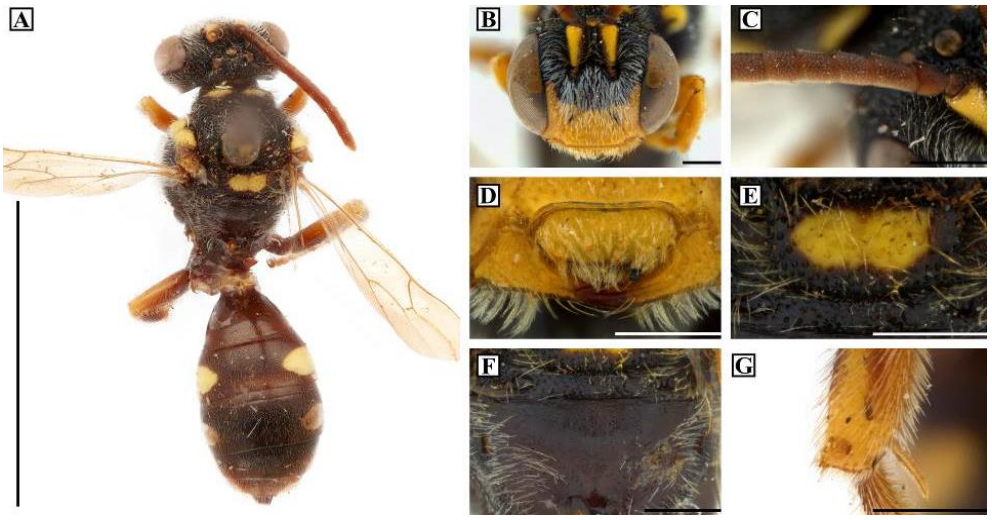

Plate 1-17. *Nomada galloisi* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

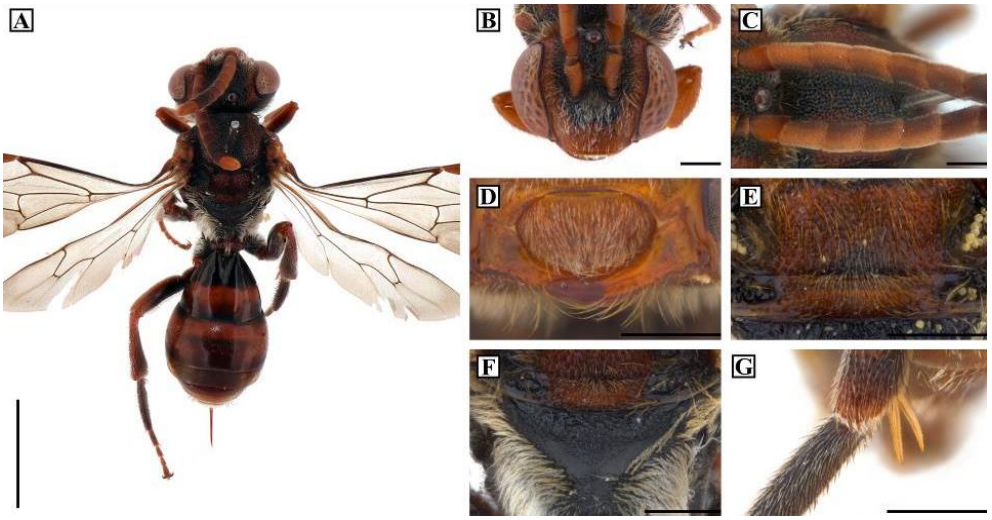

Plate 1-18. *Nomada ginran* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

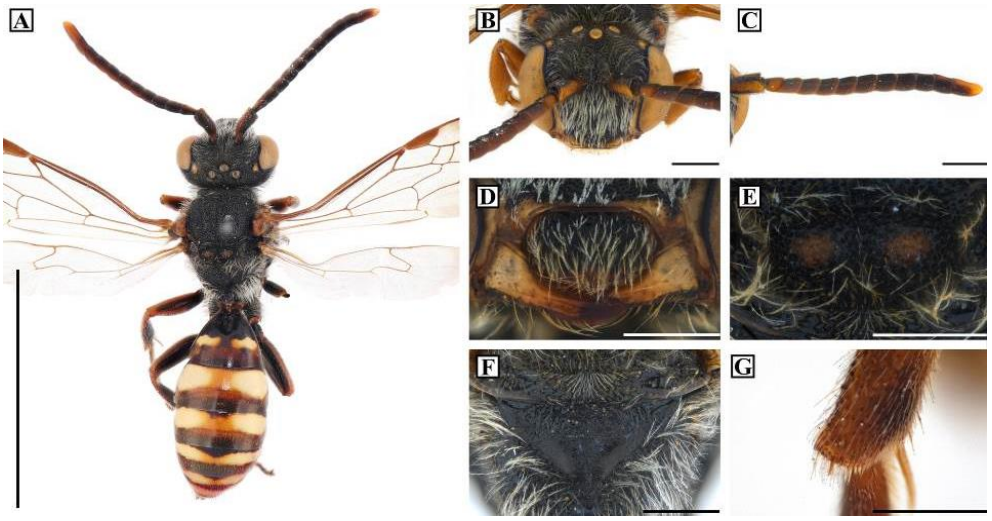

Plate 1-19. *Nomada ginran* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

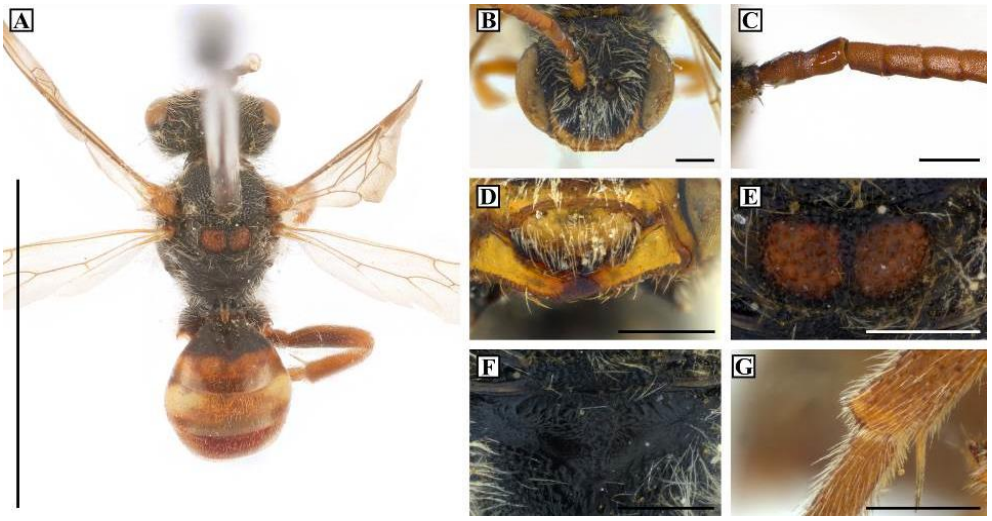

Plate 1-20. *Nomada guttulata* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

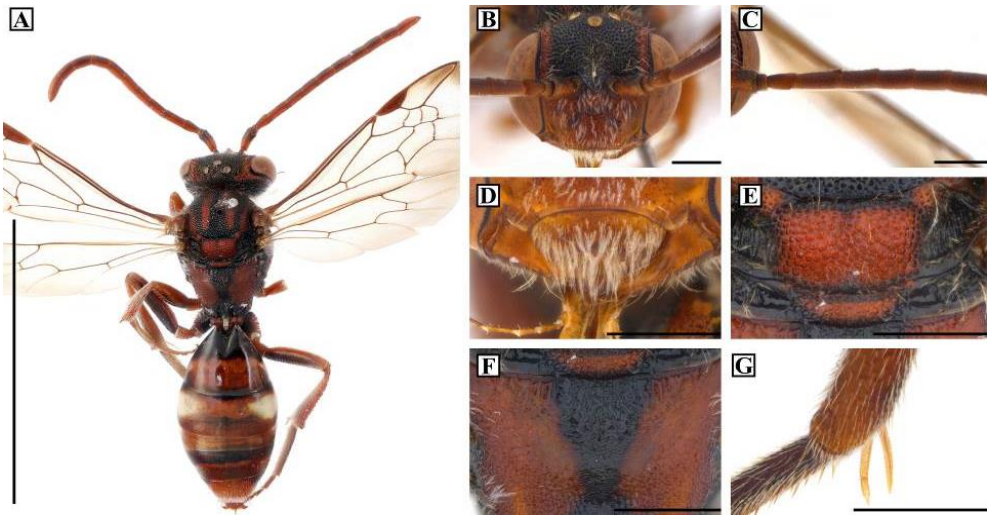

Plate 1-21. *Nomada hakonensis* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

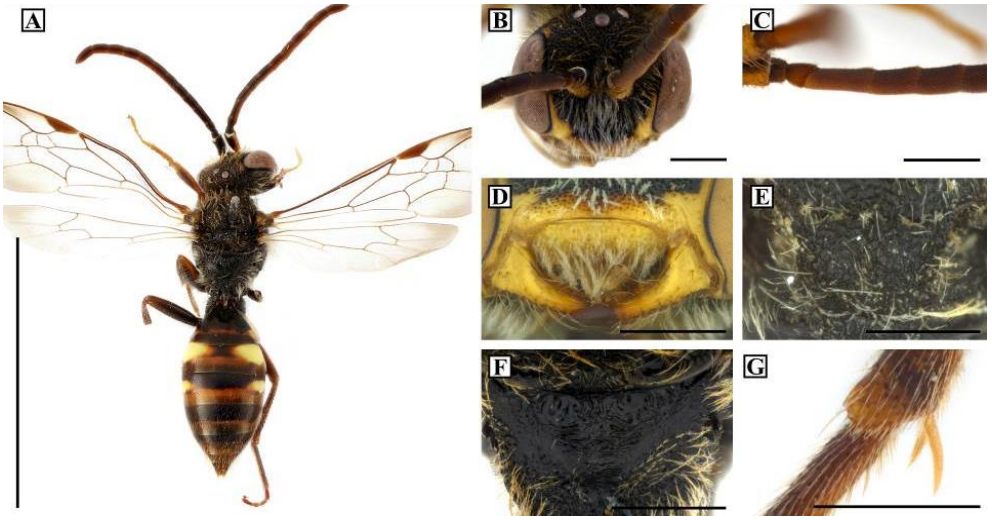

Plate 1-22. *Nomada hakonensis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

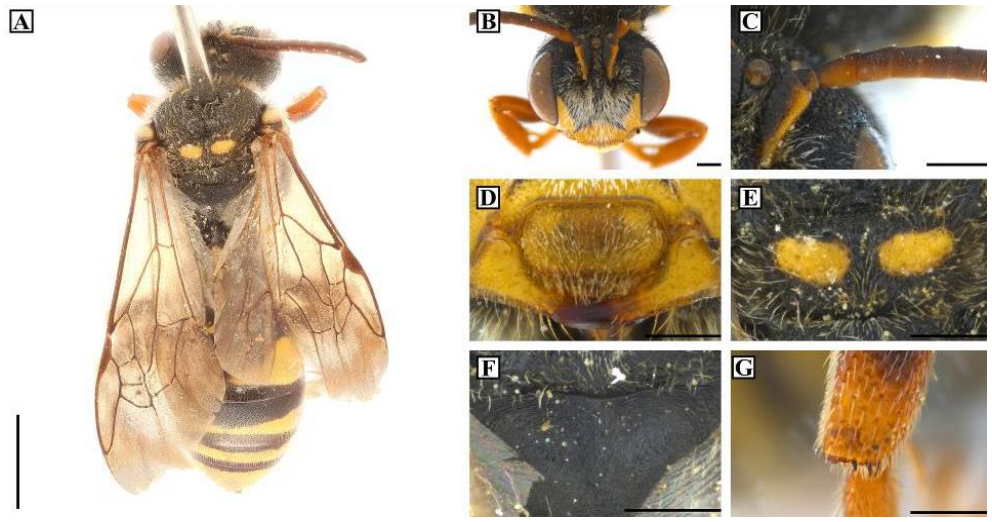

Plate 1-23. *Nomada hakusana hakusana* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

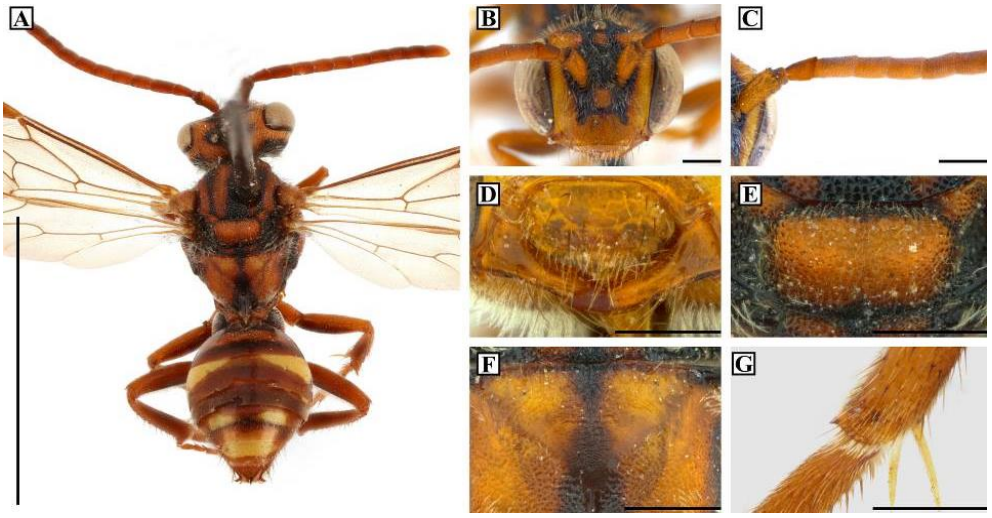

Plate 1-24. *Nomada harimensis* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

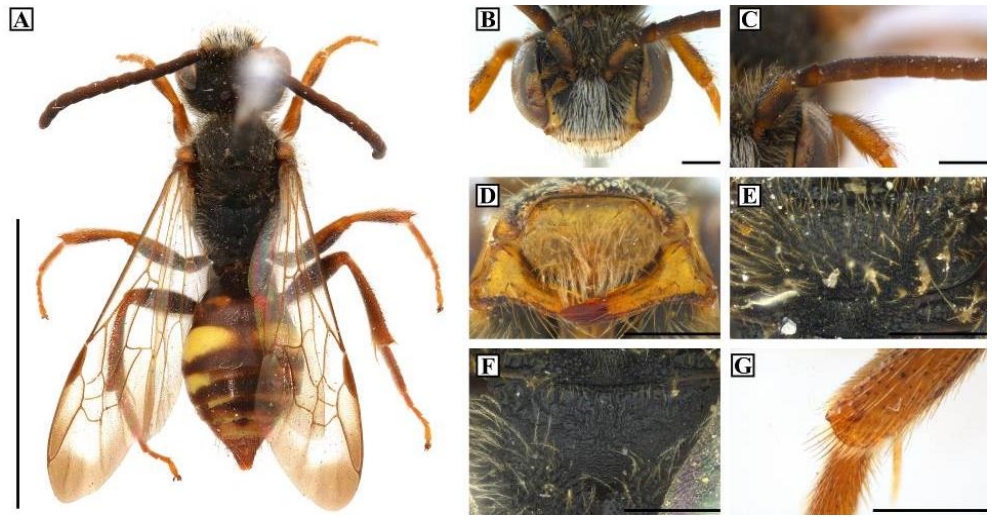

Plate 1-25. *Nomada harimensis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

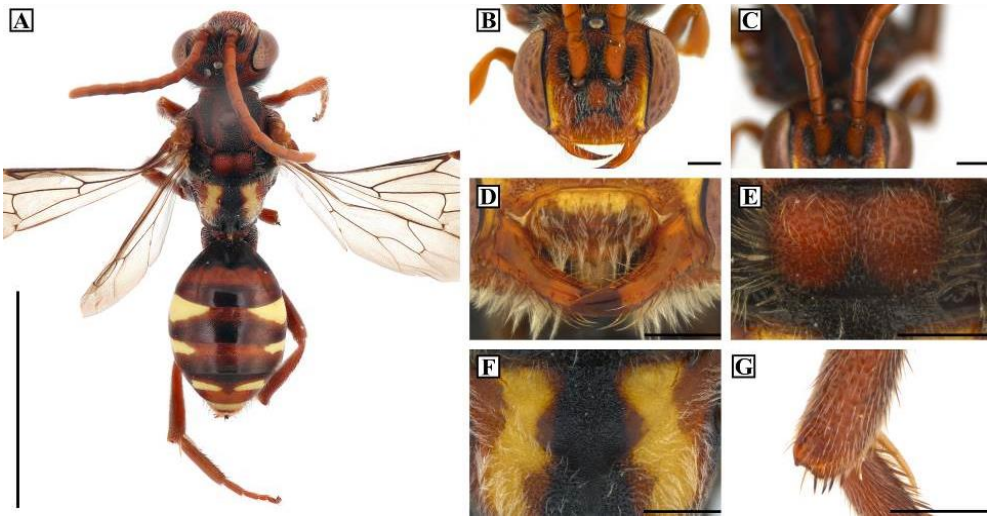

Plate 1-26. *Nomada icazti* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

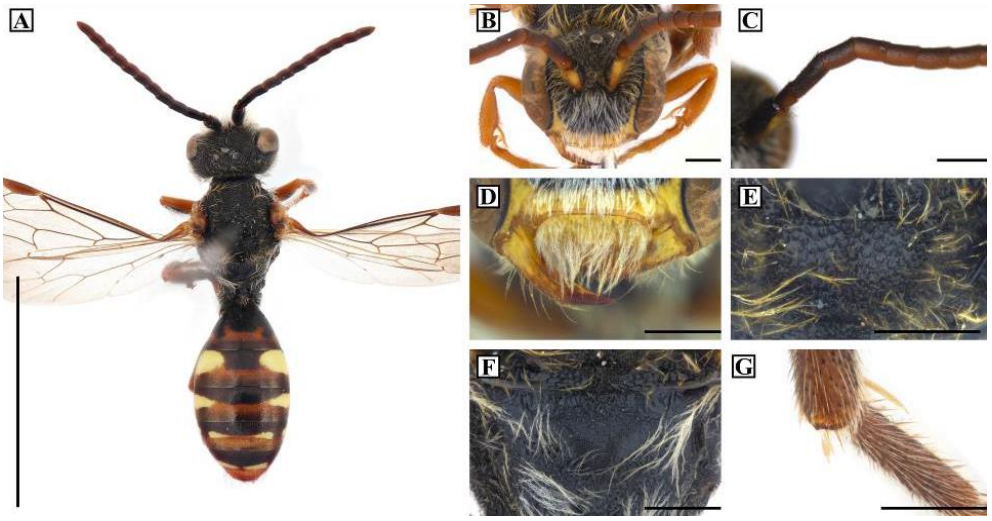

Plate 1-27. *Nomada icazti* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

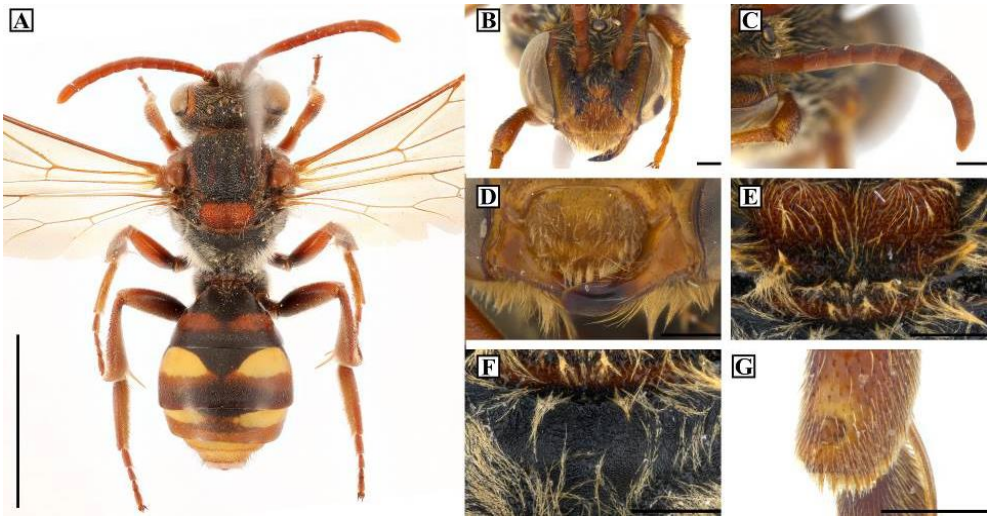

Plate 1-28. *Nomada japonica* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

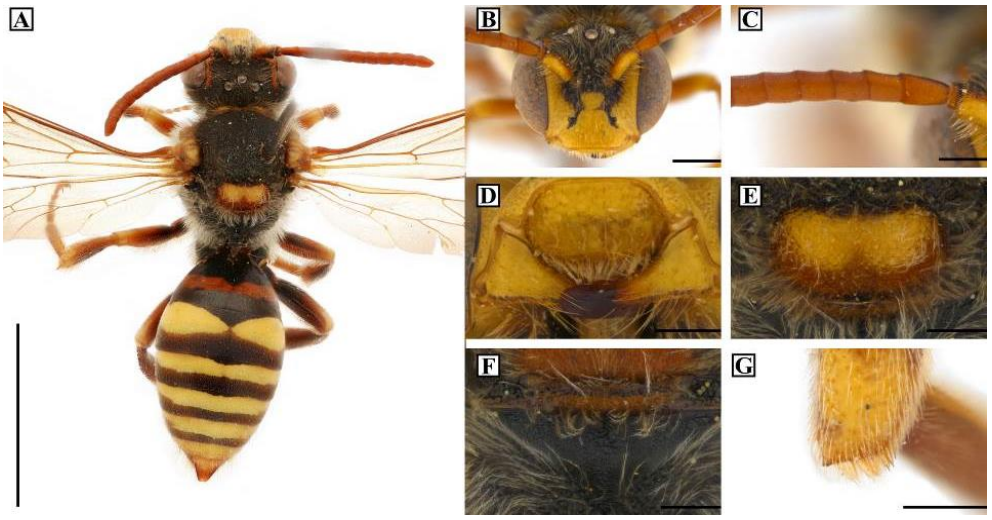

Plate 1-29. *Nomada japonica* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

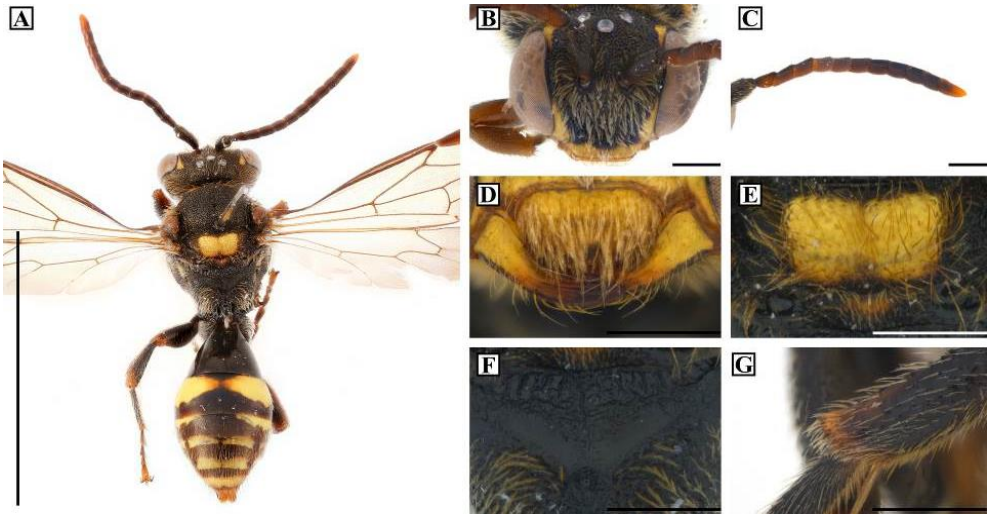

Plate 1-30. *Nomada kaguya* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

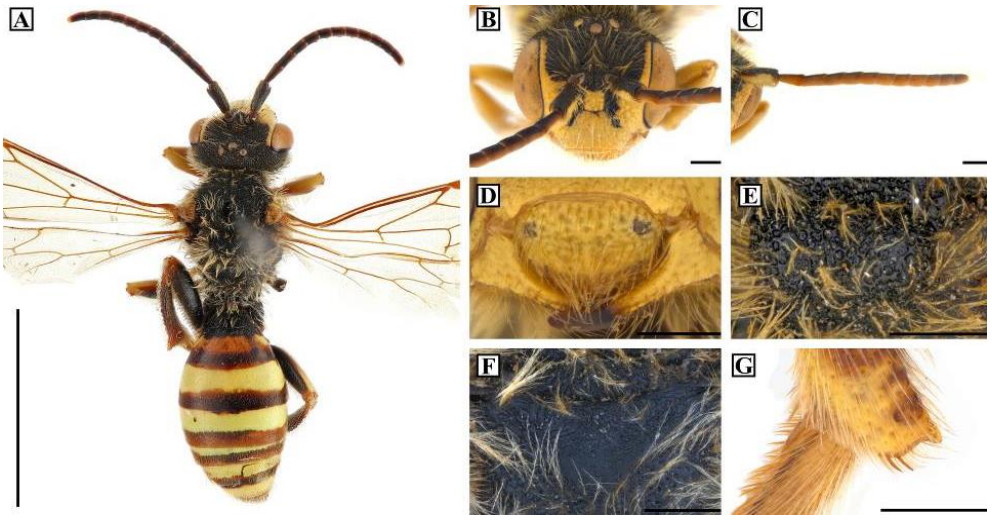

Plate 1-31. *Nomada lathburiana* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

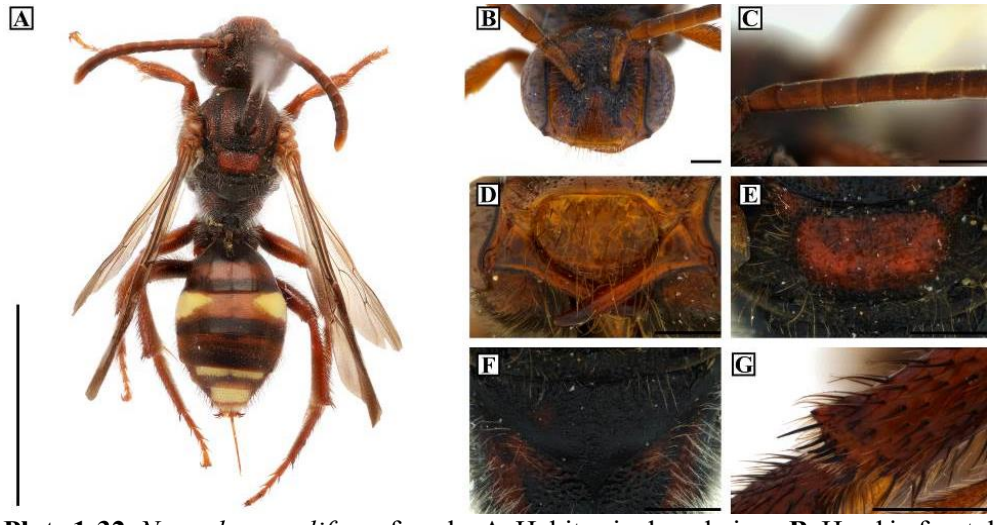

Plate 1-32. *Nomada maculifrons* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

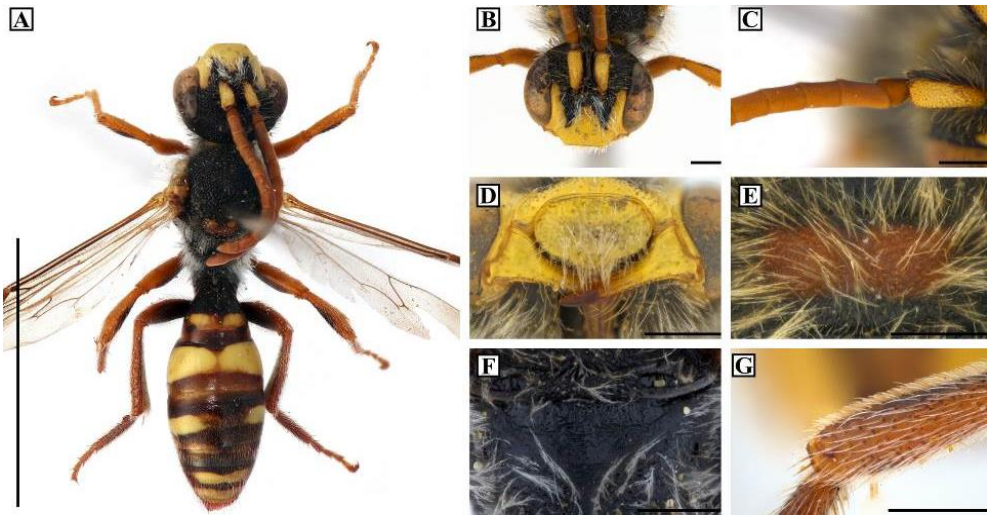

Plate 1-33. *Nomada maculifrons* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

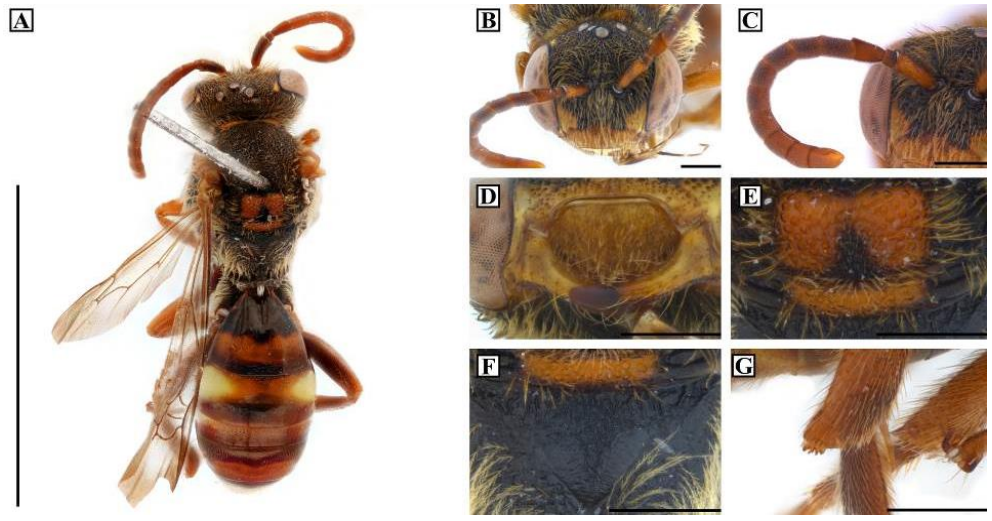

Plate 1-34. *Nomada nipponica* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

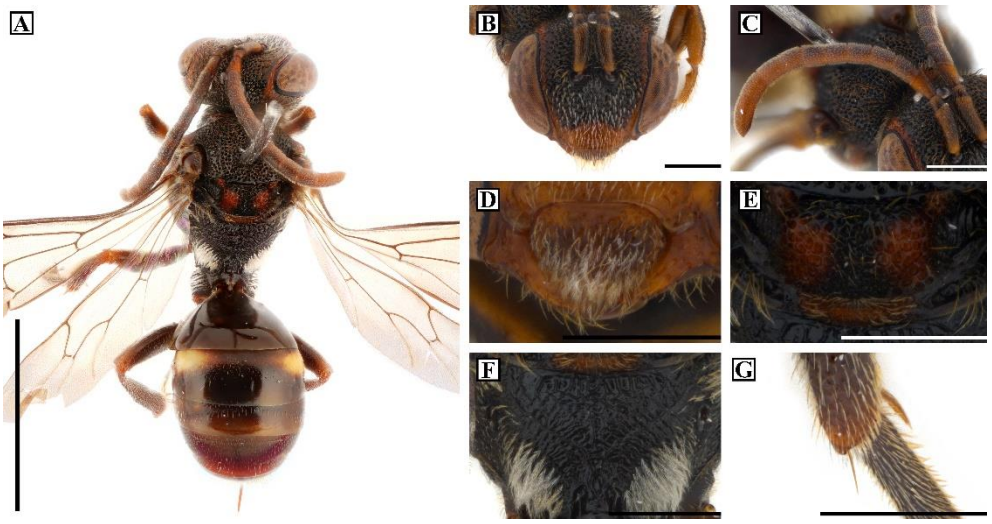

Plate 1-35. *Nomada okubira* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

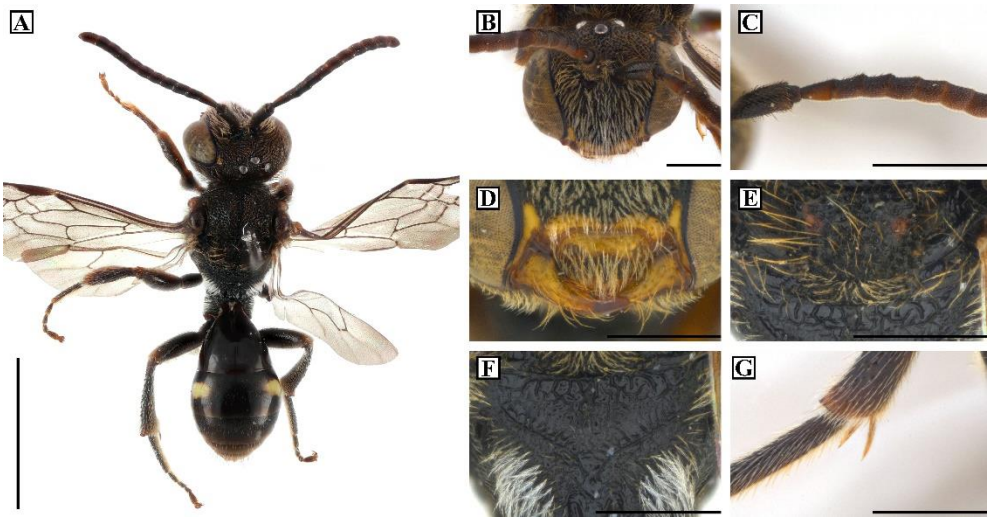

Plate 1-36. *Nomada okubira* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

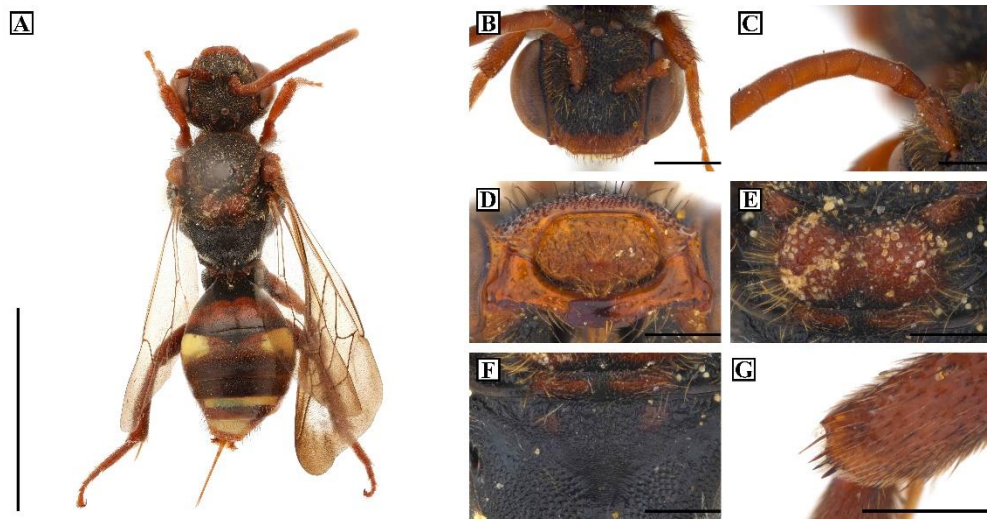

Plate 1-37. *Nomada opaca* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

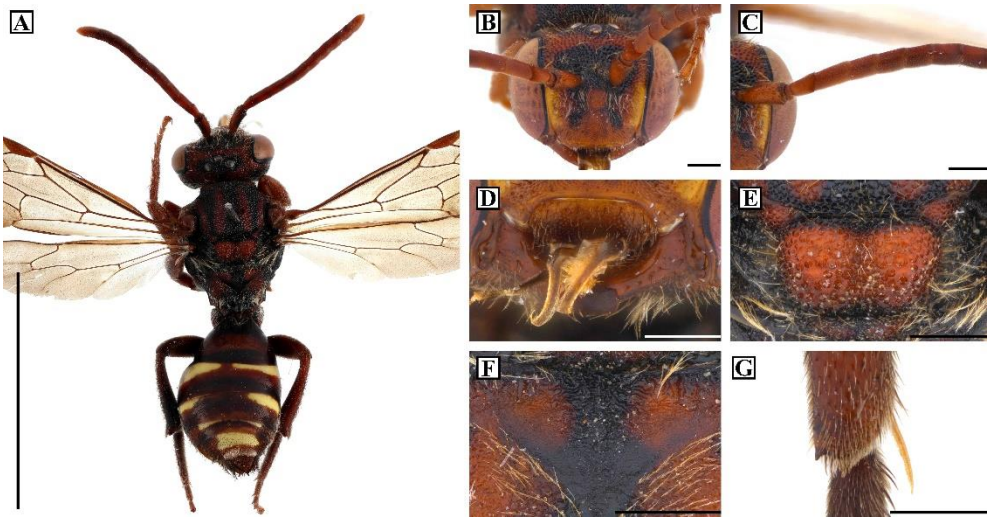

Plate 1-38. *Nomada pacifica* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

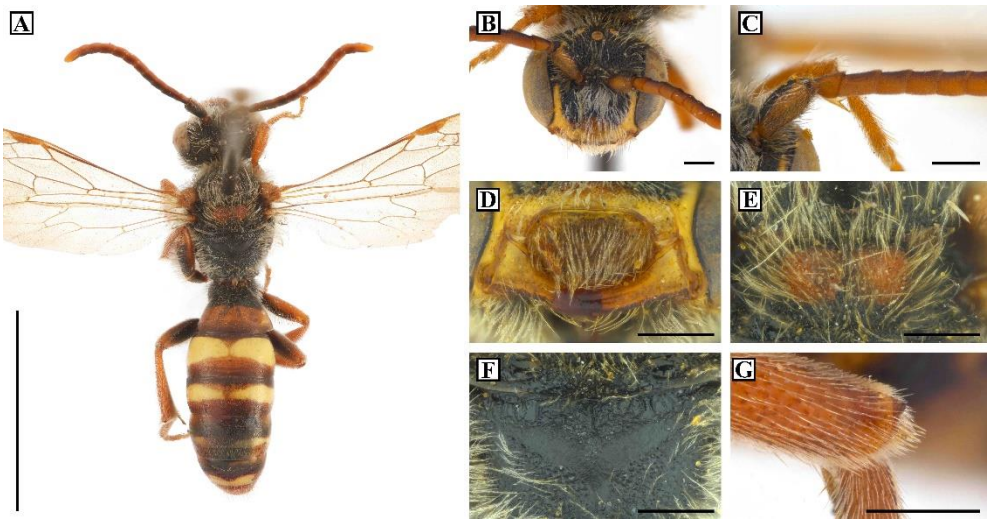

Plate 1-39. *Nomada pacifica* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

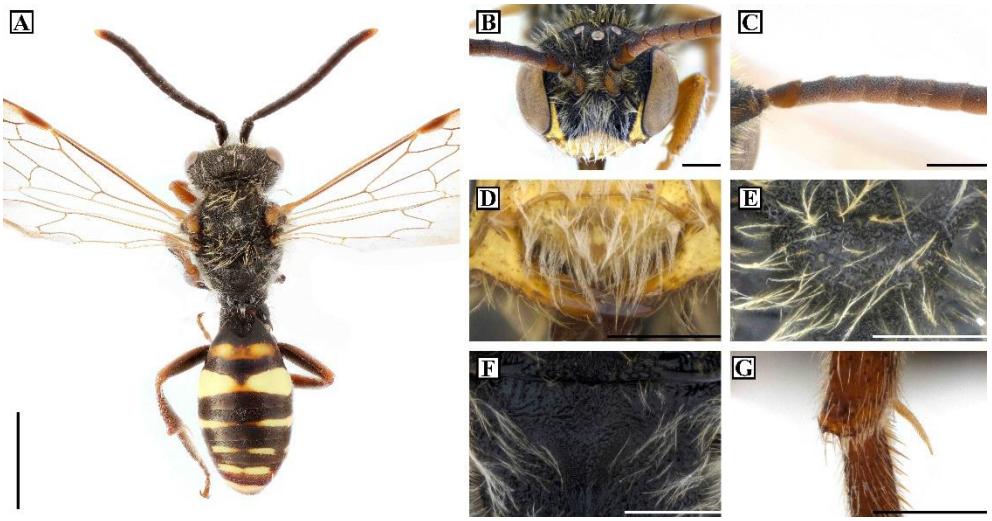

Plate 1-40. *Nomada panzeri orientis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

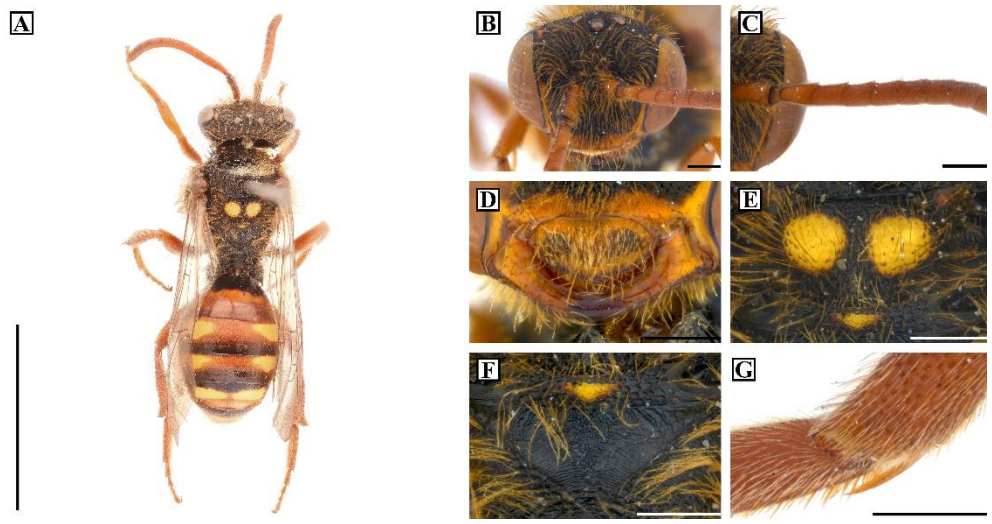

Plate 1-41. *Nomada pekingensis* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

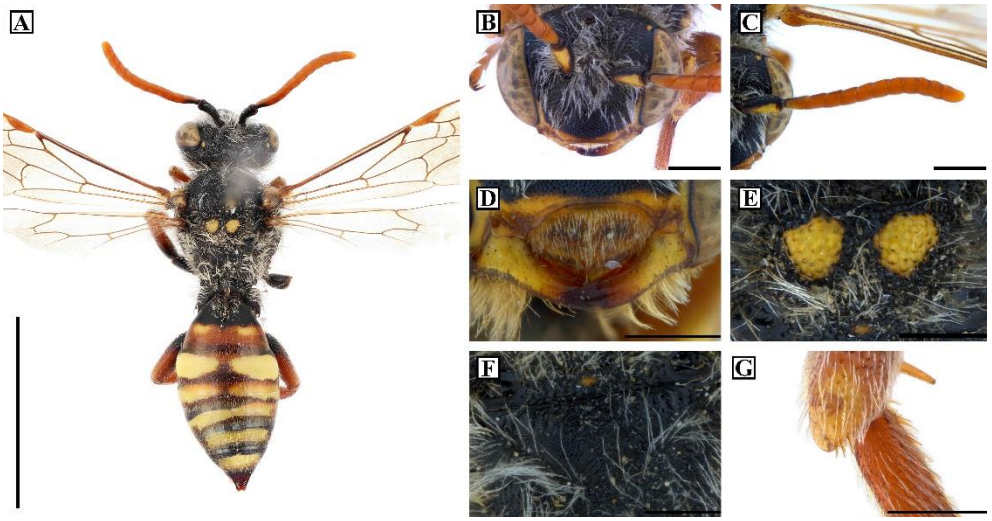

Plate 1-42. *Nomada pekingensis* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

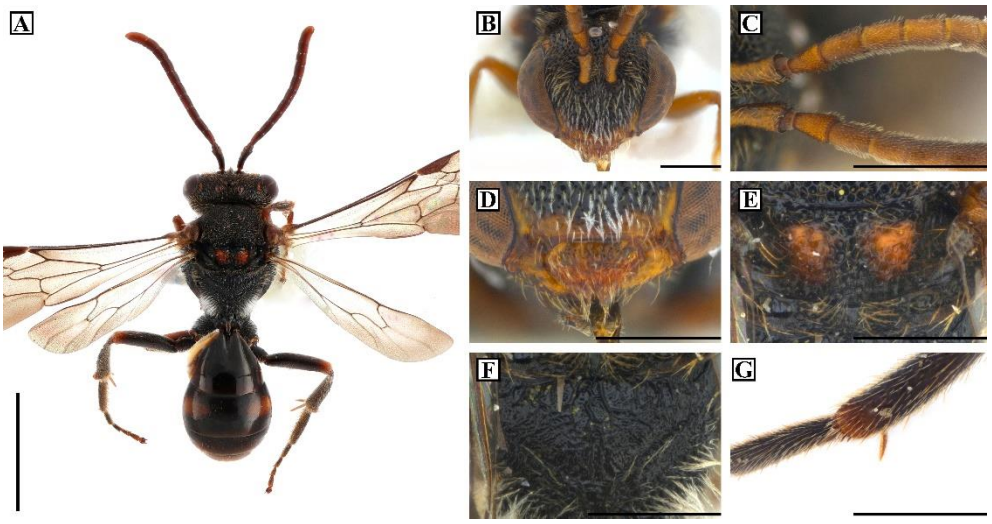

Plate 1-43. *Nomada puawskii* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

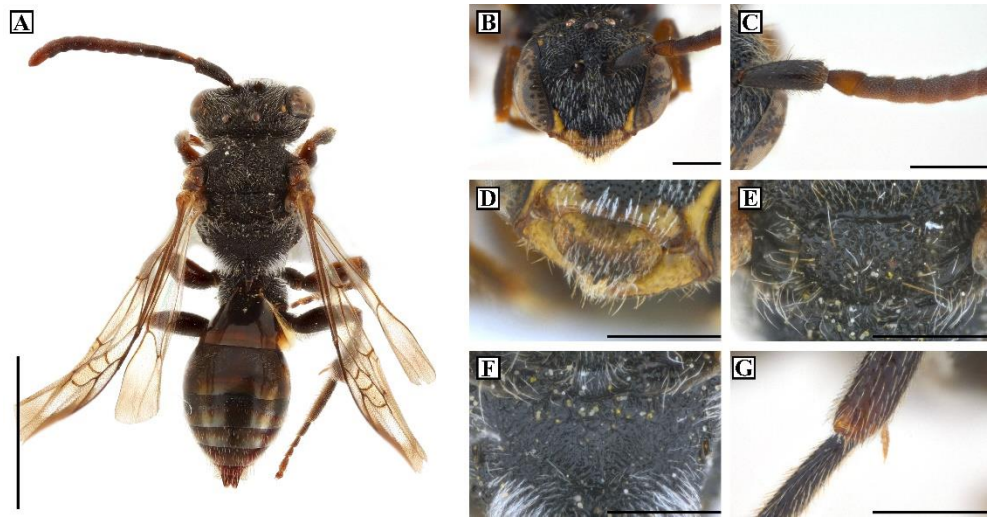

Plate 1-44. *Nomada pulawskii* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

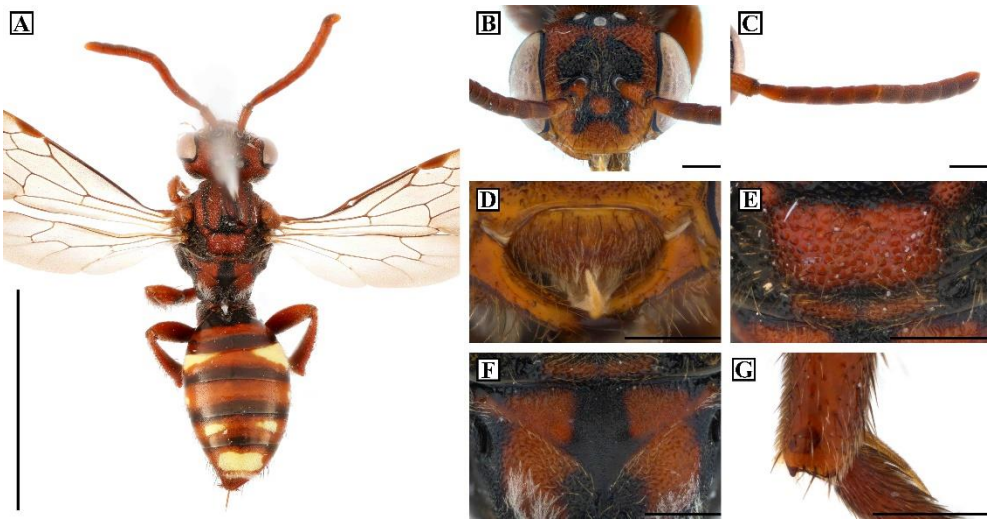

Plate 1-45. *Nomada sabaensis* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

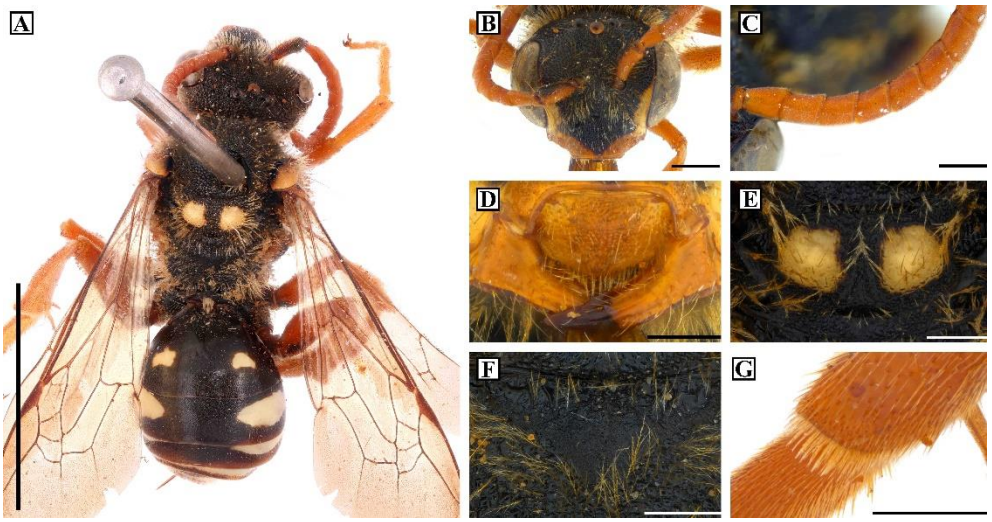

Plate 1-46. *Nomada sexfasciata* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

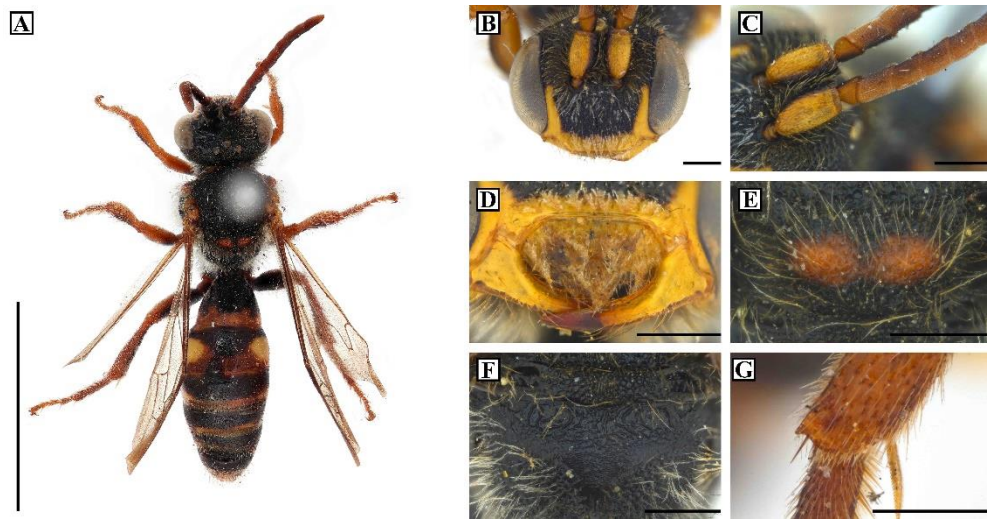

Plate 1-47. *Nomada shirakii* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

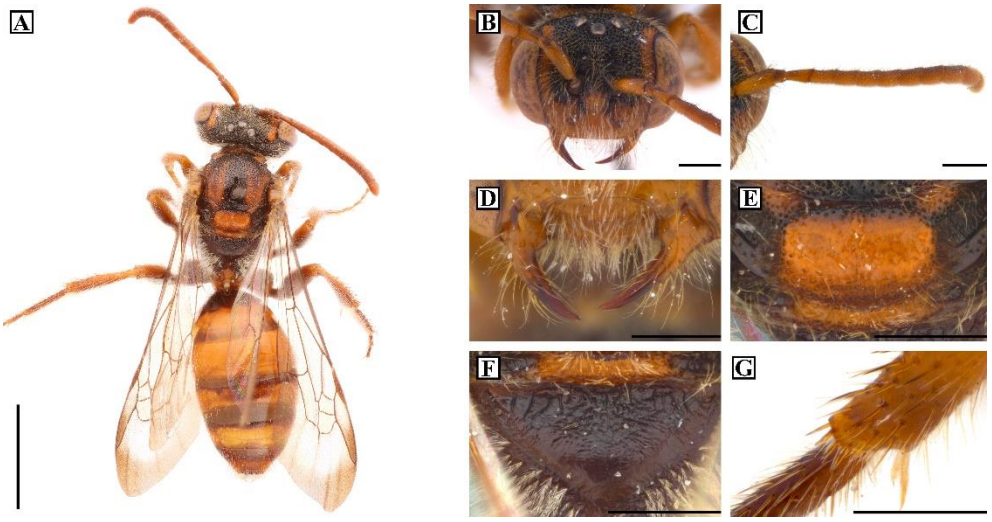

Plate 1-48. *Nomada taicho* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

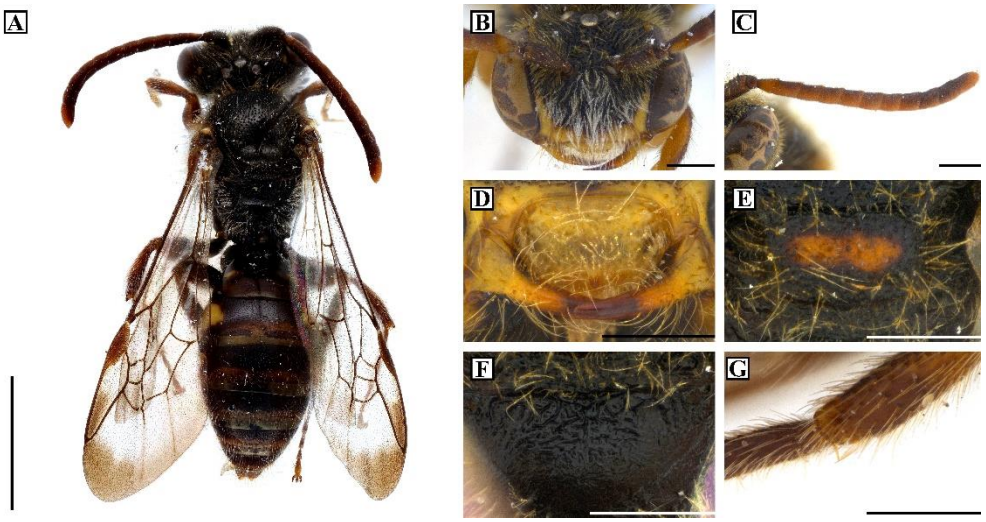

Plate 1-49. *Nomada taicho* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

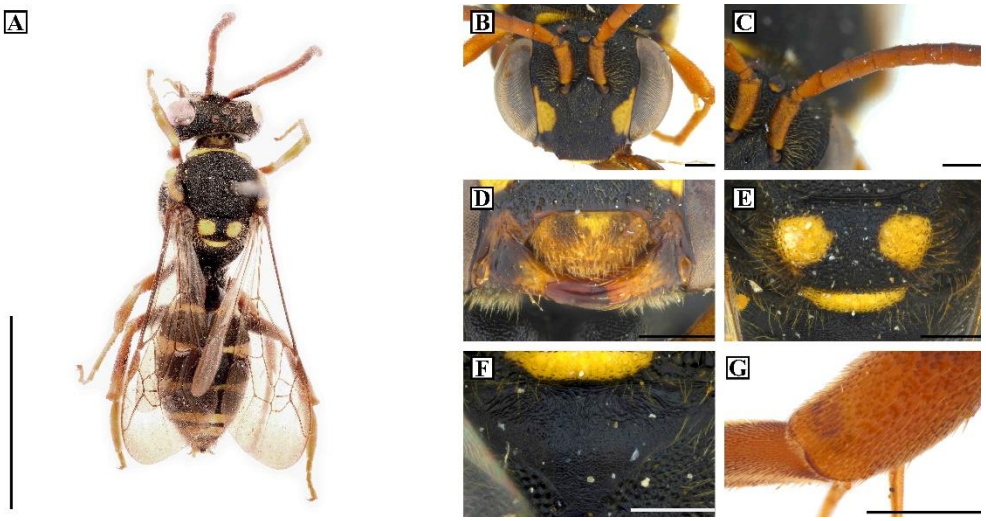

Plate 1-50. *Nomada tsunekiana* female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 5 mm for A, 0.5 mm for B–G).

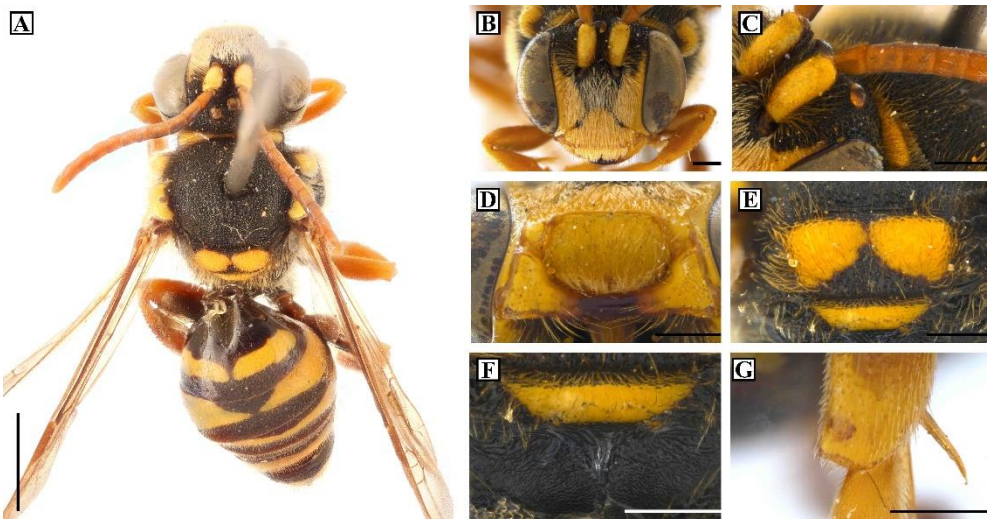

Plate 1-51. *Nomada tsunekiana* male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

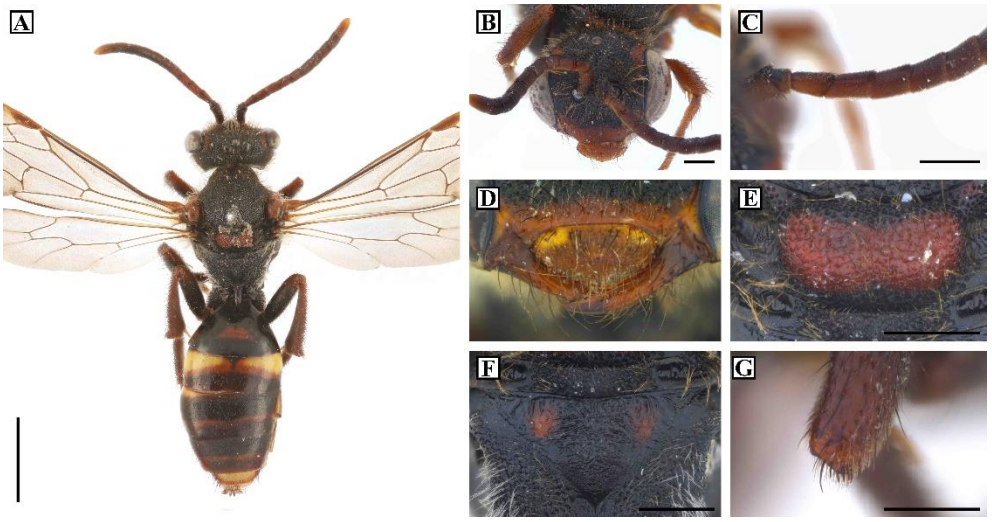

Plate 1-52. *Nomada* sp. nov. 1. female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

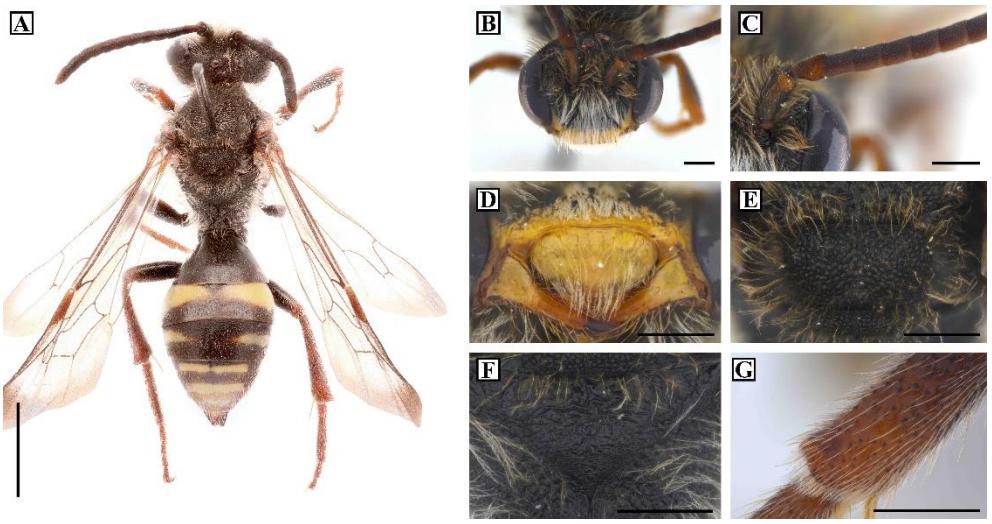

Plate 1-53. *Nomada* sp. nov. 1. male. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

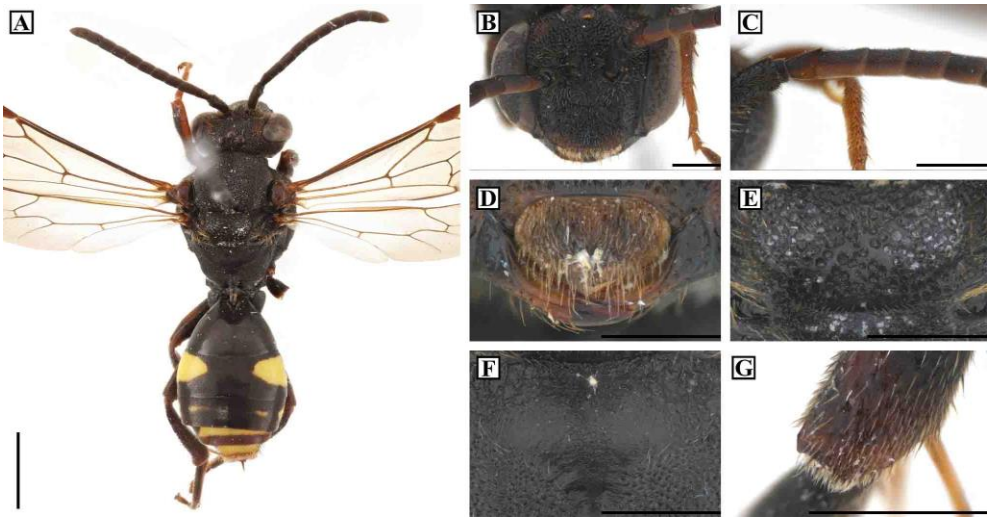

Plate 1-54. *Nomada* sp. nov. 2 female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

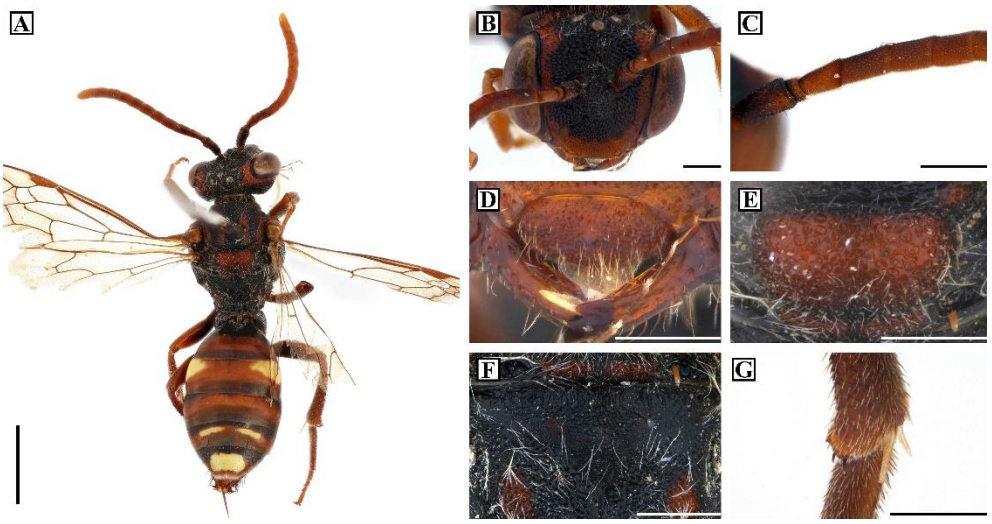

Plate 1-55. *Nomada* sp. nov 3. female. **A,** Habitus in dorsal view; **B,** Head in frontal view; **C,** Antennae; **D,** Labrum and Mandible; **E,** Scutellum; **F,** Propodeal triangle; **G,** HTS (Scale bar 2 mm for A, 0.5 mm for B–G).

Plates 2. Male terminalia

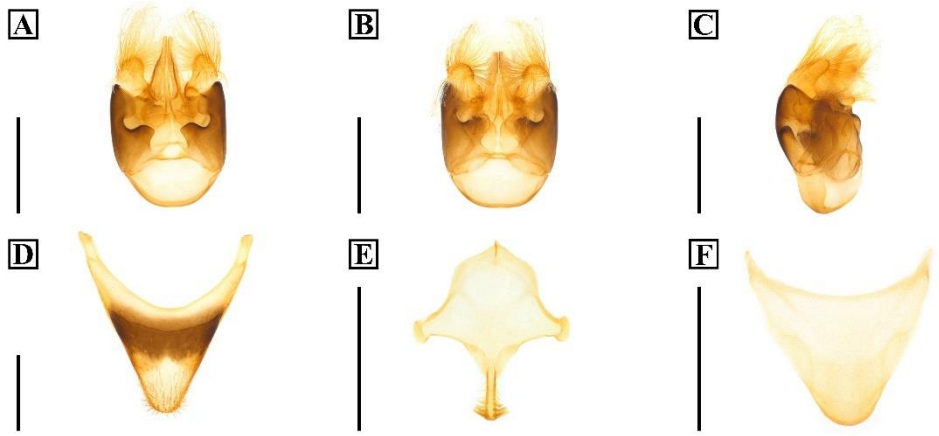

Plate 2-1. Male terminalia of *Nomada amurensis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

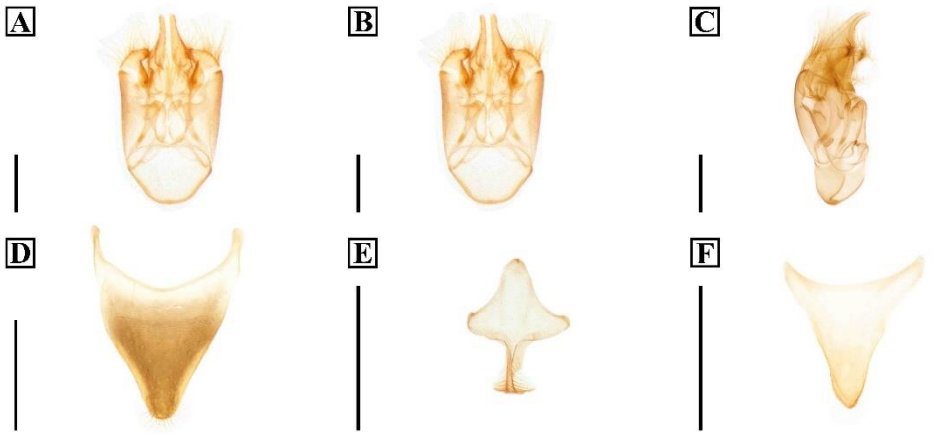

Plate 2-2. Male terminalia of *Nomada aswensis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

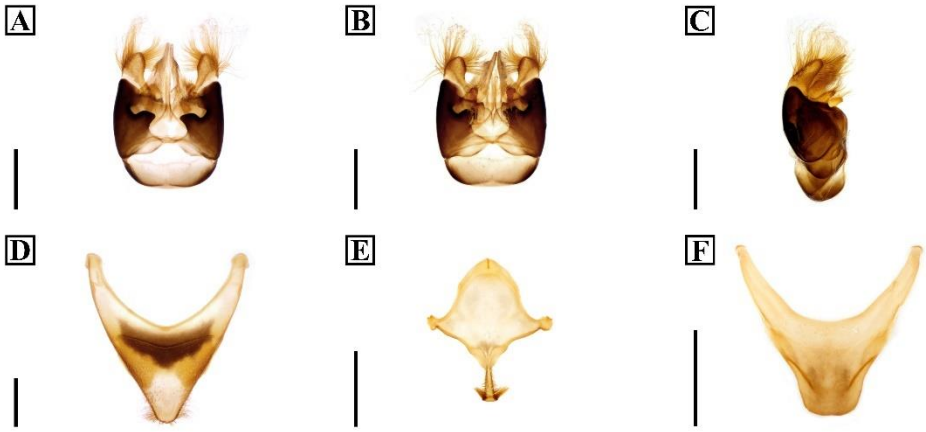

Plate 2-3. Male terminalia of *Nomada calloptera*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

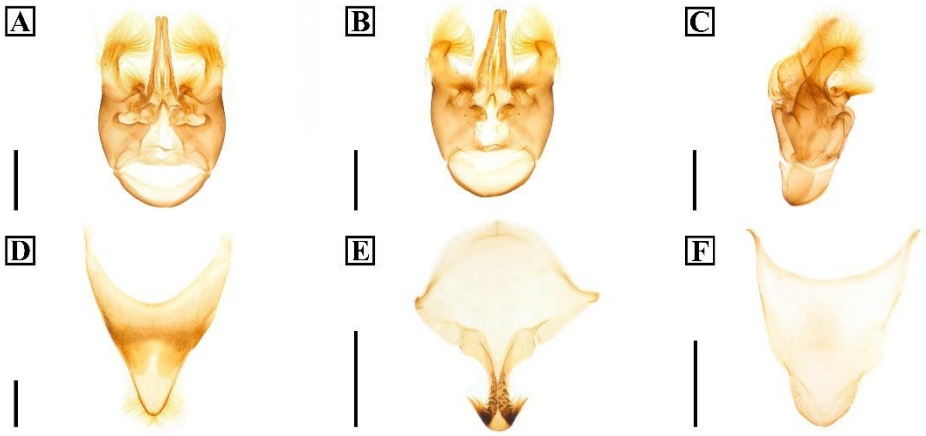

Plate 2-4. Male terminalia of *Nomada comparata*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

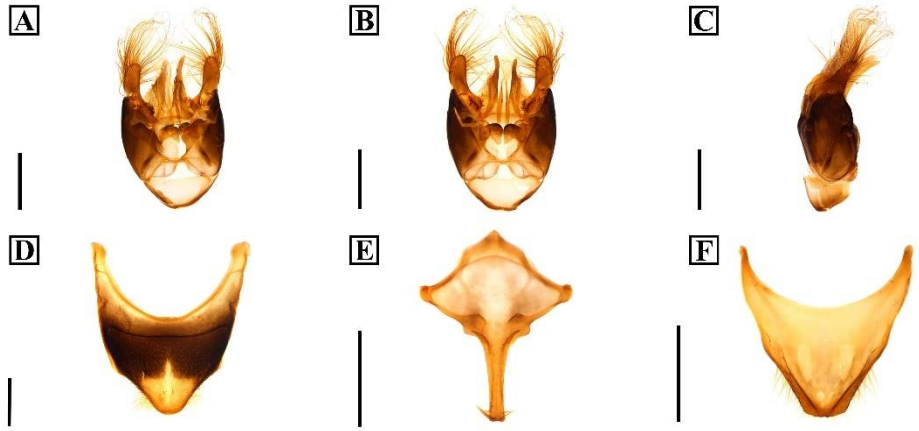

Plate 2-5. Male terminalia of *Nomada esana*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

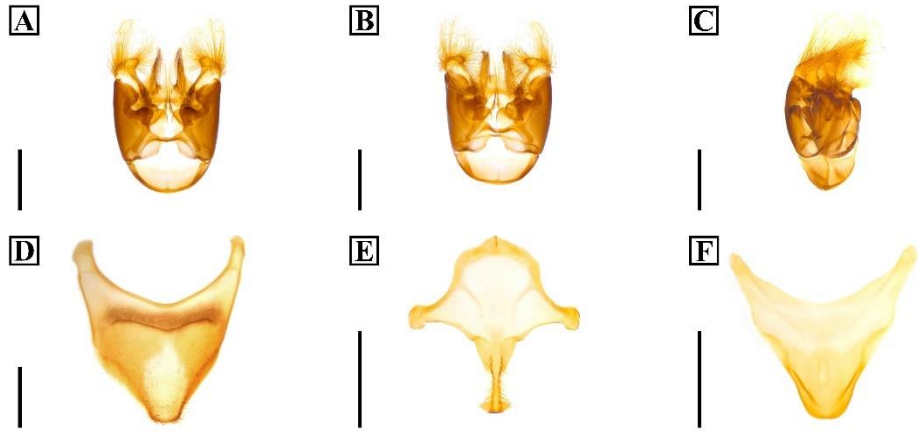

Plate 2-6. Male terminalia of *Nomada fervens*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

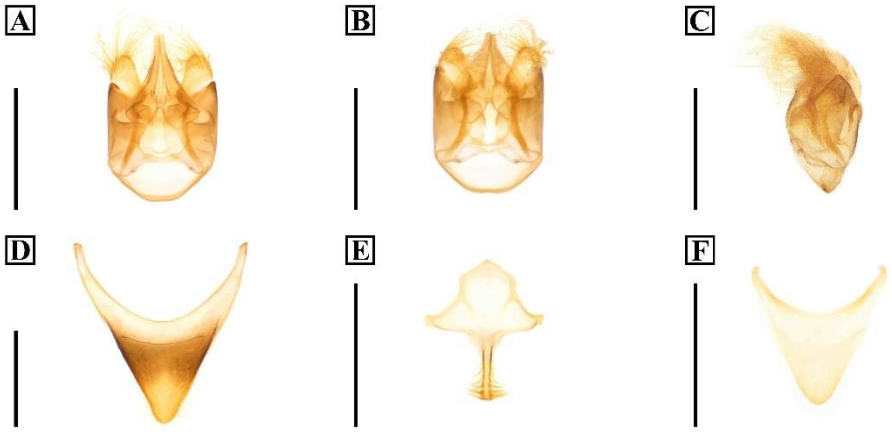

Plate 2-7. Male terminalia of *Nomada flavoguttata*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

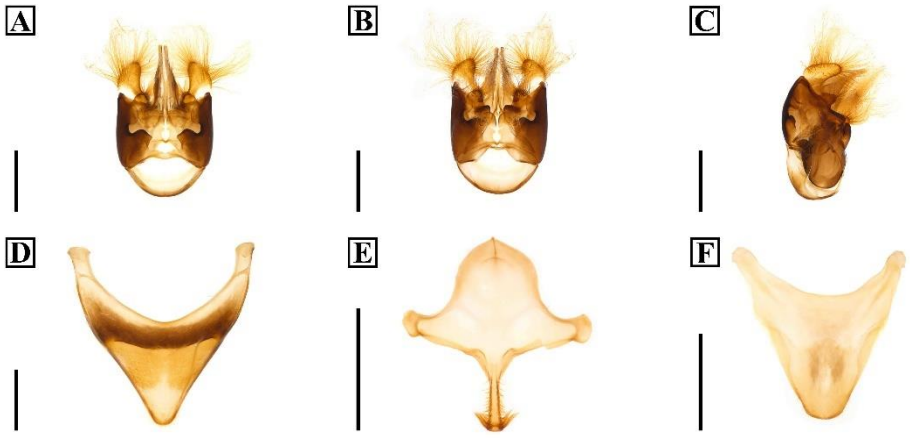

Plate 2-8. Male terminalia of *Nomada fulvicornis jezoensis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

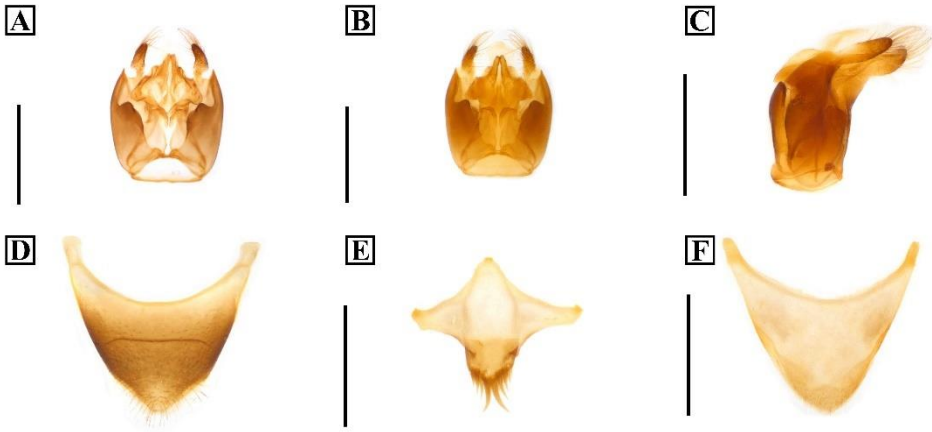

Plate 2-9. Male terminalia of *Nomada galloisi*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

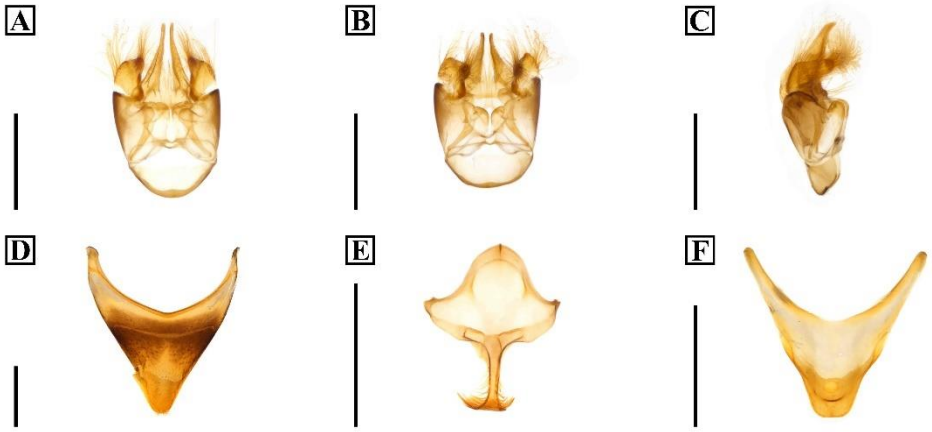

Plate 2-10. Male terminalia of *Nomada ginran*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

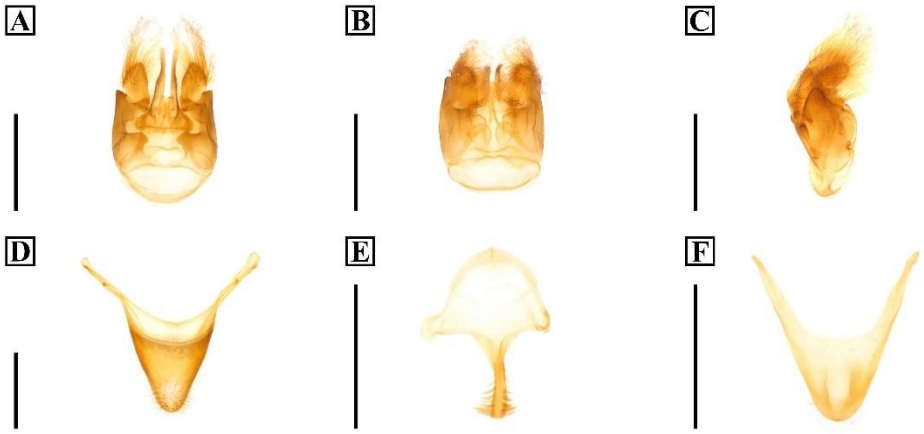

Plate 2-11. Male terminalia of *Nomada guttulata*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

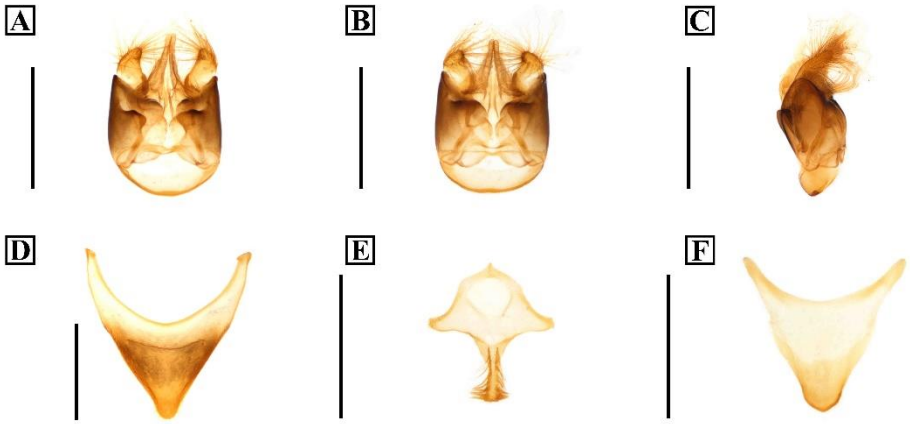

Plate 2-12. Male terminalia of *Nomada hakonensis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

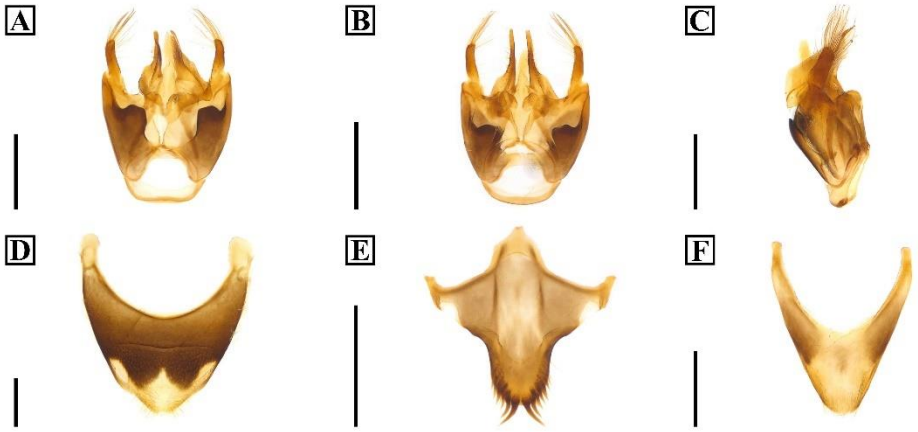

Plate 2-13. Male terminalia of *Nomada hakusana hakusana*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

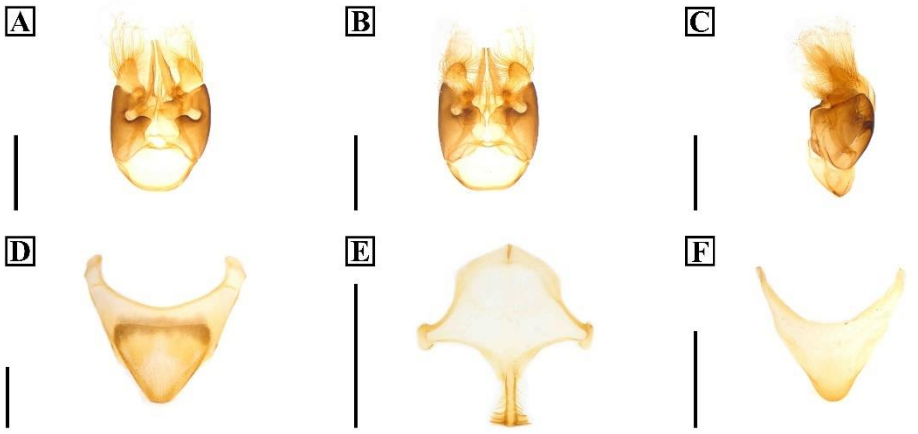

Plate 2-14. Male terminalia of *Nomada harimensis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

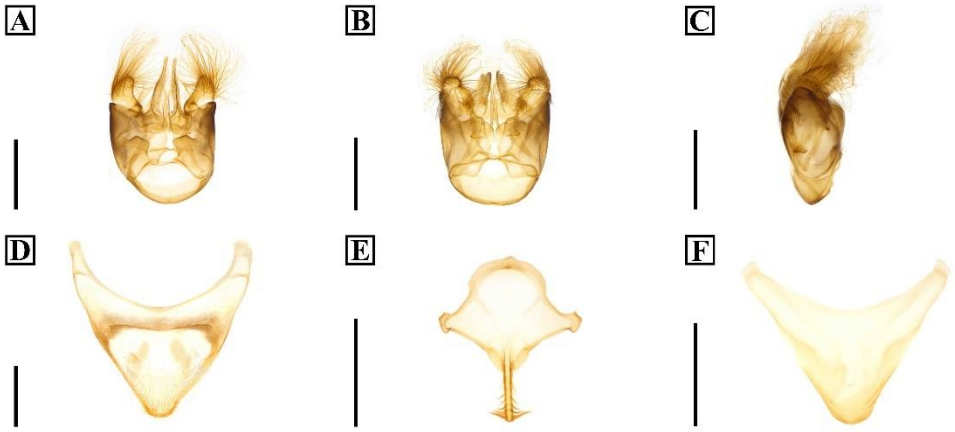

Plate 2-15. Male terminalia of *Nomada icazti*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

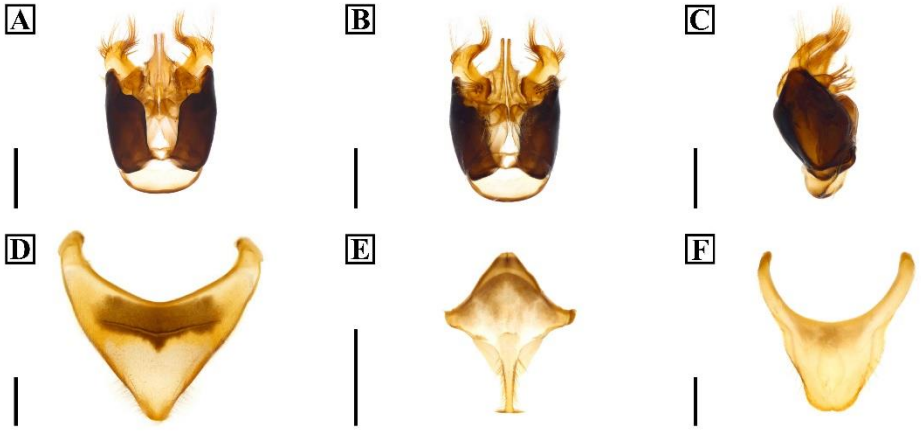

Plate 2-16. Male terminalia of *Nomada japonica*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

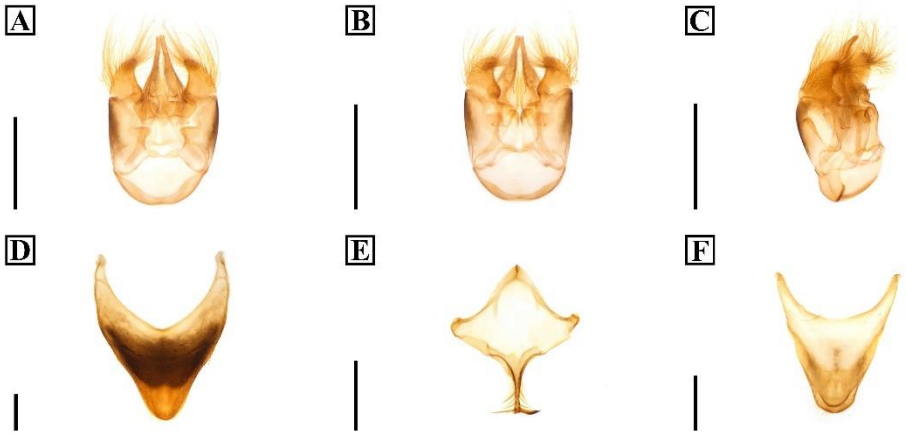

Plate 2-17. Male terminalia of *Nomada kaguya*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

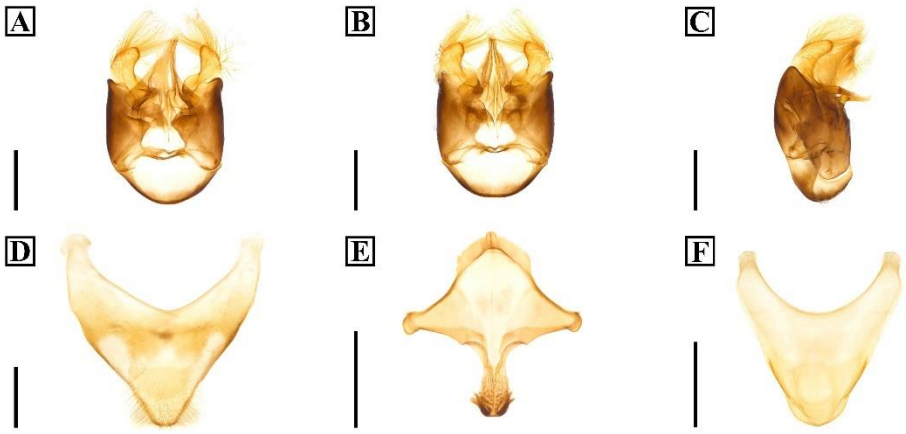

Plate 2-18. Male terminalia of *Nomada lathburiana*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

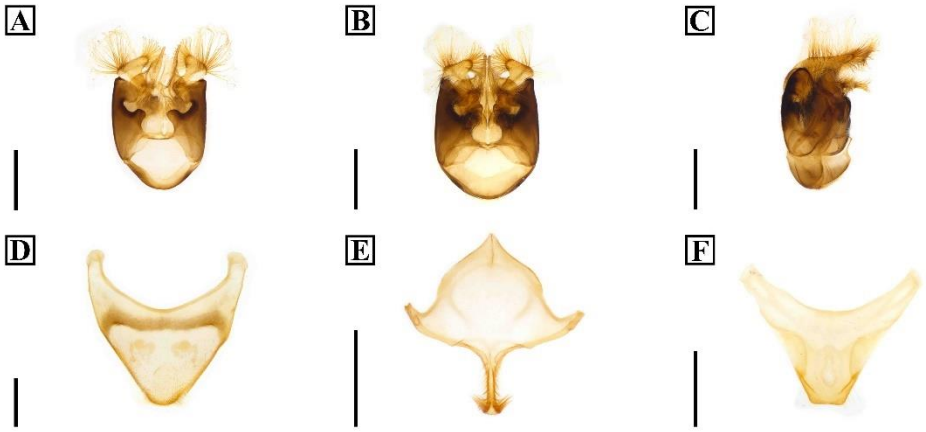

Plate 2-19. Male terminalia of *Nomada maculifrons*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

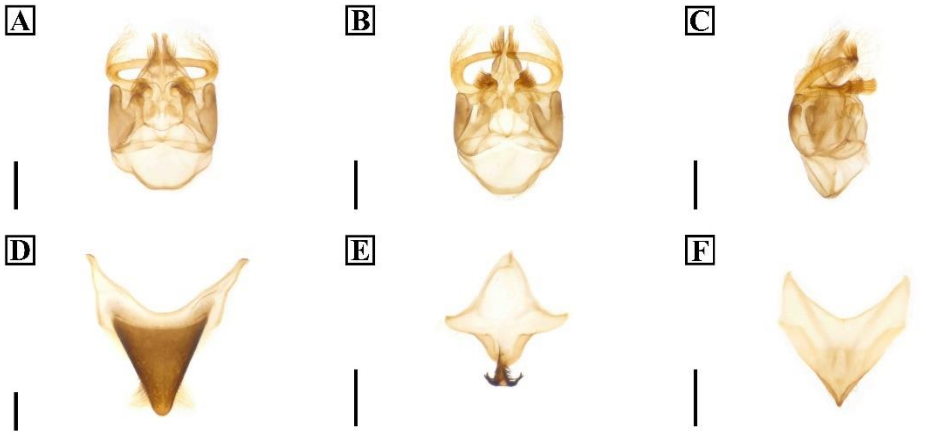

Plate 2-20. Male terminalia of *Nomada okubira*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

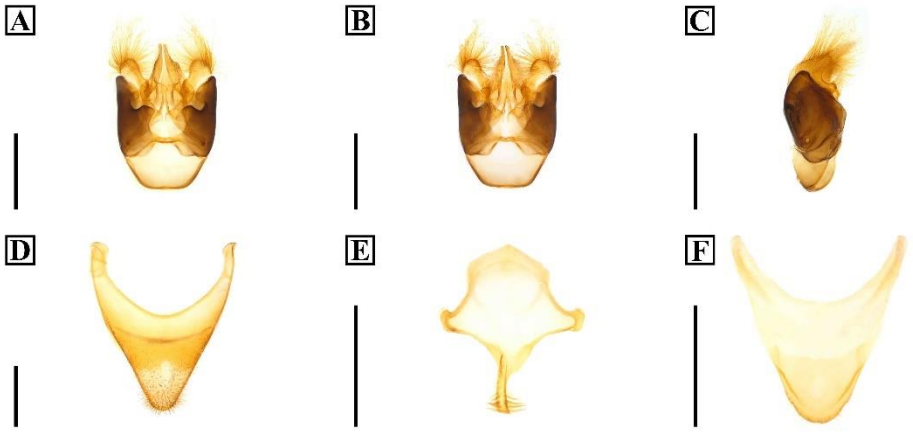

Plate 2-21. Male terminalia of *Nomada pacifica*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

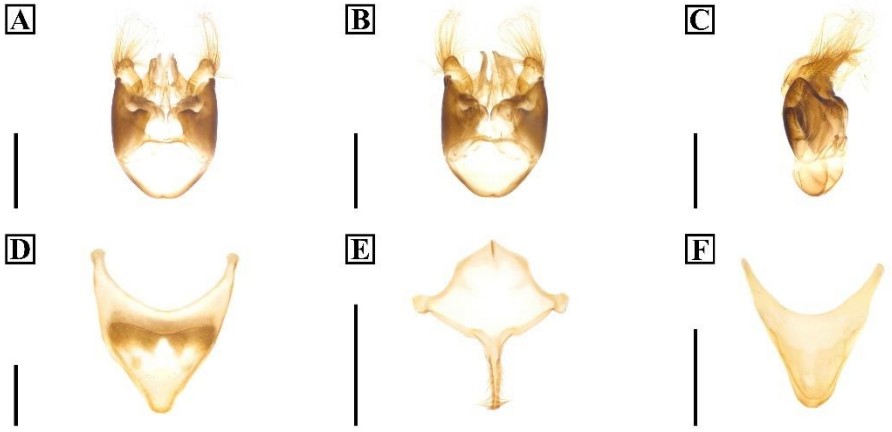

Plate 2-22. Male terminalia of *Nomada panzeri orientis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

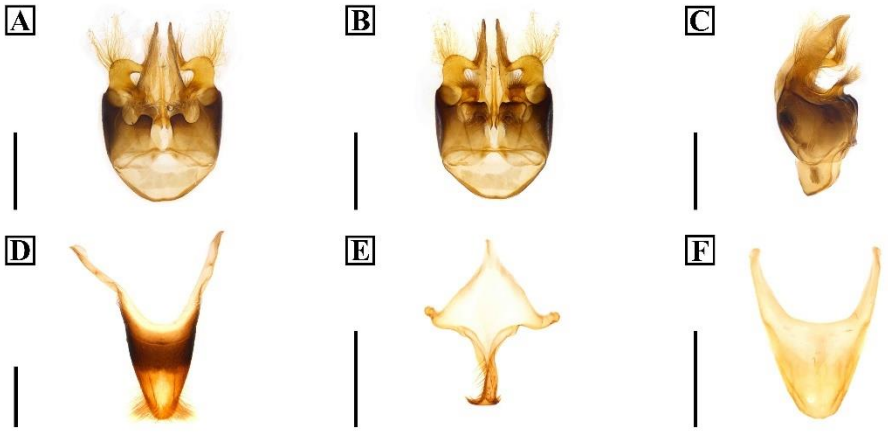

Plate 2-23. Male terminalia of *Nomada pekingensis*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

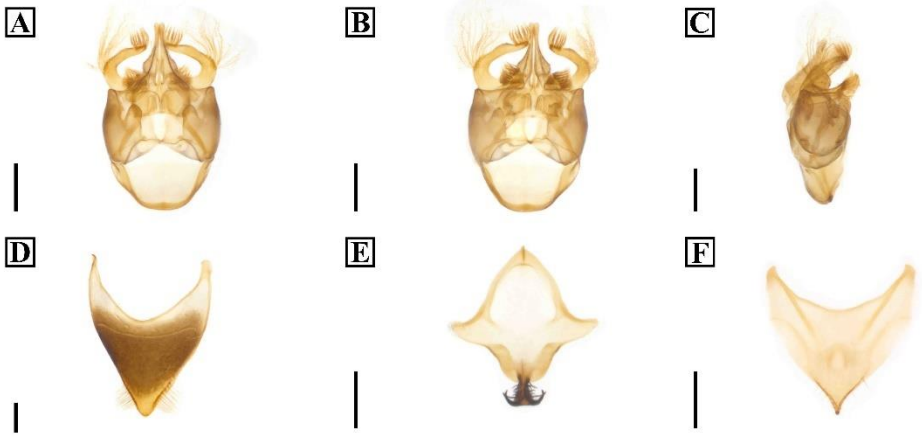

Plate 2-24. Male terminalia of *Nomada pulawskii*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

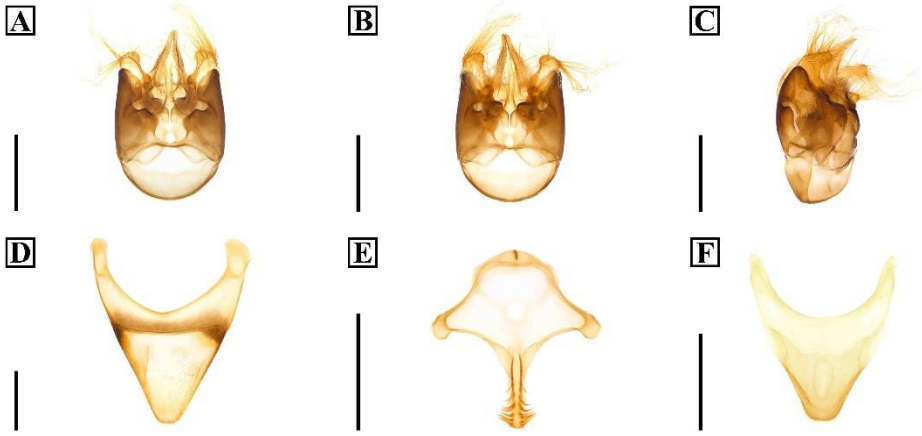

Plate 2-25. Male terminalia of *Nomada shirakii*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

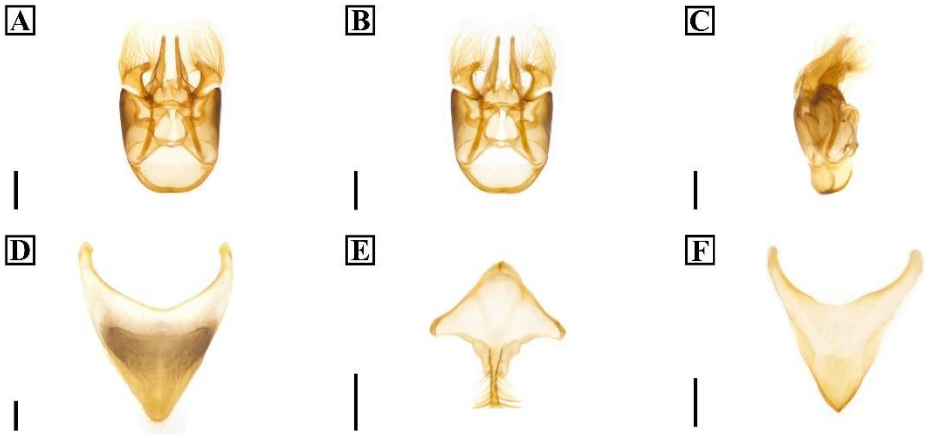

Plate 2-26. Male terminalia of *Nomada taicho*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

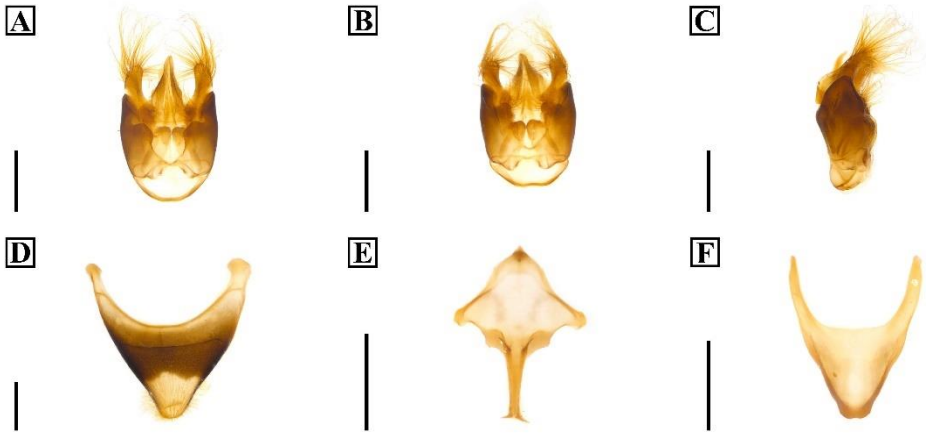

Plate 2-27. Male terminalia of *Nomada tsunekiana*. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

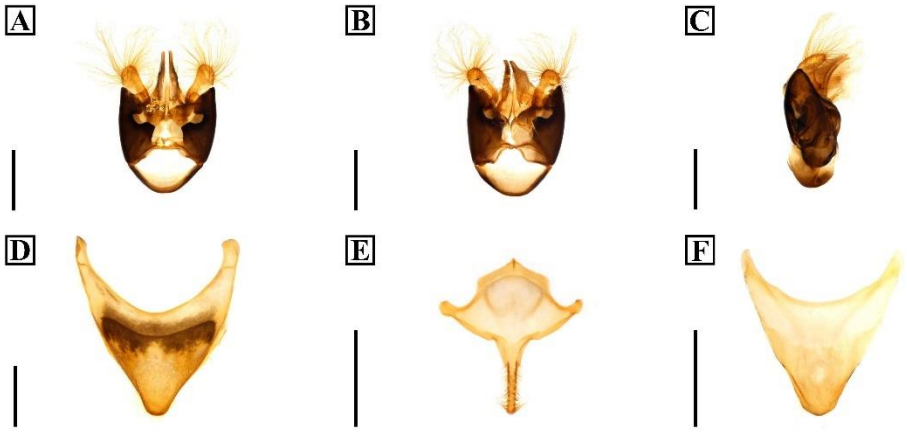

Plate 2-28. Male terminalia of *Nomada* sp. nov. 1. **A,** Genital capsule in ventral view; **B,** Genital capsule in dorsal view; **C,** Genital capsule in lateral view; **D,** 7th tergum in dorsal view; **E,** 8th sternum in ventral view; **F,** 7th sternum in ventral view (Scale bar 0.5 mm)

Plates 3. Living appearance of adult (Photo: Wonwoong Kim & Kayun Lim)

Plate 3-1. *Nomada comparata* Cockerell, 1911 **쌍발톱알락꽃벌**. **A,** female; **B,** male

Plate 3-2. *Nomada ginran* Tsuneki, 1973 **흰털허리알락꽃벌**. **A,** female; **B,** male

Plate 3-3. *Nomada hakonensis* Cockerell, 1911 **긴더듬이알락꽃벌** (**A,** female); Nomada japonica Smith, 1873 **왜알락꽃벌**(**B,** male)

Plate 3-4. *Nomada taicho* Tsuneki, 1973 넓적머리알락꽃벌. **A,** female; **B,** male

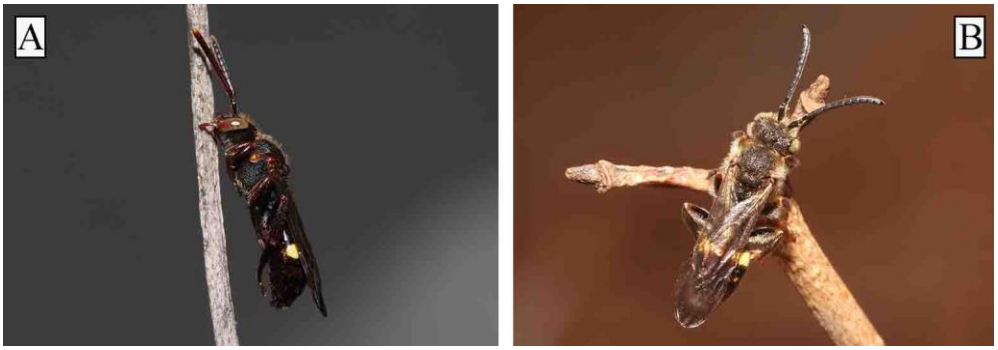

Plate 3-5. *Nomada* sp. nov. 1. **A,** female; **B,** male

국문초록

알락꽃벌속에 대한 분류 및 알락꽃벌아과의 계통, 진화학적 연구

서울대학교 대학원
농생명공학부 곤충학전공
임가윤

본 연구는 한반도산 알락꽃벌속에 대한 분류 및 알락꽃벌아과에 대한 계통 진화학적 연구로써, 총 세가지 연구로 구성되어 있다. 첫번째는 한반도에 서식하는 알락꽃벌속의 분류학적 검토, 두번째는 분자마커를 이용한 알락꽃벌아과의 계통분석 및 알락꽃벌속의 종군 재구성, 마지막으로 세번째는 분자마커를 이용한 절취기생성 꽃벌류와 숙주의 몸 크기의 진화론적 변화를 추론하는 연구이다.

첫 번째 연구에서는 45 종의 한반도산 알락꽃벌속에 대한 분류학적 연구가 수행되었으며, 이를 통하여 3 종의 미기록종 (*Nomada aswensis* Tsuneki, *Nomada fusca* Schwarz, *Nomada pulawskii* Tsuneki)과 3 종의 신종이 확인되었다.

두 번째 연구에서는 6 개의 분자마커를 이용하여 알락꽃벌아과 및 알락꽃벌속 종군의 계통관계를 확인한 결과, 알락꽃벌아과는 단계통으로 나타났으며 알락꽃벌속과 가장 근연한 족은 Hexepeolini 로 나타났다.

더불어 기존 형태기반으로 분류되었던 알락꽃벌속의 종군 중 일부가 측계통으로 확인되어 추후 추가적인 종군 재구성 연구가 필요할 것으로 확인되었다.

세 번째 진화연구에서는 원시적인 알락꽃벌아과는 계통학적으로 근연한 그룹에 기생하였으나 점차 다양한 분류군의 숙주를 선택하는 방향으로 진화하였으며, 기생자의 몸 크기가 숙주의 크기와 양의 관계가 있다는 해리슨의 법칙이 알락꽃벌아과내에서 적용 가능함을 확인하였다.

검색어: 알락꽃벌속, 알락꽃벌아과, 뻐꾸기벌, 절취기생, 해리슨법칙, 한반도

감사의 글

2020 년도에 입학하여 2 년 반 동안의 석사과정 동안 정말 많은 것을 배웠고, 성장할 수 있었던 것 같습니다. 가장 먼저 실험실에서 공부할 수 있도록 허락해주시고 부족한 저에게 연구 관련 지도뿐만 아니라 진로에 대해 다양한 조언을 해주신 지도교수님, 이승환 교수님께 감사드립니다. 벌을 연구하는 교수님의 제자로서 부족함이 없는 연구자가 될 수 있도록 미국에서도 정진하겠습니다. 또한 분류학 외에도 여러 연구 분야를 접하게 해주신 이준호 교수님, 이시혁 교수님, 제연호 교수님, 이광범 교수님, 탁준형 교수님, 또한 이번에 졸업논문 심사를 해주신 강창구 교수님께도 깊은 감사 인사를 드립니다.

더불어 알락꽃벌을 분류군으로 정하고 얼마되지 않았을 때, 분류 연구를 위해 전폭적으로 도와주시고 표본대여를 허락해주신 이흥식 박사님과, 박사님을 포함한 '벌 볼 일 있는 사람들' 모임원들, 그 중 특히 오흥윤, 강의영, 조수정 선생님께 감사드립니다. 선뜻 표본을 기증해주고 항상 열심히 필드를 다니는 준서에게도 감사와 응원을 보냅니다.

그다음으로 계통분류학이라는 같은 길을 걷고 있는 든든한 실험실원들에게 감사드리고자 합니다. 가장 먼저, 표본 제작 방법을 알려주시고 항상 잘 챙겨주신 염문옥 선생님께 감사와 존경을 표하고자 합니다. 또한 퇴근할 때마다 늘 데려다주시고, 고민이 있을 때마다 시간을 내 주신 소라 언니, 실장이자 인생의 선배로서 다양한 조언을 해주신 민호 오빠, 학기 초 분류군 설정부터 헤매면서 한창 힘들어할 때 여러 네트워크에 연결해 주시고 격려해주신 건호 오빠, 적절한 당근과 채찍으로 옳은 길로 이끌어주는 승현 오빠, 양봉후계자라며 많이 아껴준 진영 오빠, 채집 때마다 많은 도움을 받은 민혁 오빠, 분류학이 생소하게 느껴졌던 제게 정말 많은 가르침을 주신 분류학의 아버지와도 같은 덕영 오빠, 언제나 살갑게 대해주시는 진배 오빠, 유머 코드가 잘 맞는 민석 오빠, 언제나 자기 일처럼 도와줬던 재석 오빠, 그리고 실험실에서 인턴으로 일하며 여러모로 많은 도움을 받은 원웅이, 지원이, 성검이, 주형이에게도 감사합니다.

표본을 검경하기 위해 석사과정 동안 여러 기관을 방문했는데 이를 허락해주신 이종욱 교수님, 이봉우 박사님, 김일권 박사님, 김창준 박사님, 이승규 박사님, 이관석 박사님, 송정훈 박사님께도 감사드리고, DNA 샘플 대여를 허락해주신 Finnish Museum of Natural History 의 Gunilla Ståhls 박사님, 기꺼이 필요한 사진 데이터를 제공해주신 김철민 박사님, 또 선뜻 알락꽃벌 표본을 빌려주시고 동정에 많은 도움을 주신 Jan Smit, Keiichi Otsui 씨, 그리고 채집 표본을 기증해주신 Alexander ganse 선생님께도 감사를 전합니다.

계통 논문 주제를 구상하고 구체화할 때 가장 시간이 많이 소요되고 어려웠던 점은 몸 크기 데이터를 확보하는 것이었습니다. 이를 위해 연락했을 때 번거로울 수 있었을 텐데도 연구에 도움을 주신 Brigit Jauker 와 Frank Jauker 박사님, Gerardo Quintos 씨, Douglas Yanega 박사님, 데이터를 활용하지는 못했지만 많은 시간을 내어주신 Joseph Monks 박사님, 늘 알락꽃벌 연구를 응원해주시고 동정 관련 조언을 해주신 Sam Droege 씨, 통계에 관하여 도움을 주신 준호씨, 그리고 논문화에 크게 기여해주신 Michael Orr 박사님에게도 진심으로 감사드립니다.

마지막으로 어떤 길을 선택하던 믿고 지지해주시는 부모님과 가족들, 유학 가는 길을 응원해준 소꿉친구들인 가영이, 수현이, 원규, 도도, 그리고 현구와 윤혁 오빠를 포함한 핌프 동아리 사람들에게도 고맙다는 말을 꼭 전하고 싶습니다.

끝으로 지면의 제한으로 인하여 언급하지 못한 모든 분들께 감사드립니다. 지금까지 받은 도움들 절대 잊지 않고 저도 남에게 도움이 되는 사람이 될 수 있도록 최선을 다하겠습니다.