

The evolutionary history of the cleoptoparasitic bee genus *Nomada* with
an emphasis on the species of North America

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Abstract

Approximately 12% of all bee species found in North America are brood parasitic and exhibit significant morphological adaptations that allow them to successfully parasitize a host nest. Of the different genera of cleptoparasitic bees, the most diverse and taxonomically challenging is the genus *Nomada*, which has approximately 800 species and can be found on every continent except Antarctica. Due to their enigmatic nature, very little is known regarding *Nomada* biology, evolution, and population dynamics. Further complicating studying *Nomada* is inconsistency in species concepts due to immense variation within and between species and the lack of updated taxonomic tools needed to identify species. This dissertation aims to address gaps pertaining to the evolutionary history, biogeography, and population dynamics of *Nomada* at both a global and a more local North American level. The first global phylogeny and biogeography for the genus is presented here. *Nomada* was found to have a Holarctic origin around 65 million years ago and subsequently dispersed into the southern hemisphere at least three times while also dispersing throughout the Nearctic and Palearctic multiple times over various land bridges. To explore phylogeographic patterns as well as population genetic structure and diversity, the North American endemic species *Nomada articulata* was used as a model, a first for a cleptoparasitic bee. It is suggested that the Wisconsinan glaciation influenced *N. articulata* populations by dividing the species along an east-west gradient but over time, these populations dispersed, creating a single panmictic population that persists to the present. Furthermore, *N. articulata* is suggested to be a species complex with two possible new and unknown species of *Nomada* in the southern United States. Lastly, newly updated keys are provided with the aim to help remedy the lack of updated species level keys for the genus in eastern North America. As a result, fully illustrated keys are provided for five of the seven *Nomada* species groups found in eastern Canada and the United States covering male and female characters for 15 different species. Additionally, one new synonymy is presented and updated information pertaining to the biology, evolution, and taxonomy is included. The research presented here provides an important first step towards understanding the evolution and diversification of *Nomada* and how, more broadly, cleptoparasitic bees became one of the most successful groups of bees.

Dedication

Dedicated to my parents Michael and Margie for supporting me throughout all of my academic endeavors and to everyone who has contributed to every step I have taken to get me here, from a naïve undergraduate at Colorado State University to a slightly less naïve research technician at Michigan State University and Masters student at the University of New Hampshire. I also dedicate this to myself because if I can survive alone in a small bachelor pad in a foreign country separated from my family during the worst of the COVID-19 pandemic, I can survive anything.

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Statement of Authorship

I, Katherine Odanaka, am the sole author of Chapters 1, and 5 of my doctoral dissertation titled “A global phylogeny and biogeography of the cleptoparasitic bee genus *Nomada* Scopoli with the phylogeography and updated taxonomic keys to a selection of eastern North American species.” Chapters 2 and 3 were the result of a collaborative effort between the following individuals and myself: Michael Branstetter, Kerrigan Tobin, and Sandra Rehan. For Chapter 3 Farida Samad-zada was an additional collaborator. Chapter 4 is the result of collaboration between myself, Laurence Packer and Sandra Rehan. For all three chapters, I am the primary author and writer. Furthermore, all analyses and results presented are my own. MB, KT, SR, FSZ and LP contributed significantly to these projects and therefore I have listed them as coauthors for each individual manuscript that was produced from these three chapters; one of which was already published (Chapter 2) and one that is in review at the time of submission of this dissertation (Chapter 3). For Chapters 2 and 3, MB and KT assisted in generating data by extracting DNA from specimens, as well as data curation and in providing feedback for the finalized manuscripts that were submitted for peer review. For Chapter 3 FSZ assisted in initial data generation and taught me the methodology for the analyses used. Furthermore, FSZ provided feedback for the manuscript version of Chapter 3 that was submitted for peer review. For Chapter 4, LP assisted in conceptualization and helped with editing and providing feedback. SR, as my advisor, assisted in the conceptualization of all three projects as well as providing funding and helped with editing and providing feedback for the finalized manuscripts. Michael Branstetter, Kerrigan Tobin, Sandra Rehan, Farida Samad-zada, and Laurence Packer all consented to being co-authors on these papers, respectively. Lastly, the self-citations within the Introduction and Chapters 3 and 4 (Odanaka et al., 2022) refer to Chapter 2.

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Chapter 1 Introduction

Parasites are important, but often overlooked, organisms that provide valuable information which improve our understanding of community ecology, biogeography, and diversification (Cook et al., 2017, Gagne et al., 2022). The parasitic lifestyle is usually unidirectional due to intense modifications in behavior, physiology, and dietary limitations which ultimately binds the parasite to its host (Haelewaters et al., 2018, Litman, 2019; Litman et al., 2013, Muche et al., 2022); however, there are instances of organisms secondarily adapting back to a free-living lifestyle (e.g. Xu et al., 2016). Moreover, parasitism has been shown to provide many ecosystem services, such as regulation and stabilization of food webs (Hudson et al., 2006; Lafferty et al., 2006), maintenance of host populations (Dobson et al., 2008) and stabilization of competition between hosts (Hudson & Greenman, 1998), which if lost would have immense ecological consequences.

No lineage of parasitic bee has ever reverted back to pollen collecting (Dehon et al., 2017; Litman, 2019; Litman et al., 2013); all obligatory parasitic bees have lost the ability to collect pollen and construct nests; instead, they evolved mechanisms and behaviours adapted for stealth and defense, including spines, a reduced pygidial plate, and faster production of mature oocytes (Bohart, 1970; Lhomme & Hines, 2019; Litman, 2019; Michener, 2007; Rozen, 2003). The relationship between parasitic bees and their hosts frequently, but not always, follows Muller's Law (Muller, 1871). Also known as Emery's Rule, Muller's Law is divided into either a strict or loose form and states that parasitic organisms are often closely related to (loose) or are sister lineages (strict) to their hosts (Gibbs et al., 2012; Litman et al., 2013; Muller, 1971; Sless et al., 2022; Smith et al., 2007). How Muller's Law effects the different parasitic lineages depends on the age of the group and the type of parasitism expressed (Gibbs et al., 2012; Litman et al., 2013; Sless et al., 2022; Smith et al., 2007).

Two types of parasitism exist in bees (Litman et al., 2013): social parasitism and cleptoparasitism (sometimes called brood parasitism (Litman, 2019; Michener, 2007)), with cleptoparasitic lineages vastly outnumbering those that exhibit social parasitism. Approximately 13% of bee species found globally and about 30% of all apid bees are considered as brood parasites (Danforth et al., 2019), in which the parasitic female lays eggs in the nests of other

bees. Once the first egg hatches, the hospicidal and highly mobile parasite larva proceeds to kill and consume any remaining eggs of the host and parasite with a pair of scythe like mandibles (Michener, 2007; Rozen, 1991). The larva then molts, assumes a more grub-like form, and then consumes the host provisioned pollen ball (Michener, 2007; Rozen, 1991).

The most diverse and taxonomically challenging genus of cleptoparasitic bees is the *Nomada*, with over 16 species groups and ~800 species worldwide (Ascher & Pickering, 2024), Alexander, 1994; Alexander & Schwarz, 1994; Michener, 2007). The next most speciose cuckoo bee genus is *Coelioxys* (Megachilidae) with less than 500 species (Ascher and Pickering, 2023). Recently, molecular support was provided for 14 of the original 16 species groups (Odanaka et al., 2022) as well as the first biogeographic analysis for the genus (Odanaka et al., 2022). Straka et al (2024) further expanded upon the findings of Odanaka et al (2022) when the majority of the 16 species groups found in the Palaearctic were organized into 13 new or resurrected subgenera. Currently, three endemic North American species groups (the *vincta*, *adducta* and *belfragei* groups) are not placed into subgenera while the former *odontophora* species group is now elevated to genus status (*Acanthonomada*) (Straka et al., 2024).

Nomada are slender, wasplike bees and are often coloured red or black with white or yellow markings (Michener, 2007). These bees generally occur in low frequencies and most of their females' behaviour revolves around successfully finding and invading hosts' nests. At present, few studies have been successful in documenting *Nomada* behaviour, and the majority focus on nest scouting and copulation (Abrams & Eickwort, 1980; Cane, 1983; Eickwort & Abrams, 1980; Linsley & MacSwain, 1955; Rozen, 1977). Females primarily use olfactory cues to locate suitable nests but switch to visual cues for finding nest entrances (Cane, 1983; Schindler et al., 2018). How *Nomada* avoid host detection when entering a nest is still unknown but odor mimetism is strongly suggested (Tengö & Bergstrom, 1976, 1977; Velez-Ruiz & Smith-Pardo, 2013). Males are known to transfer topical pheromones to females during copulation by grabbing the female's antenna with their own; chemical analyses of some of these compounds were matched to chemicals present in *Andrena* and *Melitta* hosts (Schindler et al., 2018; Tengö & Bergstrom, 1976, 1977).

Members of the genus *Andrena* make up the majority of *Nomada*'s hosts and the tight relationship between *Andrena* and *Nomada* can be seen in the shared phenology of the host-

parasite pairs and coevolutionary history (Balfour et al., 2018; Lim et al., 2022; Straka et al., 2024). Many *Andrena* are constrained by season, only occurring for short periods in the spring or late summer, which match with the phenology for many of the *Nomada* species. While *Andrena* species are the main target, *Nomada* females scouting aggregations that contain multiple genera show no response differences and will attempt entry into any open nest regardless of what genus actually made it (Cane, 1983). This suggests that *Nomada* speciation may occur due to opportunistic host switching and possibly explains why some *Nomada* species parasitize genera outside of *Andrena* (Cane, 1983). An example of a species that has multiple hosts in two different genera is *Nomada imbricata* Smith, which has been recorded as a definite host on *Andrena vicina* Smith and *Halictus parallelus* Say (Alexander 1991). *N. imbricata* has also been recorded as a nest parasite of *Andrena regularis* (Schrader & LaBerge 1978), *A. barbara* (Hall & Ascher, 2011), and *A. dunningi* (Hall & Ascher, 2011). While *N. imbricata* is an extreme example of a species using many different hosts, other *Nomada* are only currently known from a single host. For example, *N. crotchii* is a confirmed parasite of *Andrena prunorum* as specimens from the Los Angeles Natural History Museum are labeled as being reared from nest cells of *A. prunorum* (personal observation but see Alexander, 1991 for probable record). Other known *Nomada* with single hosts include *Nomada banksi* (nest parasite on *Andrena asteris*) (Espinoza, et al., 2023) and *N. vineta* (on *A. helianthi*) (Gibbs et al., 2023). Other known hosts include species found in *Colletes*, *Eucera*, *Lasioglossum*, and *Agapostemon* (Michener, 2007).

Although *Nomada* are commonly collected in bee and pollinator surveys, their identification remains difficult because of little and seemingly inconsistent morphological variation between species resulting in many collected specimens remaining wholly unidentified or only identified to genus. Within North America there are few identification keys available for determining species of *Nomada* and when available, they are either outdated or confusing to use due to the lack of illustration and inconsistent terminology (Ascher & Pickering, 2024; Broemeling, 1988; Broemeling & Moalif, 1988; Evans, 1972; Mitchell, 1962; Snelling, 1986). Despite the challenges in identification, the confusion surrounding *Nomada* taxonomy in North America has been improving with the use of molecular methods in validating species concepts (Droege et al., 2010; Gibbs et al., 2023).

Nomada and other cleptoparasitic genera have the potential to be valuable bioindicators of the overall bee community health in a given environment due to their total dependence on their hosts and restrictive habitat requirements (Odanaka & Rehan, 2019; Sheffield et al., 2013); if an environment can support a cleptoparasitic community, it is healthy enough to support healthy populations of the host as well. Ultimately, little is known regarding *Nomada* evolution, biology, and ecology. Therefore, the overall purpose of this thesis is threefold: 1) document the global phylogeny and historical biogeography *Nomada*; 2) determine the phylogeography of a widespread species; and 3) produce an updated taxonomic key for the species of eastern North America.

By exploring these topics, I aim to expand our understanding of *Nomada*, and therefore cleptoparasitic bees, especially in the realms of evolution, biogeography and population genetics as well as provide a clear key that facilitates easy identification of *Nomada* species. Currently, no parasitic bee species have been included in a population genetics study; therefore, it is difficult to assess how parasitic bee populations respond to landscape and climate change over long periods of time. Furthermore, *Nomada* are commonly collected in bee surveys but are almost never included in analyses due to the lack of a reliable way to separate species; thus, lowering their ability to be important indicators of bee community health. By providing a new key that includes clear images and descriptions, more *Nomada* may be included in important ecological surveys.

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Chapter 2: Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements

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Abstract

The genus *Nomada* Scopoli (Hymenoptera: Apidae) is the largest genus of brood parasitic bees with nearly 800 species found across the globe and in nearly all biogeographic realms except Antarctica. There is no previous molecular phylogeny focused on *Nomada* despite their high species abundance nor is there an existing comprehensive biogeography for the genus. Using ultraconserved element (UCE) phylogenomic data, we constructed the first molecular phylogeny for the genus *Nomada* and tested the monophyly of 16 morphologically established species groups. We also estimated divergence dates using fossil calibration points and inferred the origin and of this genus around the globe. Our phylogeny recovered 14 of the 16 previously established species groups as monophyletic. The *superba* and *ruficornis* groups, however, were recovered as non-monophyletic and need to be re-evaluated using morphology. Divergence dating and historic biogeographic analyses performed on the phylogenetic reconstruction indicates that *Nomada* most likely originated in the Holarctic ~65 Mya. Geodispersal into the southern hemisphere occurred three times; once during the Eocene into the Afrotropics, once during the Oligocene into the Neotropics, and once during the Miocene into Australasia. Geodispersal across the Holarctic was most frequent and occurred repeatedly throughout the Cenozoic era, using the De Geer, Thulean, and the Bering Land Bridges. This is the first instance

of a bee using both the Thulean and De Geer land bridges and has implications of how early bee species dispersed throughout the Palearctic in the late Cretaceous and early Paleogene.

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Introduction

Nearly 13% of all bee species globally and around 20% of all bee species in the family Apidae exhibit the cleptoparasitic behavioral trait known as brood parasitism (Danforth, Minckley, & Neff, 2019). An ancient trait found within four different bee families (Cardinal, Straka, & Danforth, 2010;), brood parasites play important ecological roles within their ecosystems. Brood parasites are known to be the main cause of brood damage (Minckley & Danforth, 2019); however, the dependency of brood parasites on their hosts make them important indicators of bee community health (Odanaka & Rehan, 2019; Sheffield, Pindar, Packer, & Kevan, 2013). Recent work indicates that the majority of brood parasitic bees (excluding the genera *Aglae* and *Exacerbate* (Euglossini), and *Ctenoplectrina* (Ctenoplectrini)) are found within the apid subfamily Nomadinae (Bossert et al., 2019; Cardinal et al, 2010; Sless et al., 2022).

The genus *Nomada* is the largest genus of brood parasites with an estimated 795 species found globally (Alexander & Schwarz, 1994; Litman et al., 2013). While members of the genus *Andrena* are common hosts, *Nomada* are known to parasitize species from other bee families including Apidae, Halictidae, Melittidae, and Colletidae. *Nomada* are most species diverse across the Holarctic region and use a mode of parasitism dubbed “open cell” or “larva-open strategy” (Litman et al., 2013). Adult female *Nomada* seek out and deposit eggs into host nest cells that are still being provisioned. After egg laying, a hospicidal larva emerges and kills any remaining host eggs or larvae in the cell (Litman, 2019; Litman et al., 2013; Rozen, 1991).

Historically, *Nomada* taxonomy has been ambiguous; Snelling in the 1980’s separated *Nomada* in the Western Hemisphere across three genera and ten subgenera based off of genus group names that had been proposed between 1880’s and 1940’s (Snelling, 1986). *Nomada* was last reorganized into 16 species groups by Alexander (1994) using morphological cladistic methods (App. table 1). This revision of the genus transferred some of Snelling’s subgenera into species groups and created new groups for species that were formerly unplaced (= *incertae sedis*) (Alexander, 1994). Of the currently recognized 16 species groups, the majority are found in either the Holarctic, Palearctic, or Nearctic regions; however, every ecoregion except Antarctica is represented (Alexander, 1994; Michener, 2007). Since the establishment of the 16 species

groups there have been no subsequent studies, molecular or morphological, to validate these groups or examine the phylogenetic relationships among them.

There is currently no comprehensive assessment of the historical biogeography of *Nomada*. Consequently, the age and origin of the genus is rather uncertain. There are two putative hypotheses regarding the region of origin. The first hypothesis suggests that the Neotropics might be the region of origin for *Nomada* due to the diversity and abundance of species found within South America (Michener, 1979, 2007). Despite the high diversity and abundance, nearly all *Nomada* species found in the Neotropics were sorted into what eventually became the *vegana* species group (Alexander & Schwarz, 1994). From the Neotropics, it has further been suggested that *Nomada* later dispersed northward into the Holarctic and then outwards into the remaining ecoregions (Michener, 1979, 2007). The second hypothesis is based on cladistic results indicating that the “basal” clade of the genus originated in the Afrotropics, specifically South Africa (Alexander, 1989, 1991). This conclusion was drawn primarily based on the finding that the *gigas* group was the most plesiomorphic and had the least amount of shared characteristics with any of the other species groups (Alexander, 1989, 1991). However, Alexander (1991) also noted that there are not many apomorphic characters shared by all the *Nomada* groups. It was further suggested by Alexander (1991) that *Nomada* then dispersed northward from the Afrotropics into the Palearctic and then into the remaining ecoregions. Despite differences in region of origin, both hypotheses predicted a tropical southern hemisphere origin of the genus with dispersal into the northern hemisphere and then back into the remaining southern hemisphere ecoregions.

Here we provide the first global molecular phylogeny of *Nomada* representing all 16 species groups and all ecoregions where the genus occurs. We also infer the group’s historical biogeography using divergence dating and model-based biogeographic reconstruction methods. The objectives are threefold: 1) construct the first global molecular phylogeny of *Nomada* covering all known species groups, 2) determine the age and origin of the genus, and 3) map the historical biogeography of this genus including representation from all known ecoregions; in doing so, we test the two competing hypotheses regarding the origin of the genus.

Methods

2.1 Sample collection

A total of 144 individuals were used in the phylogenetic analyses for this study. Of these individuals, 142 represent unique species. The ingroup included 119 taxa, of which 114 were newly sequenced (App. table 2). The sampled *Nomada* represented all 16 species groups and the six biogeographic realms where the genus is found. For the outgroup, 23 taxa representing all four apid subfamilies (Anthophorinae, Apinae, Nomadinae, Xylocopinae) were included (App. table 2), 16 of which are newly sampled. Data for five ingroup and seven of the outgroup taxa were retrieved from several recent publications (Freitas et al. 2020; Grab et al. 2019; Sless et al. 2022). Samples used in this study were obtained through loans from various institutions as well as recent field collections from around the world. For rooting our phylogenetic trees we used the apid subfamily Anthophorinae.

2.2 DNA extraction

DNA was extracted from pinned specimens using non-destructive methods and Zymo Quick-DNA Miniprep Plus Kits (Zymo Research, Irvine, CA, USA). Whole body specimens were carefully removed from the pins and placed into individual tubes with a Proteinase-K digestion buffer solution. Tubes were then incubated overnight at 55°C and extracted according to manufacturer protocols, with the modifications noted in Branstetter et al. (2021). Following extraction, specimens were washed in 95% ethanol, dried and re-mounted back on the pin. DNA concentration was checked using a Qubit 3.0 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA) and quality was assessed using a TapeStation instrument (Agilent, Santa Clara, CA, USA).

2.3 UCE library preparation and enrichment

We used UCE phylogenomics to generate our sequence data (Faircloth et al., 2012) and followed the protocols outlined in Branstetter et al. (2017). We used a bee-ant specific probe set (Grab et al., 2019), which is just a subset version of the principal (Branstetter et al., 2017), to enrich 2,545 UCE loci. The probes are synthesized and available through Arbor Biosciences (Ann Arbor, MI, USA).

Extracted samples were first sheared to fragment sizes of ~400-600 bp using a Qsonica sonicator (Q800R2; Qsonica, Newton, CT, USA). Older samples were not sheared due to their already degraded status; all other samples were sonicated for either 30, 60, or 90 seconds depending on their quality. Illumina libraries were generated using KAPA HyperPrep kits (Roche Sequencing, Pleasanton, CA, USA) and custom dual-indexing adapters (Glenn et al., 2019). Fragmented DNA was purified and concentrated using an in house paramagnetic-bead solution (Rohland & Reich, 2012). Once the final bead cleaning was complete, sample DNA concentration was measured using a Qubit 3 fluorometer and then pooled into 12 groups containing 9-10 samples of equimolar concentrations.

Enrichment of the samples followed protocols from both Arbor Biosciences (v4 protocol; day1) and a standard UCE protocol (Blumenstiel et al., 2010; day 2) split over two consecutive days. After enrichment, each pool was quantified using qPCR, combined into one sample and then sent off for sequencing.

2.4 Sequencing and data processing

Sequencing, data processing, and phylogenetic analysis follow similar methods outlined in (Branstetter, Muller, Griswold, Orr, & Zhu, 2021). A total of 116 samples were sent to Novogene Inc. (Sacramento, CA, USA) for single lane multiplexed sequencing using Illumina HiSeq X. Our newly generated UCE data were then combined with data from five previously sequenced *Nomada* samples and 23 outgroup samples (Freitas et al. 2020; Grab et al. 2019; Sless et al. 2022). All newly sequenced data are available on NCBI (SRR18055085 – SRR18055199; App. table 2). We extracted UCE data from already published genomes using the “Harvesting UCE Loci from Genomes” tutorial found at (<https://phyluce.readthedocs.io/en/latest/tutorial-three.html>) and described in Faircloth (2017). Raw sequence reads were demultiplexed using BBTools (Bushnell, 2014) and the reads were then cleaned, trimmed, and assembled using the package Phyluce v1.6 (Faircloth, 2016) and its associated programs. Specifically, raw reads were trimmed using Illumiprocessor v2.0 (Faircloth, 2013), a wrapper for the software Trimmomatic (Bolger, Lohse, & Usadel, 2014) and then assembled using Spades (Bankevich et al., 2012). Contigs matching UCE loci were identified and extracted using the program LastZ v1.0 (Harris, 2007) within Phyluce and then aligned using MAFFT v7.130b (Katoh & Standley, 2013). Alignments were trimmed using Gblocks (Talavera & Castresana, 2007), with reduced

stringency parameters ($b1=0.5$, $b2=0.5$, $b3=12$, $b4=7$) and the publicly available program Spruceup (Borowiec, 2019), which trims poorly aligned sequence from individual samples rather than columns. For the Spruceup analysis we used Jukes-Cantor distances, a guide tree, and a lognormal cutoff of 0.88. All other settings were left at default values. We then removed empty alignment columns using a custom script and filtered alignments for 75% taxon occupancy.

2.5 Phylogenetic trees

We analyzed our data using concatenated and species tree approaches. For the supermatrix we first examined the effects of partitioning the data by testing several different partitioning schemes: no partitioning, partitioning by locus, and partitioning using the Sliding Window Site Characteristics based on Entropy method (SWSC-EN; Tagliacollo & Lanfear, 2018). The SWSC-EN partitioning scheme divides UCE loci into three separate regions, a main core and a right and left flank (Tagliacollo & Lanfear, 2018). The core region of UCEs is more conserved while the flanking regions are more variable (Faircloth et al., 2012). The initial set of partitions identified by the SWSC-EN algorithm were merged using ModelFinder2 (Kalyaanamoorthy, Minh, Wong, Von Haeseler, & Jermin, 2017), which is part of IQ-Tree v2.1.1 (Nguyen, Schmidt, Von Haeseler, & Minh, 2015). For the analysis we used *reclusterf*, AICc, and the GTR + G model of sequence evolution. The resulting best-fit partitioning scheme reduced the number of data subsets to 1601. Maximum likelihood analyses were then conducted on each partitioning scheme using IQ-tree v2.1.1. For each analysis we used the GTR + F + G4 model of sequence evolution and measured branch support by conducting 1000 ultrafast bootstrap replicates (UFB; Hoang et al., 2018) and 1000 replicates of the SH-like approximate likelihood ratio test (Guindon et al., 2010; Hoang et al., 2018). To test the concatenated data for potential biases, we converted the matrix to RY-coding using a Phyluce script, and then analyzed the data in IQ-Tree using the SWSC-EN partitioning scheme and the “-MFP” option for model testing. Phylogenetic inference can be influenced by the potential negative impact of data saturation and base composition bias (Phillips & Penny, 2003). RY coding has been shown to reduce these negative impacts and the approach has been used to improve phylogenetic results in bees (Praz & Packer, 2014).

For species tree inference, we estimated individual gene trees for all loci using IQ-Tree and the standard DNA alignments, i.e. not converted to RY coding. We used the “-m MFP”

option for model selection and estimated branch support by conducting 1000 UFB replicates. We collapsed nodes receiving less than 10% support using Newick Utilities (Junier & Zdobnov, 2010). Using the gene trees as input, we carried out a standard species tree analysis using the summary-based method implemented in the program Astral III (Zhang, Sayyari, & Mirarab, 2017). Species tree branch supports were assessed based on local posterior probabilities.

2.6 Divergence dating and biogeography

We time dated the SWSC-EN partitioned tree from the above analyses using the program MCMCTree v4.9j found in PAML (Yang, 1997, 2007) and the R package MCMCTreeR (Puttick, 2019). The SWSC-EN tree was selected for dating because the SWSC-EN partitioning scheme had the best model fit and results among phylogenetic analyses were highly congruent. We secondarily calibrated the root node of the tree using a normal distribution prior with a mean age of $104.4 \text{ Mya} \pm 10 \text{ Mya}$ which was previously found in Cardinal, Buchmann, & Russell (2018). For all other calibrated nodes, we used fossil calibrations and applied skew normal prior distributions. Nine different outgroup fossils were used to calibrate the analysis, including one thought to be a brood parasite (App. table 3). We tested three data matrices: all loci, 1000 clocklike loci, and 500 clocklike loci. Clocklikeness was assessed using the program SortaDate (Smith et al. 2018), which measures root-to-tip variance within gene trees and then sorts them from highest to lowest variance. The 500 most clocklike loci were thus the loci with the least root-to-tip variance.

In addition to our main dating analyses described above, we tested an alternative fossil calibration scheme in which we replaced the fossil *Protomelecta brevipennis*, Cockerell (calibrating crown Nomadinae) with the fossil *Paleoepeolus micheneri* Dehon et al. (calibrating stem Epeolini). Both of these fossils have somewhat uncertain placement within Apidae; however, we ultimately favored the use of *P. brevipennis* due to recent criticism regarding the placement of *P. micheneri* within the Nomadinae (Onuferko et al., 2019). We also tested several different prior distributions with the *P. micheneri* fossil calibration to see if changing the prior produced a noticeable effect on ages. We tested uniform, skew normal, Cauchy, and modified Cauchy distributions, all based on the same minimum and maximum ages for the fossils. The results using *P. micheneri* were very similar to the results using *P. brevipennis* and can be found in the supplement (App. table 4; Supp images 1h-k).

We carried out the approximate likelihood dating method implemented in MCMCTree and used a relaxed lognormal clock model with independent rates and a GTR+G model of sequence evolution. We did not partition the data sets. Four independent runs were conducted on each data matrix and once complete, Tracer v1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018) was used to investigate convergence across runs. Runs were then combined and a final summary tree with mean and 95% Highest Posterior Densities (HPD) was generated.

After dating the trees, we investigated the historical biogeography of *Nomada* using the R program BioGeoBEARS (Matzke, 2013). Three different biogeographic models were tested on each of the three main data matrices: the dispersal, extinction, cladogenesis model (DEC; (Ree, Moore, Webb, & Donoghue, 2005; Ree & Smith, 2008), a modified version of the dispersal-vicariance model that uses maximum likelihood (DIVA-like; Ronquist, 1997), and a derived version of the Bayesian Analysis of Biogeography model (BayArea-like; Landis, Matzke, Moore, & Huelsenbeck, 2013) that also uses maximum likelihood. We additionally tested the versions of each model that includes jump dispersal (+j) however, based on current criticism of the +j parameter, we did not include those results (Ree & Sanmartín, 2018). We do provide the results in the supplement (App. table 5). We considered six ecoregions in our models: Nearctic, Neotropics, Palearctic, Afrotropics, Indomalaya, and Australasia. We set the maximum range size to six so that all ecoregions were considered in analysis. Selection of the best fit model was done using AIC scores within the program.

Results

3.1 Molecular Phylogeny

We used a data matrix filtered for 75% taxon occupancy for our downstream analysis which consisted of 2,014 loci, a total of 1,431,861 bp, and 752,356 bp informative sites. The mean locus length was 710.95 bp and the total amount of missing data was 30.1%. All five trees (no partitioning, by locus partitioning, SWSC partitioning, ry-coding, and species) tested were mostly congruent with only minor differences in placement of various species within the clades (App. Fig. 1).

All generated phylogenies support the monophyly of the genus and reveal that the sister group to all other *Nomada* is the *odontophora* species group, a small species group found in the eastern Mediterranean (Fig. 1). Trees indicated that 14 of the 16 previously established species groups are monophyletic, providing molecular confirmation for the majority of the morphological distinctions of the different groups (Alexander, 1994). Two exceptions are the *superba* and *basalis* species groups, which need to be merged into one monophyletic clade, and paraphyly of the large *ruficornis* clade. For the *superba* and *basalis* groups, the results indicate that the *basalis* species group is nested within the *superba*, thus uniting them as a single monophyletic species group. For the *ruficornis* group, analyses revealed that the group is paraphyletic, with one large main clade and one smaller clade that is sister to the *bifasciata* species group. Interestingly, while the largest main *ruficornis* clade was composed of species found throughout the Holarctic, those that clustered in the smaller clade are restricted to eastern North America and therefore should be recognized as a new species group in order to preserve monophyly.

3.2 Dating analysis and historical biogeography

Of the three data matrices tested (all loci, 1000 clocklike loci, 500 clocklike loci), we selected the all loci analysis as the main result, given that there was little variation in dates among trees, suggesting that our analyses were not biased by the inclusion of less clocklike loci. Additionally, we found the most support for the DEC biogeographic model (AIC: 339.28) performed on the all loci tree. Our dated chronogram with biogeography focusing on the ingroup (Fig. 2; App. Fig. 2) reveals that *Nomada* diverged from the rest of the Nomadinae in the late Cretaceous (stem: 79 Mya, CI: 93-63 Mya) in the Nearctic. Our divergence dating also supports a crown age for *Nomada* around 65 Mya (95% CI: 83-48 Mya) and DEC analysis places the most recent common ancestor (MRCA) for the group originating in the Holarctic during the early Paleocene (66-56 Mya). Nearly all *Nomada* species groups had crown ages between the late Oligocene to the mid Miocene (28.1-13.8 Mya) with the exception of the younger *belfragei* group whose crown age was in the late Miocene (11.6-7.2 Mya).

The two oldest species groups (*odontophora* and *vineta*) were found to be confined to the Palearctic as early as ~65 Mya (CI: 83-48 Mya) and to the Nearctic ~ 57 Mya (CI: 74-37 Mya) respectively. Dispersal into the southern hemisphere was subsequently recorded in three species

groups: into the Afrotropics by *gigas* ~21 Mya (CI: 36-5 Mya), into the Neotropics by *vegana* (CI: 36-20 Mya), and into the Indomalaya and Australasian regions by *furva* (CI: 30-14 Mya). Three species groups (*adducta*, *erigeronis*, *belfragei*) are confined to the Nearctic, however, our analyses indicates that the MRCAs for both *erigeronis* and *belfragei* reached the Nearctic independently around 33 Mya (CI: 46-25 Mya) while the MRCA for *adducta* arrived much earlier, ~46 Mya (65-33 Mya) from somewhere across the Palearctic. Two species groups, *superba*+*basalis* and *ruficornis*, both have Holarctic distributions; our model suggests that while *superba*+*basalis* only dispersed once into the Nearctic ~ 16 Mya (CI: 25-6 Mya), *ruficornis* dispersed no less than five times between ~19-10 Mya (CI: 27-4 Mya). The remaining five species groups (*integra*, *roberjeotiana*, *bifasciata*, *trispinosa*, *armata*) are confined to the Palearctic.

Discussion

4.1 Phylogeny

Here we provide the first comprehensive molecular phylogeny of *Nomada* to date with representation of 119 species, all currently recognized species groups, and all major biogeographic regions. We propose that the crown age for *Nomada* is between 60-70 Mya. This proposed age is older than previous estimates for the group which fall anywhere from ~61 Mya (Bossert et al., 2020) and ~20-23 Mya (Cardinal et al., 2010; Cardinal et al., 2018). However, recent phylogenetic analyses have pushed the crown age for all bees to between 130-100 Ma (Branstetter et al., 2017; Cardinal & Danforth, 2013; Sann et al., 2018). Specifically Cardinal and Danforth (2013) and Sann et al (2018) recovered an origin for bees between 123-128 Mya while Branstetter et al (2020), using similar methods to the ones used in this study, recovered a crown age closer to 100 Mya. The main difference between our estimate for the crown age and those previously estimated for the genus is most likely due to the depth of sampling; older analyses included at most three Holarctic species of *Nomada* (Bossert et al., 2020; Cardinal et al., 2010; Cardinal et al., 2018;) mostly found in the *ruficornis* group. We used over 100 species and included all known species groups and biogeographic realms where *Nomada* occurs.

Interestingly, because Cardinal et al., (2018) only included species from the *ruficornis* group, their estimated age for *Nomada* matches the age we recovered for the same species group, indicating that our results are comparable.

Our phylogeny showed strong support for all but two of the morphologically defined species groups originally outlined by Alexander (1994) and we identified the *odontophora* species group as sister to the remaining groups in *Nomada*. Our finding that the *odontophora* group is sister to all other species groups contrasts with the predictions made by both Michener (2007) and Alexander (1994). Previously, Michener (2007) predicted that the *vegana* group would be “basal” based on their species diversity and location in the southern hemisphere; however, our molecular phylogeny indicates that this group originated later when its ancestor dispersed into the Neotropics from the Nearctic (~28 Mya). Alternatively, Alexander (1994) predicted that the *gigas* species group was sister to the remaining *Nomada* groups based primarily on male genitalia characters. Our results place the *gigas* group as more derived within the genus (Fig. 1).

In his detailed cladistic work, Alexander (1989, 1991) found little support for the monophyly of *superba* as a group as well as little support for a sister group relationship between *superba* and *basalis*, noting that observable and clearly defining characters for *superba* were difficult to determine. Our results provide support for the union of the *superba* and *basalis* groups into one monophyletic clade. The *ruficornis* group is a large and historically problematic clade that was assumed to be paraphyletic, mainly due to the absence of defining characters that unite the species found in the group (Alexander, 1989). In our analyses, *ruficornis* was indeed found to be paraphyletic, however, not to the extent that would be assumed for such a large clade composed of species that do not belong in any other species group. Our analyses imply that there are only two separate clades: one large main clade sister to the *armata* group, and a smaller second smaller clade more closely related to the *bifasciata* group. Interestingly, this smaller group is composed solely of eastern North American species and it should be further investigated such that after revision, a new species group could be established.

4.2 Historical biogeography

Both Michener (2007) and Alexander (1994) proposed a southern hemisphere origin for *Nomada* with subsequent dispersal northward into the remaining ecoregions. Specifically,

Michener (2007) predicted an origin in the Neotropics while Alexander (1994) predicted an Afrotropical origin. Our biogeographic results offer an alternative to these predictions and we found strong support that the stem ancestor for *Nomada* originally diverged from the sister clade consisting of Hexepeolini, Neolarrini, Townsendiellini and Biastini in the Nearctic ~79 Mya during the Late Cretaceous period. The brood parasitic bee genus *Epeolus*, was also found to have most likely originated in the Nearctic (Onuferko, Bogusch, Ferrari, & Packer, 2019) and distribution data for the tribe Hexepeolini also indicate that they are confined to the Nearctic region (Bossert et al., 2020), lending support for the origin being in the Western hemisphere. Furthermore, the cleptoparasitic tribe Neolarrini, like the genus *Epeolus* most likely originated within the Nearctic as well (Sless et al., 2022). The MRCA for *Nomada* had a Holarctic origin during the early Paleocene with the ancestor dispersing into the Palearctic from the Nearctic between 79-65 Mya, most likely via the northern De Geer land bridge. The De Geer land bridge connected eastern North America to Europe via a northern passage through Greenland and was exposed between 71-63 Mya (Brikiatis, 2014). Around this same time, the Turgai Strait was open to terrestrial organisms, allowing for geodispersal (gene flow and dispersal that occurs once a physical barrier is removed) across all of Eurasia (Akhmetiev et al., 2012). Although the Bering Land Bridge (BLB) was exposed between 66-65.5 Mya and could have been used as an alternate route, it is unlikely for two reasons. The first reason is that around the Cretaceous-Paleogene boundary (66 Mya) the BLB was located at a higher latitude than what is observed today and therefore acted more as a filter route for organisms geodispersing across it (Brikiatis, 2014; McKenna, 2003). Secondly, movement by *Nomada* across the Holarctic region was most likely already happening prior to the estimated first opening of the BLB since *odontophora* diverged from the rest of *Nomada* ~65 Mya within the Palearctic.

The first instance of back geodispersal into the Nearctic occurred in the *vincta* group ~57 Mya, most likely via the Thulean Land Bridge (TLB) as the De Geer route closed ~6 Mya prior (Brikiatis, 2014) and the presence of the Turgai Strait would have hindered movement across the BLB (Brikiatis, 2014; Sanmartín, Enghoff, & Ronquist, 2001). The only other recorded instance of bees using the TLB is found in the Ancyilaini (Praz & Packer, 2014) who are thought to have used the land bridge to reach the Palearctic from North America ~57-56 Mya; however, the TLB was an important connector between the Palearctic and Nearctic for many other taxa including toads (Pramuk, Robertson, Sites, & Noonan, 2007), crocodilids (Puértolas, Canudo, & Cruzado-

Caballero, 2011), grasshoppers (Chintauan-Marquier et al., 2014), glass lizards (Lavin & Girman, 2019), and magnolias (Hebda & Irving, 2004) around this time.

Our analysis indicates that *Nomada* geodispersed into the southern hemisphere at least three times during the course of their evolutionary history; each dispersal event resulting in a distinct species group (*gigas*, *vegana*) or species (*furva*). The first instance of southward geodispersal occurred during the middle Eocene (stem age: 45 Mya) when the MRCA of the *gigas* species group diverged from the *integra* group and moved into the Afrotropics. By the mid Cretaceous, Africa had already been isolated from the rest of Gondwana and Laurasia, but various intermittent routes would reconnect it to the other landmasses, allowing for faunal and floral exchange (Gheerbrant & Rage, 2006). These frequent and bidirectional interchanges occurred most likely between Africa and Laurasia via two routes: the Mediterranean Tethyan Sill, whose exposure was periodic from the Jurassic to the Paleogene and closely tied to falling sea levels, and a later eastern Iranian route that emerged in the mid Eocene (Gheerbrant & Rage, 2006). Using the mid Eocene stem age of *gigas* group, we can infer that the eastern Iranian route was the most probable scenario, however, we cannot rule out use of the Mediterranean Tethyan Sill. The latter scenario would match geodispersal patterns proposed for Sericini scarab beetles (Eberle, Fabrizi, Lago, & Ahrens, 2017), the extinct predatory mammals of the family Hyenodontidae (Solé, 2013) and monitor lizards (Vidal et al., 2012).

The second instance of geodispersal by *Nomada* into the southern hemisphere occurred between the Nearctic and the Neotropics by the diverse *vegana* species group shortly after the Eocene-Oligocene transition (~34 Mya). This corresponds to a floral shift within South America as tropical biomes gave way to more temperate and grassland habitats (Houben, van Mourik, Montanari, Coccioni, & Brinkhuis, 2012; Pound & Salzmann, 2017; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). Two possible routes taken by *vegana* to reach South America include use of the Isthmus of Panama (IP) and via island hopping through the Antilles region. Movement of *vegana* through the IP is questionable as completion of the isthmus was predicted to have happened ~3-4 Mya (Coates & Stallard, 2013; Jackson & O'Dea, 2013), some 30 Mya after the divergence of the *vegana* group from its sister species group, *erigeronis*. However, there is some evidence that the IP may have formed much earlier than expected, possibly in the middle Miocene (Montes et al., 2015) or near the Oligocene-Miocene boundary (Bacon et al., 2015) or

even existed as a chain of islands in late Eocene (Montes et al., 2012). Our analyses indicated that *Nomada* were already present in the Neotropics no later than ~20 Mya and therefore cannot rule out dispersal over an Oligocene-Miocene IP emergence nor an island stepping geodispersal. It is known that bee faunas in Southeast Asia and the Caribbean used scattered islands to disperse between landmasses (Michener, 1979) so it is feasible that *Nomada* island hopped between North and South America. Other organisms are found to have possibly dispersed across the IP prior to its estimated complete closure including *Ceratina* bees (Rehan et al., 2010), *Dynastes* beetles (Huang, 2016), palms (Bacon, Mora, Wagner, & Jaramillo, 2013), and *Boa* snakes (Head, Rincon, Suarez, Montes, & Jaramillo, 2012).

The third southern geodispersal happened when the *furva* group reached Australia ~10 Mya. During the late Miocene (~12-7 Mya), the Australian continent drifted towards southeast Asia, leading to an extension of the Sula Spur (Torsvik & Cocks, 2016) and provided a steppingstone like connection between Indonesia and Australia. Many organisms such as *Tylomelania* freshwater snails (von Rintelen, Stelbrink, Marwoto, & Glaubrecht, 2014), passerines in the Oriolidae (Jönsson et al., 2019) and *Spathius* parasitoid wasps (Zaldívar-Riverón et al., 2018) traversed this connection in order to disperse into or out of Australia.

Various *Nomada* species groups dispersed into the Nearctic between 46-10 Mya most likely across the Bering Land Bridge (BLB). The species groups *adductua*, *belfragei*, and *erigeronis* are all confined to North America and have MRCA's that were found across the Holarctic. Our results indicate that the ancestors for these groups geodispersed back into the Nearctic between 46-33 Mya, shortly after the start of the Eocene-Oligocene transition (~34 Mya). During this time period, major climatic shifts caused the vegetation of the BLB to transition from boreotropical to forests of mixed deciduous and coniferous trees (Sanmartín et al., 2001). Both the Holarctic *superba+basalis* and the *ruficornis* groups would have used the BLB to geodisperse to the Nearctic ~19-10 Mya. The BLB was a common route used by bees; genera from at least three families are known to have traversed it either to reach the Nearctic or the Palearctic: Apidae (Dorchin, López-Urbe, Praz, Griswold, & Danforth, 2018; Hines, 2008; Onuferko et al., 2019; Praz & Packer, 2014; S. Rehan & Schwarz, 2015); Colletidae (Ferrari et al., 2020); Megachilini (Branstetter et al., 2021; Trunz, Packer, Vieu, Arrigo, & Praz, 2016).

Conclusions

Here we constructed the first molecular phylogeny and biogeography for the *Nomada* using genome wide next-generation sequencing techniques. Overall, there was strong support for 14 of the 16 previously established species groups and additional support for one previously unknown group. *Nomada* most likely originated in the early Paleogene somewhere across the Holarctic in the latter half of the Cretaceous and began to radiate following the K-Pg extinction event. Throughout their evolutionary history, geodispersal for *Nomada* predominantly occurred between the Nearctic and Palearctic; ten independent geodispersal events using multiple existing land bridges, including the first instance of a bee crossing the De Geer land bridge, were recorded. Three geodispersal events gave rise to the three southern hemisphere species groups. Although all species groups were sampled, future studies should include more representation within the smaller clades such as *trispinosa*, *odontophora*, and *belfragei*. With nearly 800 species worldwide, *Nomada* are the most diverse and widespread of the brood parasitic apid bees. This well resolved phylogeny and historical biogeography provide an important first step towards a deeper understanding of both *Nomada* diversification and cleptoparasitic bee evolution more broadly.

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Fig. 1. Phylogram of *Nomada* with the outgroup in grey and each species group. All support values are 100/100 unless indicated.

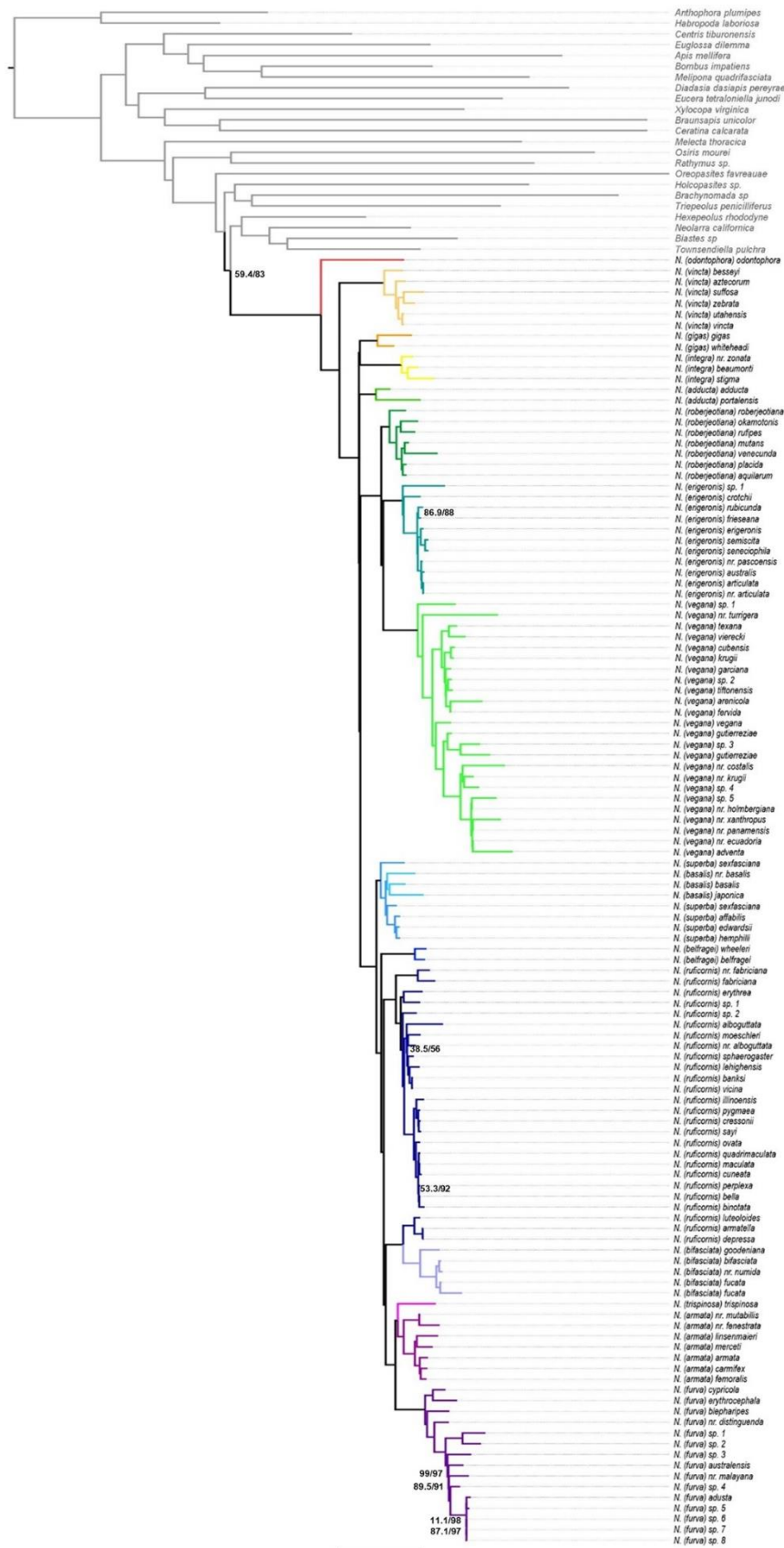
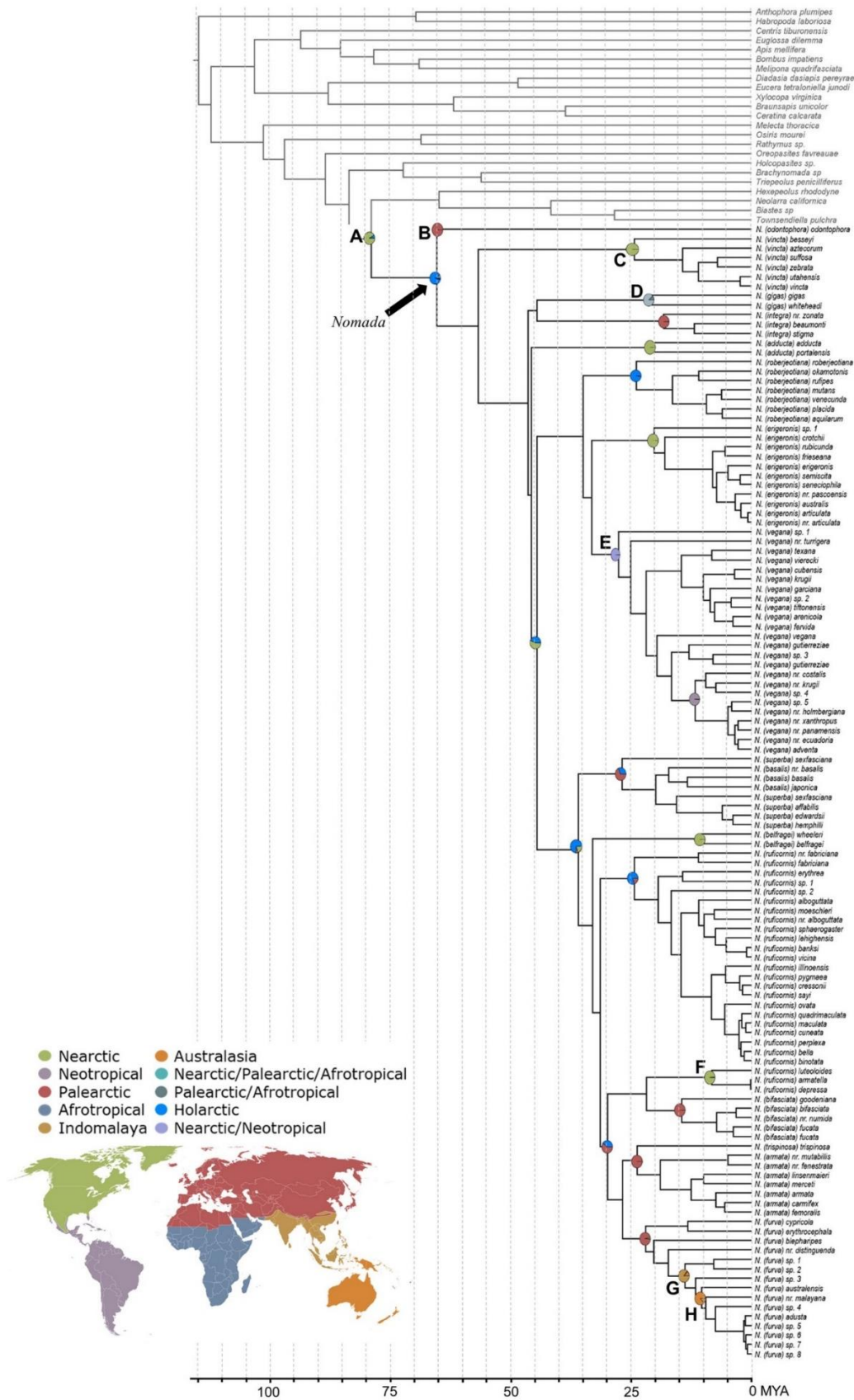


Fig. 2 Biogeography of the ingroup *Nomada* represented in our dated phylogeny. Each pie represents the probability of the ancestral region. The six included regions in our analysis are Nearctic, Neotropics, Palearctic, Afrotropics, Indomalaya, and Australasia. Large letters indicate important biogeographic events: A) most recent common ancestor of the sister stem group and *Nomada* emerges in the Nearctic; B) *odontophora* originates in the Palearctic; C) first instance of back geodispersal into the Nearctic; D) *gigas* emerges in the Afrotropics and is first dispersal into the southern hemisphere; E) movement into the Neotropics and second dispersal into southern hemisphere; F) new unnamed species group emerges in the Nearctic; G) third southern hemisphere dispersal into the Indomalaya; H) dispersal into Australasia and last new biogeographical region. Map image by Lokal_Profil distributed under a CC BY-SA 3.0 license.



Appendix

Table S1: List of the old subgenera of *Nomada*, with the current species group designations, the type specimens if known for the original subgenera, and the known geographic range for the species group. The species groups designated with a (¹) are groups that were created using subgenera that were published previously. The groups designated with a (²) are groups that have no type specimen listed and therefore the name giver is assumed. This information was pulled from Alexander & Schwarz, 1994.

Old subgenera	Current species groups	Type specimens	Geographic range
<i>Cephen</i> , <i>Aphelonomada</i> , <i>Hypochrotaenia</i> , <i>Micronomada</i> , <i>Nomadosoma</i> , <i>Polybiapis</i>	<i>Vegana</i>	<i>Cephen</i> : <i>N. texana</i> (Cresson, 1872) <i>Aphelonomada</i> : <i>N. cruralis</i> (Moure, 1960) <i>Hypochrotaenia</i> : <i>H. parvula</i> (Holmberg, 1886) <i>Micronomada</i> : <i>N. modesta</i> (Cresson, 1863) <i>Nomadosoma</i> : <i>Pasites pilipes</i> (Cresson, 1865) <i>Polybiapis</i> : <i>P. minimus</i> (Coclerell, 1916)	Neotropical, nearctic

	<i>Gigas</i>	<i>gigas</i> (Friese, 1905)	Southern Africa
<i>Asteronomada</i>	<i>Adducta</i>	<i>adducta</i> (Cresson, 1878)	Nearctic
<i>Pachynomada</i>	<i>Vincta</i>	<i>vincta</i> (Say, 1837)	Nearctic
<i>Acanthonomada</i>	<i>Odontophora</i>	<i>odontophora</i> (Kohl, 1905)	Palearctic
<i>Centrias, Nomadula</i>	<i>Erigeornis</i>	<i>Centrias</i> : <i>N. erigeronis</i> (Robertson, 1897) <i>Nomadula</i> : <i>N. articulata</i> (F. Smith, 1854)	Nearctic
<i>Gnathias, Heminomada, Lamproapis, Nomada</i> s. str., <i>Phor, Xanthidium</i>	<i>Ruficornis</i>	<i>Nomada</i> : <i>Apis ruficornis</i> (Linnaeus, 1758) <i>Gnathias</i> : <i>N. bella</i> (Cresson, 1863) <i>Heminomada</i> : <i>N. oblitterata</i> (Cresson, 1863) <i>Lamproapis</i> : <i>L. maculipennis</i> (Cameron, 1902)	Holarctic

			<i>Phor</i> : <i>N. integerrima</i> (Dalla Torre, 1896) <i>Xanthidium</i> : <i>N. luteola</i> (Olivier, 1811)	
		<i>Armata</i> ¹	Includes <i>fuscicornis</i> group (Schwarz, 1977)	Palearctic
<i>Phelonmada</i>	<i>Belfragei</i>		<i>Phelonomada</i> : <i>N. belfragei</i> (Cresson, 1878)	Nearctic
<i>Holonomada</i>	<i>Superba</i>		<i>Superba</i> : <i>N. superba</i> (Cresson, 1863)	Holarctic
<i>Laminomada</i>	<i>Basalis</i>		<i>Laminomada</i> : <i>N. hesperia</i> (Cockerell, 1903b)	Holarctic
<i>Nomadita</i> , <i>Callinomada</i>	<i>Roberjeotiana</i>		<i>Nomadita</i> : <i>Nomadita montana</i> (Mocsary, 1894) <i>Callinomada</i> : <i>N. antonita</i> (Cockerell, 1909)	Holarctic, sub-Saharan

	<i>Bifasciata</i> ²	No type listed; assuming <i>N. bifasciata</i> (Olivier, 1811)	Palearctic
	<i>Trispinosa</i> ²	No type listed; assuming <i>N. trispinosa</i> (Schmiedeknecht, 1882)	Palearctic
	<i>Integra</i> ¹	Includes <i>cinctiventris</i> group (Schwarz, 1967)	Palearctic
	<i>Furva</i> ¹	Includes <i>furva</i> group (Stockhert, 1943)	Palearctic, oriental, to Australia

Table S2: List of species used in phylogeny

Supplement table 2: List of all species used in this study. Newly sequenced species are indicated by a (*), sequences taken from a previously sequenced genome are indicated by (†), and species that have no symbol are species that were previously sequenced. The Natural History Museum of Los Angeles County is abbreviated to NHMLA.

Genus	Subgenus/ Species group	Species	Describer	Year	Identifier	In/Out group	Holding Institution	Accession #s	Notes
<i>Anthophora</i>		<i>plumipes</i>	Pallas	1772		out			
<i>Habropoda</i>		<i>laboriosa</i> †	Fabricius	1804		out		PRJNA339959	Lowe, T. M., & Eddy, S. R. 1997
<i>Centris</i>		<i>tiburonensis</i>	Cockerell	1923		out			
<i>Euglossa</i>		<i>dilemma</i> †	Bembé & Eltz	2011		out		PRJNA388474	Brand, P., et al., 2017
<i>Apis</i>		<i>mellifera</i> †	Linnaeus	1758		out		PRJNA477511	Wallberg A et al., 2019
<i>Bombus</i>		<i>impatiens</i> †	Cresson	1863		out		PRJNA70395	Sadd, B. M., et al., 2015
<i>Melipona</i>		<i>quadrifasciata</i>	Lepeletier	1836		out		PRJNA279820	
<i>Diadasia</i>	<i>Dasiapis</i>	<i>pereyrae</i>	Holmberg	1903		out	USDA Logan Bee Lab	SAMN14907487	
<i>Eucera</i>	<i>Tetraloniella</i>	<i>junodi</i>	Friese	1909		out	USDA Logan Bee Lab	SAMN14907504	
<i>Xylocopa</i>		<i>virginica</i>	Linnaeus	1771		out	Cornell University	SAMN09061455	
<i>Braunsapis</i>		<i>unicolor</i>	Smith	1854		out			
<i>Ceratina</i>		<i>calcarata</i>	Robertson	1900		out	Rehan Bee Lab	PRJNA340002	

<i>Melecta</i>		<i>thoracica</i>	Cresson	1875		out			Sless, T.J.L., et al., (2021)
<i>Osiris</i>		<i>mourei</i>	Michener	1854		out			Sless, T.J.L., et al., (2021)
<i>Rhathymus</i>		<i>sp</i>	Lepeletier & Serville			out		SRR13781625	Sless, T.J.L., et al., (2021)
<i>Oreopasites</i>		<i>favreauae</i>	Rozen	1992		out		SRR13781635	Sless, T.J.L., et al., (2021)
<i>Holcopasites</i>		<i>sp</i>	Ashmead			out			Sless, T.J.L., et al., (2021)
<i>Brachynomada</i>		<i>sp</i>	Holmberg			out			Sless, T.J.L., et al., (2021)
<i>Triepeolus</i>		<i>penicilliferus</i>	Brues	1903		out			Sless, T.J.L., et al., (2021)
<i>Hexepeolus</i>		<i>rhododyne</i>	Linsley & Michener			out		SRR13781676	Sless, T.J.L., et al., (2021)
<i>Neolarra</i>		<i>californica</i>	Michener	1939		out		SRR11497538	Sless, T.J.L., et al., (2021)
<i>Biastes</i>		<i>sp</i>	Panzer			out		SRR13781607	Sless, T.J.L., et al., (2021)
<i>Townsendiella</i>		<i>pulchra</i>	Crawford	1916		out		SRR13781611	Sless, T.J.L., et al., (2021)
<i>Nomada</i>	<i>adducta</i>	<i>adducta</i> *	Cresson	1878	D.K. Broemelling	in	USDA Logan Bee Lab	SRR18055171	
<i>Nomada</i>	<i>adducta</i>	<i>portalensis</i> *	Broemeling	1989	D.K. Broemelling	in	NHMLA	SRR18055170	allotype
<i>Nomada</i>	<i>armata</i>	<i>armata</i>	Herrich-Schäffer	1839	K. Odanaka	in	Packer Bee Lab	SRR18055141	

<i>Nomada</i>	<i>armata</i>	<i>carmifex</i> *	Mocsáry	1883	M. Schwarz	in	USDA Logan Bee Lab	SRR18055185	
<i>Nomada</i>	<i>armata</i>	<i>femoralis</i> *	Morawitz	1869	M. Schwarz	in	USDA Logan Bee Lab	SRR18055157	
<i>Nomada</i>	<i>armata</i>	<i>linsenmaieri</i> *	Schwarz	1974	M. Schwarz	in	USDA Logan Bee Lab	SRR18055096	
<i>Nomada</i>	<i>armata</i>	<i>merceti</i> *	Alfken	1909	M. Schwarz	in	USDA Logan Bee Lab	SRR18055151	
<i>Nomada</i>	<i>armata</i>	<i>nr. fenestrata</i> *			K. Odanaka	in	NHMLA	SRR18055135	
<i>Nomada</i>	<i>armata</i>	<i>nr. mutabilis</i> *			K. Odanaka	in	NHMLA	SRR18055195	
<i>Nomada</i>	<i>basalis</i>	<i>basalis</i> *	Herrich- Schäffer	1893	M. Schwarz	in	USDA Logan Bee Lab	SRR18055113	
<i>Nomada</i>	<i>basalis</i>	<i>japonica</i> *	Smith	1873	Smith	in	NHMLA	SRR18055191	
<i>Nomada</i>	<i>basalis</i>	<i>nr. basalis</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055139	
<i>Nomada</i>	<i>belfragei</i>	<i>belfragei</i> *	Cresson	1878	R.R. Snelling	in	NHMLA	SRR18055172	
<i>Nomada</i>	<i>belfragei</i>	<i>wheeleri</i> *	Cockerell	1903	R.R. Snelling	in	NHMLA	SRR18055169	
<i>Nomada</i>	<i>bifasciata</i>	<i>bifasciata</i> *	Olivier	1812	M. Schwarz	in	USDA Logan Bee Lab	SRR18055126	
<i>Nomada</i>	<i>bifasciata</i>	<i>fucata</i> *	Panzer	1798	M. Schwarz	in	USDA Logan Bee Lab	SRR18055101	
<i>Nomada</i>	<i>bifasciata</i>	<i>fucata</i> *	Panzer	1798	L. Packer	in	Packer Bee Lab	SRR18055102	
<i>Nomada</i>	<i>bifasciata</i>	<i>goodeniana</i> *	Kirby	1802	Kocourek	in	NHMLA	SRR18055100	
<i>Nomada</i>	<i>bifasciata</i>	<i>nr. numida</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055142	
<i>Nomada</i>	<i>erigeronis</i>	<i>articulata</i> *	Smith	1854	M. Veit	in	Rehan Bee Lab	SRR18055099	
<i>Nomada</i>	<i>erigeronis</i>	<i>australis</i> *	Mitchell	1962	T.J. Wood	in	Isaacs Lab	SRR18055098	

<i>Nomada</i>	<i>erigeronis</i>	<i>crotchii</i> *	Cresson	1878	T. Griswold	in	USDA Logan Bee Lab	SRR18055097	
<i>Nomada</i>	<i>erigeronis</i>	<i>erigeronis</i> *	Robertson	1897	J. Gibbs	in	Isaacs Lab	SRR18055187	
<i>Nomada</i>	<i>erigeronis</i>	<i>frieseana</i> *	Cockerell	1904	B. Alexander	in	USDA Logan Bee Lab	SRR18055186	
<i>Nomada</i>	<i>erigeronis</i>	<i>nr. articulata</i>			K. Odanaka	in	Isaacs Lab	SRR18055086	
<i>Nomada</i>	<i>erigeronis</i>	<i>nr. pascoensis</i>			K. Odanaka	in	Gord Hutchings personal collection	SRR18055177	
<i>Nomada</i>	<i>erigeronis</i>	<i>rubicunda</i> *	Olivier	1812	T.J. Wood	in	Isaacs Lab	SRR18055184	
<i>Nomada</i>	<i>erigeronis</i>	<i>semiscita</i> *	Cockerell	1904	T. Griswold	in	USDA Logan Bee Lab	SRR18055183	
<i>Nomada</i>	<i>erigeronis</i>	<i>seneciophila</i> *	Mitchell	1962	D. Jones	in	NHMLA	SRR18055182	
<i>Nomada</i>	<i>erigeronis</i>	<i>sp. 1</i> *			K. Odanaka	in	NHMLA	SRR18055095	
<i>Nomada</i>	<i>furva</i>	<i>adusta</i> *	Smith	1875	M. Schwarz	in	USDA Logan Bee Lab	SRR18055181	
<i>Nomada</i>	<i>furva</i>	<i>australensis</i> *	Perkins	1912	L. Packer	in	Packer Bee Lab	SRR18055180	
<i>Nomada</i>	<i>furva</i>	<i>blepharipes</i> *	Schmiedeknecht	1882	M. Schwarz	in	USDA Logan Bee Lab	SRR18055162	
<i>Nomada</i>	<i>furva</i>	<i>cypricola</i> *	Mavromoustakis	1955	M. Schwarz	in	USDA Logan Bee Lab	SRR18055161	
<i>Nomada</i>	<i>furva</i>	<i>erythrocephala</i> *	Morawitz	1871	M. Schwarz	in	USDA Logan Bee Lab	SRR18055160	
<i>Nomada</i>	<i>furva</i>	<i>nr. distinguenda</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055132	
<i>Nomada</i>	<i>furva</i>	<i>nr. malayana</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055176	

<i>Nomada</i>	<i>furva</i>	<i>sp. 1*</i>			K. Odanaka	in	Royal Ontario Museum	SRR18055189	
<i>Nomada</i>	<i>furva</i>	<i>sp. 2*</i>			K. Odanaka	in	Royal Ontario Museum	SRR18055188	
<i>Nomada</i>	<i>furva</i>	<i>sp. 3*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055134	
<i>Nomada</i>	<i>furva</i>	<i>sp. 4*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055179	
<i>Nomada</i>	<i>furva</i>	<i>sp. 5*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055133	
<i>Nomada</i>	<i>furva</i>	<i>sp. 6*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055112	
<i>Nomada</i>	<i>furva</i>	<i>sp. 7*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055110	
<i>Nomada</i>	<i>furva</i>	<i>sp. 8*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055136	
<i>Nomada</i>	<i>gigas</i>	<i>gigas*</i>	Friese	1905	R.R. Snelling	in	NHMLA	SRR18055159	
<i>Nomada</i>	<i>gigas</i>	<i>whiteheadi*</i>	Eardley & Schwarz	1991	T. Griswold	in	USDA Logan Bee Lab	SRR18055173	
<i>Nomada</i>	<i>integra</i>	<i>beaumonti*</i>	Schwarz	1967	M. Schwarz	in	USDA Logan Bee Lab	SRR18055158	
<i>Nomada</i>	<i>integra</i>	<i>nr. zonata*</i>			K. Odanaka	in	Packer Bee Lab	SRR18055140	
<i>Nomada</i>	<i>integra</i>	<i>stigma*</i>	Fabricius	1804	Kokouretl	in	NHMLA	SRR18055156	
<i>Nomada</i>	<i>odontophora</i>	<i>odontophora*</i>	Kohl	1905	M. Schwarz	in	USDA Logan Bee Lab	SRR18055155	
<i>Nomada</i>	<i>roberjeotiana</i>	<i>aquilarum*</i>	Cockerell	1903	K. Odanaka	in	Gord Hutchings personal collection	SRR18055175	
<i>Nomada</i>	<i>roberjeotiana</i>	<i>mutans*</i>	Cockerell	1910	R.R. Snelling	in	NHMLA	SRR18055122	

<i>Nomada</i>	<i>roberjeotiana</i>	<i>okamotonis</i> *	Matsumura	1912	D.K. Broemelling	in	NHMLA	SRR18055121	
<i>Nomada</i>	<i>roberjeotiana</i>	<i>placida</i> *	Cresson	1863	M. Killewald	in	Isaacs Lab	SRR18055120	
<i>Nomada</i>	<i>roberjeotiana</i>	<i>roberjeotiana</i> *	Panzer	1799	W.J. Pulawski	in	USDA Logan Bee Lab	SRR18055119	
<i>Nomada</i>	<i>roberjeotiana</i>	<i>rufipes</i> *	Fabricius	1793	M. Schwarz	in	USDA Logan Bee Lab	SRR18055118	
<i>Nomada</i>	<i>roberjeotiana</i>	<i>venecunda</i> *	Cresson	1879	R.R. Snelling	in	NHMLA	SRR18055117	
<i>Nomada</i>	<i>ruficornis</i>	<i>alboguttata</i> *	Herrich-Schäffer	1839	M. Schwarz	in	Rehan Bee Lab	SRR18055116	
<i>Nomada</i>	<i>ruficornis</i>	<i>armatella</i> *	Cockerell	1903	K. Odanaka	in	York University	SRR18055115	
<i>Nomada</i>	<i>ruficornis</i>	<i>banksi</i> *	Cockerell	1903	K. Odanaka	in	Raine Lab	SRR18055094	
<i>Nomada</i>	<i>ruficornis</i>	<i>bella</i> *	Cresson	1863	T.J. Wood	in	Isaacs Lab	SRR18055093	
<i>Nomada</i>	<i>ruficornis</i>	<i>binotata</i> *	Robertson	1903	T.J. Wood	in	Isaacs Lab	SRR18055092	
<i>Nomada</i>	<i>ruficornis</i>	<i>cressonii</i>	Robertson	1893		in	Cornell University	SRR7120313	Grab, H. et al., 2019
<i>Nomada</i>	<i>ruficornis</i>	<i>cuneata</i> *	Robertson	1903	T.J. Wood	in	Isaacs Lab	SRR18055091	
<i>Nomada</i>	<i>ruficornis</i>	<i>depressa</i> *	Cresson	1863	K. Odanaka	in	York University	SRR18055090	
<i>Nomada</i>	<i>ruficornis</i>	<i>erythraea</i> *	Dalla Torre	1896	R.R. Snelling	in	NHMLA	SRR18055089	
<i>Nomada</i>	<i>ruficornis</i>	<i>fabriciana</i> *	Linné	1767	P.M.F. Verhoeff	in	NHMLA	SRR18055154	
<i>Nomada</i>	<i>ruficornis</i>	<i>illinoensis</i> *	Robertson	1900	T.J. Wood	in	Isaacs Lab	SRR18055152	
<i>Nomada</i>	<i>ruficornis</i>	<i>lehighensis</i> *	Cockerell	1903	T.J. Wood	in	Isaacs Lab	SRR18055150	
<i>Nomada</i>	<i>ruficornis</i>	<i>luteoloides</i>	Robertson	1895		in	Cornell University	SRR7120314	Grab, H. et al., 2019
<i>Nomada</i>	<i>ruficornis</i>	<i>maculata</i>	Cresson	1863		in	Cornell University	SRR7120368	Grab, H. et al., 2019
<i>Nomada</i>	<i>ruficornis</i>	<i>moeschleri</i>	Alfken	1913	K. Odanaka	in	NHMLA	SRR18055149	

<i>Nomada</i>	<i>ruficornis</i>	<i>nr alboguttata</i> *			K. Odanaka	in	Guelph Insect Collection	SRR18055178	
<i>Nomada</i>	<i>ruficornis</i>	<i>ovata</i>	Robertson	1903		in	Cornell University	SRR7120367	Grab, H. et al., 2019
<i>Nomada</i>	<i>ruficornis</i>	<i>perplexa</i> *	Cresson	1863	T.J. Wood	in	Isaacs Lab	SRR18055148	
<i>Nomada</i>	<i>ruficornis</i>	<i>pygmaea</i>	Cresson	1863		in	Cornell University	SRR7120370	Grab, H. et al., 2019
<i>Nomada</i>	<i>ruficornis</i>	<i>quadrimaculata</i> *	Robertson	1903	T.J. Wood	in	Isaacs Lab	SRR18055147	
<i>Nomada</i>	<i>ruficornis</i>	<i>sayi</i> *	Robertson	1893	T.J. Wood	in	Isaacs Lab	SRR18055088	
<i>Nomada</i>	<i>ruficornis</i>	<i>sp. 1</i> *			K. Odanaka	in	Minckley personal collection	SRR18055165	
<i>Nomada</i>	<i>ruficornis</i>	<i>sp. 2</i> *			K. Odanaka	in	Texas A&M	SRR18055146	
<i>Nomada</i>	<i>ruficornis</i>	<i>sphaerogaster</i> *	Cockerell	1903	T.J. Wood	in	Isaacs Lab	SRR18055087	
<i>Nomada</i>	<i>ruficornis</i>	<i>vicina</i> *	Cresson	1863	M. Veit	in	Rehan Bee Lab	SRR18055085	
<i>Nomada</i>	<i>superba</i>	<i>affabilis</i> *	Cresson	1879	M. Minnick	in	Miami University	SRR18055199	
<i>Nomada</i>	<i>superba</i>	<i>edwardsii</i> *	Cresson	1878	T. Griswold	in	USDA Logan Bee Lab	SRR18055198	
<i>Nomada</i>	<i>superba</i>	<i>hemphilli</i> *	Cockerell	1903	E. Miliczky	in	NHMLA	SRR18055196	
<i>Nomada</i>	<i>superba</i>	<i>sexfasciana</i> *	Panzer	1799	L. Packer	in	Packer Bee Lab	SRR18055144	Unknown species not sexfasciana
<i>Nomada</i>	<i>superba</i>	<i>sexfasciana</i> *	Panzer	1799	K. Odanaka	in	USDA Logan Bee Lab	SRR18055145	
<i>Nomada</i>	<i>trispinosa</i>	<i>trispinosa</i> *	Schmiedeknecht	1882	M. Kocourek	in	Rehan Bee Lab	SRR18055143	
<i>Nomada</i>	<i>vegana</i>	<i>adventa</i> *	Smith	1860	K. Odanaka	in	NHMLA	SRR18055194	
<i>Nomada</i>	<i>vegana</i>	<i>arenicola</i> *	Swenk	1913	D.K. Broemelling	in	Texas A&M	SRR18055131	
<i>Nomada</i>	<i>vegana</i>	<i>cubensis</i> *	Cresson	1865	J.A. Genaro	in	Packer Bee Lab	SRR18055106	

<i>Nomada</i>	<i>vegana</i>	<i>fervida</i> *	Smith	1854	T.J. Wood	in	Isaacs Lab	SRR18055105	
<i>Nomada</i>	<i>vegana</i>	<i>garciana</i> *	Cockerell	1907	K.W. Wright	in	Texas A&M	SRR18055168	
<i>Nomada</i>	<i>vegana</i>	<i>gutierreziae</i> *	Cockerell	1896	D.K. Broemelling	in	Texas A&M	SRR18055166	
<i>Nomada</i>	<i>vegana</i>	<i>gutierreziae</i> *	Cockerell	1896	R. Minckley	in	Minckley personal collection	SRR18055167	
<i>Nomada</i>	<i>vegana</i>	<i>krugii</i> *	Cresson	1878	J.A. Genaro	in	Packer Bee Lab	SRR18055164	
<i>Nomada</i>	<i>vegana</i>	<i>nr krugii</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055114	
<i>Nomada</i>	<i>vegana</i>	<i>nr. costalis</i> *			K. Odanaka	in	NHMLA	SRR18055111	
<i>Nomada</i>	<i>vegana</i>	<i>nr. ecuadoria</i> *			K. Odanaka	in	Texas A&M	SRR18055192	
<i>Nomada</i>	<i>vegana</i>	<i>nr. holmbergiana</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055174	
<i>Nomada</i>	<i>vegana</i>	<i>nr. panamensis</i> *			K. Odanaka	in	USDA Logan Bee Lab	SRR18055138	
<i>Nomada</i>	<i>vegana</i>	<i>nr. turrigera</i> *			K. Odanaka	in	NHMLA	SRR18055108	
<i>Nomada</i>	<i>vegana</i>	<i>nr. xanthopus</i> *			K. Odanaka	in	NHMLA	SRR18055193	
<i>Nomada</i>	<i>vegana</i>	<i>sp. 1</i> *			K. Odanaka	in	NHMLA	SRR18055107	
<i>Nomada</i>	<i>vegana</i>	<i>sp. 2</i> *			K. Odanaka	in	Texas A&M	SRR18055137	
<i>Nomada</i>	<i>vegana</i>	<i>sp. 3</i> *			K. Odanaka	in	Texas A&M	SRR18055163	
<i>Nomada</i>	<i>vegana</i>	<i>sp. 4</i> *			K. Odanaka	in	U.C. Riverside Insect Collection	SRR18055190	
<i>Nomada</i>	<i>vegana</i>	<i>sp. 5</i> *			K. Odanaka	in	Packer Bee Lab	SRR18055109	
<i>Nomada</i>	<i>vegana</i>	<i>texana</i> *	Cresson	1872	Karen Wright	in	Texas A&M	SRR18055130	
<i>Nomada</i>	<i>vegana</i>	<i>tiftonensis</i> *	Cockerell	1903	Michael Veit	in	Isaacs Lab	SRR18055129	
<i>Nomada</i>	<i>vegana</i>	<i>vegana</i> *	Cockerell	1903	T.J. Wood	in	Isaacs Lab	SRR18055128	

<i>Nomada</i>	<i>vegana</i>	<i>vierecki*</i>	Cockerell	1903	D.K. Broemelling	in	Texas A&M	SRR18055127	
<i>Nomada</i>	<i>vincta</i>	<i>aztecorum*</i>	Cockerell	1903	T. Griswold	in	USDA Logan Bee Lab	SRR18055125	
<i>Nomada</i>	<i>vincta</i>	<i>besseyi</i>	Cockerell	1905	K. Odanaka	in	Isaacs Lab	SRR18055153	
<i>Nomada</i>	<i>vincta</i>	<i>suffosa*</i>	Cockerell	1922	D.K. Broemelling	in	NHMLA	SRR18055124	
<i>Nomada</i>	<i>vincta</i>	<i>utahensis*</i>	Moalif	1988	D.K. Broemelling	in	USDA Logan Bee Lab	SRR18055123	
<i>Nomada</i>	<i>vincta</i>	<i>vincta*</i>	Say	1837	D. Drons	in	Minnesota State	SRR18055104	
<i>Nomada</i>	<i>vincta</i>	<i>zebrata*</i>	Cresson	1878	D.K. Broemelling	in	NHMLA	SRR18055103	

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Table S3: Fossils used in this project.

Placement	Fossil	Species Author	Other References	Paleobiod b.org link	Fossil Deposit	Deposit Age (paleobiodb)	Deposit Time (paleobiodb)	Min	Max	Notes
Root (Apidae)	secondary calibration		Cardinal et al. 2018	n/a	n/a	n/a	n/a	94.4	114.4	The estimated mean and 95% HPD for crown Apidae in Cardinal et al. (2018) is 104.4 (94.8-113.5). For MCMCTree we applied a normal distribution with mean and 95% CI set to 104.4 Ma $\pm$ 10 Ma. In MCMCTree this is a SkewNormal distribution with the shape parameter set to 0.
Melipona + Bombus	<i>Cretotrigona prisca</i>	Michener & Grimaldi 1988		https://paleobiodb.org/classic/basicTaxonInfo?taxon_no=214589	New Jersey Amber	66.0-70.6	Late/Upper Maastrichtian (Cretaceous)	66	91	We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used

										default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).
Anthophora + Habropoda	<i>Paleohabropoda oudardi</i>	Michez & Ramont 2009	Michez et al. 2009	https://paleobiodb.org/classic/basicTaxonInfo?taxon_no=180931	Menat Formation	59.2-61.6	Selandian (Paleocene)	59.2	95	We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older

										nodes estimated in Cardinal et al. (2018).
										We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).
Euglossa + Bombus	<i>Euglossa moronei</i>	Engel 1999	https://paleobiodb.org/classic/basicTaxonInfo?taxon_no=255331	Dominican Amber	13.82-20.44	Burdigalian - Langhian (Miocene)	13.8	91		
Apis + Bombus	<i>Apis henshawi</i>	Engel 1998	https://paleobiodb.org/classic?accessionSearch&collection	Rott Formation	23.0-28.4	Chattian (Oligocene)	23	91		We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We

			ction_no= 152455						input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).
Ceratina + Braunsapis	<i>Boreallo dape baltica</i>	Engel 2001a	https://palaeobiology.org/classic/basicTaxonInfo?taxon_no=216530	Baltic Amber	33.9-38.0	Priabonian (Eocene)	33.9	73	We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are

										listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).
Xylocopa + Ceratina	<i>Xylocopa gabrielae</i>	Engel 2001b		https://paleobiodb.org/classic/basicTaxonInfo?taxon_no=200584	Florissant Formation	33.9-37.2	Chadronian (Oligocene)	33.9	94	We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).
Melecta + Oreopasites	<i>Protomel ecta brevipennis</i>	Cockerell 1908	Zeuner & Manning 1976	https://paleobiodb.org/classic/basicTaxonInfo?taxon_no=200584	Florissant Formation	33.9-37.2	Chadronian (Oligocene)	33.9	104	We used MCMCTreeR to set the parameters of a

										Info?taxon _no=2346 20	SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).
Tetralonia + Diadasia	<i>Tetralonia a berlandi</i>	Theobald 1937	Zeuner & Manning 1976	https://palaeobiologydatabase.org/classic/basicTaxonInfo?taxon_no=210889	Célas, Gard, France	33.9-38.0	Priabonian (Eocene)	33.9	88	We used MCMCTreeR to set the parameters of a SkewNormal distribution for MCMCTree. We input the min/max age estimates listed here and used default parameters in MCMCTree R to calculate the	

distribution. The exact distribution parameters are listed. The max age was estimated based on ages of older nodes estimated in Cardinal et al. (2018).

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Table S4: Chart comparing the results of original divergence dating using *Protomelecta brevipennis* and the divergence dating using *Paleoepolus micheneri*

	root node age	crown age	crown range	Fossil Used
original	1.15	0.65	0.46-0.83	<i>Protomelecta brevipennis</i>
skew normal	1.17	0.7	0.71-1.00	<i>Paleoepolus micheneri</i>
uniform	1.13	0.66	0.43-0.83	<i>Paleoepolus micheneri</i>
Couchy	1.17	0.69	0.49-0.88	<i>Paleoepolus micheneri</i>
Couchy mod	1.17	0.71	0.57-0.86	<i>Paleoepolus micheneri</i>

Table S5: Biogeography AIC (a) and AICc (b)

a)

	LnL	numparams	d	e	j	AIC	AIC_wt
DEC	-167.5946	2	0.08993069	8.85E-02	0	339.1893	5.16E-11
DIVALIKE	-179.0816	2	0.13896958	1.00E-12	0	362.1631	5.30E-16
BAYAREALIKE	-191.1077	2	0.03826743	1.62E+00	0	386.2154	3.17E-21

b)

	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-167.5946	2	0.08993069	8.85E-02	0	339.275	5.39E-11
DIVALIKE	-179.0816	2	0.13896958	1.00E-12	0	362.2488	5.53E-16
BAYAREALIKE	-191.1077	2	0.03826743	1.62E+00	0	386.3011	3.31E-21

Chapter 3: Support for the refugia within refugia hypothesis in a North American cleptoparasitic bee

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Abstract

The genus *Nomada* is the most diverse and speciose of the cleptoparasitic bees, yet very little is known about their phylogeography. Studying *Nomada* populations can be difficult since they occur in small numbers within the landscape; however, some species are abundant and widespread enough that studying their populations is possible. Understanding the genetic diversity of cleptoparasitic bees is valuable because they tend to be less abundant and potentially more vulnerable to extinction than their hosts. *Nomada articulata* Smith is a common nest parasite of *Agapostemon virescens* (Fabricius) and *Agapostemon sericeus* (Forster) and is found throughout the US and Canada. To explore phylogeographic patterns as well as population genetic structure and diversity within *Nomada articulata*, we sequenced nuclear ultraconserved elements and mitochondrial genes from 74 individuals sampled from across North America. Our results suggest that *N. articulata* may be a species complex, as half of the specimens from the southern US grouped with other species outside the main *N. articulata* clade in both UCE and mitochondrial phylogenetic trees. Furthermore, our results indicate that historically, *Nomada articulata* may have been divided into two separate populations along an east-west gradient, but due to environmental and landscape changes over time, it currently consists of a single panmictic population. We present here the first phylogeographic study for a *Nomada* species and provide

insights into understanding how cleptoparasitic bee populations respond to environmental changes over time.

Keywords: cleptoparasite, phylogeography, Wisconsinan glaciation, ultra-conserved elements, native bees, phylogenomics, population genomics

Introduction

Global biodiversity is being lost at an alarming rate due to a multitude of factors such as climate change, habitat loss, and land conversion (Cardinale et al., 2012; Hallmann et al., 2017; Potts et al., 2010, Sánchez-Bayo & Wyckhuys, 2019). As populations diminish in size or in extreme cases are entirely lost, the genetic diversity within species will decrease as well (Hoban et al., 2022). Genetic diversity allows organisms to respond and adapt to changes in their environment and contributes to the overall stability and resilience of species through time (Booy et al., 2000; González et al., 2020). As populations become more homogenous due to the loss of genetic diversity, their ability to adapt to change becomes diminished and their chances of extinction rises (Hoban et al., 2023; Raffard et al., 2019; Vellend & Geber, 2005). Genetic diversity can also be used as an indicator for biodiversity which can then be integrated into decisions regarding ecological restoration and conservation (Hoban et al., 2023).

The majority of global pollination services in agriculturally dominant landscapes are provided by bees (Kennedy et al., 2013; Khalifa et al., 2021) and there is evidence that bees contribute substantially to pollination in urbanized environments (Cohen et al., 2021; Lowenstein et al., 2015). However, due to multiple stressors such as disease (Yordanova et al., 2022), the use of agrochemicals (Siviter et al., 2021), and human mediated changes to the environment for agriculture and urbanization, overall bee species diversity has been declining (Ayers & Rehan, 2021; Kremen et al., 2002). Bees are especially sensitive to changes in their environment as they are dependent on the quality and quantity of flowers in order to provide pollen and nectar for their young and the availability of suitable nesting locations (Potts et al., 2003; Vaudo et al., 2015). Habitat fragmentation in addition to the loss of floral and nesting provisions can reduce population size, which can ultimately lead to disconnected and isolated bee communities

(Ferreira et al., 2015; Suni & Brosi, 2012). The resulting loss of connectivity between populations increases the chances of inbreeding depression which may result in a negative feedback loop due to the production of sterile males that may further increase inbreeding depression within the population (Zayed & Packer, 2005). Social bees only comprise 9% of all bee species (Danforth et al., 2019), yet they are often the focus of population and conservation genetics research (Kelemen & Rehan, 2021), leaving the majority of bee species highly underrepresented in studies of population and conservation genetics and phylogeography.

About 13% of all bees are considered brood parasites, outnumbering the global diversity of the more iconic eusocial species such as bumble bees and honey bees (Danforth et al., 2019). Once a female brood parasite gains entrance into a host nest, either by opening a closed nest herself or by entering an open nest that is currently being provisioned, she will either kill the host larvae and lay her eggs on the provided pollen ball or will leave the host offspring and lay her eggs within the brood cell lining. The first parasitic larvae to emerge will kill the remaining eggs and the host offspring and then proceed to consume the provisioned pollen. Cleptoparasitic bees are intrinsically tied to their hosts and therefore can act as a reflection of the health of their host in an environment (Odanaka & Rehan, 2019; Sheffield et al., 2013). Generally, if a host population is doing well, they will be able to support a robust parasitic community; however, if the host population is doing poorly, due to changes in habitat or climate, the parasitic community will be diminished or absent and often the parasites will be the first to be extirpated from an environment (Westrich, 1996).

An astonishing 30% of all apid bees exhibit the brood parasitic life history (Danforth et al., 2019) and the most diverse of these bees is the genus *Nomada* (Alexander & Schwarz, 1994). Found on all continents except Antarctica (which has no bees), this genus contains approximately 800 species and is divided into over 16 different species groups (Alexander & Schwarz, 1994; Odanaka et al., 2022; Straka et al., 2024). Despite being such a large and diverse genus, very little is known regarding the population dynamics of cleptoparasitic lineages, like *Nomada*. Studying *Nomada* populations can be difficult due to their solitary and parasitic nature; often only occurring in small numbers or found in passive traps. Despite their semi-rarity, some *Nomada* species can occur in high enough numbers, usually associated with nest aggregations of their hosts, such that studying their populations is possible.

Nomada articulata Smith, 1854 is a common spring species within the North American endemic *N. erigeronis* species group (Alexander & Schwarz, 1994) and is encountered between April and August (Ascher & Pickering, 2024). As a species, *N. articulata* is at least 2 million years old (Odanaka et al., 2022) and unlike most *Nomada* species, which use members of the genus *Andrena* as hosts, *N. articulata* parasitizes nests of the sweat bees *Agapostemon virescens* (Fabricius) and *Agapostemon sericius* (Forster) (Alexander, 1991). *Nomada articulata* individuals are distinctive and relatively easy to identify, unlike most *Nomada*, with the only other species that is similar in appearance being its sister species, *Nomada australis* Mitchell (Mitchell, 1962). Females of *N. articulata* have an entirely red abdomen and distinctive hind tibial spines which separates them from *N. australis* (Mitchell, 1962). Additionally, *N. articulata* females have a narrower head width when compared to *N. australis*. Males are more often confused with *N. australis*, however coloration on the thorax and shape of the antenna set *N. articulata* apart (Mitchell, 1962). This species is an ideal candidate to examine cleptoparasitic bee population structure based on their abundance, large geographic range (which spans from the Atlantic coast to the Rocky Mountains), ease of identification and availability of samples.

Although UCEs are primarily used in phylogenetic studies, they have been increasingly used to examine gene flow and phylogeography (Branstetter & Longino, 2019; Stiller et al., 2021; Tonione et al., 2022; Zarza et al., 2016, 2018). One benefit of using targeted methods such as UCEs for population genetics is that mitochondrial DNA is routinely collected as a byproduct, allowing for the simultaneous analysis of both nuclear DNA and mtDNA (Amaral et al., 2015; Branstetter et al., 2021). Compared to SNP datasets generated from restriction site sequencing methods, e.g. RADseq, UCE data are also more easily integrated into other studies due to the fact that the same loci are targeted across all Hymenoptera (Zhang et al., 2019).

The objectives of this study are threefold; to 1) examine phylogeographic patterns within the species; 2) determine if *N. articulata* is one species or potentially a complex of morphologically similar species; and 3) examine population structure and genetic diversity within the species. This study is the first assessment of the phylogeography and population genetics of any North American *Nomada* species and provides important insights into how populations of cleptoparasitic bees have been influenced by environmental change over time.

Materials and Methods

Specimen sampling

A total of 85 individuals of *Nomada articulata* from across North America were acquired, reviewed for species determination, and used for both nuclear and mitochondrial gene-based tree construction (Fig. S1; Table S1). In order to have representatives from the entire range, specimens were selected from various museum collections and were sorted into four geographic regions (West, South, Midwest, Northeast) (Fig. S1; Table S1). Due to the use of museum specimens, collection dates ranged from 1903-2019. Overall, 75 individuals were newly sequenced while the remaining 10 were previously sequenced (Odanaka et al., 2022). A total of 11 outgroup species, consisting of the remaining five known eastern *N. erigeronis* group species and an additional six *N. erigeronis* group species from western North America, were used as outgroups to both root the tree and test the species status of *N. articulata*. Of the original 74 individuals identified as *N. articulata*, only 59 were found to be true representatives of the species (see results section). Consequently, only these 59 samples were used subsequently for population genetic analysis (Fig. 1).

DNA extraction, library preparation, sequencing, and data processing

DNA extraction, library preparation, sequencing and data processing followed the same protocol of Odanaka et al., (2022). Briefly, we used non-destructive methods and Zymo Quick-DNA Miniprep Plus Kits (Zymo Research, Irvine, CA, USA) for DNA extraction. Specimens were gently removed from their original pin, placed into individual tubes containing Proteinase-K and then incubated overnight. Extractions were done following a modified protocol (Branstetter et al., 2021) and once finished, bees were then washed, cleaned of debris and remounted on their pin. The concentration and quality of the DNA was checked using both a Qubit 3.0 (Thermo Fisher Scientific, Waltham, MA, USA) fluorometer and a TapeStation (Agilent, Santa Clara, CA, USA). Sequence data were generated using a previously published protocol (Branstetter et al., 2017) and a bee-ant specific probe set (Grab et al., 2019). DNA samples were sheared using a Qsonica sonicator (Q800R3; Newton, CT, USA) to obtain base fragments with a mean length of 400-600 bp. Kapa HyperPrep kits (Roche Sequencing, Pleasanton, CA, USA) and custom dual-indexing adapters (Glenn et al., 2019) were then used to create the Illumina-ready libraries. A magnetic-bead solution (Rohland & Reich, 2012) was used

to purify and concentrate the fragmented DNA samples and libraries. After concentrating the DNA, samples were pooled into equimolar batches of 10 samples and then enriched for UCEs over a two day period. Following enrichment, pools were quantified using Qubit and qPCR and then combined into a single sequencing pool and shipped to Novogene (Sacramento, CA, USA) for sequencing using Illumina HiSeq X. Once sequencing was completed, BBTools (Bushnell, 2014) was used to demultiplex the raw reads and the package Phyluce v1.6 (Faircloth, 2016) was used to clean and trim the demultiplexed reads. SPAdes (Bankevich et al., 2012), found within the Phyluce package was used for assembly of the trimmed reads. After the reads were aligned, they were trimmed using both Gblocks (parameters: b1 = 0.5, b2 = 0.5, b3 = 12, b4 = 7) (Talavera & Castresana, 2007) and Spruceup (parameters: distances = Jukes Cantor, lognormal cutoff = 0.88, all other parameters = default and included a guide tree) (Borowiec, 2019), then empty alignment columns were removed and the entire dataset was filtered for 75% taxon occupancy.

Mitochondrial data

The DNA barcode gene *cytochrome oxidase I* (COI) was successfully extracted from the UCE assemblies of 65 individuals (22 outgroup specimens; 43 ingroup specimens) using MitoFinder v1.4.1 (Allio et al., 2020) and a reference genome for *Thyreus decorus* found on NCBI (GenBank accession NC_057192.1). The output files from MitoFinder were then manually inspected to find the entire COI gene for each individual and moved to a single alignment containing all 65 COI genes. We aligned the COI gene data with MAFFT (Katoh & Standley, 2013) and visually examined the alignments in MEGA (Tamura et al., 2007) to identify the barcode region. TrimAl (Capella-Gutiérrez et al., 2009) was then used to externally and internally trim the alignment file, leaving only the COI barcode region. The resulting matrix was translated and visually inspected to ensure no pseudogenes were incorporated.

Phylogenetic trees

We used the program IQ-TREE v2.1.1 (Minh et al., 2020) to analyze both COI and nuclear UCE-based trees. For the UCE data, partitioning was conducted using the Sliding Window Site Characteristics based on Entropy method (SWSC-EN; Tagliacollo & Lanfear, 2018). The resulting data subsets (three for each UCE locus) were merged using ModelFinder2

(Kalyaanamoorthy et al., 2017), which is found within IQ-TREE2. For COI, alignments were input directly into IQ-TREE2 after being trimmed and were analyzed without partitioning. For merging the SWSC-EN data subsets, we used rclusterf, AICc, and GTR+G within IQ-TREE. For phylogenetic inference, we used the merged partitioning scheme for the UCE dataset and GTR+G as the model of sequence evolution for both the UCE and COI datasets. To assess clade support we performed 1000 ultrafast bootstrap replicates (UFB).

Mapping and variant calling

Fastq files containing trimmed read data were mapped to the *Nomada fabriciana* genome from NCBI (GenBank accession PRJEB44833) using the default parameters and the function “bwa mem” in BWA v.0.7.17 (Li & Durbin, 2009). BamTools v.2.5.1 (Barnett et al., 2011) was then used to check the mapping statistics of the processed reads. The mapped reads were then checked for any instances of duplication, but not deleted, using GATK v.4.2.5 (MarkDuplicates function) (McKenna et al., 2010) and files were indexed using SAMtools v.1.17 (index function) (Li et al., 2009). The functions mpileup and call within bcftools (Li, 2011) were used for multi-sample variant calling on the mapped reads. The maximum depth was set to 8000 while variant calling and base quality was filtered for values higher than 40 or 20 bp respectively. SNPs were then filtered using VCFtools v.0.1.16 (Danecek et al., 2011) such that only biallelic SNPs were retained. For filtering, minimum mean depth was 10, max mean depth was 100, and any SNPs missing more than 5% of the data were excluded. We then controlled for linkage disequilibrium by pruning variants from the filtered SNPs using the function “indep” in PLINK (Purcell et al., 2007) and the settings 50, 5, and 0.2 for the window size, step size, and the r^2 threshold respectively. Lastly, indels were then removed from the pruned and filtered SNPs using VCFtools and the function “remove-indels”. The resulting filtered, cleaned, and pruned SNPs were then used for the population genetics analyses.

Population genetics analysis

Older specimens can have highly degraded DNA which can influence extraction and sequencing. Due to the wide age range of our samples (1903-2019; Table S1) and the inclusion of male specimens, we analyzed our data four times: once with a dataset that included all specimens (combined), once with only contemporary specimens, once with only female

specimens, and once with only female contemporary specimens. Historic samples were not analyzed separately due to low sample size in the western population. Bees were sexed and then designated as historic (captured prior to 1987) and contemporary (captured between 1988 to present). The cutoff of 1987 used here has been used to denote historical collection dates in multiple bee studies examining historical populations from museum specimens (Brasil et al., 2023; Mathiasson & Rehan, 2020). Furthermore, multiple stressors started impacting bees at around this time: since the late 1980's, there has been considerable expansion of land area dedicated for urbanization (Brain, & Anderson, 2019), which coincided with the rise of commercial neonicotinoid use (Simon-Delso et al., 2015), record setting annual temperatures (NOAA, 2024), and an increase in the number of invasive bee species in North America (Rodríguez et al., 2024).

The following population genetics analyses were conducted on all four datasets using the program Genodive v3.04 (Meirmans, 2020). Hardy-Weinberg equilibrium (HWE) was first calculated using both G_{is} and F_{is} values. We then calculated the observed (H_o) and expected (H_s) heterozygotes in addition to the inbreeding coefficient (G_{is}) and the fixation index (G_{st}). In addition, we calculated pairwise F_{st} values between the different geographic regions using an AMOVA which was permuted 10,000 times.

ADMIXTURE (Alexander et al., 2009) and STRUCTURE v2.3.4 (Pritchard et al., 2000) were used to infer population organization for all datasets. We ran both programs due to differences in how each infers population structure; ADMIXTURE employs maximum likelihood in order to estimate the number of ancestral states while STRUCTURE uses a Bayesian clustering approach. For STRUCTURE, Markov chain Monte Carlo (MCMC) replicates were set to 100,000 with a burn-in period of 100,000. The number of populations (K) was set between 1-5 with 10 iterations of each. The Evanno method (Evanno et al., 2005) allows for inference of the optimal K value, however this method can be computationally taxing so the programs StrAuto (Chhatre & Emerson, 2017) and Structure Harvester (Earl & vonHoldt, 2012) were used to easily parallelize the runs, collect, and summarize the output. For the ADMIXTURE analysis, PLINK v1.9 was first used to extract SNP data from the vcf input file. SNPs were then inputted into the ADMIXTURE program in which $K=1-5$, each with 10 iterations. Visualization of both ADMIXTURE and STRUCTURE plots were made in CLUMPAK (Kopelman et al., 2015). To examine the influence of both specimen age and N .

articulata population structure, we used the same PLINK formatted SNP file from above and conducted a PCA in R v4.3.1 (R core team, 2023). Packages ggplot2 v3.4.2 (Wickham et al., 2019) and plotly v4.10.2 (Sievert, 2020) were used to then visualize the PCA.

The package TESS3 (Caye et al., 2016) was used in R to further examine population structure. TESS3 is similar to STRUCTURE but is able to additionally incorporate spatial information. The number of populations ranged from 1-5 to match the ancestral population estimates used in the STRUCTURE and ADMIXTURE analysis and all other parameters were set to default. Overlay of the TESS3 results onto a map of eastern North America was created using ARCGIS (ArcGIS Pro 3.1, Redlands, CA, USA). Lastly, the R package dartR (Gruber et al., 2018) was used to test for any effects of isolation by distance (IBD) at the population (F_{st} , Nei's D) and individual (Euclidean, Prop.shared) levels using the functions "Fst" and "D" for populations and "Euclidean" and "Prop.shared" for individuals. A total of 10,000 permutations were used for the individual level tests, however due to the low number of populations, only 23 permutations were run for the population level tests.

Results

Nuclear DNA and mtDNA trees

We could not recover COI data from all individuals, resulting in a reduction of the total number of individuals found within the finalized mitochondrial DNA tree ($n = 65$) compared to the number of individuals within the nuclear DNA tree ($n = 85$). Regardless, both the nuclear UCE and mtDNA trees indicated that not all *Nomada articulata* specimens form a single clade (Figs. 2 & S2). Of the original 74 individuals identified as *N. articulata*, 15 were placed among the outgroup samples in the final nuclear DNA tree and 12 of those 15 individuals were placed among the outgroups in the smaller mtDNA tree. This indicates that *N. articulata* is potentially comprised of multiple cryptic species or that some of the western species that we sampled also occur in the east. Within the outgroup we recovered support in both trees for an unknown clade of three related individuals that span across the south, midwest, and western parts of the United States and Canada (*Nomada* sp BLX 2886, *Nomada* sp BLX 2909, *Nomada* sp BLX 2928) (Figs. 2 & S2). Moreover, within both the nuclear UCE and mitochondrial trees we found support for a

previously unknown relationship between the primarily western *Nomada pascoensis* Cockerell (another species included in the outgroup) and another unknown southern species.

Within the main *N. articulata* clade, geographic structure can be inferred from the nuclear DNA tree, however some relationships were not recovered in the mitochondrial tree. While there is a primarily western clade present in the nuclear DNA tree, the mitochondrial tree shows western individuals to be more scattered and with low support. The samples from the remaining geographic areas were not recovered as distinct from one another on either tree, however there were two instances where individuals from the South and Midwestern populations clustered together on the nuclear DNA tree. Conversely, there were numerous clades with individuals from the three remaining populations sister to each other indicating that the three regions share a closer and more recent evolutionary history with each other than with the western population (Figs. 2 & S2).

Population genetics analysis

The results for all four datasets were similar and therefore we only detail the findings for the combined population below; results for the contemporary subset and the female only subsets can be found in the supplement (Tables S2-S5; Figs. S3-12). For H_o , G_{is} , and G_{st} results below, confidence intervals were calculated by bootstrapping over loci (Meirmans, 2020). A total of 59 confirmed *N. articulata* individuals were used for the population genetics analyses. Of these, only four specimens had a low mapping percentage (30-49%) and all were historic; all other specimens had mapping percentages ranging from 53-89%. A total of 4037 SNPs were also used for the population genetics analysis and the total number of alleles was 8,074 with only 1.38% missing data. Our HWE values for F_{is} and G_{is} were negative in all populations indicating an excess of heterozygotes (Table 1); this excess is further supported by the observed heterozygosity which was higher than expected across all populations ($H_o = 0.317$; 2.5, 97.5% CI: 0.309, 0.325) (Table 2). We found evidence of random breeding within *N. articulata* due to a negative inbreeding coefficient ($G_{is} = -0.182$; 2.5, 97.5% CI: -0.198, 0.165) as well as a low fixation value of 0.010 ($G_{st} = 0.010$; 2.5, 97.5% CI: 0.009, 0.012) across all populations (Table 2). We also found that F_{st} values across all population pairs were significantly low, ranging from 0.007 to 0.027 (for all values $p \leq 0.05$) (Table 3). Specifically, both the highest and lowest values recorded occurred in the interactions of the western population with the midwest (lowest, $F_{st} =$

0.007, $p = 0.008$) and southern (highest, $F_{st} = 0.027$, $p = 0.002$) populations. The low paired F_{st} value for the Midwest and western populations is evidence of high connectivity between the top populations. Conversely, the high F_{st} value between the southern and western populations indicates low connectivity between the two populations. The paired F_{st} values between the midwest, northeast and southern populations were between 0.008-0.009, which all support high connectivity between the three easternmost populations.

Our PCA shows some separation between contemporary and historic specimens, particularly in midwestern individuals (Fig. 3a). Additionally, our PCA indicates that western specimens cluster together with minimal overlap with the midwest population and no overlap with the southern and northeastern populations. Conversely, individuals of the midwest, southern, and northeastern populations are more separated and populations overlap with each other (Fig. 3a). This pattern is consistent even when the historical specimens are removed and only contemporary specimens are analyzed (Fig. 3b). Both STRUCTURE and ADMIXTURE returned with a $K = 1$, indicating that there is only one population present (Full STRUCTURE and ADMIXTURE: Figs. S4 & S5). Furthermore, although the TESS3 analysis uses STRUCTURE output, the cross validation results of the TESS3 analysis indicates that there is finer structure within the population that cannot be detected by the other methods (Fig. S8). R^2 and p values for the IBD test for the combined dataset were 0.749 ($p = 0.08$) and 0.839 ($p = 0.08$) for populations (Nei's D and F_{st} respectively) and 0.102 ($p = 0.05$) and 0.078 ($p = 0.17$) for individuals (Proportion shared and Euclidean respectively) (Tables S5; Fig. S9). For the female only dataset, R^2 was significant for F_{st} (0.9355, $p = 0.04$), proportion shared (0.1939, $p = 0.0089$) and Euclidean (0.1788, $p = 0.0381$) (Table S5, Fig. S11). Lastly, for the female contemporary dataset, only proportion shared was significant ($R^2 = 0.1996$, $p = 0.03$) (Table S5, Fig. S12). With the exception of F_{st} for the females only dataset, all significant values indicate that there is no correlation between isolation by distance and our other results.

Discussion

Due to their parasitic life history, and usually low abundance, very little is known about cleptoparasitic bee biology and evolution despite comprising nearly a third of all apid bees globally; even less is known regarding their population dynamics. Here we investigated the

phylogeography and genetic diversity of the relatively common cleptoparasitic bee *Nomada articulata* across its known geographic distribution. We provide evidence that historically, *N. articulata* was divided into two genetic clusters representing the eastern and western portions of its range but presently comprise only one large panmictic population. Additionally, we observe that *N. articulata* populations have high genetic diversity due to elevated levels of heterozygosity and low inbreeding across their range. Lastly, our results indicate that *N. articulata*, as currently defined by morphology, most likely represents a species complex as both nuclear UCE and mitochondrial data support at least one cryptic species within the *N. erigeronis* species group in the southeastern United States that has been considered, until now, conspecific with *N. articulata*.

Genetic diversity and phylogeography

Nomada articulata shows signs of high genetic diversity as all populations have both elevated levels of heterozygotes and low levels of inbreeding. This is noteworthy because our findings differ substantially from other studied North American bee species that have likely been impacted by the last ice age (Samad-zada et al., 2023; Shell & Rehan, 2016). During the Wisconsinan glaciation (WG) (~112 kya – 12 kya) (Dalton et al., 2022), the topography of Canada and the United States was vastly different from what it is today. Nearly all of Canada and parts of the US were under the Laurentide Ice Sheet while the US east of the Rocky Mountains was covered in temperate grassland, taiga, and boreal or temperate woodland, with the largest biome being the taiga which dominated the landscape east of the Mississippi River (Ray & Adams, 2001). Within eastern North America, many species took refuge in the eastern and southern regions (boreal and temperate woodlands) in response to the environment and climatic conditions, and experienced population declines (Dalton et al., 2022; Ray & Adams, 2001; Samad-zada et al., 2023; Shell & Rehan, 2016). As glacial ice retreated following the WG and biomes began to shift, many species moved north and westward. Consequently, their populations experienced rapid expansion and diversification, effectively decreasing genetic diversity due to founder effects which is evident in high levels of inbreeding detected in current populations (Dalton et al., 2022; Samad-zada et al., 2023; Shell & Rehan, 2016). Conversely, because *N. articulata* emerged in North America around 2 mya and was already present during the WG, the low levels of inbreeding seen in this species could indicate that populations were split between

multiple refugia across North America. These separated populations then came back into contact after glacial ice retreated and the environment became more favorable for dispersal.

Best documented in Europe, the “refugia within refugia” hypothesis (Gómez & Lunt, 2007), is a genomic pattern found in various organisms including moose (Dussex et al., 2020), crested newts (Wielstra et al., 2021) and numerous plants (Pinto-Carrasco et al., 2022; Shi et al., 2014). The hypothesis implies that little to no gene flow occurred between populations of a species divided across multiple refugia, ultimately allowing for enough differentiation to occur such that populations would be genetically distinct (Gómez & Lunt, 2007). As populations began to spread post-glaciation, contact with other formerly isolated populations increased genetic diversity and lowered inbreeding. As *N. articulata* dispersed post-glaciation, repeated mixing events where the different populations came into contact could have contributed to maintaining the elevated levels of genetic diversity, we detected. Our results are the first documentation of a North American bee population that displays the low levels of inbreeding characteristic of the refugia within refugia hypothesis.

Life history traits, such as feeding specialty and behavior, can be dovetailed with the refugia within refugia hypothesis and provide additional support for the genetic diversity observed in *N. articulata*. Together, life history traits and the refugia within refugia hypothesis are known to influence observed genetic diversity in at least three bee species including *Andrena agilissima*, a specialist oligolectic bee that exhibits high genetic diversity and low differentiation (Sousa et al., 2023) much like the observations recorded for *N. articulata* (this study). Although *A. agilissima* is a specialist and thus restricted by its nutritional needs, the host (Brassicaceae) is widely distributed and abundant; as long as *A. agilissima* has access to its host it can persist in environments such as in refugia. Accordingly, since Brassicaceae is pervasive, this allows for larger populations of *A. agilissima* which can support overall higher genetic diversity (Sousa et al., 2023). Ultimately, in *A. agilissima*, the combination of life history traits and the landscape effects due to being isolated across multiple refugia work in tandem to preserve and elevate genetic diversity (Sousa et al., 2023). Both cleptoparasitism and oligolecty are highly specialized life history traits and it is conceivable that the patterns seen in *N. articulata* genetic diversity are also a result of the availability of the host species during and post glaciation. Given that the host *Agapostemon virescens* is widespread throughout North America and very common (Ayers & Rehan, 2023; Gill & O’Neal, 2015) it is possible that *N. articulata* followed *A. virescens* as it

began to disperse from refugia after the WG. However, this assertion needs further investigation, as no continent-wide genetic diversity analyses have been conducted on *A. virescens*, whereas the northern range populations have been found to have low levels of genetic diversity and high levels of inbreeding (Samad-zada & Rehan, 2023). Future studies comparing *N. articulata* and *A. virescens*, as well as any host-parasite populations should include expanded sampling of both species.

Our ADMIXTURE and STRUCTURE analyses confirm that presently, *N. articulata* is one continuous population, however, the results from our PCA, paired F_{st} tests, and phylogenetic reconstruction provide some support for a historical division between a western population and a larger mixed population that was comprised of individuals from the Midwest, Northeast and Southern regions of Canada and the United States. Furthermore, our population genetics analyses indicate that there is some overlap between the Western and Midwestern populations but not between the Western, Southern, and Northeastern populations. These observed patterns in genetic diversity are most likely a result of isolated *N. articulata* populations that began to disperse and interbreed following the WG as the landscape transitioned into different ecological successional states over time. As mentioned previously, during the WG the predominant biome in the Midwestern and Eastern US was taiga which separated the western temperate grassland from the eastern boreal and temperate woodlands (Ray & Adams, 2001); these three biomes could have acted as refuge for *N. articulata* and kept the different populations separate. As the Laurentide Ice Sheet melted during the end of the WG, the amount of water and sediment entering the Mississippi River increased, causing mega-floods within the Mississippi Basin (Baker, 2007; Fildani et al., 2016, 2018). The subsequent flooding of the Mississippi Basin physically increased the size and flow rate of the river as well as expanded the forests that grew within the flood plain, causing new barriers to dispersal (Lyman & Edwards, 2022). The division of a species on either side of the Mississippi River is a common pattern seen in Eastern North American fauna and flora and is known as the Mississippi River discontinuity (Soltis et al., 2006). This pattern of splitting a species into distinct clusters east and west of the Mississippi occurs in plants (De La Torre et al., 2019; Prior et al., 2020; Tanaka et al., 2012) and in terrestrial (Fontanella et al., 2008; Marshall et al., 2021) and aquatic animals (Near et al., 2001; Pessino et al., 2014; Robison, 1986). Flooding from the Mississippi could have resulted in the maintenance of the eastern and western *N. articulata* populations observed in the phylogenetic reconstruction.

Over time, as the forests eventually gave way to the grassland environment seen in the present day, the different populations began to disperse and interbreed. For example, we can infer from our comparative F_{st} values that the western *N. articulata* population most likely began to migrate and intermix primarily with the midwestern population, as that area would have been most accessible, and then subsequently with the southern and northeastern populations. At the same time, the Midwest, Northeast, and Southern populations dispersed among each other with the Midwest population acting as the central melting pot for all four populations most likely due to its proximity to all the others. The panmictic population that we observe is a result of sustained dispersal and interbreeding between the different populations that was facilitated by changes in the landscape during and following the Wisconsinan glaciation.

Cryptic species

Our phylogenetic results indicate that *N. articulata* is a complex that contains cryptic species. Currently, there are 14 species within the *N. erigeronis* species group found in the west but only five known species that occur east of the Mississippi River (Alexander & Schwarz, 1994). Our results indicate that there is possibly one or two additional species distributed within the southeastern United States (Figs. 2). One clade that indicates a possible new southern species is comprised of newly sequenced individuals from the Southeast, Midwest, and the West (*Nomada* sp BLX 2886, *Nomada* sp BLX 2909, *Nomada* sp BLX 2928). This clade is sister to another clade made entirely of western species and it is supported by both the nuclear and mitochondrial trees. The southern individual within this new clade was collected in North Carolina and therefore was expected to have been related to the known eastern species, yet its closest relatives occur in Manitoba and British Columbia. The presence of additional southeastern specimens sister to *Nomada pascoensis* is also noteworthy. *Nomada pascoensis* is primarily found west of the Rocky Mountains but there are records from Colorado and North Dakota although no individuals have been found east of the Mississippi River (Ascher & Pickering, 2024). Both the nuclear DNA and mitochondrial trees support the relationship between the unnamed southeastern individuals and *N. pascoensis*. This indicates that either *N. pascoensis* has a wider distribution than is currently known or there is a new species that is closely related to it. Of the different bee genera that occur in Eastern Canada and the US, species of the genus *Nomada* are among the more difficult to identify due to inconsistencies in

morphology and color patterns thus making it easy to overlook new species. Therefore, it is not surprising that even species thought to be relatively easy to identify, like *N. articulata*, can mask cryptic species whose morphology only slightly vary and can only be distinguished through molecular methods (Packer & Taylor, 1997).

Importance of museum specimens

Nearly half of the *N. articulata* specimens used for this project were collected between 1903-1987 representing a 120 year time span. Despite their age, we were able to extract viable DNA for our population level analyses thus providing support for the use of historical specimens in studies pertaining to population genetics. Furthermore, historical specimens can provide a wealth of information (Bartomeus et al., 2018) especially when concerning the population distributions (Jacobson et al., 2018; Mathiasson & Rehan, 2020), morphologies (MacLean et al., 2018; Oliveira et al., 2016), and phenologies (Bartomeus et al., 2011; Dorian et al., 2023) of species through time and space. It is important to take age into consideration as historical specimens can have severely degraded DNA making extraction difficult; however next generation sequencing approaches, such as the enrichment and sequencing of UCEs, allow for better success at harnessing fragmented DNA (McCormack et al., 2016; Suchan et al., 2016; Tin et al., 2014). Once unlocked, the genetic information can help inform population and conservation genetics in various ways such as accounting for genotypes that are no longer present in a population due to decreases in population sizes resulting from sudden changes to the environment (Nakahama, 2021; Wandeler et al., 2007). Fragmented DNA from historical specimens can also provide information detailing the mechanisms that induced changes seen in the genetic diversity of a population of interest (Nakahama & Isagi, 2018), as well as aiding in the recovery of previously extinct species (Hennessy, 2015; Peacock et al., 2017; Robertson et al., 2011). For instance, the rediscovery of the Lord Howe Island walking stick relied on genetic material taken from museum specimens to match fresh samples from Ball's Pyramid, an uninhabited islet near the southeast coast of Lord Howe Island in Australia, to the extinct historical population on Lord Howe Island (Mikheyev et al., 2017). Furthermore in roseate terns, UCE data sequenced from historic and contemporary tissue samples were used to examine changes in genetic diversity and population connectivity due to population declines and range contractions (Byerly et al., 2022). Our success in using UCEs to obtain reliable genetic

information from historical samples adds further support for the use of museum specimens for population and conservation genetics as well as phylogeography.

Conclusions

Here we document the population structure and genetic diversity of *Nomada articulata*, a first for a cleptoparasitic bee. Our data shows how the Wisconsinan glaciation left a lasting impact on *N. articulata*, most notably in splitting the population along an east-west boundary consistent with genetic isolation divided by the Mississippi River. We also provide evidence that the patterns of genetic diversity observed in *N. articulata* populations are a result of the species fitting the refugia within refugia hypothesis, as all populations exhibited low levels of inbreeding and high heterozygosity. This is the first documented instance of this hypothesis for a cleptoparasitic and North American bee species. Moreover, we found evidence that *N. articulata* is most likely a species complex and further taxonomic research is warranted for exploring diversity in the *N. erigeronis* species group, especially in the southeastern region of the United States. Lastly, our work highlights the importance of including historical specimens in population and conservation genetics. Historical specimens can offer a snapshot of past population structure that can be useful for comparisons to present day observations. As global biodiversity continues to decline due to human mediated effects on the environment, bees will be especially vulnerable to these changes. Diligent monitoring of population structure and genetic diversity in combination with abundance and richness assessments can ultimately help inform conservation decisions for wild bees.

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Data accessibility statement:

Unprocessed Illumina reads are deposited in BioProject # PRJNA1048485

Author contributions:

Katherine A. Odanaka: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization.

Farida Samad-zada: Formal analysis, Investigation, Writing – review & editing.

Michael G. Branstetter: Methodology, Resources, Investigation, Data curation, Writing – review & editing.

Kerrigan B. Tobin: Investigation, Writing – review & editing.

Sandra M. Rehan: Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition.

Figure 1: Map of the collection locations of *Nomada articulata* individuals used in the population genetics analysis. Each dot represents one or two individuals.

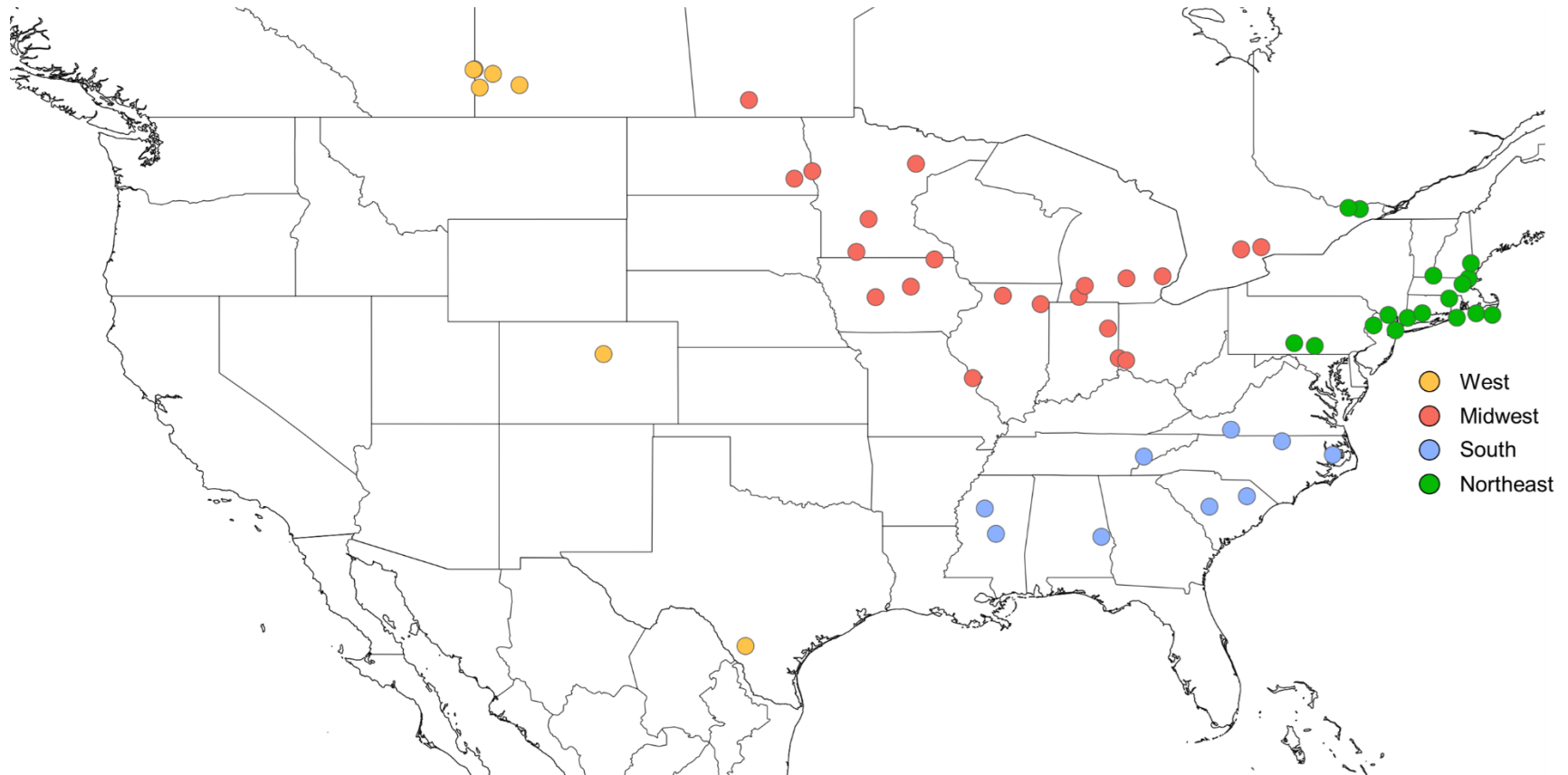


Figure 2: Cladogram of all UCE sequenced specimens within this project. Only bootstrap values higher than 75 are shown and color denotes the geographic locality the *Nomada articulata* specimen was collected. Purple colored specimens within the outgroup were initially identified as *N. articulata*.

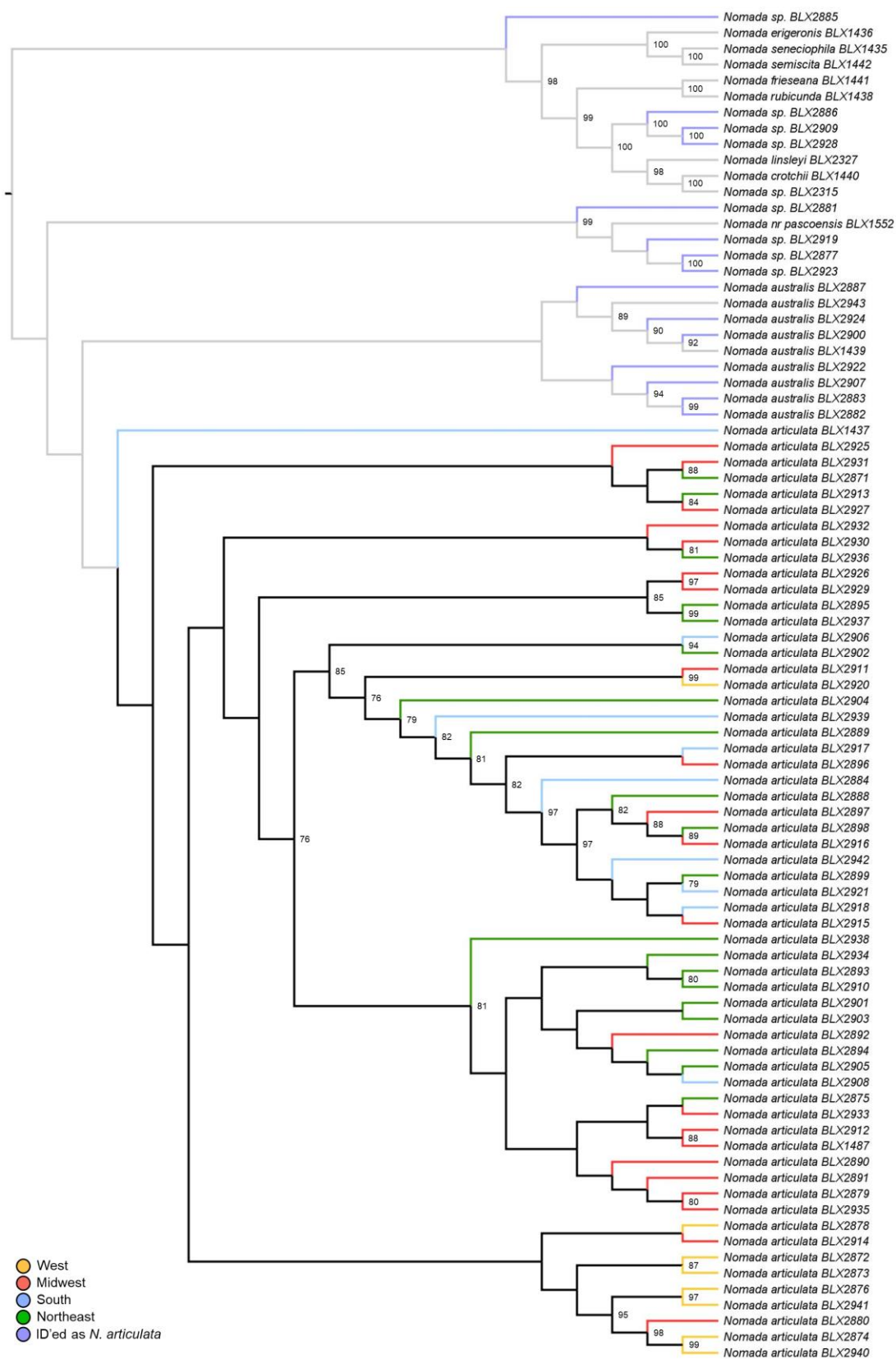
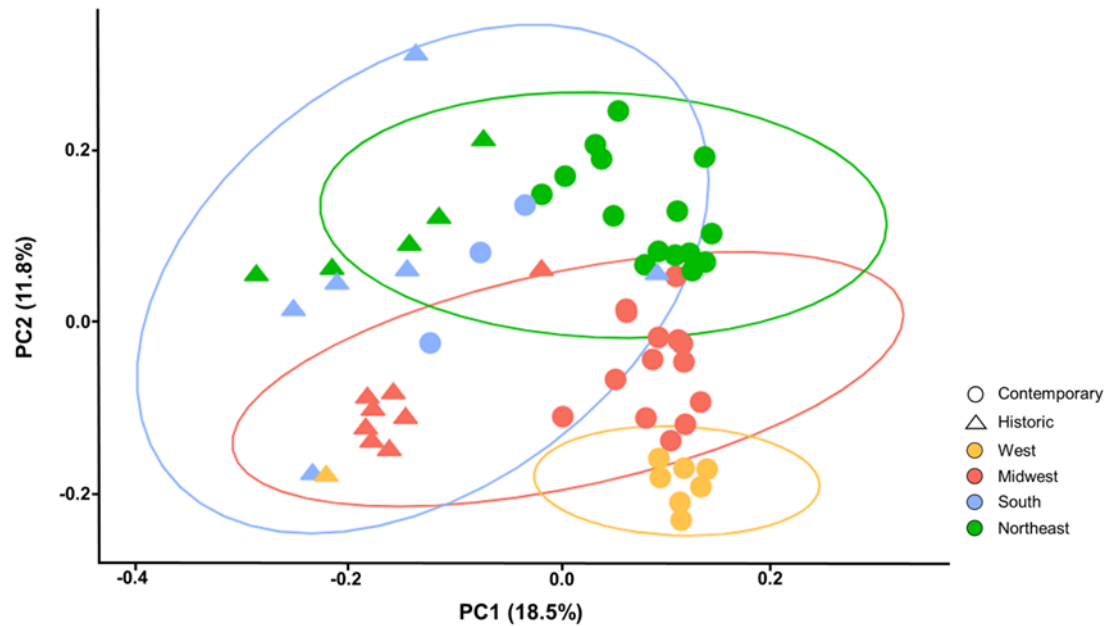


Figure 3: a) Principal component analysis for the 56 *N. articulata* individuals showing the relationship between all specimens across the four geographic locations and b) the 36 contemporary only specimens across their geographic regions. Ellipses represent 95 % confidence.

a)



b)

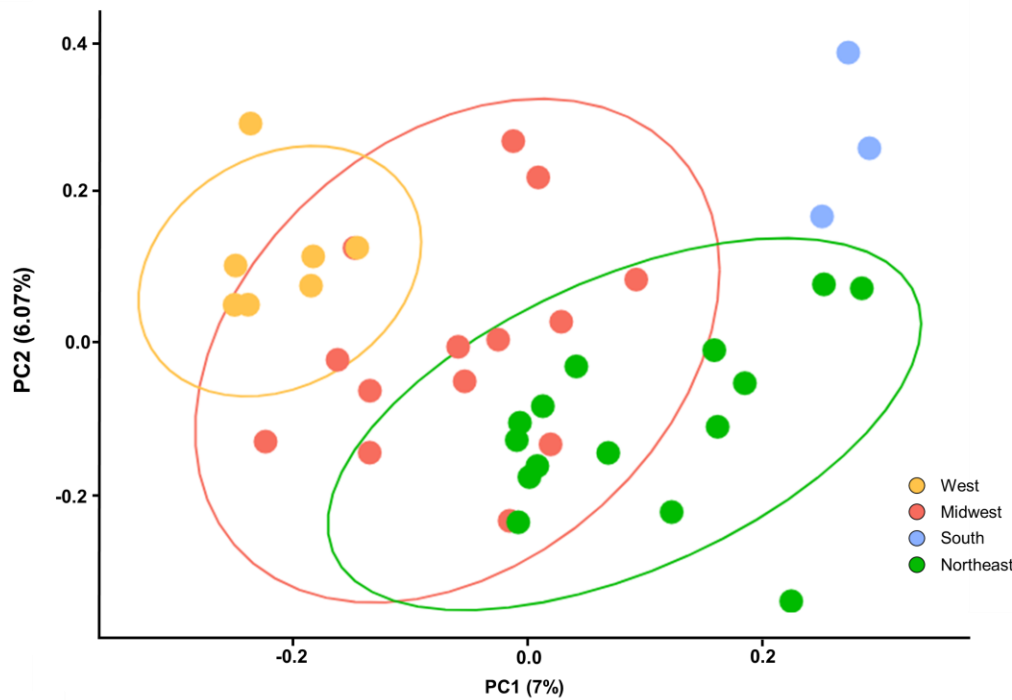


Table 1: Hardy Weinberg estimations for each population using either heterozygosity (Gis) and least squares methods (Fis). P values for all values were < 0.005

Population	Gis values	Fis values
South	-0.193	-0.193
Midwest	-0.173	-0.173
Northeast	-0.177	-0.177
West	-0.186	-0.186
Overall	-0.182	-0.196

Table 2: G statistics for heterozygosity and inbreeding across all populations. Confidence intervals were calculated using bootstrapping over loci (Meirmans, 2020).

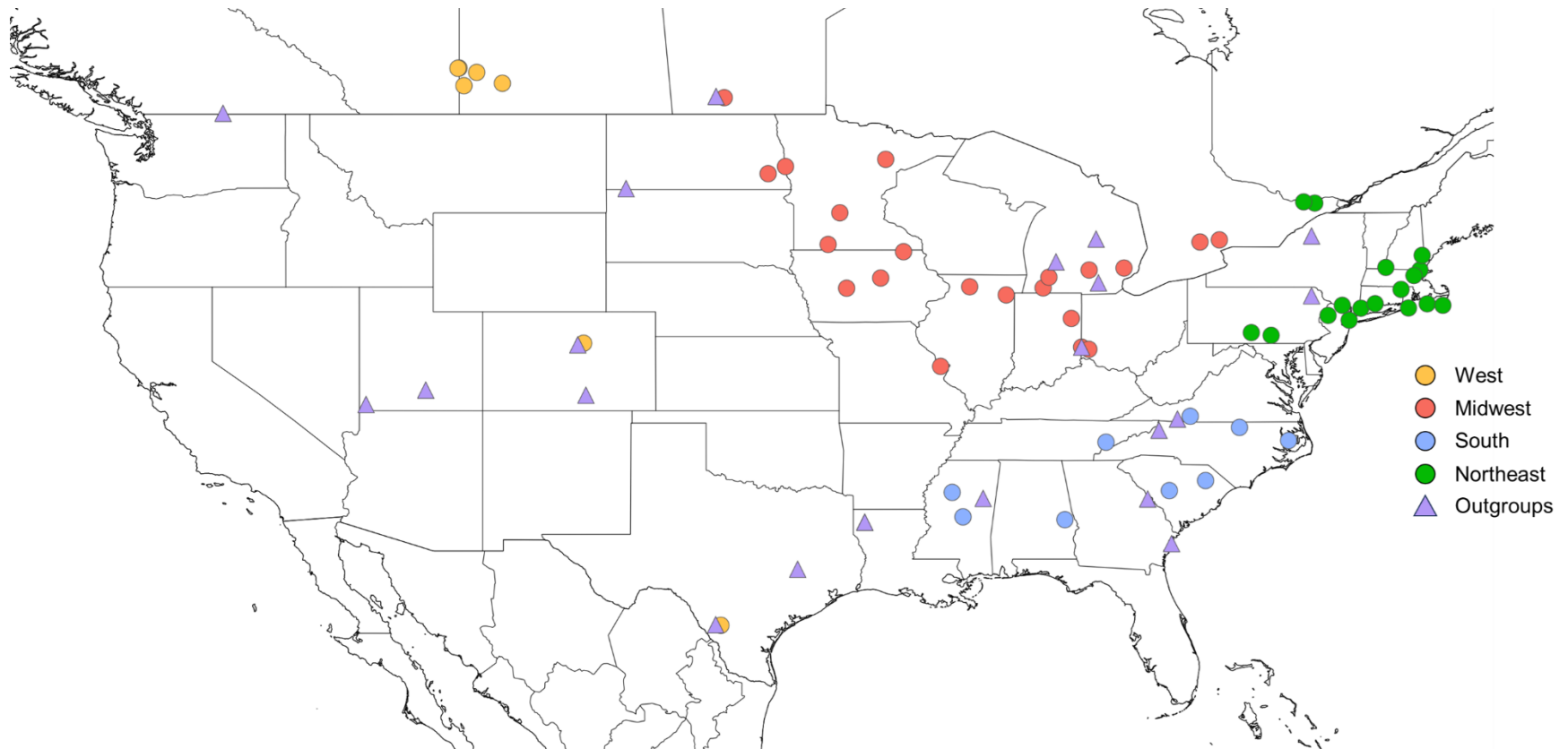
Statistic	Value	Std.Dev.	c.i.2.5%	c.i.97.5%
Observed (H_o)	0.317	0.004	0.309	0.325
Expected (H_s)	0.268	0.002	0.264	0.273
Total (H_t)	0.271	0.002	0.267	0.275
Inbreeding (G_{is})	-0.182	0.009	-0.198	-0.165
Fixation (G_{st})	0.010	0.001	0.009	0.012

Table 3: Fst values between pairs for all populations. The values below the diagonal are p-values and all are significant.

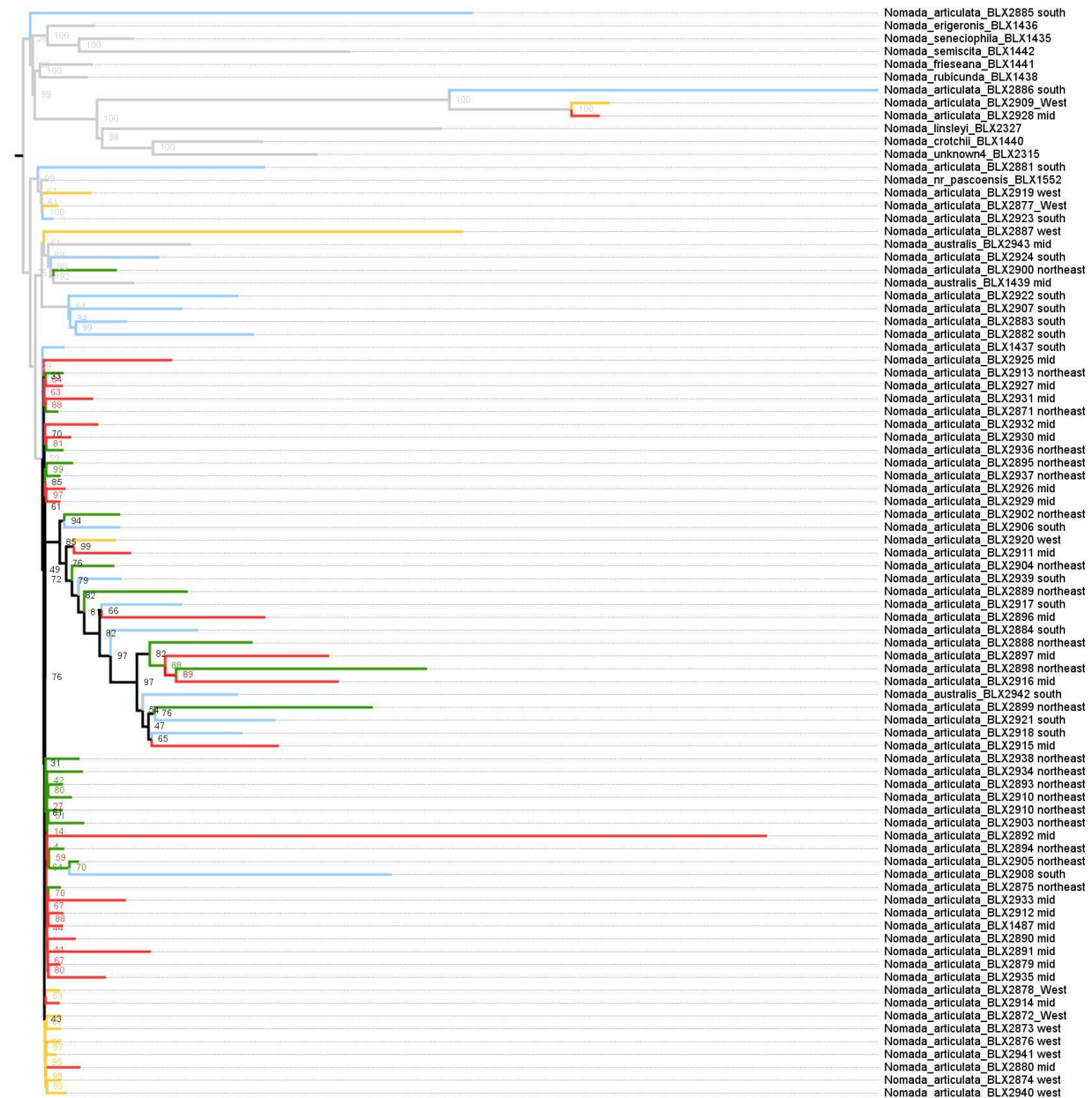
	South	Midwest	Northeast	West
South	--	0.009	0.008	0.027
Midwest	0.006	--	0.009	0.007
Northeast	0.007	0.000	--	0.019
West	0.002	0.008	0.000	--

Appendix

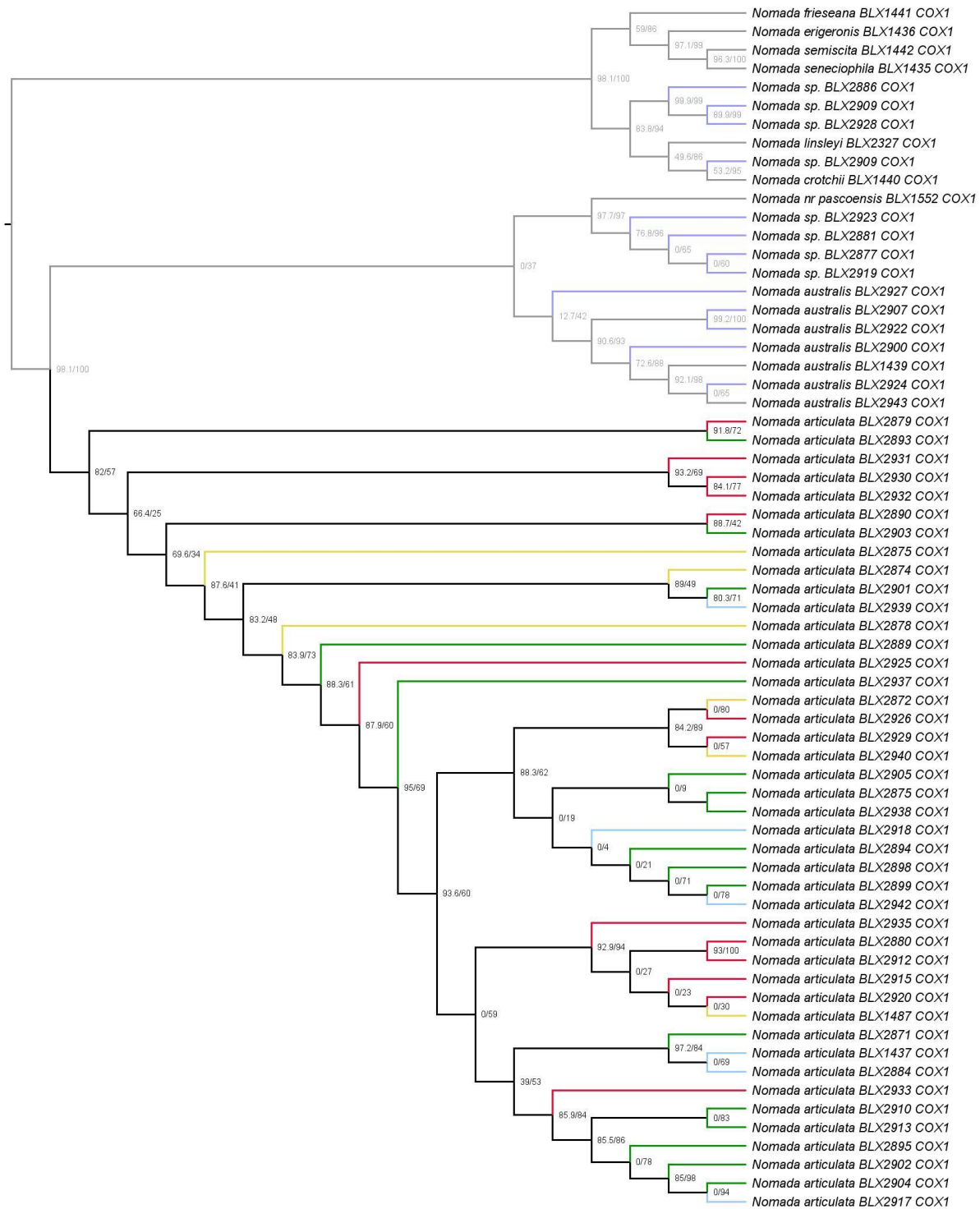
Fig. S1: Map of all specimens including those in the outgroup



Supp Fig. 2: Untransformed cladogram of all UCE sequenced specimens within this project. Color denotes the geographic locality the *Nomada articulata* specimen was collected. Purple colored specimens within the outgroup were initially identified as *N. articulata*.



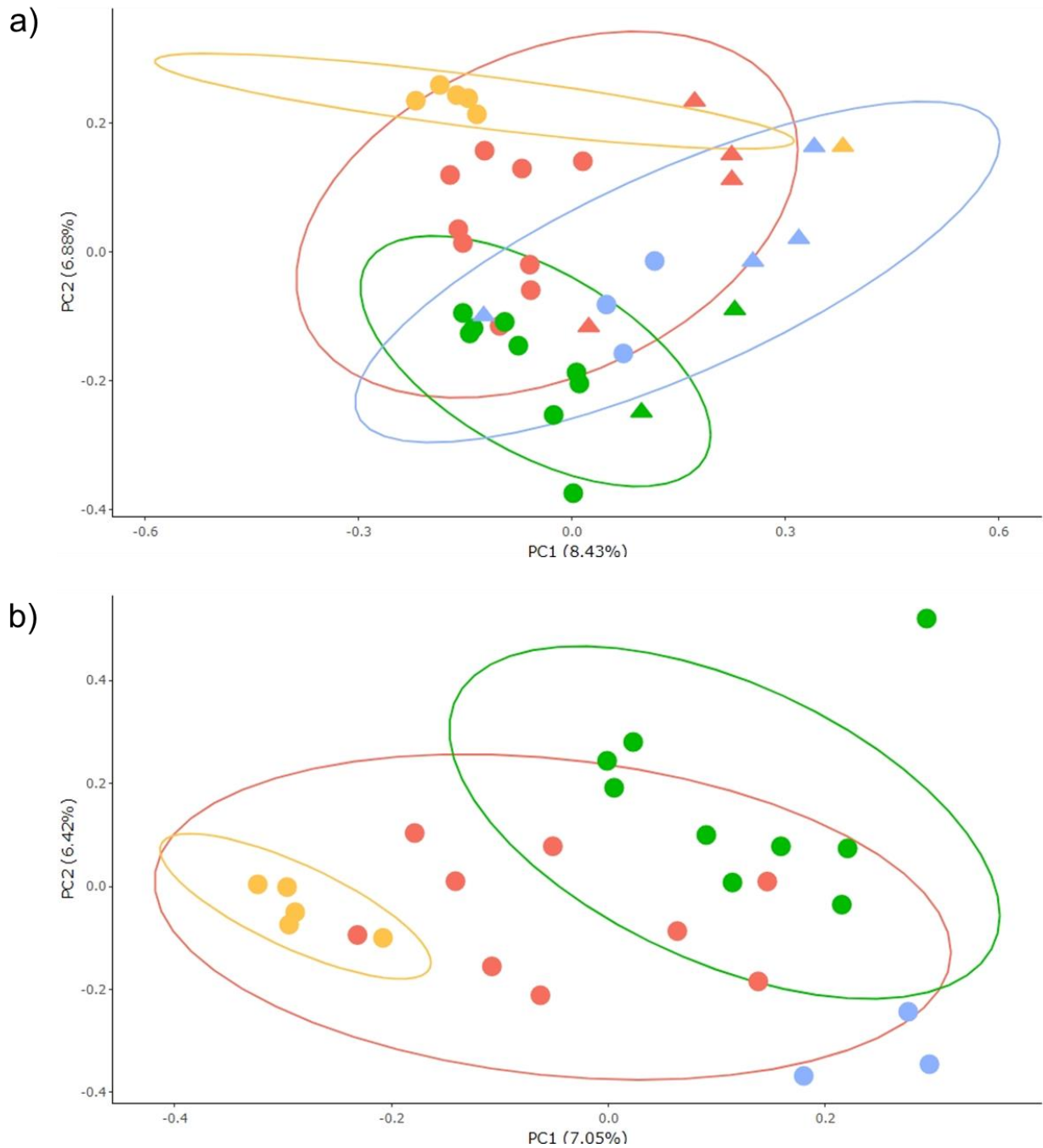
Supp Fig. 3: Cladogram of all mitochondrial sequenced specimens within this project. Color denotes the geographic locality the *Nomada articulata* specimen was collected. Purple colored specimens within the outgroup were initially identified as *N. articulata*.



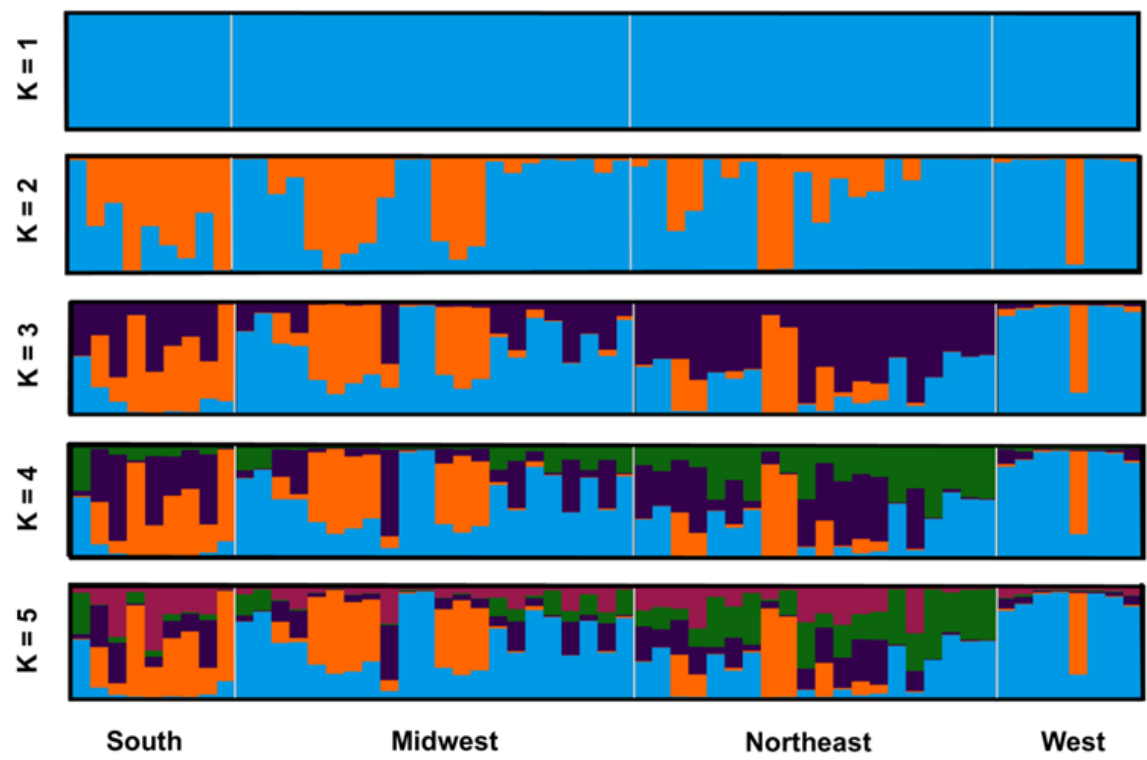
Supp Fig. 4: Untransformed cladogram of all mitochondrial sequenced specimens within this project. Color denotes the geographic locality the *Nomada articulata* specimen was collected. Purple colored specimens within the outgroup were initially identified as *N. articulata*.



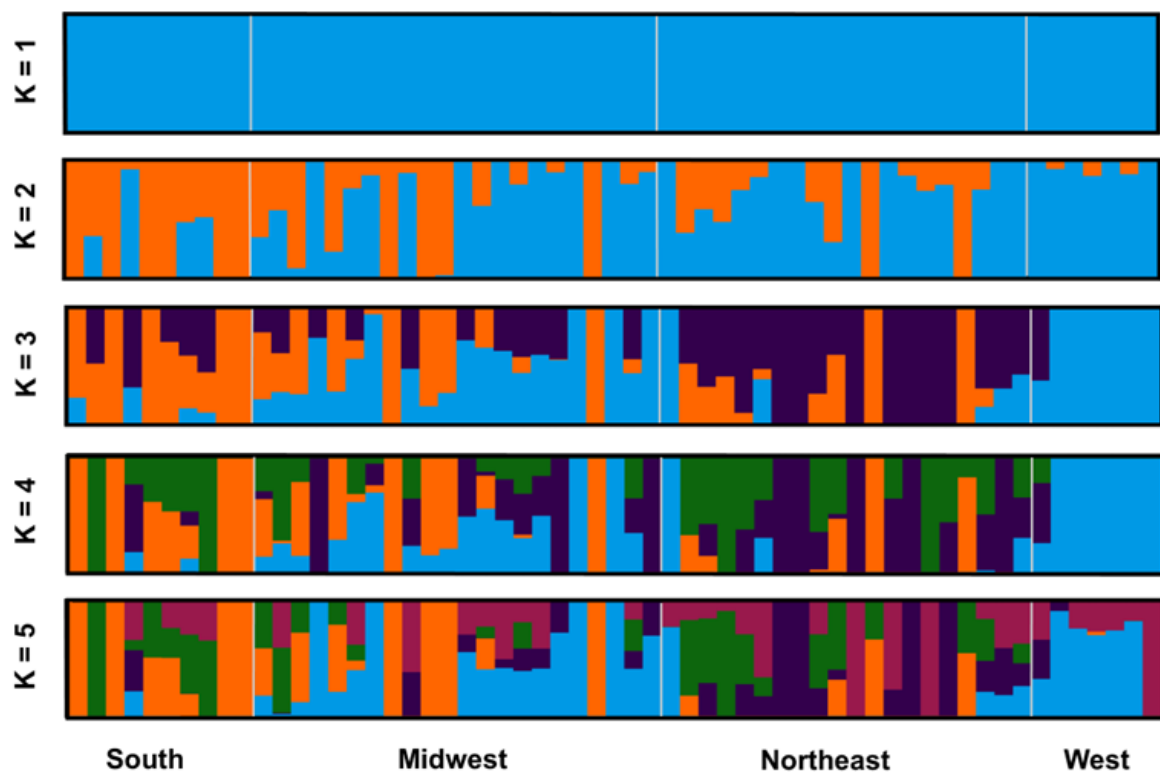
Supp Fig. 5: a) Principal component analysis for the 38 female *N. articulata* individuals showing the relationship between all specimens across the four geographic locations and b) the 26 female contemporary specimens across their geographic regions. Ellipses represent 95 % confidence.



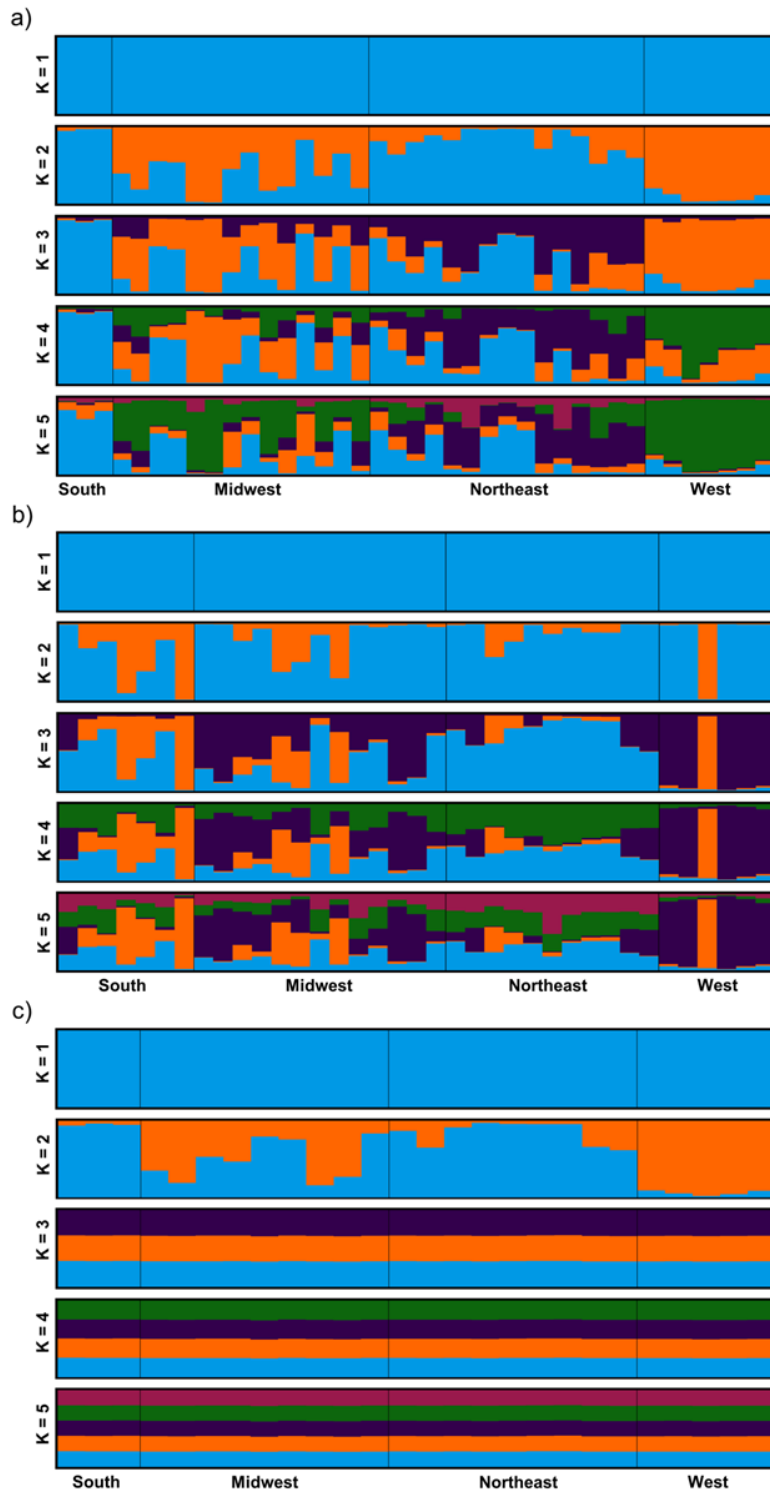
Supp. Fig. 6: Full results from STRUCTURE for all specimens



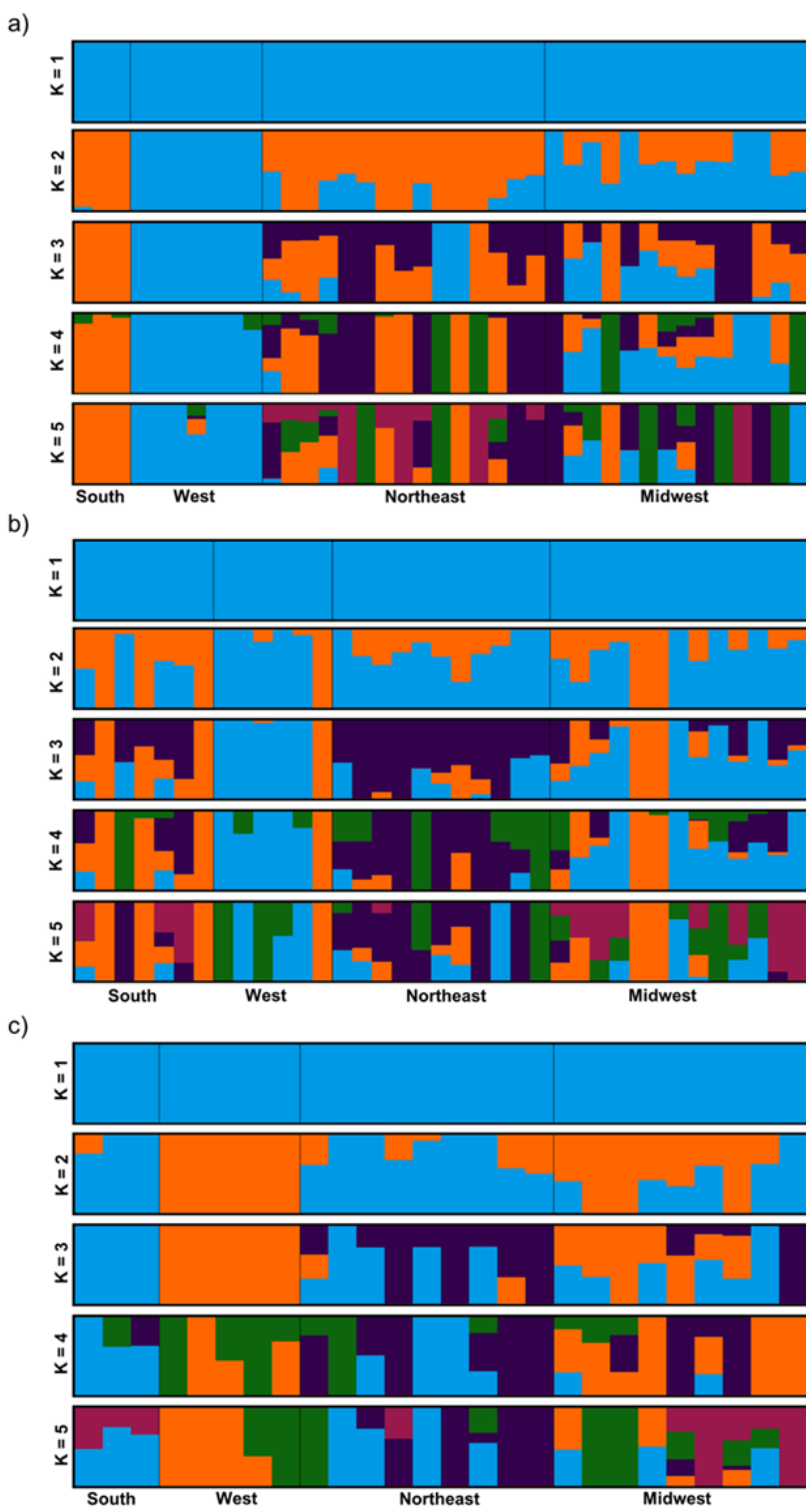
Supp. Fig. 7: Full results from ADMIXTURE for all specimens



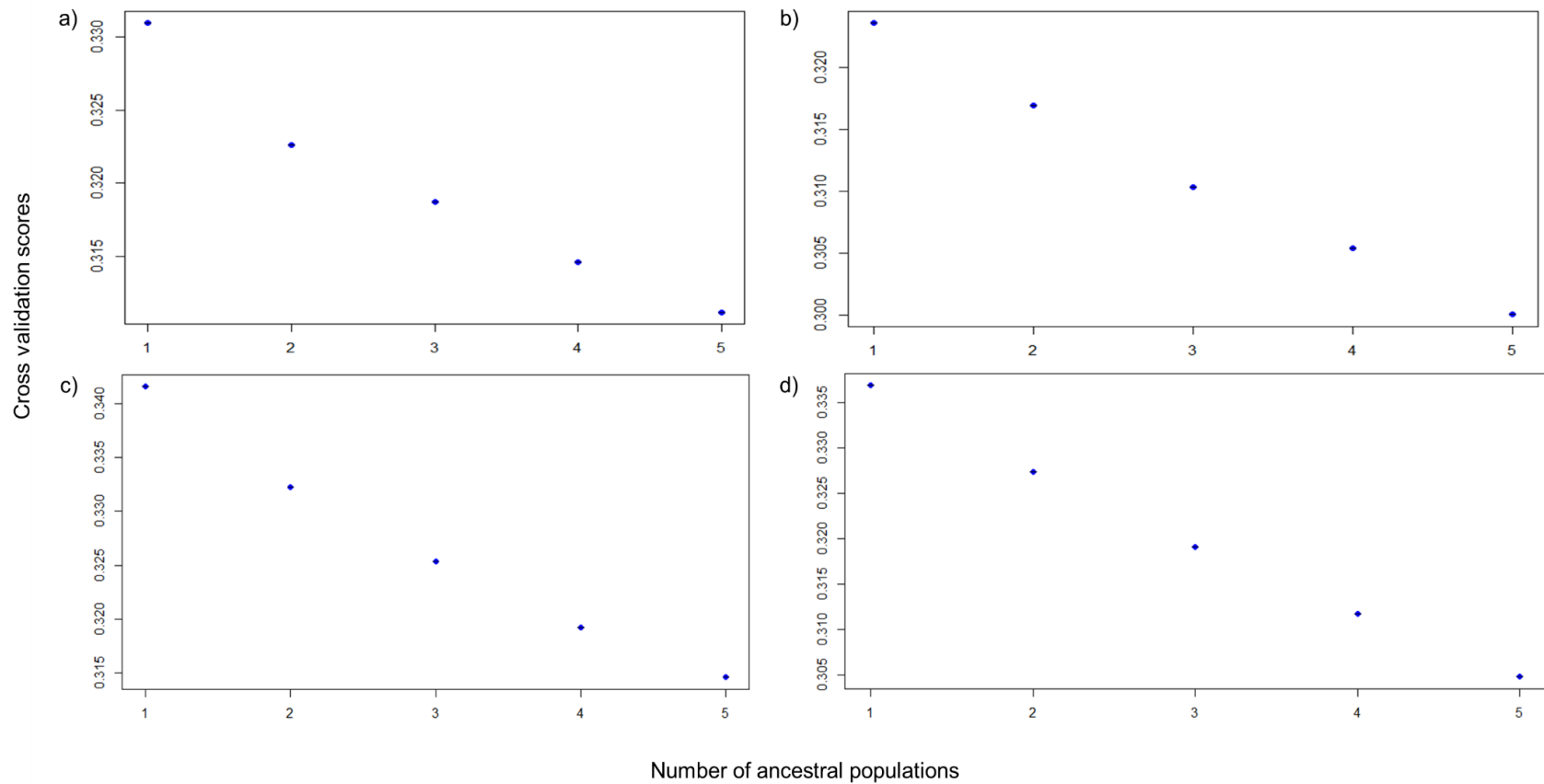
Supp Fig. 8: Remaining STRUCTURE results for a) contemporary only, b) all females, and c) all contemporary female samples



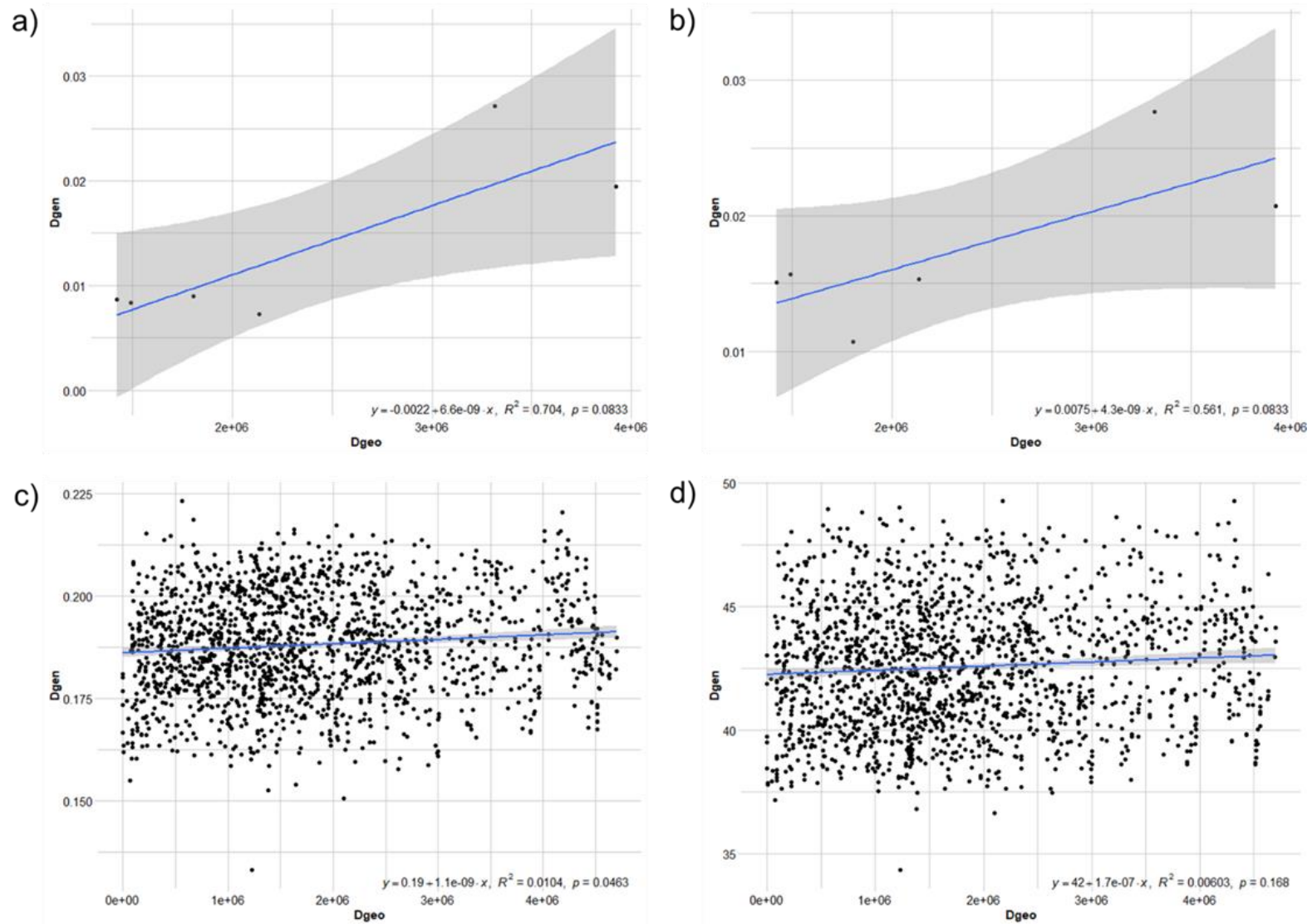
Supp. Fig. 9: Remaining ADMIXTURE results for a) contemporary only, b) all females, and c) all contemporary female samples



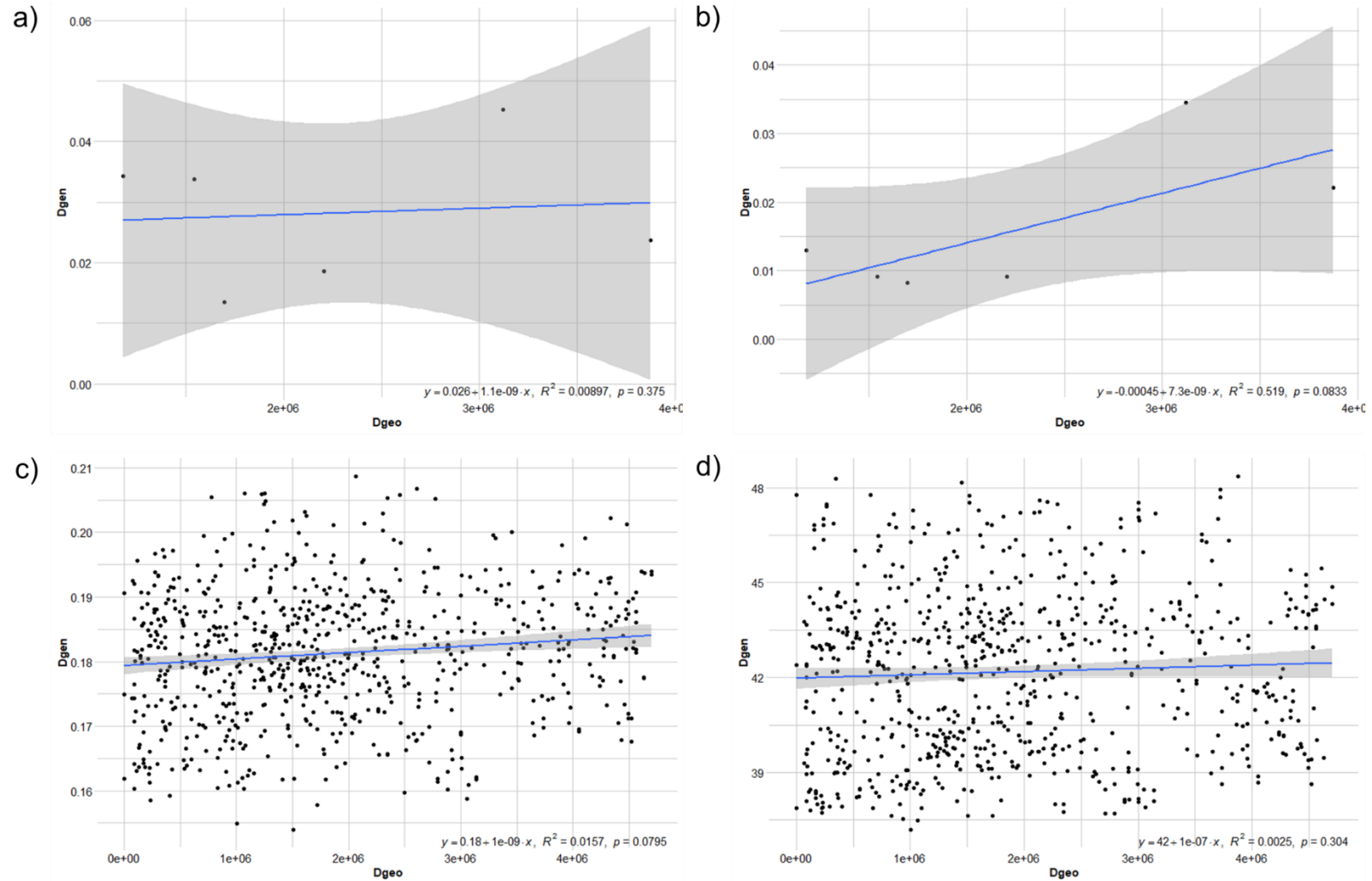
Supp. Fig. 10: TESS3 result showing no plateau of the cross validation scores. These results indicate that there is another factor, such as isolation by distance or other geological barriers, that influenced the historical population structure. a) all specimens; b) contemporary only; c) all females; d) all females contemporary



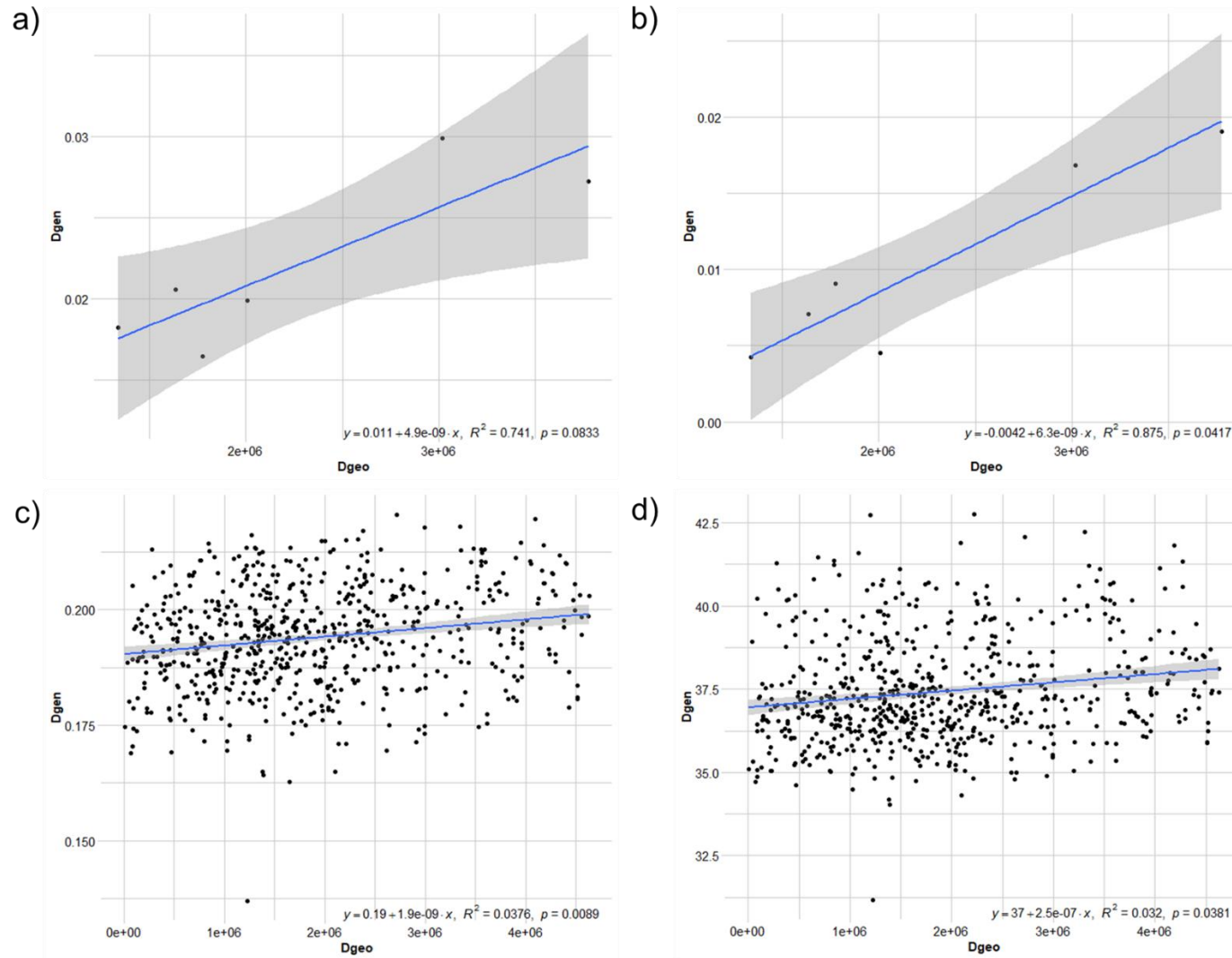
Supp. Fig. 11: Mantel test results plots for assessing isolation by distance for all specimens. a. Nei's D; b. Fst; c. Proportion shared alleles; d. Euclidean



Supp. Fig. 12: Mantel test results plots for assessing isolation by distance for all contemporary specimens. a) Nei's D; b) Fst; c) Proportion shared alleles; d) Euclidean



Supp. Fig. 13: Mantel test results plots for assessing isolation by distance for all female specimens. a) Nei's D; b) Fst; c) Proportion shared alleles; d) Euclidean



Supp. Fig. 14: Mantel test results plots for assessing isolation by distance for all female contemporary specimens. a) Nei's D; b) Fst; c) Proportion shared alleles; d) Euclidean

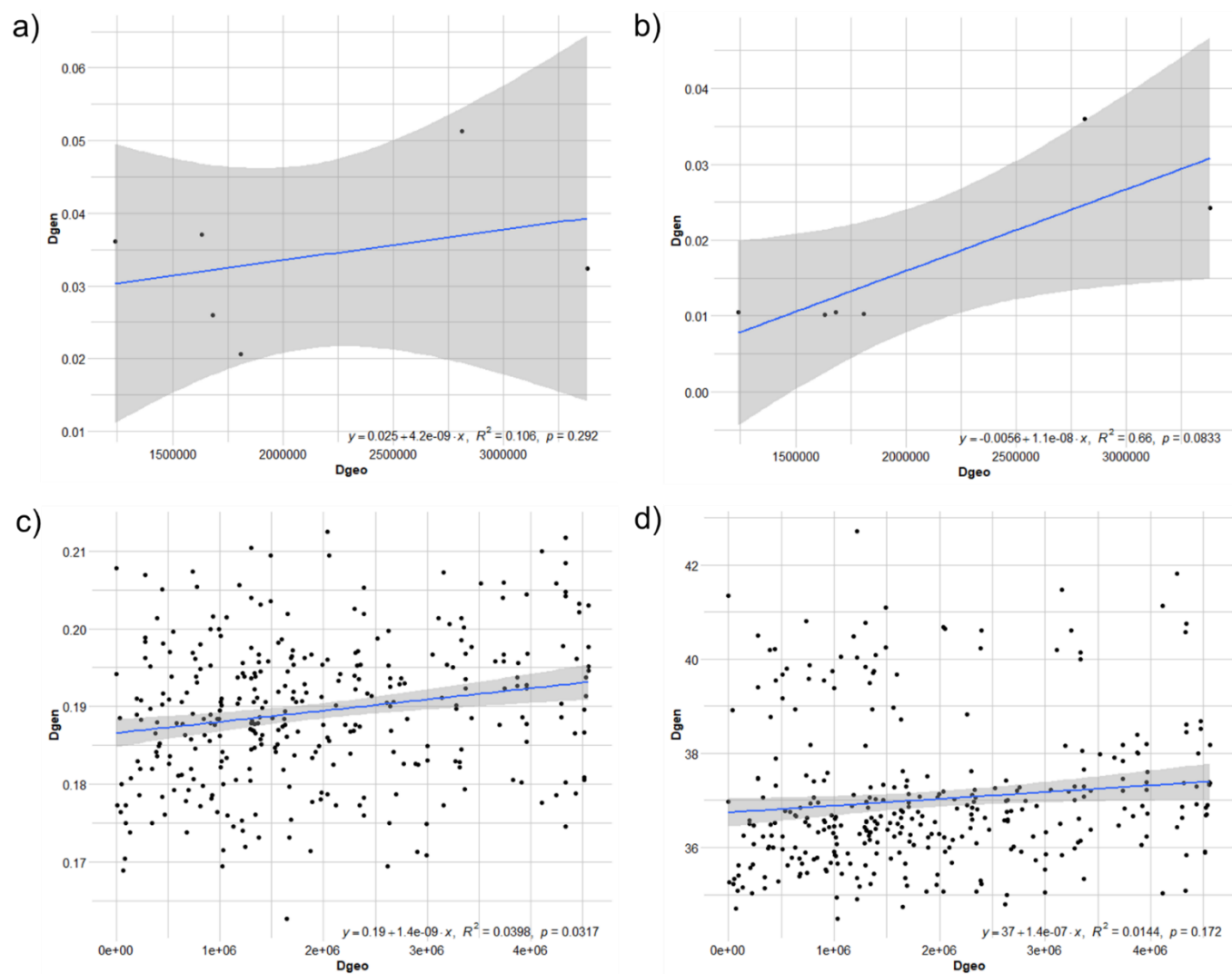


Table S1: Information for all specimens used in this study; Housing abbreviations used below: **AMNH** American Museum of Natural History **CFM** Chicago Field Museum **CLEM** Clemson University **FLSCA** Florida State Collection of Arthropods **GHC** Gordon Hutching Collection **ILMSU** Isaacs Lab Michigan State University **ISU** Iowa State University **MMC** Michael Minnick Collection **MNSD** Minnesota State Department **MSSU** Mississippi State University **MVC** Michael Veit Collection **NCSU** North Carolina State University **NHMLAC** Natural History Museum of Los Angeles County **PSU** Pennsylvania State University **RCYU** Rehan Collection York University **RHC** Russel Hopping Collection **ROM** Royal Ontario Museum **TAM** Texas A&M **TOC** Thomas Onuferko Collection **UCONN** University of Connecticut **UMB** University of Manitoba **USNPIC** U.S. National Pollinating Insects Collection

Species	BLX #	Sex	Housing collection	Collection Date	Country	State or province	Location	Age	Population
<i>seneciophila</i>	BLX1435		NHMLAC	14-Jun-2014	USA	MA	41.648, -75.494722		outgroup
<i>erigeronis</i>	BLX1436		ILMSU	2-Jul-2015	USA	MI	43.0172, -85.8381		outgroup
<i>rubicunda</i>	BLX1438		ILMSU	13-Jun-2018	USA	MI	43.941, -84.216		outgroup
<i>australis</i>	BLX1439		ILMSU	17-Jun-2017	USA	MI	42.17, -84.12		outgroup
<i>crotchii</i>	BLX1440		USNPIC	2-Jun-2003	USA	UT	37.834270, -111.353859		outgroup
<i>frieseana</i>	BLX1441		USNPIC	4-Apr-1986	USA	UT	37.254293, -113.771149		outgroup
<i>semiscita</i>	BLX1442		USNPIC	30-Apr-1981	USA	CO	37.627767, -104.868719		outgroup
<i>sp.</i>	BLX2877	f	TOC	16-Jun-2017	USA	CO	39.6677, -105.1968		outgroup
<i>sp.</i>	BLX2881	f	TAM	14-Apr-1962	USA	TX	30.588525, -96.297053		outgroup
<i>australis</i>	BLX2882	f	MSSU	17-Apr-1996	USA	LA	32.493056, -93.5825		outgroup
<i>australis</i>	BLX2883	f	MSSU	17-Apr-1996	USA	LA	32.492222, -93.579444		outgroup
<i>sp.</i>	BLX2885	f	MSSU	20-Apr-1958	USA	MS	33.453889, -88.788889		outgroup
<i>sp.</i>	BLX2886	f	MSSU	14-Jun-1981	USA	NC	36.211389, -81.668611		outgroup
<i>australis</i>	BLX2887	f	MSSU	21-Jul-1974	USA	ND	45.9833, -103.245		outgroup

<i>australis</i>	BLX2900	f	AMNH	14-Jul-1990	USA	NY	44.068611, -75.494722		outgroup
<i>australis</i>	BLX2907	f	AMNH	14-Jun-1910	USA	VA	36.664722, -80.920278		outgroup
<i>sp.</i>	BLX2909	f	GHC	19-Jun-2016	CAN	BC	49.02774601, - 119.5609691		outgroup
<i>sp.</i>	BLX2919	f	TAM	28-Mar-1987	USA	TX	28.34585, -99.615623		outgroup
<i>australis</i>	BLX2922	m	NHMLAC	22-Apr-1958	USA	GA	33.429882, -82.125907		outgroup
<i>sp.</i>	BLX2923	f	NHMLAC	21-Apr-1978	USA	GA	31.626232, -81.159809		outgroup
<i>australis</i>	BLX2924	f	NHMLAC	21-Apr-1978	USA	GA	31.626232, -81.159809		outgroup
<i>sp.</i>	BLX2928	m	UMB	2-Jun-2010	CAN	MB	49.7084, -99.6007		outgroup
<i>australis</i>	BLX2943	m	MMC	11-May-2015	USA	OH	39.572, -84.801		outgroup
<i>articulata</i>	BLX_1487	f	ILMSU	5-Jul-2016	USA	MI	41.967775, -86.358208	Contemporary	Midwest
<i>articulata</i>	BLX2879	f	MNSD	5-6-Jun-2017	USA	MN	45.00594, -94.58901	Contemporary	Midwest
<i>articulata</i>	BLX2880	f	MNSD	10-12-Jun-2014	USA	MN	43.72553, -95.0639	Contemporary	Midwest
<i>articulata</i>	BLX2890	f	AMNH	3-Jul-2014	USA	IA	43.431919, -92.009089	Contemporary	Midwest
<i>articulata</i>	BLX2891	m	AMNH	20-Jun-1917	USA	IL	42.014608, -89.332536	Historic	Midwest
<i>articulata</i>	BLX2892	m	AMNH	24-May-1903	USA	IN	40.733333, -85.216667	Historic	Midwest
<i>articulata</i>	BLX2896	f	AMNH	2-Jun-1934	USA	ND	46.877222, -96.789444	Historic	Midwest
<i>articulata</i>	BLX2897	f	AMNH	12-Jun-1934	USA	ND	46.586944, -97.4925	Historic	Midwest
<i>articulata</i>	BLX2911	f	ROM	3-Jul-1968	CAN	ON	43.823584, -80.008313	Historic	Midwest
<i>articulata</i>	BLX2912	m	ISU	29-May-2016	USA	IA	41.955417, -94.31325	Contemporary	Midwest

<i>articulata</i>	BLX2914	m	ISU	28-May-2018	USA	IA	42.367172, -92.935749	Contemporary	Midwest
<i>articulata</i>	BLX2915	m	CFM	20-Jun-1921	USA	IL	41.684722, -87.853056	Historic	Midwest
<i>articulata</i>	BLX2916	f	CFM	14-Jun-1931	USA	IL	41.684722, -87.853056	Historic	Midwest
<i>articulata</i>	BLX2925	m	NHMLAC	23-May-1977	USA	MO	38.794218, -90.508536	Historic	Midwest
<i>articulata</i>	BLX2926	f	MMC	10-Jun-2015	USA	OH	39.572, -84.801	Contemporary	Midwest
<i>articulata</i>	BLX2927	f	MMC	12-May-2015	USA	OH	39.485, -84.509	Contemporary	Midwest
<i>articulata</i>	BLX2929	f	UMB	9-Jun-2019	CAN	MB	49.6603, -99.269	Contemporary	Midwest
<i>articulata</i>	BLX2930	m	UMB	19-Jun-2015	USA	MI	42.6915, -84.497	Contemporary	Midwest
<i>articulata</i>	BLX2931	m	UMB	21-Jun-2008	CAN	ON	43.91055, -79.22443	Contemporary	Midwest
<i>articulata</i>	BLX2932	f	ILMSU	16-Jun-2014	USA	MI	42.400606, -86.126150	Contemporary	Midwest
<i>articulata</i>	BLX2933	f	ILMSU	24-May-2018	USA	MI	42.772, -83.084	Contemporary	Midwest
<i>articulata</i>	BLX2935	m	MNSD	12-14-Aug-2014	USA	MN	47.166964, -92.732307	Contemporary	Midwest
<i>articulata</i>	BLX2871	f	TOC	21-Jun-2020	CAN	ON	45.3981, -75.3623	Contemporary	Northeast
<i>articulata</i>	BLX2875	f	TOC	26-Jun-2018	CAN	QC	45.4462, -75.8131	Contemporary	Northeast
<i>articulata</i>	BLX2888	f	AMNH	17-Jun-1958	USA	CT	41.906111, -71.870278	Historic	Northeast
<i>articulata</i>	BLX2889	f	AMNH	17-May-1968	USA	CT	41.1468, -73.4949	Historic	Northeast
<i>articulata</i>	BLX2893	m	AMNH	8-Jun-2010	USA	MA	41.32485, -70.81055	Contemporary	Northeast
<i>articulata</i>	BLX2894	f	AMNH	16-Jun-2011	USA	MA	42.693035, -71.104717	Contemporary	Northeast
<i>articulata</i>	BLX2895	m	AMNH	15-Jun-2010	USA	MA	41.26504, -70.1773	Contemporary	Northeast

<i>articulata</i>	BLX2898	m	AMNH	20-May-1910	USA	NJ	40.853704, -74.824877	Historic	Northeast
<i>articulata</i>	BLX2899	m	AMNH	20-May-1910	USA	NJ	40.853704, -74.824877	Historic	Northeast
<i>articulata</i>	BLX2901	f	AMNH	29-May-2010	USA	NY	40.661667, -73.970833	Contemporary	Northeast
<i>articulata</i>	BLX2902	m	AMNH	3-Jul-1962	USA	NY	41.263337, -74.250405	Historic	Northeast
<i>articulata</i>	BLX2903	f	AMNH	21-Jun-2005	USA	PA	40.160084 , -77.931	Contemporary	Northeast
<i>articulata</i>	BLX2904	f	AMNH	21-Jun-1995	USA	RI	41.155869, -71.568624	Contemporary	Northeast
<i>articulata</i>	BLX2905	f	AMNH	21-Jun-1995	USA	RI	41.155869, -71.568624	Contemporary	Northeast
<i>articulata</i>	BLX2910	m	UCONN	20-24-May-2010	USA	CT	41.330831, -72.919719	Contemporary	Northeast
<i>articulata</i>	BLX2913	m	PSU	11-May-2017	USA	PA	40.0502, -77.1282	Contemporary	Northeast
<i>articulata</i>	BLX2934	m	MVC	4-Jun-2017	USA	NH	42.796, -72.486	Contemporary	Northeast
<i>articulata</i>	BLX2936	f	RCYU	24-Jun-2014	USA	NH	43.284785, -71.016719	Contemporary	Northeast
<i>articulata</i>	BLX2937	m	RCYU	11-Jun-2014	USA	NH	43.284785, -71.016719	Contemporary	Northeast
<i>articulata</i>	BLX2938	f	RHC	18-Jun-2011	USA	MA	42.468186, -71.348928	Contemporary	Northeast
<i>articulata</i>	BLX1437	f	MVC	18-Apr-1976	USA	AL	32.594631, -85.477732	Historic	South
<i>articulata</i>	BLX2884	f	MSSU	14-May-1991	USA	MS	33.69832, -90.0405	Contemporary	South
<i>articulata</i>	BLX2906	f	AMNH	28-May-2000	USA	VA	36.776715, -80.404415	Contemporary	South
<i>articulata</i>	BLX2908	f	CLEM	25-May-1930	USA	SC	34.177377, -79.783688	Historic	South
<i>articulata</i>	BLX2917	m	NCSU	27-May-1959	USA	NC	35.797222, -76.421944	Historic	South
<i>articulata</i>	BLX2918	m	NCSU	6-May-1955	USA	NC	36.326631, -78.410632	Historic	South

<i>articulata</i>	BLX2921	f	TAM	4-May-1950	USA	SC	33.7706, -81.249343	Historic	South
<i>articulata</i>	BLX2939	f	FLSCA	29-Jun-1995	USA	TN	35.72798, -83.813261	Contemporary	South
<i>articulata</i>	BLX2942	f	MSSU	10-Apr-1974	USA	MS	32.708472, -89.603848	Historic	South
<i>articulata</i>	BLX2872	f	TOC	11-Jun-2019	CAN	AB	50.86, -110.0068	Contemporary	West
<i>articulata</i>	BLX2873	f	TOC	11-Jun-2019	CAN	AB	50.8504, -110.0489	Contemporary	West
<i>articulata</i>	BLX2874	f	TOC	11-Jun-2019	CAN	AB	50.8504, -110.0489	Contemporary	West
<i>articulata</i>	BLX2876	m	TOC	2-Jun-2019	CAN	SK	50.1456, -109.8062	Contemporary	West
<i>articulata</i>	BLX2878	m	TOC	15-Jun-2017	USA	CO	39.7319, -104.9609	Contemporary	West
<i>articulata</i>	BLX2920	f	TAM	15-Mar-1977	USA	TX	28.324167, -99.405196	Historic	West
<i>articulata</i>	BLX2940	f	TOC	11-Jul-2019	CAN	SK	50.6834, -109.2901	Contemporary	West
<i>articulata</i>	BLX2941	f	TOC	27-Jul-2019	CAN	SK	50.2431, -108.2503	Contemporary	West

Table S2: Hardy Weinberg values using heterozygosity (Gst) and least squares methods (Fst). P-values are too small and are presented as zero by Genodive.

	Population	Gst values	Fst values	P values
All contemporary	South	-0.325	-0.325	0.000
	Midwest	-0.182	-0.182	0.000
	Northeast	-0.173	-0.173	0.000
	West	-0.225	-0.225	0.000
	Overall	-0.224	-0.197	0.000
Females only	South	-0.234	-0.234	0.000
	Midwest	-0.257	-0.257	0.000
	Northeast	-0.267	-0.267	0.000
	West	-0.231	-0.231	0.000
	Overall	-0.248	-0.264	0.000
Females contemporary	South	-0.327	-0.327	0.000
	Midwest	-0.282	-0.282	0.000
	Northeast	-0.262	-0.262	0.000
	West	-0.292	-0.292	0.000
	Overall	-0.289	-0.282	0.000

Table S3: G statistics for heterozygosity and inbreeding across all populations.

	Statistic	Value	Std.Dev.	c.i.2.5%	c.i.97.5%
All contemporary	Ho	0.332	0.004	0.323	0.341
	Hs	0.271	0.002	0.266	0.276
	Ht	0.274	0.002	0.27	0.279
	Gis	-0.224	0.009	-0.242	-0.206
	Gst	0.012	0.001	0.01	0.015
Females only	Ho	0.356	0.004	0.347	0.365
	Hs	0.286	0.002	0.281	0.29
	Ht	0.288	0.003	0.283	0.293
	Gis	-0.248	0.008	-0.263	-0.232
	Gst	0.008	0.001	0.006	0.009
Females contemporary	Ho	0.372	0.005	0.363	0.382
	Hs	0.289	0.003	0.283	0.294
	Ht	0.292	0.003	0.287	0.297
	Gis	-0.289	0.008	-0.306	-0.273
	Gst	0.013	0.001	0.01	0.015

Table S4: F_{st} for all pairs of populations resulting from AMOVA; p-values are below the diagonal and all are significant; indicative of freely breeding populations.

All contemporary		South	Midwest	Northeast	West
	South	--	0.013	0.009	0.035
	Midwest	0.037	--	0.008	0.009
	Northeast	0.08	0.000	--	0.022
	West	0.008	0.000	0.000	--
Females only		South	Midwest	Northeast	West
	South	--	0.004	0.007	0.017
	Midwest	0.073	--	0.009	0.005
	Northeast	0.016	0	--	0.019
	West	0.029	0.068	0	--
Females contemporary		South	Midwest	Northeast	West
	South	--	0.01	0.01	0.036
	Midwest	0.012	--	0.01	0.011
	Northeast	0.034	0	--	0.024
	West	0.019	0.001	0.001	--

Table S5: Mantel test results for assessing isolation by distance for all data types tested.

				Upper quantiles of permutations			
		Mantel statistic	significance	90%	95%	97.50%	99%
All	Nei's D	0.7487	0.083333	0.666	0.734	0.832	0.898
	Fst	0.8393	0.08333	0.555	0.601	0.758	0.872
	Proportion shared	0.102	0.049995	0.0785	0.1019	0.1232	0.1494
	Euclidean	0.07768	0.16768	0.104	0.133	0.158	0.182
All contemporary	Nei's D	0.09471	0.375	0.741	0.913	0.941	0.948
	Fst	0.7205	0.08333	0.674	0.704	0.81	0.887
	Proportion shared	0.1253	0.079492	0.114	0.147	0.179	0.21
	Euclidean	0.05004	0.30987	0.135	0.174	0.208	0.245
Female only	Nei's D	0.861	0.08333	0.58	0.68	0.818	0.912
	Fst	0.9355	0.041667	0.516	0.631	0.718	0.772
	Proportion shared	0.1939	0.0088991	0.0942	0.1258	0.153	0.1878
	Euclidean	0.1788	0.038096	0.123	0.162	0.2	0.24
Female contemporary	Nei's D	0.3258	0.29167	0.747	0.868	0.878	0.879
	Fst	0.8127	0.08333	0.614	0.654	0.797	0.899
	Proportion shared	0.1996	0.031697	0.132	0.175	0.209	0.251
	Euclidean	0.12	0.17228	0.159	0.203	0.252	0.319

Keys to the species groups of eastern North American *Nomada* Scopoli and to species of five of the seven species groups

Abstract

The genus *Nomada* is the largest and most diverse of all the cleptoparasitic bee genera and is routinely collected in large scale bee surveys. Despite how pervasive they are, *Nomada* in collections frequently remain difficult to identify as a result of outdated keys and the high variation in morphology within species. Provided here are updated and fully illustrated dichotomous keys to the seven *Nomada* species groups found in eastern North America in addition to keys for the identification of 15 species from five of the seven species groups. Additionally, one synonym is confirmed: *N. bessyi* Swenk is a junior synonym of *N. graenicheri* Cockerell. This synonymy, originally suggested by Droege et al. (2010) is now supported through the use of molecular data. Consequently, *N. graenicheri* is moved from the subgenus *Nomada s.s.* to the *N. vincta* species group. In addition to new taxonomic keys, this chapter provides updated information regarding *Nomada* biology and ecology such as host and floral associations and species ranges.

Introduction

About 20% of all bees in the family Apidae are considered brood parasites. in which the parasitic female lays eggs in the nests of other bees (Danforth et al., 2019). Of the different parasitic genera, the genus *Nomada* (Scopoli) is considered the most taxonomically challenging and diverse (Alexander, 1994; Alexander & Schwarz, 1994). *Nomada* and other cleptoparasitic bees are inherently linked to their specific host bee or bees; the binding of host and parasite is the result of coevolution and involved unidirectional and often extreme modifications to their behaviour and morphology (Dehon et al., 2017; Straka et al., 2024). The changes to an obligatory parasitic lifestyle include the gain of mechanisms and behaviours associated with stealth and defense, including spines, a reduced pygidial plate, and faster production of mature oocytes at

the loss of the ability to gather pollen and construct nests (Lhomme & Hines, 2019; Litman, 2019; Michener, 2007; Rozen, 2003).

Ultimately, cleptoparasitic bees like *Nomada* perform many of the ecological services that are attributed to traditional parasites such as manipulating community composition and influencing the biodiversity of their environment and therefore can be used as important ecological monitoring tools (Minckley & Danforth, 2019; Odanaka & Rehan, 2019; Sheffield et al., 2013). For example, *Nomada* and other cleptoparasitic genera can be valuable bioindicators of overall bee community health in a given environment due to their total dependence on their hosts and restrictive habitat requirements (Sheffield et al., 2013). If an environment can support a diverse and stable cleptoparasitic community, that habitat is healthy enough to support healthy and diverse populations of the hosts as well (Odanaka & Rehan, 2019). However, despite being of ecological importance and commonly collected in bee and pollinator surveys, *Nomada* identification remains very difficult due to little and seemingly inconsistent morphological variation between species resulting in many collected specimens remaining unidentified and not, or inappropriately reported, in ecological surveys.

Regardless of the taxonomic challenges, recent progress has been made in untangling the evolutionary relationships among *Nomada* species and/or species groups (Lim & Lee, 2023b; Odanaka et al., 2022; Straka et al., 2024), and creating more definite species concepts (Droege et al., 2010; Fidalgo & Paris, 2023; Gibbs et al., 2023; Kuhlmann, 2023; Lim et al., 2022; Lim & Lee, 2023a; Smit, 2018; Walker et al., 2020). This has been aided by the increasing accessibility of molecular tools. Within North America, species identification keys for *Nomada* remain largely absent (but see Ascher & Pickering 2024). The last comprehensive key for the genus was Mitchell (1962) which only dealt with species from the Eastern United States. Therefore, the overall purpose of this study is to provide keys to the species groups and to the species of five groups of *Nomada* found east of the Mississippi River in Canada and the United States.

Methods

The identification keys presented here are based upon the external morphologies visible in dry pinned specimens for both male and female specimens. Although a single initial key to species groups is included, any characters that are unique to a particular sex are clearly distinguished within the couplet. For some species groups (the *N. roberjeotiana*, *N. vincta*, and *N. vegana* species groups), males and females are essentially monomorphic and thus only one key is presented. A reminder that males and females are monomorphic is placed at the beginning of each key for the species of the *N. roberjeotiana*, *N. vincta*, and *N. vegana* species groups. Additionally, there is only one set of diagnoses under the “Diagnosis” sections for the species within these species groups. For all remaining species groups, there are separate keys and diagnoses for males and females.

A combination of morphology supported by genetic barcoding and previously sequenced ultra-conserved elements (UCEs) was used to help delimit the *Nomada* species included here. For DNA barcoding, genetic data were obtained by sequencing the 658 bp barcode region of the COI gene. A total of 380 specimens (from 52 species) were chosen and a single leg was removed from each individual and sent to the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Ontario, Canada for sequencing. Of the original 380 specimens, only 278 yielded DNA results and only 246 sequences are barcode compliant. For this chapter, data from only 93 specimens that are representative of the five species groups being addressed are presented (Table S1; Supp. Fig. 1). Failed specimens were primarily older and were originally sequenced using the Ancient DNA option offered by the CCDB. Once the data were returned, neighbor joining trees (Saitou & Nei, 1987) in the Taxon ID Tree function on the BOLD systems interface was used to check for sequences and for cross referencing species designations and relationships with the UCE tree. At times, the placement of certain individuals on the trees did not match the species identification of the specimen. These individuals were then re-examined morphologically to check for additional differences between morphological and sequence data. Barcoded specimens are uploaded on the BOLD database under the “Barcoding eastern North American *Nomada* species” project. The remaining barcodes and the neighbor-joining and UCE trees will be made public following the completion of the keys for the remaining species groups not addressed in this dissertation. See Odanaka et al (2022) for the complete methodology for obtaining the UCE sequences used here. Published UCE data are currently available on NCBI (SRR18055085 – SRR18055199). The original UCE based tree used here can be found in Supp. Fig. 2.

The anatomical and taxonomic terms used in the subsequent keys follow Michener (2007) and Smit (2018) and are illustrated in (Figs. 1-8). Additional terms used are prelobar carina (Fig. 26) and acetabular carina (Fig. 28) which follow Broemeling and Moalif (1988) and Michener and Fraser (1978) respectively. These additional characters are primarily used for identification of members of the *N. roberjeotiana* and *N. vincta* species groups. When discussing the antenna, an F followed by a number from one to ten (for females) or one to eleven (for males) designates individual flagellomeres (Fig. 5). Antennal measurements primarily compare the relative lengths of F1, F2, and F3 and are proportional to each other. Unless stated, measurements are based upon the shorter side of F1 and the middle of F2 or F3 (Figs. 11, 14). For all other measurements of length and width, such as for the head, the widest and longest margins are used (Fig. 75). For describing width measured along a horizontal axis, the term length is used (i.e. for antennal measurements) and for measurements along a vertical axis, the term height is used. When discussing the metasoma, T or S followed by a number designates one of five (females) or six (males) visible terga or sterna (Fig. 2, 3). Within certain species groups, puncture density can be used for distinguishing between species. An area is considered to be densely punctate if there is no integument surface visible and punctures are nearly contiguous (Fig. 58a). An area is considered to be sparsely punctate if the punctures are spaced farther apart and integument is visible between the punctures (Fig. 32b).

Due to multiple difficulties, such as the COVID-19 pandemic, not all primary types were physically examined; rather many of the species descriptions were based upon examination of paratypes or detailed photos of the primary type specimens found on museum databases or sent to me by the collection curator. If the type was physically examined, the label “EXAMINED” is included in the description, otherwise the species description is labeled whether photos or other types (ie paratype, homotype) were examined. Information was retrieved from the manuscript where the species was described for type specimens that are lacking online photos and were not physically examined; these specimens are labeled as “NOT EXAMINED.” Specimens used for the DNA barcoding, UCE sequencing and for morphological examination were provided by a multitude of museums and academic institutions within the US, Canada and the United Kingdom (Table S1). Species distributions and floral host association were estimated from the examined specimens and gaps were then filled by examining Discover life and published records (Ascher & Pickering, 2024; Broemeling, 1988; Broemeling & Moalif, 1988, Cockerell, 1903a, 1903b,

1903c, 1905, 1911a, 1921; Cockerell & Atkins, 1902; Cresson, 1863, 1878; Droege et al., 2010; Gibbs et al., 2017, 2023; Goldstein & Ascher, 2016; Kilpatrick et al., 2020; Mitchell, 1962; Portman et al., 2023; Robertson, 1895; Stevens, 1951; Swenk, 1912, 1915; Wolf & Ascher, 2008).

The following acronyms were used to distinguish between the different collections both in Table S1 and in species descriptions: **AMNH** (American Museum of Natural History), **ANS** (Academy of Natural Sciences, Philadelphia), **CLEM** (Clemson University Arthropod Collection, Clemson), **HE** (Hadil Elsayed personal collection), **CSU** (Colorado State University, Fort Collins), **FMNH** (Field Museum of Natural History, Chicago), **FSCA** (Florida State Collection of Arthropods, Gainesville), **GH** (Gord Hutchings personal collection), **GIC** (Guelph Insect Collection, Guelph), **INHS** (Illinois Natural History Survey, Champaign), **KU** (University of Kansas, Lawrence), **JBWM** (University of Manitoba, Winnipeg), **LACM** (Los Angeles County Museum, Los Angeles), **MSSU** (Mississippi State University, Mississippi State), **MSU** (Isaacs Lab at Michigan State University, Lansing), **MCZ** (Museum of Comparative Zoology, Harvard, Cambridge), **MM** (Michael Minnick personal collection), **MNSC** (Minnesota State Collection, Minneapolis-Saint Paul), **MV** (Michael Veit personal collection), **NCSU** (North Carolina State University, Raleigh), **NHMUK** (Natural History Museum, London, UK) **PCYU** (Packer Collection at York University, Toronto), **PSU** (Frost Entomological Museum, Penn State University, University Park), **RLGU** (Raine Lab at the University of Guelph, Guelph), **RLYU** (Rehan Lab at York University, Toronto), **ROM** (Royal Ontario Museum, Toronto), **SH** (Spencer Hardy personal collection), **TAMU** (Texas A&M at College Station, College Station), **TO** (Tom Onuferko personal collection), **UCal** (University of Calgary, Calgary), **UCF** (University of Central Florida, Orlando), **UCON** (University of Connecticut, Storrs), **UGA** (University of Georgia, Athens), **UNBSM** (University of Nebraska State Museum, Lincoln), **USNM** (U.S. National Museum, Washington DC).

All photographs used in these keys were taken of pinned specimens on a Canon EOS 7D SLR camera using a custom built imaging system. Image stacking was performed using Zerene Stacker and all photos were edited using Microsoft Powerpoint (v.2405).

Taxonomy

One of two genera found within the tribe Nomadini, *Nomada* are slender, wasplike bees and are usually coloured red or black with white or yellow markings (Michener, 2007). There are more than 16 currently recognized species groups placed within 13 different subgenera (Straka et al., 2024). The highest concentration of species diversity is in the Holarctic with the number of species groups decreasing in the southern hemisphere; only 3 species groups in comparison to the over 13 found in the northern hemisphere (Alexander, 1990, 1991; Michener, 2007; Odanaka et al., 2022). It is estimated that the most recent common ancestor for *Nomada* separated from its sister genus, *Acanthonomada*, between 49-65 million years ago and most likely in the eastern Mediterranean region (Odanaka et al., 2022; Straka et al., 2024). From there, the genus dispersed throughout the globe, however dispersal into the southern hemisphere only occurred three times, resulting in one endemic subgenus (*Afronomada*) and species group (the *N. vegana* species group) (Odanaka et al., 2022). The subgenus *Mininomada* was the third group of *Nomada* to reach the southern hemisphere (Odanaka et al., 2022). A more detailed treatment of *Nomada* biogeography can be found in Chapter 2.

Currently within *Nomada* there are four different subgenera found in eastern Canada and the United States. These are *Heminomada*, *Holonomada*, *Hypochrotaenia*, and *Nomada sensu stricto*. These four subgenera cover all eastern *Nomada* species except members of the *N. vincta* species group which previously had subgeneric status under the name *Pachynomada* but was relegated to species group status by Alexander (1989). Of the subgenera listed, only *Holonomada* and *Hypochrotaenia* are addressed in this key. Furthermore, *Hypochrotaenia* is the only subgenus to contain multiple species groups (the *N. erigeronis*, *N. roberjeotiana* and *N. vegana* species groups) in North America, two of which are endemic to the Western hemisphere. It should be noted that in the most recent taxonomic restructuring of all *Nomada* (Straka et al., 2024), there are a couple of inaccuracies in the organization of the subgenus *Hypochrotaenia* for the Western hemisphere. In particular, their recognition of the *N. elegantula* species group without molecular support is contradicted by Alexander (1994) who considered it part of the *N. roberjeotiana* species group despite singling out the three species (*N. elegantula*, *N. marginella*, *N. melanosoma*) that comprise the *N. elegantula* “group” based upon their unique morphology

(mesal part of pronotal collar compressed and appearing attached to the anterior of the scutum, margins and ridges of the pronotum absent, presence of long plumose setae on mesepisternum and propodeum, scutellum without a median groove). This decision to keep the three species as part of the *N. roberjeotiana* species group is reflected in Alexander and Schwarz (1994) as all three are listed in the *roberjeotiana* section. Future work should include these three species in order to verify if they comprise their own species group. The second error is that Straka et al. (2024) only recognize three species groups for North America: the *N. vegana*, *N. erigeronis*, and *N. elegantula* species groups within the Western hemisphere while leaving out the *N. roberjeotiana* species group. There are two eastern North American species (*N. aquilarum*, *N. placida*) and at least two western North America species (*N. mutans*, *N. venecunda*) with molecular support for their placement within the *N. roberjeotiana* species group (Odanaka et al., 2022). As listed above, the *N. elegantula* group currently only contains three species and both the *N. erigeronis* and *N. vegana* species groups comprise their own unique clades; therefore, the *N. roberjeotiana* species group must also be recognized as occurring in the Palearctic, Africa, and in the Nearctic. Lastly, Straka et al. (2024) mention a *Nomada modesta* species group and, while historically this group was valid, it should be noted that Alexander and Schwarz (1994), changed the name of this species group to the *Nomada vegana* species group due to the discovery that *N. modesta* was used to describe three different species (two in the Palearctic and one in the Nearctic).

There are about 76 species of *Nomada* found in eastern North America (Schuh et al., 2010) with the majority of species placed into the subgenus *Nomada s.s.* Overall, there has been no revision of the genus for all of North America; only selected groups as well as a couple of selected species have been adequately revised (Broemeling & Moalif, 1988; Droege et al., 2010; Evans, 1972; Michener, 2007). Of the existing identification keys for the genus, most are dated, difficult to use, and do not include new species or contain species names that have since been synonymized (Mitchell, 1962; Schuh et al., 2010). These issues, in addition to the little morphological variation between species, but high colour variation within them make identification of *Nomada* in eastern North America incredibly challenging (Mitchell, 1962; Schuh et al., 2010). To remedy some of the taxonomic issues, I present six keys, one to the species groups found in eastern Canada and the eastern United States for both sexes and five for five of the seven North American species groups. In the initial key to the species groups, those

that are bolded (the *N. erigeronis*, *N. vegana*, *N. roberjeotiana*, *N. superba* and *N. vincta* species groups) are addressed here. As mentioned in the taxonomy section above, basic terms used in the following keys are illustrated in Figs. 1-8.

Biology

Most of *Nomada* biology and behaviour revolves around, for males, finding one or more mates, and for females, successfully finding and invading hosts' nests. Currently, few studies have been successful in documenting *Nomada* behaviour, and the majority focus on nest scouting and copulation (Cane, 1983; Eickwort & Abrams, 1980; Linsley & MacSwain, 1955; Rozen, 1977; Velez-Ruiz & Smith-Pardo, 2013). Females will use olfactory cues and fly close to the ground to locate host nests; once a nest is found, they will then switch to visual cues at the entrances to check for guards or active provisioning (Cane, 1983; Schindler et al., 2018). Interestingly, if a *Nomada* female is scouting at an aggregation that contains multiple genera, she will attempt entry into any open nest regardless of what genus actually made it, suggesting that *Nomada* speciation may have occurred due to opportunistic host switching (Cane, 1983). This possibly explains why some *Nomada* species parasitize genera outside of *Andrena* such as *Colletes*, *Eucera*, *Lasioglossum*, and *Agapostemon* (Cane, 1983; Michener, 2007). Conversely, coevolution studies suggest that *Nomada* is more closely tied to the members of the family Andrenidae than might be suggested by their willingness to enter any possible host nest (Bossert et al., 2022; Straka et al., 2024). Furthermore, Straka et al. (2024) also showed that host switching occurred rarely within species groups and subgenera that occur in the Eastern hemisphere. They did not include in depth taxon sampling of Western hemisphere species which include members of the *N. erigeronis* species group which are notable cleptoparasites of *Agapostemon* species (Eickwort, 1981; Eickwort & Abrams, 1980; Gibbs et al., 2023) or members of the *N. vegana* species group which are suggested to be cleptoparasites of *Agapostemon*, *Nomia* (both Halictidae) and *Exomalopsis* (Apidae) (Snelling, 1986).

The majority of *Nomada* use *Andrena* species as hosts (Michener, 2007) and as obligatory ground nesters, *Andrena* safeguard their nests from damage by applying secretions

from their Dufour's gland to their brood cell walls (Hefetz, 1987). Prior research suggested that *Nomada* use odour mimetism to avoid host detection by identifying and matching the chemical profile of male *Nomada* mandibular secretions to the chemical compounds found in Dufour's gland secretions of the female *Andrena* (Tengö & Bergström, 1976, 1977). Specifically, these authors showed that the major compound in the mandibular gland of *Nomada* males in six parasite-host pairs corresponded exactly to the major compound in the Dufour's gland of the host (Tengö & Bergstrom, 1977). It is presumed that male *Nomada* transfer the host mimicking semiochemicals to the female cuticle through antennal grabbing (Schindler et al., 2018) or through cephalic secretions (Tengö & Bergstrom, 1977). More detailed information regarding the biology of particular *Nomada* species groups can be found in the relevant sections below.

Key to species groups for both sexes

- 3(2) F2 longer than broad and longer than each of F1, F3-F9 in females and F1, F3-F10 in males (Fig. 11a); F3-F9 in females and F3-F10 in males longer than broad (Fig. 11a); pronotal collar carinate (Fig. 12a), sometimes weakly; propodeal triangle always with coarse striae at least some of which are at least partly longitudinally oriented (if the dorsolateral striae are transverse, there are others elsewhere which are longitudinally oriented) (Fig. 13a); males always with a short spine on F3 (Fig. 74).....
.....*N. erigeronis* species group (pg 160)
- F2 shorter than F1 but longer than F3-F9 in females or F3-F10 in males (Fig. 11b); F3-F9 in females and F3-F10 in males square, slightly taller than broad (Fig. 11b); pronotal collar rounded (Fig. 12b); propodeal triangle with shallow striae that are restricted to the dorsolateral part of the sclerite and are transversely oriented (Fig. 13b), males with no spine on F3 (Fig. 11b).....*N. vegana* species group (pg. 150)
- 4(2) F2 equal to or shorter than F1 (Fig. 14b), if equal then mandible narrower at midlength than maximum width of scape (Fig. 15a) dorsal margin straight to concave; male pygidial plate entire (Fig. 16a).....5
- F2 longer than F1 (Fig. 14a) but if equal (*N. annulata*), then mandible broad, at midlength broader than maximum width of scape (11:10), breadth due to convexity of dorsal margin (Fig. 15b); male pygidial plate notched (Fig. 16b).....7
- 5(4) Propodeum with sides rounded (Fig. 17a); clypeal rim much more developed laterally, thus clypeus appearing apicolaterally angulate (Fig. 18a); scutellum angulate in profile (Fig. 19b).....
.....*N. superba* species group (pg. 146)

- Propodeal sides straight (Fig. 17b); clypeal rim not, or only slightly broader laterally thus appearing apicolaterally rounded (Fig. 18b); scutellum rounded in profile (Fig. 19a).....6

- 6(5) Labrum with a distinctly toothed or denticulate transverse apical carina (Fig. 20a); tergal maculations white or yellow, medially interrupted at least on T2-T4 (Fig. 21a); male scape rectangular (Fig. 22a).....
.....*N. roberjeotiana* species group (pg. 137)

- Labrum either lacking carina or angulate in profile but lacking teeth other than median angulation (Fig. 20b); terga with complete yellow bands (Fig. 21b); male scape bulbous or globular (Fig. 22b).....
.....*N. vincta* species group (pg. 141)

- 7(5) Head and scape with 9 stiff red hairs (Fig. 23a); apical metatibial spines in female thick and deep red to black (Fig. 24a).....
.....*N. ruficornis* species group (in part)

- Stiff red hairs absent on head (Fig. 23b); apical metatibial spines in female thin and ranging from light clear or yellow to black (Fig. 24b).....8

- 8(7) Metasoma bands T2-T5 in female or T2-T6 in male wide and complete (Fig. 21b); supraclypeal area carina rounded and same height as surrounding hair; integument primarily bright yellow; no pit behind the scape, integument flat.....*N. obliterated* species group

- Metasoma bands T2-T5 in females or T2-T6 in males incomplete; if complete bands present, supraclypeal area carina tall and protrudes higher than the surrounding hair; tegument primarily red or infrequently black

- with yellow maculations; deep pit behind scape where antenna attaches to the face.....9
- 9(8) Supraclypeal area carina tall, fin like; metasoma bands T2-T5 complete, wide; deep pits above torulus.....*N. ruficornis* species group (in part)
- Metasoma T2-T5 in females and T2-T6 in males with no complete bands, usually spots but if bands, medially interrupted and narrow; no deep pits above the torulus, surface, flat supraclypeal area variable.....
.....*N. ruficornis* species group (in part)

Nomada roberjeotiana species group

Placed into the subgenus *Hypochrotaenia* by Straka et al. (2024), the *N. roberjeotiana* species group has a Holarctic distribution (Alexander & Schwarz, 1994). Recent molecular studies have placed this group sister to the western hemisphere endemic *N. erigeronis* and *N. vegana* species groups (Odanaka et al., 2022; Straka et al., 2024). Further, these studies estimate that the most recent common ancestor (MCRA) for the *N. roberjeotiana* species group split from the *N. erigeronis* and *N. vegana* species groups between 18-35 mya (Odanaka et al., 2022; Straka et al., 2024). Interestingly, this relationship between the three species groups within the western hemisphere *Hypochrotaenia* was hypothesized prior by both Snelling and Alexander (1991) using morphological comparison and cladistic approaches respectively.

The *N. roberjeotiana* species group has a complicated taxonomic history that spans across two continents. The European monotypic genus *Nomadita* was described by Mocsary (1894) however, the genus was synonymized under *Nomada* by Dusmet (1913). In North America, Rodeck (1945) separated some members of the subgenus *Holonomada* into their own subgenus, *Callinomada* and named *Nomada antonita* Cockerell (now *Nomada snowii* Cresson)

as the type. Snelling (1986) then revived *Nomadita* as a senior synonym of *Callinomada* and then gave it subgeneric status within *Nomada*. Broemeling (1988) last revised the six North American species of *Nomadita* and a more comprehensive key with detailed characters (such as genitalia) for the eastern and western species can be found there (Broemeling, 1988). Lastly, Alexander (1989) eliminated subgenus *Nomadita* and placed the species into the *N. roberjeotiana* species group.

Of the six known members of the *N. roberjeotiana* species group in North America, only two are found in eastern North America: *Nomada aquilarum* Cockerell and *N. placida* (Fig. 25) (Broemeling, 1988). Both species are active from midsummer to fall and can be found primarily on plants with small flowers such as species of asters and goldenrods (Mitchell, 1962). Currently there are no known host data for any of North American members of the *N. roberjeotiana* species group, however it is presumed that *Andrena* subgenus *Cnemidandrena* is the host due to both groups emerging late in summer and flying in the fall (Snelling, 1986).

Members of the *N. roberjeotiana* species group can be most easily separated from other eastern North American *Nomada* by the transverse carina on the labrum (Fig. 20a). Additional characters that separate members of the *N. roberjeotiana* species group from all others except those of the *N. vincta* and *N. superba* species groups include F1 equal to or longer than F2 (Fig. 14b) and an entire pygidial plate (Fig. 16a) in males. The lack of rounded propodeal sides in members of the *N. roberjeotiana* species group (Fig. 17) separates them from those of the *N. superba* species group. Additionally, either the lack of complete pale integumental metasomal bands on T2-T5 (if female) or T2-T6 (if male) (Fig. 21) and the lack of bulbous scapes in males (Fig. 22) separates it from species of the *N. vincta* species group. Additional, but not essential and often difficult to view, characters that help separate members of the *N. roberjeotiana* species group from other North American *Nomada* are the presence of a prelobar carina (Fig. 26), the presence of either a subcarinate or carinate pre-occipital margin (Fig. 27) and a distinct acetabular carina (Fig. 28).

Diagnosis: The following combination of characteristics is diagnostic for the two species in this species group (alternative states in brackets): Mandibles simple (mandibles bidentate), procoxa with either a apicomedial denticle or no spine (procoxa with long apicomedial spine), F1 equal to

Primary type specimen: Holotype ♂ USMN No. 13183 Collection information: USA: New Mexico: White Mountains, South Fork Eagle Creek, ~8000ft, 18 VIII; Townsend; on flowers *Erigeron macranthus*, USNMENT 00533885; photos available from USMN.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. roberjeotiana* species group in eastern North America (alternative states in brackets): Facial, tergal and sternal maculations white (maculations yellow), labrum carina broken with three medial teeth (carina transverse with five teeth), apical metatibial spines short and stout (apical metatibial spines long and narrow), tegula punctate mesad and sparse to absent laterad (tegula punctate throughout).

Discussion: Found primarily in the west along the Rocky Mountains in the late summer and fall, *N. aquilarum* can occasionally be collected in Minnesota and Wisconsin in the eastern US and Manitoba in Canada. Individuals have been collected on *Erigeron*, *Grinelda*, *Lactuca*, *Melilotus* and *Solidago*, in late summer (Cockerell, 1903a; Mitchell, 1962; Stevens, 1951; Swenk, 1912).

Host information: Unknown.

Distribution: Western North America following the Rocky Mountains (CAN: YT, NWT, AB; USA: AK, NM, WY) but also in the northern prairie states (ND, MN, WI) and provinces (SK, MB).

2) *Nomada placida* (Figs. 25b, 26b, 27b, 28b, 29b, 30b, 31b, 32b, 33b, 34b, 35b, 36b)

Nomada placida Cresson, 1863. On the North American species of the genus *Nomada*. *Proceedings of the Entomological Society of Philadelphia*, 2, 280-312 (♀).

Primary type specimen: Lectotype ♀ Type No. 2600 Collection information: USA; Pennsylvania: 1863; Cresson; EXAMINED.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. roberjeotiana* species group in eastern North America (alternative states in brackets): Facial, tergal and sternal maculations yellow (maculations white), labrum carina transverse with five teeth and (carina broken with three medial teeth), apical metatibial spines long and thin (apical metatibial spines short and stout), and tegula pitting throughout (tegula pitting only close to the inner margin).

Discussion: The most commonly collected species of the *N. roberjeotiana* species group east of the Mississippi River, and in nearly all cases, the only species collected in the group. Specimens, however, can also be found in the central US. This species is found in late summer and early fall (Mitchell, 1962; Swenk, 1912).

Host information: Unknown.

Distribution: Found as far west as Nebraska and Kansas; furthest northern distribution is Ontario and farthest southern extension is Mississippi.

Nomada vincta species group

This species group is endemic to North America and was last revised by Broemeling and Moalif (1988) when the species were still members of the currently defunct subgenus *Pachynomada*; a complete guide for all the North American species with detailed character descriptions can be found there (Broemeling & Moalif, 1988). Originally, members of this species group were placed into the subgenus *Holonomada*, however Rodeck (1945) divided the former and described the new subgenus *Pachynomada* using the distinct shape of the male scape, the spines of the hind tibia, and the shape of the pronotum as unique identifying characters. He

also designated *Nomada vincta* Say as the type for the subgenus (Rodeck, 1945). *Pachynomada* was then revised by Moalif (1979) using genitalia and the shape of the hind basitarsus as the distinct characters for the subgenus. The *N. vincta* species group arose around 57 mya, most likely in the Nearctic and was considered to be the second oldest species group within *Nomada* (Odanaka et al., 2022). However, with the elevation of the *N. odontophora* species group to genus status (*Acanthonomada*, (Straka et al., 2024)), the *N. vincta* species group is now sister to all remaining *Nomada* species groups (Odanaka et al., 2022).

There are 13 known species in the group in North America, however only two can be found in the east: *N. vincta* and *Nomada graenicheri* Cockerell. The majority of the species comprising this species group can be found in Mexico and Western United States (Alexander & Schwarz, 1994). Previously, *Nomada besseyi* Swenk was considered as a third species, however recent molecular (Supp. Fig. 2) results presented here and comparison of *N. besseyi* and *N. graenicheri* specimens suggest that *N. besseyi* and *N. graenicheri* are the same species and should be synonymized. The photos of *N. graenicheri* in this key were taken from the specimens used for the molecular tree (Supp. Fig. 2) and thus represent a female originally identified as *N. besseyi* (Figs. 37a, 41a, 42a) and a male originally identified as *N. graenicheri* (Figs. 43a, 44a). The synonymizing of these species was originally put forth in Droege et al. (2010) after examination of the *N. graenicheri* holotype and comparison of the type to the description of *N. besseyi* by the authors. Both species fly from midsummer to fall and are especially attracted to members of the genus *Helianthus* for nectar (Ascher & Pickering, 2024; Broemeling & Moalif, 1988; Mitchell, 1962). There is limited host data for species of the *N. vincta* species group and at varying degrees of certainty; for instance, *Nomada utahensis* Moalif, 1988 has been reared from *Andrena* (*Callandrena*) *helianthi* Robertson, 1891 nests (Parker & Bohart, 1982) but the same species has been observed only leaving from nests of *Andrena* (*Callandrena*) *haynesi* Viereck and Cockerell (Parker & Griswold, 1982), making this association less certain. Of the two eastern species, only *N. vincta* has definitive host data and has been recorded using *A. helianthi* (Gibbs et al., 2023).

Members of the *N. vincta* species group can be separated from all other groups based upon the bulbous scape (Fig. 22b) in males, the distinct prelobar carina (Fig. 26), and the distinct acetabular carina on the upper base of the mandibles (Fig. 28a). Additional characters include the

equal lengths of F1 and F2 (Fig. 14b) and the entire pygidial plate in males (Fig. 16a) (which separates the *N. vincta* species group from all other species groups except the *N. roberjeotiana* and *N. superba* species groups), the lack of rounded propodeal sides (Fig. 17b) (present in the *N. superba* species group) and the lack of a horizontal carina across the labrum (Fig. 20b) (present in the *N. roberjeotiana* species group).

Diagnosis: The following combination of characteristics is diagnostic for the two species in this species group (alternative states in brackets): mandibles simple (mandibles bidentate), procoxa with either an apicomedial denticle or no spine (procoxa with long apicomedial spine), F1 equal to or longer than F2 (F1 shorter than F2), pygidial plate entire in males (pygidial plate notched at the tip), propodeal sides straight (propodeal sides rounded), clypeus apicolaterally and scutellum in profile rounded (clypeus apicolaterally and scutellum in profile angulate). Members of the *N. vincta* species group share the above characteristics with those in the *N. roberjeotiana* species group. The two species groups can be separated by the lack of a transverse carina on the labrum (labrum with carina), tergal maculations appearing as complete bands (tergal maculations medially interrupted) and males having bulbous scapes (male scape rectangular) in members of the *N. vegana* species group.

Other than for the usual sexual dimorphism, there are no external morphological differences between males and females in species of this species group. Therefore, the following key can be used for both males and females

- 1a Pubescence on propodeum very short, sparse, white in colour (Fig. 39a);
propodeum with no yellow maculations, completely black (Fig. 39a);
mesopleuron with transverse yellow bar (Fig. 40a).....
.....*N. graenicheri* Cockerell

- 1b Propodeum pubescence long, golden in colour (Fig. 39b); propodeum with yellow maculations (Fig. 39b); mesopleuron with yellow triangular maculation (Fig. 40b).....*N. vincta* Say

1) *Nomada graenicheri* (Figs. 37a, 38, 39a, 40a, 41a, 42a, 43a, 44a, 46)

Nomada graenicheri Cockerell, T.D.A. 1905. Some bees of the genus *Nomada* from Wisconsin. *The Canadian Entomologist*, 37, 189-191 (♀).

Primary type specimen Type ♀ USMN No. 29483 **Collection information:** USA: Wisconsin: Milwaukee, 16 VIII 1903; S. Graenicher; USNMENT 00533930; photos available from USNM.

Nomada besseyi Swenk M. H. 1912. Studies of North American Bees. *University Studies* (Lincoln, Nebraska), 12, 1-113 (♂). **New synonymy.**

Primary type specimen: Holotype ♂ 933 **Collection information:** USA: Kansas: Manhattan, 24 VIII 1908, O. A. Stevens, on flowers of *Helianthus tuberosus*, UNSMe 0372; photos sent from UNBSM.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. vincta* species group in eastern North America (alternative states in brackets): pubescence short and sparse on propodeum (pubescence long), propodeum entirely black (propodeum with yellow maculations), and mesopleuron with transverse yellow bar (mesopleuron with triangular yellow maculation).

Discussion: A relatively rare species, the UCE tree (Supp Fig. 2) and morphological data suggests that *N. besseyi* and *N. graenicheri* are the same species and therefore should be synonymized under *N. graenicheri*. *N. graenicheri*, then should be moved from the *N. ruficornis* species group (within subgenus *Nomada s.s.*) to the *N. vincta* species group.

A late summer and fall flying species, it has been collected off *Helianthus* (Cockerell, 1905; Graenicher, 1911; Swenk, 1912). Interestingly, in his original description of *N. besseyi*, Swenk (1912) made note that the species was closely allied to *N. vincta*, accurately predicting the eventual placement of the species within the same defunct subgenus *Pachynomada* by Broemeling and Moalif (1988) and into the *N. vincta* species group by Alexander (1989).

Host information: Unknown; In Cockerell's (1905) original description of *N. graenicheri*, he made note that Graenicher believed that *N. graenicheri* was a cleptoparasite of one of late summer *Andrena* as he observed both host and parasite on *Helianthus* spp. However, there is no mention of which *Andrena* spp. was the host.

Distribution: Kansas to Minnesota and Ontario, east to New Jersey and south to South Carolina.

2) *Nomada vincta* (Figs. 37b, 38, 39b, 40ab 41b, 42b, 43b, 44b, 45)

Nomada vincta Say, T. 1836. Descriptions of new species of North American Hymenoptera, and observation on some already described. *Boston Journal of Natural History*, 1, 209–305 (♀♂).

Primary type specimen: Lost Collection information: Unknown.

Nomada vincta heterochroa Cockerell. T.D.A 1921. Western bees obtained by the American Museum expeditions *American Museum Novitates*, 24(1), 1-15 (♂).

Primary type specimen: Holotype ♂ 933 Collection information: USA: Kansas: Manhattan, 24 VIII 1908, O. A. Stevens, on flowers of *Helianthus tuberosus*, UNSMe 0372.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguishes this species from all other members in the *N.vincta* species group in eastern North America (alternative states in brackets): pubescence long on propodeum (pubescence short),

propodeum with two yellow maculations (propodeum entirely black), mesopleuron with triangular yellow maculation (mesopleuron with transverse yellow bar).

Discussion: The most commonly collected and widespread species of the *N. vincta* species group in the east. Found in the late summer and early autumn (Cockerell, 1921; Mitchell, 1962; Swenk, 1912, 1915), *N. vincta* has been captured on the flowers of *Aster*, *Bidens*, *Grindelia*, *Helianthus*, *Rudbeckia*, and *Solidago* (Cockerell, 1903c; Mitchell, 1962; Swenk, 1912, 1915).

Host information: *Andrena helianthi* (Gibbs et al., 2023).

Distribution: Alberta to Colorado east to Maine and North Carolina.

Nomada superba species group

Part of subgenus *Holonomada*, the *N. superba* species group has a global Holarctic distribution. The majority of species can be found in Europe and Asia (Alexander & Schwarz, 1994; Straka et al., 2024) and within North American, most species are found in the west. The concentration of species west of the Rocky Mountains is most likely a result of the species group crossing the Bering Land Bridge into North America from Asia and then more recently, radiating out eastward from the west (Odanaka et al., 2022).

The *N. superba* species group was last revised in North America by Evans (1972) in which he noted 11 different species and three subspecies. Only two species, *Nomada superba* and *Nomada affabilis*, are found east of the Mississippi River and they are most likely collected in the late spring to midsummer (Evans, 1972). Not much is known regarding the host associations of North American *N. superba* species group members however *Nomada superba* has been documented using members of *Eucera* (*Synhalonia*) (Wolf and Ascher, 2006) and

Nomada edwardsii is a noted cleptoparasite of *Andrena perimelas* (Linsley and MacSwain, 1955).

N. superba species group members in eastern North America are separated from all other species groups by their overall larger size, rounded propodeal sides (Fig. 17a), clypeus apicolaterally and scutellum in profile angulate (Figs. 18a, 19b). Additional characters include a longer F1 when compared to F2 (Fig. 11b) and a complete, parallel sided pygidial plate in males (Fig. 16a). Although *N. roberjeotiana* and *N. vincta* species groups also have F1 greater than F2, the lack of a horizontal carina across the labrum (Fig. 20b) separates the *N. superba* species group from *N. roberjeotiana* species group and the lack of globular scapes in males (Fig. 22a) separates out *N. vincta* species group.

Diagnosis: The following combination of characteristics is diagnostic for the two species in this species group (alternative states in brackets): Mandibles simple (mandibles bidentate), procoxa with either an apicomedial denticle or no spine (procoxa with long apicomedial spine), F1 equal to or longer than F2 (F1 shorter than F2), pygidial plate entire in males (pygidial plate notched at the tip). Although members of the *N. superba* species group share the above characteristics with those in the *N. roberjeotiana* and *N. vincta* species groups, *N. superba* group members can be separated by having propodeal sides rounded (propodeal sides straight) and having clypeus apicolaterally and scutellum in profile angulate (clypeus apicolaterally and scutellum in profile rounded).

Male

- 1a Propodeum with sides yellow and/or red (Fig. 52).....*N. affabilis* Cresson
- 1b Propodeum with sides completely black (Fig. 56b).....*N. superba* Cresson

Female

- 1a Metanotum and propodeum with sides yellow (Fig. 52); apical metatibial spines in a row (Fig. 49a).....***N. affabilis* Cresson**
- 1b Metanotum and propodeum with sides black (Fig. 56b); apical metatibial spines in a patch (Fig. 49b).....***N. superba* Cresson**

1) *Nomada affabilis* (Figs. 47, 49a,c, 50, 51, 52, 53a, 54a)

Nomada affabilis Cresson, E. T. 1878. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. *Transactions of the American Entomological Society and Proceedings of the Entomological Section of the Academy of Natural Sciences*, 7, 61-136 (♂).

Primary type specimen Syntype ♂ Type No. 2593 **Collection information:** USA: New York EXAMINED.

Nomada affabilis dallensis Cockerell, T. D. A. 1911. Bees in the collection of the United States National Museum 1. *Proceedings of the United States National Museum*, 39, 635-658 (♀♂).

Primary type specimen: Type ♀ USMN No. 13434 **Collection information:** USA: Texas: Dallas, 9 IV 1906, J. C. Crawford, on dewberry, USNMENT 00533913; photos available from USMN; examined Homotype from LACM.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. affabilis* and distinguish this species from all other members in the *N. superba* species group in eastern North America (alternative states in brackets): **Male:** the propodeal sides yellow, however in some individuals there can be a mix of red and yellow (propodeal sides black);

Female: metanotum and propodeal sides yellow (metanotum and propodeal sides black), apical metatibial spines in a straight line (apical metatibial spines in a patch).

Discussion: This species seems to have a more southern distribution than *N. superba* with individuals being found as far southwest as Texas and southeast as Florida. *N. affabilis* is recorded flying between March through June and has been captured off flowers of dewberry, blackberry, *Apocymum*, *Aruncus*, *Brassica*, *Brauneria*, *Camassia*, *Cercis*, *Claytonia*, *Cornus*, *Diospyros*, *Gillenia*, *Houstonia*, *Hydrophyllum*, *Krigia*, *Malva*, *Melilotus*, *Oenothera*, *Penstemon*, *Polemonium*, *Rubus*, *Taenidia*, *Trifolium*, *Verbena*, *Viola* and *Zizia* (Cockerell, 1911a; Mitchell, 1962; Robertson, 1895).

Host information: Unknown.

Distribution: Texas to Florida, north to New York and Minnesota.

2) *Nomada superba* (Figs. 48, 49b,d, 53b, 54b, 55, 56,)

Nomada superba Cresson, E. T. 1863. On the North American species of the genus *Nomada*. *Proceedings of the Entomological Society of Philadelphia*, 2, 280-312 (♂).

Primary type specimen Holotype ♂ Type No. 2583 **Collection information:** USA: Colorado; EXAMINED.

Nomada superba malvastri Swenk M. H. 1912. Studies of North American Bees. *University Studies* (Lincoln, Nebraska), 12, 1-113 (♀).

Primary type specimen: Holotype ♀ **Collection information:** USA: Nebraska: Sioux Co: War Bonnet Canyon, 16 VI 1901, M. Cary, on *Malvastrum*.

Nomada superba nebrascensis Swenk M. H. 1912. Studies of North American Bees. *University Studies* (Lincoln, Nebraska), 12, 1-113 (♀).

Primary type specimen: ♀ 4 **Collection information:** USA: Nebraska: West Point.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. superba* and distinguish this species from all other members in the *N. superba* species group in eastern North America (alternative states in brackets): **Male:** the propodeal sides completely black (propodeal sides yellow, sometimes mix of red and yellow); **Female:** metanotum and propodeal sides black (metanotum and propodeal sides yellow) and the apical metatibial spines in a patch (apical metatibial spines in a straight line).

Discussion: This species appears to have a more northern distribution than *N. affabilis*, however, records on Discover life indicate that *N. superba* may be distributed as far south as Georgia. Additionally, there is a record on Discover Life that shows a specimen of *N. superba* in British Columbia; however, this is a possible misidentification. *N. superba* occurs in the spring through mid-summer and has been captured on flowers from *Brauneria*, *Camassia*, *Cardamine*, *Comandra*, *Coreopsis*, *Cornus*, *Erigeron*, *Fragaria*, *Geranium*, *Heracleum*, *Houstonia*, *Krigia*, *Lithospermum*, *Malvastrum*, *Melilotus*, *Mepeta*, *Nothoscordum*, *Oxalis*, *Phlox*, *Prunus*, *Ranunculus*, *Rubus*, *Salix*, *Senecio*, *Sisyrinchium*, *Stachys*, *Stellaria*, *Trifolium*, and *Zizia* (Mitchell, 1962; Swenk, 1912).

Host information: *Eucera* (*Synhalonia*) (Wolf & Ascher, 2008).

Distribution: Southern Ontario to the north, Colorado and Wyoming to the west, Georgia to the south, and Washington DC to the east.

Nomada vegana species group

Part of subgenus *Hypochrotaenia* (with *N. roberjeotiana* and *N. erigeronis* species groups) (Straka et al., 2024), members of the *N. vegana* species group are endemic to the Western hemisphere; this species group is the only one found in South America (Alexander & Schwarz, 1994). Recent studies place the MRCA of the *N. vegana* species group splitting from the MCRA of *N. roberjeotiana* species group between 18-35 mya and around 16-33 mya from the MCRA of the *N. erigeronis* species group (Odanaka et al., 2022; Straka et al., 2024).

Comprised of ~54 species, the *N. vegana* species group reaches its greatest diversity in the Neotropics (~23 species in southern Mexico, Central America, and South America [*Nomada mexicana* Cresson's specific collection in Mexico is unknown, the collector, François Sumichrast, was known to collect in southern Mexico] and six species from the Caribbean) (Alexander & Schwarz, 1994). Outside of the Neotropics the *N. vegana* species group is well represented in the western US (20 spp.) while only four species are found in eastern North America (Alexander & Schwarz, 1994). Many of the species within the *N. vegana* species group superficially resemble members of the genus *Hylaeus* due to their distinct yellow facial maculations and overall black integument however, members of the *N. vegana* species group are much larger in size.

The *N. vegana* species group has gone through many taxonomic changes; most recently the group was moved into the resurrected subgenus *Hypochrotaenia* (Straka et al., 2024). Originally, non-Caribbean, eastern North American species of this group were placed into either the genus *Cephen* (Robertson, 1903) or the subgenus *Micronomada* (Cockerell & Atkins, 1902) however Swenk (1912) synonymized the former under the latter. Interestingly, Robertson (1903) had originally suspected that *Cephen* and *Micronomada* would be the same genus yet chose to keep them separate due to being unable to examine the *Micronomada* type *Nomada modesta* Cresson. *Micronomada* was then placed by Snelling (1986) under the genus *Hypochrotaenia* Holmberg along with two other subgenera, *Hypochrotaenia* and *Aphelonomada* Snelling. Alexander (1989) then separated the subgenera *Micronomada*, *Aphelonomada*, and *Hypochrotaenia* from the genus *Hypochrotaenia* and elevated them as their own species group, the *Nomada modesta* species group while eliminating the genus *Hypochrotaenia*. The original “*N. modesta*” name was later changed to “*N. vegana*” when it was found that “*Nomada modesta*”

referred to three different species, two palearctic species found in the *ruficornis* species group and the North American *N. modesta* (Alexander & Schwarz, 1994). *Hypochrotaenia* was recently resurrected at the subgeneric level, by Straka and colleagues (2024) and includes the *N. vegana*, *N. erigeronis*, and *N. roberjeotiana* species groups in eastern North America. It should be noted that prior to the widespread use of molecular methods, the relationship between the three species groups within the western hemisphere *Hypochrotaenia* was hypothesized by both Snelling (1986) and Alexander (1991) using morphology and cladistic approaches respectively.

At the species level, three of the four eastern *N. vegana* species (*N. fervida* Smith, *N. texana* Cresson, and *N. tiftonensis* Cockerell) were revised in Droege et al. (2010). Notable changes were the synonymizing of *N. fervida* with *N. wisconsinensis* Graenicher and the reorganizing of both *N. texana* and *N. tiftonensis* (Droege et al., 2010). Specifically, Droege et al. (2010) synonymized *N. tiftonensis* with *N. modesta riverstonensis* Cockerell and found that *N. heiligbrodtii* Cresson was a junior synonym of *N. texana*. By recognizing that *N. heiligbrodtii* was a junior synonym, this elevated *N. tiftonensis* back to species status, as it was previously considered to be a synonym of *N. heiligbrodtii* (Droege et al., 2010; Mitchell, 1962). Lastly, Gibbs et al (2023) synonymized *N. arenicola* Swenk with *N. fervida*.

It is presumed that species in the *N. vegana* species group have specialized nesting requirements; for example, *N. fervida* is a known sand specialist and it is presumed that *N. tiftonensis* also inhabits sandy environments (Droege et al., 2010).

Members of the *N. vegana* species group seem to specialize on at least three different genera: *Agapostemon*, *Exomalopsis* and *Nomia* (Snelling, 1986). There are no known confirmed host records for any of the eastern Canada and US members in the *N. vegana* species group however, one species *N. fervida* is presumed to be a nest parasite of *A. splendens* yet in Williams et al., (2017) one citation used (Eickwort, 1981) to support this association does not state this. Despite this citation error, the assumption that *N. fervida* and *A. splendens* are associated with each other is also posited by Droege et al (2010) due to their shared restriction to sandy habitats, (which Williams and colleagues correctly cite). Outside of eastern Canada and the US, there are host records for at least four other species. *Nomada cubensis* Cresson is a known cleptoparasite of *Exomalopsis globosa* (Raw, 1997) and *E. similis* Cresson (Raw, 1977) (these two species are now synonymized under *E. similis* Cresson), *N. formula* Viereck is known to use *Agapostemon*

texanus Cresson (Eickwort & Abrams, 1980a; Eickwort, 1981), *N. gutierreziae* Cockerell was found to use *E. crenulata* (now *Anthophorula crenulata* (Timberlake) (Parker, 1984)), *N. suavis* Cresson is a known cleptoparasite of *Nomia melanderi* Cockerell (Bohart, 1970), and lastly *N. medellinenses* Velez-Ruiz & Smith-Pardo which is associated with nests of *E. aburraensis* Velez-Ruiz & Smith-Pardo (Velez-Ruiz & Smith-Pardo, 2013).

Diagnosis: The following combination of characteristics is diagnostic for the four species in this group (alternative states in brackets): mandible simple (mandible bidentate), procoxa with long apicomedial spine (apicomedial spine lacking). While members of the *N. erigeronis* species group share the previous characteristics, members of the *N. vegana* species group can be further separated from the *N. erigeronis* species group by the rounded pronotal collar (angulate and carinate), propodeal triangle with shallow striae (propodeal triangle with coarse striae), F2 shorter than F1 but longer than F3-F9 in females or F3-F10 in males (F2 longer than F1, F3-F9 or F3-F10), F3-F10 in females or F3-F10 in males slightly taller than broad and appearing square (F3-F10 or F3-F10 longer than broad, rectangular) and male flagellomeres lacking ornamentation, especially on F3 (male F3 with short spine).

Other than for the usual sexual dimorphism, there are no external morphological differences between males and females in species of this species group. Therefore, the following key can be used for both males and females

- 1 Propodeal sides with yellow patches (Fig. 66).....*N. vegana* Cockerell
- Propodeum all black.....2
- 2(1) Apical metatibial spines forming a large patch (Fig. 59a).....
.....*N. fervida* Smith

- Apical metatibial spines arranged in a single row.....3
- 3(2) Metasoma with T3 entire (Fig. 64a); metasomal sterna with interrupted yellow or white bands (Fig. 65a); hind coxa red (Figs. 57b, d).....
.....*N. texana* Cresson
- Metasoma with T3 median break (Fig. 64b); metasomal sterna black with no maculations (Fig. 65b); hind coxa black, (Fig. 57c).....
.....*N. tiftonensis* Cockerell

1) *Nomada fervida* (Figs. 57a, 58, 59a, 60, 61)

Nomada fervida Smith, F. S. 1854. *Catalogue of the hymenopterous insects in the collection of the British Museum Part 2 Apidae*. London: British Museum (♀).

Primary type specimen Type ♀ B.M. Type HYM 17B.580 **Collection information:** USA: Georgia, *Nomada fervida* Type Sm., *fervida* Type SM., NHMUK014025104; EXAMINED.

Nomada arenicola Swenk M. H. 1912. Studies of North American Bees. *University Studies* (Lincoln, Nebraska), 12, 1-113 (♀).

Primary type specimen: ♀ **Collection information:** USA: Nebraska: Neligh; NOT EXAMINED

Nomada crassula Cockerell, T. D. A. 1903. North American bees of the genus *Nomada*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 55, 580-614 (♀).

Primary type specimen: Type ♀ USMN No. 13171 **Collection information:** USA: Louisiana (2563), USNMENT 00533909; photos available from USMN.

Nomada wisconsinensis Graenicher, S. 1911. Bees of Northern Wisconsin. *Bulletin of the Public Museum of the City of Milwaukee*, 1, 221-249 (♀♂).

Primary type specimen: Lectotype ♀ 29752 **Collection information:** USA: Randall: Wisconsin: Burnett Co., Aug 5-7, 1909, TYPE, *Nomada wisconsinensis* Graen ♀, Lectotype ♀ *Nomada wisconsinensis* Graenicher des Droege et al.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. vegana* species group in eastern North America (alternative states in brackets): the propodeal sides all black (propodeal sides with yellow maculations) and apical metatibial spines forming a large patch composed of smaller spines (apical metatibial spines in a line).

Discussion: Gibbs et al., (2023) synonymized *N. fervida* and *N. arenicola* based on molecular data and the lack of morphological differences between the two species. This species occurs most commonly between March through September and inhabits sandy soils (Droege et al., 2010; Gibbs et al., 2023; Mitchell, 1962). *N. fervida* has been collected from flowers of *Amorpha*, *Asclepias*, *Bidens*, *Ceanothus*, *Euphorbia*, *Heterotheca*, *Melilotus*, *Polygonum*, *Silphium*, and *Verbena* (Gibbs et al., 2023; Mitchell, 1962; Swenk, 1912, 1915).

Host information: Unknown. There is some speculation that *N. fervida* is a nest parasite of *Agapostemon splendens* due to their shared habitat (Droege et al., 2010) but there has been no concrete evidence yet.

Distribution: As far south as Florida and Georgia to New England in the north and to Colorado, Texas and Manitoba in the west.

2) *Nomada texana* (Figs. 57b, 58, 59b, 62a, 63a, 64a, 65a)

Nomada texana Cresson, E. T. 1872. Hymenoptera Texana. *Transactions of the American Entomological Society*, 4, 153-292 (♀♂).

Primary type specimen Lectotype, ♀ Lectotype 2598 **Collection information:** USA: Texas, 163, ♀, Belfrage, G.W., Boll, J.; examined lectotype #2561 at ANS.

Nomada heiligbrodtii Cresson, E. T. 1878. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. *Transactions of the American Entomological Society*, 7, 61-136 (♀♂).

Primary type specimen: Lectotype ♀ **Collection information:** USA: Texas.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. vegana* species group in eastern North America (alternative states in brackets): the propodeal sides all black (propodeal sides with yellow maculations) and apical metatibial spines in a straight line (apical metatibial spines forming a large patch composed of smaller spines). Although *N. tiftonensis* and *N. texana* share the previous characters, *N. texana* can be further distinguished by T3 entire (T3 medially interrupted), S3-S4 with interrupted yellow or white bands (S3-S4 with no bands) and hind coxa red (hind coxa black).

Discussion: Found flying in the throughout the late spring to the early fall, *N. texana* can be captured off flowers of *Asclepias*, *Bidens*, *Brassica*, *Chamaechrista*, *Chrysopsis*, *Engelmannia*, *Gaillardia*, *Gossypium*, *Haplopappus*, *Helianthus*, *Heterotheca*, *Marilaunidium*, *Marrubium*, *Monarda*, *Pithecolobium*, *Ratibida*, *Rudbeckia*, *Pyrrhopappus*, *Solidago*, *Verbesina*, *Veronica* (Cockerell, 1911a; Mitchell, 1962; Swenk, 1912, 1915).

Host information: Unknown.

Distribution: A fairly large range from Arizona, Nevada and Idaho in the west to Florida, up to New Hampshire in the east and as far south as Mexico. There are some records on Discover Life from California and Mexico but these were not examined. However, since there are records of the species in Nevada it is plausible that the species has a coast to coast distribution.

3) *Nomada tiftonensis* (Figs. 57c, 58, 59c, 62b, 63b, 64b, 65b)

Nomada tiftonensis Cockerell, T. D. A. 1903. North American bees of the genus *Nomada*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 55, 580-614 (♂).

Primary type specimen Holotype ♂ Type No. 10165 **Collection information:** USA: Georgia: Tifton; examined paratype at ANS.

Nomada modesta var *riverstonensis* Cockerell, T. D. A. 1903. North American bees of the genus *Nomada*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 55, 580-614 (♀).

Primary type specimen: Holotype ♀ Type No. 10158 **Collection information:** USA: New Jersey: Burlington Co.: Riverton, VII.31.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. vegana* species group in eastern North America (alternative states in brackets): the propodeal sides all black (propodeal sides with yellow maculations) and apical metatibial spines in a straight line (apical metatibial spines forming a large patch composed of smaller spines). Although *N. texana* and *N. tiftonensis* share the previous characters, *N. tiftonensis* can be further distinguished by T3 medially interrupted (T3 entire), S3-S4 with no bands, completely black (S3-S4 with interrupted white and yellow) and hind coxa black (hind coxa red.)

Discussion: Originally treated as its own species, *N. tiftonensis* was synonymized, along with *Nomada modesta riverstonensis*, under the name *N. heiligbrodtii* by Mitchell (1962). Droege et

al (2010) then synonymized *N. heiligbrodtii* with *N. texana* but separated out both *N. tiftonensis* and *N. modesta riverstonensis*, ultimately synonymizing the latter two into *N. tiftonensis*. The separation of *N. tiftonensis* and *N. texana* as separate species is supported by morphological characters, DNA barcoding, and UCE sequencing (Droege et al., 2010; Odanaka et al., 2022). Can be found on *Bidens*, *Chrysopsis*, *Haplopappus*, and *Solidago* (Mitchell, 1962).

Host information: Unknown.

Distribution: From Ontario in the north, westwards to Minnesota and south to Georgia.

4) *Nomada vegana* (Figs. 57d, 58, 59d, 66, 67)

Nomada vegana Cockerell, T. D. A. 1903. North American bees of the genus *Nomada*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 55, 580-614 (♀).

Primary type specimen: ♀ **Collection information:** USA: New Mexico: Las Vegas, A. Garlic, July, 12, 1899; NOT EXAMINED

Nomada modesta Cresson, E. T. 1863. On the North American species of the genus *Nomada*. *Proceedings of the Entomological Society of Philadelphia*, 2, 280-312 (♀♂).

Primary type specimen: Type ♀; Type No. 2599 **Collection information:** USA: Illinois ♀ Cresson, 1863; EXAMINED.

Nomada modesta var *vegana* Cockerell, T. D. A. 1903. North American bees of the genus *Nomada*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 55, 580-614 (♀).

Primary type specimen: ♀ **Collection information:** USA: New Mexico: Las Vegas, A. Garlic, July, 12, 1899; NOT EXAMINED

Nomada vegana var *nitescens* Cockerell, T. D. A. 1903. The bees of the genus *Nomada* found in Colorado, with a table to separate all the species of the Rocky Mountains. *Bulletin Colorado Agricultural Experiment Station*, 94, 69-85 (♀).

Primary type specimen: Type ♀ Type No. 27704 **Collection information:** USA: Col: Ft. Collins, 8-8-99, abdomen off when received, *N. vegana* v. *nitescens* Ckll TYPE, *Nomada vegana* ckll, USNMMENT 00533957; photos available from USNM.

Diagnosis: The following combination of characteristics is diagnostic for either sex and distinguish this species from all other members in the *N. vegana* species group in eastern North America (alternative states in brackets): propodeum with yellow maculations (propodeum all black). It should be noted that this species will occasionally have a nearly all black form with thin banding on the metasoma and reduced yellow maculations on the head, thorax and metasoma, however the propodeum will still have yellow maculations.

Discussion: The taxonomy for this species is confusing due to the original species name of “*modesta*”. The first instance of synonymizing “*vegana*” and “*modesta*” was in Alexander and Schwarz’s checklist (1994), noting that “*modesta*” was already used twice for two different European species and then once in North America. Interestingly, in Snelling’s 1986 partitioning on *Nomada*, both *N. vegana* and *N. modesta* are treated as separate species even though prior, *N. vegana* was treated as a variant of *N. modesta*. Lastly, it should be noted that the now defunct subgenus *Micronomada* was founded on the *N. modesta* var *vegana* form further confusing the taxonomy (Cockerell, 1903b; Cockerell & Atkins, 1902) as the *vegana* variant is distinguished from *modesta*, but never treated as fully separate until 1994 when the two species were synonymized (Alexander & Schwarz, 1994).

Found from late June through September, *N. vegana* can be caught foraging on flowers of *Amorpha*, *Asclepias*, *Cephalanthus*, *Chrysopsis*, *Cucurbita*, *Eryngium*, *Gaillardia*, *Helianthus*, *Helenium*, *Kuhnistera*, *Linum*, *Marilaundium*, *Medicago*, *Mentha*, *Petalostemum*,

Pycnanthemum, *Ratibida*, *Rhus*, *Solidago*, *Symphoricarpos*, *Verbena*, and *Verbesnia* (Cockerell, 1903c; Mitchell, 1962; Swenk, 1912, 1915).

Host information: Unknown.

Distribution: From the Rocky Mountains in the west to the Atlantic coast in the east. There are some records of this species in Mexico however they were not examined and therefore cannot be confirmed.

Nomada erigeronis species group

Along with the *N. roberjeotiana* and *N. vegana* species groups, the *N. erigeronis* species group is currently placed within the subgenus *Hypochrotaenia* (Straka et al., 2024). It is estimated that the MRCA of the *N. erigeronis* species group split from the MCRA of *N. roberjeotiana* species group between 18-35 mya and around 16-33 mya from the MCRA of the *N. vegana* species group (Odanaka et al., 2022; Straka et al., 2024). Prior to the widespread use of molecular methods, the relationship between the three species groups within the western hemisphere *Hypochrotaenia* was hypothesized by both Snelling (1986) and Alexander (1991) using morphology and cladistic approaches respectively.

Much like the *N. vegana* species group, members of the *N. erigeronis* species group are endemic to the Western hemisphere but in the case of *N. erigeronis* species group, they are mostly restricted to the US and Canada (Alexander & Schwarz, 1994). Of the 19 species within this species group, only five are found in eastern Canada and the US (Alexander & Schwarz, 1994). The number of eastern species may increase, however, as results from Chapter 3 of this dissertation has found possible evidence of one or two new species inhabiting the southeastern region of the US.

Originally, species found within the *N. erigeronis* species group were placed either into the genus *Centrias* or into the subgenus *Nomadula*. *Centrias* was described by Robertson (1903) and contained both *Nomada articulata* Smith and *Nomada erigeronis* Robertson, designating the latter as the type. For *Nomadula*, Cresson described this subgenus based upon the spine on the first coxa, puncturing on the abdomen, and the male antenna, designating *N. articulata* as the type (Cockerell, 1903b). Interestingly, both Robertson (1903) and Cresson (1903b) published their redescrptions within two months of each other (June and August respectively); as a result, *N. articulata* was moved from the genus *Centrias* to the subgenus *Nomadula*, making *Centrias* a monotypic genus. The next taxonomic change occurred when Snelling (1986) synonymized *Nomadula* and *Centrias* under the genus *Centrias*. Alexander (1994) then stripped *Centrias* of generic status, delegating it as a species group under the genus *Nomada*, and renamed it the *erigeronis* species group.

Of the five species found in eastern North America, only *N. articulata* has confirmed host associations (*Agapostemon virescens* and *A. sericus*) (Abrams & Eickwort, 1980, 1981; Alexander, 1991; Eickwort, 1981; Eickwort & Abrams, 1980a). There is one record of *N. articulata* using *Andrena alleghaniensis* as a host, however this observation was only noted as a “probable” association as the author could not find any evidence of successful parasitism (Alexander, 1991). The remaining four species only have presumed hosts (see below) and more research is needed to confirm the associations (Ascher & Pickering, 2024; Gibbs et al., 2023; Stevens, 1951).

Members of the *N. erigeronis* species group can be easily separated from all other species groups by the spine located on the inner margin on the first coxa (Fig. 10), long F2 (Fig. 11b) and carinate pronotal collar (Fig. 12b) in both females and males. Additionally, the presence of a spine on F3 (Fig. 11b) can separate *N. erigeronis* species group males from the males of the *N. vegana* species group.

Diagnosis: The following combination of characteristics is diagnostic for the five species in this species group (alternative states in brackets): mandible simple (mandible bidentate), procoxa with long apicomedial spine (apicomedial spine lacking). While members of the *N. vegana* species group share the previous characteristics, members of the *N. erigeronis* species group can

be further separated from the *N. vegana* species group by the angulate and carinate pronotal collar (pronotal collar rounded), propodeal triangle with coarse striae (propodeal triangle with shallow striae), F2 longer than F1, F3-F9 in females or F3-F10 in males (F2 shorter than F1 but longer than F3-F9 or F3-F10), F3-F9 in females or F3-F10 in males longer than broad and appearing rectangular (F3-F10 or F3-F10 slightly taller than broad, appearing square) and male F3 with short spine and sometimes on F4-F10 (flagellomeres lacking ornamentation, especially on F3).

Male

- 1 F2 and F3 equal or nearly equal (Fig. 74e); edges of F3-F9 pointed with spines identical to the one found in centre of F3 (Fig. 74e); F5-F8 with pairs of spines (Fig. 74e); found in the southern US only.....
.....*N. seneciophila* Mitchell
- F2 longer than F3, sometimes twice as long (Figs. 74a,b,c,d); spines not found under F4-F11, if there are structures, these are rounded and not resembling spine under F3 (Figs. 74a,b,c,d); F5-F8 without pairs of spines; much wider distribution.....2
- 2(1) Scutellum with bright yellow (Fig. 88b); spine on F3 flattened and wide, not pointed like a thorn (Fig. 74d); hind femora straight and not carinate (Fig. 87a); S3 and S4 (sometimes S2) with nearly complete bright yellow bands, may be interrupted in some individuals.....*N. rubicunda* Olivier
- Scutellum red or black; spine on F3 pointed (Fig. 74a,b,c); hind femora curved with carination on edge (Fig. 87b); sterna without complete bright yellow bands, if maculated, yellow is dull and patchy.....3

3(2) Scape distinctly bulbous (Fig. 82); scutellum red, but in lighter individuals may have yellow and red (Fig. 84c); axilla, tegula, pronotal collar, and metanotum bright yellow (Fig. 83c, 84c); T2-T4 and S2-S4 with apical impressed areas deeply and distinctly impressed in relation to rest of respective tergum or sternum (Fig. 86); T2 with thick yellow maculation that is narrowly interrupted in the centre, sometimes appearing as a single band (Fig. 85c).....***N. erigeronis* Robertson**

- Scape not bulbous; scutellum never with red and yellow; axilla red or black; tegula never yellow; pronotal collar if yellow, small maculations; tegument punctures shallow; tergal rims not noticeably depressed and maculations appear flush with rest of terga.....4

4(3) Mesoscutum with red, can be variable from nearly completely red to small red streaks (Fig. 76b,c); axilla red (Fig. 76a,c); F3 with spine only, other flagellomeres with small nearly indistinguishable bumps if any at all (Fig. 74a); scutellum variable completely red to red and black (Fig. 77b,c); propodeal triangle variable with some red to completely black (Fig. 77b,c); pronotal collar yellow (Fig. 76b,c).....***N. articulata* Smith**

- Mesoscutum all black with no red (Fig. 79b); axilla may be red but mostly black (Fig. 79b); F3-F7 with denticles (Fig. 74b) and F8-F10 with carination on inner margins (Fig. 74b); scutellum either with red maculations or completely black (Fig. 80b,c); propodeal triangle completely black (Fig. 80b,c); pronotal collar usually black but sometimes with small yellow maculations (Fig. 79b).....***N. australis* Mitchell**

Female

- 1 [Southern US distribution only]; metasoma with unique pattern of maculation, spots laterally on T1-T3, T4 with a transverse band and T5 with two large spots, as in Figure 92a; propodeal triangle with red dots (Fig. 91a); F2 and F3 nearly equal; apical metatibial spines 4 dark red, curved, and longer than surrounding hair (Fig. 73e).....
.....*N. seneciophila* **Mitchell**
- Can be found outside southern US; metasoma maculations either absent (Fig.), whitish (Fig.) or more extensive with a broad band on T5 as in Fig. 92a ; propodeal triangle with no red dots (Fig. 77a, 80a, 84a,b, 88a); F2 much longer than F3 (Fig. 14a);.....2
- 2(1) Metasoma with maculations.....3
- Metasoma completely red with no maculations.....4
- 3(2) Maculations on T3-T5 cream coloured, no pale maculations on T1(on T2 if maculation present, it is vague) (Fig. 89a); integument punctures shallow; axillae yellow (Fig. 88a); pronotal collar red (Fig. 71a); tergal and sternal apical impressed areas not noticeably depressed; apical metatibial spine singular, flat and paddle like (Fig. 73d).....*N. rubicunda* **Olivier**
- Two colour variants: western individuals more red (Fig. 70b), eastern individuals black (Fig. 70a). Maculations T1-T5 bright yellow; tegument with deep punctures (Fig. 85a,b); axillae and pronotal collar bright yellow (Figs. 83a,b; 84a,b); T2-T4 and S2-S4 with apical impressed areas deeply and distinctly impressed in relation to rest of respective tergum or sternum (Fig. 86); apical metatibial spines between 4-6, long and thin (Fig. 73c).....
.....*N. erigeronis* **Robertson**

- 4(2) Apical metatibial spines short, nearly hidden by surrounding hair (Fig. 73a); head only slightly wider than long, not appearing rectangular and not as wide as in *N. australis* (Fig. 75a); females usually dark red in colour (Fig. 68a), never red-orange***N. articulata* Smith**
- Apical metatibial spines longer than surrounding hairs, flat and dark red (Fig. 73b); head much wider than long, nearly rectangular and obvious even with the naked eye and clearly wider than in *N. australis* (Fig. 75); females light red in colour (Fig. 69a).....***N. australis* Mitchell**

1) *Nomada articulata* (Figs. 68, 73a, 74a, 75a, 76, 77, 78, 87b)

Nomada articulata Smith, F. S. 1854. *Catalogue of the hymenopterous insects in the collection of the British Museum Part 2 Apidae*. London: British Museum (♂).

Primary type specimen Type ♂ B.M. Type HYM 17B 586 **Collection information:** ES NA
Nomada articulata Type Sm., Type H.T., NHMUK014025110; EXAMINED.

Nomada americana Kirby, W. 1837. *Fauna Boreali Americana pt 4* London, John Murray (♀).

Primary type specimen Type missing.

Nomada americana dacotana Cockerell, T. D. A. 1903. North American bees of the genus *Nomada*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 55, 580-614 (♂).

Primary type specimen ♂ **Collection information:** USA: South Dakota: Brookings, June 8; NOT EXAMINED.

Nomada bilobata Swenk M. H. 1912. Studies of North American Bees. *University Studies* (Lincoln, Nebraska), 12, 1-113 (♀).

Primary type specimen: ♀ **Collection information:** USA: Nebraska: Cuming Co: West Point. June 22, 1905 (H.S. Smith); NOT EXAMINED.

Nomada incerta Cresson, 1863. On the North American species of the genus *Nomada*. *Proceedings of the Entomological Society of Philadelphia*, 2, 280-312 (♀).

Primary type specimen: Type ♀; Type No. 2563 **Collection information:** USA: Illinois ♀ Cresson.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. articulata* and distinguish this species from all other members in the *N. erigeronis* species group in eastern North America (alternative states in brackets): **Males:** F2 longer than F3 (F2 and F3 are nearly equal), scutellum red or black (scutellum with yellow), hind femur curved with carinate edge (hind femora straight with no carination), scape rectangular (scape bulbous), scutellum, tegula, and terga never yellow (scutellum, tegula, and terga yellow), tegument punctures shallow (punctures deep), and terga rims and maculations flush with the rest of the terga (rims depressed and maculations appearing elevated). The previous characters are shared between *N. articulata* and its closest relative *N. australis*, however *N. articulata* can further be distinguished by having mesoscutum and axilla red (mesoscutum completely black, axilla red or black), and only F3 with spine underneath (F4-F7 with denticles and F8-F10 with carination). **Females:** the propodeal triangle without red maculations (propodeal triangle with two red maculations), F2 longer than F3 (F2 and F3 nearly equal) and metasoma with no maculations (metasoma with maculations). The previous characters are shared between *N. articulata* and its closest relative *N. australis*, however *N. articulata* can further be distinguished by having apical metatibial spines short and hidden in surrounding hair (apical metatibial spines longer than surrounding hairs) and head narrow, appearing taller than broad (head rectangular appearing broader than longer).

Discussion: Of the different members of the *N. erigeronis* species group, this species is the most well studied, mostly due to its wide range and because one of the hosts, *Agapostemon virescens*, is common and communal. This species flies in the spring and summer and is known from flowers of *Achillea*, *Amorpha*, *Apocynum*, *Aruncus*, *Asclepias*, *Brassica*, *Callirhoe*, *Camassia*, *Ceanothus*, *Chrysanthemum*, *Convolvulus*, *Coreopsis*, *Crataegus*, *Crepis*, *Dianthera*, *Erigeron*, *Fragaria*, *Geranium*, *Houstonia*, *Hypochaeris*, *Krigia*, *Lactuca*, *Malva*, *Melilotus*, *Meriolix*, *Neota*, *Nothoscordum*, *Oenothera*, *Oxalis*, *Potentilla*, *Ranunculus*, *Rubus*, *Rudbeckia*, *Sedum*, *Senecio*, *Symphoricarpos*, *Taenidia*, *Taraxacum*, *Trifolium*, and *Zizia* (Cockerell, 1903c, 1911b, 1911a; Gibbs et al., 2023; Mitchell, 1962; Stevens, 1951; Swenk, 1912).

Host information: This species is confirmed to use two different host species *Agapostemon sericeus* and *A. virescens* (Abrams & Eickwort, 1980, 1981; Eickwort & Abrams, 1980a). There is another record of this bee using *Andrena alleghaniensis* however the association between the two was only based on observation of *N. articulata* entering the nest and is considered dubious because no *Nomada* were reared from assumed parasitized nests (Alexander, 1991).

Distribution: From the Rocky Mountains east to the Atlantic coast. Interestingly, there are Discover Life specimens found in California, however I examined these specimens and they are not *N. articulata*. Instead, they are an unknown western species that is also a member(s) of the *N. erigeronis* species group.

2) *Nomada australis* (Figs. 69, 73b, 74b, 75b, 79, 80, 81, 87b)

Nomada australis Mitchell, T. D. 1962. Bees of the Eastern United States Vol 2. *North Carolina Agricultural Experiment Station Technical Bulletin*, 152, 1-557 (♀).

Primary type specimen Holotype ♀ Type No. 75213 **Collection information:** USA: FL: Highlands Hammock State Park. T.B. Mitchell, April 5, 1959, on *Bidens*, USNMMENT 00533890; paratype and allotype examined.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. articulata* and distinguish this species from all other members in the *N. erigeronis* species group in eastern North America (alternative states in brackets): **Males:** F2 longer than F3 (F2 and F3 are nearly equal), scutellum red or black (scutellum with yellow), hind femur curved with carinate edge (hind femora straight with no carination), scape rectangular (scape bulbous), scutellum, tegula, and terga never yellow (scutellum, tegula, and terga yellow), tegument punctures shallow (punctures deep), and terga rims and maculations flush with the rest of the terga (rims depressed and maculations appearing elevated). The previous characters are shared between *N. australis* and its closest relative *N. articulata*, however *N. australis* can further be distinguished by having mesoscutum completely black and the axilla red or black (mesoscutum and axilla red), and F4-F7 with denticles and F8-F10 with carination (only F3 with a spine). **Females:** the propodeal triangle without red maculations (propodeal triangle with two red maculations), F2 longer than F3 (F2 and F3 nearly equal) and metasoma with no maculations (metasoma with maculations). The previous characters are shared between *N. australis* and its closest relative *N. articulata*, however *N. australis* can further be distinguished by having apical metatibial spines longer than surrounding hairs (apical metatibial spines short and hidden in surrounding hair) and head rectangular, appearing broader than tall (head narrow appearing taller than broad).

Discussion: This species is most closely related to *N. articulata*. Recorded off of flowers of *Bidens*, *Cornus*, *Erigeron*, *Gypsophila Ilex*, and *Senecio* (Gibbs et al., 2023; Mitchell, 1962).

Host information: The host of *N. australis* is presumably *Agapostemon splendens* based upon co-occurrences of the two species (Gibbs et al., 2023).

Distribution: This species has a wide range from as far west and north as Manitoba and stretches along the entire Atlantic coast in both the US and Canada.

3) *Nomada erigeronis* (Figs. 70, 73c, 74c, 82, 83, 84, 85, 86, 87b)

Nomada erigeronis Robertson, C. 1897. North American Bees-Descriptions and Synonyms. *Transactions of the Academy of Science of St. Louis*, 7, 315-356.

Primary type specimen Holotype ♀ **Collection information:** Unknown, INHS Insect Collection 179661.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. erigeronis* and distinguish this species from all other members in the *N. erigeronis* species group in eastern North America (alternative states in brackets): **Males:** F2 longer than F3 (F2 and F3 are nearly equal), scutellum red or black (scutellum yellow), and hind femur curved with carinate edge (hind femora straight with no carination). *N. erigeronis* is further separated by having scape bulbous (scape rectangular), scutellum, tegula, and terga yellow (scutellum, tegula, and terga never yellow), tegument punctures deep (punctures shallow), and T1-T6 rims depressed and maculations appearing elevated (T1-T6 rims not depressed and maculations flush with the rest of terga). **Females:** the propodeal triangle without red maculations (propodeal triangle with two red maculations), F2 longer than F3 (F2 and F3 nearly equal) and metasoma with maculations (metasoma with no maculations). The previous characters are shared between *N. erigeronis* and *N. rubicunda*, however *N. erigeronis* can further be distinguished by having maculations T1-T5 bright yellow (maculations white), tegument punctures deep (punctures shallow), axillae and pronotal collar yellow (axillae yellow but pronotal collar red), and having 4-6 apical metatibial spines that are long and thin (singular apical metatibial spine, flat and paddle like).

Discussion: This species flies from late spring through the summer and can be found on flowers of *Brauneria*, *Campanula*, *Coreopsis*, and *Erigeron* (Mitchell, 1962; Swenk, 1912).

Host information: Presumably *Andrena helianthiformis* however there is no given explanation for the assumption other than that the two species occur at the same time (Stevens, 1951).

Distribution: Found as far west as Nebraska and Kansas, as far north as North Dakota, Minnesota and Ontario, and as far east and south as the entire Atlantic Coast.

4) *Nomada rubicunda* (Figs. 71, 73d 74d, 87a, 88, 89)

Nomada rubicunda Olivier, G. 1811. *Encyclopedie Methodique. Dictionnaire des Insectes Vol. 8.* Paris, Panckoucke.

Primary type specimen: Unknown **Collection information:** Carolina, M. Bofe; NOT EXAMINED

Nomada torrida Smith, F. S. 1854. *Catalogue of the hymenopterous insects in the collection of the British Museum Part 2 Apidae.* London: British Museum (♀).

Primary type specimen Type B.M. Type HYM 17B585 **Collection information:** 506 Georgia *Nomada torrida* Type Sm., *torrida* Type Sm., Type H.T., NHMUK014025109; photos available from NHMUK.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. rubicunda* and distinguish this species from all other members in the *N. erigeronis* species group in eastern North America (alternative states in brackets): **Males:** F2 longer than F3 (F2 and F3 are nearly equal), scutellum yellow (scutellum red or black), and hind femora rounded with straight edge (hind femur curved with carinate edge). **Females:** the propodeal triangle without red maculations (propodeal triangle with two red maculations), F2 longer than F3 (F2 and F3 nearly equal) and metasoma with maculations (metasoma with no maculations). The previous characters are shared between *N. rubicunda* and *N. erigeronis*, however *N. rubicunda* can further be distinguished by having maculations T3-T5 white (maculations yellow), tegument

punctures shallow (punctures deep), axillae yellow but pronotal collar red (axillae and pronotal collar yellow) and having a singular apical metatibial spine, flat and paddle like (4-6 apical metatibial spines that are long and thin).

Discussion: Flying in the spring to early summer, *N. rubicunda* seems to be restricted to sandy soils (Cockerell, 1911a; Gibbs et al., 2023). This species has been recorded off of *Crataegus*, *Fragaria*, *Mellilotus*, and *Rubus* (Mitchell, 1962).

Host information: Presumably *Agapostemon splendens* due to both species being restricted to sandy habitats (Gibbs et al., 2017, 2023).

Distribution: As far west as Wyoming, as far north as Ontario and Manitoba, and as far east and south as the entire Atlantic Coast.

5) *Nomada seneciophila* (Figs. 72, 73e, 74e, 87b, 90, 91, 92)

Nomada seneciophila Mitchell, T. D. 1962. Bees of the Eastern United States Vol 2. *North Carolina Agricultural Experiment Station Technical Bulletin*, 152, 1-557 (♀).

Primary type specimen Holotype ♀ USNM No 75224 **Collection information:** USA: North Carolina: Wake Co, May 7, 1960, ♀, T.D. Mitchell, on *Senecio*, USNMENT00533985; photos available at USNM; paratype examined.

Diagnosis: The following combination of characteristics is diagnostic for the female and male of *N. seneciophila* and distinguish this species from all other members in the *N. erigeronis* species group in eastern North America (alternative states in brackets): **Males:** F2 compared to F3 nearly equal in length (F2 longer than F3) and F3-F9 edges with pointed spines identical to spine found under F3 and F5-F8 with paired spines (F3-F9 with no spines on edges that look identical to the one found on F3 and F5-F8 with no paired spines). **Females:** the propodeal triangle with two red

maculations (propodeal triangle with no maculations) and F2 compared to F3 nearly equal in length (F2 longer than F3), and four apical metatibial spines curved and longer than the surrounding hair (apical metatibial spines variable).

Discussion: This species is regionally restricted to the southeastern US and is possibly a specialist on members of the plant genus *Jacobaea* (Mitchell, 1962). *N. seneciophila* has also been collected off *Rubus* in addition to ragwort (Mitchell, 1962). This species is named after the genus *Senecio*, of which ragwort used to belong to; therefore, future work should focus on collecting individuals off ragwort especially in areas where plant is considered an invasive and noxious weed as it would be interesting if the *Nomada* is following the plant as it disperses.

Host information: *Andrena gardineri* is considered a possible host (Ascher & Pickering, 2024).

Distribution: As far west as Texas and as far north and east as Maryland.

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Figures

1

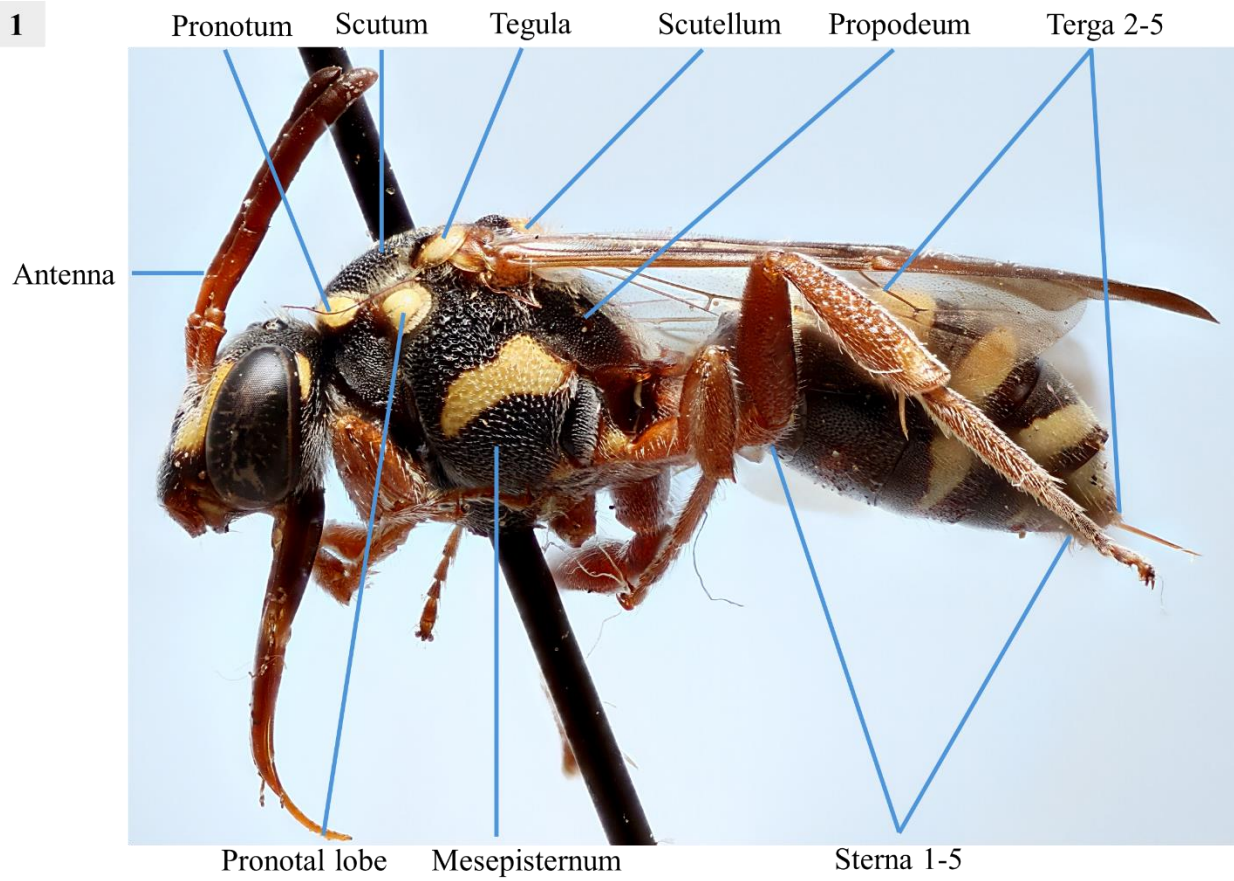


Figure 1. Lateral image showing major structures of *N. tiftonensis*.

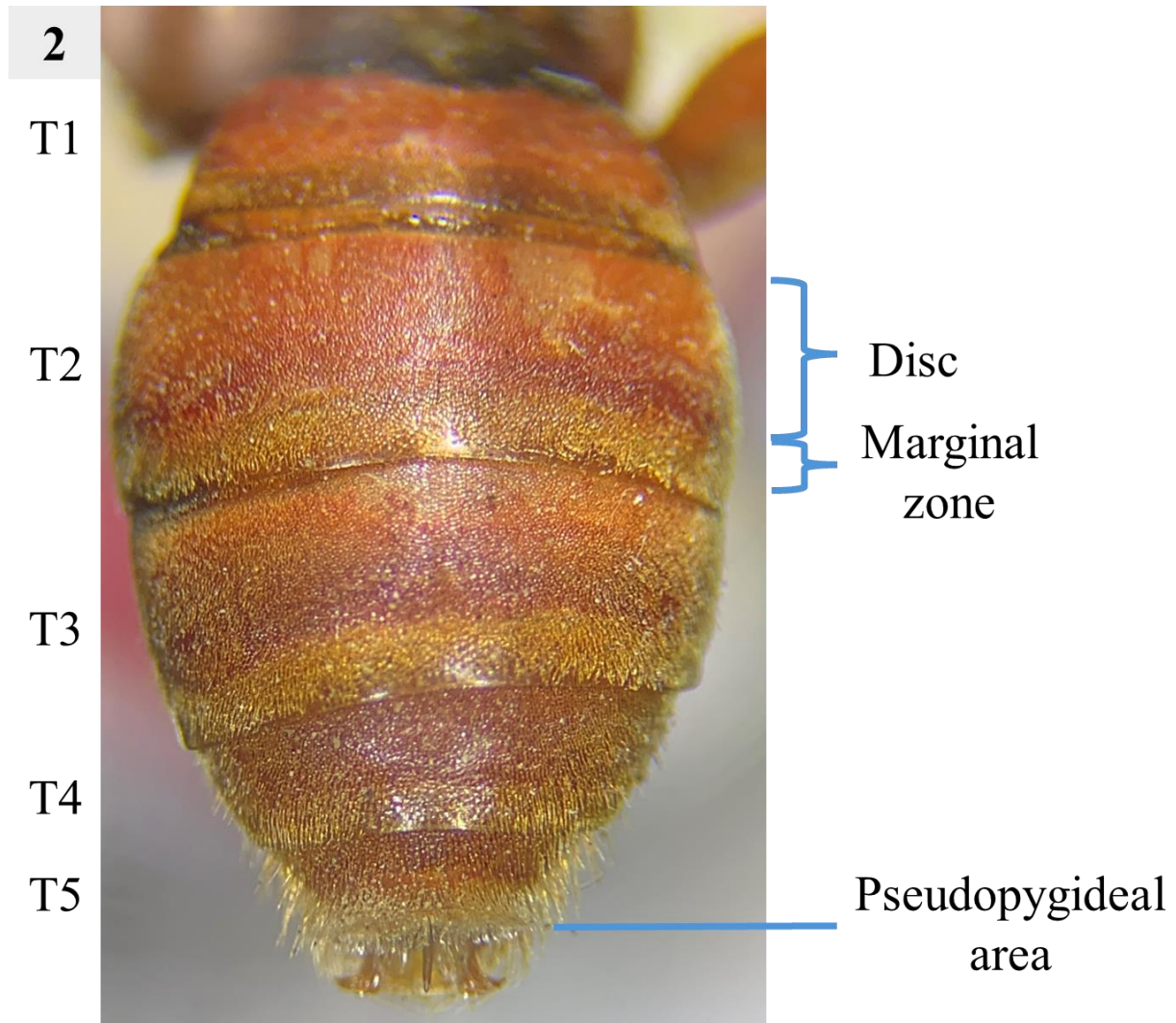
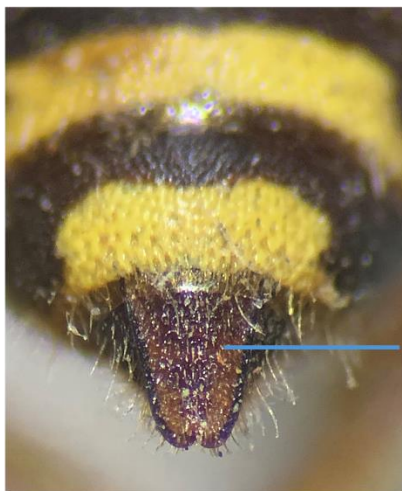


Figure 2. Dorsal surface of the metasoma of *N. crudelis*.

3a



Male

3b

T4

T5

Pygideal
plate



Pseudopygideal
area

Female

Figure 3. Structures of the apical external segments of the metasoma of male(a) and female (b) of *N. electa*.

4



Figure 4. Dorsal surface of the thorax of *N. erigeronis* to show the structures

5

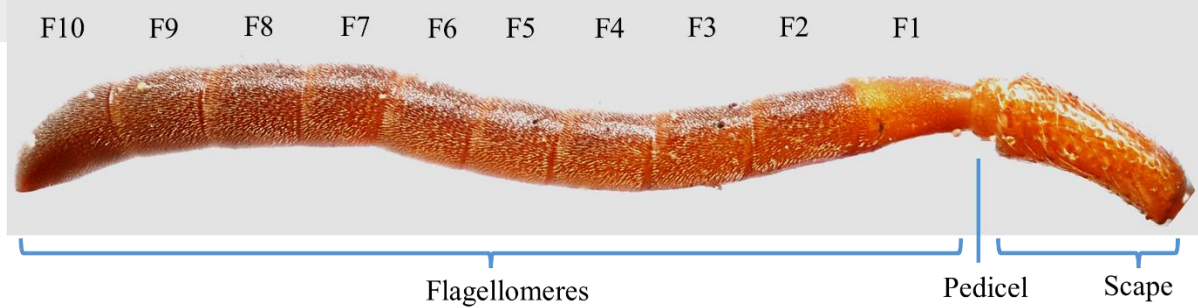


Figure 5. Female antenna of *N. fervida*; the male antenna will have an additional flagellomere (F11). Additionally, in many species of *Nomada*, the pedicel is recessed into the scape in males (see Fig. 55b).

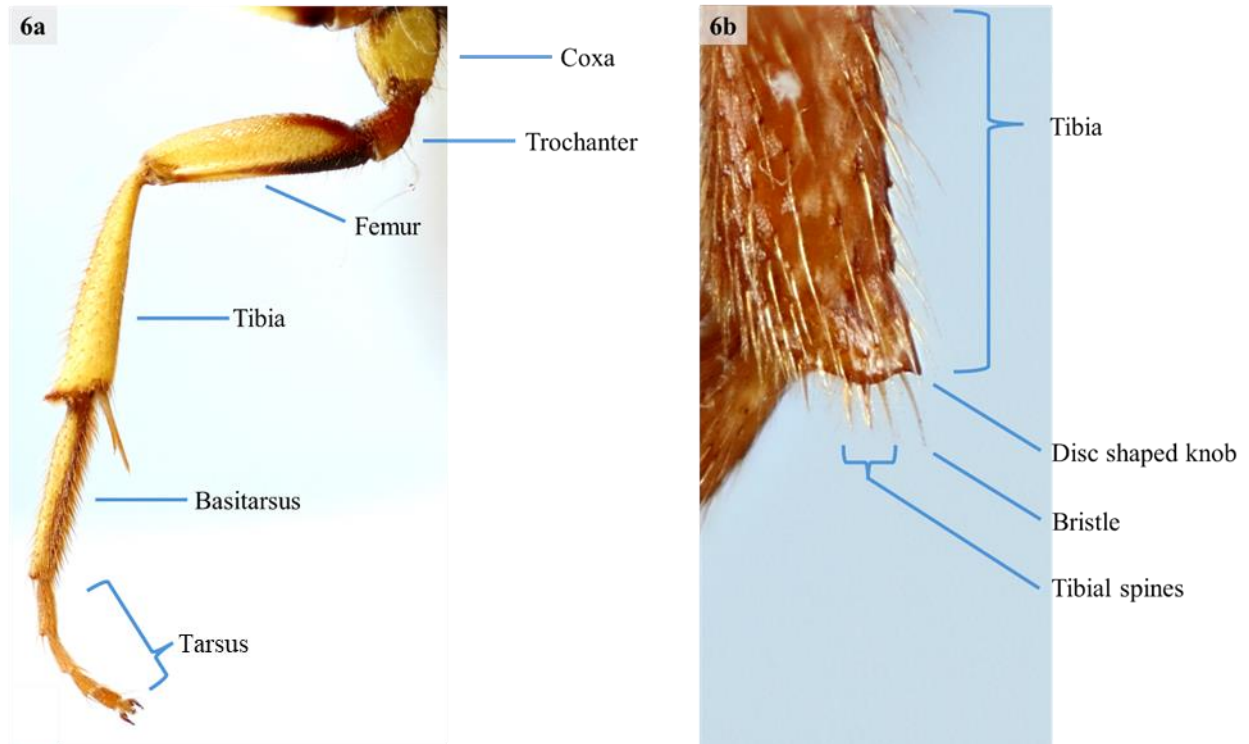


Figure 6. Diagram illustrating a) the structures of the leg of *N. sulphurata* and b) the apex of the tibia in *N. xanthura*.

7

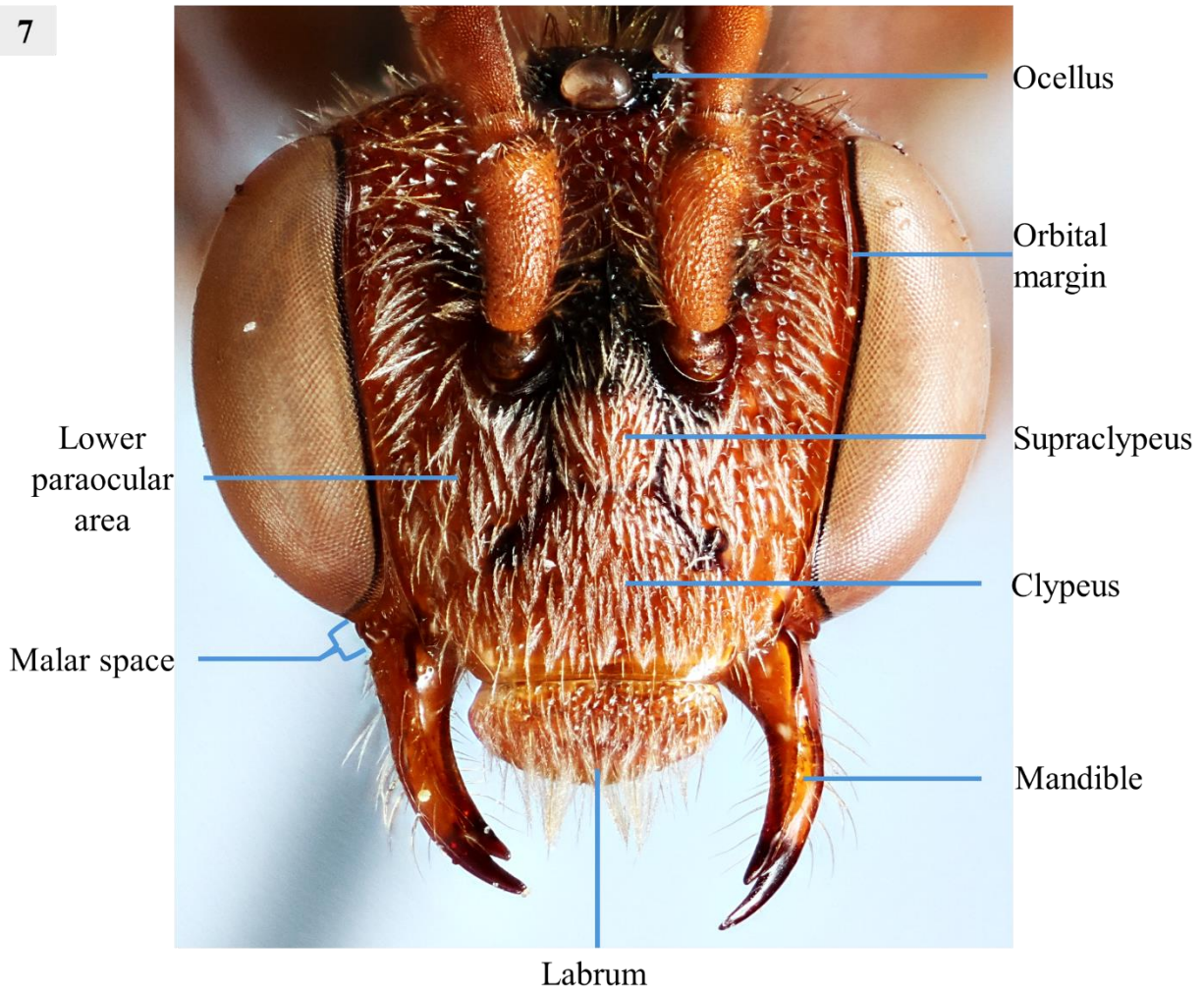


Figure 7. Diagram illustrating the structures of the head (*N. maculata*).

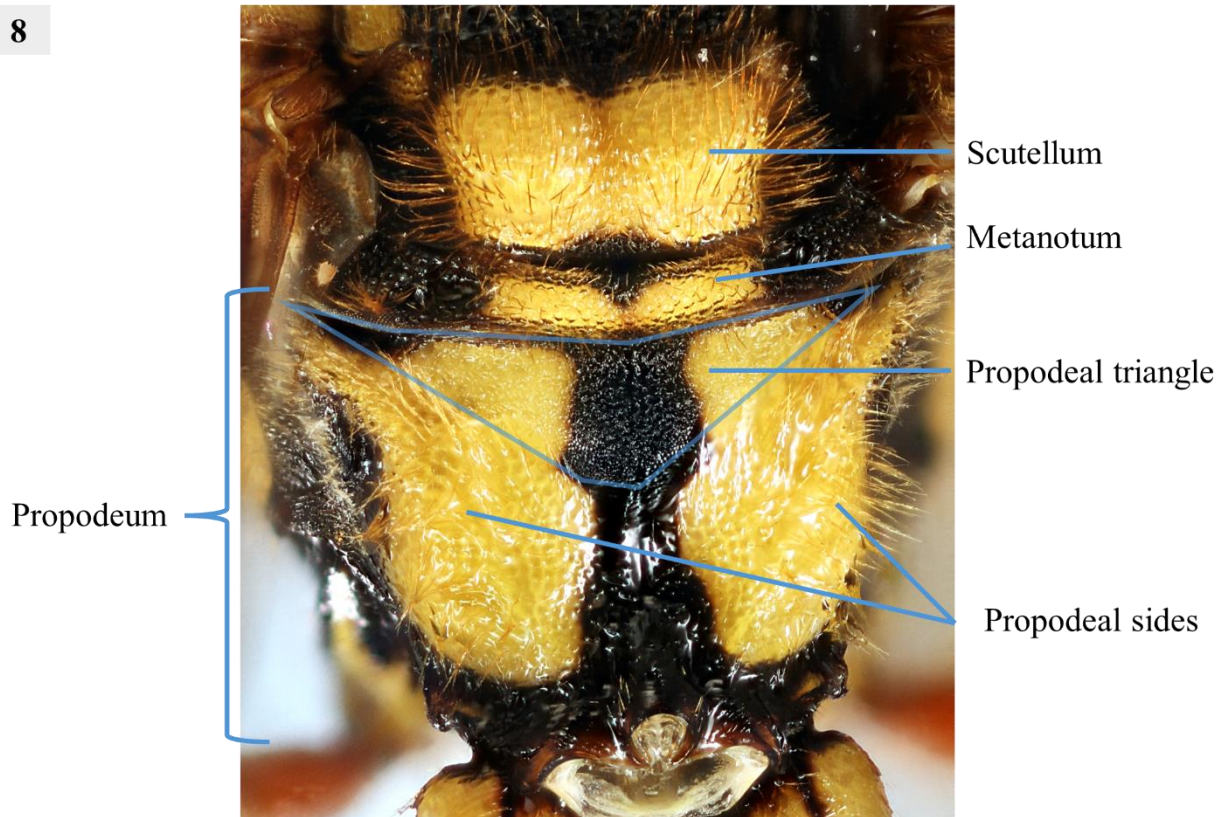


Figure 8. Diagram illustrating the posterior structures of the mesosoma in *N. sulphurata*. The propodeal triangle and the metapostnotum., which is used in identifying other bee groups, are the same structure.

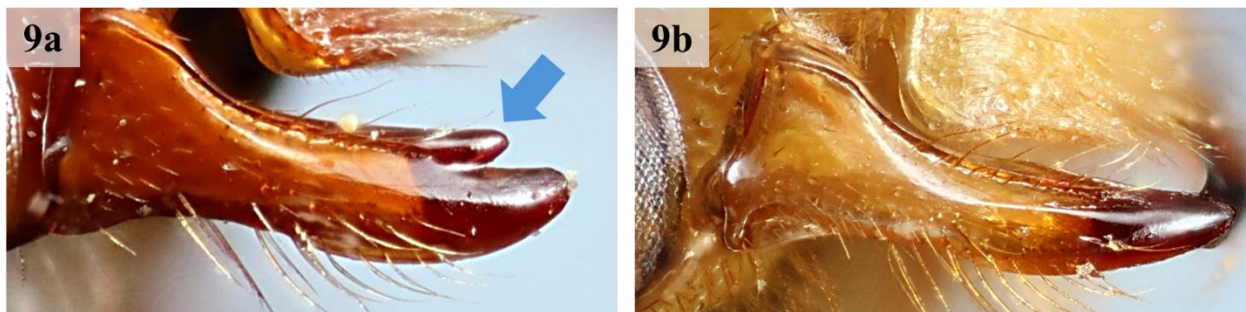


Figure 9. Mandibles a) bidentate in *N. maculata*, with a subapical tooth and resembling a mitten and b) non-bidentate in *N. sulphurata*, with no subapical tooth, this is the most common form.

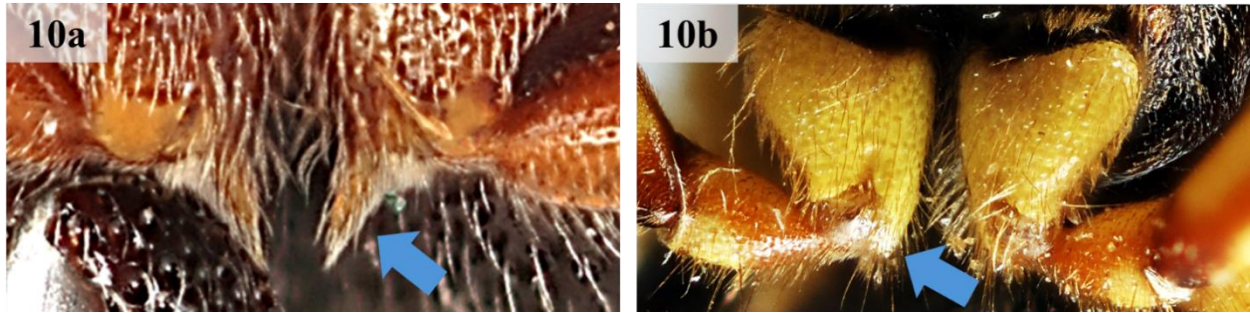


Figure 10. Anterior (or pro-) coxa showing a) long spine characteristic of the *N. erigeronis* and *N. vegana* species groups (here in *N. fervida*) and b) absence of a long spine in *N. sulphurata*.

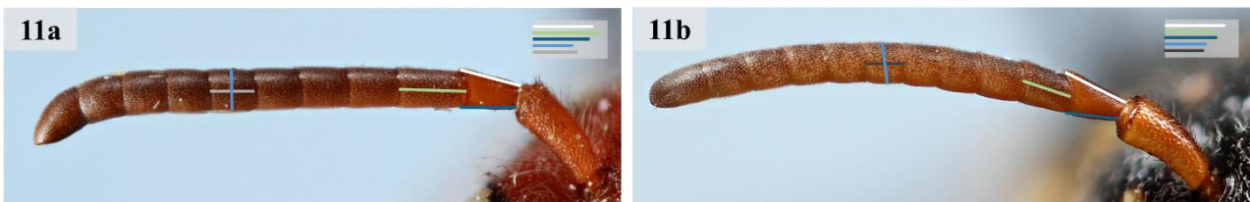


Figure 11. Differences in antennal structures between the a) *N. erigeronis* b) and *N. vegana* species groups. Members of *N. erigeronis* species group a) have a longer F2 than F1 and middle segments longer than tall, rectangular. Members of *N. vegana* species group b) have F2 shorter than F1 and middle segments shorter than tall.

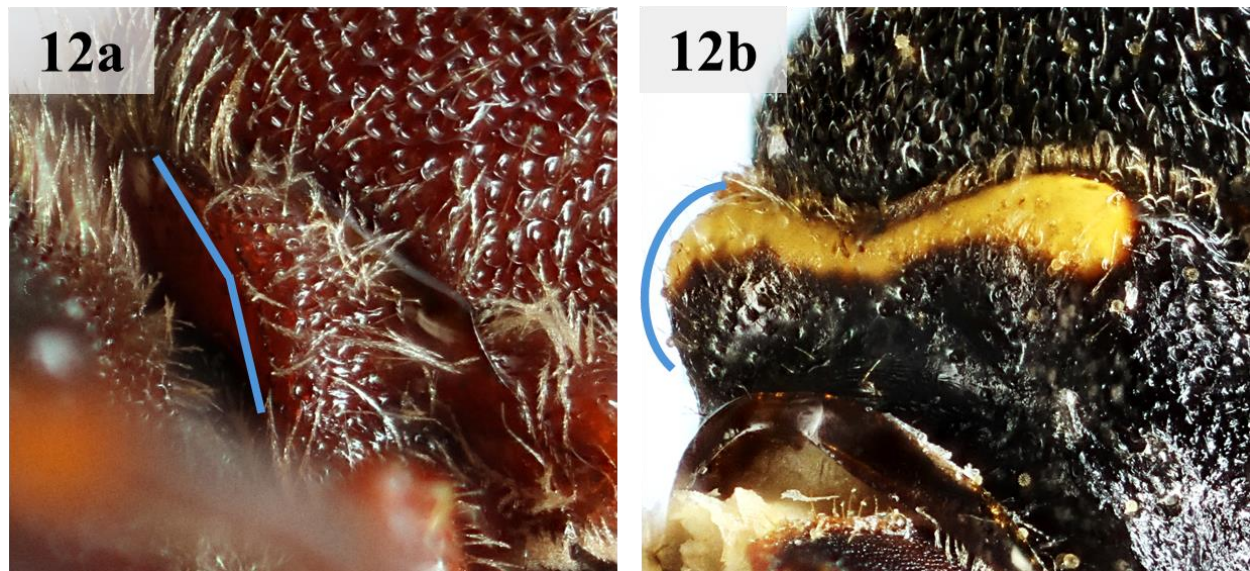


Figure 12. Difference in pronotal collar shape between the *N. erigeronis* (a) and *N. vegana* species groups (b). Members of *N. erigeronis* species group a) will have a carinate or subcarinate pronotal collar while members of *N. vegana* species group b) will have a rounded one.

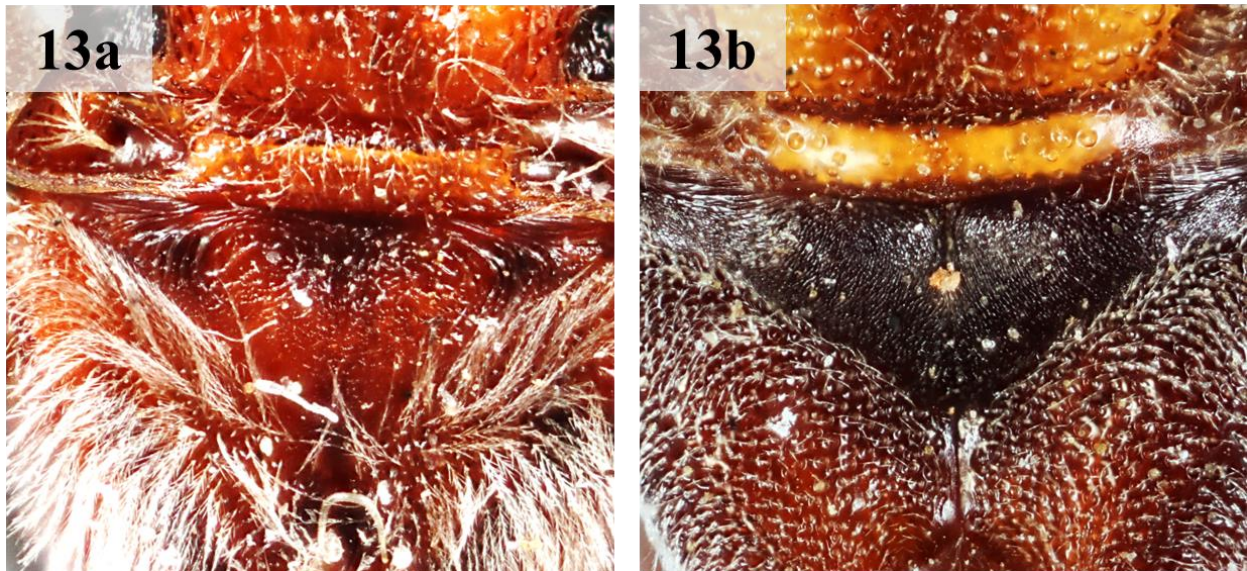


Figure 13. Propodeal triangle differences between members of *N. erigeronis* (a) and *N. vegana* (b) species groups. Members of the *N. erigeronis* species group a) have coarse striae that are vertical or nearly vertical in the anterolateral corners; integument of the propodeal triangle and surrounding areas similar. Members of the *N. vegana* species group b) have shallow striae that are horizontal anterolaterally; integument of the propodeal triangle different from the surrounding area, it is weakly sculptured and imbricate while the surrounding integument is coarsely punctured.

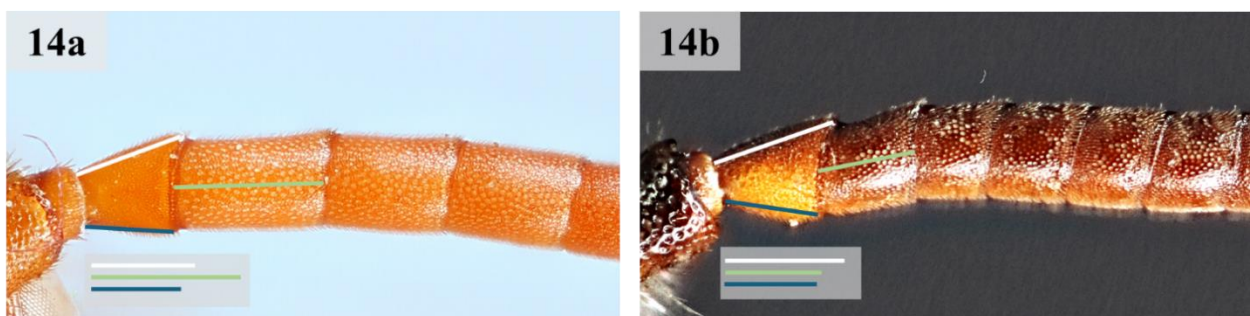


Figure 14. Basal flagellomeres a) both long and short edges of F1 shorter than F2 in *N. dentariae*) and b) long edge of F1 longer than F2 but short edge shorter or equal to F2 in *N. aquilarum*. Coloured lines demonstrate the relative lengths.

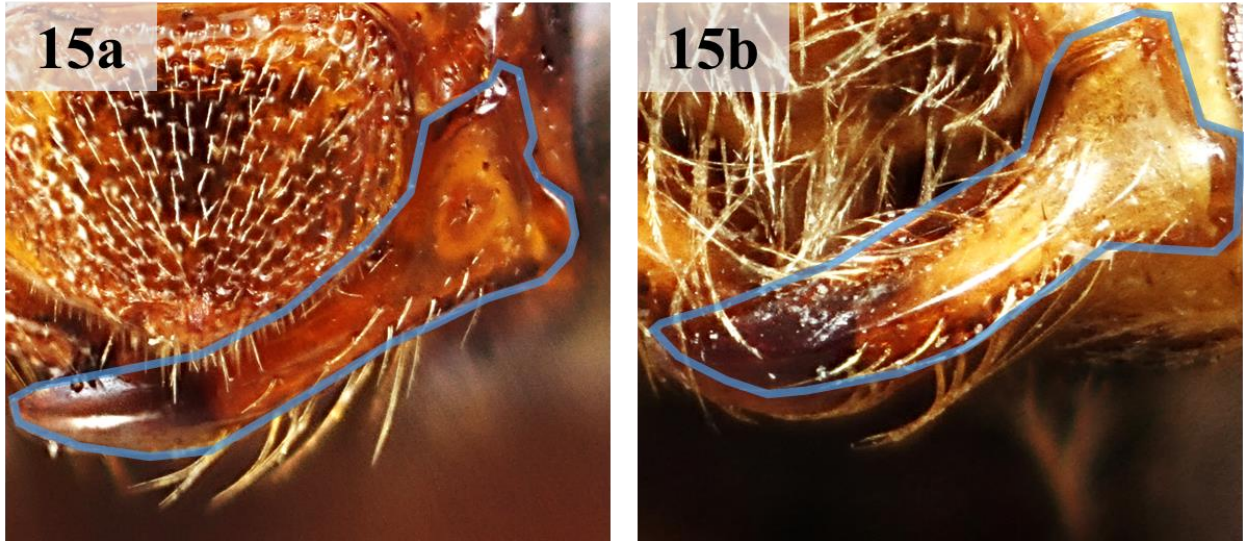


Figure 15. Differences in mandible thickness showing a) the more common narrower mandible in *N. fervida* and b) the broad mandible characteristic of *Nomada annulata*.



Figure 16. Male pygidial plate a) entire in *N. superba* and b) notched in *N. texana*.



Figure 17. Depiction of the a) convex propodeal lateral surface characteristic of members of the *N. superba* species group (here *N. superba*) and b) the more common straight condition in all other species groups (here *N. sulphurata*).

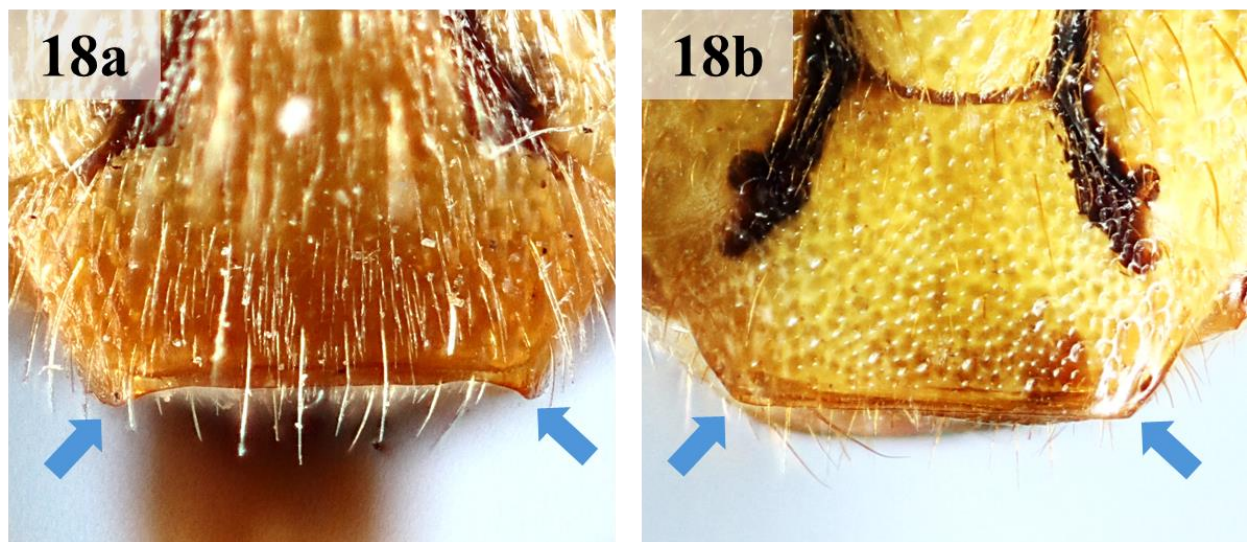


Figure 18. Apical margin of the clypeus showing a) angulate apicolateral margin found in members of the *N. superba* species group (here *N. superba*) and b) the more common rounded edges (here *N. sulphurata*).

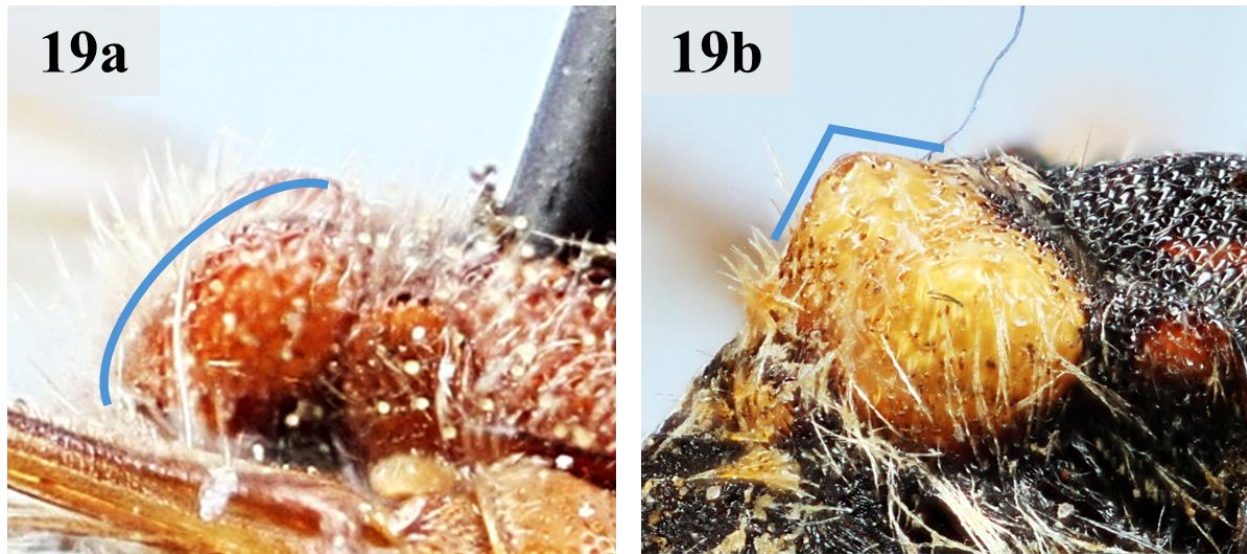


Figure 19. Shape of the scutellum in profile showing the a) more common rounded form (here *N. seneciophila*) and b) the characteristic angulate scutellum of members of the *N. superba* species group (here *N. superba*).

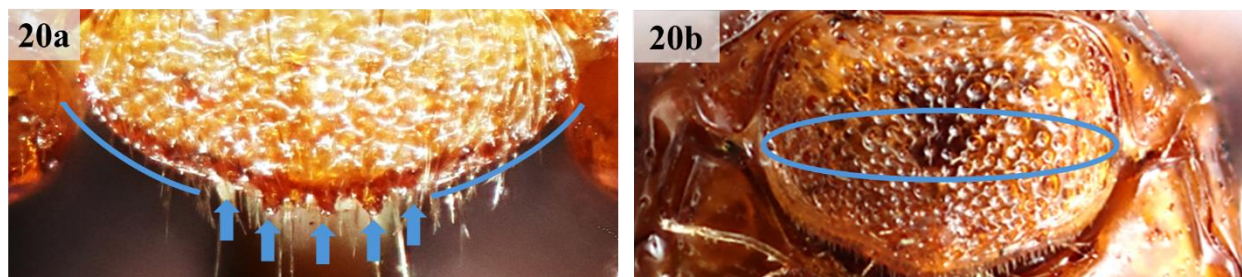


Figure 20. Labrum showing a) the transverse carina bearing teeth found in members of the *N. roberjeotiana* species group (here *N. placida*, note the five characteristic teeth indicated by the arrows see pg 138-142 for more) and b) a front view of a labrum with a circle highlighting the lack of a median transverse carina (here *N. fervida*).

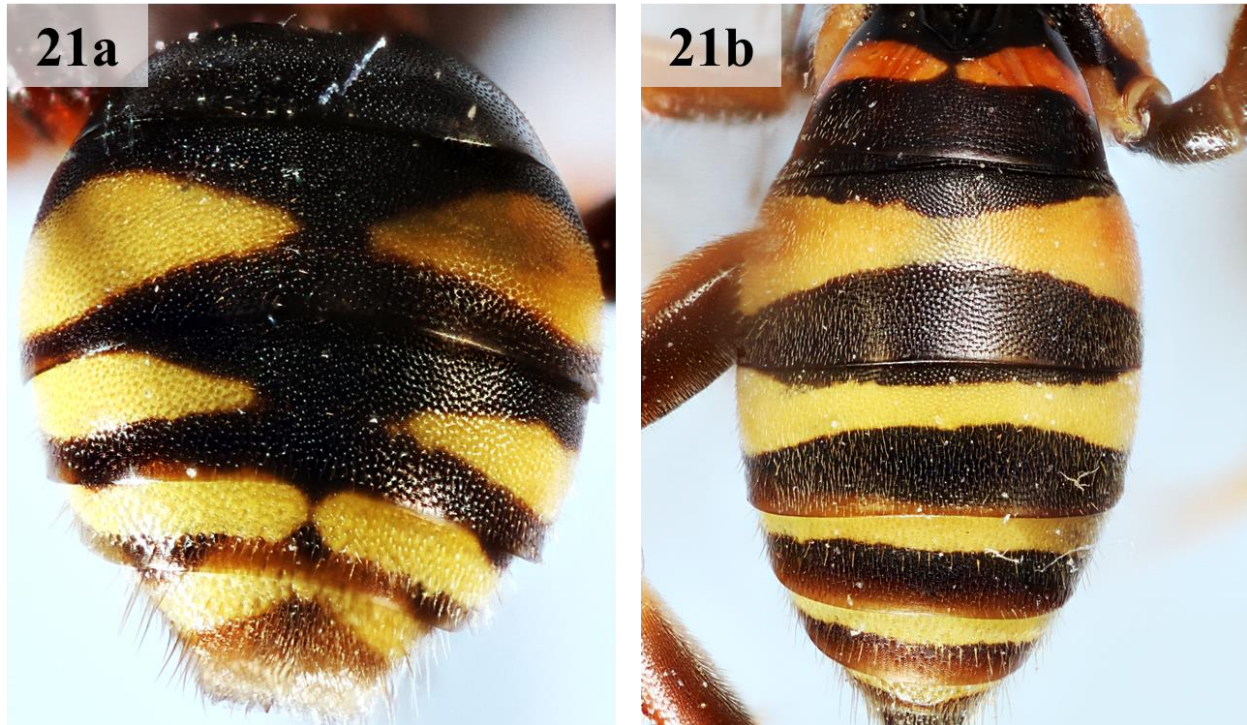


Figure 21. Differences in metasomal maculations in a) members of the *N. roberjeotiana* species group, which have incomplete bands that are broken in the middle on T2-T4 (here *N. placida*) and b) members of the *N. vincta* species group which have complete banding on T2-5 and usually T1. This specimen has a small break in the banding of T1, making it unusual (here *N. vincta*) See page 203 Fig. 41 for other examples of *N. vincta* species group members.



Figure 22. Differences in the shape of the male scape; a) the more common cylindrical shape found in both males and females (here *N. sulphurata*) and b) the globular and swollen scape of males of the *N. vincta* species group (here *N. graenicheri*).

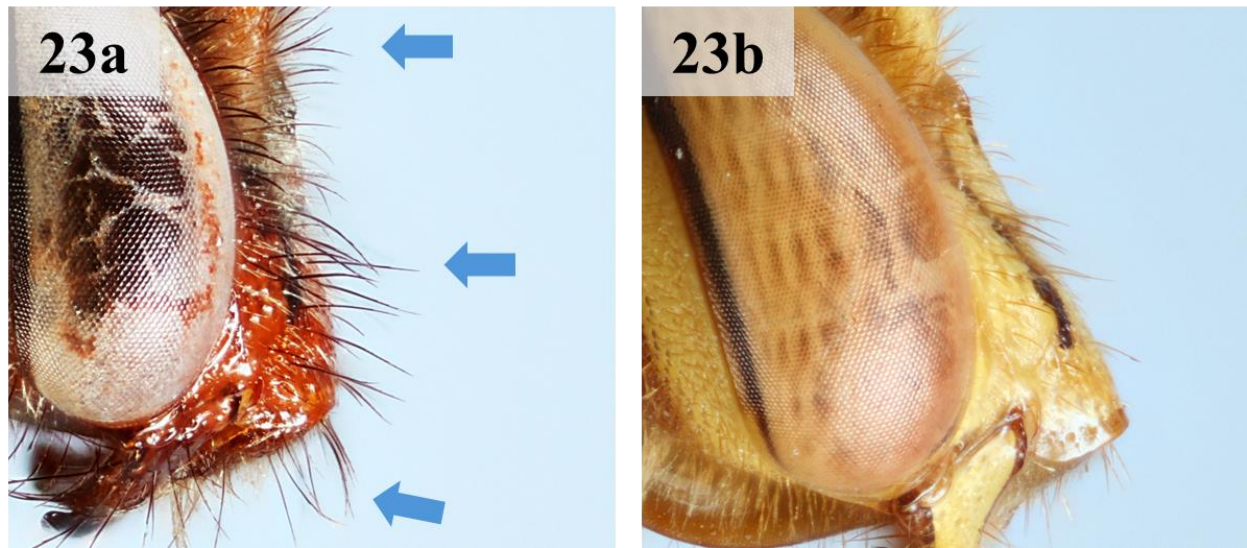


Figure 23. The a) presence (here *N. valida*) or b) absence (here *N. superba*) of red bristles on the face and scape. These bristles are dark red, stiff, and resemble an eyelash. If coloured hairs are present (b) they are not dark red.

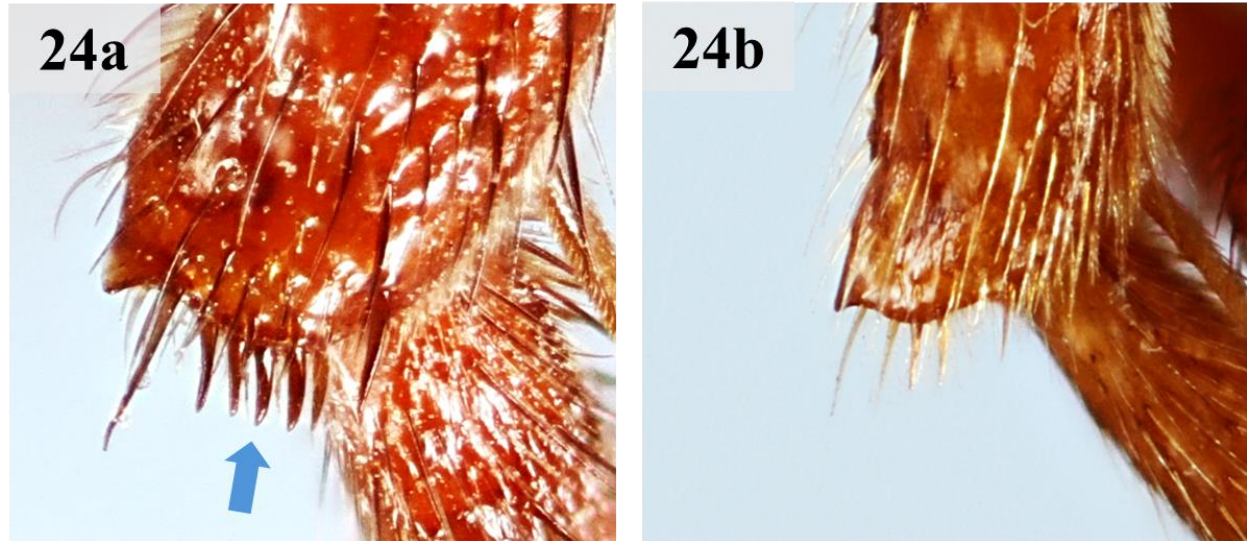


Figure 24. Apical metatibial spines characteristic of a) members of the *N. ruficornis* species group that have distinctive red bristles; thick and dark red (here *N. valida*) and b) the more common light reddish spines found in species across the *N. ruficornis* and *N. heminomada* species groups (here *N. xanthura*). Remember that in counting apical metatibial spines, the long

hair close to the disc shaped knob on the left side of the tibia is not counted (see Fig. 6b for diagram).

25a



25b



Figure 25. Lateral view of a) female *Nomada aquilarum* and b) male *Nomada placida*. Note that males and females within each species resemble each other except for standard sexual dimorphism.

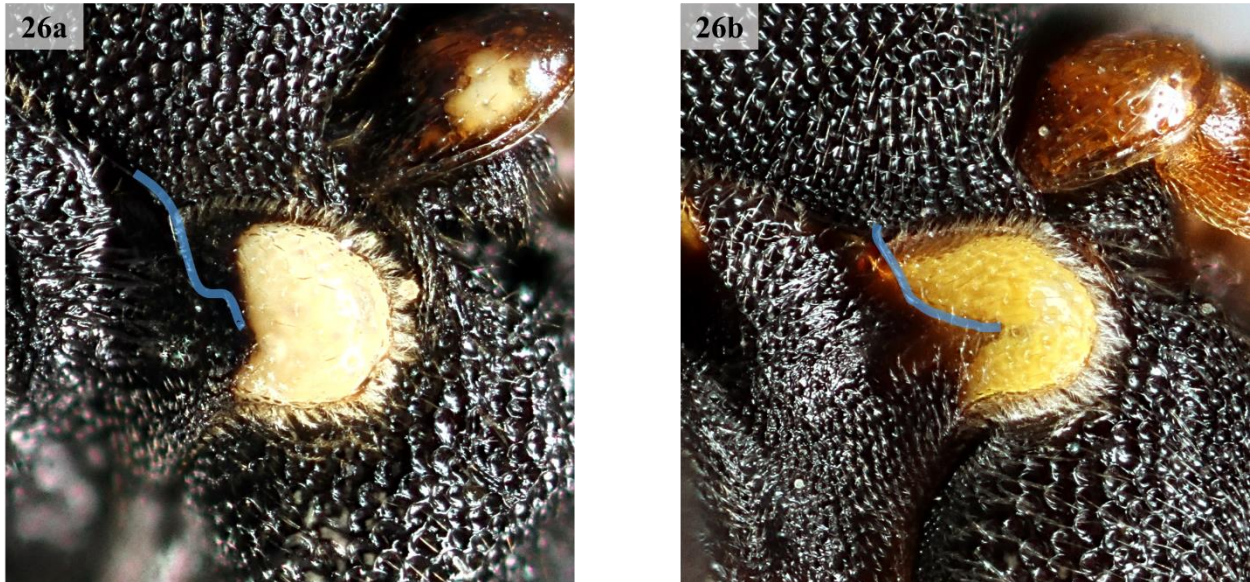


Figure 26. The prelobar carina (also known as the pronotal lateral carina) in members of the *N. roberjeotiana* species group: a) is almost vertical with a ventral sinuation in *N. aquilarum*; b) gradually curved in *N. placida*.



Figure 27. The pre-occipital margin is either a) rounded as in *N. aquilarum* or b) angulate as in *N. placida*.



Figure 28. Acetabular carina is found dorsally at the base of the mandible; a) acetabular carina well defined in *N. aquilarum* and b) rudimentary in *N. placida*.



Figure 29. Faces of a) *N. aquilarum* demonstrating clypeus and paraocular areas with characteristic cream colored maculations and b) *N. placida* with these areas with characteristic bright yellow maculations.



Figure 30. Mesosomal posterior surfaces for a) *N. aquilarum* where the scutellum has a cream coloured maculation and b) *N. placida* where both the scutellum and metanotum bright yellow.



Figure 31. Metasoma demonstrating the a) cream coloured maculations, shallow and sparser punctures in *N. aquilarum* and b) bright yellow maculations, coarse and dense punctation in *N. placida*.



Figure 32. Dorsal view of the maculations and punctation on the thorax of a) *N. aquilarum* with white markings and coarse slightly spaced punctuation; b) *N. placida* with yellow maculations and smaller denser punctures

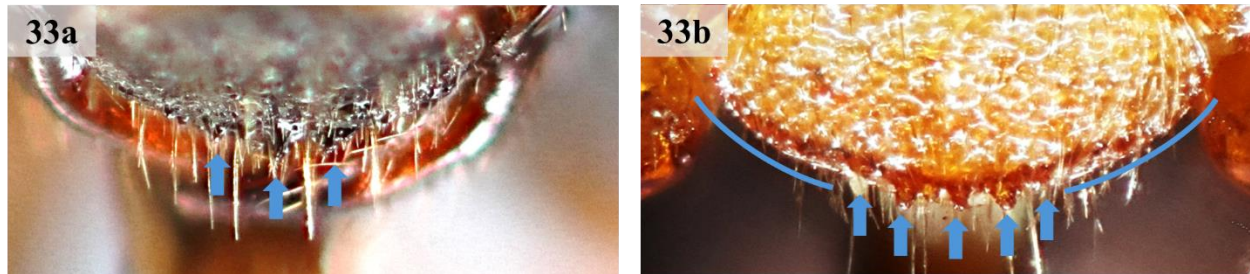


Figure 33. Dorsal view of the apicomedian carina found on the labrum in a) *N. aquilarum* and b) *N. placida*. Note the incomplete carina with three teeth in *N. aquilarum* (a) and the complete transverse carina (lateral blue lines) with five teeth in *N. placida* (b).

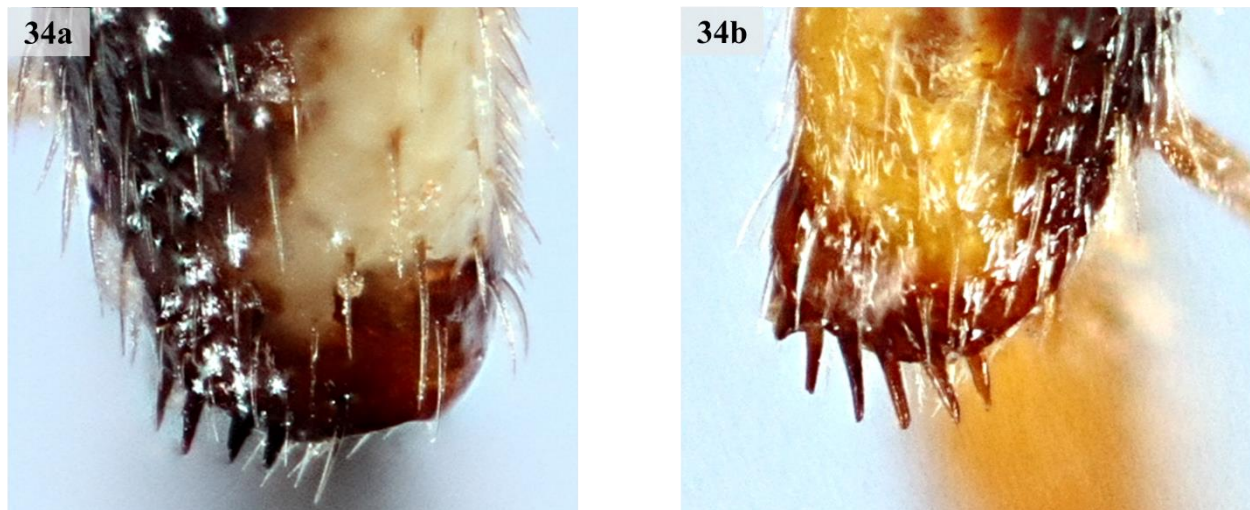


Figure 34. Apical metatibial spines of female in a) *N. aquilarum* with four short and stout spines and b) *N. placida* which has four or five (five in this image) long, narrow spines.

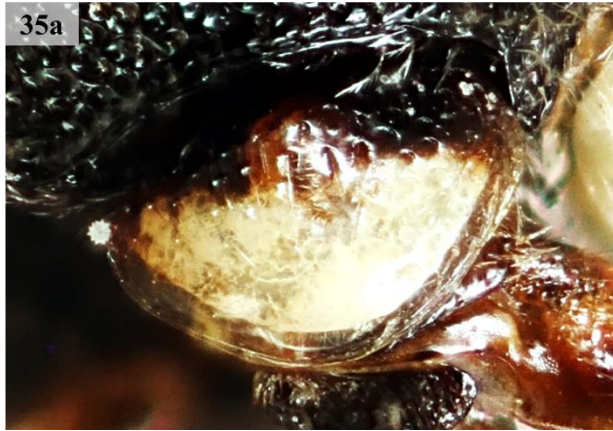


Figure 35. Dorsal view of the tegula demonstrating how a) pitting is limited to the medial portion in *N. aquilarum* and b) is throughout the tegula in *N. placida*.



Figure 36. Metasomal sterna of a) *N. aquilarum* and b) *N. placida* showing the differences in maculation shape and colour. a) *N. aquilarum* will have maculations cream coloured and separated while b) *N. placida* has them yellow and complete.



Figure 37. Lateral images of female a) *N. graenicheri* and b) *N. vincta*. Note that males and females within each species resemble each other except for standard sexual dimorphism.



Figure 38. Dorsal view of the thorax representative of members of the *N. vincta* species group (here *N. vincta*) showing the metasoma black and pronotal collar, pronotal lobe, tegula, scutellum, with colour. *N. graenicheri* will only differ by having these structures cream coloured instead of yellow.



Figure 39. Postero-dorsal view of the posterior of the mesosoma in a) *N. graenicheri* showing the few hairs of the propodeum, cream coloured maculations on the scutellum and metanotum, and lack of maculations on the propodeal sides. b) *N. vincta* showing the long golden pubescence

on the propodeum and bright yellow maculations on the scutellum, metanotum, and propodeal sides.

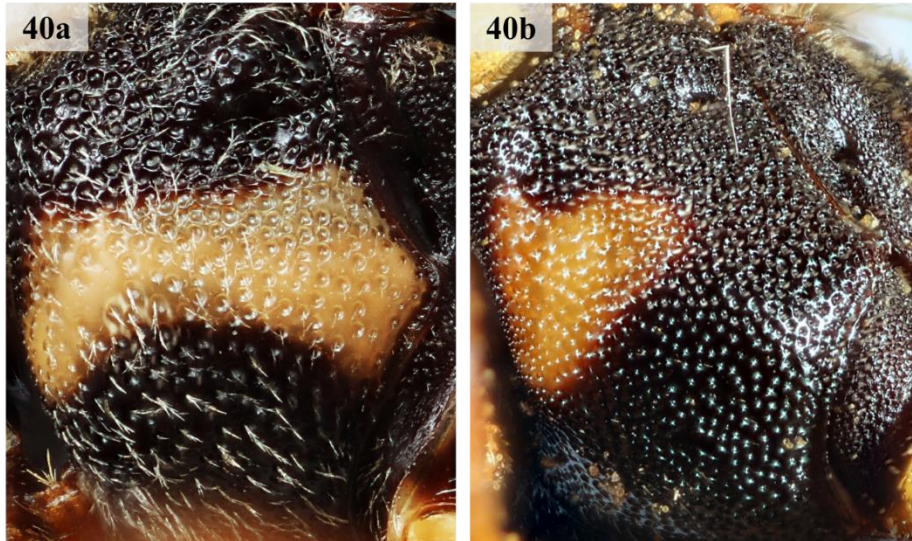


Figure 40. Lateral view of the mesepisternum of a) *N. graenicheri* displaying a transverse cream or yellow bar shaped maculation and b) *N. vincta* displaying a yellow, triangular, anterior maculation.



Figure 41. Dorsal view of the metasoma of a) *N. graenicheri* and b) *N. vincta* showing the differences in maculation colour

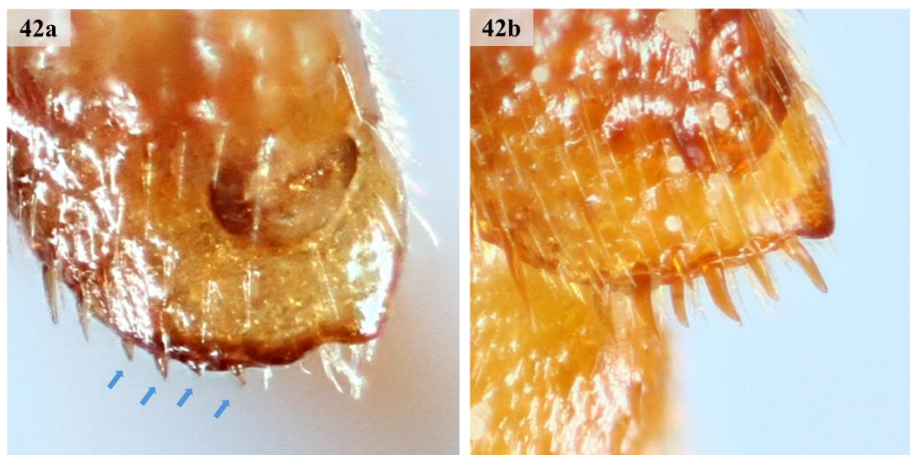


Figure 42. Apex of metatibia of female to show spines in: a) *N. graenicheri* which are minute and conical and b) *N. vincta* in which they are long and thick.



Figure 43. The shape of scapes in male members of the *N. vincta* species group: a) *N. graenicheri* and b) *N. vincta* showing the characteristic globular shape found in members of the *vincta* species group. a) *N. graenicheri* has outer edges curved while b) *N. vincta* has outer margin “S” shaped

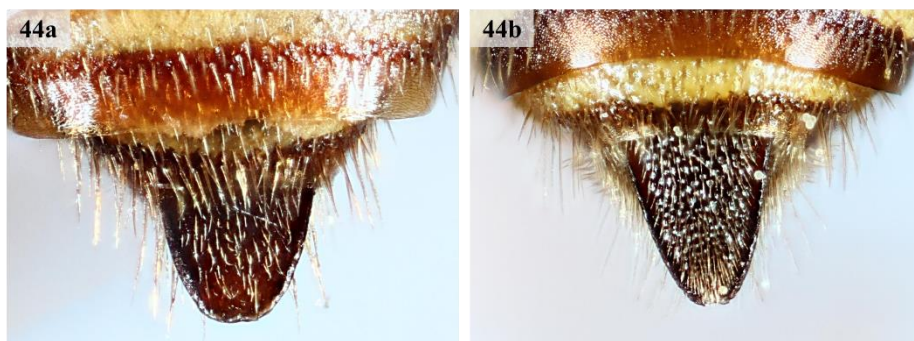


Figure 44. The pygidial plate in male a) *N. graenicheri* and b) *N. vincta* in dorsal view. Note the differences in shape: a) in *N. graenicheri* it is broadly rounded apically, parallel sided basally and overall more U-shaped, whereas; b) in *N. vincta* it is triangular and more V-shaped.



Figure 45. *N. vincta* face: a) female and b) male which is easily identifiable by the enlarged scape.



Figure 46. Female *N. graenicheri* face. Male will have the same maculations on the paraocular area, clypeus, and supraclypeal area, but the scape will be globular as in Fig. 43a.



Figure 47. Lateral images of *N. affabilis*: a) female and b) male.



Figure 48. Lateral images of *N. superba*: a) female and b) male.

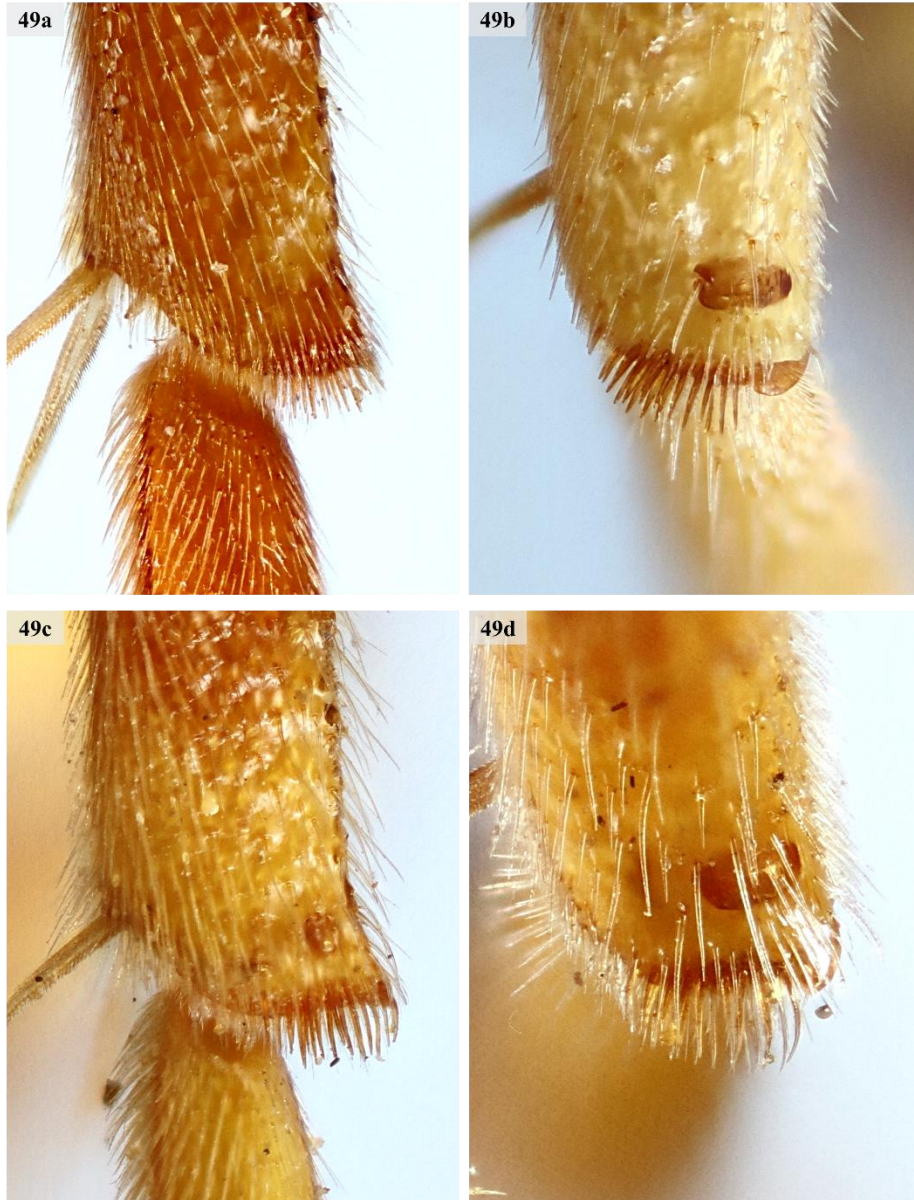


Figure 49. Apex of metatibia to show spines in the female(top: a,b) and male (below: c,d). a,c) *N. affabilis* and b,d) *N. superba*.



Figure 50. Variation in the colour of head in a, b) female and c) male *N. affabilis*. Note the reduced amount of black in (a) compared to (b).



Figure 51. Variation in the extent of red on the mesoscutum of a, b) female and c) male *N. affabilis*.

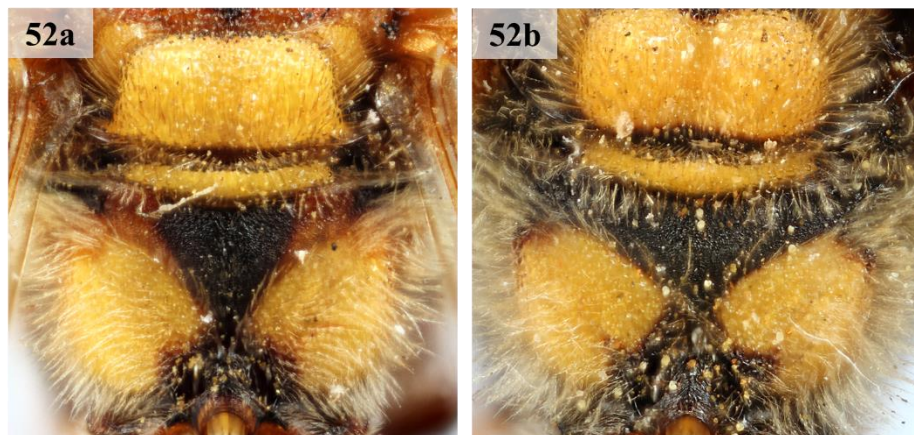


Figure 52. The a) presence or b) absence of red within the propodeal triangle of *N. affabilis*.



Figure 53. Metasoma of a) *N. affabilis* and b) *N. superba* displaying the differences in maculation colour. a) *N. affabilis* will have maculations more orange-yellow and in b) *N. superba* they will be bright yellow.



Figure 54. Male pygidial plate in a) *N. affabilis* and b) *N. superba*. Note the differences in shape: a) in *N. affabilis* it is more triangular and V-shaped, whereas; b) in *N. superba* it is broadly rounded apically, parallel sided basally, and more U-shaped.



Figure 55. *N. superba* face: a) female and b) male showing differences in maculation colour and density and length of facial foveae.

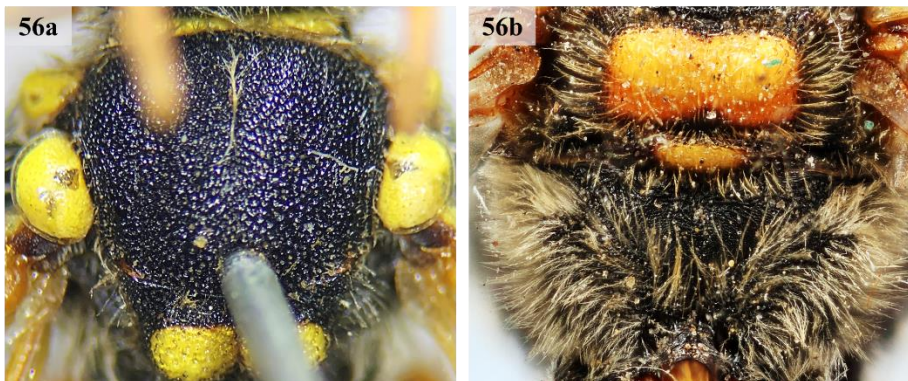


Figure 56. A a) dorsal and b) postero-dorsal view of the posterior of the mesosoma of *N. superba* where both sexes lack maculations on the mesoscutum and propodeal sides.

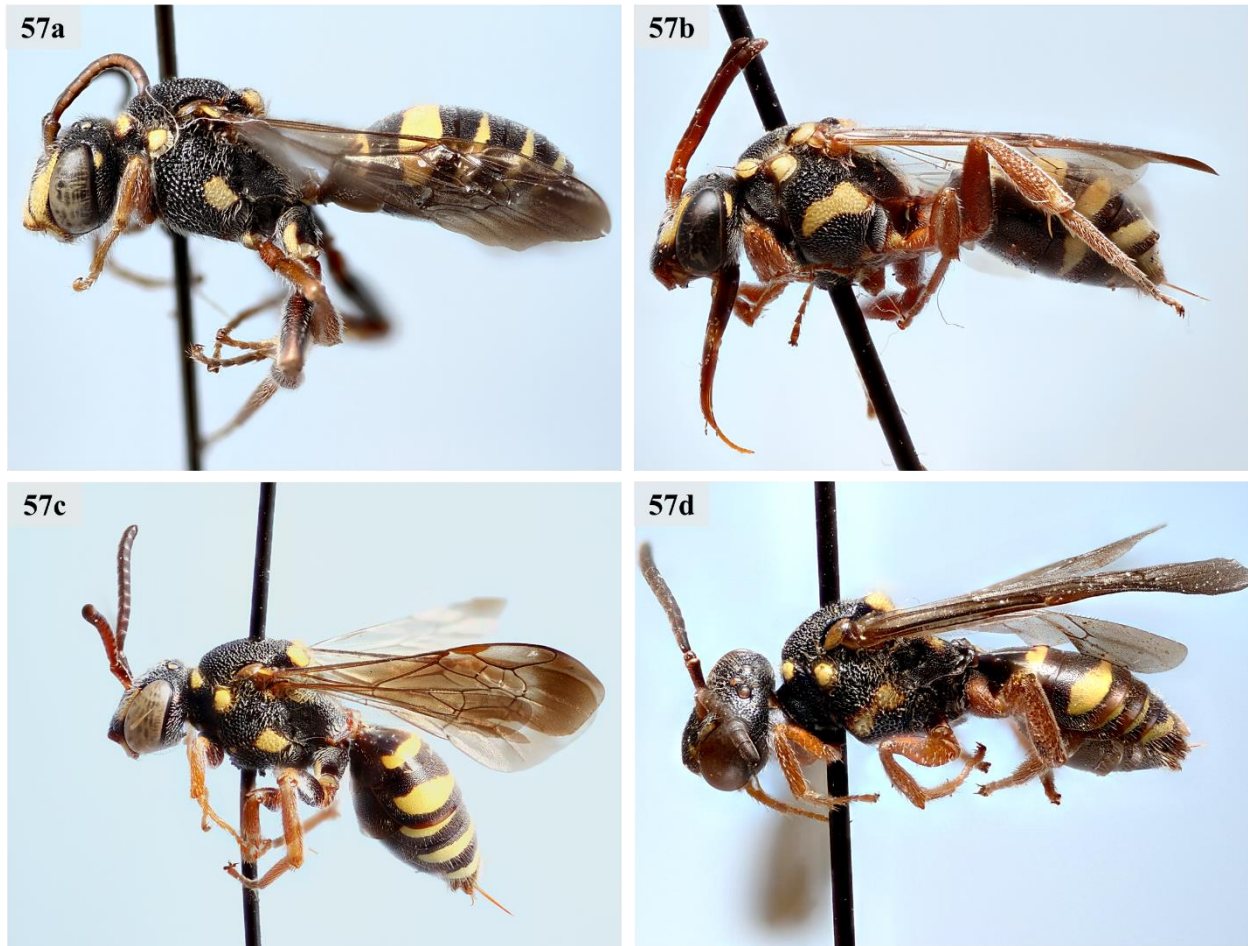


Figure 57. Lateral images of female a) *N. fervida*, b) *N. texana*, c) *N. tiftonensis*, and d) *N. vegana*. Within each species, males and females are nearly identical, other for standard sexual dimorphism.



Figure 58. Dorsal view of the thorax typical of eastern members of the *N. vegana* species group (*N. vegana*) showing pronotal collar, pronotal lobes and scutellum yellow. With the exception of *N. texana* which has tegula yellow, tegula orange.



Figure 59. Apical metatibial spines in females of the *N. vegana* species group (lateral view except when stated otherwise): a) the dense patch of small spines characteristic of *N. fervida*; b) the blunt and square spines characteristic of *N. texana*; c) long, tapered and often curved spines found in *N. tiftonensis*; d) underside view of the short, apical metatibial spines of *N. vegana* which are often not detectable in lateral view due to being hidden in the surrounding hair

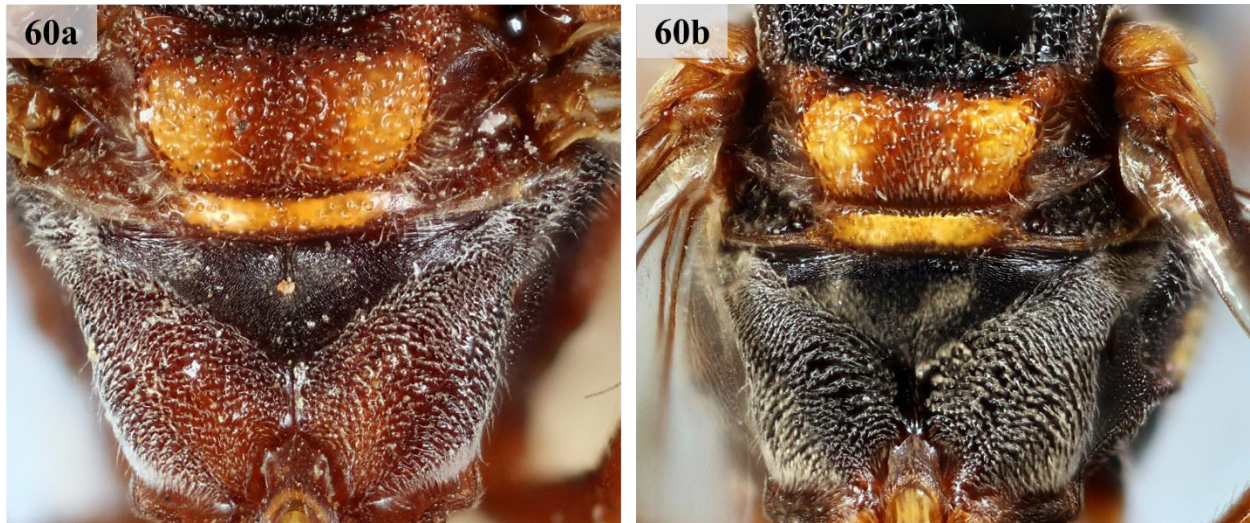


Figure 60. Posteror-dorsal view of the posterior of the mesosoma of *N. fervida* in posterodorsal view displaying variation in the amount of red present: a) propodeal sides completely red but propodeal triangle black; b) the more common propodeal sides and propodeal triangle both completely black.

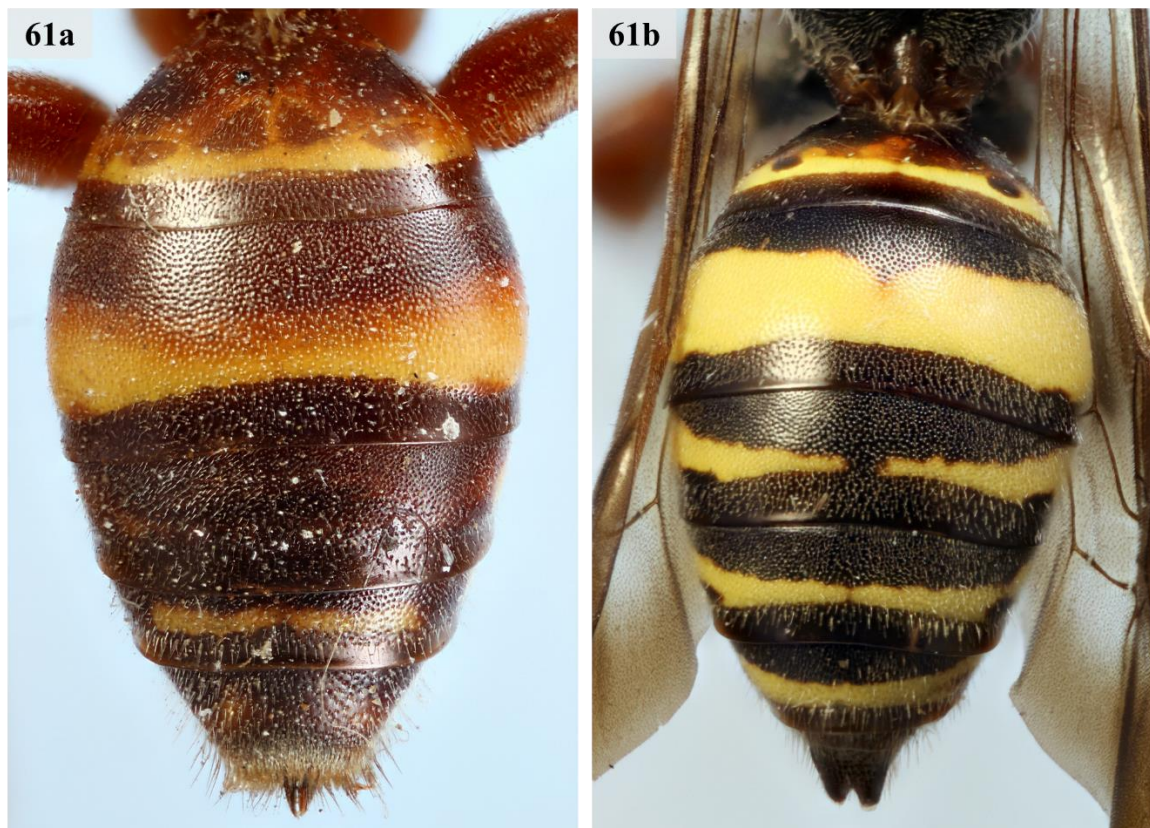


Figure 61. Metasoma of a) female and b) male *N. fervida* in dorsal view displaying the variation of red present. Most individuals, male and female, will be similar to the colouration found in (b).

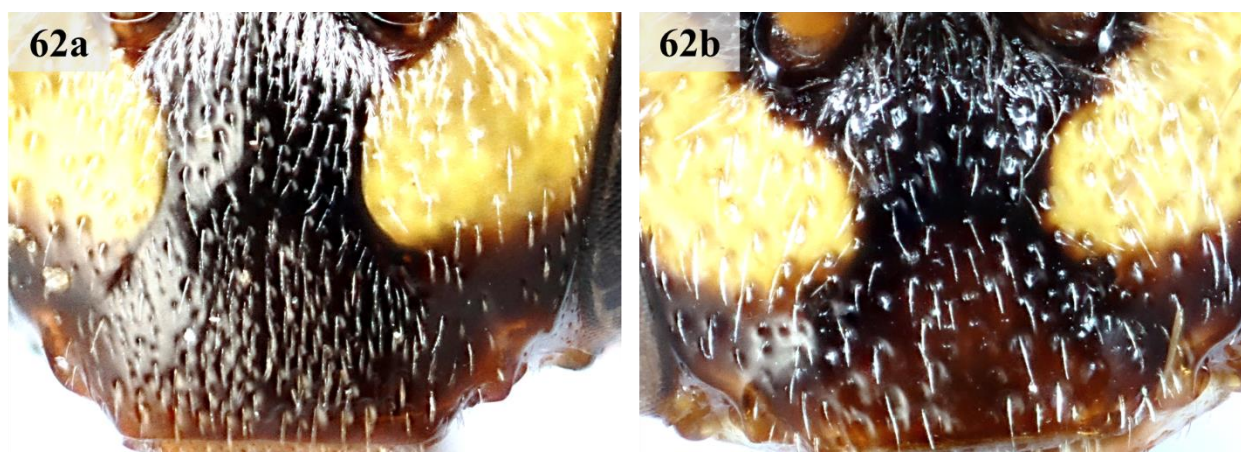


Figure 62. Differences in the density and shape of shallow pitting on the clypeus of females of:
a) *N. texana* where the punctures are dense and smaller in comparison to those of the
supraclypeal and paraocular areas and b) *N. tiftonensis* where the punctures are sparse and nearly
identical in size.

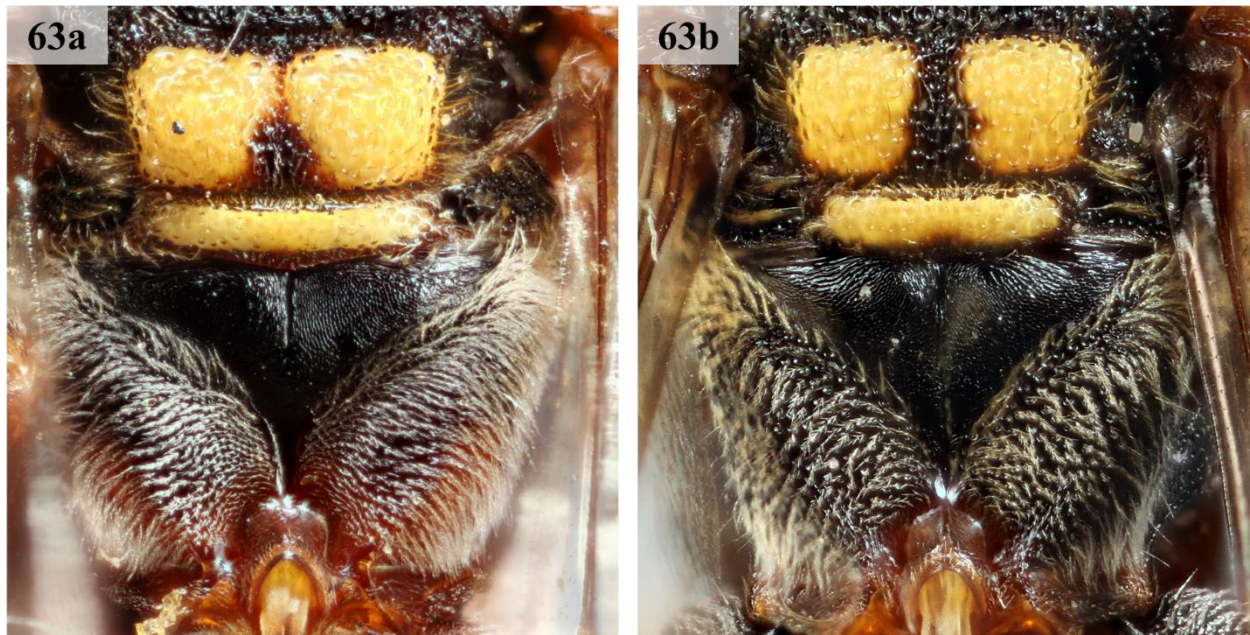


Figure 63. Propodeum in postero-dorsal view for a) *N. texana* and b) *N. tiftonensis* to show differences in scutellum maculation shape. a) Scutellum maculations in *N. texana* nearly touch apically and metanotum wide while in b) *N. tiftonensis* maculations separated and metanotum short

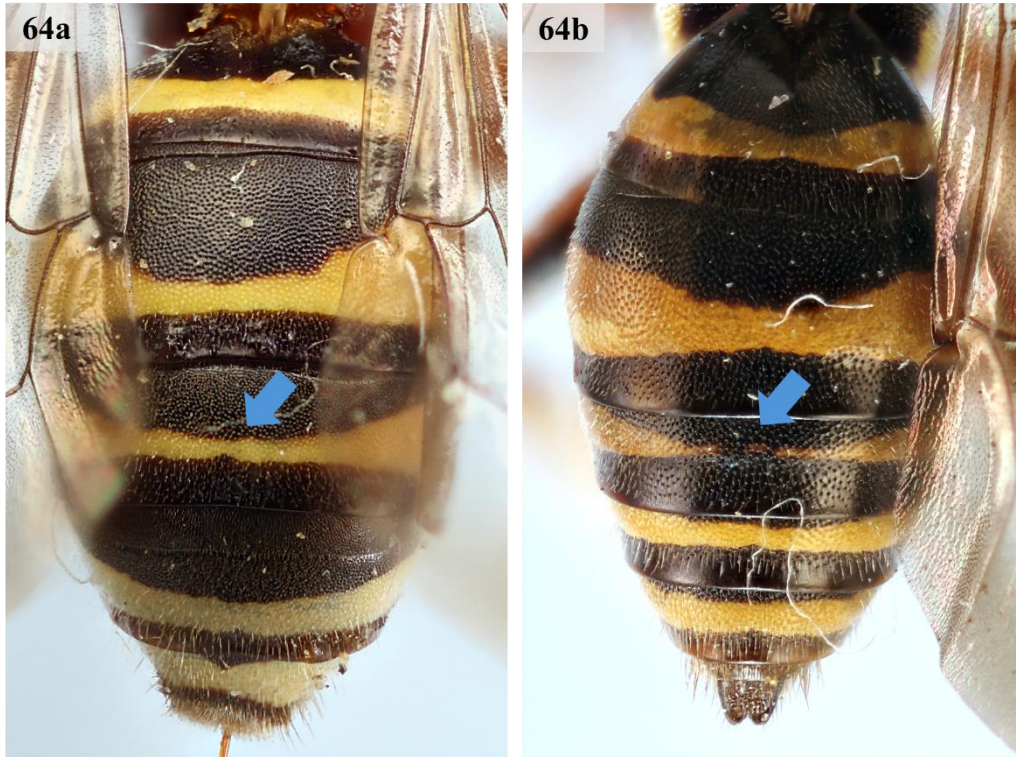


Figure 64. Metasoma, dorsal view, showing the a) absence (*N. texana*) or b) presence (*N. tiftonensis*) of a central break in the maculation on T3.



Figure 65. Metasoma sterna showing the a) presence (*N. texana*) or b) absence (*N. tiftonensis*) of maculations.

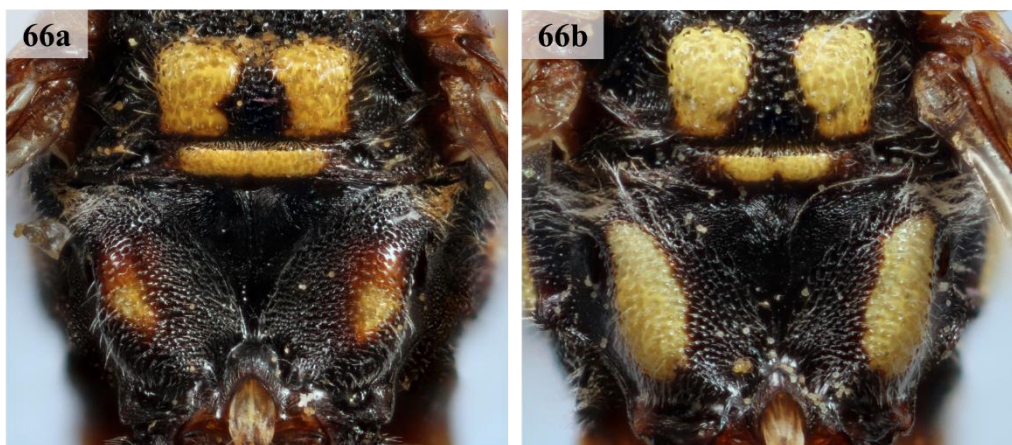


Figure 66. Postero-dorsal view of the posterior of the propodeum showing the variation in propodeal maculation size and colour in *N. vegana*: a) small yellow and red maculations; b) large yellow maculations with no red. The more common form in both males and females is displayed in (b).



Figure 67. Metasoma of female *N. vegana* (that of the male has the same colour pattern).



Figure 68. Lateral images of *N. articulata* a) female and b) male.



Figure 69. Lateral images of *N. australis* a) female and b) male.



Figure 70. Lateral images of *N. erigeronis* a) female dark form, b) female red form and c) the male.

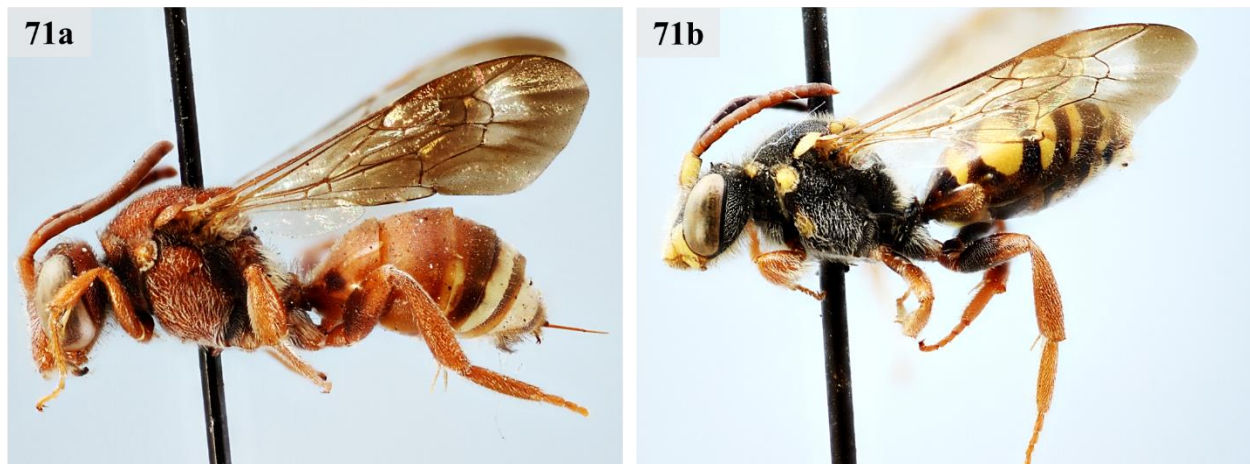


Figure 71. Lateral images of *N. rubicunda* a) female and b) male.



Figure 72. Lateral images of *N. seneciophila* a) female where arrows denote relatively obscure maculations and b) male where metasomal maculations are obscured by the wings. See Fig. 92b for a clear image.

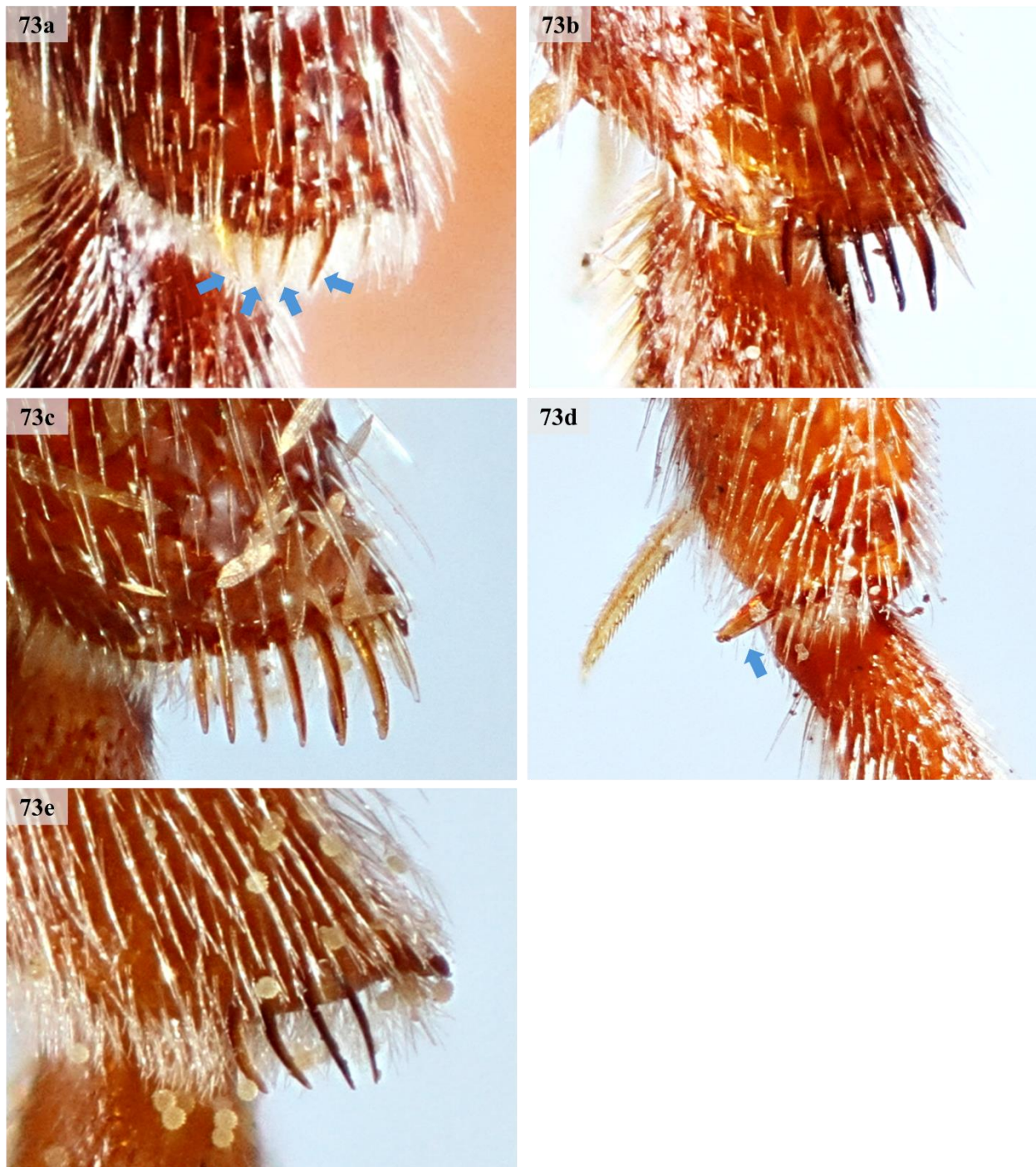


Figure 73. Apical metatibial spines of female of each member of the *N. erigeronis* species group: a) *N. articulata*, b) *N. australis*, c) *N. erigeronis*, d) *N. rubicunda*, and e) *N. seneciophila*.



Figure 74. Flagellum of males showing the spines on F3-F9. a) *N. articulata*: F3 spine only, b) *N. australis*: F4-F6 paired spines with those of F4 most similar to those of F3 and those of F4-F5 more rounded, c) *N. erigeronis*: F3 spine only, d) *N. rubicunda*: F3 spine rounded (insert), not sharply and conically pointed like others, F4-F5 with small bumps, e) *N. seneciophila*: F4-F9 with paired spines similar to those of F3.

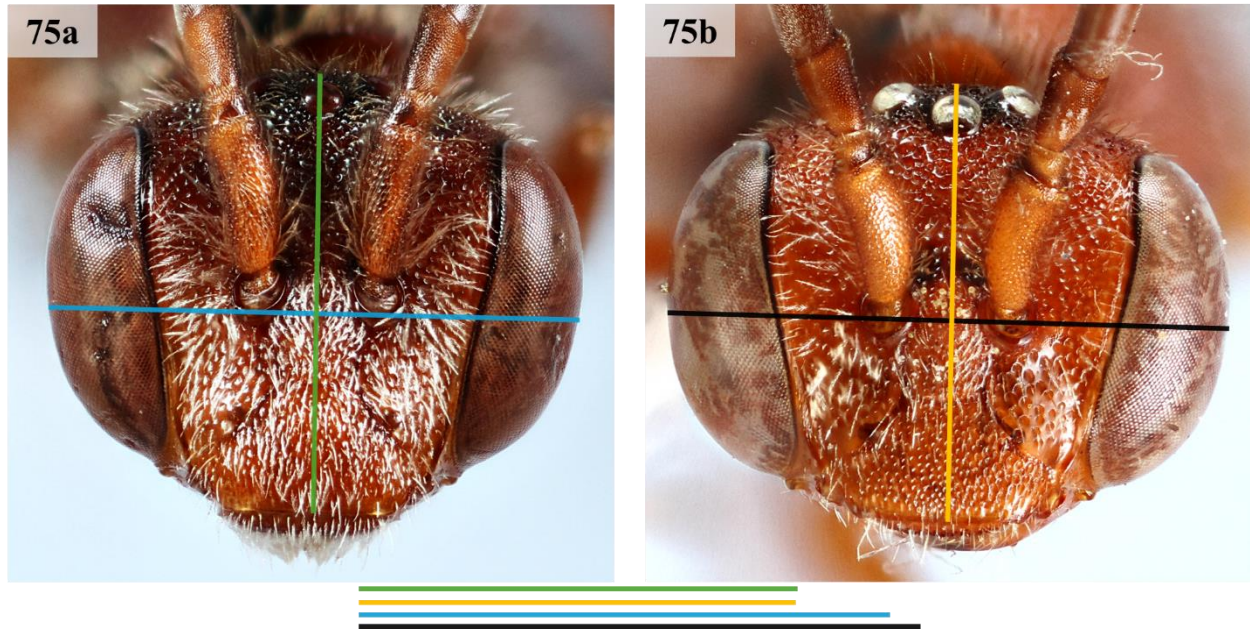


Figure 75. Diagram illustrating the comparative differences in width and length of the head in a) *N. articulata* and b) *N. australis*. Overall, *N. articulata* has a narrower head in comparison to the head of *N. australis*.



Figure 76. Dorsal view of *N. articulata* thorax illustrating the inter- and intrasexual variation in colour: a) females are always primarily red; b, c) male red on the mesoscutum varies from b) nearly none to c) extensively red.



Figure 77. Posterior half of mesosoma, postero-dorsal view of *N. articulata* illustrating inter- and intrasexual variation in the amount of red on the propodeal triangle: a) female and b, c) male: a) female completely red, b) male partly red to c) completely black.



Figure 78. Metasoma of a) female and b, c) male *N. articulata* illustrating the variation in colour; a) female always red with no maculations, b, c) males vary in colour from b) darker to c) more red, and both distinctly maculated.



Figure 79. Dorsal view of the thorax for a) female and b) male *N. australis*; a) female mesoscutum always red but the black median stripe varies from nearly absent (here) or as in Fig. 76a; b) male mesoscutum always black, in contrast to many males of *N. articulata*.



Figure 80. Mesoma posterior half in postero-dorsal view to show variation in colour of *N. australis*; a) female scutellum, propodeum, and metanotum will always be red, males vary with b) ornamented individuals having red on scutellum and metanotum to c) males with scutellum and metanotum completely black.



Figure 81. Metasoma of a) female and b, c) male *N. australis* illustrating the variation in colour and size of the maculations. a) females always have a completely red metasoma; males range from b) red to c) mostly blackish. T1 maculation for males can be b) present or c) absent and T3-T6 tergal bands can be b) complete or c) medially interrupted



Figure 82. Face of male *N. erigeronis* illustrating the swollen scape and indetectably recessed pedicel.



Figure 83. Dorsal view of the thorax showing colour variation in the mesoscutum of a, b) female and c) male individuals. Female mesoscutum commonly a) black or black with red laterally however, b) individuals in the western and southwestern part of its range will be nearly all red, c) male mesoscutum always black.



Figure 84. Postero-dorsal view of the scutellum, metanotum, and propodeum demonstrating the variation in colour found in *N. erigeronis* a, b) female and c) male individuals. Females in a) the eastern part of the range will have propodeum completely black while those found in the b) southwest and west will have propodeum completely or near completely red, c) males have propodeum completely black.



Figure 85. Metasoma of a, b) female and c) male *N. erigeronis* illustrating variation in colour. a, c) metasoma with black integument is more common in females and ubiquitous in males however, b) metasoma with red integument is more common in females in the west and southwest.

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Figure 86. Metasoma sterna displaying the characteristic coarse, deep punctures found throughout the body, depressed rims, and elevated discs for males and females of *N. erigeronis*.

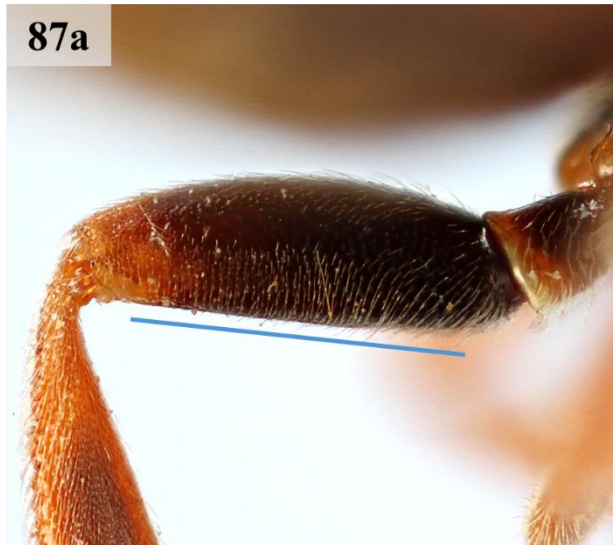


Figure 87. Male hind femur showing the a) straight edge characteristic of *N. rubicunda* and the b) curved edge found in all other members of the *N. erigeronis* species group.



Figure 88. Postero-dorsal view of the scutellum, metanotum, and propodeum of a) female and b) male *N. rubicunda* to show the difference in colour.



Figure 89. Metasoma of *N. rubicunda*: a) female, T3-T5 with distinctive ivory bands, b) male with yellow bands.



Figure 90. Dorsal view of the thorax for a) female and b) male *N. seneciophila* to show difference in colour



Figure 91. Postero-dorsal view of the scutellum, metanotum, and propodeal triangle for *N. seneciophila*. a) Female showing the extensive red including two spots on the propodeal triangle and b) male all black scutellum and propodeal triangle, but red-marked metanotum.



Figure 92. Metasoma of *N. seneciophila* dorsal views: a) female with pale markings on T2-T5. Note that T3 has faded paired yellow maculations (arrow) that may resemble those found on T1 for females of *N. erigeronis* T1 (Fig. 85a) and T4 also has maculations that require a lateral view Fig. 72a; b) male showing more extensive maculations.

Appendix

Table S1: All the specimens used in this project for DNA barcoding and morphological examination. Specimens with SRR numbers were taken from Chapter 2 (Table S2) and specimens that have BLX numbers but no SRR numbers are specimens used in a project that is currently in progress. Identifications were made by and checked by me, with the exception for some specimens taken from Chapter 2. Specimen identifiers for these individuals are listed in Table S2. Specimens with BOLD numbers that have a (*) are included in the tree in Supp. Fig.1. Specimens that have BOLD numbers but no (*) could not be included into the tree because they were not barcode compliant.

Code	Country	State	Co	Location	Sex	Species	Species group	Author	Year	Collector	Date	Notes	BLX #	BOLD	Accession number
ANHM	USA	NY	Lewis	Natural Bridge	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	E.L. Quinter	14-Jul-90	14-16-July-1990	BLX2900		
ANHM	USA	NJ	Warren	Hackettstown	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854		20-May-10		BLX2899		
CLEM	USA	SC	Florence	Florence	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	O. L. Cartwright	25-May-30		BLX_2908	KONoProj_307	
FMNH	USA	IL	Cook	Palos	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Pearson	20-Jun-21		BLX2915		
JBWM	CAN	Manitoba	Glenboro-South Cypress	Spruce Woods Provincial Park; Spirit Sands; trailhead	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Gibbs	9-Jun-19		BLX2929		
KU	USA	MA	Suffolk		m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Rykken	31-May-11	31-May-1-June, 2011; 9118			
KU	USA	NY	Ulster	Olivera	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	N. Dietrich	8-Jun-34	paratype for australis; included note says may be colour variant of articulata rather than true australis; agree with assessment as the antenna flagellomeres do not match that of true australis, cannot examine abdomen because it is missing			
KU	USA	MI	Lapeer	13 mi N. Lapeer	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	C. Sabrosky	30-May-37				
KU	USA	NY	Seneca	Junius Ponds 6 mi NW of Waterloo	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854		18-May-86				
LACM	USA	GA	Liberty	St. Catherine's Island	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	GC Eickwort	21-Apr-78			KONoProj_301	
LACM	USA	NJ	Bergen	Englewood	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	Jerry Rozen	1-Jul-82			KONoProj_302	

LACM	USA	ND	Ransom	1 mi SE McLeod	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	JR Powers	23-Jun-61			KONoProj_303
LACM	USA	MO	St. Charles		m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Johnson	23-May-77			KONoProj_304
LACM	USA	GA	Liberty	St. Catherine's Island	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	A Hook, J Krispyn	21-Apr-78			KONoProj_309
LACM	USA	GA	Richmond	Ft. Gordon	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	RR Snelling	4/220/1958			KONoProj_311
MM	USA	OH	College Comer	8959 Jones Rd	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	Michael Minnick	10-Jun-15	pan trap, forest/corn/ag edge	BLX2926	KONoProj_134
MM	USA	OH	College Comer	8959 Jones Rd	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	Michael Minnick	11-May-15	Vane trap, forest/soy/ag edge		KONoProj_158
MNSC	USA	MN	Otter tail	Maplewood State Park	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	D. Drons	12-Jun-18			KONoProj_136
MNSC	USA	MN	Swift	Clair Rollings WMA	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	A. Fulton, K. Jokela	17-18-Jun- 2015	pan trap		KONoProj_138
MNSC	USA	MN	Sibley	Indian Lake WVA	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	K. Jokela	25-Jun-15	Cirsium arvense		KONoProj_139
MSU	USA	MI	Ottawa	Mame, 2 km S	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Brokaw	4-Jun-15	trt:OP extra, Leucanthemum vulgare		KONoProj_132
MSU	USA	MI	Van Buren	Grand Junction, 1 km S	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Brokaw	5-Jun-17	trt:OP extra, Coreopsis lanceolata		KONoProj_133
MSU	USA	MI	Allegan	3mi WSW Fennville	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	J. Tuell et al.	12-Jun-06			KONoProj_155
MV	USA	CT	Hartford	South Windsor Forest	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	M.F. Veit	29-May-17			KONoProj_146
MV	USA	MA	Bamstable	Mashpee Preserve	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	M.F. Veit	14-Jun-14		BLX_1437	SRR18055099
PCYU	CAN	ON	Essex	Point Pelee National Park, Maintenance Camp	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	S. Fotheringham	15-16-Jun- 2009			KONoProj_152*
PSU	USA	PA	Centre	Harmer Orchard; standard apple	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	D.J. Biddinger	13-Jun-08	Apple orchard; yellow pan trap		KONoProj_147
PSU	USA	PA	Adams	Rouzer FREC Pollinator Small Plot	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	D.J. Biddinger	31-May-18	May 31 - June 7, 2018; NRCS pollinator strip; blue vane trap 1		KONoProj_148
PSU	USA	PA	Adams	3 mi nw York Springs; Lerew Orch. Town Hill	m	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	D.J. Biddinger	11-May-17	May 11-18, 2017; tart cherry; blue vane trap 3	BLX 2913	
RLUG	CAN	ON	Northumberland	NCC-Webber Natue Reserve	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	M. Matkowski, K. Verboom	8-Jun-17	yellow pan trap		
RLYU	USA	NH	Strafford		f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854		30-Jun-15	pan		KONoProj_137
TAMU	USA	SC	Lexington	Pelion	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	W.F. Chamberlain	4-May-50			KONoProj_305
TAMU	USA	TX	Dimmit	Chaparral W.M.A	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T. Friedlander	15-Mar-77	March 15-16, 1977		KONoProj_308
TO	USA	CO	Jefferson	Westminister, W Big Dry Creek	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	18-Jun-17			KONoProj_144
TO	USA	CO	Denver	Denver Zoo	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	S. Tessier	17-Jun-17			KONoProj_145

TO	CAN	QC		CMN (Natural Heritage Campus) Gatineau	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	26-Jun-18			KONoProj_150*
TO	CAN	ON		Ottawa, 2155 Carolodd Dr, Ottawa	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	21-Jun-20	net		KONoProj_151
TO	CAN	SK		North Bitter Lake, Tumstall (stabilizing dune)	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	16-Jun-19	yellow pans		KONoProj_153
TO	CAN	SK		7.6 km NNW Webb (active dune)	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	1-Jun-19	yellow pans		KONoProj_154*
TO	CAN	ON		Ottawa (field near Moodie station)	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	4-Jun-20			KONoProj_159
TO	CAN	AB		11.8 km SSW Empress (stabilizing dune)	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	11-Jun-19	yellow pans	BLX2874	
UCAL	CAN	AB	Pincher Creek	MD of Pincher Creek	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	M. Evans	2-Jul-09	Pan trap		KONoProj_135*
UCAL	CAN	AB	Pincher Creek	MD of Pincher Creek	f	<i>articulata</i>	<i>erigeronis</i>	Smith	1854	M. Evans	24-Jun-09	Pan trap		KONoProj_281*
KU	USA	FL	Lake	Ocala National Forest Alexander Spring Camp	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	G. C. Eickwort	31-Mar-74			
KU	USA	AR	Scott	Boles	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	R. H. Beamer	27-May-50			
KU	USA	NJ	Atlantic	1 mi N of junction 561+563 Immanuel	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	R. C. Miller	14-Jun-75	3B		
LACM	USA	GA	Richmond	Ft. Gordon	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	RR Snelling	26-Apr-59	paratype		KONoProj_321
LACM	USA	MD	Prince George	Bowie	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	RR Snelling	26-May-68			KONoProj_322
MM	USA	IN	Cedar Grove	3128 Sparks Rd	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	Michael Minnick	22-May-15	pan traps, forest/soy ag edge		KONoProj_166
MNSC	USA	MN	Lake of the Woods	Norris Camp	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	G. Nordquist A. Maleski	16-17-Jun-2015	pan trap		KONoProj_163*
MSU	USA	MI	Eaton	Pottersville, Thomapple River at Pinch Highway	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	T.J. Wood	3-Jun-18			KONoProj_162*
MSU	USA	MI	Oakland	Bald Mountain Rec Area, East Graham Lake	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	T.J. Wood	24-May-18			KONoProj_164*
MSU	USA	MI	Macomb	Washington Inwood Hiking trails	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	T.J. Wood	24-May-18			KONoProj_165*
MSU	USA	MI	Benzie	Pere Marquette State Forest, S of Grass Lake	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	T.J. Wood	27-May-18			KONoProj_167
MSU	USA	MI	Washentaw	Sharonville SGA: east unit	f	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	T.J. Wood	17-Jun-17		BLX_1439	SRR18055098
MV	USA	MA	Middlesex	Groton, Groton Town	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	M.F. Veit	17-May-14			KONoProj_160*

PSU	USA	PA	Adams	Rouzer FREC	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	D.J. Biddinger	24-May-16	Net collected; buttercup;	KONoProj_157
PSU	USA	PA	Adams	E. Divley; Standard Apple	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	D.J. Biddinger	3-Jun-08	Ranunculus sp. blue pan trap; apple orchard	KONoProj_168*
RLUG	CAN	ON	Peterborough	NCC-Webber Nature Reserve	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	S. Dunlop, G. Landon	11-Jun-19	white pan trap	
RLYU	USA	NH	Carroll	Conway	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962		27-Jun-15		KONoProj_161
UCON	USA	CT	New Haven	CAES Campus	f	<i>australis</i>	<i>erigeronis</i>	Smith	1854	T. Zamillo	31-May-10	pan trap; 31-May-3-Jun-2010	KONoProj_140*
UCON	USA	CT	Middlesex	Stewart B. McKinney NWR	m	<i>australis</i>	<i>erigeronis</i>	Mitchell	1962	K. Vagos	12-25-May-2014	pan trap	KONoProj_261*
ISU	USA	IA	Greene	Peckum	m	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897	M. Mackert	2-Jul-18		
KU	USA	AR	Izard		f	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897		14-Jun-14	4	
KU	USA	ND	Slope	Mammoth	f	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897	O. A. Stevens	4-Jul-18	11515; <i>Brauneria pallida</i>	
KU	USA	TX	Dallam, Hartley	Dalhart	m	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897	R. H. Beamer	8-Jun-50		
KU	USA	TX	Dallam, Hartley	Dalhart	m	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897	R. H. Beamer	8-Jun-50		
KU	USA	MT			m	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897				
LACM	USA	IL	Macoupin	Carlinville	f	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897	Charles Robertson			
MSU	USA	MI	Ottawa	Mame, 2 km S	m	<i>erigeronis</i>	<i>erigeronis</i>	Robertson	1897	J. Brokaw	2-Jul-15	<i>Rudbeckia hirta</i>	BLX_1436
KU	USA	SC	Beaufort	Parris Island	f	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	J. F. Reinert	2-Apr-81	2-9 April 1981	
KU	USA	NC	Dare	Kill Devil Hills	f	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	K. V. Krombein	2-Jun-48		
KU	USA	IN	Morgan	Miller	f	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	W. J. Gerhard	30-May-19		
KU	USA	GA	Richmond	Augusta	m	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	R. R. Snelling	6-Apr-59		
KU	USA	GA	Richmond	Augusta	m	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	R. R. Snelling	10-Apr-59		
MSU	USA	MI	Bary	Middleville SGA, Pamalee Rd	f	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	T.J. Wood	10-Jun-17		KONoProj_27*
MSU	USA	MI	Gladwin	Grim Hills, Grim Rd Cross x Center Fireline Rd	f	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	T.J. Wood	13-Jun-18		KONoProj_28*
MSU	USA	MI	Gladwin	Grim Hills, Grim Rd Cross x Center Fireline Rd	f	<i>rubicunda</i>	<i>erigeronis</i>	Olivier	1812	T.J. Wood	13-Jun-18		BLX_1438
LACM	USA	AL	Lee	Auburn	m	<i>seneciophilla</i>	<i>erigeronis</i>	Mitchell	1962	D. Jones	18-Apr-76	on Senecio	BLX_1435
KU	USA	NC	Buncombe	Swannanoa	f	<i>seneciophilla</i>	<i>erigeronis</i>	Mitchell	1962	J. C. Crawford	14-Jun-24	AC33827	
KU	USA	GA	Murray	Fort Mountain	f	<i>seneciophilla</i>	<i>erigeronis</i>	Mitchell	1962	P. W. Fattig	22-May-38		
KU	USA	NC	Wake	Raleigh	m	<i>seneciophilla</i>	<i>erigeronis</i>	Mitchell	1962	T. B. Mitchell	8-May-34	Rubus	
KU	USA	NC	Buncombe	Black Mountain	m	<i>seneciophilla</i>	<i>erigeronis</i>	Mitchell	1962	J. C. Crawford	28-Apr-27	A.C. 33827; <i>Fragaria virginiana</i>	
TAMU	USA	TX	Immit	Catarina	f	<i>sp.</i>	<i>erigeronis</i>	Smith	1854	A. Hook	28-Mar-87		KONoProj_310

TO	USA	CO	Denver	Denver Botanic Gardens	f	sp.	<i>erigeronis</i>	Smith	1854	T.M. Onuferko	15-Jun-17			KONoProj_143
UCAL	CAN	AB	Pincher Creek	MD of Pincher Crak	f	sp.	<i>erigeronis</i>	Smith	1854	M. Evans	2-Jul-09	Pan trap		KONoProj_280
GH	CAN	YT	Takhini	Klondike	f	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	G. Hutchings	3-Aug-11		BLX_1553	SRR18055175
JBWM	CAN	MB		Jordan	f	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	Martini M.	2-Aug-19	net		
JBWM	CAN	MB	West Lake-Gladstone	Westboume	f	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	J. Gibbs	22-Aug-08			
JBWM	CAN	MB		Jordan	f	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	Martini M.	2-Aug-19	net		
JBWM	CAN	MB		Saint Laurent BP4 7km NNE Saint Laurent	m	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	Martini M.	5-Aug-20	Solidago gigantea		
JBWM	CAN	MB		Saint Laurent BP4 7km NNE Saint Laurent	m	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	Martini M.	5-Aug-20	Solidago gigantea		
JBWM	CAN	MB		Saint Laurent BP4 7km NNE Saint Laurent	m	<i>aquilarum</i>	<i>roberjeotiana</i>	Cockerell	1903	Martini M.	5-Aug-20	Solidago gigantea		
FMNH	USA	IL	Cook	Matteson	m	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863	J. Pearson	18-Jul-31			
FSCA	USA	NC	Haywood	I-40 near Waterville Lake	m	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863	H.V. Weems Jr.	16-Oct-85			
JBWM	USA	MI	Van Buren	Almena, 4.5 km NNE	f	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863	J. Gibbs	3-Sep-14			
LACM	USA	NY	Tompkins		f	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863	R.A. Morse	16-Aug-60	Solidago sp		
LACM	USA	VA	Fairfax	Scott Run	f	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863	AS Menke & DR Miller	6-Sep-69			
MSU	USA	MI	Berrien	SWMREC SR1 Block 3	m	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863		1-Sep-15			KONoProj_49
MSU	USA	MI	Berrien	SWMREC	m	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1872	SARE	21-Aug-15	Oligoneuron rigidum		KONoProj_81*
MSU	USA	MI	Berrien	SWMREC SR2 Block 1	m	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863		27-Aug-15		BLX_1464	SRR18055120
TO	CAN	ON		Bruce Pitt Dog Park (Ottawa)	f	<i>placida</i>	<i>roberjeotiana</i>	Cresson	1863	T. M. Onuferko	9-Aug-21	Euthamia graminifolia		
MM	USA	OH	Hamilton	4328-4496 Trenton Oxford Rd	f	<i>articulata</i>	<i>ruficornis</i>	Smith	1854	Michael Minnick	12-May-15	pan traps, forest/soy ag edge	BLX2927	KONoProj_156*
CLEM	USA	SC	Pickens	Clemson College	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878	E. C. Murdoch	18-May-28			
FSCA	USA	FL	Wakulla	Wakulla Springs	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878	G.B. Fairchild	30-Apr-82			
LACM	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878		15-May-37			KONoProj_288
LACM	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	5-Apr-29			KONoProj_289
LACM	USA	GA	Paulding	Dallas	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	P.W. Fattig	7-May-52			KONoProj_290
LACM	USA	GA	Richmond	Augusta	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	W.H. Cross	9-May-53			KONoProj_291
LACM	USA	TN	Union	9 mi SE La Follette	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	B.L. Freeman	7-Jun-73			KONoProj_292

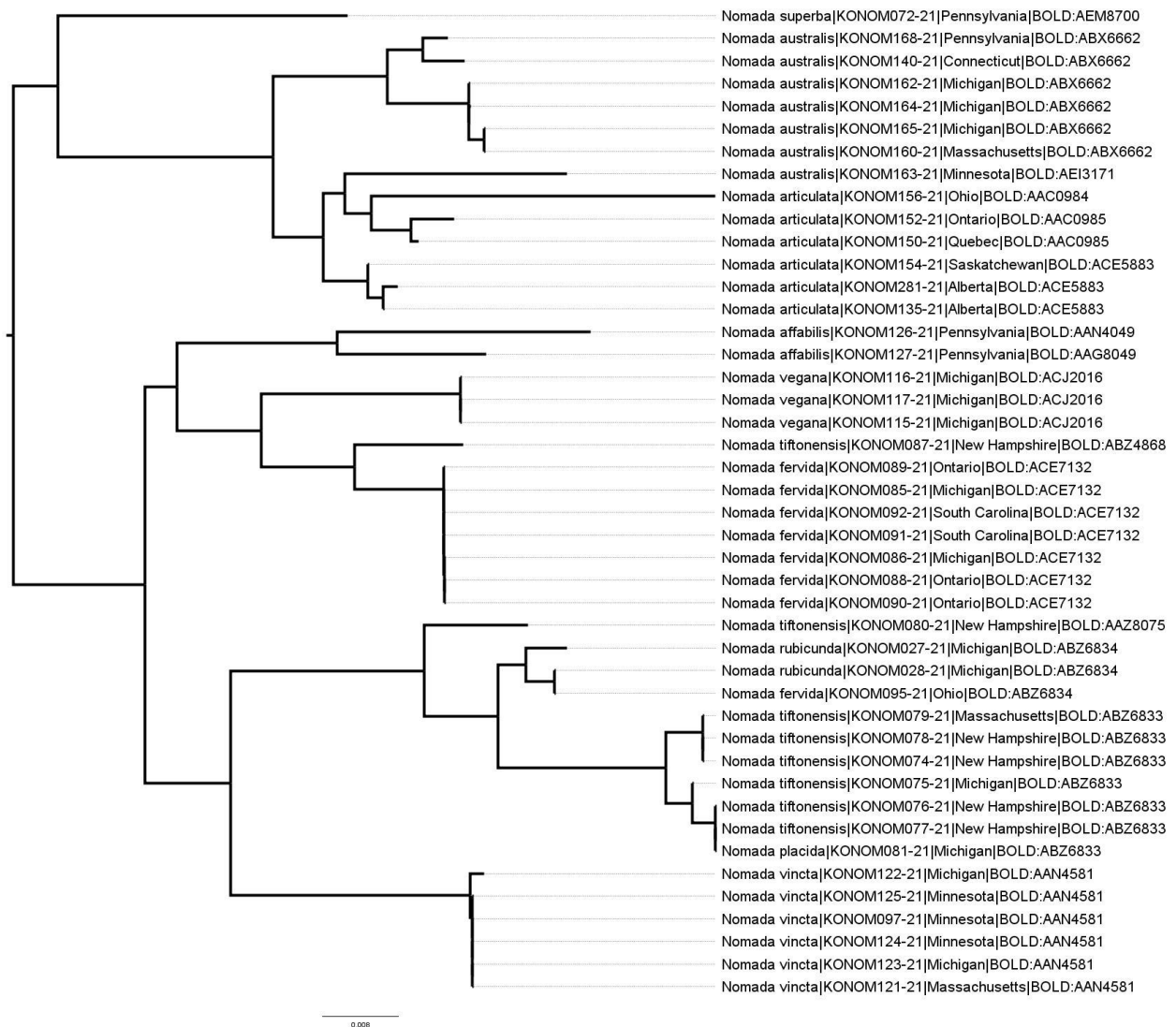
LACM	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T. D. Mitchell	9-May-38		
LACM	USA	GA	Bartow; Polk	Taylorsville	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878	P. W. Fattig	30-Apr-39		
MM	USA	IN	Cedar Grove	9104 Lohrey Rd	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	Michael Minnick	2-Jun-15	BLX_1491	SRR18055199
MM	USA	IN	Cedar Grove	9104 Lohrey Rd	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	Michael Minnick	2-Jun-15	BLX_1492	
NCSU	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	15-May-61		
NCSU	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	30-Apr-61		
NCSU	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878		10-May-41		
NCSU	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	C.S. Brimley	17-May-32		
NCSU	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	26-May-51		
NCSU	USA	NC	Wake	Raleigh	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	22-Apr-54		
NCSU	USA	NC	Wake	Raleigh	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	5-May-34	Rubus	
NCSU	USA	NC	Wake	Raleigh	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878		26-Apr-42		
NCSU	USA	NC	Wake	Raleigh	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878		1-May-30		
NCSU	USA	NC	Wake	Raleigh	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878	T.B. Mitchell	26-Apr-28		
PSU	USA	PA	Adams	Rouzer FREC	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	D.J. Biddinger	12-Jun-13	June 12-19, 2013; NRCS pollinator strip; blue vane trap 1	KONoProj_126*
PSU	USA	PA	Adams	.5 mi se Arendtsville	m	<i>affabilis</i>	<i>superba</i>	Cresson	1878	D.J. Biddinger	7-Jun-08	Catalpa blossom	KONoProj_127*
UGA	USA	GA	Clarke		f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	M. Tupper	19-May-40		
UGA	USA	GA	Clarke	Athens	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	M. Arden	10-May-41		
UGA	USA	GA	Clarke	Athens	f	<i>affabilis</i>	<i>superba</i>	Cresson	1878	W. Hightboy	20-Apr-47		
LACM	USA	TX	Dallas, Collin, Denton, Kaufman, Rockwall	Dallas	f	<i>affabilis dallasensis</i>	<i>superba</i>			J.C. Crawford	9-Apr-06	on dewberry	KONoProj_286
LACM	USA	TX	Dallas, Collin, Denton, Kaufman, Rockwall	Dallas	f	<i>affabilis dallasensis</i>	<i>superba</i>			J.C. Crawford	9-Apr-06	on dewberry	KONoProj_287
LACM	USA	TX	Dallas, Collin, Denton, Kaufman, Rockwall	Dallas	f	<i>affabilis dallasensis</i>	<i>superba</i>			J.C. Crawford	9-Apr-06	homotype, on dewberry	KONoProj_293
FSCA	USA	IL	Platt	Allerton Park	m	<i>superba</i>	<i>superba</i>	Cresson	1863	Lloyd R. Davis Jr.	19-May-73		
LACM	USA				f	<i>superba</i>	<i>superba</i>	Cresson	1863	Charles Robertson	1970		
MSU	USA	MI	Van Buren	Breedsville, 1 km SW	m	<i>superba</i>	<i>superba</i>	Cresson	1863	K. Mason	25-May-14		KONoProj_73
PSU	USA	PA	Adams	3 mi nw York Springs; Lerew Orch	m	<i>superba</i>	<i>superba</i>	Cresson	1863	D.J. Biddinger	5-May-16	May 5-12, 2016; tart cherry; Blue vane trap 5	KONoProj_72*
PSU	USA	PA	Adams	Town Hill 3 mi nw York Springs; Lerew Orch	m	<i>superba</i>	<i>superba</i>	Cresson	1863	D.J. Biddinger	12-May-16	May 12-19, 2017; tart cherry; Blue vane trap 2	BLX 2308
ROM	CAN	ON		Point Pelee National Park	m	<i>superba</i>	<i>superba</i>	Cresson	1863	NYLB	14-Jun-20		

CLEM	USA	SC	Charleston	Rosebank field WF, 3m	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	M. Jenkins	16-May-18	On Verbena sp.	KONoProj_90*
CLEM	USA	SC	Bamwell	EREC field WF, 95m	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	M. Jenkins	13-Jul-17	On Gaillardia pulchella	KONoProj_91*
CLEM	USA	SC	Bamwell	EREC field WF, 95m	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	M. Jenkins	23-Jun-17	On Cosmos sulfureus	KONoProj_92*
GIC	CAN	ON	Norfolk	Manestar Track, 6 km NNW St. Williams	f	<i>fervida</i>	<i>vegana</i>	Smith	1854	M. Buck	25-Jul-00	wisconsinensis	KONoProj_88*
GIC	CAN	ON	Kent	Rondeau P.P. group campground	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	M. Buck	11-Jul-05	wisconsinensis	KONoProj_89*
GIC	CAN	ON	Bruce	Inverhuron Provincial Park	f	<i>fervida</i>	<i>vegana</i>	Smith	1854	M. Buck	25-Jul-03	wisconsinensis; dunes	KONoProj_95*
HE	CAN	ON	Norfolk	Long Point NWA WPWC	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	Hadil Elsayed	15-Jun-22	malaise trap; 15 June-6 July, 2022	
HE	CAN	ON	Norfolk	Long Point NWA WPWC	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	Hadil Elsayed	15-Jun-22	malaise trap; 15 June-6 July, 2022	
MSU	USA	MI	Berrien	Grand Mere State Park	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	T.J. Wood	29-Jul-17		KONoProj_85*
MSU	USA	MI	Berrien	Grand Mere State Park	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	T.J. Wood	29-Jul-17		KONoProj_86*
MSU	USA	MI	Berrien		m	<i>fervida</i>	<i>vegana</i>	Smith	1854	T.J. Wood	29-Jul-17		BLX_1503 SRR18055105
NCSU	USA	OH	Erie	Lake Lab Cedar Point	f	<i>fervida</i>	<i>vegana</i>	Smith	1854		4-Jul-17	44	
NCSU	USA	NC	Swain	Bryson City	f	<i>fervida</i>	<i>vegana</i>	Smith	1854	T.B. Mitchell	28-Jul-22	Koelia	
NCSU	USA	NC	Buncombe	Swannanoa	f	<i>fervida</i>	<i>vegana</i>	Smith	1854	T.B. Mitchell	6-Sep-24	Helianthus outum	
NCSU	USA	NC	Swain	Bryson City	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	T.B. Mitchell	28-Jul-22	Koelia	
UCF	USA	FL	St. Johns	Crescent Beach	m	<i>fervida</i>	<i>vegana</i>	Smith	1854	H.G. Hall	5-Sep-10	Bidens alba	
ANHM	USA	AZ	Cochise	2 mi N of Portal	m	<i>texana</i>	<i>vegana</i>	Cresson	1872	J.S. Ascher, C. Dong	31-Aug-08		
CSU	USA	TX	Ward	Monahans Sandhills State Park	f	<i>texana</i>	<i>vegana</i>	Cresson	1872	H. E. Evans & W. Rubink	1-Jun-74	6/1-2/1974	
CSU	USA	TX	Ward	Monahans Sandhills State Park	f	<i>texana</i>	<i>vegana</i>	Cresson	1872	H. E. Evans & W. Rubink	1-Jun-74	6/1-2/1974	
CSU	USA	CO	Prowers	Carlton	m	<i>texana</i>	<i>vegana</i>	Cresson	1872	H. E. Evans & W. Rubink	6-Jun-74		
FSCA	USA	TX	Hidalgo	Bentsen R. Grande Valley State Park nr Mission	f	<i>texana</i>	<i>vegana</i>	Cresson	1872	C. Porter	1-Apr-86		
NCSU	USA	AL	Morgan	Decatur	f	<i>texana</i>	<i>vegana</i>	Cresson	1872	G.E. Bohart	Aug-44		
NCSU	USA	AL	Morgan	Decatur	m	<i>texana</i>	<i>vegana</i>	Cresson	1872	G.E. Bohart	1-Aug-44		
NCSU	USA	NC	Wake	Raleigh	m	<i>texana</i>	<i>vegana</i>	Cresson	1872		31-Jul-52		
NCSU	USA	NC	Wake	Raleigh	m	<i>texana</i>	<i>vegana</i>	Cresson	1872	C.S. Brimley	23-Jul-26		
NCSU	USA	MI	Muskegon		m	<i>texana</i>	<i>vegana</i>	Cresson	1872	R.R. Dreisbach	2-Aug-44		
TAMU	USA	TX	Dawson	20 miles west of Lamesa	f	<i>texana</i>	<i>vegana</i>	Cresson	1872	W.F. Chamberlain	26-May-97		BLX_1504 SRR18055130

TAMU	USA	TX	Hale	Cotton Center	m	<i>texana</i>	<i>vegana</i>	Cresson	1872	Henry Cobb	9-Aug-79	Compositae at 1400-1600		
ISU	USA	IA	Muscatine	Muscatine	f	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903	W.W. Darlington	15-Sep-42			
MSU	USA	MI	Kalamazoo	Au Sabo Land Preserve	m	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903	T.J. Wood	29-Jul-17			KONoProj_75*
MV	USA	MA	Middlesex	Groton, Groton Town	m	<i>tiftonensis</i>	<i>vegana</i>	Cresson	1872	M.F. Veit	14-Aug-16			KONoProj_79*
MV	USA	MA	Middlesex		f	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903	M.F. Veit	2-Sep-08		BLX_1501	SRR18055129
RLYU	USA	NH	Strafford		f	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903		7-Aug-14	pan		KONoProj_74*
RLYU	USA	NH	Strafford	Lee, Dairy	f	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903		22-Aug-16	pan		KONoProj_76*
RLYU	USA	NH	Strafford	Madbury, Kingman	m	<i>tiftonensis</i>	<i>vegana</i>	Cresson	1872		17-Aug-16	pan		KONoProj_77*
RLYU	USA	NH	Strafford		m	<i>tiftonensis</i>	<i>vegana</i>	Cresson	1872		20-Jul-16	pan		KONoProj_78*
RLYU	USA	NH	Strafford		m	<i>tiftonensis</i>	<i>vegana</i>	Cresson	1872		3-Aug-16	pan		KONoProj_80*
RLYU	USA	NH	Strafford		m	<i>tiftonensis</i>	<i>vegana</i>	Smith	1854		13-Aug-15	pan		KONoProj_87*
SH	USA	VT			m	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903	S. Hardy	24-Jul-20			
SH	USA	VT			m	<i>tiftonensis</i>	<i>vegana</i>	Cockerell	1903	S. Hardy	21-Jul-20			
CLEM	USA	SC	Bamwell	EREC field WF, 95m	f	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	M. Jenkins	29-Jun-17	On Citrullus lanatus		
CLEM	USA	SC	Bamwell	EREC field WF, 95m	f	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	M. Jenkins	29-Jun-17	On Citrullus lanatus		
CLEM	USA	SC	Bamwell	EREC field WF, 95m	f	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	M. Jenkins	29-Jun-17	On Citrullus lanatus		
CSU	USA	CO	Prowers	Carlton	m	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	H. E. Evans	6-Jun-74	on Tamarix		
CSU	USA	CO	Bent	Hasty	m	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	H. E. Evans	26-Jun-74	Malaise trap		
MSU	USA	MI	Lenawee		m	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	T.J. Wood	28-Jul-18			KONoProj_115*
MSU	USA	MI	Bemien		f	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	T.J. Wood	29-Jul-17			KONoProj_116*
MSU	USA	MI	Lenawee		f	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	T.J. Wood	8-Jul-18			KONoProj_117*
MSU	USA	MI	Monroe		f	<i>vegana</i>	<i>vegana</i>	Cockerell	1903	T.J. Wood	30-Jul-17		BLX_1502	SRR18055128
LACM	USA	NC	Swain	Bryson City	m	<i>graeenicheri</i>	<i>vincta</i>	Cockerell	1905		26-Aug-23	Helianthus sp	BLX_2272	
MSU	USA	MI	St. Clair	Algonac State Park	f	<i>graeenicheri</i>	<i>vincta</i>	Cockerell	1905	T.J. Wood	2-Sep-17		BLX_1475	SRR18055153
ANHM	USA	ND	Williams	Williston	m	<i>vincta</i>	<i>vincta</i>	Say	1837	O.A. Stevens	15-Aug-15	Grindelia squarosa		
FMNH	USA	IL	Cook	Palos	m	<i>vincta</i>	<i>vincta</i>	Say	1837	J. Pearson	30-Aug-31			
ISU	USA	IA	Woodbury, Plymouth	Sioux City	f	<i>vincta</i>	<i>vincta</i>	Say	1837	Jean Laffoon	3-Sep-56			
ISU	USA	IA	Guthrie	Cretsinger	m	<i>vincta</i>	<i>vincta</i>	Say	1837	M. Mackert	25-Aug-18			
LACM	USA	NE	Cuming	West Point	f	<i>vincta</i>	<i>vincta</i>	Say	1837		2-Sep-00			
LACM	USA	NE	Scotts Bluff	Mitchell	f	<i>vincta</i>	<i>vincta</i>	Say	1837	L. M. Gates	29-Jul-13			
MNSC	USA	MN	Big Stone	Rothi WPA	m	<i>vincta</i>	<i>vincta</i>	Say	1837	A. Fulton, K. Jokela	24-25-Aug-2015	pan trap		KONoProj_124*
MNSC	USA	MN	Lac Qui Parle	Bail Out WMA	m	<i>vincta</i>	<i>vincta</i>	Say	1837	A. Fulton, K. Jokela	24-25-Aug-2015	pan trap		KONoProj_125*

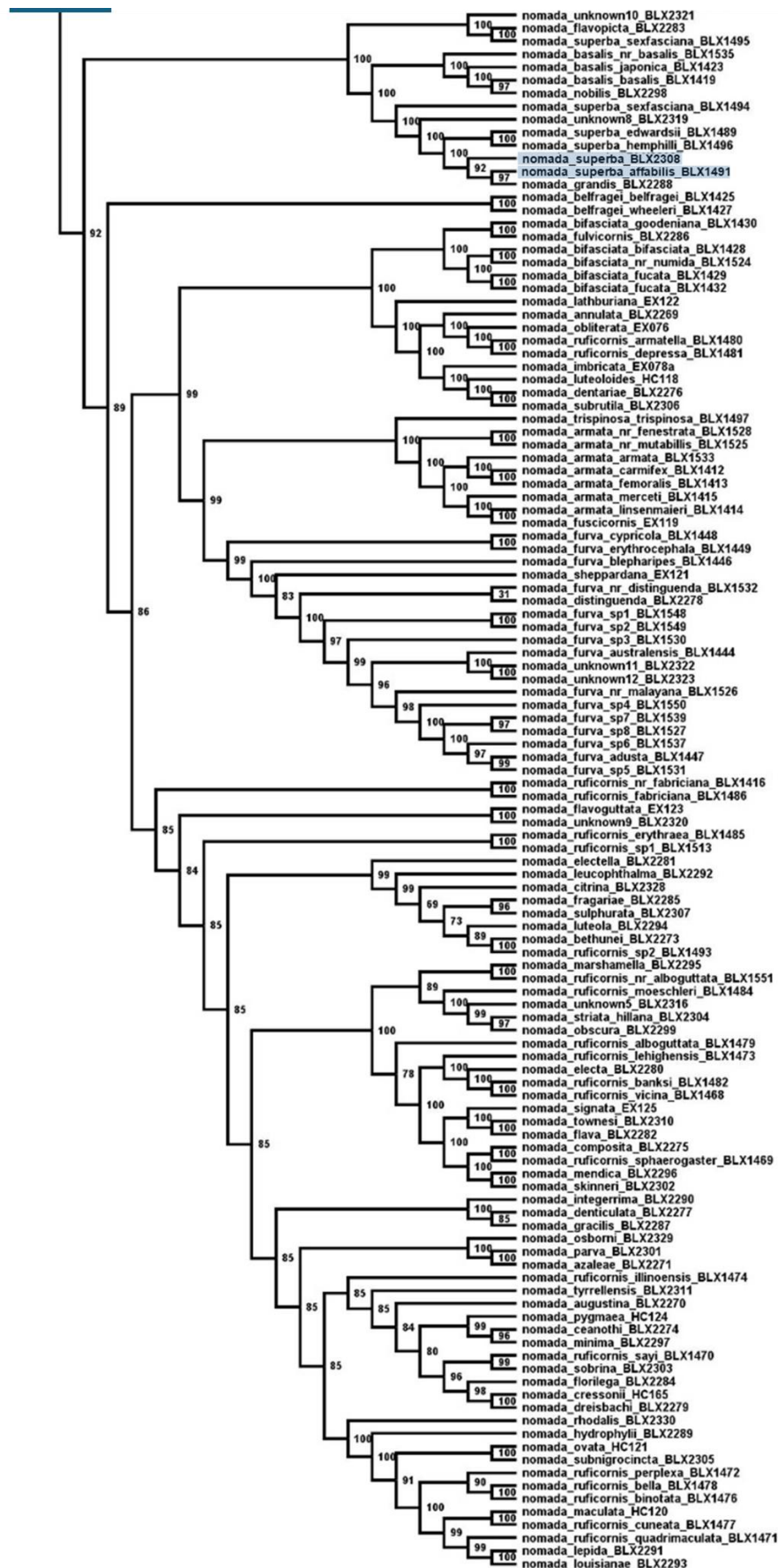
MNSC	USA	MN	Swift	Clair Rollings WMA	f	vineta	vineta	Say	1837	A. Fulton, K. Jokela	24-25-Aug-2015	pan trap	KONoProj_97*	
MNSC	USA	MN	Lac Qui Parle	Bail Out WMA	f	vineta	vineta	Say	1837	A. Fulton, K. Jokela	24-25-Aug-2015	pan trap	BLX_1515	SRR18055104
MSSU	USA	MS	Okitbbeh	Osborn	m	vineta	vineta	Say	1837	Beverly Smith	22-Oct-00	on Aster sp. in Black Belt Prairie		
MSU	USA	MI	St. Clair		f	vineta	vineta	Say	1837	T.J. Wood	2-Apr-17		KONoProj_122*	
MSU	USA	MI	St. Clair		m	vineta	vineta	Say	1837	T.J. Wood	2-Apr-17		KONoProj_123*	
MV	USA	MA	Franklin		m	vineta	vineta	Say	1837	M.F. Veit	24-Aug-16		KONoProj_121*	

Supp. Fig. 1: Neighbor joining tree using the BOLD aligner and the Kimura distance model for specimens that were barcode compliant. All five species groups and ten of the fifteen species are represented in the tree.



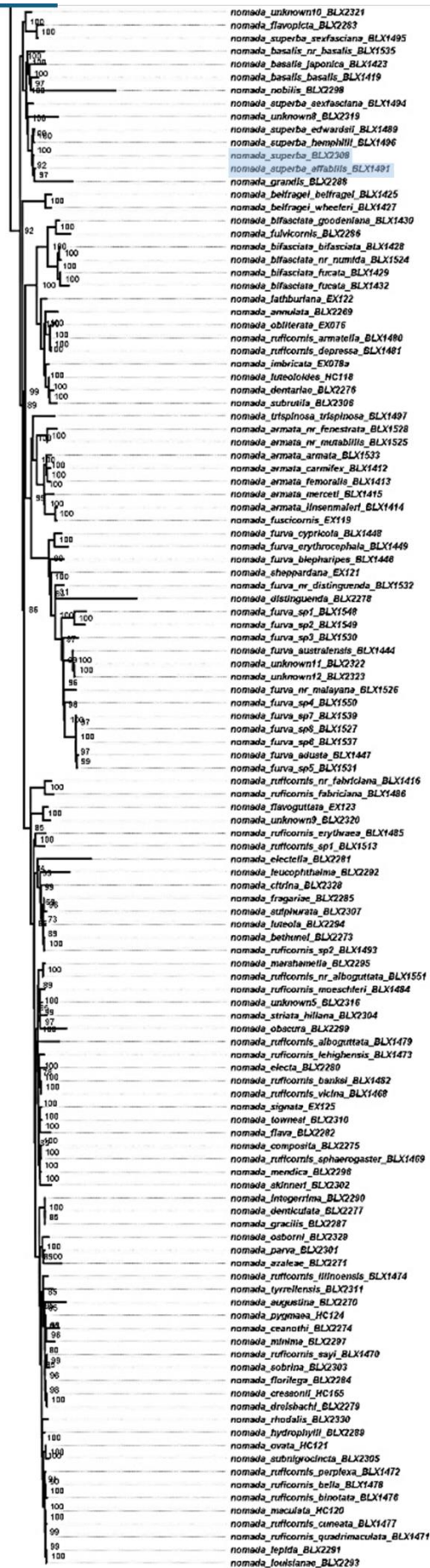
Supp Fig. 2: Updated UCE phylogram containing all species and species groups. Synonymized species are also included (*N. graenicheri* and *N. besseyi*, *N. arenicola* and *N. fervida*). The species addressed in this chapter are highlighted blue. These relationships were compared to the BOLD trees and morphological features to determine species delimitation.





Supp Fig. 3: Untransformed version of the phylogram in Supp. Fig. 2 showing branch lengths. Synonymized species are also included (*N. graenicheri* and *N. besseyi*, *N. arenicola* and *N. fervida*). The species addressed in this chapter are highlighted blue. These relationships were compared to the BOLD trees and morphological features to determine species delimitation.





Chapter 5 General Conclusion and Future Directions

Parasites perform many important ecosystem services such that if the parasites were lost from a given environment, there would be immense ecological consequences (Dobson et al., 2008; Hudson & Greenman, 1998; Hudson et al., 2006; Lafferty et al., 2008). Likewise, *Nomada* and other cleptoparasitic bees are ecologically important and occupy a unique space within bee communities, acting more as predators that contribute to population control (Minckley & Danforth, 2019) as well as be indicators of healthy bee communities (Odanaka & Rehan, 2019; Sheffield et al., 2013). Despite their ecological importance, there remains a dearth of knowledge surrounding *Nomada* and cleptoparasitic bee biology, evolution, and their population dynamics. This dissertation aims to fill these gaps by first documenting the global phylogeny and historical biogeography of *Nomada*; then determining the phylogeography of a widespread North American species; and lastly by producing updated taxonomic keys for the seven species groups of *Nomada* found in eastern North America and to species for five of these groups.

In Chapter 2, I provide the first global phylogeny and biogeography for the genus *Nomada*. Prior, *Nomada* was estimated to have an origin in the southern hemisphere (either South America (Michener, 1979) or South Africa (Alexander, 1991)) and that the genus then dispersed into the Northern Hemisphere and then back into the remaining continents in the Southern Hemisphere. Further, there was no molecular support for the 16 different species groups that *Nomada* species were placed in. This study found that *Nomada* emerged as a genus around 65 mya in the Holarctic region, however the first species group, *N. odontophora* (now the genus *Acanthonomada*), emerged in the eastern Mediterranean region. From there, *Nomada* dispersed into the Nearctic and then down into the Neotropics. In the Eastern hemisphere, *Nomada* dispersed from the Palaearctic into the Afrotropics, while at the same time dispersing into the eastern Palaearctic region, then into the Indomalayan region and lastly into Australasia. Additionally, 14 of the original 16 species groups were found to be monophyletic. The remaining two species groups (*N. superba* and *N. ruficornis* species groups) were found to be paraphyletic and one new species group was found. This work suggested that the *N. superba* and *N. basalis* species groups should be united thus rendering the group monophyletic. For the *N. ruficornis* species group, members were divided between a large clade and a smaller but distinct and separate clade that is sister to the *N. bifasciata* species group. By designating this smaller clade

as a new species group, the *N. ruficornis* species group is now rendered monophyletic. This study was foundational as it provided the very first global molecular phylogeny for *Nomada*, established a hypothesis for the origin of the genus and its biogeography, and provided molecular support for the different species groups that prior could only be determined by morphology.

In Chapter 3, I analyze the phylogeographic patterns and population genetic structure of the common eastern North American *Nomada* species *Nomada articulata*. Overall, it was found that *N. articulata* is most likely a species complex as our genetic results indicated that half our southern individuals fell outside of the main *N. articulata* clade. One important clade was comprised of three individuals that most likely represent a new species while another clade suggested either a range expansion of a single western species or a second entirely new species within the Southeast region of the United States. Additionally, the results suggest that during the last glacial period, *N. articulata* may have been divided along an east to west gradient into two different populations. However, as the landscape and climate changed over time, these separate populations dispersed towards each other and ultimately merged, thus creating a large panmictic population. This study was the first to characterize the phylogeography of a species of a cuckoo bee and to provide insights into how changes in landscape and climate influence the structure of cleptoparasitic bee populations over time.

In Chapter 4, using morphological characters and molecular support, I developed a new key to the seven species groups of *Nomada* in eastern North America (*N. erigeronis*, *N. oblitterata*, *N. roberjeotiana*, *N. ruficornis*, *N. superba*, *N. vegana* and *N. vincta* species groups) and new keys to identify the species of five of them (*N. erigeronis*, *N. roberjeotiana*, *N. superba*, *N. vegana*, and *N. vincta* species groups). The construction of new keys and descriptions provided the opportunity to amass the scattered knowledge regarding eastern North American *Nomada* and document it in one place. Newly updated information includes sequenced DNA data, updated phenologies, and confirmed host-parasite relationships. Furthermore, the keys are fully illustrated with photographs of each character important for *Nomada* identification to facilitate ease of identification. Molecular data supported only one synonymization, *Nomada besseyi* under the name *Nomada graenicheri*, which had been proposed earlier but needed more evidence to support the claim (Droege et al., 2010). *Nomada* identification has been challenging and of the existing identification keys for the genus, most are dated, difficult to use and

understand, and do not include new species or contain species names that have been synonymized (Mitchell, 1962; Schuh et al., 2010). These issues, in addition to the little morphological variation, but high colour variation within species make identification of *Nomada* in eastern North America incredibly challenging (Mitchell, 1962; Schuh et al., 2010). The results of this chapter provide essential keys that will aid in the identification of *Nomada* captured in eastern North America and new information pertaining to their biology and ecology.

Further research is needed to fully understand how *Nomada* diversified and became the most speciose of all the cleptoparasitic bee genera. The studies in this dissertation provide an initial examination of the ability of members of *Nomada* to globally disperse and endure changes in both climate and landscape over time, ultimately highlighting the adaptability of the genus. This opens the door for new studies delving more into the host-cleptoparasite relationship such as determining the extent and ability of *Nomada* to find and evade hosts and using genomics to further examine if cleptoparasitic bees, such as *N. articulata*, were able to avoid genetic pitfalls of being isolated during the Wisconsinan glaciation by following their hosts. Additional taxonomic studies are needed to address the two species groups that were not included in this dissertation and provide updated keys to species for them as well. Future taxonomic work should also include in depth examination of the type specimens that were not available for study. As more knowledge pertaining to cleptoparasitic bee biology, evolution, and ecology is obtained, these findings can be used in making more informed conservation decisions that benefit both cleptoparasitic and non-cleptoparasitic bees.

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Appendices

Appendix A: Permissions



Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements

Author: Katherine A. Odanaka, Michael G. Branstetter, Kerrigan B. Tobin, Sandra M. Rehan

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United States Department of Agriculture

Research, Education, and Economics
Agricultural Research Service

June 21, 2024

Department of Biology
York University
Toronto, ON

To Whom It May Concern:

I am writing to confirm that I am a co-author on the two articles listed below and that I give permission to Ph.D. candidate Katherine Odanaka to include these articles in her Ph.D. Dissertation. My name is Michael G. Branstetter, the date is June 21, 2024, and I am Research Entomologist with the USDA-ARS Pollinating Insects Research Unit. The articles are titled:

- (1) "Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements" and
- (2) "Support for the refugia within refugia hypothesis in a North American cleptoparasitic bee"

If you have any further questions or concerns, please feel free to contact me.

Sincerely,

Michael Branstetter

Michael G. Branstetter, Ph.D.
Research Entomologist
USDA-ARS Pollinating Insects Research Unit

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9 August 2024

To whom it may concern,

I am a co-author of both "Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements" and "Support for the refugia within refugia hypothesis in a North American cleptoparasitic bee".

I give my permission for these articles to be included in Katherine Odanaka's dissertation.

Sincerely,

Kerrigan Tobin

A handwritten signature in black ink, appearing to read 'KBT', with a stylized, wavy line extending from the end.

To whom it may concern,

This letter is to confirm that as a co-author of “Support for the refugia within refugia hypothesis in a North American cleptoparasitic bee”, I give permission for the article to be included in Katherine Odanaka’s dissertation.

Farida Samad-zada

June 25th, 2024