

New suggestion of the species group reconstruction of genus *Nomada* Scopoli, 1770 (Hymenoptera, Apidae) from Korea

Kayun Lim^{1,2}, Seunghwan Lee^{2,3}

1 Utah State University, Department of Biology, 5305 Old Main Hill, Logan, UT 84322-5305, USA **2** Insect Biosystematics Laboratory, Research Institute for Agriculture and Life Sciences, Seoul National University, Seoul 151-921, Republic of Korea **3** Department of Agricultural Biotechnology, Seoul National University, Seoul 151-921, Republic of Korea

Corresponding author: Seunghwan Lee (seung@snu.ac.kr)

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Abstract

Genus *Nomada*, which includes approximately 800 species, is the largest genus in the subfamily Nomadinae and the sole genus in the tribe Nomadini. Its taxonomic classification is particularly challenging due to high morphological variations, making it one of the most controversial groups in the subfamily. In order to shed light on the complex classification of *Nomada* species and their tribal position, this study conducted a multi-locus phylogeny using one mitochondrial gene (COI) and five nuclear protein-coding genes (EF1 α , Nak, Opsin, Pol II, Wingless). The study focused on expanding the knowledge of some East Palearctic species, with the ultimate goal of reviewing species groups of *Nomada* present in Korea. In this study, we suggest that the *ruficornis* species group is polyphyletic. Some species should be moved to more appropriate species groups as follows: *N. tsunekiana*, *N. emarginata*, and *N. flavopicta* into the *basalis* species group; *N. aswensis*, *N. kaguya*, and *N. taicho* into the *armata* species group.

Keywords

Bees, Cleptoparasite, *Nomada*, Nomadinae, Molecular phylogeny, Multi-locus

Introduction

Nomada, the only genus in the tribe Nomadini and the largest genus in the subfamily Nomadinae, is composed of around 800 species (Smit 2018). This genus has a predominantly Holarctic distribution in all continents except Antarctica (Alexander 1994). Due to the high morphological diversity exhibited by this genus, its classification into subgroups has been a contentious issue, particularly at the species level, where identification is challenging. For example, the genus has been divided into various subgenera or even designated as new genera by Nearctic taxonomists, while most Palearctic taxonomists have insisted on the species group concept (Snelling 1986; Alexander 1994). Thereafter, Alexander (1994) reconstructed the genus using the species group concept in *Nomada* which are *adducta*, *armata*, *basalis*, *belfragei*, *bifasciata*, *erigeronis*, *furva*, *gigas*, *integra*, *odontophora*, *roberjeotiana*, *ruficornis*, *superba*, *trispinosa*, *vegana*, and *vincta*. Of these, the *ruficornis* species group, which is the largest among the 16 established groups, may be a paraphyletic group due to the lack of apomorphic characters (Alexander 1994). 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 a 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 that belong to the *ruficornis* species group are more like the remnants of the species that cannot be merged into the other species group (Mitai and Tadauchi 2007).

Nomada species from Korea have been classified into species groups primarily based on the work of Mitai and Tadauchi (Mitai and Tadauchi 2003, 2004, 2005, 2006, 2007, 2008), with an update by Won and Kim (Won and Kim 2013). Initially, molecular phylogenetics using a COI marker was employed by Won to resolve the species group complex of the *Nomada* in his Ph.D. dissertation (Won 2006). However, as the number of recorded species within Korea has increased and with improvements in molecular phylogenetics, further research is necessary to expand upon the previous study, which was limited in scope by analyzing 12 species and using a single marker.

Recently, with the advancement of phylogenomics and the use of ultra-conserved elements (UCEs), Sless et al. (2022) provided the new classification of the subfamily Nomadinae using UCE and Odanaka et al. (2022) showed paraphyly of *ruficornis* species group. On the other hand, Lim et al. (2022) noted that with variations in taxon sampling, the *ruficornis* species group is polyphyletic. However, the taxon sampling of the study was mainly focused on the species that have host information. 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 from Korea, which is currently subject to incomplete and controversial systematic classifications.

Methods

Taxon sampling

For this study, we included 74 species as an ingroup and selected 6 species from Ammobatoidini, Neolarrini, and Hexepeolini as an outgroup (See Suppl. material 1). Outgroup species were chosen due to its close relationship with *Nomada* based on Sless et al. (2022) and availability in NCBI database. To clarify the validity of the species group concept by Alexander (1994), we included *Nomada ruficornis*, *N. roberjeotiana*, *N. bifasciata*, *N. armata*, *N. furva*, as they represent the type species of various species groups. In total, sampling in this study encompasses 8 species groups out of the 16 species groups. We added 44 more *Nomada* species from Lim et al. (2022), out of which 17 species were newly sequenced for this study, and the remaining sequences were obtained from NCBI (Suppl. material 1).

DNA extraction, PCR amplification, and sequencing

To extract total genomic DNA, we ground up either the detached midleg, head of the alcohol vouchers or dried specimens. The wet lab work protocol was consistent with the supplementary information 3 from Lim et al. (2022). We utilized one mitochondrial protein-coding gene, namely the cytochrome oxidase subunit I gene (COI), and five nuclear protein-coding genes (EF-1 α , long-wavelength rhodopsin (opsin), NaK, pol II, and wingless) to maintain consistency with Lim et al. (2022). All DNA vouchers were deposited in the Insect Biosystematics Laboratory at Seoul National University.

Sequencing alignments

We utilized SeqMan Pro version 7.1.0 (DNASTAR, Inc., Madison, WI, U.S.A.) to assemble, check, and trim the raw sequence data. The sequence alignment of all six genes was conducted using MAFFT version 7 (<https://mafft.cbrc.jp/alignment/server/>), and the sequences were adjusted in Mega 7 with the amino acid translation option. In cases where the length of certain genes differed between the NCBI data and the newly obtained sequences, longer sequences were removed. Finally, the aligned sequences were combined using SequenceMatrix Windows ver. 1.8 (Vaidya et al. 2011).

Phylogenetic analyses

We conducted phylogenetic analyses using two methods, Bayesian inference (BI) and Maximum likelihood (ML). Different potential partitioning schemes, considering codon position and genes, and nucleotide substitution models were assessed using ModelFinder2 (Kalyaanamoorthy et al. 2017) within IQ-TREE 2.2.3 (Minh et al. 2020) using “TEST-

NEWMERGE” option. Following the implementation of the most suitable partitioning scheme and substitution models, IQ-TREE2 generated a ML tree, and nodal supports were determined through 1000 ultrafast bootstrap replicates (Hoang et al. 2018).

On the other hand, because some models, such as TIM, TNe, TN models, were not applicable in MrBayes 3.2.7 for BI (Ronquist et al. 2012), we excluded the unavailable models in MrBayes by using the “-mset” option to restrict the testing procedure with the “TESTMERGEONLY” (See Suppl. material 2). To conduct the MrBayes analysis, we ran 20 million Markov chain Monte Carlo (MCMC) generations, and trees were sampled every 100 generations. We executed one cold chain and three heated chains for each MCMC analysis. We examined the outcome with Tracer 1.7.1 (Rambaut et al. 2018) and discarded the first 2,500,000 sampled trees as burned in.

Results

The dataset used for the phylogenetic reconstruction contained 660 bp of COI, 442 bp of *ef1a*, 870 bp of *Nak*, 459 bp of *Opsin*, 840 bp of *Pol2*, 456 bp of *Wng*, for a total of 3727 bp of the nucleotide sequence. Phylogenies obtained through BI and ML support for the monophyly of *Nomada*.

Although the monophyly of the tribe Nomadini remains notably stable, the *ruficornis* species group showed polyphyly, which is consistent with Lim et al. (2022). For example, *N. imbricata* and *N. lathburiana*, previously categorized within the *ruficornis* species group, were nested within the *bifasciata* species group. Similarly, *N. tsunekiana*, *N. emarginata*, and *N. flavopicta* were clustered with the *basalis* species group. Furthermore, the *roberjeotiana* species group showed paraphyly in both ML and BI. Notably, the *bifasciata* species group formed a well-supported subclade (BS=88, PP=97) with *N. lathburiana* and *N. imbricata*, previously considered part of the *ruficornis* species group.

When it comes to the *armata* species group, it was also revealed as paraphyletic due to the *N. kaguya* and *N. asuensis*, which were previously treated as the *ruficornis* species group as well, and *N. taicho*, formerly treated as *furva* species group according to the Alexander and Schwarz (1994). Because multiple species that were originally placed within the *ruficornis* species group radiated into multiple species groups, a polyphyly of this species group was confirmed in this study.

Discussion

Phylogeny of subfamily Nomadinae

Alexander first 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 and Tadauchi 2007; Proshchalykin and Lelej 2010; Smit 2018; Lim et al. 2022; Odanaka et al. 2022; Lim and Lee 2023). However, he mentioned that one of the species groups, the *ruficornis* species group, may be a paraphyletic group that belongs to a remnant of a more comprehensive clade without relatively distinct apomorphic subunits such as in *armata* and *basalis* species group (Alexander 1994; Mitai and 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 and Tadauchi 2004). However, it was reconstructed as a member of the *armata* species group later (Mitai and Tadauchi 2007). Won also indicated in his PhD thesis that the *bifasciata* species group, *trispinosa* 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 Odanaka et al. (2022), the largest number of *Nomada* was exploited for phylogenetic analysis compared to the previous investigations and suggested that the *ruficornis* species group is paraphyletic, with highlighting potential new species group. In this study, we suggest that the *ruficornis* species group is polyphyletic, which is congruent with Lim et al. (2022) but with the expanded sampling of East Palearctic species. The discrepancy between the previous classification and redesignation will be discussed below based on Fig. 1.

Node A.

Nomada tsunekiana Schwarz, 1999, which is distributed only in Korea has been considered as the *ruficornis* species group (Won and Kim 2013). However, it formed a subclade within the *basalis* species group in this study. According to Alexander (1994), the diagnostic characters of the *basalis* species group were as follows: 1) mandible simple and round at tip; 2) first flagellar segment. evidently longer than the 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, the 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 as 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 a distinctly shorter first flagella to belong to the *ruficornis* species group (Fig. 2). 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 the *ruficornis* species group and possess no setae on the hind tibiae (Smit 2018). The complexity of the *roberjeotiana* species group might have arisen due to the sampling limitation because the analyses for *N. obtusifrons* and *N. argentata* were based on only COI data. Therefore, a more comprehensive taxon sampling should be conducted to enhance the resolution of the *roberjeotiana* species group.

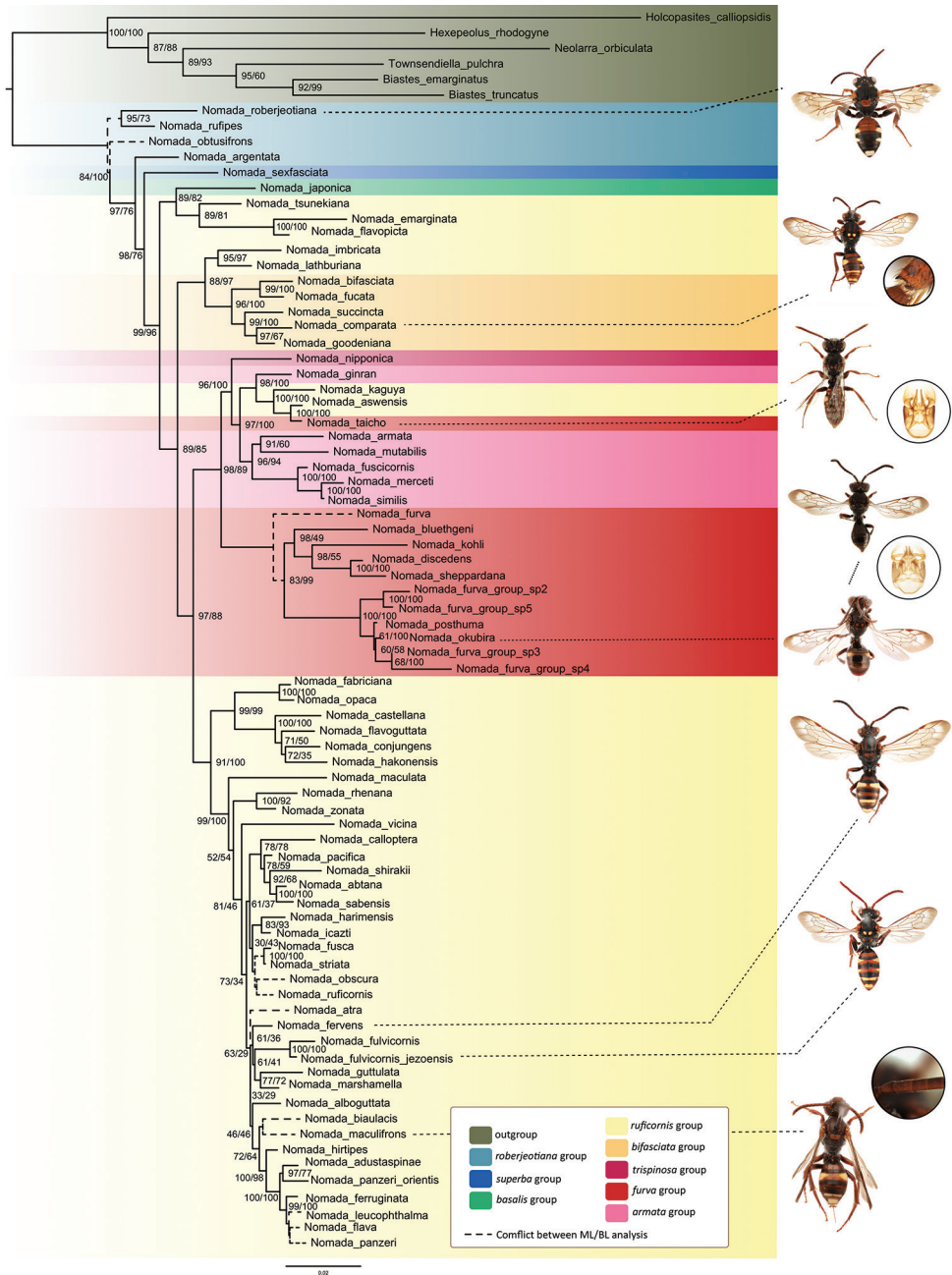


Figure 1. Phylogenetic trees (ML/ BI) of genus *Nomada* (Photo: Kayun Lim).

Node B.

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 or three in number on the margin of hind tibiae of the females (Alexander 1994).

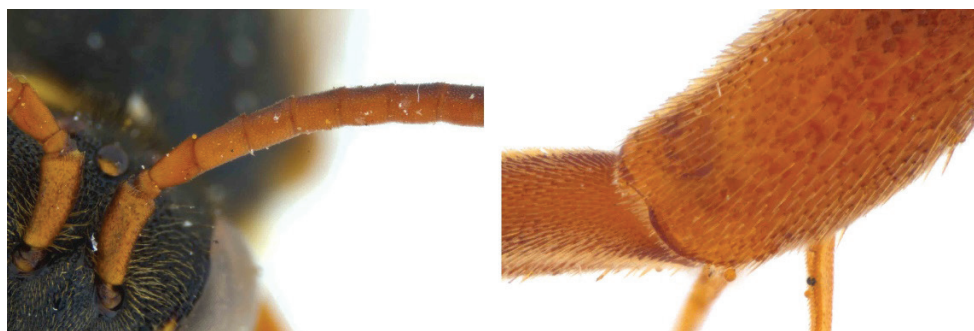


Figure 2. *N. tsunekiana* female. left, antennae in ventral view; right, hind tibiae (Photo: Kayun Lim).

However, the species group formed the subclade with *N. lathburiana*, and *N. imbricata*, which were placed in the *ruficornis* species group (Alexander 1994), indicating the classification of *bifasciata* species group may need modification as the apomorphic character for it cannot be applied to these two species. Otherwise, the new species group must be designated with *N. lathburiana* and *N. imbricata*. For example, the females of *N. lathburiana* possess three or four stout and straight setae (Smit 2018), and females of *N. imbricata* usually have about three, posteriorly curved setae on their hind tibiae (Personal observation). Alexander (1994) agreed that *N. imbricata* has a similar appearance to the species in the *bifasciata* species group, but he did not include the *N. imbricata* in the *bifasciata* species group because males did not have the apomorphic morphology. Consequently, further investigation of morphology with the increased taxon sampling must be conducted to resolve these species group complexes.

Node C.

The expanded multi-gene phylogeny in this study supports the designation of *N. ginran* within the *armata* species group, as proposed by Mitai and 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* were previously treated as the *ruficornis* species group, and *N. nipponica*, which was previously considered as the *trispinosa* species group, also formed the same clade with *N. armata*. Moreover, *N. taicho*, formally classified as the *furva* species group by Alexander and Schwarz (1994), was nested in the *armata* species group. Therefore, it might be plausible to move *N. aswensis* and *N. kaguya* to the *armata* species group. Traditionally, the *ruficornis* species group has been considered to have evidently shorter first flagellum than the second, while it is nearly equal in length in *N. aswensis* females (Mitai and Tadauchi 2007). Also, *N. kaguya* shares morphological characteristics with *N. aswensis* and *N. ginran*, such as stout setae and a generally small body size of less than 8 mm (Won and Kim 2013). However, its first flagellum is distinctly shorter than the second one, suggesting that flagellum length may not serve as a definitive apomorphic character for the *ruficornis* species group. Therefore, the redesignation of

the *ruficornis* species group with vast sampling 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 lacks the 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 the *furva* species group.

Conclusion

In this study, the review of species groups in genus *Nomada*, with a particular focus on the East Palearctic species, was conducted. Most of the species groups from the traditional classification by Alexander (1994) did not form monophyly. However, this discrepancy may not necessarily stem from inaccuracies in the traditional classification but rather from exceptions found among East Palearctic species, especially those from Northeast Asia. This is attributed to Alexander’s limited examination of collections by Tsuneki, a *Nomada* taxonomist from Japan. Consequently, the current classification must be expanded with these exceptions as described in the discussion and some species should be moved to the appropriate species group, including *N. tsunekiana*, *N. emarginata*, and *N. flavopicta* into the *basalis* species group, and *N. aswensis*, *N. kaguya*, and *N. taicho* into the *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 the *basalis* species group or remain nested within the *bifasciata* group. The updated species list with species group reconstruction can be found in Table 1.

Table 1. Species list of *Nomada* from Korea with new suggestion of the species group designation.

No.	Recorded species	Previous species group	This study
1	<i>Nomada abtana</i> Tsuneki, 1973	<i>ruficornis</i>	<i>ruficornis</i>
2	<i>Nomada adustaspinae</i> Lim & Lee, 2023	<i>ruficornis</i>	<i>ruficornis</i>
3	<i>Nomada amurensis</i> Radoszkowski, 1876	<i>ruficornis</i>	<i>ruficornis</i>
4	<i>Nomada aswensis</i> Tsuneki, 1973	<i>ruficornis</i>	<i>armata</i>
5	<i>Nomada atra</i> Lim & Lee, 2023	<i>ruficornis</i>	<i>ruficornis</i>
6	<i>Nomada bialacis</i> Lim & Lee, 2023	<i>ruficornis</i>	<i>ruficornis</i>
7	<i>Nomada calloptera</i> Cockerell, 1918	<i>ruficornis</i>	<i>ruficornis</i>
8	<i>Nomada comparata</i> Cockerell, 1911	<i>bifasciata</i>	<i>bifasciata</i>
9	<i>Nomada esana</i> Tsuneki, 1973	<i>ruficornis</i>	<i>ruficornis</i>
10	<i>Nomada fervens</i> Smith, 1873	<i>ruficornis</i>	<i>ruficornis</i>
11	<i>Nomada flavoguttata</i> (Kirby, 1802)	<i>ruficornis</i>	<i>ruficornis</i>
12	<i>Nomada fulvicornis jezoensis</i> Matsumura, 1912	<i>ruficornis</i>	<i>ruficornis</i>
13	<i>Nomada fusca</i> Schwarz, 1986	<i>ruficornis</i>	<i>ruficornis</i>
14	<i>Nomada galloisi</i> Yasumatsu & Hirashima, 1953	<i>roberjeotiana</i>	<i>roberjeotiana</i>
15	<i>Nomada ginran</i> Tsuneki, 1973	<i>armata</i>	<i>armata</i>
16	<i>Nomada guttulata</i> Schenck, 1861	<i>ruficornis</i>	<i>ruficornis</i>
17	<i>Nomada hakonensis</i> Cockerell, 1911	<i>ruficornis</i>	<i>ruficornis</i>

No.	Recorded species	Previous species group	This study
18	<i>Nomada hokusana hokusana</i> Tsuneki, 1973	<i>roberjeotiana</i>	<i>roberjeotiana</i>
19	<i>Nomada harimensis</i> Cockerell, 1914	<i>ruficornis</i>	<i>ruficornis</i>
20	<i>Nomada icazti</i> Tsuneki, 1976	<i>ruficornis</i>	<i>ruficornis</i>
21	<i>Nomada japonica</i> Smith, 1873	<i>basalis</i>	<i>basalis</i>
22	<i>Nomada kaguya</i> Hirashima, 1953	<i>ruficornis</i>	<i>ruficornis</i>
23	<i>Nomada koreana</i> Cockerell, 1926	<i>ruficornis</i>	<i>ruficornis</i>
24	<i>Nomada lathburiana</i> (Kirby, 1802)	<i>ruficornis</i>	<i>ruficornis</i>
25	<i>Nomada leucophthalma</i> (Kirby, 1802)	<i>ruficornis</i>	<i>ruficornis</i>
26	<i>Nomada maculifrons</i> Smith, 1869	<i>ruficornis</i>	<i>ruficornis</i>
27	<i>Nomada montverna</i> Tsuneki, 1973	<i>ruficornis</i>	<i>ruficornis</i>
28	<i>Nomada nipponica</i> Yasumatsu & Hirashima, 1951	<i>trispinosa</i>	<i>armata</i>
29	<i>Nomada okamotoi</i> Matsumura, 1912	<i>roberjeotiana</i>	<i>roberjeotiana</i>
30	<i>Nomada okubira</i> Tsuneki, 1973	<i>furva</i>	<i>furva</i>
31	<i>Nomada opaca</i> Alfken, 1913	<i>ruficornis</i>	<i>ruficornis</i>
32	<i>Nomada pacifica</i> Tsuneki, 1973	<i>ruficornis</i>	<i>ruficornis</i>
33	<i>Nomada panzeri orientis</i> Tsuneki, 1973	<i>ruficornis</i>	<i>ruficornis</i>
34	<i>Nomada pekingensis</i> Tsuneki, 1986	<i>trispinosa</i>	<i>trispinosa</i>
35	<i>Nomada pulawskii</i> Tsuneki, 1973	<i>furva</i>	<i>furva</i>
36	<i>Nomada pyrifer</i> Cockerell, 1918	<i>ruficornis</i>	<i>ruficornis</i>
37	<i>Nomada roberjeotiana aino</i> Tsuneki, 1973	<i>roberjeotiana</i>	<i>roberjeotiana</i>
38	<i>Nomada sabaensis</i> Tsuneki, 1973	<i>ruficornis</i>	<i>ruficornis</i>
39	<i>Nomada sexfasciata</i> Panzer, 1799	<i>superba</i>	<i>superba</i>
40	<i>Nomada shirakii</i> Yasumatsu & Hirashima, 1951	<i>ruficornis</i>	<i>ruficornis</i>
41	<i>Nomada shoyozana</i> Tsuneki, 1986	<i>roberjeotiana</i>	<i>roberjeotiana</i>
42	<i>Nomada striata</i> Fabricius, 1793	<i>ruficornis</i>	<i>ruficornis</i>
43	<i>Nomada taicho</i> Tsuneki, 1973	<i>furva</i>	<i>armata</i>
44	<i>Nomada temmasana temmasana</i> Tsuneki, 1986	<i>roberjeotiana</i>	<i>roberjeotiana</i>
45	<i>Nomada tsunekiana</i> Schwarz, 1999	<i>ruficornis</i>	<i>basalis</i>

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Supplementary material I

NCBI accession numbers

Authors: Kayun Lim, Seunghwan Lee

Data type: docx

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Supplementary material 2

Model selection for BI

Authors: Kayun Lim, Seunghwan Lee

Data type: docx

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