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THE EVOLUTION OF DIET BREADTH IN MELISSODES BEES (APIDAE: EUCERINI)

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THE EVOLUTION OF DIET BREADTH IN *MELISSODES* BEES (APIDAE: EUCERINI)

by

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DISSERTATION

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The evolution of diet breadth in *Melissodes* bees (Apidae: Eucerini)

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ABSTRACT

The relationship between phytophagous insects and their host plants has interested scientists since Darwinian times. Using modern phylogenetic inference, we are able to investigate these patterns using, not only the phylogenies of the insects, but the evolutionary relationships among the plants they feed on as well. The relationships between bees and the plants they pollinate were traditionally seen as mutualistic and were treated separately from the research investigating the antagonistic relationships between phytophagous insects and their host plants. However, recent phylogenetic studies have made great progress including bee-host relationships in with the larger body of work on phytophagous insects.

The genus *Melissodes* Latreille in the tribe Eucerini is a widespread and common group of bees. There are 129 described *Melissodes* species that range throughout the western hemisphere with the center of diversity in the warm

deserts of southwestern North America. Here, we present a species-level phylogeny using five loci for 89 species of *Melissodes*. We confirm all of the subgeneric delineations constructed by LaBerge, with the exception of *Heliomelissodes* which renders *Eumelissodes* paraphyletic, and we discuss the unexpected placement of a few taxa. We combine this analysis with previous data to support the placement of *Melissodes* within the tribe Eucerini and add a temporal component. We find a southwestern North American origin for the genus with a model that supports widespread sympatric speciation.

This work represents the first analysis to incorporate a taxon dense phylogeny of bees, molecular barcoding of pollen to identify host plants, and a host plant phylogeny to assess the evolution of diet breadth in bees. The use of molecular barcodes to discern host identities allowed a more detailed look into specialization of bees within the major clades of the super-diverse plant family, Asteraceae. Here we assess the value of using barcoding techniques for pollen identification and the merits of various ways of inferring ancestral diet breadth. We find, not one, but three general patterns of host plant evolution within a single genus of bees. Finally, we place our findings in the context of historical biogeography and current theory on the evolution of diet breadth.

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Abstract

The genus *Melissodes* Latreille in the tribe Eucerini is a widespread and common group of bees. There are 129 described *Melissodes* species that range throughout the western hemisphere with the center of diversity in the warm deserts of southwestern North America. Despite its widespread nature and importance in agriculture, the evolutionary relationships among the species have never been investigated. Here, we present a species-level phylogeny using five loci for 89 species of *Melissodes*. We confirm all of the subgeneric delineations constructed by LaBerge, with the exception of *Heliomelissodes* which renders *Eumelissodes* paraphyletic, and we discuss the unexpected placement of *M. tristis* Cockerell, *M. paucipuncta* LaBerge, *M. dagosus* Cockerell, and *M. pexa* LaBerge. We combine this analysis with previous data to support the placement of *Melissodes* within the tribe Eucerini and add a temporal component. We find a southwestern North American origin for the genus with a model that supports widespread sympatric speciation.

Fig. 1: Various species of *Melissodes.* Photos by J.S. Wilson

Introduction

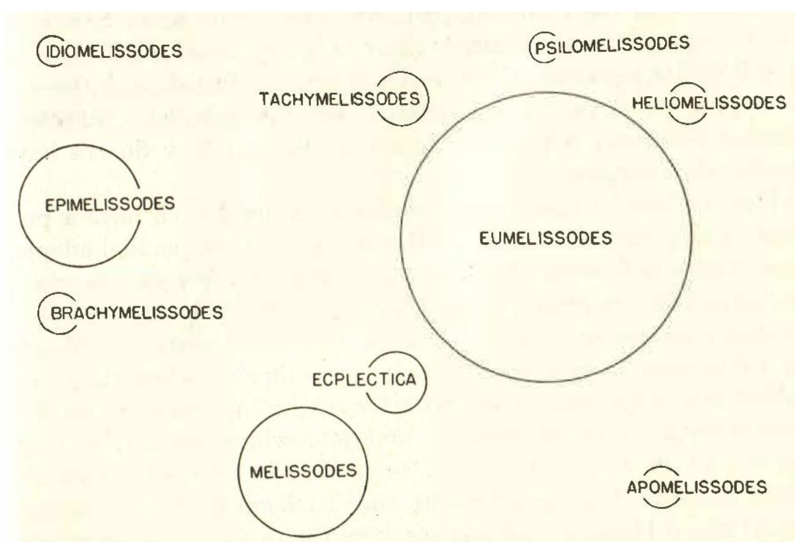
The genus *Melissodes* Latreille is a diverse genus of medium sized, setaceous bees in the tribe Eucerini (Apinae). The males of most species in the tribe have long antennae that typically reach past the metasoma (Michener, 2007), lending the tribe the common name of 'long-horned bees' (Fig. 1). *Melissodes* is the second largest genus in the tribe with 129 described species ranging from Canada to Argentina. Distinguishing features that separate *Melissodes* from the rest of the tribe include a narrow or concave apicolateral margin of the tegulae and simple mandibles. The males have an angular tooth on either side of the pygidial plate and the females have short hair obscuring the basitibial plate (Michener, 2007).

Melissodes are widespread and important pollinators in both natural and agricultural settings. They are either solitary or gregarious ground-nesters with most species emerging in mid- to late summer. They are mentioned as prominent pollinators of sunflower (Parker *et al.*, 1981), canola (Morandin & Winston, 2005), cantaloupe (Winfree *et al.*, 2007), watermelon (Kremen *et al.*, 2002), alfalfa

(LaBerge, 1956a), cotton (LaBerge, 1956a), coffee (Jha & Vandermeer, 2010), and anecdotally on many other crops. Many of the species are polylectic (pollinate plants in two or more families) while others are restricted to Asteraceae pollen hosts and a very few are oligolectic on other plant families (Wright, unpublished data). Asteraceae specialization may require physiological (Müller & Kuhlmann, 2008; Sedivy *et al.,* 2008; Sedivy *et al.,* 2011; Williams, 2003) and/or behavioral adaptations (Cane, 2017). Although *Melissodes* are prominent in many agricultural and ecological studies, they are rarely identified below the genus level because of the difficulty of identifying *Melissodes* to species. Many of the characters in the current keys refer to setal color or placement of apical hair bands, but color may be variable and setae can be missing in older specimens.

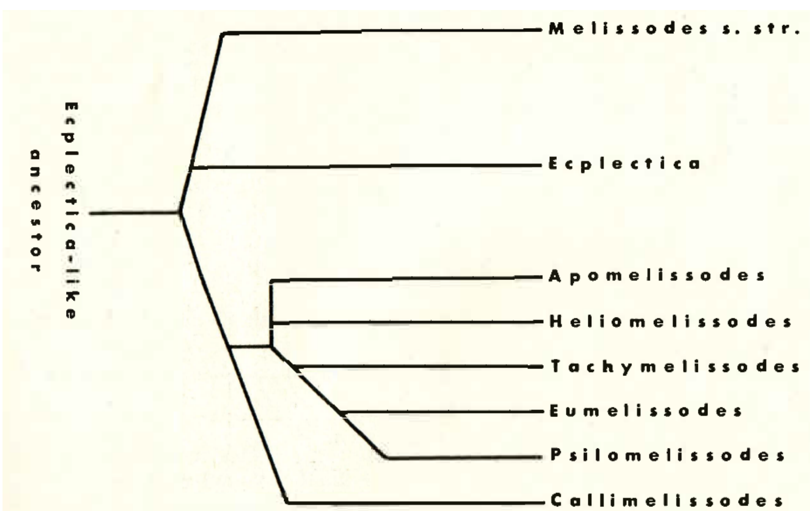
Wallace LaBerge revised this genus in a three publication series (LaBerge, 1956a; 1956b; 1961). In Part I, LaBerge recognized eleven subgenera, eight of which were newly described. Divisions among the subgenera were made largely according to male genitalic characters. He also recognized that the genus was probably polyphyletic and noted three subgenera, *Epimelissodes* Ashmead, *Brachymelissodes* LaBerge, and *Idiomelissodes* LaBerge, as being in a distinct group (Group 1). These three subgenera were subsequently placed in the genus *Svastra* Holmberg (LaBerge, 1957; Michener *et al.*, 1955; Moure & Michener, 1955). LaBerge is credited with the discovery of the synapomorphy that unites the current *Melissodes* and separates it from what is now called *Svastra*; this being the narrow or concave apical edge of the tegulae. The close relationship between *Melissodes* and *Svastra* has long been recognized and a study using modern molecular techniques found them to be sister taxa (Hedtke *et al.*, 2013). The other eight subgenera (Group 2) are currently recognized as constituting the genus *Melissodes.*

Fig. 2 Pre-Hennigean phyletic representation of the genus *Melissodes* from LaBerge (1956a). "FIG. 1. Diagrammatic representation of the relationships of the subgenera of *Melissodes* Latreille. The area of each circle indicates the approximate number of species in each subgenus, *Psilomelissodes* being unity. The distances between the perimeters of adjacent circles represent degree of relationship. The subgenera *Epimelissodes*, *Idiomelissodes* and *Brachymelissodes* form a distinct group and are not closely related to any one of the remaining subgenera."



In Part I, LaBerge (1956a) depicted the relationships of the subgenera in a diagram (Fig. 2). In LaBerge's estimation, *Ecplectica* Holmberg, the only South American subgenus of Group 2, is the basal group from which *Eumelissodes* LaBerge and *Melissodes* s.s. were derived and he hypothesized that *Apomelissodes* LaBerge, *Tachymelissodes* LaBerge, *Psilomelissodes* LaBerge, and *Heliomelissodes* LaBerge were all derived from the largest subgenus, *Eumelissodes*.

Fig. 3: Phyletic relationship of the subgenera of *Melissodes* based on 19 characters from LaBerge (1961). "FIG. 2. Dendogram showing the relationships of the subgenera of *Melissodes* Latreille. The lengths of the various lines are of no significance."

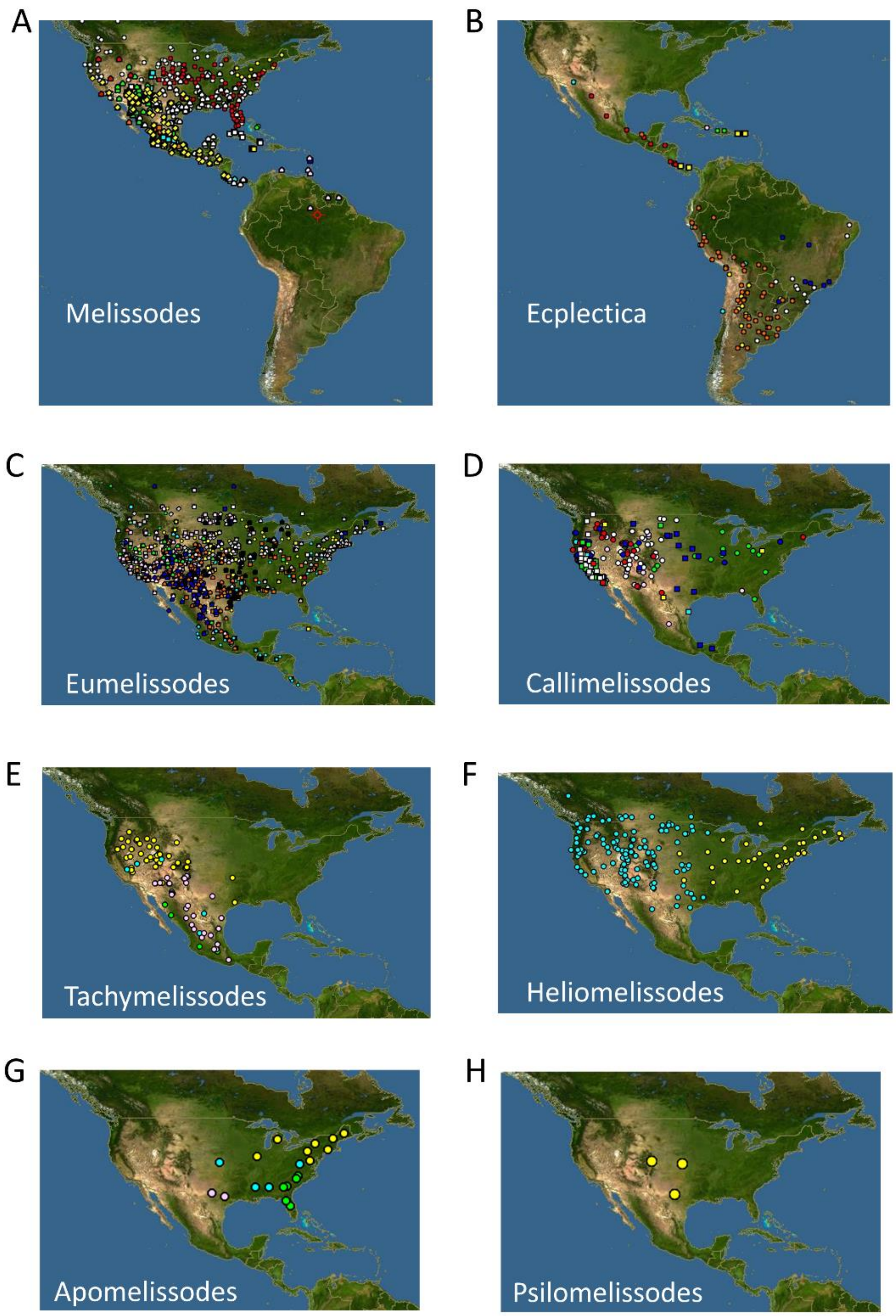


Subsequently, in Part III LaBerge (1961) added *Callimelissodes* and proposed a new phylogenetic hypothesis based on 'primitiveness' vs. 'specialization' of 19 morphological characters (Fig. 3). He proposed that while a *Eumelissodes*-like ancestor was possible, the shared specialized characters of the *Eumelissodes* group supports an *Ecplectica*-like ancestor with *Melissodes* s.s. derived from *Ecplectica* and the rest forming a separate clade. No further phylogenetic hypothesis has been proposed within this group to date.

While *Melissodes* ranges throughout North and South America, each subgenus has a more restricted distribution (Fig. 4). *Ecplectica* has only ten described species with five in South America, three in the Antillean islands, one species ranging from Panama north to Mexico, and no locality information found for the tenth species. *Melissodes* s.s. has 24 species mostly from southwestern North America (including Mexico), with only five species that occur further north or east, and six species that occur in the Antillean islands (one of which also occurs on the mainland of South America crossing into northern Brazil). *Tachymelissodes* has only four species. Three are in southwestern North America and one is more widespread throughout the western United States, north to Washington. *Callimelissodes*, with 14 species, has its center of diversity in the western United States with four species extending east of the Mississippi and two of these also extending south into Mexico. *Apomelissodes* has four species that occur in the eastern United States, with two as far west as Texas. *Heliomelissodes* consists of two species, both with large distributions in North America, one primarily east of the Mississippi and one west of it. *Psilomelissodes* is a monotypic subgenus that is restricted to Texas, Kansas and Nebraska. Finally, the largest subgenus, *Eumelissodes*, has 72 described species ranging from British Columbia to Maine and south to Cuba and Panama. Most of the diversity is in the western United States and Mexico with about one third of the species ranging further east, one fifth found further north into Canada, and only two species in Central America, and one in Cuba (Ascher & Pickering, 2017; Michener, 2007).

For the tribe Eucerini, Michener (2007) listed thirty-three genera with the acknowledgement that much work was needed to better circumscribe them. Two papers have investigated the relationships among many of the Eucerini genera (Cardinal & Danforth, 2013; Praz & Packer, 2014), including *Melissodes.* And most recently, the *Eucera* Scopoli complex has undergone a major reclassification based on molecular and morphological data, in which Dorchin *et al*. (2018a) have reassigned six previously recognized genera to subgeneric status in the genus *Eucera* and erected one new genus (Dorchin *et al.,* 2018b). This leaves the tribe Eucerini with 28 genera, *Eucera* being the largest and only cosmopolitan genus. There are three genera that occur only in the eastern hemisphere and the rest are in the western hemisphere. Of those, six genera span North and South America, fifteen are Neotropical, and only two genera are solely Nearctic. Even though relatively few genera occur in North America as compared to South America, the majority of species of the two largest genera, *Eucera* and *Melissodes*, are primarily Nearctic.

Fig. 4: Distribution maps of each currently recognized subgenus of *Melissodes*. Maps created in Discover Life (Ascher & Pickering, 2017)



The two primary objectives of this study are (i) to present the first molecular phylogeny of the genus *Melissodes* and test monophyly of the genus and subgenera and (ii) to understand the evolutionary relationships among these groups and contrast them with the groupings proposed by LaBerge (1956a, 1961). Based on the resulting phylogeny and divergence time estimates, we also propose a novel biogeographical hypothesis regarding the origin and diversification of *Melissodes*. This work will provide a framework for the future revision of the genus and a reference for studying the evolution of host plant specialization within this genus.

Materials and Methods

Taxon Sampling

Specimens were either borrowed from entomological collections (7 institutions), or collected by the first author (Appendix A). Our outgroup sampling included one species of *Exomalopsis* Spinola and one species of *Anthophorula* Cockerell in the tribe Exomalopsini. Within Eucerini, we included thirteen species of *Eucera* in five subgenera per Dorchin *et al.* (2018); two *Xenoglossa* Smith, three *Xenoglossodes* Ashmead, one *Peponapis* (Say), one *Syntrichalonia* LaBerge, and six *Synhalonia* Patton, as well as one species each of *Martinapis* Cockerell and *Florilegus* (Cresson), and five species of the sister genus *Svastra*.

The ingroup consisted of two of the four species of *Apomelissodes* (50%), twelve of fourteen species of *Callimelissodes* (86%), three of the ten recognized species of *Ecplectica* (30%) plus one undetermined species, 53 of the 72 described species of *Eumelissodes* (74%) plus four undetermined or undescribed species, both species of *Heliomelissodes* (100%), thirteen of 24 *Melissodes* s.s. (54%), the only species of *Psilomelissodes* (100%), and three of the four species of *Tachymelissodes* (75%). This provided a total of 89 of the 129 described species of *Melissodes* (69%) plus 5 undescribed or undetermined taxa. A complete list of taxa and institutions where vouchers were deposited is presented in Appendix A. All identifications were made or confirmed by the author using LaBerge's keys

(LaBerge, 1956a, 1956b, 1961) and reference material from the USDA-ARS Pollinating Insects Research Unit in Logan, UT and the American Museum of Natural History in New York, NY.

In addition, DNA sequences from 11 taxa that overlap the breadth of this analysis were acquired from GenBank. These data came from Cardinal & Danforth (2013) and included a complementary taxon from each of the outgroup taxa in Exomalopsini, as well as five taxa in Emphorini and Ancylini, three overlapping taxa within Eucerini, and a single sequence from within *Melissodes*. Because there are no fossils within *Melissodes*, these additional taxa along with the large number of outgroup taxa included by the authors were used to more strongly place *Melissodes* within the phylogeny as well as to provide an estimation of the age of these groups, since the Cardinal & Danforth (2013) analysis was calibrated with fossils.

We included some specimens that could not be confidently identified. To confirm that the unknown specimens were molecularly distinct, we ran a preliminary phylogenetic analysis using maximum likelihood. We compared the position of the unknown specimens to their sister species on the resulting phylogeny. For pairs with extremely short or no branch length separating them, we assumed that the unknown specimen was conspecific with its sister and removed it from the analysis. If the branch length separating them was long, comparable to the branch length between known species pairs on the tree, we assumed the specimen represented a distinct taxon and was left in the analysis. Most likely ‘nspwhite’, ‘mystery’, ‘affpersonatellus’ and ‘unk15’ represent undescribed species because they are morphologically distinct from the known species. ‘Ec_sp’ and ‘Unk11’ may be described species, but the author could not confirm the species identifications. Types of *Ecplectica* and a group of small morphologically similar *Eumelissodes* would have to be examined to confirm this, but revisionary work was deemed outside the scope of this study.

Character Sampling

DNA was extracted from a single mesothoracic leg using Qiagen DNeasy® Blood and Tissue Kits (Valencia, CA, USA) following the manufacturer’s protocol. Polymerase chain reactions (PCR) were performed using an Eppendorf Mastercycler ep gradient S Thermal Cycler® (Eppendorf, Hamburg, Germany) with TaKaRa Amplitaq™ (Applied Biosystems, Foster City, CA, USA). Various primers and temperature regimes were used to amplify five gene fragments including a fragment of mitochondrial DNA spanning cytochrome *c* oxidase I (791 bps), tRNA-Leucine (132 bps), and cytochrome *c* oxidase II (251 bps) and four nuclear gene fragments. The nuclear loci were RNA polymerase II (839 bps), arginine kinase (547 bps) with one intron (445 bps), the F2 copy of elongation factor 1-alpha (730 bps) with one intron (281 bps), and opsin (421 bps) with two introns (908 bps). See Appendix B for a list of primers. In a few cases, introns were removed, usually from genera far removed from *Melissodes* that could not be aligned.

For the taxa from Cardinal & Danforth (2013) we used six loci from the Cardinal & Danforth (2013) study; three of which overlapped with the current analysis (EF1a, Opsin, and PolII) and an additional three; 18S (782 bps), NaK (1,460 bps), and Wingless (455 bps) that did not. (bps = aligned base pairs)

PCR amplicons were visualized using gel electrophoresis, cleaned with ExoSAP-IT™ (USB-Affymetrix, Cleveland, OH, USA), purified with Sephadex® G-50 (GE Healthcare, Uppsala, Sweden) to prepare for sequencing using ABI Prism Big Dye™ (v3.1; Invitrogen, Fairfax, VA, USA). Sequencing was conducted with an ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) in the Biology Department of the University of New Mexico. We sequenced the amplicons in both directions (see Appendix A for fragments that were only successful in a single direction) and the resulting data were edited in Sequencher® (Gene Codes, 1999).

Data analysis

Individual gene sequences were aligned using MUSCLE (Edgar, 2004) implemented in MEGA6 (Tamura *et al*., 2011) using the default parameters. Introns were only problematic in a few cases and sections were removed only when alignment was ambiguous (GenBank sequences were complete). Gaps were treated as missing data. All eight aligned loci were concatenated and organized in Mesquite (Maddison & Maddison, 2018). In cases where multiple sequences for the same species were amplified and the combination of those sequences created a longer fragment than each alone, these fragments were made into contigs that were used in the final analysis, but only if there were no base pair differences in the sections that did overlap. This treatment resulted in a total of 8,059 aligned base pairs (6,293 coding, 1,634 intron, and 132 tRNA). All sequences were submitted to GenBank (Appendix A).

PartitionFinder (Lanfear *et al.*, 2012) was used for model selection and finding the best fit partitioning scheme. Both mitochondrial and nuclear protein-coding genes were partitioned by codon positions. Introns, tRNA, and 18S rRNA were treated as single data blocks, resulting in a total of 42 data blocks. The greedy search algorithm was used to find the best fit scheme, which was determined by the Bayesian Information Criterion (BIC), implemented in PartitionFinder. PartitionFinder suggested 8 partitions, which were used for all subsequent analyses. Maximum Likelihood (ML) and Bayesian analyses (BA) were run in RAxML 7.2.8 (Stamatakis et al. 2008) and MrBayes V3.2.6 (Ronquist *et al*., 2012), respectively on XSEDE (Extreme Science and Engineering Discovery Environment, https://www.xsede.org) through the CIPRES Science Gateway (Miller et al. 2011). For the ML analyses, we used the best-fit partitioning scheme recommended by PartitionFinder with the GTRCAT model applied to each partition and nodal support was evaluated using 1,000 replications of rapid bootstrapping implemented in RAxML. For the BA analyses, we also used the best-fit partitioning scheme and partition-specific models recommended by

PartitionFinder and default priors, and two independent analyses were conducted each with four runs with four chains each for 100 million generations, sampling every 2,500 generations. We plotted the likelihood trace for each run to assess convergence in Tracer V1.6 (Rambaut, Suchard, Xie, & Drummond, 2014), and discarded an average of 25% of each run as burn-in.

MCMCTree (Yang 2007) was used to perform Bayesian estimation of species divergence time. We used an unpartitioned dataset and analyzed under the HKY85 model with gamma with five rate parameters. We first estimated overall substitution rate using point calibration 0.71 (71 mya) at root, and estimated the gradient and Hessian of the branch lengths at the maximum likelihood estimates, which were used to estimate time and rate. We set the clock as independent, the gamma prior for kappa to a = 6, b = 2, and the gamma prior for alpha to a = 1, b = 1. The prior distribution of overall substitution rate assuming the gamma distribution was estimated to be a = 1, b = 1.81, and the Dirichlet-gamma prior for sigma2 to a = 1, b = 4.5. Since there are no fossils known within the ingroup, we took four node ages (+/-3.9 my) from the fossil-calibrated tree by Cardinal & Danforth (2013) as our calibration points (root age splitting Exomalopsini = 71 mya; Emphorini = 63 mya; the node separating *Florilegus* from the remaining eucerines = 23 mya; and the split between the *Eucera* complex and *Melissodes* + *Svastra* = 14 mya, see Fig. 5). This is a loose estimation of divergence times and should be interpreted as such. The first 2,000 generations of the MCMC chains were discarded as burnin and then trees were sampled every 200 generations until a posterior distribution of 10,000 was reached (2,000,000 iterations). We ran two independent MCMC chains to test for convergence. MCMCTree analysis was run using the parallel version of paml4.9e (Yang 2007) implemented in Texas A&M University High Performance Research Computing Ada Cluster.

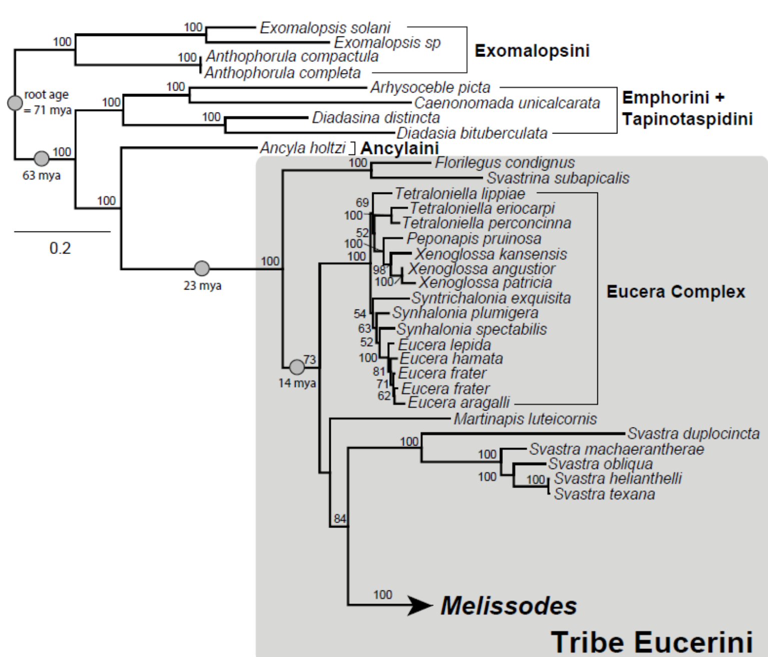
Ancestral ranges were inferred for the ingroup (*Melissodes*) using the time calibrated tree in BioGeoBEARS (Matzke, 2013) in R (R Core Team, 2013). Eight geographical areas (A=South America, B=Central America, C=Mexico excluding the Baja peninsula, D=Southern California and Baja California, E=United States and Canada west of the Rocky Mountains, F=Great Plains, G= east of the Mississippi River, and H=West Indies) were defined and a distribution range for each species was determined based on maps from Discover Life (Ascher & Pickering, 2017) and data collected by the author. We tested six models implemented in the program (DEC [dispersal-extinction cladogenesis], DEC+J [including founder event speciation], DIVALIKE [Dispersal-Vicariance Analysis], DIVALIKE+J, BAYAREALIKE [Bayesian] and BAYAREALIKE+J) using default parameters. Likelihood values of these models were compared using likelihood ratio test and the Akaike Information Criterion (AIC) to directly compare how well the different models fit the data (Matzke, 2013, 2014).

Results

Phylogenetic relationships among outgroups

All tribal relationships were consistent with the phylogeny of Cardinal & Danforth (2013). Within Eucerini, *Svastra* was sister to *Melissodes*. *Martinapis* was sister to *Melissodes* + *Svastra* and the *Eucera* complex was sister to the larger clade. *Florilegus* + *Svastrina* formed the basal clade of Eucerini. The ML tree (Fig. 5) and the BA (Wright 2018) consensus tree were in agreement except for the placement of *Syntrichalonia.* The ML tree placed *Syntrichalonia* as sister to the *Synhalonia* + *Eucera* clade whereas the BA tree placed it as sister to the entire *Eucera* complex.

Fig 5. Maximum Likelihood tree of outgroups with bootstrap support values. Grey circles reflect calibration points from Cardinal & Danforth (2013). Taxa within the Eucera complex now represent subgenera of Eucera (Dorchin et al. 2018).

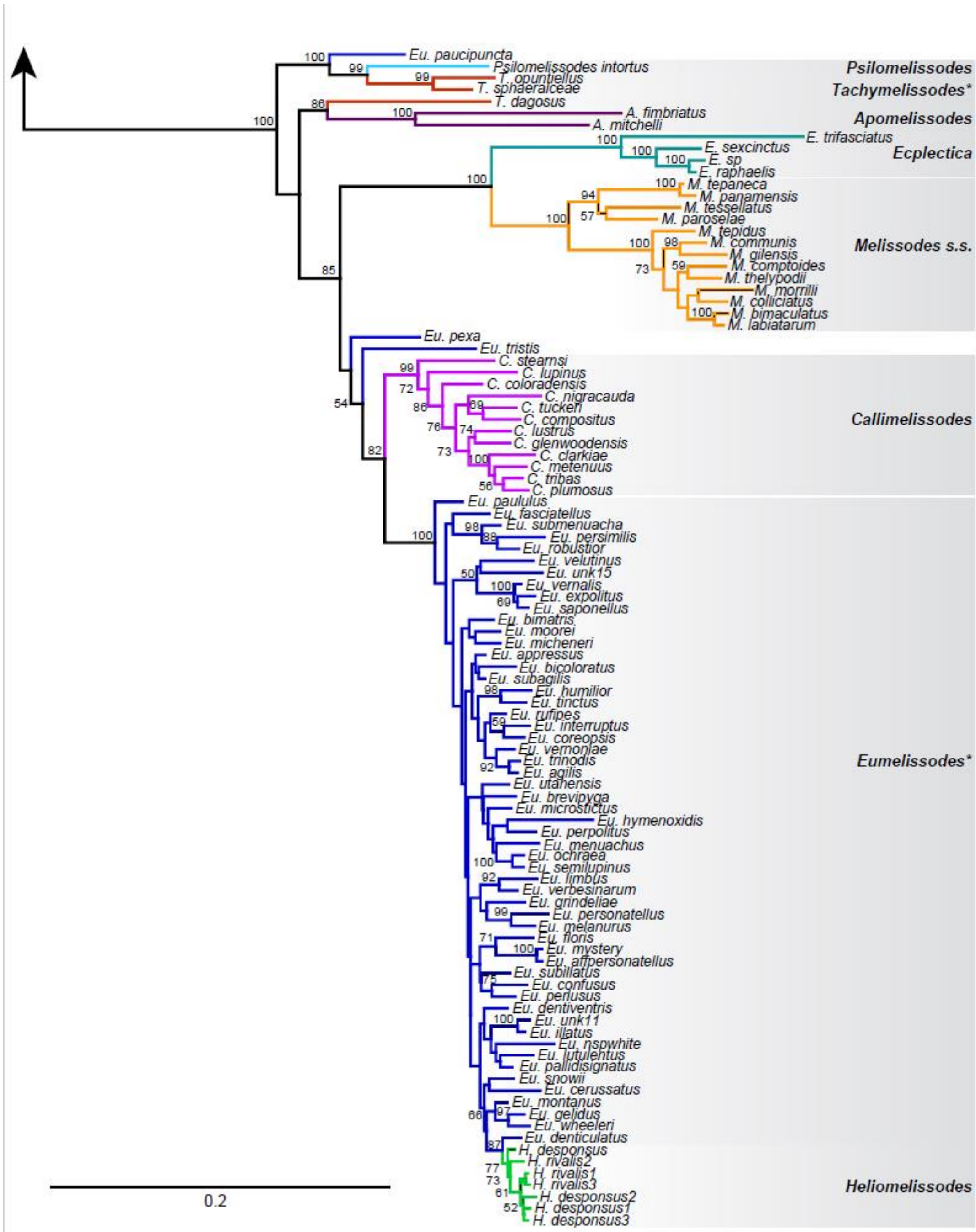


Phylogeny of Melissodes

We recovered the genus *Melissodes* (Fig. 6) as monophyletic. In terms of subgenera, *Apomelissodes*, *Melissodes* s.s., *Ecplectica*, *Callimelissodes,* and *Heliomelissodes* were found to be monophyletic, while *Tachymelissodes* and *Eumelissodes* were paraphyletic. *Psilomelissodes*, which is monotypic, was found near the base of *Melissodes*. The earliest diverging lineage within *Melissodes* was a clade that consisted of *Melissodes* (*Eumelissodes*) *paucipuncta* LaBerge, *Psilomelissodes*, and two species of *Tachymelissodes*. Next was a clade that consisted on *Apomelissodes* and *Melissodes* (*Tachymelissodes*) *dagosus* Cockerell. The remaining species within the genus consisted of two large clades, one formed by *Melissodes* s.s. and *Ecplectica,* another formed by *Callimelissodes*, most of *Eumelissodes*, and *Heliomelissodes*. *Heliomelissodes* was nested within *Eumelissodes* rendering *Eumelissodes* paraphyletic.

Within *Melissodes*, the species were largely resolved into the subgenera delimited by LaBerge with few exceptions. *Melissodes* (*Eumelissodes*) *paucipuncta* LaBerge was placed sister to *Psilomelissodes* + *Tachymelissodes* with strong nodal support. *Melissodes* (*Tachymelissodes*) *dagosus* Cockerell was placed as sister to *Apomelissodes*. Finally, *Melissodes* (*Eumelissodes*) *pexa* LaBerge and *M.* (*Eumelissodes*) *tristis* were both placed basally to *Callimelissodes* + *Eumelissodes,* but with low support values. The unexpected

Fig. 6: Maximum Likelihood tree of *Melissodes* with bootstrap support values (only shown >50). Paraphyletic species are indicated with *. Subgenera are color coded (Dark blue = *Eumelissodes*, light purple = *Callimelissodes*, green = *Heliomelissodes*, orange = *Melissodes* s.s., teal = *Ecplectica*, dark plum = *Apomelissodes*, red = *Tachymelissodes*, turquoise = *Psilomelissodes*.



placement of these four *Eumelissodes* species was consistent in both the ML and BA trees.

The relationships among the species within each subgenus were less resolved. Many small clades were consistent between the ML and BA analyses, but the relationships among these clades were inconclusive, especially in the hyperdiverse *Eumelissodes*. The alignment and newick trees for both the ML and BA analyses were deposited in Mendeley (Wright, 2018).

Divergence time and Historical biogeography of Melissodes

Our divergence time estimate analysis found that the genus *Melissodes* diverged from its relatives in Eucerini about 15 mya (Fig. 7). The diversification of major subgenera continued to occur throughout the Miocene and most of the present-day species came into existence by the end of the Pliocene. The BioGeoBEARS analysis suggested that the ancestral range of the common ancestor of *Melissodes* was western North America (Fig. 8). Among the six tested models, we found the BAYAREALIKE+J model (Landis *et al.*, 2013) to be the best fit to the data based on the AIC (Table 1).

Table 1. Likelihood scores from six BioGeoBEARS models.

model	LnL	params	d	e	j	AIC	AIC_wt
DEC	-424.2363	2	0.0281	0.0000	0.0000	852.4726	0.0000
DEC+J	-423.3709	3	0.0277	0.0000	0.0070	852.7419	0.0000
DIVALIKE	-434.5127	2	0.0322	0.0000	0.0000	873.0255	0.0000
DIVALIKE+J	-434.3300	3	0.0317	0.0000	0.0031	874.6600	0.0000
BAYAREALIKE*	-351.2543	2	0.0061	0.0893	0.0000	706.5086	0.3869
BAYAREALIKE+J*	-349.7940	3	0.0054	0.0823	0.0044	705.5880	0.6131

*p-value = 0.087

After the genus diverged from its relatives, the two smallest clades, consisting of *Tachymelissodes*, *Apomelissodes*, and *Psilomelissodes*, remained in the southwest or moved eastward (Fig. 8). The *Melissodes* s.s clade mainly diverged in western North America with some lineages moving east while others colonized Central America, eventually giving rise to the *Ecplectica* group in South America. The divergence of the *Callimelissodes* + *Eumelissodes* clade took place in the middle Miocene, and the two lineages continuously diversified in the same region and multiple small clades or species expanded to eastern North America. The analysis calculated lower dispersal parameter value (d=0.0054) than the extinction parameter value (e=0.0823), and the founder event speciation parameter value (j=0.0044) was also low. Given the relatively higher parameter value of extinction than the other two parameters, we can infer that many of the changes from the ancestral ranges were due to local range extinction.

Fig. 7: Time calibrated MCMCtree. Node ages estimated from Cardinal & Danfoth (2013). See Fig. 5 for calibration points.

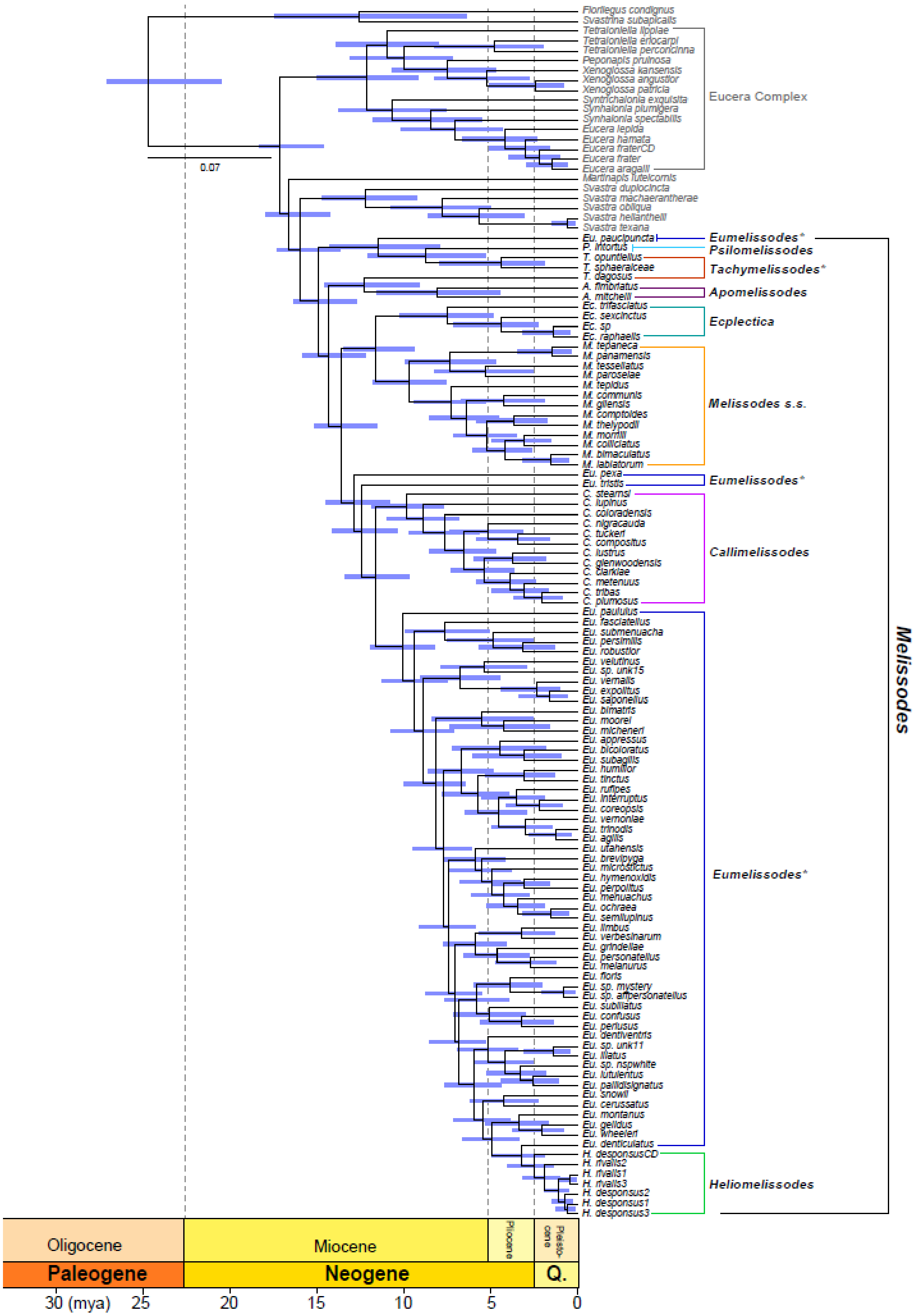
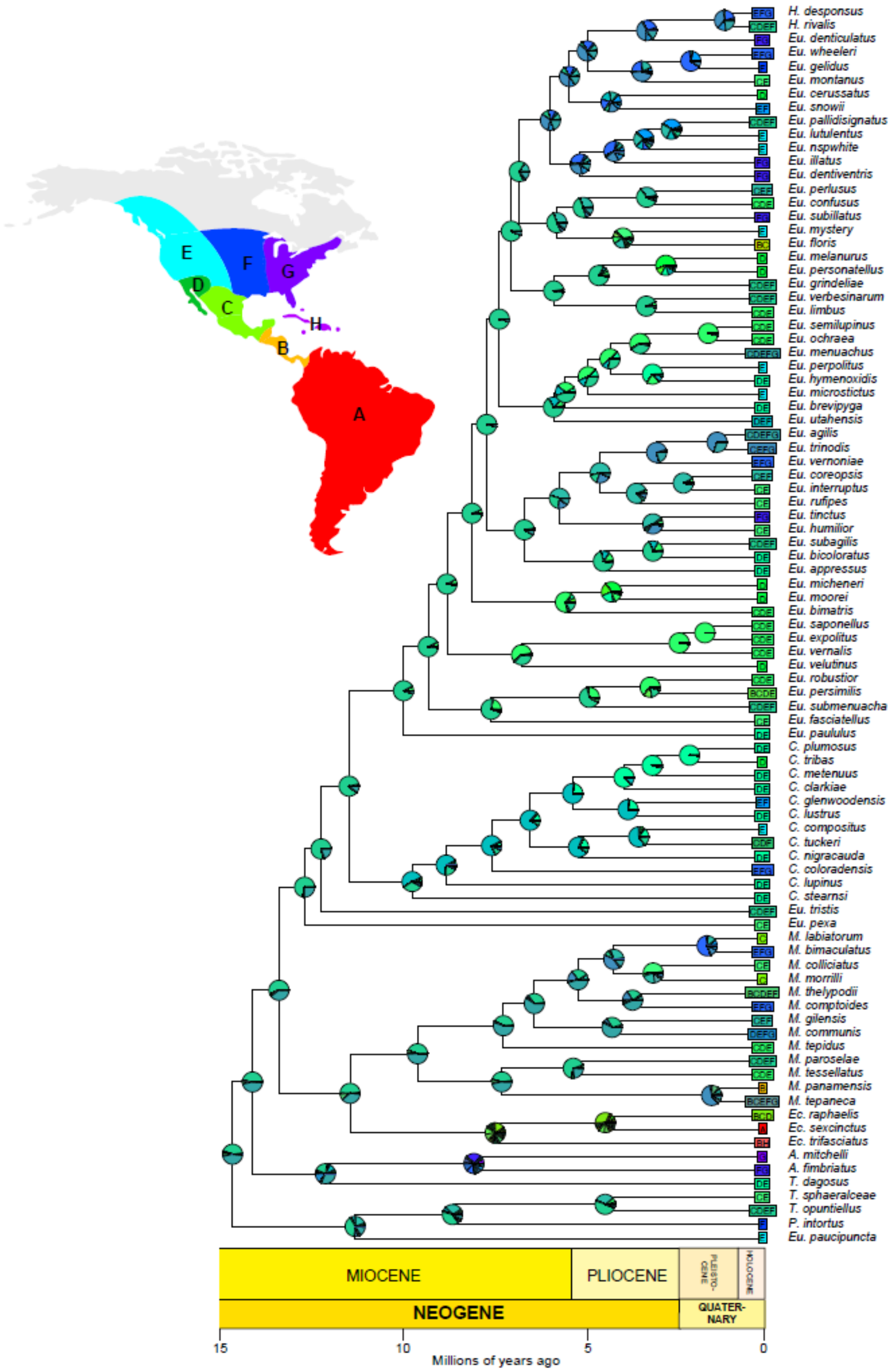


Fig. 8: BioGeoBEARS tree based on time calibrated MCMCtree. Ranges (A = South America, B = Central America, C = Mexico excluding the Baja Peninsula, D = Southern California and the Baja Peninsula, E = west of the Rocky Mountains, F = Great Plains, G = east of the Mississippi River, H = West Indies)



Discussion

Phylogenetic relationships among outgroups

This study represents the first comprehensive molecular phylogeny of the long-horned bee genus *Melissodes*. Few papers have been published on the Eucerini in general. Cardinal & Danforth (2013) presented a Bayesian phylogeny of all bees that included four eucerine representatives (including one *Melissodes*) that placed Eucerini sister to Ancylaini. All relationships among taxa in the current study and in Cardinal & Danforth are equivalent, which is not suprising considering we used much of their data. In 2014, Praz & Packer presented a more in depth look at the Ancylaini and its relationship to Eucerini, which included 13 eucerine genera (again with one *Melissodes*). The relationships among taxa that are included in both this study and Praz & Packer are congruent except for the placement of *Tetraloniella* relative to *Eucera*. Finally, Dorchin *et al*. (2018) provided a thorough revision of the Eucera complex, sinking many genera to subgeneric standing and erecting one new genus (Dorchin et al., 2018b). The Dorchin study included eight eucerine genera with four representatives of *Melissodes*. Both Dorchin's tree and the ML tree from this study place *Syntrichalonia* as sister to the *Eucera* + *Synhalonia* subgenera, whereas the BA tree from this study places it outside the entire *Eucera* complex. The Dorchin *et al*. study more thoroughly covers the Eucera complex. Therefore, the former placement is more reliable.

Phylogeny of Melissodes

The sister relationship among the subgenera *Ecplectica* and *Melissodes* s.s. is not surprising, however the original assessment of LaBerge (1956a, 1961) that these subgenera are basal to all other *Melissodes* is not supported in these analyses. Instead, *Tachymelissodes*, *Apomelissodes*, *Psilomelissodes* and *M.* (*Eumelissodes*) *paucipuncta* comprise the basal clades. The subgenera *Melissodes* s.s., *Ecplectica,* and *Callimelissodes* are each monophyletic with strong support with *Melissodes* s.s. + *Ecplectica* sister to *Callimelissodes* + *Eumelissodes*. The subgenus *Heliomelissodes* is monophyletic, but renders *Eumelissodes* paraphyletic and in the next generic revision, should be synonymized with *Eumelissodes*.

Although the pre-Hennigian approach that LaBerge used was inadequate for inferring the relationships among the subgenera, his placement of most species in their respective subgenera is consistent with this phylogeny with a few exceptions. *M.* (*Eumelissodes*) *paucipuncta* is morphologically quite distinct with very sparse punctures and the males have much shorter antennae than typical *Eumelissodes*. The placement of this species with *M*. (*Psilomelissodes*) *intortus* Cresson, *M.* (*Tachymelissodes*) *opuntiellus* Cockerell and *M.* (*T*.) *sphaeralceae* Cockerell is morphologically consistent as these three species also have short male antennae. The placement of *M*. (*Tachymelissodes*) *dagosus* with *Apomelissodes* rather than the two other *Tachymelissodes* is surprising because of its western distribution whereas all the other *Apomelissodes* are eastern. However, the apical hair bands and protruding clypeus place it with

Apomelissodes whereas the male antennal length is short and contradicts this placement. These two small clades are relatively well supported and, in a future revision, will require a more thorough study of their morphologies.

Melissodes (*Eumelissodes*) *tristis* is a widespread and morphologically distinctive species. It is a hyper-generalist, pollinating at least 26 genera in 13 plant families (unpublished data). The females have a broadly hyaline apical edge on T1, a single row of dark erect hairs posterior to the apical hair band on T3, few to no punctures in the interband zone of T2 and the scutellum, and a shiny boss on the clypeus. In the males, the antennal configuration is consistent with *Eumelissodes* but clypeus is entirely dark and they do not share the synapomorphic *Callimelissodes* trait of having a broadly convex hyaline apical edge of S4. Nor does *M. tristis* share the ecological trait of oligolecty on Asteraceae as are many of the *Callimelissodes* and *Eumelissodes*. Instead, its dietary patterns are more consistent with those of a broad generalist, as are most of the *Melissodes* s.s. Finally, *Melissodes* (*E*.) *pexa* is a morphologically typical but rare species with very little known about its biology. These two species are basal to *Eumelissodes* + *Callimelissodes*. Retention of these two species in *Eumelissodes* would render it paraphyletic and their phylogenetic positions suggest that they are distinct from most of the *Eumelissodes*, but without other compelling information, it would be premature to make any taxonomic changes based on molecular evidence alone.

Although individual small clades within *Eumelissodes* are well supported and consistent between the ML (Fig. 5) and the BA analyses, the backbone is poorly supported and the relationships among the smaller clades are unresolved. The Cardinal & Danforth (2013) study estimated 13.74 mya since the split of the *Melissodes* + *Svastra* clade from the *Eucera* clade, while our study proposes a slightly older age of 16.63 mya for the same clade. The *Melissodes* clade is estimated to have diverged from Svastra 15.97 mya , and therefore it represents a relatively young radiation.

Combining results from Cardinal & Danforth (2013), Praz & Packer (2014), Dorchin *et al.* (2018) and this study, a comprehensive picture of the tribe Eucerini and its placement within the larger Apinae is coming to light. A meta-analysis combining all these data with exemplars from *Gaesischia* and *Cubitalia* and denser taxon sampling for *Svastra, Melissoptila, Thygater*, and *Alloscirtetica* would more fully round out our understanding of the tribe Eucerini.

Historical biogeography of Melissodes

A western North American origin of *Melissodes* was indicated by the biogeographic analysis. This is consistent with the center of diversity of the group. The model selection of the BAYAREALIKE+J (LnL = -351.08) model suggests widespread sympatric speciation followed by range extinction and possible founding events with little indication of speciation resulting from vicariance. Dorchin *et al.* (2018) concluded that *Eucera,* the only other large

Eucerini genus, also originated in western North America with two subsequent dispersals to the eastern hemisphere.

The two basal clades of *Melissodes* likely originated in western North America with *Apomelissodes* and *Psilomelissodes* expanding eastward. The most recent common ancestor (MRCA) of *Melissodes* s.s. and *Ecplectica* also originated in western North America with *Ecplectica* expanding south through Central America and into South America and *Melissodes* s.s diversifying in situ as well as expanding eastward. *Callimelissodes* apparently had a wide distribution over much of North America followed by range contractions where most were limited to west of the Rocky Mountains and only a few species remained in the Great Plains. The MRCA of *Eumelissodes* was likely very widespread from Mexico east through the Great Plains. Several lineages then diversified in situ with subsequent range contractions in the western portion of the continent and several lineages expanded eastward.

In *Melissodes*, many of the sister taxa couplets are sympatric rather than allopatric (~80%). This combined with the biogeographical analysis suggests speciation due to factors other than vicariance. For herbivores, host switching is often implicated in sympatric speciation (Berlocher & Feder, 2002). However, in *Melissodes*, more than half of the species are oligolectic on or within the family Asteraceae and many specialize within the two largest North American clades of

Asteraceae; the Heliantheae Alliance (HA) and the North American clade of Astereae (NAC) (Wright, unpublished data).

Although the timing of major events such as mountain, grassland and desert formation in North America are still debated, it is clear that during the Miocene (23-5.3 mya), North America saw major changes including increased aridity and cooler temperatures (Wilson & Pitts, 2010). The grasslands of North America may have started as patchy, isolated habitats as early as the Early-Middle Eocene, but the expansive grasslands that are notable today, may have formed as late as the Middle-Late Miocene (Strömberg, 2011). Also, the warm deserts of southwestern North America may have formed as recently as 10,000 years ago (Wilson & Pitts, 2010). The origin of the Asteraceae groups that thrive in these habitat types evolved much earlier. Both the NAC (Brouillet *et al*., 2009; Noyes & Rieseberg, 1999) and the HA (Baldwin, 2009) have similar patterns of a North American origin and disjunct distributions in South America. In fact, analyses of both groups point to a southwestern origin in the warm deserts of North America with a rapid Oligocene-Early Miocene diversification (Funk et al. 2009). The grasslands and arid regions, where Asteraceae thrive, were patchy and probably ephemeral as drier climates allowed grasslands and parklands to expand while the forests contracted (Strömberg, 2011).

This study indicates that the *Melissodes* radiation occurred from the Middle to Late Miocene. This followed or was concurrent with the diversification of North

American Asteraceae. This is significant because of the large number of *Melissodes* species that specialize on Asteraceae. Although the results of this study indicate sympatric speciation as a major speciation mechanism, followed by range extinction, the resolution of the geographic ranges used in this study may not have been on a fine enough scale to rule out localized, short-term allopatry during this time of ecological change.

There is some evidence that the pollen of Asteraceae is chemically defended and/or difficult to digest by bee larvae (Sedivy *et al.*, 2011). Specialization on this abundant and widespread group of flowering plants, combined with an adaptation for digesting their pollens, may be implicated as a cause for the radiation of Melissodes, or at least the subgenus *Eumelissodes*. Further investigation into the evolution of diet breadth of *Melissodes* is needed.

In summary, we found that the previously delimited subgenera hold true with the exception of (i) two species (*M. paucipuncta* and *M. dagosus*) that are well supported in other clades, (ii) two species (*M. tristis* and *M. pexa*) with low support at the nodes leaving them with ambiguous placement, and (iii) *Heliomelissodes* imbedded within *Eumelissodes* rendering it paraphyletic. The biogeographical analysis suggests that the genus originated in southwestern North America and speciation occurred under widespread sympatry followed by range extinction. The diversification of *Melissodes* follows the formation of the North American deserts and grasslands and the diversification of the two largest

North American clades of Asteraceae. The information gained in this study can be used as a basis for future studies on the evolution of this group of important pollinators.

Chapter 2: Evolution of diet breadth in *Melissodes* (Apidae: Eucerini)

Short title: Diet breadth

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Abstract

The relationship between phytophagous insects and their host plants has interested scientists since Darwinian times. Using modern phylogenetic inference, we are able to investigate these patterns using, not only the phylogenies of the insects, but the evolutionary relationships among the plants they feed on as well. The relationships between bees and the plants they pollinate were traditionally seen as mutualistic and were treated separately from the research investigating the antagonistic relationships between phytophagous insects and their host plants. However, recent phylogenetic studies have made great progress including bee-host relationships in with the larger body of work on phytophagous insects. This work represents the first analysis that incorporates a taxon dense phylogeny of bees, molecular barcoding of pollen to identify host plants, and a host plant phylogeny to assess the evolution of diet breadth in bees. The use of molecular barcodes to discern host identities allowed a more detailed look into specialization of bees within the major clades of the super-diverse plant family, Asteraceae. Here we assess the value of using the barcoding techniques for pollen identification and the merits of various ways of inferring ancestral diet breadth. We investigate the strength and location of phylogenetic signal and rate changes in speciation. We find, not one, but three general patterns of host plant evolution within a single genus of bees, *Melissodes* Latreille, and that most cladogenesis events occur in the absence of a change in diet breadth. And we place our findings in the context of historical biogeography and current theory on the evolution of diet breadth.

Key Words: Apidae, Eucerini, Melissodes, diet breadth, phylogenetic diversity, oscillation hypothesis, constraint hypothesis

Introduction:

The degree of host plant specialization of pollinating bees has long interested entomologists (Robertson 1925). Adult bees drink nectar for energy, but do not specialize on nectar hosts. Females collect pollen to provision their nests for larval nutrition and some species specialize on particular pollen hosts. Categories of pollen specialization range from monolecty (specialization on a single species of plant), to oligolecty (specialization on a single family of plants), through to broad polylecty (pollinating multiple families of plants) with a multitude of categories in between (Cane and Sipes 2006). These terms represent qualitative groupings on a continuum of diet breadth. The traditional view holds that oligolecty is a derived condition from a more generalist ancestor (Waser 1998). But with more species-level phylogenetic studies becoming available, it is has been suggested that most bees are ancestrally oligolectic and the evolution of polylecty from oligolecty is more common than the other way around (Danforth et al. 2013, Praz et al. 2008, Sedivy et al. 2008). So far, ten studies have used phylogenetic methods to investigate bee diet (Dellicour et al. 2013, Haider et al. 2014, Larkin et al. 2008, Michez et al. 2008, Müller 1996, Müller and Kuhlmann 2008, Patiny et al. 2007, Sedivy et al. 2008, Sedivy et al. 2013, Sipes and Tepedino 2005). Danforth et al. (2013) includes a short review on this subject.

If diet breadth is a heritable trait and there are costs associated with host switching or adding potential hosts to a bee's diet, then adaptation to a particular plant group could be viewed as a type of constraint. Constraints, either physiological, morphological, or neurological, should evolve after or in concert with specialization. Once constraints are in place, they would enhance conservation of diet breadth in bee lineages and prevent host switching or changes in diet breadth away from the ancestral condition (Bernays 2001, Haider et al. 2014, Praz *et al*. 2008, Sedivy et al. 2011, Sedivy et al. 2013). There is empirical evidence to support this idea in bees. For example, laboratory reared bees in the family Megachilidae have been shown to have variable reproductive success when larvae were reared on different types of pollen (Praz et al. 2008, Williams 2003). This phylogenetic constraint implies that bee species that are closely related should have more similar diets than bees that are more distantly related, especially if the progression to polylecty is additive.

Host plant specialization may facilitate speciation and there are several models that describe this evolutionary dynamic. The escape and radiate model (Ehrlich and Raven, 1964) posits that increased speciation would occur after access to an underutilized niche is gained through adaptive radiation. However, phylogenetic studies across many organisms show that conservation of dominant traits in radiations is common (for a review, see Webb et al. 2002). The oscillation hypothesis (Janz and Nylin 2008) suggests that specialist lineages go through brief periods of generalism that fuel the next phase of speciation back towards specialization. Sedivy et al. (2008) define this cycle in a more precise manner under the constraint hypothesis. They postulate that bees start as specialists, then during a time of pollen limitation (selection pressures towards generalization), they overcome these constraints to enter a polylectic phase. In some cases, selection pressures then lead them back towards specialization. If the pollen shortage is lifted, they revert to their ancestral host, if not, they become specialized on a different host. These new specialists then develop new constraints. If there are no selection pressures to lead them back to specialization, they remain generalists. The musical chairs hypothesis (Hardy and Otto 2014), on the other hand, refers to host switching of specialist herbivores and the ease with which certain lineages switch back and forth due to retention of genetic variation for ancestral diet breadth.

Diet breadth is an ecological trait of a species and it can only be described from understanding the natural history of the organisms. It is nearly impossible to estimate the full diet breadth of a particular bee species from field observations or through feeding experiments, and thus an alternative method of estimation is needed. A common method is to infer diet breadth from ecological data recorded in museum specimens, but host information on labels can often be misleading. Host associations are based on pollen usage, not nectar sources, and often nectar sources are more variable and taxonomically broad than the pollen hosts (Robertson 1925). Label data often contain information on the species of plant the bee was collected from but do not typically distinguish between nectaring and pollen collection. Alternatively, morphological identification of pollen taken directly from the scopae of female bee specimens can be used to avoid the problems associated with label data. However, pollen morphology is difficult and nearly impossible to distinguish at lower taxonomic levels for certain plants such as Asteraceae. Recently, methods of molecular identification of pollens have been used. For example, the internal transcribed spacer unit 1 (ITS1) gene fragment is a reliable barcode for most plant taxa (Gemeinholzer et al. 2006, Hollingsworth 2011, Li et al. 2011) and has been used to identify pollen from the gut contents of *Colletes* Latreille bees (Wilson et al. 2010). It can be used for generic and often species level identification for most North American plants.

Once the number and type of plant species that a bee species utilizes as hosts are determined, they can be used as raw data for measuring diet breadth. However, there is no consensus on how best to quantify diet breadth. Because of the diversity of flowering plants that are insect pollinated, counting plant families and other taxonomic groups to measure diet breadth can be problematic because taxonomic categories are human constructs. Even if these groupings represent monophyletic groups, not all plant families are equal in size or relationship to one another. To account for this and to devise a more realistic quantitative measure of diet breadth, methods have been developed that take into consideration the phylogenetic relationships of the plants.

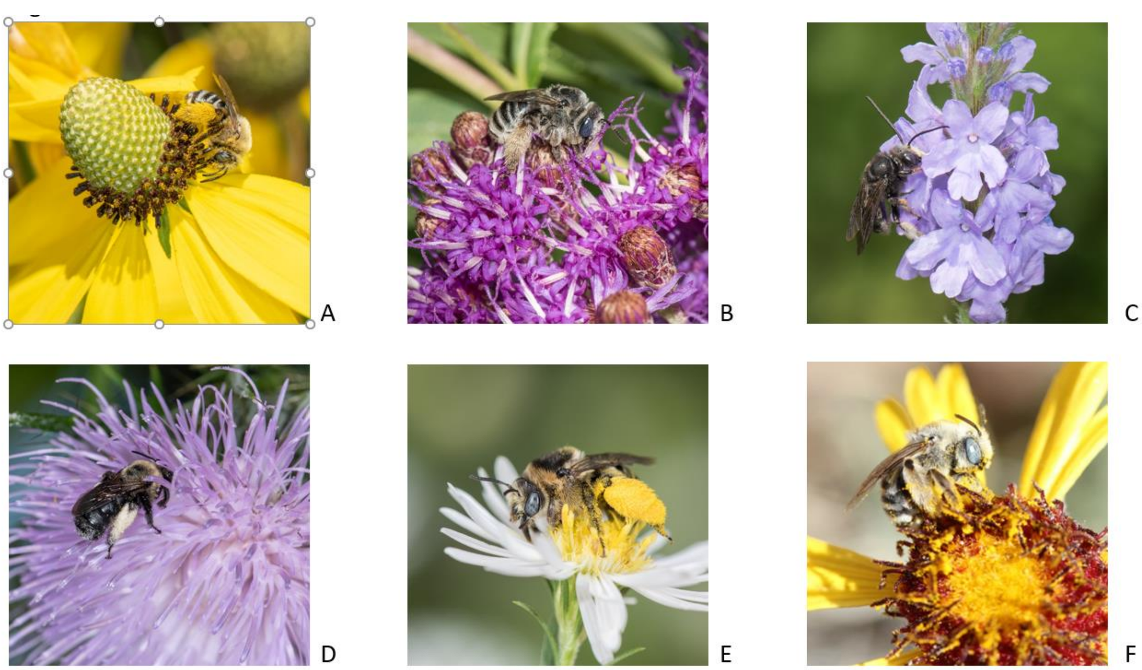
Faith's Phylogenetic Diversity (Faith 1996) was first developed as a measure of diversity for communities in a conservation context. Symons and Beccaloni (1999) then used the Root Phylogenetic Diversity Index (RPD) to measure diet breadths of phytophagous insects. RPD is the combined branch lengths (including the root) of all species in a community mapped onto a phylogenetic tree. In the case of pollinators, their diet breadth can be measured as the combined branch lengths of all species of host plants of a given species of pollinator, mapped onto a larger host plant phylogeny.

These measures solve the problem of quantifying diet breadth, but in comparative studies, the measurement of diet breadth may not be as important as the identity of the hosts. Two bee species may be quantitatively equal in the respective RPDs of their diets, but they may each pollinate two very different plant taxonomic groups. Phylogenetic Beta Diversity, the amount of overlap of branch lengths on a phylogenetic tree for two communities divided by the total branch lengths for both communities, can be used to look at the phylogenetic overlap of two communities. This was also first applied in a conservation ecology framework, but likewise, has been used in host/parasite or host/herbivore relationships (Graham and Fine 2008, Pellissier et al. 2013, Poulin et al. 2011, Scordato and Kardish 2014) and can be applied to diet breadth of bees as well. This method is more robust to sampling error because, when not all the hosts are known, this method can show the proportion of branches that overlap even when the tips of the host tree do not match.

Categorical data, taxonomic counts, and RPD can be treated as phenotypic characters to investigate the ancestral states throughout the bee phylogeny. But because diet breadth is a range, not a single phenotypic character, diet breadth ranges can also be assessed in the same way that geographic ranges are treated when inferring ancestral geographic ranges. Diet breadth can be assessed by treating the plant phylogeny as a geographic map; where each clade on the plant phylogeny is treated as a geographic range. The relationships among clades on a phylogeny have similar characteristics to geographic ranges on a map. Not all areas are the same size, each pair of them is separated by different distances, and the strengths of the barriers between them are variable. In a phylogenetic tree, clades are of different sizes, some are more closely related to each other, and there may be different types of barriers between them. As an example, Asteraceae is a much larger family than Polemoniaceae, it is much more closely related to Apiaceae than it is to Polemoniaceae, and differences in pollen chemistry, corolla shape, and other phenotypes could deter switching or adding a new plant group to a bee's diet. These phenotypic differences may prevent host range switching just as vicariance caused by mountain or glacial formation may prevent geographic range switching.

The R package BioGeoBEARS (Matzke, 2013) allows comparison of three common models; the Dispersal-Extinction Cladogenesis (DEC), DIspersal-Vicariance Analysis (DIVALIKE), and a Bayesian model (BAYAREALIKE). All three models contain parameters to account for dispersal, extinction, and narrow sympatry. In the context of host range these would be widening the diet breadth, narrowing the diet breadth, and allowing speciation to occur in a specialist insect without a host switching event. DIVALIKE and DEC also contain parameters to account for vicariance, which in terms of the host plant phylogeny would be cladogenesis where the daughter species had a more narrow diet than the parent species. Finally, BAYAREALIKE, which does not include parameters for vicariance, includes a parameter for widespread sympatry, which would imply cladogenesis events without changes in overall diet breadth. Three additional models are created by adding a parameter for founder event speciation (+J) to each of the above. In the host plant phylogeny, founder event speciation would be a cladogenesis event that included host switching for one of the daughter species.

Fig. 9: Various species of Melissodes. A-E photos by Heather Holm; F photo by Olivia Messinger-Carril.



All of these methods to investigate ancestral diet on categorical, continuous, or in a biogeographic context, can be used to evaluate the above mentioned theories on the evolution of diet breadth. In this study, we investigate the evolution of diet breadth in the bee genus *Melissodes* (Fig. 1, Apidae: Eucerini), which has its center of diversity in southwestern North America (Michener 2007). Many of the species in *Melissodes* are considered polylectic, most of the remaining species specialize on Asteraceae, and a few specialize within other plant families.

Asteraceae specialization is common in bees and many types of bees have evolved specialized hairs (Müller 1996) and behaviors specific to Asteraceae pollination (Cane 2017). Yet Asteraceae is suspected of having chemically unpalatable pollen (Dötterl and Vereecken 2010, Nicolson and Human 2013) and certain bee larvae cannot be reared on Asteraceae pollen unless they are specialists on Asteraceae (Praz et al. 2008, Williams et al. 2003). Alternatively, Asteraceae pollen may confer some level of protection from brood parasitism (Spear et al. 2016). Müller and Kuhlmann (2008) coined the term 'Asteraceae paradox' meaning, that while many species of bees are specialists on Asteraceae, most generalists avoid Asteraceae. Asteraceae is one of the largest plant families on the planet and there is a recent phylogeny of the entire family (Funk et al. 2009b). The three major subfamilies that occur in North America are the Carduoideae (thistles), Cichorioideae (lettuce and dandelions), and the Asteroideae (the largest subfamily). Within Asteroideae, the North American clade of Astereae (NAC) and the Heliantheae Alliance (HA) are the two largest radiations of Asteraceae in North America.

In this study we were able to empirically identify the diet breadth of 52 species of *Melissodes* using molecular techniques that allowed us to discern specialization within the super-diverse Asteraceae. We use the bee phylogeny from Wright et al. (2008) to assess relatedness among the bees and we build a host plant phylogeny to assess diet breadth of each bee species in a phylogenetic context. We append the empirical data of diet breadth with information from the literature to expand the taxonomic scope of the study. We use ancestral character state reconstruction, ancestral range reconstruction (BioGeoBEARS), Pagel's statistics, and Phylogenetic Beta Diversity to look at the evolution and overlap of bee diets and investigate if diet breadth affects speciation/extinction rates. Using these tools we can test whether or not the patterns seen in host utilization of *Melissodes* fit previous hypotheses about the evolution of diet breadth. Specifically, is the most common recent ancestor (MRCA) of *Melissodes* a specialist or a generalist? Are there frequent or rare shifts between oligolecty and polylecty? Do host switches rather than changes in breadth play a major role in the diversification of this genus? Do polylectic species include Asteraceae in their diet? Finally, do changes in diet co-occur with changes in speciation rates? Throughout our attempts to answer all these questions, we have also gained valuable insight as to the ability of different analyses to answer these complex questions.

Materials and Methods:

Estimation of diet breadth: In order to understand how diet breadth evolved throughout the diversification of *Melissodes*, we first estimated the diet breadth of 52 species by molecularly identifying pollen samples collected from the female scopae of museum specimens. A total of 1,441 museum specimens, borrowed from 23 insect collections, 20 individual researchers, and collected by the senior author, were used for gathering the pollen samples. Identifications of the bees were made or confirmed by the senior author to the species level. If the specimen label had a host genus recorded, the sample was only processed if that genus of plant had not yet been recorded for that species of bee. Only one specimen from each locality, host, and date was processed. An effort was made to maximize the host range and geographical range for each species of bee. In determining the diet breadth of each species, we deemed that enough data were gathered if one of the following criteria was met: (i) at least 20 samples had successful pollen DNA identifications (see below) to the generic level; (ii) less than 20 samples were attempted because all remaining samples available to the author had host label information that matched a genus already designated for that species; or (iii) at least three different host plant families were represented and less than twenty samples were available for that species.

Pollen identification: From each female bee specimen, pollen was scraped using a new insect pin into a wide bottom micro-centrifuge tube with a single 5mm disposable glass bead and crushed using a Qiagen TissueLyser II machine at a frequency of 30 Hz. for 60 seconds. DNA was extracted using Qiagen DNeasy® Plant Mini Kits (Valencia, CA, USA) following the manufacturer's protocol. PCR reactions were run on an Eppendorf Mastercycler ep gradient S Thermal Cycler® (Eppendorf, Hamburg, Germany) with TaKaRa Amplitaq™ (Applied Biosystems, Foster City, CA, USA). Various primers (Table 2) and temperature regimes were used to amplify the internal transcribed spacer unit 1 (ITS1). Fragments were visualized using gel electrophoresis and purified with ExoSAP-IT™ (USB-Affymetrix, Cleveland, OH, USA) then prepared for sequencing using ABI Prism Big Dye™ (v3.1; Invitrogen, Fairfax, VA, USA) and purified with Sephadex® G-50 (GE Healthcare, Uppsala, Sweden). Sequencing was conducted with an ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) in the Biology Department of the University of New Mexico. Sequencing was run in a single direction and edited in Sequencher® (Gene Codes, 1999).

Table 2. Primers for ITS1

code	direction	sequence	reference
7A	forward	GAGTCATCAGCTCGCGTTGACTA	Tate & Simpson 2003
2B	reverse	CTCGATGGAACACGGGATTCTGC	Tate & Simpson 2003
5	forward	GGAAGGAGAAGTCGTAACAAGG	Tate & Simpson 2003
rev	reverse	CTTTTCCTCCGCTTATTGATATG	Little et al. 2004
1	forward	AGAAGTCGTAACAAGGTTTCCGTAGG	Tate & Simpson 2003
4	reverse	TCCTCCGCTTATTGATATGC	Tate & Simpson 2003

This procedure typically resulted in 500-600 bps (minimum = 242 bps, maximum = 903 bps). The ITS1 gene fragment of the pollen was searched against the National Center for Biotechnology Information (NCBI) Basic Logical Alignment Search Tool nucleotide (BLASTn) database optimized for highly similar sequences (megablast). To ensure that the NCBI database was complete enough to perform this task, we performed a preliminary search and confirmed that all plant genera that were listed on bee specimen labels had at least one ITS1 gene fragment in the database. In most cases, the highest ranked match resulted in one or a few species in a particular plant genus, but occasionally the sequence equally matched several genera in a family. The generic level of identification was only accepted when the identity matched above 98% and only one genus matched to the highest ‘identity’ with the highest ‘max score’ and lowest ‘E value’ in the BLAST results.

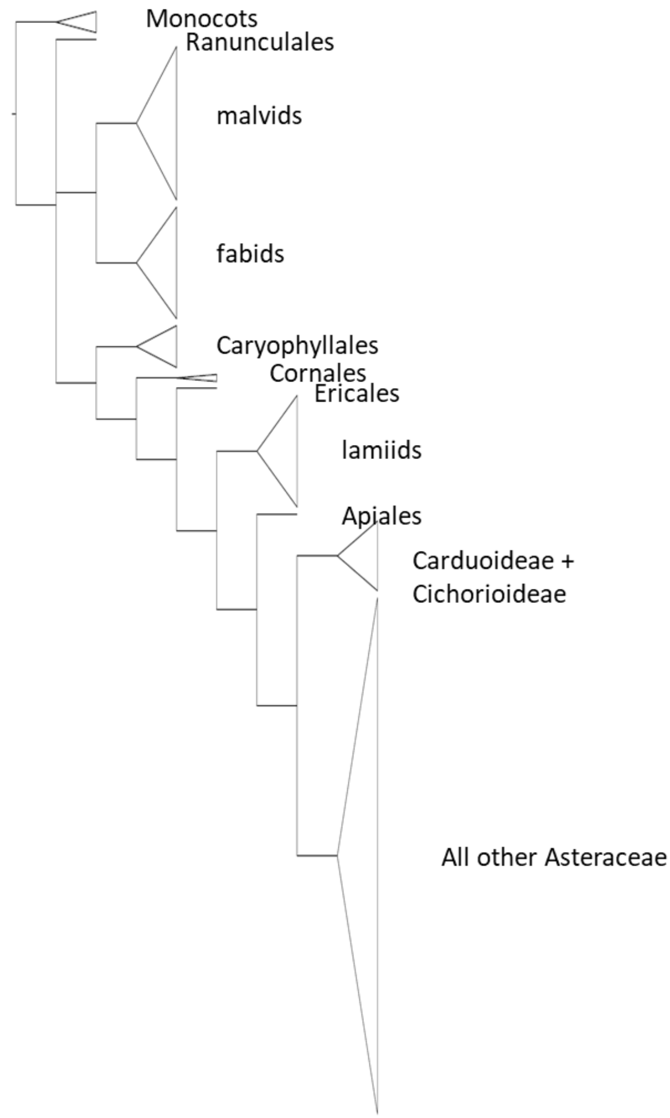
Because most female *Melissodes*, even if they are generalists, only visit one species of flower in a single foraging trip, most samples contained pollen from a single plant species and Sanger sequencing was sufficient for data generation. However, a portion of the samples had multiple pollen species in a single load and our methods were not able to read these sequences. To identify the pollen from these samples, we used a metabarcoding method by performing amplicon sequencing, targeting a portion of the chloroplast trnL intron. In short, we used two rounds of PCR generated amplicons that contained adaptor sequence to allow for subsequent indexing and Illumina sequencing. After PCR normalization and pooling, sample library pools were sent for sequencing on an Illumina MiSeq (San Diego, CA) in the CU Boulder BioFrontiers Sequencing Center using the v2 300-cycle kit (cat# MS-102-2002). After basic quality control and trimming, the trnL amplicons were processed via the UPARSE pipeline (Edgar 2013). Taxonomy was assigned via the SINTAX protocol (http://www.drive5.com/usearch/manual/utax_user_train.html) available in usearch v8.861 (Edgar 2010). To assign taxonomy to each OTU, an SINTAX trnL reference database was constructed by downloading any annotated GenBank (Benson 2005) records that contain the trnL gene. The amplicon region bounded by the trnL c & h primers (Taberlet 2007) was extracted from the GenBank records using the UTAX protocol. All extracted amplicon regions were dereplicated to 100% sequence identity and any identical sequence across lineages are collapsed to the lowest-common-ancestor. Closed-reference OTUs were generated by searching against the trnL reference database at 100% sequence similarity. Results for these samples were included in the diet breadth data if they comprised greater than 10% of the OTUs for a given sample.

Bee specimens with successful pollen sequences were labeled with the pollen sample ID number and vouchered at the Museum of Southwestern Biology at the University of New Mexico or the specimens were labeled and returned to their respective owners (Appendix C). Because the pollen samples came from bees and not from the identified plant specimens, they are considered environmental samples according to NCBI and therefore were not deposited in GenBank. The pollen sequences are available in Appendix D.

Measurements of diet breadth: Based on the molecular identification of the pollen samples collected from the museum specimens, we estimated the diet breadth of each species using three different methods. The first method was an ecological estimate of diet breadth in which each bee was assigned to be either oligolectic (a particular host family), polylectic (multiple host families), or generalist with a strong preference for Asteraceae (all but one sample were identified as Asteraceae). The second method was a taxonomic estimate of the diet breadth in which the number of plant host families, tribes, and genera of all sampled pollen hosts of each bee species was tallied. The last method was a phylogenetic estimate of diet breadth in which we calculated the root phylogenetic diversity (RPD) of host plants utilized by each species. This was calculated as the sum of all branch lengths on the host plant tree (see below) for all the host plant genera for each species of bee using the pd tool in Picante (Kembel et al. 2010) in R (R Core Team, 2013).

To calculate the RPD of host plants, we first estimated the host plant phylogeny. For each plant genus identified from the pollen samples using the BLASTn search (160 genera), the most common or widespread species that was matched to the data was used as a representative of that genus. For example, seven species of *Helianthus* were found to be matches to different pollen DNA samples, but *Helianthus annuus* Linnaeus was used as the representative species for the genus. For these genera, the ITS1 + 5.8S + ITS2 gene fragment available on GenBank was downloaded and aligned using the same tools listed above. This produced 919 aligned bps. A maximum likelihood (ML) analysis was run in RAxML V7.0.3 (Stamatakis 2006) using default parameters on CIPRES (Miller *et al.*, 2011), starting with a random tree, and bootstrap support was calculated with 1000 replicates. Because this tree was based on less than 1,000 bps of nucleotide data and is missing most of the species of the entire Angiosperm group, the basal relationships were constrained in accordance with the Angiosperm Phylogeny Group III (APG III, Fig. 10, modified from Chase & Reveal 2009).

Fig. 10: Constraints placed on maximum likelihood phylogenetic tree of host plants, modified from APG III (Chase and Reveal 2009).

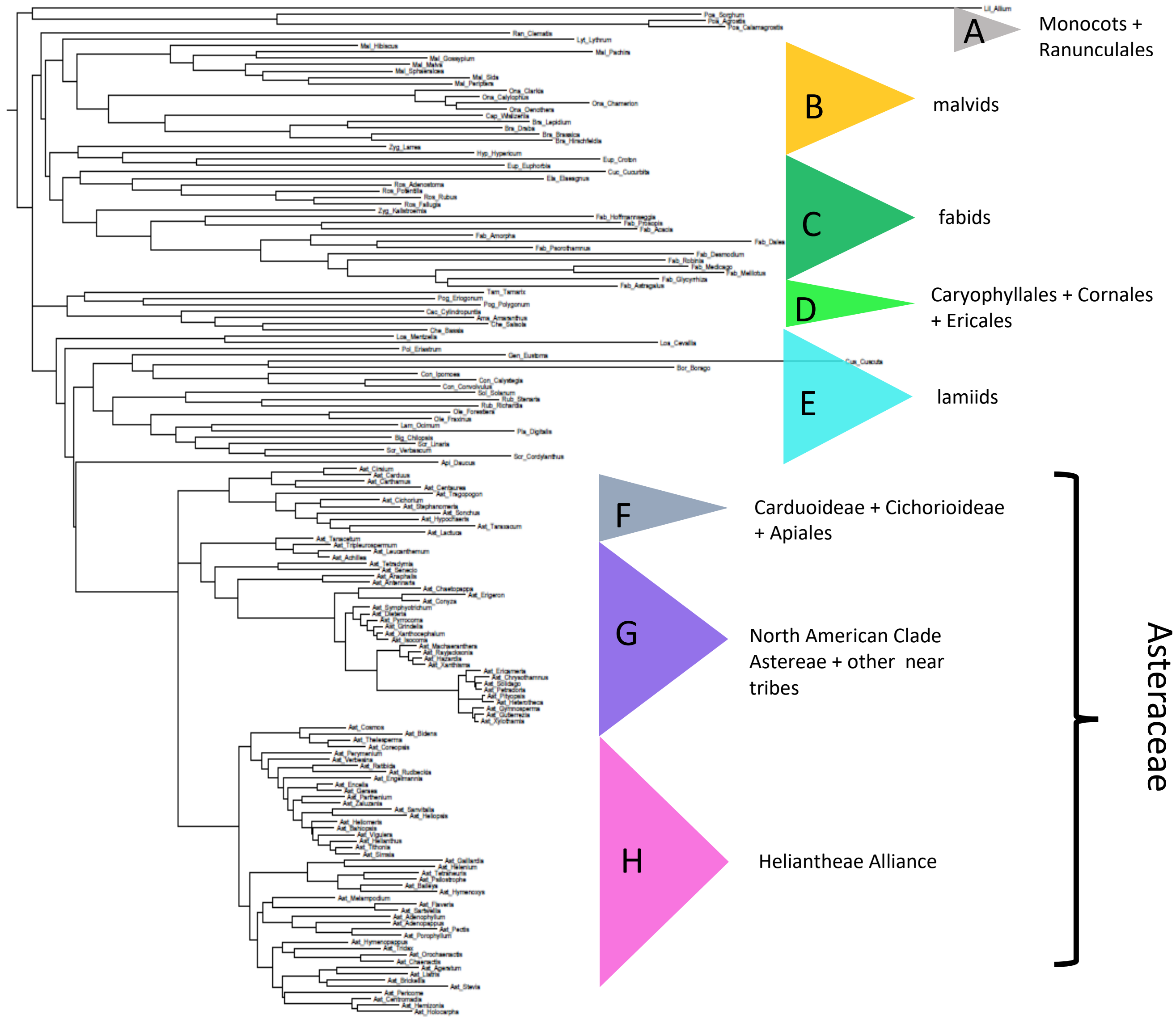


Ancestral character state reconstruction: To study how diet breadth evolved throughout the phylogeny of *Melissodes*, we used Ancestral Character State Reconstruction (ACR) using the ace function in package ape (Paradis et al. 2004) in R. The ML bee phylogeny from Chapter 1 was pruned to the 52 species for which we had diet data. The ecological estimate of diet breadth was converted into three categorical schemes. The first scheme divided *Melissodes* into four groups (Asteraceae = all host records were in the Asteraceae family, Polemoniaceae = all host records were in the Polemoniaceae family, Generalist = more than one host family, and Strong Preference = all but one of the host records were in the Asteraceae family with a single sample from another family). The second scheme replaced Strong Preference with Asteraceae, assuming that the ten species whose diet records show all samples were within Asteraceae with the exception of a single sample, were Asteraceae specialists who occasionally collect pollen from alternate families. The third scheme replaced Strong Preference with Generalist, assuming that these ten species are really generalists, but the data on hand under-sampled their true diet breadth. All three schemes were analyzed under three different models available in ape; ER = equal rates across the entire tree, SYM = forward changes and reversals had equal rates, and ARD = different rates across the entire tree in both directions. Log-likelihoods and the Akaike Information Criterion (AIC) were used to assess the fit of each model and models with more parameters were tested for significance against the next model down with fewer parameters.

The taxonomic estimate of diet breadth was converted into continuous variables in which the number of higher taxonomic groups (genus, tribe, family) of the host plants for each bee species was treated as a character. Counts of families and genera are straight forward, but because Asteraceae is one of the largest families of plants in the world, we compiled a third taxonomic count data set where tribes within Asteraceae were treated equally to all other families. The phylogenetic estimate of diet breadth using the RPD of host plants for each bee species was also treated as a continuous variable. For all of these estimates, ACR analyses were performed in R using the fastAnc and contMap functions in the package phytools (Revell 2012) with confidence intervals calculated for each node.

Ancestral host range reconstruction: We used BioGeoBEARS to study the ancestral ranges of diet breadths of bees. Because BioGeoBEARS requires a time calibrated tree, we used the time calibrated MCMC tree from Chapter 1, pruned to match the species for which we have diet breadth data. Eight host ranges (A=monocots + Ranunculales, B=malvids, C=fabids, D=Caryophyllales + Ericales + Cornales, E=lamiids, F=Carduoideae + Cichorioideae,+ Apiales G=the North American clade of Astereae + Senecioninae + Gnaphalieae + Anthemideae, and H=the Heliantheae Alliance) were defined according to the host plant phylogeny (Fig. 11) and a matrix of each species of bee and their host ranges was constructed. Ranunculales (one sample) was placed with the monocots as it is basal to all other eudicots. Cornales (two genera in four

Fig. 11: Maximum likelihood phylogeny of host plants with clades categorized for BioGeoBEARS analysis for inferring ancestral host plant ranges in *Melissodes*.



samples) and Ericales (one genus) were placed with the Caryophyllales. And Apiales (one sample) was treated with the Carduoideae + Cichorioideae because it is basal to the Asterales. We tested six models implemented in the program using default parameters. Likelihood values of these models were compared using likelihood ratio test and the AIC to directly compare how well the different models fit the data (Matzke, 2013, 2014).

Ancestral host range reconstruction with additional data from the literature: The empirical diet breadth data generated in this study covers 52 of the 129 described species of *Melissodes*. The original *Melissodes* phylogeny published in Wright et al. (2018) contained 89 of the 129 species. In order to broaden the taxonomic scope of this study we collected additional diet data from Wallace LaBerge's revisionary work on the genus (LaBerge 1959a, 1959b, 1961). In his species descriptions, LaBerge included sections on bionomics and flower records. When he was confident of his observations, he included the host specialization in these accounts. Although there is no empirical evidence to confirm his conclusions, LaBerge was considered the expert on this group and had more first-hand knowledge than anyone else. He did not simply rely on the flower records to make these conclusions and often commented that although a bee was collected on other flowers, he was confident it was oligolectic on a particular group. He also mentioned directly looking at the pollen from certain bees in order to ascertain their diet preferences. From these records, we were able to generate literature-based data for additional 25 species. This information was not detailed enough to estimate RPD so only the ancestral range analyses were rerun with the additional data.

Beta Diversity of Host Plants: In order to compare diet breadths of closely related species of bees to more distantly related species of bees, we made pairwise comparisons of the phylogenetic distance between each pair of species of bee and the phylogenetic beta diversity of their hosts. Phylogenetic beta diversity was calculated using the phylosor function in the package picante in R on the host plant phylogeny and mean pairwise distance between each pair of bee species was calculated using the cophenetic function in the package ape in R on the bee phylogeny. These measurements were then regressed to determine if there was a significant correlation between the relatedness of the bees and the overlap of their diets.

Pagel's Phylogenetic Signal Metrics: To test whether there was phylogenetic signal on the bee tree in the phylogenetic estimate of diet breadth and where the signal is strongest, we calculated Pagel's λ, δ and κ (Münkemüller 2012) using the pgls function in the package caper (Orme *et al*., 2018) in R. Pagel's λ indicates whether or not there is phylogenetic signal in the tree (1 = the phenotype evolves according to Brownian motion; 0 = no phylogenetic signal, something other than phylogenetic relationship is responsible to the phenotypic change across the tree). Kappa tests whether the phenotypic change across the tree occurs early in the tree or towards the tip (<1 = phenotypic change occurred early in the tree, 1= gradualistic change from the base to the tips, >1 = most of the change occurred towards the tips of the tree. Delta indicates the effect of branch length on the phylogenetic signal (<1 = punctuational evolution, change in phenotype occurred with relatively short branch lengths, 0 = gradualistic change, >1 = longer branch lengths have more than expected phenotypic change). We repeated the analyses after pruning the tree to just the *Eumelissodes* + *Callimelissodes* clade to see if the location and strength of the phylogenetic signal changed when zooming in on this inner clade.

Diversification analysis: To test for changes in speciation and/or extinction rates across the phylogenetic tree, we used the time calibrated bee phylogeny from Wright et al. (2018) which included all available species of *Melissodes*, not just the ones for which we had diet breadth data. We ran the program Bayesian Analysis of Macroevolutionary Mixtures (BAMM, Rabosky, 2014) for 500,000,000 generations, sampling every 50,000 and limited the smallest clade to 5 species. Because we know that we did not include all the known species of *Melissodes* (89 of 129 known species), we adjusted the program to account for known missing species within each subgenus. We used the package BAMMtools (Rabosky et al., 2014) in R to determine priors and to interpret the results.

Results:

Molecular identification of pollen samples: A total of 1,441 pollen samples were taken from *Melissodes* females and were subject to DNA extraction, PCR amplification of ITS1 gene, and Sanger sequencing. A total of 426 samples did not successfully amplify at all (30%) and 210 samples had more than one species of pollen making the sequences unreadable using Sanger sequencing methods (15%). For those samples that were properly amplified and sequenced, 724 samples (50%) resulted in angiosperm DNA sequences and 79 samples resulted in fungal DNA (5%). The fungal sequences were typically indoor molds that are common in insect collections. Of the samples with more than one species of DNA, 70 samples were successfully processed using metabarcoding techniques.

Generic level matches of the ITS1 gene fragment from pollen samples to known Angiosperm DNA sequences deposited in the NCBI nucleotide database were accepted if the match had >98% identity and no other genera matched equally well using the ‘max score’ and ‘E-value’ provided by the search. Most of the time, the BLAST results matched equally to a single species or several species in a genus. For example, a specimen collected from a bee with the host label indicating that it was collected from *Helianthus anomolus* S.F. Blake matched *H. anomolus* with 99% identity, 512 max score and E value = 5e-141. It matched to *H. annuus* plus ten other species of *Helianthus* with 99% identity, 505 max score and E value 8e-139. The rarity of *H. anomolus* and better score increased our confidence of the species level identification. There were very few cases where the pollen was obviously from contamination. One sample matched *Platanus* x*hispanica* Mill. Ex Münchh., the London planetree, which is a common wind pollinated ornamental tree that was planted outside the laboratory where the samples were processed. Not all wind pollinated plants were excluded as *Melissodes* is known to collect pollen from wind pollinated plants (personal observation, Cane et al. 1992). A list bee specimens, summary label information, BLAST identifications, and specimen repository locations can be found in Appendix C.

Of the bee specimens, 295 had host information on the labels. In comparing the label information to the BLAST results of the pollen samples, 83% of the DNA BLAST results matched the label data to the family level, 55% to genus, and 40% to species. These were most likely bees that were collected on a flower that they were nectaring on and not collecting pollen from. The bias in these results leans heavily towards Asteraceae. For the bee specimens with label data that states that they were collected on Asteraceae, 97.5% of their pollen samples also matched to Asteraceae. Of bee specimens that were collected from all other families, only 45.7% matched to the family level and, of the mismatched samples, 46% were bees that were collected from a non-Asteraceae plant, but the pollen matched to Asteraceae instead.

Table 3: Summary diet breadth for 52 *Melissodes* species.

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
Melissodes (Callimelissodes)												
coloradensis	9	1.2873	1	3	4	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Eupatorieae	*Liatris*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
compositus	14	3.4240	3	4	8	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Liliaceae					*Allium*
							Onagraceae					*Clarkia*
glenwoodensis	13	1.1936	1	2	6	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
lupinus	14	2.0988	1	4	10	Asteraceae	Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Encelia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Madieae	*Centromadia*
							Asteraceae	Asteroideae	yes	no	Madieae	*Hemizonia*
							Asteraceae	Asteroideae	yes	no	Madieae	*Holocarpha*
							Asteraceae	Carduoideae	no	no	Cardueae	*Centaurea*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
lustrus	5	0.9151	1	2	4	NAC	Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
Melissodes (Callimelissodes) cont.												
metenuus	12	5.0371	6	11	12	Generalist	Apiaceae					*Daucus*
							Asteraceae	Asteroideae	no	no	Anthemideae	*Tanacetum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	no	Gnaphalieae	*Anaphalis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Hypochaeris*
							Hypericaceae					*Hypericum*
							Onagraceae					*Chamerion*
							Plantaginaceae					*Digitalis*
							Scrophulariaceae					*Verbascum*
plumosus	5	1.9199	2	4	5	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Adenophyllum*
							Asteraceae	Carduoideae	no	no	Cardueae	*Centaurea*
							Polygonaceae					*Eriogonum*
stearnsi	15	4.7203	6	7	8	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Brassicaceae					*Brassica*
							Brassicaceae					*Hirschfeldia*
							Cuscutaceae					*Cuscuta*
							Lamiaceae					*Ocimum*
							Polygonaceae					*Eriogonum*
							Rosaceae					*Adenostoma*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
Melissodes (Eumelissodes)												
agilis	18	1.5281	1	3	6	Asteraceae	Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Rudbeckia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Simsia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Sonchus*
appressus	5	1.1356	1	2	3	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
bicoloratus	5	1.4266	1	3	4	Asteraceae	Asteraceae	Asteroideae	no	yes	Astereae	*Chrysothamnus*
							Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Tetradymia*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Stephanomeria*
bimatris	17	1.9813	2	3	9	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Bahiopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Tamaraceae					*Tamarix*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
confusus	29	3.2417	1	8	19	Asteraceae	Asteraceae	Asteroideae	no	yes	Astereae	*Chrysothamnus*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gymnosperma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Pyrrocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Bidens*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Cosmos*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Hymenoxys*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Heliomeris*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Heliopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Simsia*
							Asteraceae	Asteroideae	yes	no	Millerieae	*Tridax*
							Asteraceae	Asteroideae	yes	no	Perityleae	*Pericome*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Asteraceae	Carduoideae	no	no	Cardueae	*Carduus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
coreopsis	22	3.3798	2	7	15	Generalist	Asteraceae	Asteroideae	no	no	Anthemideae	*Leucanthemum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Solidago*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Coreopsis*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Gaillardia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Ratibida*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Carduoideae	no	no	Cardueae	*Carduus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Polygonaceae					*Polygonum*
fasciatellus	15	1.4771	1	2	7	Asteraceae	Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Taraxacum*
grindeliae	11	2.5668	1	6	9	Asteraceae	Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Petradoria*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Coreopsis*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Hymenoxys*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Ratibida*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Taraxacum*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
humilior	8	1.4773	1	3	6	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
hymenoxidis	7	1.5395	1	2	6	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Chrysothamnus*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Pyrrocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Gaillardia*
interruptus	18	2.8345	2	6	9	Generalist	Asteraceae	Asteroideae	yes	no	Coreopsideae	*Bidens*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Cosmos*
							Asteraceae	Asteroideae	yes	no	Eupatorieae	*Stevia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Perymenium*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Simsia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Tithonia*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Adenopappus*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Tragopogon*
							Loasaceae					*Cevallia*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
limbus	21	2.7545	2	5	13	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Pityopsis*
							Asteraceae	Asteroideae	no	yes	Astereae	*Solidago*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Baileya*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Hymenoxys*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Parthenium*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Sanvitalia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Flaveria*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Pectis*
							Zygophyllaceae					*Kallstroemia*
menuachus	20	2.4988	2	3	12	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Viguiera*
							Fabaceae					*Hoffmannseggia*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
microstictus	31	3.8379	2	8	18	Generalist	Asteraceae	Asteroideae	no	no	Anthemideae	*Achillea*
							Asteraceae	Asteroideae	no	no	Anthemideae	*Tripleurospermum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Hazardia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Solidago*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	no	no	Gnaphalieae	*Anaphalis*
							Asteraceae	Asteroideae	no	no	Gnaphalieae	*Antennaria*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Helenium*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Asteraceae	Carduoideae	no	no	Cardueae	*Carduus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Centaurea*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Hypericaceae					*Hypericum*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
montanus	21	2.3683	1	4	16	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Chrysothamnus(+5)*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gymnosperma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Xanthocephalum(+3)*
							Asteraceae	Asteroideae	no	yes	Astereae	*Xylothamia(+1)*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Bidens*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Coreopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Heliomeris*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Heliopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Sanvitalia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Simsia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Tithonia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Viguiera*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Porophyllum*
pallidisignatus	20	3.3786	2	8	14	Generalist	Asteraceae	Asteroideae	no	no	Anthemideae	*Tanacetum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Solidago*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Coreopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Engelmannia*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Asteraceae	Carduoideae	no	no	Cardueae	*Centaurea*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Taraxacum*
							Rosaceae					*Potentilla*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
paucipuncta	3	2.0083	3	3	3	Generalist	Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Cactaceae					*Cylindropuntia*
							Fabaceae					*Acacia*
perpolitus	5	0.8733	1	1	2	NAC	Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
persimilis	12	1.5123	1	4	7	HA	Asteraceae	Asteroideae	yes	no	Chaenactideae	*Chaenactis*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Bidens*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Cosmos*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Tithonia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Porophyllum*
rufipes	5	1.0134	1	2	3	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Hazardia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Rayjacksonia(+1)*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Hymenoxys*
saponellus	3	2.2525	4	4	5	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Convolvulaceae					*Convolvulus*
							Loasaceae					*Mentzelia*
							Malvaceae					*Malva*
semilupinus	12	1.9586	2	4	7	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Loasaceae					*Mentzelia*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
snowii	22	4.2717	3	8	15	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Xanthisma*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Baileya*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Asteraceae	Carduoideae	no	no	Cardueae	*Carthamus*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Taraxacum(+3)*
							Brassicaceae					*Draba*
							Fabaceae					*Dalea*
subagilis	19	1.2853	1	2	7	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
subillatus	13	2.5234	1	6	9	Asteraceae	Asteraceae	Asteroideae	no	no	Anthemideae	*Leucanthemum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Erigeron*
							Asteraceae	Asteroideae	no	yes	Astereae	*Solidago(+4)*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Coreopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Ratibida*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Rudbeckia*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Sonchus*
submenuacha	6	0.7429	1	1	2	HA	Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
trinodis	27	3.8517	4	8	13	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Solidago(+1)*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Coreopsis*
							Asteraceae	Asteroideae	yes	no	Eupatorieae	*Ageratum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Heliopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Ratibida*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Rudbeckia*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Cichorium*
							Convolvulaceae					*Calystegia(+1)*
							Elaeagnaceae					*Elaeangus*
							Fabaceae					*Medicago*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
tristis	33	10.8252	13	17	26	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Chaetopappa*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	yes	no	Coreopsideae	*Thelesperma*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Hymenoxys*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Encelia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Geraea*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	no	no	Senecioneae	*Senecio*
							Bignoniaceae					*Chilopsis*
							Brassicaceae					*Lepidium*
							Chenopodiaceae					*Salsola*
							Fabaceae					*Dalea*
							Fabaceae					*Glycyrrhiza(+7)*
							Fabaceae					*Melilotus*
							Fabaceae					*Psorothamnus*
							Loasaceae					*Mentzelia*
							Malvaceae					*Sphaeralcea*
							Onagraceae					*Oenothera*
							Polygonaceae					*Eriogonum*
							Rosaceae					*Fallugia*
							Scrophulariaceae					*Cordylanthus*
							Tamaraceae					*Tamarix*
							Zygophyllaceae					*Kallstroemia(+6)*
							Zygophyllaceae					*Larrea*
utahensis	11	1.2160	1	2	7	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Chrysothamnus*
							Asteraceae	Asteroideae	no	yes	Astereae	*Dieteria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Ericameria*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Eumelissodes)* cont.**												
velutinus	3	0.7222	1	1	1	Polemoniaceae	Polemoniaceae					*Eriastrum*
verbesinarum	25	2.1643	1	4	13	Asteroideae	Asteraceae	Asteroideae	no	yes	Astereae	*Chaetopappa*
							Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Isocoma*
							Asteraceae	Asteroideae	no	yes	Astereae	*Machaeranthera*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Xanthisma*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Baileya*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Hymenoxys*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Encelia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Pectis*
vernalis	14	2.2804	2	5	8	Generalist	Asteraceae	Asteroideae	yes	no	Chaenactideae	*Orochaenactis*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Baileya*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Psilostrophe*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Bahiopsis*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Encelia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Stephanomeria*
							Malvaceae					*Malva*
vernoniae	4	2.4712	3	4	4	Generalist	Asteraceae	Asteroideae	yes	no	Eupatorieae	*Liatris*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Fabaceae					*Medicago*
							Solanaceae					*Solanum*
wheeleri	7	1.4874	1	3	6	HA	Asteraceae	Asteroideae	yes	no	Helenieae	*Baileya*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Ratibida*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Rudbeckia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Pectis*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
Melissodes (Heliomelissodes)												
desponsus	4	1.6068	2	2	3	Generalist	Asteraceae	Carduoideae	no	no	Cardueae	*Carduus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Fabaceae					*Astragalus*
rivalis	26	6.0403	7	10	12	Generalist	Asteraceae	Asteroideae	yes	no	Eupatorieae	*Brickellia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Centaurea*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Hypochaeris(+1)*
							Convolvulaceae					*Convolvulus(+4)*
							Fabaceae					*Acacia*
							Malvaceae					*Gossypium*
							Malvaceae					*Malva*
							Plantaginaceae					*Digitalis*
							Poaceae					*Agrostis*
							Scrophulariaceae					*Linaria*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
Melissodes (Melissodes)												
bimaculatus	26	9.9261	11	14	19	Generalist	Amaranthaceae					*Amaranthus*
							Asteraceae	Asteroideae	no	no	Anthemideae	*Leucanthemum*
							Asteraceae	Asteroideae	no	yes	Astereae	*Gutierrezia*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Verbesina*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Cichorium*
							Asteraceae	Cichorioideae	no	no	Cichorieae	*Lactuca*
							Boraginaceae					*Borago*
							Convolvulaceae					*Calystegia*
							Convolvulaceae					*Ipomoea*
							Cucurbitaceae					*Cucurbita*
							Fabaceae					*Medicago*
							Fabaceae					*Melilotus*
							Malvaceae					*Gossypium*
							Malvaceae					*Hibiscus*
							Malvaceae					*Sphaeralcea*
							Oleaceae					*Forestiera(+4)*
							Onagraceae					*Oenothera*
							Poaceae					*Sorghum*
							Polygonaceae					*Polygonum*
colliciatus	5	3.5380	5	5	5	Generalist	Chenopodiaceae					*Salsola*
							Euphorbiaceae					*Croton*
							Fabaceae					*Dalea*
							Malvaceae					*Sphaeralcea*
							Zygophyllaceae					*Kallstroemia*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)

species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Melissodes)* cont.**												
communis	24	6.7837	7	10	15	Generalist	Asteraceae	Asteroideae	yes	no	Coreopsideae	*Bidens*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Porophyllum*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Convolvulaceae					*Convolvulus*
							Fabaceae					*Amorpha(+1)*
							Fabaceae					*Dalea*
							Fabaceae					*Medicago*
							Gentianaceae					*Eustoma*
							Onagraceae					*Calylophus*
							Onagraceae					*Oenothera*
							Rosaceae					*Fallugia*
							Rosaceae					*Rubus*
							Rubiaceae					*Richardia*
							Rubiaceae					*Stenaria*
comptoides	7	3.4694	5	5	5	Generalist	Amaranthaceae					*Amaranthus*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Euphorbiaceae					*Euphorbia*
							Fabaceae					*Melilotus*
							Malvaceae					*Gossypium*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Melissodes)* cont.**												
gilensis	16	8.3900	6	8	15	Generalist	Asteraceae	Asteroideae	no	yes	Astereae	*Grindelia*
							Asteraceae	Asteroideae	no	yes	Astereae	*Heterotheca*
							Asteraceae	Asteroideae	no	yes	Astereae	*Symphyotrichum*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Carduoideae	no	no	Cardueae	*Cirsium*
							Cucurbitaceae					*Cucurbita*
							Fabaceae					*Acacia*
							Fabaceae					*Calamagrostis*
							Fabaceae					*Desmodium*
							Fabaceae					*Melilotus*
							Fabaceae					*Robinia*
							Malvaceae					*Malva*
							Malvaceae					*Sphaeralcea*
							Onagraceae					*Oenothera*
							Ranunculaceae					*Clematis*
paroselae	16	5.3725	7	8	10	Generalist	Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Asteraceae	Asteroideae	yes	no	Tageteae	*Pectis*
							Brassicaceae					*Lepidium*
							Capparaceae					*Wislizenia*
							Fabaceae					*Acacia*
							Fabaceae					*Psorothamnus*
							Malvaceae					*Sida*
							Malvaceae					*Sphaeralcea*
							Oleaceae					*Fraxinus*
							Zygophyllaceae					*Kallstroemia*

Table 3: Summary diet breadth for 52 *Melissodes* species (cont.)												
species	sample #	PD	Family #	Tribe #	Genus #	Ecological specialization	blast_family	blast_subfamily	HA	NA	blast_tribe	blast_genus
***Melissodes (Melissodes)* cont.**												
tepaneca	11	5.8407	6	8	11	Generalist	Asteraceae	Asteroideae	yes	no	Eupatorieae	*Ageratum*
							Asteraceae	Asteroideae	yes	no	Helenieae	*Tetraneuris*
							Asteraceae	Asteroideae	yes	no	Heliantheae	*Simsia*
							Fabaceae					*Dalea*
							Fabaceae					*Prosopis*
							Gentianaceae					*Eustoma*
							Lythraceae					*Lythrum*
							Malvaceae					*Pachira*
							Malvaceae					*Periptera*
							Malvaceae					*Sida*
							Orchidaceae					*Aspidogyne*
thelypodii	13	4.0990	7	7	9	Generalist	Asteraceae	Asteroideae	yes	no	Heliantheae	*Helianthus*
							Chenopodiaceae					*Bassia(+1)*
							Convolvulaceae					*Convolvulus*
							Fabaceae					*Medicago*
							Fabaceae					*Melilotus*
							Malvaceae					*Gossypium*
							Malvaceae					*Sphaeralcea*
							Orchidaceae					*Aspidogyne*
							Zygophyllaceae					*Kallstroemia*

In total, we were able to identify enough pollen samples from museum specimens in order to estimate the diet breadth of 52 species of *Melissodes*. See Table 3 for a summary of generic level identifications of the pollen samples resulting from the BLAST search for each of these 52 *Melissodes* species.

Host plant phylogeny: The host plant tree is not a 'true' plant phylogeny, as it is based on a relatively small amount of data, both in terms of molecular data and taxon sampling, and was only constrained on a very broad scale. The largest discrepancy was that *Larrea* and *Kallstroemia*, the only two Zygophyllaceae in the tree, did not place as sister to each other.

Ancestral Character State Reconstruction. Using the ecological estimate of diet breadth, the model with the highest log-likelihood, and that made the most biological sense, was the second categorical scheme that treated species with a Strong Preference for Asteraceae as though they were strict Asteraceae specialists (Fig. 12A; Schemes 1 and 3 are presented in Fig. 12B & C). The log-likelihood of the ARD model was higher, but was not significantly different from the SYM model (LnL = -32.56, Table 4). The MRCA of these bees was most likely polylectic. There was a roughly equal probability that the MRCA of *Melissodes* s.s. + *Eumelissodes* + *Callimelissodes* was oligolectic or polylectic.

Fig. 12: Ancestral character state reconstruction on ecological data. A. Scheme 2, treating generalists with a strong preference for Asteraceae as Asteraceae specialists; B. Scheme 1, treating generalists with a strong preference for Asteraceae as a separate group; C. Scheme 3, treating generalists with a strong preference for Asteraceae as a generalist.

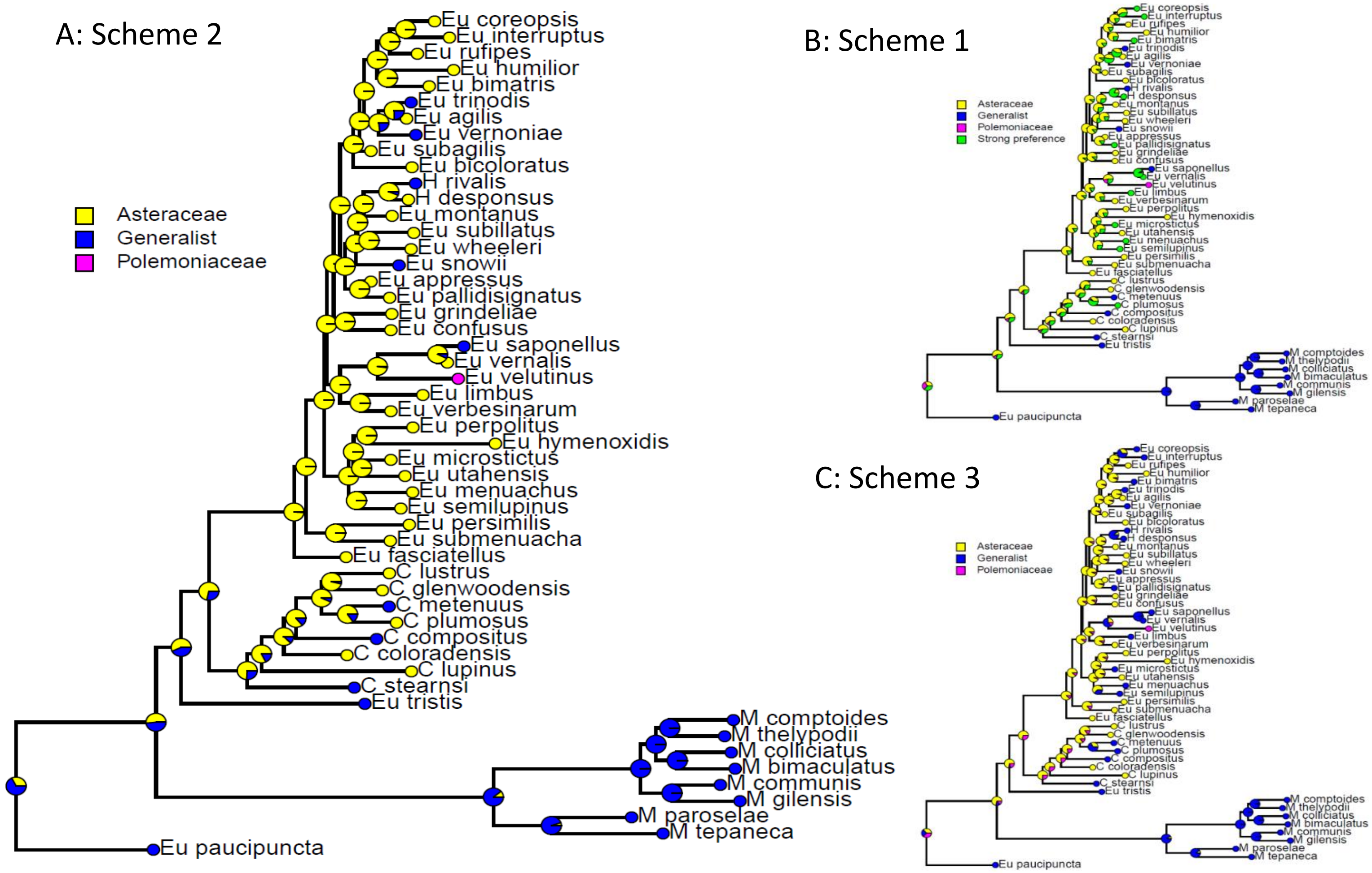
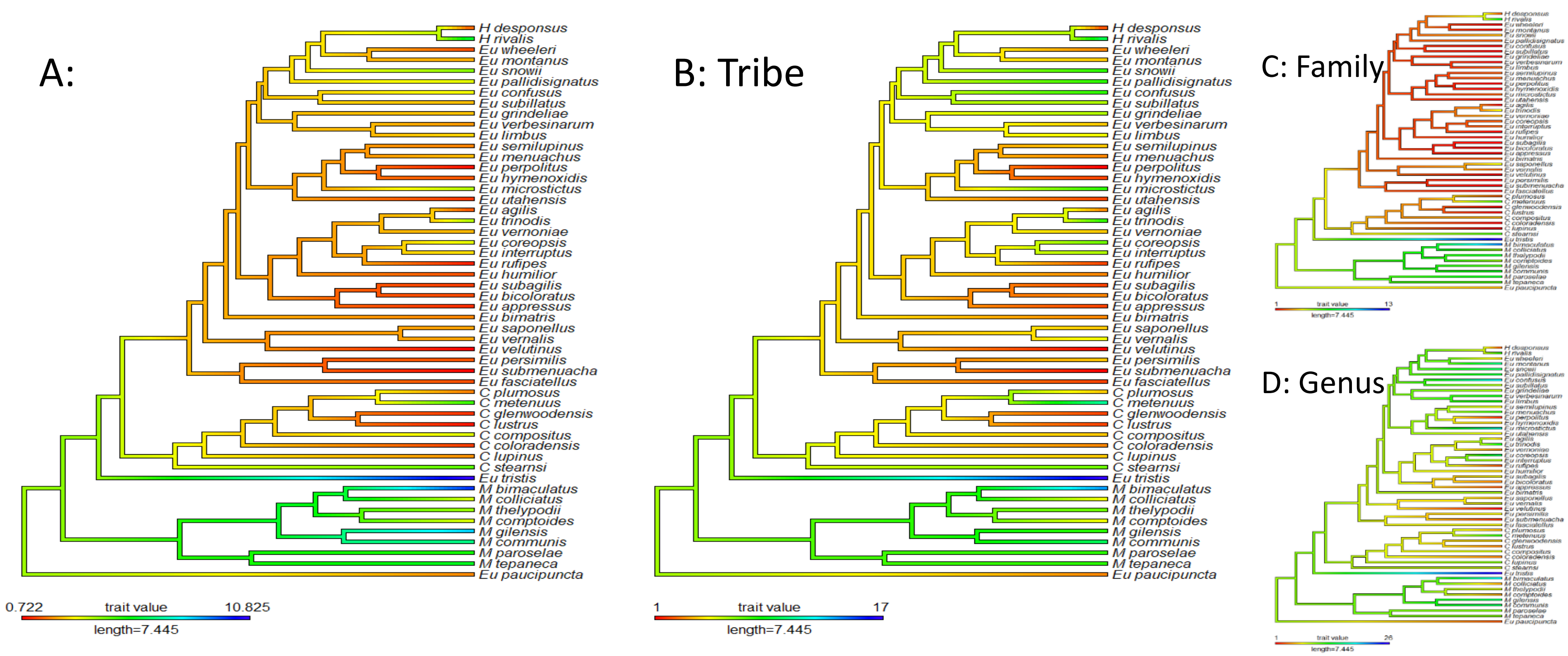


Fig. 13: Ancestral character state reconstruction on taxonomic and phylogenetic data. A. Phylogenetic diversity (RPD) of host plants; B. Tribe Richness, counts of host plant families, treating tribes of Asteraceae equal to other families; C. Family richness, counts of host plant families; D. Genus richness, counts of host plant genera.



And the common ancestor of *Callimelissodes* + *Eumelissodes* was most likely oligolectic on Asteraceae.

Table 4. Ancestral Character State Reconstruction of ecological measurements
Log-likelihoods of each model and probabilities of diet breadth at root node

	Log-likelihood	Asteraceae	Generalist	Polemoniaceae	Strong Preference
Scheme 1					
ER	-64.49342	0.232	0.415	0.176	0.176
SYM	-56.44592	0.205	0.627	0.002	0.166
ARD	-51.08812	0.33	0	0.319	0.351
Scheme 2					
ER	-37.50038	0.235	0.663	0.102	
SYM*	-32.55791	0.325	0.675	0.001	
ARD*	-30.86503	0.503	0	0.497	
Scheme 3					
ER	-50.94534	0.284	0.477	0.239	
SYM	-39.61793	0.498	0.5	0.002	
ARD	-37.49806	0.359	0.284	0.356	

*ARD and SYM not significantly different

Using the phylogenetic estimate of diet breadth (RPD) as a continuous trait in an ancestral character reconstruction shows similar patterns to the ecological data (Fig. 13a). If diet breadth evolution is additive or subtractive, meaning that species acquire or lose host plants in a stepwise fashion, this is a good visual representation of the likely progression of changes in diet breadth throughout the tree. In comparison to the phylogenetic estimation of diet breadth, the taxonomic estimation of diet breadth either over- or underestimated ancestral states depending on which taxonomic level was used. Family richness (Fig. 13c) overestimated specialization, genus richness (Fig. 13d) underestimated specialization, and tribe richness (Fig. 13b) was the most similar to the phylogenetic analysis.

Table 5. BioGeoBEARS model comparisons for empirical diet breadth data.							
	LnL	numparams	dispersal	extinction	founder_event	AIC	AIC_wt
DEC	-255.6	2	0.036	1.00E-12	0	515.2	1.70E-14
DEC+J	-255.6	3	0.036	1.00E-12	1.00E-05	517.2	6.30E-15
DIVALIKE	-261.9	2	0.039	1.00E-12	0	527.8	3.20E-17
DIVALIKE+J	-261.9	3	0.039	1.00E-12	1.00E-05	529.8	1.20E-17
BAYAREALIKE*	-224.2	2	0.016	0.04	0	452.4	0.73
BAYAREALIKE+J*	-224.2	3	0.016	0.04	1.00E-05	454.4	0.27
*not significantly different							

Ancestral host range reconstruction: In the BioGeoBEARS analysis, the BAYAREALIKE+J model had the highest log likelihood (-224.21) and the J parameter improved the fit of the model according to the AIC (Table 5). The J component represents founder event speciation, and in the case of host plants, would suggest host switching events, not a gradual change in diet breadth. The BAYAREALIKE+J model suggests that the MRCA of *Melissodes* was a generalist (Fig. 14), but the ancestor of *Callimelissodes* + *Eumelissodes* was most likely a specialist on Asteroideae (G+H). Only two lineages became more specialized on just the Helianthus Alliance (H only) and a few lineages widened their diet breath to include Carduoideae and/or Cichorioideae (F+G+H) and therefore encompass all of Asteraceae. Polylecty evolved several times within the *Eumelissodes* + *Callimelissodes* clade but always includes Asteraceae as well as other plant families. As expected *Melissodes* s.s. are all polylectic and all but one of the *Melissodes* s.s. species collected pollen from Asteraceae as well as other families.

Fig. 14: Ancestral host range reconstruction (BioGeoBEARS) on empirical data; model = BAYAREALIKE+j.

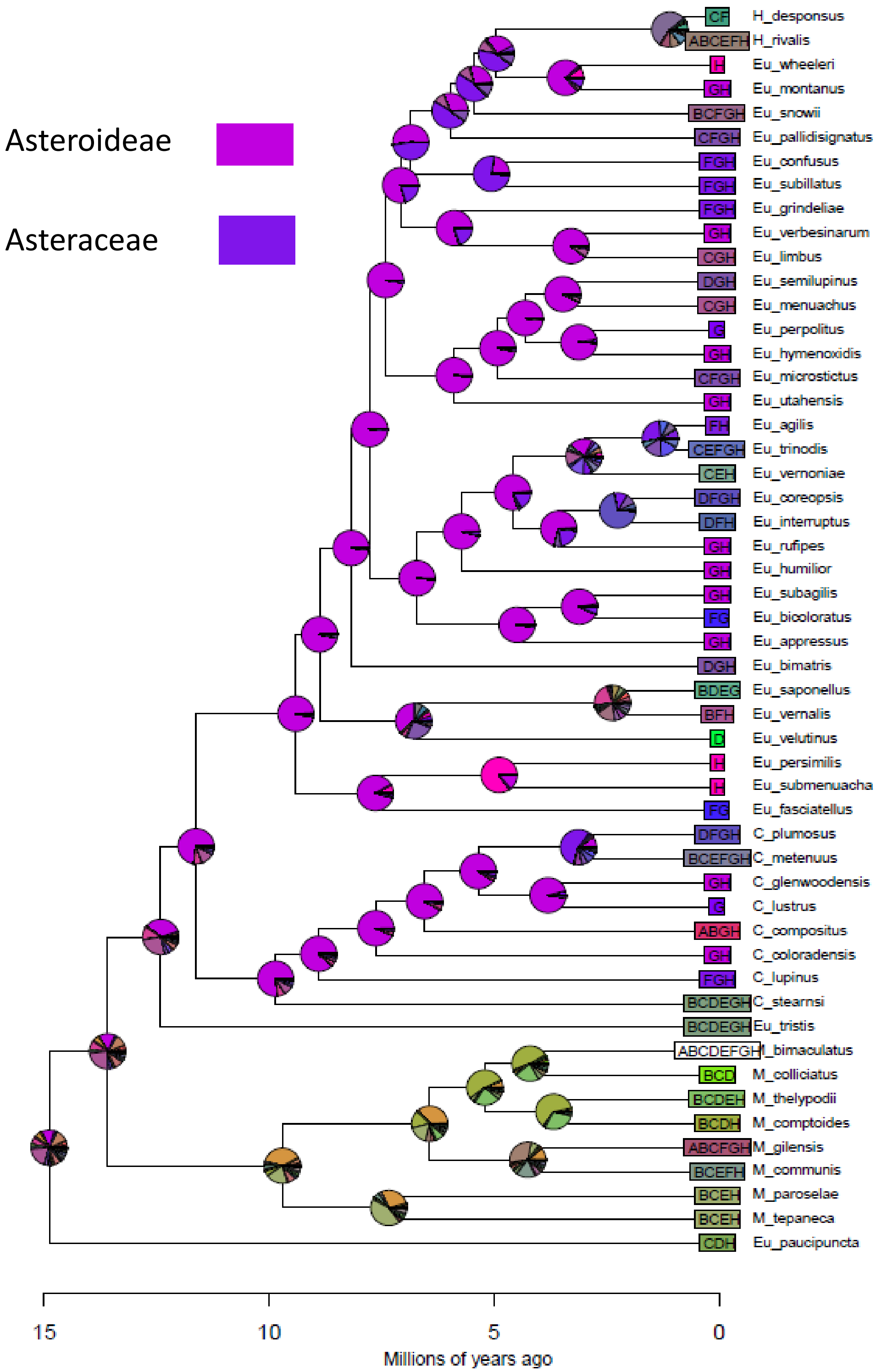
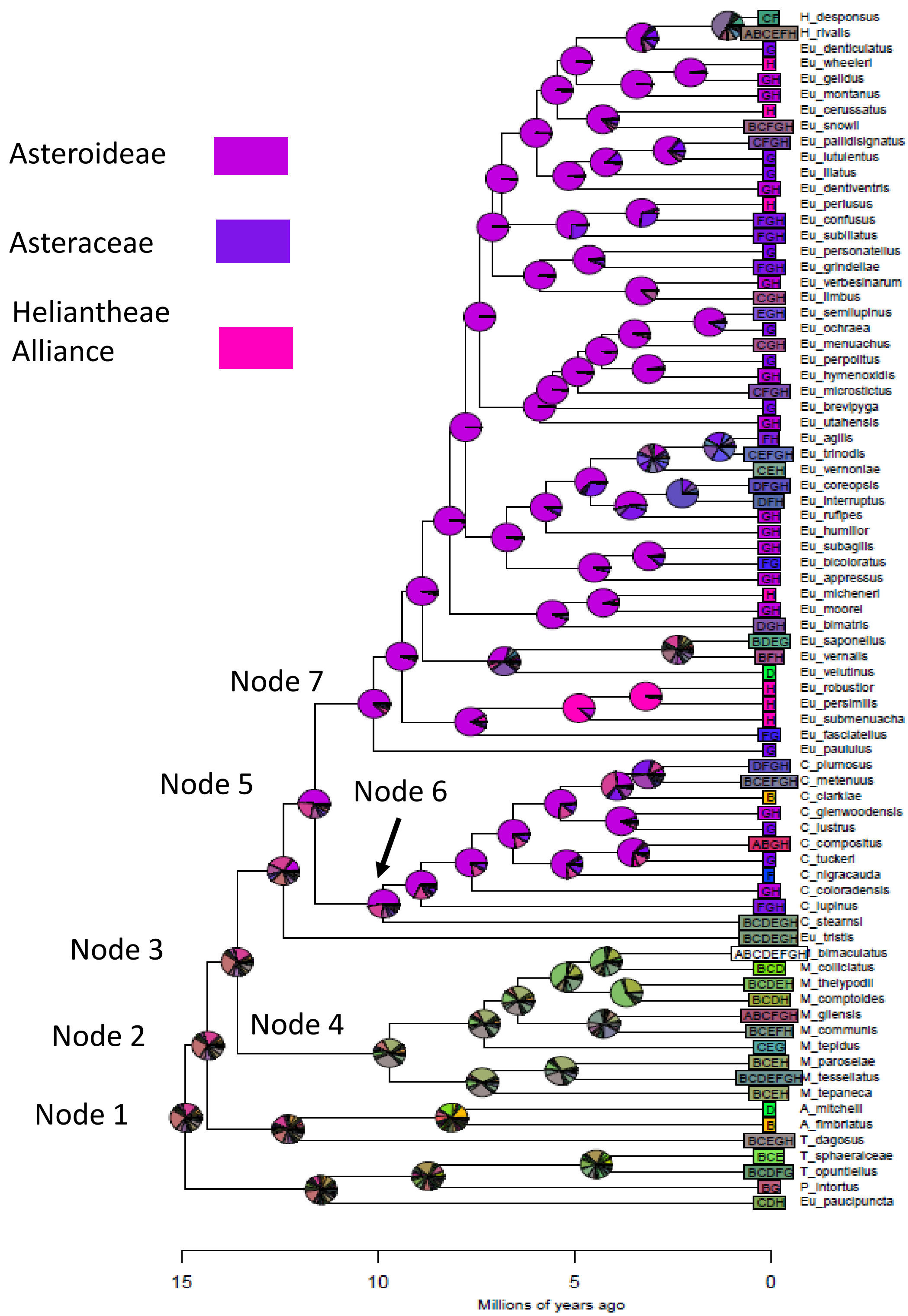


Fig. 15: Ancestral host range reconstruction (BioGeoBEARS) on empirical data and data taken from the LaBerge (1956a, b, and 1961); model = BAYAREALIKE+j. Individual node labels are referred to directly in the text.



Ancestral host range reconstruction with additional data from the literature: With data from the literature, The BAYARELIKE+J model again fit the data best (LnL = -320.25; Table 6) and the overall patterns of ancestral ranges were the same (Fig. 15).

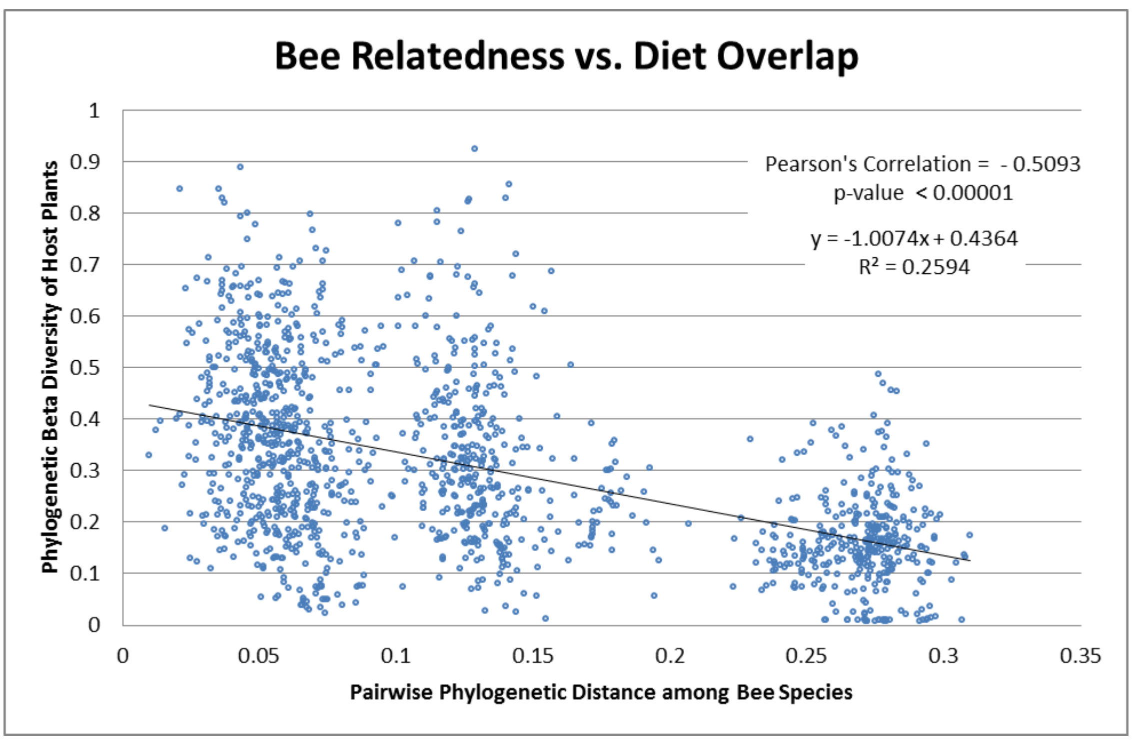
Table 6. BioGeoBEARS model comparisons for empirical and literature diet breadth data.

	LnL	numparams	dispersal	extinction	founder_event	AIC	AIC_wt
DEC	-350.6	2	0.032	4.00E-08	0	705.2	4.70E-14
DEC+J	-350.6	3	0.032	1.00E-12	0.0004	707.2	1.80E-14
DIVALIKE	-358	2	0.036	1.00E-12	0	719.9	3.10E-17
DIVALIKE+J	-358	3	0.036	1.00E-12	1.00E-05	721.9	1.10E-17
BAYAREALIKE*	-320.3	2	0.015	0.064	0	644.5	0.73
BAYAREALIKE+J*	-320.2	3	0.015	0.063	0.0005	646.5	0.27

*not significantly different

Probabilities of each range or range combination at important nodes can tell us more about the evolution of diet breadth in this group (Fig. 15). For the root node (node 1 on Fig. 15) of all *Melissodes*, the combined probability that the host diet of the MRCA of the entire genus included pollen from Asteroideae was 98.6% and the probability that it included either the NAC or the HA plus at least one non-Asteraceae group was 98.1%. The other group that was best represented at the root was the malvids. Moving inwards, the next important node is the one splitting *Apomelissodes* + *Psilomelissodes* + *Tachymelissodes* from *Melissodes* s.s. + *Callimelissodes* + *Eumelissodes* (node 2). At this node the ranges that were most probable were those that included Asteroideae plus malvids (comb. prob. = 69.4). The same was true for the node splitting *Melissodes* s.s. from *Eumelissodes* + *Callimelissodes* (node 3; comb. prob. = 74.7). At the node at the base of all *Melissodes* s.s.(node 4), the two ranges with the highest independent probabilities were malvids + fabids + lamiids + Asteroideae (BCEGH) with a probability of 29.0 and malvids + fabids + lamiids + HA (BCEH) with a probability of 20.4. The node splitting *Callimelissodes* from *Eumelissodes* (node 5) had a 46.5 probability that the host range was Asteroideae and a combined probability of 33.8 for the Asteroideae + either the malvids or the Caryophyllales. The MRCA of *Callimelissodes* (node 6), the host range was most probably Asteroideae (51.3) or Asteroideae + malvids (20.5). And finally at the base of *Eumelissodes* (node 7) specialization on Asteroideae had a probability of 86.3 and only 6.1 probability that the MRCA fed on Asteroideae + malvids.

Fig. 16: Regression of pairwise measurements of phylogenetic distance among bee species against pairwise beta diversity of their diet breadths. Clumping of three clouds are the result of distances between the three major subgenera of Melissodes.



Beta diversity of host plants: Pairwise measurements of phylogenetic distance of the bee species was negatively correlated with pairwise measurements of phylogenetic beta diversity of the host plants (-0.5093, p-value < 0.0001, Fig. 16).

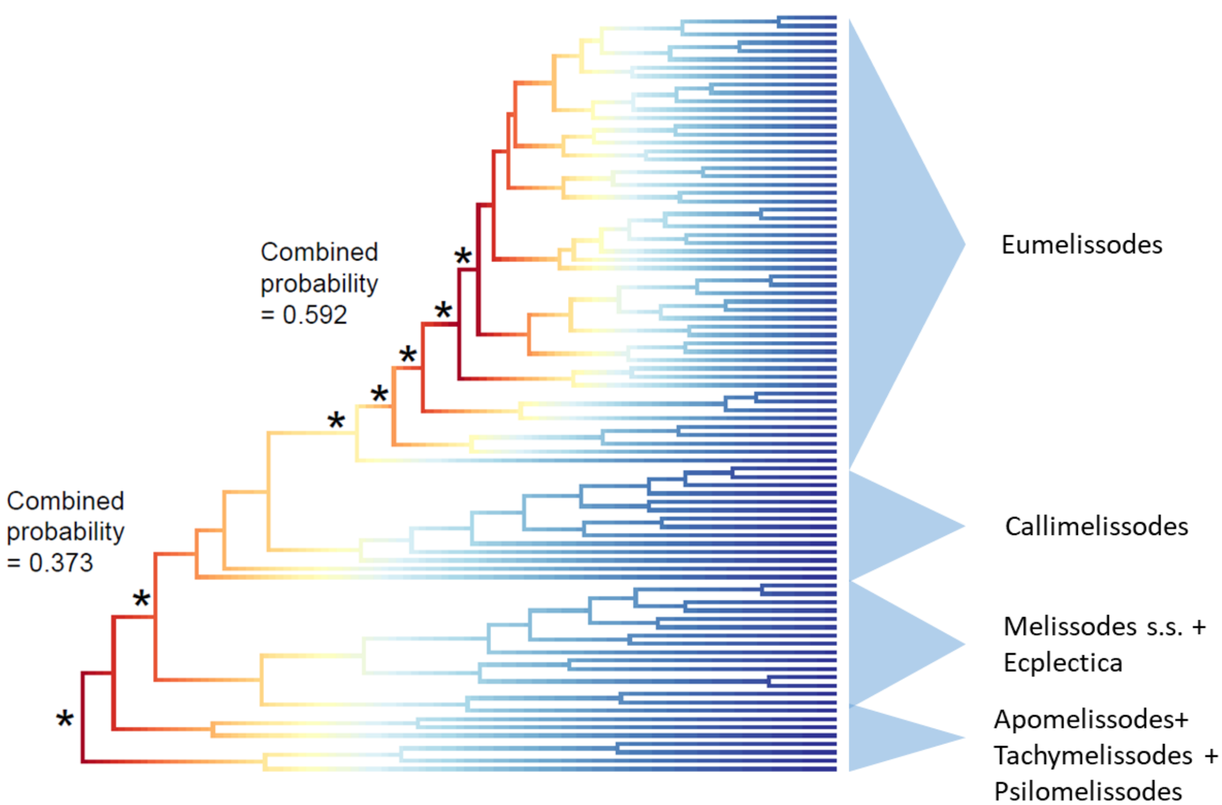
Pagel's phylogentic signal metrics: Treating the root phylogenetic diversity (RPD) as the continuous trait, there was phylogenetic signal (λ) of 0.804, where 1 indicates Brownian motion along a phylogenetic tree. The δ was not significantly different to 1 or 3 (1.795) and indicates that the signal was either gradualistic or stronger towards the tips. The κ was not significantly different to 1 (0.941), indicating gradualistic change along branches. When only the *Callimelissodes* + *Eumelissodes* clade was analyzed without *Melissodes* s.s., the λ did not change much (0.810), but the δ was not significantly different to 0.5 or 1 which indicates phenotypic change early in the tree or gradualistic. Finally the κ was not significantly different to 0 or 0.5 indicating punctuational change (Table 7).

Table 7. Pagel's Phylogenetic Signal Metrics

Entire tree		
Lambda	0.804	Significantly different from 0 and 1.
Delta	1.795	Not significantly different from 1 or 3.
Kappa	0.941	Not significantly different from 1.
Eumelissodes + Callimelissodes clade only		
Lambda	0.81	Significantly different from 0 and 1.
Delta	0.579	Not significantly different from 0 or 0.5.
Kappa	0.328	Not significantly different from 0 or 0.5.

Speciation and extinction rates: The BAMM analysis reached convergence. The highest probability indicated a single shift in speciation/extinction rates in the tree (p = 0.6100) and the Bayes factors also support this conclusion. There were seven probable locations where this shift occurred with a combined probability of 0.592 that it occurred at the base of the *Eumelissodes* clade and 0.373 that it occurred near the base of the entire tree (Fig. 17).

Fig. 17: Bayesian Analysis of Macroevolutionary Mixtures (BAMM, Rabosky, 2014) run on the original data from Wright et al. (2018) for 500,000,000 generations, sampling every 50,000 accounting for known missing species from each subgenus (89 of 129 known species). Although the analysis indicates only a single rate change, there are seven probable locations of that rate change. Asterisks(*) indicate probable locations of rate changes.



Discussion:

This work represents the most taxonomically dense phylogenetic diet analysis to date that incorporates the host plant phylogeny to assess diet breadth in bees. The use of molecular barcodes to discern host identities allowed a more detailed look into the role of the major Asteraceae clades in North America. In this discussion we assess the value of using the ITS1 gene fragment for pollen identification and the merits of various ways of inferring ancestral diet breadth. We provide a more detailed account of what ancestral range analysis can tell us about important nodes within the *Melissodes* phylogeny and an overview of what all of these analyses, in combination, tell us about the evolution of diet breadth in this group of pollinators. We review how well *Melissodes* confirms or contradicts the various theories about the direction and frequency of changes in diet breadth, the effect these changes may have on speciation rates, and evaluate the special role that Asteraceae plays. We conclude with placing what we have learned in a historical context of what we know about the environment in North America during the Miocene and Pliocene.

Barcoding for pollen identification: Using the ITS1 gene fragment as a barcode with traditional Sanger sequencing is relatively inexpensive and works well if there is only a single species in the pollen sample. However, much progress has been made in using metabarcoding techniques for these applications (de Vere et al. 2017). In comparing label data to sequencing results, it is clear that label data cannot be used to discern pollen host records. Morphological and/or molecular techniques are needed to verify the pollen identity. In the case of Asteraceae, molecular techniques work best because of the difficulty in identifying Asteraceae pollen below the tribal level from morphological characters alone. The molecular barcoding allowed for a much more detailed look into specialization not only on the family Asteraceae, but within the largest clades of North American Asteraceae. The BLAST function in the NCBI nucleotide database is more than adequate to resolve genus level (and in some cases species level) identifications for North American angiosperms with as few as 250 bps of the ITS1 gene fragment. (It should be noted here that early attempts at using the chloroplast gene fragment rbcL using 1F/724R (Savolainen et al. 2000) were made but the BLAST results were not nearly as precise as the ITS1 fragment. No quantitative comparisons were made.)

Table 8. PCR success rate of pollen samples by years.

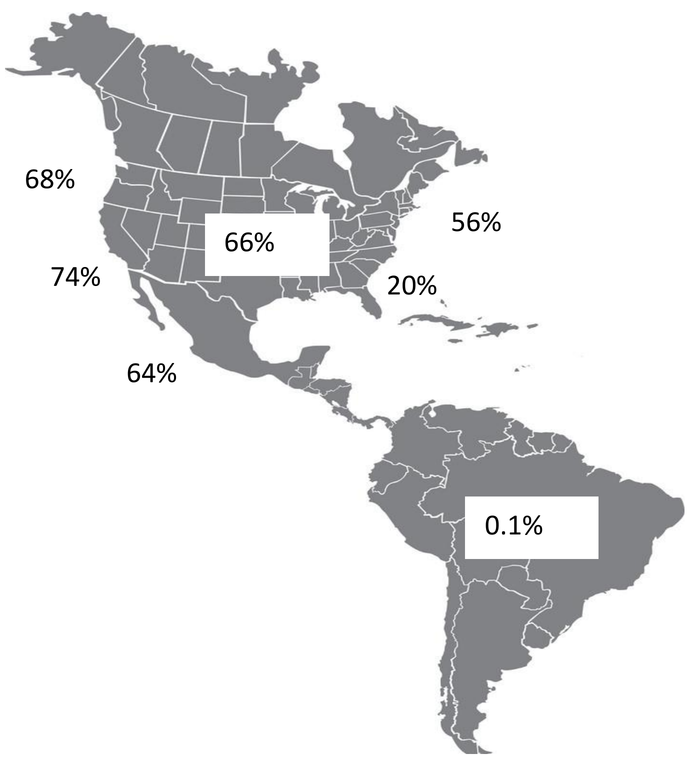
years	1931 - 1940	1941 - 1950	1951 - 1960	1961 - 1970	1971 - 1980	1981 - 1990	1991 - 1995	1996 - 2000	2001 - 2005	2006 - 2010	2011 - 2015
good	0	0	8	6	11	6	14	46	163	152	526
total	5	7	31	48	28	38	49	98	254	210	672
%	0	0	26	13	39	16	29	47	64	72	78

Age, collection method, and geography strongly affected successful amplification. Less than 50% of samples that were more than fifteen years old amplified, while samples less than five years old had a 78% success rate (Table 8). The bee specimen labels often had information of trap type used or host flower. Samples with host plant information were assumed to be net collected. Of samples with this information, 107 were from some type of trap and 368 were net

Table 9. PCR success rates by collection methods.

	Trap		From flowers	
	number	%	number	%
good	107	44	368	57
multiple	64	26	92	14
fungus	15	6	27	4
No sequence	55	23	160	25

Fig. 18: Map indicating geographic variation in the percent success rate of sequencing pollen samples using Sanger sequencing from insect collections and individual researchers. Northwest = BC, OR, WA, MT, ID, and WY; Southwest = CA, NV, UT, CO, AZ and NM; Midwest = ND, SD, MN, WI, IA, NE, IL, KS, MO, OK, and TX; Northeast = MI, IN, OH, KY, WV, VA, MD, DE, NJ, NY, PA, CT, RI, MA, NH, VT and ME. Southeast = AR, LA, TN, NC, SC, GA, FL, AL, and MS; Mexican and Panama samples combined; all South American samples combined.



collected from flowers. Samples from net collected bees had 57% successful amplification whereas samples from traps had 44% success. Twenty-six percent of the trap samples had more than one species of pollen per sample (and therefore were unreadable using Sanger sequencing) compared to 14% for net collected samples. This was probably due to contamination of pollen from other bees in the trap, and because of this, no trapped bee samples were used for metabarcoding. The number of samples with fungal DNA or no amplification was equivalent between collection methods (Table 9). Location of the institutions from which the specimens were borrowed also affected success of amplification. Specimens from the southeast USA had only 20% success rate compared to 74% for the southwest (Fig. 18). The success of amplification of specimens from collections in different regions seemed to correlate to humidity of the regions. Humidity control is rare in University-based insect collections but may affect the preservation of DNA in specimens.

Merit of analytical tools in assessing evolution of diet breadth: The ACR analyses on the ecological estimate of diet were found to be very sensitive to the subjective categories that were imposed on the data. ACR is useful when comparing phenotypic traits that are undeniably discrete, but due to the subjective nature of categorizing diet breadth, it is unsuitable for these purposes. Using phylogenetic diversity of the host plants of each species of bee as a continuous variable in ACR led to a more informative visualization of the changes in diet breadth over time. Although this analysis did provide confidence intervals around each node, we found the interpretation of the results not as straightforward as the ancestral range reconstructions (see below). Similar to the ecological estimate, using the taxonomic estimate of diet breadth was also extremely sensitive to which taxonomic ranking was used. However, treating the tribes of Asteraceae equal to all other families of plants led to results most similar to the phylogenetic ACR. Phylogenetic diversity of host plants is a much better measure of diet breadth than taxonomic counts. However, it still has the problem of taking a complex and structured system and reducing it to a number. For example, a bee that pollinates 20 species of very closely related sunflowers may have the same RPD as a bee that pollinates only two species of more distantly related roses. The RPD measure does not recognize identity, it is only a measure of branch length. In order to compare identity, phylogenetic beta diversity measures the amount of overlap of the identities of the hosts of two species of bees, using overlapping branch length as a measurement. Using biogeographical tools to infer the ancestral host ranges was by far the most informative. Probabilities of ancestral ranges at particular nodes are relatively easy to interpret and allowed insight that the other methods did not (see next section).

Evolution of diet breadth in *Melissodes*: Through these analyses, we have learned that the MRCA of *Melissodes* was most probably a generalist whose host plant repertoire included the Asteroideae as well as at least one other non-Asteraceae group of plants, most likely the malvids (Fig 7). The MRCA of the subgenus *Melissodes* s.s. not only retained the polylectic diet of its ancestors, but also broadened its diet to include more host plant groups; the two ranges with the highest independent probabilities were malvids + fabids + lamiids + Asteroideae (BCEGH) and the same but without the NAC (BCEH). At this stage, fabids and lamiids were added as being most likely part of the ancestral diet of *Melissodes* s.s. Moving away from *Melissodes* s.s., the nodes ancestral to *Eumelissodes* +*Callimelissodes* had higher probabilities for Asteroideae and lower probabilities that the diet included any non-Asteraceae pollen. This culminated at the MRCA of *Eumelissodes* (node 7) where this trend towards specialization on Asteroideae was stronger and less than ten percent probability that the MRCA fed on Asteroideae + malvids. Within the *Eumelissodes* + *Callimelissodes,* reversion to polylecty occurred near the tips in many lineages (at least nine times) as did further specialization within Asteraceae onto either the NAC or the HA (at least ten times). In only two cases did a host switching event occur onto a non-Asteraceae family (*M. velutinus* (Cockerell) onto Polemoniacea and *M. clarkiae* LaBerge onto Onagraceae).

Although the ancestral range analysis did reveal specialization on Asteroideae to be the most common ancestral host range for the *Callimelissodes* + *Eumelissodes*, specialization on one of the two groups within Asteroideae (the HA or the NAC) was common for extant species. Also, expanding diet breadth to incorporate the Carduoideae + Cichorioideae was not uncommon. Although there are frequent changes back and forth between these groups, it is apparent that there is some discerning factor that *Melissodes* recognizes among these groups. More information is needed about the pollen chemistry within Asteraceae (Dötterl and Vereecken 2010).

In summary, these analyses indicated that MRCA of all *Melissodes* was a generalist. The subgenus, *Melissodes* s.s., has remained polylectic to the present day. The MRCA of both *Callimelissodes* and *Eumelissodes* has a high probability of being Asteroideae specialists, not including any non-Asteraceae groups, but this is higher for the *Eumelissodes* MRCA. There are ten species that are generalists but with a strong preference for Asteraceae. There is phylogenetic signal in diet breadth and closer related bees have more similar diets. There was a single speciation rate increase that occurred near the base of Eumelissodes. This occurred after, not in concert with specialization on Asteroideae. Finally, speciation events occurred in the absence of changes in diet.

How does *Melissodes* fit with current theory? It was once thought that bees were ancestrally generalists, which evolved host plant specialization over time and then were more prone to extinction. However, with more bee phylogenies becoming available, the opposite pattern emerges as the more prevalent case. Most bee groups have been shown to be ancestrally oligolectic with changes to polylecty more common than once thought (Danforth et al. 2013, Praz et al. 2008, Sedivy et al. 2008, but see Haider et al. 2014). However, it is difficult to generalize because it depends on the taxonomic scope of each study. The MRCA of *Melissodes* was a generalist, but if we were to broaden the scope of the study to include its sister genus, *Svastra* Holmberg, or the entire tribe of Eucerini, we may see a different picture all together. Transitions from polylecty to oligolecty appear to have occurred only twice in *Melissodes*; at the base of the *Callimelissodes* + *Eumelissodes* and the perhaps at the base of *Apomelissodes*.

But the reversal to polylecty near the tips is common, as is the further specialization within the Asteraceae.

While selection pressures that favor specialization are generally accepted (e.g. competition theory, optimal foraging theory), conditions that favor polylecty are often overlooked. These would occur when the foraging season of a particular bee species was longer than that of individual host plant species (Sedivy et al 2008) or when the geographic range of the bee is larger than than of individual host plants (Moldenke 1975). There are several studies that have correlated range size with diet breadth (for a meta-analysis, see Slatyer et al. 2013). And most bee species that are active from the spring through the fall are polylectic. The oscillation hypothesis (Janz and Nylin 2008) allows for evolution of diet breadth to swing back and forth between polylecty and oligolecty, but maintains that the polylectic phase would be brief. The constraint hypothesis of Sedivy et al. (2008) is more detailed and flexible allows for a scenario in which the generalist diet state could be maintained if selection pressures for specialization did not outweigh the benefits of being a generalist.

In *Melissodes* we see three distinct patterns of evolution of diet breadth. *Melissodes* s.s. is a polylectic clade and none of the species within have evolved back towards oligolecty. Within *Callimelissodes* + *Eumelissodes* we see a trend towards specialization on Asteroideae but most speciation events within these groups do not coincide with a change in diet. If most oscillations between oligolecty and polylecty resulted in respecialization on the original host (Asteroideae), these transitions would be lost to history because our knowledge of the past is restricted to what we know about extant species. The multitude of transitions that we see at the tips, both towards polylecty and towards increased specialization, suggest that these may indeed represent transitional stages in an ongoing oscillation between constraints and release of constraints due to fluctuating selection pressures.

Asteraceae, a paradox or a gateway? The Asteraceae Paradox (generalist bees avoid Asteraceae pollen) is not evident in *Melissodes*. In fact, Asteraceae is included within the host plant repertoire in all but one species of generalist in the genus. In the case of *Melissodes*, Asteraceae pollen appears to be the gateway pollen. Once a bee species can utilize Asteraceae pollen, perhaps all other pollen types are relatively easy to incorporate into the diet. Praz et al. (2008) found that although the non-Asteraceae specialists could not survive on Asteraceae pollen, the one Asteraceae specialist bee in the study had good survivability on all other pollen types except for Ranunculaceae. This may also explain the multiple reversions to polylecty seen in the *Callimelissodes* + *Eumelissodes* clade and the high proportion of Melissodes that are generalists with a strong preference for Asteraceae.

Asteraceae pollen may be unpalatable, but many phytophagous insects specialize on plants with low nutrition or even toxic defenses. Asteraceae species are widespread, common in all open habitats, and tend to have very predictable bloom phenology. Even during severe droughts in arid environments, many Asteraceae plants, such as *Helianthus annuus* and *Ericameria nauseosa* (Pall. Ex Pursh) G.L. Nesom & Baird, bloom more predictably than most other flowering plants and in dry years can be the only available pollen source (pers. obs.). Finally, as mentioned above, Asteraceae feeding may provide protection from parasitism (Spear et al. 2016). If physiological constraints particular to Asteraceae are overcome by a bee lineage, the benefits of retaining this physiological adaptation may outweigh the costs.

Historical context: Wright et al. (2018) suggested that sympatry, followed by range extinction was the best fit biogeography model and that vicariance had little effect on speciation. In the current analysis, we infer that cladogenesis most often occurred without a change in host range and, in *Eumelissodes*, the speciation rate increased. This implies that something other than vicariance and diet shifts was responsible for cladogenesis and the increase rate of speciation within the *Eumelissodes*.

Wright *et al.* (2018) estimated a divergence time of around 15 mya for *Melissodes* and 10 mya for each of the three major subgenera. The highest clustering of lineage divergence occurred in the late Miocene and Pliocene. The Miocene (23-5.3 mya) was a time of fluctuation around the globe, including North America. The formation of the grasslands and warm deserts began at this time, which may have facilitated the divergence and spread of the two largest clades of North American Asteraceae. The Helianthus Alliance and the North American Clade of Astereae both had major radiations in North America during the Oligocene-Early Miocene (Funk et al. 2009a). However, it wasn't until much later that these two biomes became expansive. In fact the widespread grasslands and deserts that are notable today may have arisen as recently as 7-5 mya (Strömberg 2011) and 10,000 years ago (Wilson and Pitts, 2010), respectively. During the Miocene, these habitats were patchy, isolated, and probably ephemeral areas surrounded by forest. The species that thrive in these habitats, such as the Asteroideae and *Melissodes*, may not have been as widespread as they are today, but instead may have experienced something more akin to meta-population dynamics or refugia that could facilitate allopatric speciation. The BioGeoBEARS range delimitation used in Wright *et al.* (2018) was too coarse to register fine scale changes and there is too little known about the fluctuations of the grasslands as they gained a larger and larger presence throughout the Miocene. We acknowledge that the null hypothesis of allopatric speciation must not be dismissed without further evidence to the contrary.

Conclusions: Within the three subgenera for which we have empirical diet breadth data, we see three very different patterns. In *Melissodes* s.s. we see a clade of broadly polylectic species that have retained this wide diet breadth through speciation events to the present day. After specialization onto Asteraceae, we see one clade (*Eumelissodes*) with an increased rate of speciation and another (*Callimelissodes*) with no indication of increased rates of speciation. And, we see cladogenesis events in the absence of changes in diets. The constraint hypothesis includes scenarios in which both oligolecty and polylecty endure through evolutionary time, but it still doesn't explain cladogenesis without changes in diets or the speciation rate increase in *Eumelissodes*. There are several explanations. (i) The higher rate of speciation is really an increased rate of undocumented extinction events in the rest of the phylogeny. (ii) The oscillations between the polylectic and oligolectic phases almost always result in respecialization on the ancestral diet and therefore the polylectic phases are lost to history. (iii) Allopatric speciation, not changes in diet is responsible for cladogenesis, yet undetectable at the scale of Wright et al. (2018).

This study brings to light the evolutionary history of diet breadth in an important group of North American pollinators. As more phylogenetic studies become available, more natural history data on diet is amassed, and more information on the chemistry of pollen is acquired, the larger picture of the evolution of diet breadth in bees will come to light.

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APPENDIX A: Bee voucher specimens, GenBank numbers and instituitions.

Taxa					GenBank accession numbers									
Tribe	Genus	Subgenus	species	Sample Number	EF1a	ArgK	Opsin	PolII	COI/tRNA /COII	18S	NaK	Wingless	comments on sequences	Repository
Ancylini	Ancyla	NA	holtzi	NA	GU244913	----------	GU245235	GU245352	----------	GU244591	GU245057	GU245510		C&D
Emphorini	Diadasia	Coquillettapis	bituberculata	NA	GU244927	----------	AF344594	GU245367	----------	GU244606	GU245074	GU245527		C&D
Emphorini	Diadasina	NA	distincta	NA	GU244929	----------	GU245248	GU245369	----------	GU244608	GU245076	GU245529		C&D
Eucerini	Eucera	Peponapis	pruinosa	49	MG257000	MG257166	MG257311	MG257463	MG384533	----------	----------	----------		MSBA
Eucerini	Eucera	Synhalonia	aragalli	255	MG257017	MG257099	MG257242	MG257390	MG384461	----------	----------	----------		MSBA
Eucerini	Eucera	Synhalonia	frater1	256	MG257018	MG257100	----------	MG257391	MG384462	----------	----------	----------		MSBA
Eucerini	Eucera	Synhalonia	frater2	NA	----------	----------	GU245232	GU245385	----------	GU244626	GU245094	GU245547		C&D
Eucerini	Eucera	Synhalonia	hamata1	171	MG257006	MG257045	MG257189	MG257334	MG384409	----------	----------	----------		MSBA
Eucerini	Eucera	Synhalonia	hamata2	311	----------	MG257133	MG257277	MG257427	MG384497	----------	----------	----------	ArgK, reverse	MSBA
Eucerini	Eucera	Synhalonia	lepida	172	MG257007	MG257046	MG257190	MG257335	MG384410	----------	----------	----------		MSBA
Eucerini	Eucera	Synhalonia	plumigera	365	----------	MG257152	----------	MG257449	MG384519	----------	----------	----------		MSBA
Eucerini	Eucera	Synhalonia	spectabilis	364	----------	MG257151	----------	MG257448	MG384518	----------	----------	----------		MSBA
Eucerini	Eucera	Syntrichalonia	exquisita	251	----------	MG257096	----------	MG257386	MG384457	----------	----------	----------		MSBA
Eucerini	Eucera	Xenoglossa	angustior	NA	----------	----------	GU245233	GU245386	----------	GU244627	GU245095	GU245548		C&D
Eucerini	Eucera	Xenoglossa	kansensis	253	MG256981	MG257097	----------	MG257388	MG384459	----------	----------	----------	EF1a, forward	MSBA
Eucerini	Eucera	Xenoglossa	patricia	260	----------	MG257104	----------	MG257395	MG384466	----------	----------	----------		MSBA
Eucerini	Eucera	Xenoglossodes	eriocarpi	252	MG257013	----------	MG257240	MG257387	MG384458	----------	----------	----------	EF1a, forward	MSBA
Eucerini	Eucera	Xenoglossodes	lippiae	254	MG257016	MG257098	MG257241	MG257389	MG384460	----------	----------	----------		MSBA
Eucerini	Eucera	Xenoglossodes	perconcinna	278	MG257021	MG257115	MG257258	MG257408	MG384478	----------	----------	----------		MSBA
Eucerini	Florilegus	Florilegus	condignus	290	MG256983	MG257122	MG257266	MG257416	MG384486	----------	----------	----------		MSBA
Eucerini	Martinapis	Martinapis	luteicornis1	170	MG256976	MG257044	MG257188	MG257333	MG384408	----------	----------	----------		MSBA
Eucerini	Martinapis	Martinapis	luteicornis2	310	MG256986	MG257132	MG257276	MG257426	MG384496	----------	----------	----------		MSBA
Eucerini	Melissodes	Apomelissodes	fimbriatus	372	----------	MG257156	MG257301	MG257453	MG384523	----------	----------	----------		MSBA
Eucerini	Melissodes	Apomelissodes	mitchelli	301	----------	MG257127	MG257271	MG257421	MG384491	----------	----------	----------	PolII, reverse	MSBA
Eucerini	Melissodes	Callimelissodes	clarkiae	370	MG250073	MG257154	MG257299	MG257451	MG384521	----------	----------	----------		BLCU
Eucerini	Melissodes	Callimelissodes	coloradensis	175	MG250020	MG257049	MG257193	MG257338	MG384413	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	compositus	152	MG257004	MG257038	MG257181	MG257326	MG384402	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	glenwoodensis	160	MG250016	MG257040	MG257184	MG257329	MG384405	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	lupinus	121	MG257001	MG257028	MG257171	MG257316	MG384392	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	lustrus	136	MG250011	MG257032	MG257175	MG257320	MG384396	----------	----------	----------	ArgK, reverse	MSBA
Eucerini	Melissodes	Callimelissodes	metenuus	236	MG250049	MG257089	MG257233	MG257379	MG384451	----------	----------	----------		BLCU
Eucerini	Melissodes	Callimelissodes	nigracauda	281	MG257022	MG257118	MG257261	MG257411	MG384481	----------	----------	----------		BLCU
Eucerini	Melissodes	Callimelissodes	plumosus1	191	MG250026	MG257058	MG257201	MG257347	MG384422	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	plumosus2	194	MG250029	MG257061	MG257204	MG257350	MG384425	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	plumosus3	358	MG256998	MG257149	MG257296	MG257446	MG384516	----------	----------	----------		BLCU
Eucerini	Melissodes	Callimelissodes	plumosus4	211	MG250039	MG257073	MG257216	MG257362	MG384437	----------	----------	----------		BLCU
Eucerini	Melissodes	Callimelissodes	stearnsi	192	MG250027	MG257059	MG257202	MG257348	MG384423	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	tribas1	193	MG250028	MG257060	MG257203	MG257349	MG384424	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	tribas2	289	MG257024	MG257121	MG257265	MG257415	MG384485	----------	----------	----------		MSBA
Eucerini	Melissodes	Callimelissodes	tuckeri	371	MG250074	MG257155	MG257300	MG257452	MG384522	----------	----------	----------		OSEC
Eucerini	Melissodes	Ecplectica	raphaelis	300	MG256984	MG257126	MG257270	MG257420	MG384490	----------	----------	----------		UCRC
Eucerini	Melissodes	Ecplectica	sexcinctus	306	MG256985	MG257131	MG257275	MG257425	MG384495	----------	----------	----------	EF1a, forward	UFVB
Eucerini	Melissodes	Ecplectica	sp.	233	MG256980	MG257087	MG257231	MG257377	MG384449	----------	----------	----------		BLCU
Eucerini	Melissodes	Ecplectica	trifasciatus	350	----------	MG257147	MG257292	MG257442	MG384512	----------	----------	----------		MSBA

Eucerini	Melissodes	Eumelissodes	aff.personatellus	323	MG257027	MG257139	MG257284	MG257434	MG384505	----------	----------	----------	EF1a, forward	MSBA
Eucerini	Melissodes	Eumelissodes	agilis	131	MG250010	MG257031	MG257174	MG257319	MG384395	----------	----------	----------	ArgK, reverse	MSBA
Eucerini	Melissodes	Eumelissodes	appressus	338	MG256993	MG257144	MG257289	MG257439	MG384509	----------	----------	----------		MSBA
Eucerini	Melissodes	Eumelissodes	bicoloratus	212	MG250040	MG257074	MG257217	MG257363	MG384438	----------	----------	----------		BLCU
Eucerini	Melissodes	Eumelissodes	bimatris	382	MG250075	MG257159	MG257303	MG257455	MG384526	----------	----------	----------		MSBA
Eucerini	Melissodes	Eumelissodes	brevipyga	269	MG250059	----------	MG257251	MG257401	MG384472	----------	----------	----------		MSBA
Eucerini	Melissodes	Eumelissodes	cerussatus	213	MG257010	MG257075	MG257218	MG257364	MG384439	----------	----------	----------		BLCU
Eucerini	Melissodes	Eumelissodes	confusus	143	MG257002	MG257035	MG257178	MG257323	MG384399	----------	----------	----------		MSBA
Eucerini	Melissodes	Eumelissodes	coreopsis1	244	MG257014	MG257092	MG257236	MG257382	MG384454	----------	----------	----------		MSBA
Eucerini	Melissodes	Eumelissodes	coreopsis2	189	MG250024	MG257056	MG257199	MG257345	MG384420	----------	----------	----------	ArgK, reverse , Opsin, reverse	MSBA
Eucerini	Melissodes	Eumelissodes	denticulatus1	214	MG257011	MG257076	MG257219	MG257365	----------	----------	----------	----------	ArgK, reverse , Opsin, forward	BLCU

Appendix B: Primers and references for PCR of bee specimens.

Gene fragment	Primer code	sequence	direction	Reference
COI/tRNA/COII	Jerry	CAACATTTATTTTGATTTTTTGG	Forward	Simon et al. 1994
	Pat	TCCAATGCACTAATCTGCCATATTA	Reverse	Simon et al. 1994
	2195	TTGATTTTTTGGTCATCCAGAAGT	Forward	Simon et al. 1994
	EmbCOIF4	ACWTCAGCWACYATAATYATTGC	Forward	Miller pers. comm.
	EmbCOIIR1	CATATCTTCARTATCATTGATGAC	Reverse	Miller pers. comm.
EF1α_F2copy	haF2for1	GGGYAAAGGWTCCTTCAARTATGC	Forward	Danforth et al. 1999
	F2rev1	AATCAGCAGCACCTTTAGGTGG	Reverse	Danforth et al. 1999
	for1deg	GYATCGACAARCGTACSATYG	Forward	Magnacca and Danforth 2007
	EmphF2for	GCCTGGGTATTGGATAAGCTGAA	Forward	Sipes and Wolf 2001
	EmphF2rev	TGGATTGTTYTTRGAGTCACCAG	Reverse	Sipes and Wolf 2001
	haF2for1mel	GGGAAAAGGVTCSTTCAARTAYGC	Forward	Wright
	melfor1	GCACATCRCBYTRTGGAAGT	Forward	Wright
	melrev1	ARTACTCCVGTYTCCACACG	Reverse	Wright
	melrev3	CGAACCTGMAGRGGAAGACG	Reverse	Wright
PolII	polfor2a	AAYAARCCVGTYATGGGTATTGTRCA	Forward	Danforth et al. 2006
	polrev2a	AGRTANGARTTCTCRACGAATCCTCT	Reverse	Danforth et al. 2006
	for2	TGGGAYGSYAAAATGCCKCAACC	Forward	Danforth et al. 2006
	rev2	TTYACAGCAGTATCRATRAGACCTTC	Reverse	Danforth et al. 2006
	melF1	TTCTWRCCYAGYTGGGATGG	Forward	Wright
	melR1	CCTCTGGATTCAGGACCGTA	Reverse	Wright
Opsin	for3(mod)	TTCGAYAGATACAACGTRATCGTNAARGG	Forward	Almeida and Danforth 2009
	rev(mod)	ATANGGNGTCCANGCCATGAACCA	Reverse	Almeida and Danforth 2009
	OPforEuc	GATAGGTACAACGTAATCGTGAAA	Forward	Dorchin et al. 2017
	OPrevEuc	TGAACCACAGCGAGATCGTCATAA	Reverse	Dorchin et al. 2017
ArgK	For2	GACAGCAARTCTCTGCTGAAGAA	Forward	Magnacca and Danforth 2007
	Rev2	GGTYTTGGCATCGTTGTGGTAGATAC	Reverse	Magnacca and Danforth 2007
	melF2	TGTTCGATCARYYGAAGACG	Forward	Wright
	melR1	CGGTCACCCTCCTTGAAYAR	Reverse	Wright
	melR2	TCGTCRATCAACTTYTGCTG	Reverse	Wright

Primers with Wright as a reference were developed by the primary author for this study.
Miller pers. comm. were developed by the second author for use on Embioptera.

APPENDIX C: Bee identifiecation, label information and repository for all bee specimens with pollen samples.

num	Genus	subgenus	species	label_host_family	label_host_genus	label_host_species	state	month	year	repository
1001	Melissodes	C	coloradensis	vane trap	na	n	NE	9	2014	OSEC
1121	Melissodes	C	coloradensis	vane trap	na	na	NE	9	2014	OSEC
1123	Melissodes	C	coloradensis	vane trap	na	na	NE	9	2014	OSEC
1125	Melissodes	C	coloradensis	vane trap	na	na	NE	9	2014	OSEC
370	Melissodes	C	coloradensis	Asteraceae	Helianthus	annuus	NM	9	2011	MSBA
372	Melissodes	C	coloradensis	Asteraceae	Helianthus	mollis	IL	8	1995	INHS
582	Melissodes	C	coloradensis	Asteraceae	Liatris	pynostachya	IA	8	2002	SUI
1002	Melissodes	C	coloradensis	vane trap	na	n	NE	9	2014	OSEC
769	Melissodes	C	coloradensis	na	na	na	SD	9	2011	BIML
911	Melissodes	C	compositus	na	na	na	AZ	8	2014	BLCU
910	Melissodes	C	compositus	na	na	na	AZ	8	2014	BLCU
1293	Melissodes	C	compositus	na	na	na	UT	8	1994	BLCU
376	Melissodes	C	compositus	na	na	na	NM	9	2012	MSBA
388	Melissodes	C	compositus	na	na	na	NV	9	1960	INHS
382	Melissodes	C	compositus	na	na	na	CA	6	1982	UCDC
383	Melissodes	C	compositus	Asteraceae	Heterotheca	psammophila	NM	9	1999	BLCU
380	Melissodes	C	compositus	Asteraceae	Heterotheca	villosa	NM	8	2012	MSBA
387	Melissodes	C	compositus	na	na	na	AZ	9	2008	BLCU
384	Melissodes	C	compositus	na	na	na	NM	9	2010	BLCU
389	Melissodes	C	compositus	na	na	na	CA	8	1957	INHS
375	Melissodes	C	compositus	Asteraceae	Dieteria	canescens	NM	9	2009	MSBA
377	Melissodes	C	compositus	na	na	na	NM	9	2012	AMNH
379	Melissodes	C	compositus	Asteraceae	Helianthus	annuus	NM	9	2002	MSBA
400	Melissodes	C	glenwoodensis	Asteraceae	Dieteria	canescens	NM	9	2009	MSBA
395	Melissodes	C	glenwoodensis	Asteraceae	Dieteria	canescens	UT	9	2003	BLCU
1107	Melissodes	C	glenwoodensis	na	na	na	MT	8	2009	MSBA
1218	Melissodes	C	glenwoodensis	na	na	na	ND	9	2009	MSBA
1220	Melissodes	C	glenwoodensis	na	na	na	ND	9	2004	MSBA
399	Melissodes	C	glenwoodensis	Asteraceae	Ericameria	nauseosa	NM	9	2012	MSBA
773	Melissodes	C	glenwoodensis	na	na	na	SD	9	2011	BIML
774	Melissodes	C	glenwoodensis	na	na	na	SD	9	2010	BIML

396	Melissodes	C	glenwoodensis	Asteraceae	Ericameria	na	UT	8	2009	BLCU
397	Melissodes	C	glenwoodensis	Cleomaceae	Cleome	serrulata	UT	9	2003	BLCU
390	Melissodes	C	glenwoodensis	na	na	na	CO	9	1992	FSCA
908	Melissodes	C	glenwoodensis	Asteraceae	Gutierrezia	sarothrae	UT	9	2005	BLCU
398	Melissodes	C	glenwoodensis	Rosaceae	Fallugia	paradoxa	NM	9	2003	MSBA
1226	Melissodes	C	lupinus	na	na	na	CA	9	1999	UCRC
1222	Melissodes	C	lupinus	na	na	na	CA	8	2005	AMNH
964	Melissodes	C	lupinus	bluevane	na	na	ID	7	2012	MSBA
965	Melissodes	C	lupinus	bluevane	na	na	ID	na	2012	MSBA
411	Melissodes	C	lupinus	na	na	na	CA	9	2006	AMNH
721	Melissodes	C	lupinus	Asteraceae	Encelia	californica	CA	4	2014	MSBA
1223	Melissodes	C	lupinus	na	na	na	CA	6	2000	AMNH
418	Melissodes	C	lupinus	Asteraceae	Grindelia	squarrosa	UT	7	2012	BLCU
730	Melissodes	C	lupinus	Asteraceae	Helianthus	annuus	CA	6	2012	MSBA
416	Melissodes	C	lupinus	Asteraceae	Hemizonia	congesta	CA	9	2010	UCRC
1224	Melissodes	C	lupinus	Asteraceae	Heterotheca	villosa	Canada	7	1991	SEMC
417	Melissodes	C	lupinus	Asteraceae	Holocarpa	heermannii	CA	9	2002	BLCU
419	Melissodes	C	lupinus	Asteraceae	Calycadenia	pauciflora	CA	8	2010	UCRC
413	Melissodes	C	lupinus	pantrap	na	na	UT	8	1997	BLCU
424	Melissodes	C	lustrus	Asteraceae	Ericameria	nauseosa	CA	8	2012	MSBA
423	Melissodes	C	lustrus	Asteraceae	Grindelia	camporum	CA	8	2012	MSBA
1126	Melissodes	C	lustrus	Asteraceae	Grindelia	na	ID	9	2012	CIDA
720	Melissodes	C	lustrus	Asteraceae	Isocoma	menziesii	CA	9	2014	MSBA
428	Melissodes	C	lustrus	na	na	na	CA	10	1978	UCRC
1095	Melissodes	C	metenuus	bluevane	na	na	OR	8	2014	OSAC
1047	Melissodes	C	metenuus	bluevane	na	na	OR	7	2015	OSAC
1108	Melissodes	C	metenuus	na	na	na	MT	8	2009	MSBA
1110	Melissodes	C	metenuus	Asteraceae	Heterotheca	villosa	MT	na	2011	MSBA
1090	Melissodes	C	metenuus	bluevane	na	na	OR	7	2014	OSAC
1093	Melissodes	C	metenuus	bluevane	na	na	OR	7	2014	OSAC
1094	Melissodes	C	metenuus	bluevane	na	na	OR	7	2014	OSAC
1028	Melissodes	C	metenuus	Asteraceae	Gaillardia	aristata	MT	7	2014	MSBA
1092	Melissodes	C	metenuus	bluevane	na	na	OR	7	2014	OSAC

1041	Melissodes	C	metenuus	bluevane	na	na	OR	7	2015	OSAC
1043	Melissodes	C	metenuus	bluevane	na	na	OR	7	2015	OSAC
1045	Melissodes	C	metenuus	bluevane	na	na	OR	7	2015	OSAC
1310	Melissodes	C	plumosus	Asteraceae	Centaurea	solstitialis	CA	5	1997	BLCU
369	Melissodes	C	plumosus	na	na	na	CA	6	1959	UCRC
367	Melissodes	C	plumosus	Onagraceae	Clarkia	unguiculata	CA	6	2011	BLCU
913	Melissodes	C	plumosus	Polygonaceae	Eriogonum	fasciculatum	CA	6	2012	BLCU
447	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	MSBA
728	Melissodes	C	stearnsi	Asteraceae	Helianthus	annuus	CA	6	2012	MSBA
924	Melissodes	C	stearnsi	Brassicaceae	Hirschfeldia	incana	CA	6	2012	BLCU
922	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	BLCU
929	Melissodes	C	stearnsi	Paparavaceae	Eschscholzia	californica	CA	6	2012	BLCU
926	Melissodes	C	stearnsi	Lamiaceae	Trichostema	lanceolatum	CA	6	2012	BLCU
445	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	BLCU
918	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	BLCU
923	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	BLCU
925	Melissodes	C	stearnsi	Lamiaceae	Trichostema	lanceolatum	CA	6	2012	BLCU
920	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	BLCU
444	Melissodes	C	stearnsi	pantrap	na	na	CA	6	2012	BLCU
927	Melissodes	C	stearnsi	Lamiaceae	Trichostema	lanceolatum	CA	6	2012	BLCU
928	Melissodes	C	stearnsi	Lamiaceae	Trichostema	lanceolatum	CA	6	2012	BLCU
921	Melissodes	C	stearnsi	Polygonaceae	Eriogonum	fasciculatum	CA	6	2012	BLCU
619	Melissodes	EU	agilis	Asteraceae	Verbesina	encelioides	CO	9	2012	UCMC
1331	Melissodes	EU	agilis	na	na	na	AZ	9	2009	AMNH
618	Melissodes	EU	agilis	na	na	na	CO	7	2012	UCMC
1128	Melissodes	EU	agilis	Lamiaceae	lavendula	na	ID	8	2001	CIDA
1017	Melissodes	EU	agilis	Asteraceae	Helianthus	maximilliani	MT	8	2014	MSBA
748	Melissodes	EU	agilis	bluevane	na	na	TX	7	2014	OSEC
31	Melissodes	EU	agilis	Asteraceae	Amauriopsis	dissecta	AZ	9	2012	MSBA
33	Melissodes	EU	agilis	Asteraceae	Helianthus	annuus	AZ	9	2012	MSBA
38	Melissodes	EU	agilis	na	na	na	MEX	11	2012	CEET
35	Melissodes	EU	agilis	Asteraceae	Verbesina	encelioides	NM	10	2011	MSBA
36	Melissodes	EU	agilis	Asteraceae	Helianthus	annuus	NM	7	2012	MSBA

34	Melissodes	EU	agilis	Asteraceae	Helianthus	anomalus	UT	8	2003	BLCU
667	Melissodes	EU	agilis	na	na	na	MEX	10	2014	CEET
1328	Melissodes	EU	agilis	Asteraceae	Cirsium	arvense	ND	8	2012	MSBA
1332	Melissodes	EU	agilis	Asteraceae	Verbesina	encelioides	NM	10	2011	MSBA
1014	Melissodes	EU	agilis	vane trap	na	n	NE	9	2014	OSEC
32	Melissodes	EU	agilis	Asteraceae	Cirsium	wrightii	NM	9	2011	MSBA
963	Melissodes	EU	appressus	Asteraceae	Heterotheca	na	NM	9	2014	BLCU
1333	Melissodes	EU	appressus	Asteraceae	Heterotheca	na	NM	9	2014	BLCU
723	Melissodes	EU	appressus	Asteraceae	Isocoma	acrodenia	CA	10	2014	MSBA
724	Melissodes	EU	appressus	Asteraceae	Isocoma	menziesii	CA	9	2014	MSBA
1334	Melissodes	EU	bicoloratus	pantrap	na	na	WY	9	2004	BLCU
43	Melissodes	EU	bicoloratus	na	na	na	UT	8	1980	BLCU
45	Melissodes	EU	bicoloratus	Brassicaceae	Thelypodium	integrifolium	UT	6	2003	BLCU
44	Melissodes	EU	bicoloratus	Linaceae	Linum	aristatum	UT	8	2003	BLCU
1336	Melissodes	EU	bicoloratus	na	na	na	UT	7	2007	BLCU
53	Melissodes	EU	bimatris	Asteraceae	Machaeranthera	canescens	UT	9	2005	BLCU
900	Melissodes	EU	bimatris	Asteraceae	Ericameria	nauseosa	CA	9	2013	BLCU
50	Melissodes	EU	bimatris	Asteraceae	Chrysothamnus	viscidiflorus	ID	9	1972	BLCU
897	Melissodes	EU	bimatris	Asteraceae	Chrysothamnus	na	NV	9	2005	BLCU
898	Melissodes	EU	bimatris	Asteraceae	Chrysothamnus	viscidiflorus	NV	9	2004	BLCU
899	Melissodes	EU	bimatris	Asteraceae	Chrysothamnus	na	UT	9	2005	BLCU
94	Melissodes	EU	bimatris	na	na	na	UT	9	2000	BLCU
52	Melissodes	EU	bimatris	na	na	na	CA	9	1994	BLCU
58	Melissodes	EU	bimatris	na	na	na	NM	10	2002	MSBA
57	Melissodes	EU	bimatris	pantrap	na	na	UT	9	2008	BLCU
1338	Melissodes	EU	bimatris	pantrap	na	n	NM	10	2004	MSBA
895	Melissodes	EU	bimatris	Asteraceae	Gutierrezia	sarothrae	UT	9	2005	BLCU
56	Melissodes	EU	bimatris	Lamiaceae	Marrubium	vulgare	UT	9	2003	BLCU
719	Melissodes	EU	bimatris	Asteraceae	Isocoma	acrodenia	CA	10	2014	MSBA
54	Melissodes	EU	bimatris	Asteraceae	Isocoma	acrodenia	AZ	9	2001	BLCU
46	Melissodes	EU	bimatris	Asteraceae	Grindelia	squarrosa	UT	9	1965	BLCU
896	Melissodes	EU	bimatris	Asteraceae	Viguiera	na	CA	9	2013	BLCU
682	Melissodes	EU	confusus	na	na	na	MEX	8	2013	CEET

79	Melissodes	EU	confusus	Asteraceae	Cirsium	na	NM	7	2009	BLCU
889	Melissodes	EU	confusus	Asteraceae	Chrysothamnus	depressus	UT	7	2002	BLCU
67	Melissodes	EU	confusus	Asteraceae	Cirsium	na	UT	7	2008	BLCU
683	Melissodes	EU	confusus	na	na	na	MEX	9	2013	CEET
643	Melissodes	EU	confusus	na	na	na	AZ	8	2014	AMNH
644	Melissodes	EU	confusus	na	na	na	AZ	8	2014	AMNH
68	Melissodes	EU	confusus	Asteraceae	Erigeron	subtrinervis	CO	7	2012	MSBA
884	Melissodes	EU	confusus	na	na	na	AZ	8	2009	BLCU
75	Melissodes	EU	confusus	na	na	na	MEX	8	2013	CEET
883	Melissodes	EU	confusus	Clusiaceae	Hypericum	na	NV	8	2005	BLCU
642	Melissodes	EU	confusus	na	na	na	AZ	8	2014	AMNH
885	Melissodes	EU	confusus	na	na	na	AZ	8	2014	BLCU
882	Melissodes	EU	confusus	na	na	na	UT	8	2001	BLCU
881	Melissodes	EU	confusus	Asteraceae	na	na	UT		2001	
65	Melissodes	EU	confusus	Asteraceae	na	na	NM	7	2009	BLCU
62	Melissodes	EU	confusus	na	na	na	CO	7	2012	UCRC
66	Melissodes	EU	confusus	Asteraceae	Hymenoxys	hoopesii	AZ	8	2012	EMEC
76	Melissodes	EU	confusus	Asteraceae	Cirsium	parryi	AZ	8	2012	EMEC
81	Melissodes	EU	confusus	Campanulaceae	Campanula	rotundifolia	AZ	8	2012	MSBA
64	Melissodes	EU	confusus	na	na	na	NM	7	2009	BLCU
69	Melissodes	EU	confusus	Asteraceae	Heliomeris	multiflora	AZ	8	2012	EMEC
63	Melissodes	EU	confusus	Asteraceae	na	na	UT	7	2008	BLCU
886	Melissodes	EU	confusus	na	na	na	AZ	8	2014	BLCU
887	Melissodes	EU	confusus	Asteraceae	Senecio	spartoides	NV	8	2004	BLCU
671	Melissodes	EU	confusus	na	na	na	MEX	11	2014	CEET
687	Melissodes	EU	confusus	na	na	na	MEX	10	2014	CEET
669	Melissodes	EU	confusus	na	na	na	MEX		2014	CEET
611	Melissodes	EU	coreopsis	Asteraceae	Ratibida	columnifera	CO	6	2012	UCMC
610	Melissodes	EU	coreopsis	na	na	na	CO	7	2013	UCMC
606	Melissodes	EU	coreopsis	yellowvane	na	na	CO	6	2013	UCMC
1003	Melissodes	EU	coreopsis	vane trap	na	n	NE	8	2014	OSEC
1018	Melissodes	EU	coreopsis	Asteraceae	Erigeron	speciosus	MT	7	2014	MSBA
547	Melissodes	EU	coreopsis	Asteraceae	Gaillardia	pulchella	TX	5	2013	MSBA

605	Melissodes	EU	coreopsis	Asteraceae	Grindelia	squarrosa	CO	9	2012	UCMC
782	Melissodes	EU	coreopsis	na	na	na	SD	9	2011	BIML
781	Melissodes	EU	coreopsis	na	na	na	SD	8	2011	BIML
783	Melissodes	EU	coreopsis	na	na	na	SD	8	2011	BIML
608	Melissodes	EU	coreopsis	yellowvane	na	na	CO	9	2013	UCMC
545	Melissodes	EU	coreopsis	Asteraceae	Helianthus	annuus	NM	7	2012	MSBA
543	Melissodes	EU	coreopsis	na	na	na	NM	9	2010	MSBA
980	Melissodes	EU	coreopsis	vane trap	na	na	TX	9	2014	OSEC
607	Melissodes	EU	coreopsis	Asteraceae	Gaillardia	aristata	CO	6	2012	UCMC
634	Melissodes	EU	coreopsis	Asteraceae	Leucanthemum	vulgare	KS	6	2013	MSBA
1252	Melissodes	EU	coreopsis	Asteraceae	Machaeranthera	na	CO	7	1999	UCMC
609	Melissodes	EU	coreopsis	Asteraceae	Verbesina	encelioides	CO	9	2012	UCMC
784	Melissodes	EU	coreopsis	na	na	na	SD	7	2010	BIML
1250	Melissodes	EU	coreopsis	Asteraceae	Solidago	na	CO	7	1996	UCMC
1129	Melissodes	EU	coreopsis	Polygonaceae	Polygonum	bicorne	NE	8	2014	OSEC
544	Melissodes	EU	coreopsis	Asteraceae	Cirsium	wrightii	NM	9	2011	MSBA
85	Melissodes	EU	fasciatellus	Asteraceae	Grindelia	squarrosa	AZ	9	2012	MSBA
1348	Melissodes	EU	fasciatellus	Asteraceae	Ericameria	nauseosa	AZ	9	2012	MSBA
1345	Melissodes	EU	fasciatellus	na	na	na	AZ	9	2009	AMNH
1353	Melissodes	EU	fasciatellus	Asteraceae	Gutierrezia	na	NM	9	2001	UCMC
1349	Melissodes	EU	fasciatellus	na	na	na	NM	9	2011	AMNH
1350	Melissodes	EU	fasciatellus	na	na	na	NM	8	2011	AMNH
1352	Melissodes	EU	fasciatellus	na	na	na	NM	9	2011	AMNH
86	Melissodes	EU	fasciatellus	Asteraceae	Heterotheca	na	NM	8	2005	BLCU
84	Melissodes	EU	fasciatellus	na	na	na	NM	9	2012	AMNH
87	Melissodes	EU	fasciatellus	na	na	na	NM	9	2010	BLCU
1351	Melissodes	EU	fasciatellus	Asteraceae	Haplopappus	na	NM	9	2010	BLCU
83	Melissodes	EU	fasciatellus	Asteraceae	Haplopappus	na	NM	8	2011	UCRC
1347	Melissodes	EU	fasciatellus	na	na	na	NM	9	2011	AMNH
904	Melissodes	EU	fasciatellus	Asteraceae	Machaeranthera	parviflora	AZ	9	2014	BLCU
905	Melissodes	EU	fasciatellus	Asteraceae	Gutierrezia	na	NM	9	2014	BLCU
504	Melissodes	EU	grindeliae	Asteraceae	Thelesperma	simplicifolium	AZ	9	2012	MSBA
505	Melissodes	EU	grindeliae	Asteraceae	Erigeron	na	NM	8	2009	MSBA

970	Melissodes	EU	grindeliae	Asteraceae	Ericameria	nauseosa	UT	8	2014	BLCU
891	Melissodes	EU	grindeliae	Asteraceae	na	na	UT	7	2001	BLCU
971	Melissodes	EU	grindeliae	Asteraceae	na	na	UT	7	2001	BLCU
890	Melissodes	EU	grindeliae	Ranunculaceae	Ranunculus	na	UT	7	2001	BLCU
1356	Melissodes	EU	grindeliae	na	na	na	AZ	8	2013	MSBA
892	Melissodes	EU	grindeliae	Asteraceae	na	na	UT	6	2001	BLCU
1267	Melissodes	EU	grindeliae	na	na	na	NM	8	2009	BLCU
972	Melissodes	EU	grindeliae	Asteraceae	na	na	UT	7	2002	BLCU
507	Melissodes	EU	grindeliae	Asteraceae	Petradoria	pumilis	UT	7	2001	BLCU
506	Melissodes	EU	grindeliae	Asteraceae	Senecio	spartoides	UT	8	2001	BLCU
1361	Melissodes	EU	humilior	Asteraceae	na	na	NM	9	2009	MSBA
511	Melissodes	EU	humilior	Asteraceae	Isocoma	coronopifolia	NM	8	2011	MSBA
1362	Melissodes	EU	humilior	Asteraceae	Heterotheca	villosa	NM	9	2009	MSBA
509	Melissodes	EU	humilior	Asteraceae	Ericameria	nauseosa	NM	8	2009	MSBA
510	Melissodes	EU	humilior	Asteraceae	Isocoma	pluriflora	NM	9	2012	MSBA
1364	Melissodes	EU	humilior	na	na	na	NM	9	2012	AMNH
1363	Melissodes	EU	humilior	Asteraceae	Senecio	na	NM	9	2012	MSBA
508	Melissodes	EU	humilior	Asteraceae	Senecio	na	NM	9	2012	MSBA
948	Melissodes	EU	hymenoxidis	Asteraceae	Chrysothamnus	depressus	UT	7	2002	BLCU
516	Melissodes	EU	hymenoxidis	Asteraceae	na	na	UT	7	2000	BLCU
1027	Melissodes	EU	hymenoxidis	Asteraceae	Erigeron	speciosus	MT	7	2014	WIBF
1026	Melissodes	EU	hymenoxidis	Asteraceae	Gaillardia	aristata	MT	7	2014	WIBF
1269	Melissodes	EU	hymenoxidis	Asteraceae	Grindelia	na	WY	8	2000	UCMC
1366	Melissodes	EU	hymenoxidis	na	na	na	UT	7	2008	BLCU
517	Melissodes	EU	hymenoxidis	Asteraceae	Ericameria	nauseosa	CA	9	2009	UCRC
706	Melissodes	EU	interruptus	na	na	na	MEX	11	2014	CEET
692	Melissodes	EU	interruptus	na	na	na	MEX	11	2012	CEET
695	Melissodes	EU	interruptus	na	na	na	MEX	9	2014	CEET
699	Melissodes	EU	interruptus	na	na	na	MEX	10	2014	CEET
702	Melissodes	EU	interruptus	na	na	na	MEX	10	2014	CEET
691	Melissodes	EU	interruptus	na	na	na	MEX	10	2012	CEET
675	Melissodes	EU	interruptus	na	na	na	MEX	9	2014	CEET
697	Melissodes	EU	interruptus	na	na	na	MEX	9	2014	CEET

698	Melissodes	EU	interruptus	na	na	na	MEX	9	2014	CEET
140	Melissodes	EU	interruptus	na	na	na	MEX	9	2012	CEET
696	Melissodes	EU	interruptus	na	na	na	MEX	9	2014	CEET
700	Melissodes	EU	interruptus	na	na	na	MEX	10	2014	CEET
701	Melissodes	EU	interruptus	na	na	na	MEX	10	2014	CEET
694	Melissodes	EU	interruptus	na	na	na	MEX	8	2013	CEET
677	Melissodes	EU	interruptus	na	na	na	MEX	10	2014	CEET
703	Melissodes	EU	interruptus	na	na	na	MEX	10	2014	CEET
143	Melissodes	EU	interruptus	na	na	na	MEX	12	2011	CEET
673	Melissodes	EU	interruptus	na	na	na	MEX	9	2014	CEET
523	Melissodes	EU	limbus	na	na	na	AZ	8	2008	BLCU
528	Melissodes	EU	limbus	na	na	na	AZ	8	2010	AMNH
1276	Melissodes	EU	limbus	na	na	na	AZ	8	2007	AMNH
1279	Melissodes	EU	limbus	na	na	na	AZ	8	2007	AMNH
930	Melissodes	EU	limbus	Asteraceae	Machaeranthera	na	NM	8	2001	BLCU
973	Melissodes	EU	limbus	na	na	na	MEX	9	1998	BLCU
776	Melissodes	EU	limbus	Asteraceae	Flaveria	chlorifolia	NM	9	2011	MSBA
522	Melissodes	EU	limbus	Asteraceae	Pectis	angustifolia	AZ	9	2008	BLCU
950	Melissodes	EU	limbus	Asteraceae	Verbesina	na	NM	9	2008	BLCU
760	Melissodes	EU	limbus	na	na	na	NM	8	2008	BLCU
524	Melissodes	EU	limbus	Asteraceae	Baileya	multiradiata	AZ	5	2007	AMNH
520	Melissodes	EU	limbus	Asteraceae	Gutierrezia	na	NV	9	1997	BLCU
527	Melissodes	EU	limbus	Asteraceae	Hymenoxys	hoopesii	AZ	8	2012	MSBA
951	Melissodes	EU	limbus	na	na	na	AZ	9	2008	BLCU
521	Melissodes	EU	limbus	Asteraceae	na	na	AZ	9	2008	BLCU
635	Melissodes	EU	limbus	na	na	na	NM	8	2014	AMNH
529	Melissodes	EU	limbus	na	na	na	AZ	8	2010	AMNH
531	Melissodes	EU	limbus	na	na	na	NM	5	2012	AMNH
775	Melissodes	EU	limbus	Rosaceae	Fallugia	paradoxa	NM	8	2014	MSBA
530	Melissodes	EU	limbus	na	na	na	AZ	8	2011	AMNH
949	Melissodes	EU	limbus	Asteraceae	Grindelia	squarrosa	NM	8	2013	BLCU
96	Melissodes	EU	menuachus	na	na	na	OR	9	1959	BLCU
1284	Melissodes	EU	menuachus	na	na	na	ND	9	2009	MSBA

1374	Melissodes	EU	menuachus	Asteraceae	Erigeron	subtrinervis	NM	7	2012	EMEC
755	Melissodes	EU	menuachus	Asteraceae	Chrysothamnus	viscidiflorus	UT	8	2002	BLCU
1375	Melissodes	EU	menuachus	Asteraceae	Grindelia	squarrosa	UT	8	2001	SEMC
92	Melissodes	EU	menuachus	Asteraceae	Grindelia	squarrosa	NM	9	2012	MSBA
1005	Melissodes	EU	menuachus	vane trap	na	n	NE	9	2014	OSEC
622	Melissodes	EU	menuachus	yellowvane	na	na	CO	9	2013	UCMC
1037	Melissodes	EU	menuachus	na	na	na	MEX	8	2013	CEET
906	Melissodes	EU	menuachus	na	na	na	AZ	8	1997	BLCU
93	Melissodes	EU	menuachus	na	na	na	CO	7	2012	UCRC
1282	Melissodes	EU	menuachus	Asteraceae	Isocoma	pluriflora	NM	8	2014	MSBA
89	Melissodes	EU	menuachus	na	na	na	MT	8	1963	BLCU
90	Melissodes	EU	menuachus	Asteraceae	Machaeranthera	canescens	NM	9	2009	MSBA
95	Melissodes	EU	menuachus	Asteraceae	Helianthus	annuus	NM	9	2002	MSBA
1372	Melissodes	EU	menuachus	Asteraceae	na	na	AZ	9	2006	FSCA
1373	Melissodes	EU	menuachus	Asteraceae	na	na	WY	8	2000	UCMC
1370	Melissodes	EU	menuachus	Asteraceae	Verbesina	encelioides	NM	9	2007	MSBA
907	Melissodes	EU	menuachus	Asteraceae	na	na	NM	9	2010	BLCU
967	Melissodes	EU	microstictus	bluevane	na	na	WA	7	2013	BLCU
1061	Melissodes	EU	microstictus	bluevane	na	na	OR	7	2015	OSAC
1023	Melissodes	EU	microstictus	Asteraceae	Carduus	nutans	MT	7	2014	MSBA
1102	Melissodes	EU	microstictus	na	na	na	MT	8	2015	WIBF
1024	Melissodes	EU	microstictus	Asteraceae	Centaurea	stoebe	MT	7	2014	MSBA
1072	Melissodes	EU	microstictus	bluevane	na	na	OR	7	2014	OSAC
1113	Melissodes	EU	microstictus	na	na	na	MT	8	2009	MSBA
102	Melissodes	EU	microstictus	Asteraceae	Ericameria	bloomeri	CA	9	2004	BLCU
1025	Melissodes	EU	microstictus	Asteraceae	Erigeron	speciosus	MT	7	2014	MSBA
101	Melissodes	EU	microstictus	na	na	na	ID	8	1963	BLCU
100	Melissodes	EU	microstictus	Asteraceae	Grindelia	squarrosa	UT	7	2012	BLCU
1114	Melissodes	EU	microstictus	na	na	na	ID	7	2014	MSBA
1103	Melissodes	EU	microstictus	na	na	na	MT	8	2015	WIBF
1115	Melissodes	EU	microstictus	na	na	na	MT	8	2010	MSBA
104	Melissodes	EU	microstictus	Asteraceae	Cirsium	na	UT	7	2012	BLCU
866	Melissodes	EU	microstictus	Asteraceae	Hazardia	whitneyi	CA	8	2009	BLCU

860	Melissodes	EU	microsticta	Asteraceae	Dieteria	canescens	CA	7	2014	BLCU
861	Melissodes	EU	microstictus	Asteraceae	na	na	CO	8	2014	BLCU
1022	Melissodes	EU	microstictus	Asteraceae	Cirsium	vulgare	MT	7	2014	MSBA
865	Melissodes	EU	microstictus	na	na	na	CA	6	2006	BLCU
868	Melissodes	EU	microstictus	Asteraceae	Pyrrocoma	apargioides	CA	7	2004	BLCU
1116	Melissodes	EU	microstictus	Asteraceae	na	na	MT	8	2009	MSBA
867	Melissodes	EU	microstictus	Asteraceae	Symphyotrichum	spathulatum	CA	9	2006	BLCU
869	Melissodes	EU	microstictus	Asteraceae	Erigeron	peregrinus	CA	8	2005	BLCU
863	Melissodes	EU	microstictus	na	na	na	CA	8	2004	BLCU
864	Melissodes	EU	microstictus	na	na	na	CA	8	2004	BLCU
103	Melissodes	EU	microstictus	Scrophulariaceae	Mimulus	pulsiferae	CA	8	2004	BLCU
99	Melissodes	EU	microstictus	na	na	na	Canada	8	1963	BLCU
859	Melissodes	EU	microstictus	Malvaceae	Sidalcea	malviflora	CA	7	2006	BLCU
862	Melissodes	EU	microstictus	na	na	na	CA	8	2006	BLCU
1056	Melissodes	EU	microstictus	bluevane	na	na	OR	7	2015	OSAC
1059	Melissodes	EU	microstictus	bluevane	na	na	OR	7	2015	OSAC
118	Melissodes	EU	montanus	na	na	na	MEX	11	2012	CEET
942	Melissodes	EU	montanus	na	na	na	UT	8	2001	BLCU
116	Melissodes	EU	montanus	na	na	na	MEX	8	2013	CEET
638	Melissodes	EU	montanus	na	na	na	AZ	9	2013	AMNH
637	Melissodes	EU	montanus	na	na	na	AZ	9	2013	AMNH
106	Melissodes	EU	montanus	Asteraceae	Helianthus	annuus	AZ	9	2012	MSBA
612	Melissodes	EU	montanus	Asteraceae	Grindelia	squarrosa	CO	9	2012	UCMC
110	Melissodes	EU	montanus	Asteraceae	Heliomeris	multiflora	AZ	9	2012	MSBA
109	Melissodes	EU	montanus	Asteraceae	Heliomeris	multiflora	AZ	9	2012	MSBA
111	Melissodes	EU	montanus	Asteraceae	Heliomeris	multiflora	AZ	9	2012	MSBA
113	Melissodes	EU	montanus	na	na	na	NM	8	2009	BLCU
613	Melissodes	EU	montanus	Asteraceae	Chrysothamnus	na	CO	10	2012	UCMC
108	Melissodes	EU	montanus	Asteraceae	Ericameria	na	NM	10	2010	BLCU
662	Melissodes	EU	montanus	na	na	na	MEX	10	2014	CEET
712	Melissodes	EU	montanus	na	na	na	MEX	10	2014	CEET
107	Melissodes	EU	montanus	Asteraceae	Thelesperma	simplicifolium	AZ	9	2012	MSBA
660	Melissodes	EU	montanus	na	na	na	MEX	10	2014	CEET

112	Melissodes	EU	montanus	na	na	na	TX	9	1990	BLCU
709	Melissodes	EU	montanus	na	na	na	MEX	9	2014	CEET
661	Melissodes	EU	montanus	na	na	na	MEX	9	2014	CEET
117	Melissodes	EU	montanus	na	na	na	MEX	8	2013	CEET
937	Melissodes	EU	pallidisignatus	na	na	na	WA	7	1999	BLCU
1105	Melissodes	EU	pallidisignatus	Asteraceae	Centaurea	maculosa	MT	8	2015	WIBF
129	Melissodes	EU	pallidisignatus	Asteraceae	Chrysothamnus	viscidiflorus	NV	9	1979	BLCU
1154	Melissodes	EU	pallidisignatus	Asteraceae	na	na	ID	8	2007	WFBM
939	Melissodes	EU	pallidisignatus	Asteraceae	Engelmannia	pinnatifida	NM	7	2009	BLCU
133	Melissodes	EU	pallidisignatus	Asteraceae	Ericameria	nauseosa	AZ	9	2012	MSBA
1106	Melissodes	EU	pallidisignatus	Asteraceae	Erigeron	speciosus	MT	7	2015	MSBA
128	Melissodes	EU	pallidisignatus	Asteraceae	Grindelia	squarrosa	NM	9	2012	MSBA
1100	Melissodes	EU	pallidisignatus	na	na	na	UT	9	2011	MSBA
940	Melissodes	EU	pallidisignatus	pantrap	na	na	WA	7	2010	BLCU
938	Melissodes	EU	pallidisignatus	Asteraceae	Gutierrezia	sarothrae	UT	9	2005	BLCU
124	Melissodes	EU	pallidisignatus	na	na	na	AZ	8	2009	BLCU
131	Melissodes	EU	pallidisignatus	na	na	na	MEX	7	2013	CEET
1104	Melissodes	EU	pallidisignatus	na	na	na	MT	8	2015	WIBF
127	Melissodes	EU	pallidisignatus	Asteraceae	Solidago	velutina	NM	8	2009	BLCU
1029	Melissodes	EU	pallidisignatus	na	na	na	MT	8	2014	WIBF
132	Melissodes	EU	pallidisignatus	Brassicaceae	Sisymbrium	altissimum	WA	8	2004	BLCU
936	Melissodes	EU	pallidisignatus	na	na	na	AZ	8	2009	BLCU
130	Melissodes	EU	pallidisignatus	na	na	na	CA	8	2005	UCRC
126	Melissodes	EU	pallidisignatus	na	na	na	CO	7	2012	UCRC
135	Melissodes	EU	paucipuncta	Cactaceae	Cylindropuntia	na	AZ	4	2013	MSBA
231	Melissodes	EU	paucipuncta	Cactaceae	Cylindropuntia	na	AZ	4	2013	MSBA
232	Melissodes	EU	paucipuncta	Cactaceae	Cylindropuntia	na	AZ	4	2013	MSBA
947	Melissodes	EU	perpolitus	Asteraceae	Grindelia	squarrosa	UT	8	2013	BLCU
136	Melissodes	EU	perpolitus	Asteraceae	Gutierrezia	na	NM	9	2003	MSBA
944	Melissodes	EU	perpolitus	Asteraceae	na	na	UT	8	2013	BLCU
946	Melissodes	EU	perpolitus	Asteraceae	Chrysothamnus	na	UT	8	2013	BLCU
945	Melissodes	EU	perpolitus	na	na	na	UT	8	2013	BLCU
713	Melissodes	EU	persimilis	na	na	na	MEX	9	2014	CEET

672	Melissodes	EU	persimilis	na	na	na	MEX	11	2014	CEET
147	Melissodes	EU	persimilis	Asteraceae	Verbesina	encelioides	NM	10	2010	BLCU
148	Melissodes	EU	persimilis	Asteraceae	Viguiera	stenoloba	NM	10	2010	BLCU
149	Melissodes	EU	persimilis	Asteraceae	Viguiera	dentata	NM	10	2010	BLCU
150	Melissodes	EU	persimilis	Asteraceae	Senecio	na	NM	10	2010	BLCU
714	Melissodes	EU	persimilis	na	na	na	MEX	10	2014	CEET
715	Melissodes	EU	persimilis	na	na	na	MEX	10	2014	CEET
716	Melissodes	EU	persimilis	na	na	na	MEX	10	2014	CEET
717	Melissodes	EU	persimilis	na	na	na	MEX	10	2014	CEET
718	Melissodes	EU	persimilis	na	na	na	MEX	10	2014	CEET
146	Melissodes	EU	persimilis	na	na	na	NM	9	2010	BLCU
526	Melissodes	EU	rufipes	Asteraceae	Helenium	thurberi	MEX		2007	
155	Melissodes	EU	rufipes	na	na	na	MEX		2013	
1038	Melissodes	EU	rufipes	na	na	na	MEX	7	2013	CEET
1039	Melissodes	EU	rufipes	na	na	na	MEX	7	2013	CEET
1040	Melissodes	EU	rufipes	na	na	na	MEX	7	2013	CEET
156	Melissodes	EU	saponellus	Asteraceae	na	na	UT	9	2003	BLCU
932	Melissodes	EU	saponellus	Convolvulaceae	Convolvulus	na	UT	6	2013	BLCU
931	Melissodes	EU	saponellus	na	na	na	UT	6	1997	BLCU
157	Melissodes	EU	semilupinus	Asteraceae	Ericameria	nauseosa	UT	9	2001	BLCU
159	Melissodes	EU	semilupinus	pantrap	na	na	UT	9	2008	BLCU
1378	Melissodes	EU	semilupinus	na	na	na	NM	8	2011	UCRC
163	Melissodes	EU	semilupinus	Asteraceae	Machaeranthera	gracilis	NM	9	2009	MSBA
1379	Melissodes	EU	semilupinus	Asteraceae	Verbesina	encelioides	NM	9	2007	MSBA
160	Melissodes	EU	semilupinus	Euphorbiaceae	Croton	texensis	NM	9	2008	MSBA
164	Melissodes	EU	semilupinus	Asteraceae	Machaeranthera	canescens	NM	9	2004	MSBA
161	Melissodes	EU	semilupinus	na	na	na	NM	9	2008	MSBA
1380	Melissodes	EU	semilupinus	pantrap	na	na	NM	10	2006	MSBA
162	Melissodes	EU	semilupinus	Asteraceae	Palafoxia	sphacelata	NM	9	2006	MSBA
166	Melissodes	EU	semilupinus	na	na	na	NM	9	2005	MSBA
158	Melissodes	EU	semilupinus	Asteraceae	na	na	UT	9	2001	BLCU
175	Melissodes	EU	snowii	Asteraceae	Ericameria	nauseosa	NM	9	2004	MSBA
1384	Melissodes	EU	snowii	Asteraceae	Baileya	multiradiata	NM	9	2003	MSBA

1382	Melissodes	EU	snowii	Asteraceae	Palafoxia	sphacelata	NM	9	2006	MSBA
1299	Melissodes	EU	snowii	Asteraceae	Ericameria	nauseosa	UT	8	2001	BLCU
1385	Melissodes	EU	snowii	na	na	na	NM	9	2005	MSBA
1389	Melissodes	EU	snowii	Asteraceae	Grindelia	na	NM	8	2000	UCMC
1388	Melissodes	EU	snowii	Asteraceae	Psilostrophe	tagetina	NM	10	2005	MSBA
1391	Melissodes	EU	snowii	na	na	na	UT	9	1983	BLCU
991	Melissodes	EU	snowii	vane trap	na	na	TX	8	2014	OSEC
167	Melissodes	EU	snowii	Asteraceae	Palafoxia	sphacelata	NM	9	2006	MSBA
1320	Melissodes	EU	snowii	Asteraceae	Isocoma	pluriflora	NM	8	2014	MSBA
168	Melissodes	EU	snowii	Asteraceae	Machaeranthera	canescens	NM	9	2009	MSBA
169	Melissodes	EU	snowii	Asteraceae	Hymenopappus	filifolius	NM	10	2005	MSBA
170	Melissodes	EU	snowii	Asteraceae	Machaeranthera	gracilis	NM	9	2009	MSBA
172	Melissodes	EU	snowii	na	na	na	NM	9	2005	MSBA
1383	Melissodes	EU	snowii	Asteraceae	Cirsium	na	NM	7	2009	BLCU
1387	Melissodes	EU	snowii	Fabaceae	Dalea	lanata	NM	9	2004	MSBA
171	Melissodes	EU	snowii	Asteraceae	Baileya	multiradiata	NM	9	2003	MSBA
173	Melissodes	EU	snowii	Fabaceae	Psorothamnus	scoparius	NM	9	2004	MSBA
1112	Melissodes	EU	subagilis	na	na	na	MT	8	2013	MSBA
176	Melissodes	EU	subagilis	Asteraceae	Grindelia	squarrosa	NM	8	2012	MSBA
788	Melissodes	EU	subagilis	na	na	na	SD	8	2011	BIML
789	Melissodes	EU	subagilis	na	na	na	SD	8	2011	BIML
790	Melissodes	EU	subagilis	na	na	na	SD	9	2011	BIML
952	Melissodes	EU	subagilis	Asteraceae	Chrysothamnus	na	UT	8	2013	BLCU
754	Melissodes	EU	subagilis	Asteraceae	Helianthus	annuus	UT	8	2009	BLCU
1392	Melissodes	EU	subagilis	na	na	na	AZ	8	2012	UCRC
179	Melissodes	EU	subagilis	na	na	na	AZ	8	2003	BLCU
753	Melissodes	EU	subagilis	na	na	na	AZ	8	2012	UCRC
177	Melissodes	EU	subagilis	Asteraceae	Haplopappus	na	NM	9	2010	BLCU
178	Melissodes	EU	subagilis	na	na	na	AZ	9	2009	AMNH
1300	Melissodes	EU	subagilis	na	na	na	AZ	9	2012	AMNH
182	Melissodes	EU	subagilis	Asteraceae	Helianthus	annuus	NM	9	2002	MSBA
180	Melissodes	EU	subagilis	na	na	na	AZ	8	2008	BLCU
787	Melissodes	EU	subagilis	na	na	na	SD	9	2011	BIML

679	Melissodes	EU	subillatus	na	na	na	IL	7	2014	MSBA
185	Melissodes	EU	subillatus	na	na	na	NY	6	2005	AMNH
1393	Melissodes	EU	subillatus	na	na	na	IL	7	2014	MSBA
1303	Melissodes	EU	subillatus	na	na	na	MN	7	2015	MSBA
1304	Melissodes	EU	subillatus	na	na	na	MN	7	2015	MSBA
680	Melissodes	EU	subillatus	na	na	na	IL	7	2014	MSBA
575	Melissodes	EU	subillatus	Asteraceae	Solidago	nemoralis	IA	7	2004	SUI
184	Melissodes	EU	subillatus	Asteraceae	Rudbeckia	hirta	NJ	6	2011	MSBA
563	Melissodes	EU	subillatus	Asteraceae	Solidago	rigida	ND		2012	
578	Melissodes	EU	subillatus	Fabaceae	Dalea	purpurea	*IA*	7	2004	SUI
1394	Melissodes	EU	subillatus	Fabaceae	Amorpha	canescens	IA	7	2002	SUI
579	Melissodes	EU	subillatus	Asteraceae	Heliopsis	helianthoides	IA	7	2004	SUI
192	Melissodes	EU	submenuacha	na	na	na	AZ	9	2008	BLCU
193	Melissodes	EU	submenuacha	na	na	na	AZ	8	2010	AMNH
191	Melissodes	EU	submenuacha	Asteraceae	Verbesina	encelioides	NM	9	2010	BLCU
1395	Melissodes	EU	submenuacha	Asteraceae	Helianthus	annuus	NM	9	2012	MSBA
1396	Melissodes	EU	submenuacha	Asteraceae	Verbesina	encelioides	NM	9	2012	MSBA
1306	Melissodes	EU	submenuacha	Zygophyllaceae	Kallstroemia	grandiflora	NM	8	2000	SEMC
201	Melissodes	EU	trinodis	na	na	na	PA	7	2011	MSBA
1159	Melissodes	EU	trinodis	bluevane	na	na	PA	7	2014	PennState
1176	Melissodes	EU	trinodis	vane trap	na	na	NE	8	2014	OSEC
596	Melissodes	EU	trinodis	Asteraceae	Helianthus	pauciflorus	IA	8	2004	SUI
199	Melissodes	EU	trinodis	Asteraceae	Grindelia	squarrosa	SD	8	2012	MSBA
1015	Melissodes	EU	trinodis	vane trap	na	n	NE	8	2014	OSEC
1016	Melissodes	EU	trinodis	vane trap	na	n	NE	8	2014	OSEC
1175	Melissodes	EU	trinodis	vane trap	na	na	NE	9	2014	OSEC
1161	Melissodes	EU	trinodis	bluevane	na	na	PA	7	2011	PennState
1164	Melissodes	EU	trinodis	bluevane	na	na	PA	7	2013	PennState
1165	Melissodes	EU	trinodis	bluevane	na	na	PA	8	2015	PennState
1166	Melissodes	EU	trinodis	bluevane	na	na	PA	7	2015	PennState
1167	Melissodes	EU	trinodis	bluevane	na	na	PA	7	2015	PennState
1169	Melissodes	EU	trinodis	bluevane	na	na	PA	8	2015	PennState
1170	Melissodes	EU	trinodis	bluevane	na	na	PA	8	2015	PennState

1171	Melissodes	EU	trinodis	bluevane	na	na	PA	8	2015	PennState
1168	Melissodes	EU	trinodis	bluevane	na	na	PA	7	2015	PennState
1158	Melissodes	EU	trinodis	Asteraceae	Helianthus	divaricatus	PA	7	2014	PennState
594	Melissodes	EU	trinodis	Asteraceae	Ratibida	pinnata	IA	8	2002	SUI
568	Melissodes	EU	trinodis	Asteraceae	Cirsium	na	ND	8	2011	E UMSP
592	Melissodes	EU	trinodis	Asteraceae	Aster	ericoides	IA	9	2002	SUI
198	Melissodes	EU	trinodis	Asteraceae	Sonchus	oleraceus	NM	8	2010	MSBA
591	Melissodes	EU	trinodis	Asteraceae	Aster	laevis	IA	9	2004	SUI
590	Melissodes	EU	trinodis	Asteraceae	Liatris	pynostachya	IA	8	2002	SUI
626	Melissodes	EU	trinodis	bluevane	na	na	CO	8	2013	UCMC
600	Melissodes	EU	trinodis	Asteraceae	Aster	novae-angliae	IA	9	2002	SUI
627	Melissodes	EU	trinodis	yellowvane	na	na	CO	7	2013	UCMC
28	Melissodes	EU	tristis	Fabaceae	Psorothamnus	na	AZ	9	2008	BLCU
831	Melissodes	EU	tristis	na	na	na	NV	5	2004	BLCU
836	Melissodes	EU	tristis	Asteraceae	Encelia	virginensis	NV	6	2005	BLCU
767	Melissodes	EU	tristis	Asteraceae	Ericameria	nauseosa	NM	9	2013	MSBA
837	Melissodes	EU	tristis	Asteraceae	Geraea	canescens	NV	5	2005	BLCU
826	Melissodes	EU	tristis	Asteraceae	Isocoma	tenuisecta	AZ	8	2013	BLCU
838	Melissodes	EU	tristis	Asteraceae	Machaeranthera	tanacetifolia	NM	8	2014	BLCU
21	Melissodes	EU	tristis	Fabaceae	Melilotus	officinalis	NM	6	2012	MSBA
823	Melissodes	EU	tristis	Asteraceae	Senecio	flaccidus	NV	7	2004	BLCU
27	Melissodes	EU	tristis	Asteraceae	Erigeron	na	NM	6	1991	BLCU
828	Melissodes	EU	tristis	Fabaceae	Prosopis	glandulosa	NV	5	2004	BLCU
824	Melissodes	EU	tristis	Brassicaceae	Lepidium	na	NM	8	2001	BLCU
747	Melissodes	EU	tristis	bluevane	na	na	TX	8	2014	OSEC
15	Melissodes	EU	tristis	Fabaceae	Dalea	leporina	NM	7	2004	MSBA
24	Melissodes	EU	tristis	Boraginaceae	Cryptantha	na	UT	6	2001	BLCU
14	Melissodes	EU	tristis	Convolvulaceae	Ipomoea	leptophylla	NM	6	2004	MSBA
26	Melissodes	EU	tristis	Fabaceae	Dalea	carthegenesis	MEX	5	1997	BLCU
20	Melissodes	EU	tristis	Fabaceae	Melilotus	officinalis	NM	6	2012	MSBA
19	Melissodes	EU	tristis	Malvaceae	Sphaeralcea	na	NM	na	na	AMNH
827	Melissodes	EU	tristis	Loasaceae	Metzelia	na	AZ	8	2014	BLCU
768	Melissodes	EU	tristis	Malvaceae	Sphaeralcea	polychroma	NM	8	2014	MSBA

22	Melissodes	EU	tristis	Malvaceae	Sphaeralcea	ambigua	NV	6	2004	BLCU
25	Melissodes	EU	tristis	Asteraceae	Petradoria	pumila	UT	7	2001	BLCU
30	Melissodes	EU	tristis	Malvaceae	Sphaeralcea	coccinea	UT	5	2000	BLCU
835	Melissodes	EU	tristis	Hydrophyllaceae	Phacelia	crenulata	NV	4	2005	BLCU
833	Melissodes	EU	tristis	Lamiaceae	Salvia	dorrii	NV	6	2005	BLCU
839	Melissodes	EU	tristis	Polygonaceae	Eriogonum	deflexum	NV	8	2004	BLCU
16	Melissodes	EU	tristis	Cactaceae	Opuntia	polyocantha	NM	5	2002	MSBA
822	Melissodes	EU	tristis	Scrophulariaceae	Cordylanthus	parviflorus	NV	7	2005	BLCU
23	Melissodes	EU	tristis	Tamaricaceae	Tamarix	na	UT	6	2003	BLCU
29	Melissodes	EU	tristis	Malvaceae	Sphaeralcea	na	TX	4	1966	INHS
18	Melissodes	EU	tristis	Zygophyllaceae	Larrea	tridentata	NM	8	2010	MSBA
842	Melissodes	EU	utahensis	Asteraceae	Chrysothamnus	viscidiflorus	NV	8	2004	BLCU
844	Melissodes	EU	utahensis	Asteraceae	Grindelia	squarrosa	UT	8	2005	BLCU
846	Melissodes	EU	utahensis	Asteraceae	Dieteria	canescens	NV	9	2004	BLCU
845	Melissodes	EU	utahensis	Asteraceae	Chrysothamnus	na	UT	8	2013	BLCU
630	Melissodes	EU	utahensis	Asteraceae	Grindelia	squarrosa	CO	8	2012	UCMC
203	Melissodes	EU	utahensis	na	na	na	CA	10	1980	BLCU
843	Melissodes	EU	utahensis	Asteraceae	Gutierrezia	microcephala	NV	9	2004	BLCU
847	Melissodes	EU	utahensis	Asteraceae	Bebbia	juncea	NV	9	2005	BLCU
205	Melissodes	EU	utahensis	pantrap	na	na	UT	9	2008	BLCU
848	Melissodes	EU	utahensis	Asteraceae	na	na	UT	8	2013	BLCU
209	Melissodes	EU	velutinus	Polemoniaceae	Eriastrum	densifolium	CA	6	2011	UCRC
211	Melissodes	EU	velutinus	Polemoniaceae	Eriastrum	na	CA	6	2011	UCRC
678	Melissodes	EU	velutinus	Boraginaceae	Cryptantha	intermedia	CA	7	2013	MSBA
854	Melissodes	EU	verbesinarum	Tamaricaceae	Tamarix	ramosissima	AZ	5	2014	BLCU
856	Melissodes	EU	verbesinarum	na	na	na	NV	6	2004	BLCU
218	Melissodes	EU	verbesinarum	Asteraceae	Baileya	multiradiata	NM	8	2010	BLCU
850	Melissodes	EU	verbesinarum	Asteraceae	Stephanomeria	na	NV	10	2005	BLCU
858	Melissodes	EU	verbesinarum	na	na	na	NV	5	2004	BLCU
853	Melissodes	EU	verbesinarum	Asteraceae	Encelia	virginensis	NV	7	2005	BLCU
633	Melissodes	EU	verbesinarum	Asteraceae	Grindelia	squarrosa	CO	8	2013	UCMC
632	Melissodes	EU	verbesinarum	bluevane	na	na	CO	9	2013	UCMC
857	Melissodes	EU	verbesinarum	na	na	na	NV	9	2004	BLCU

222	Melissodes	EU	verbesinarum	na	na	na	AZ	5	2004	MSBA
223	Melissodes	EU	verbesinarum	Asteraceae	Hymenoxys	hoopesii	AZ	8	2012	MSBA
213	Melissodes	EU	verbesinarum	Asteraceae	Isocoma	pluriflora	NM	9	2012	MSBA
219	Melissodes	EU	verbesinarum	Asteraceae	Ericameria	nauseosa	NM	8	2009	MSBA
849	Melissodes	EU	verbesinarum	Asteraceae	na	na	AZ	9	2008	BLCU
59	Melissodes	EU	verbesinarum	na	na	na	NV	10	1998	BLCU
212	Melissodes	EU	verbesinarum	Asteraceae	Psilostrophe	tagetina	NM	10	2005	MSBA
228	Melissodes	EU	verbesinarum	Asteraceae	Machaeranthera	pinnatifida	NM	9	2004	MSBA
227	Melissodes	EU	verbesinarum	na	na	na	NM	9	2005	MSBA
229	Melissodes	EU	verbesinarum	Asteraceae	Machaeranthera	tanacetifolia	NM	9	2003	MSBA
216	Melissodes	EU	verbesinarum	Asteraceae	Pectis	angustifolia	AZ	9	2008	BLCU
226	Melissodes	EU	verbesinarum	na	na	na	AZ	8	2011	AMNH
639	Melissodes	EU	verbesinarum	na	na	na	AZ	8	2014	AMNH
217	Melissodes	EU	verbesinarum	Asteraceae	na	na	AZ	9	2008	BLCU
215	Melissodes	EU	verbesinarum	na	na	na	CA	9	1980	BLCU
1314	Melissodes	EU	vernalis	na	na	na	AZ	5	2012	AMNH
875	Melissodes	EU	vernalis	Asteraceae	Baileya	multiradiata	NV	6	2005	BLCU
1401	Melissodes	EU	vernalis	Asteraceae	Baileya	multiradiata	NM	5	2005	MSBA
873	Melissodes	EU	vernalis	Asteraceae	Encelia	virginensis	NV	5	2005	BLCU
874	Melissodes	EU	vernalis	Malvaceae	Sphaeralcea	ambigua	NV	6	2005	BLCU
871	Melissodes	EU	vernalis	Asteraceae	Bebbia	juncea	CA	4	2013	BLCU
872	Melissodes	EU	vernalis	Asteraceae	Encelia	na	CA	4	2013	BLCU
870	Melissodes	EU	vernalis	Asteraceae	Psilostrophe	cooperi	NV	5	2004	BLCU
879	Melissodes	EU	vernalis	na	na	na	NV	6	2004	BLCU
880	Melissodes	EU	vernalis	Asteraceae	Stephanomeria	exigua	NV	6	2005	BLCU
876	Melissodes	EU	vernalis	Asteraceae	Atrichoseris	platyphylla	NV	5	2005	BLCU
878	Melissodes	EU	vernalis	Asteraceae	Chaenactis	freemontii	NV	6	2004	BLCU
877	Melissodes	EU	vernalis	Malvaceae	Sphaeralcea	na	NV	6	2005	BLCU
625	Melissodes	EU	vernoniae	bluevane	na	na	CO	8	2013	UCMC
1156	Melissodes	EU	vernoniae	vane trap	na	na	NE	7	2014	OSEC
624	Melissodes	EU	vernoniae	bluevane	na	na	CO	8	2013	UCMC
1317	Melissodes	EU	wheeleri	na	na	na	AZ	9	1991	AMNH
239	Melissodes	EU	wheeleri	na	na	na	AZ	9	2008	BLCU

186	Melissodes	EU	wheeleri	Asteraceae	Rudbeckia	hirta	KS	7	2010	MSBA
758	Melissodes	EU	wheeleri	na	na	na	AZ	8	2008	AMNH
235	Melissodes	EU	wheeleri	na	na	na	AZ	8	2011	AMNH
236	Melissodes	EU	wheeleri	Asteraceae	Rudbeckia	hirta	TX	5	2013	MSBA
240	Melissodes	EU	wheeleri	Asteraceae	Gaillardia	na	TX	5	1953	SEMC
237	Melissodes	EU	wheeleri	Asteraceae	Verbesina	na	NM	8	2004	UCRC
1136	Melissodes	H	desonsus	bluevane	na	na	PA	8	2014	PennState
1231	Melissodes	H	desonsus	na	na	na	MN	7	2015	MSBA
1232	Melissodes	H	desonsus	na	na	na	MN	7	2015	MSBA
983	Melissodes	H	rivalis	vane trap	na	na	TX	7	2014	OSEC
491	Melissodes	H	rivalis	Asteraceae	Centaurea	americana	NM	7	2009	BLCU
555	Melissodes	H	rivalis	Asteraceae	Cirsium	arizonicum	AZ	9	2012	MSBA
493	Melissodes	H	rivalis	Asteraceae	Cirsium	na	UT	7	2008	BLCU
494	Melissodes	H	rivalis	Asteraceae	Cirsium	na	UT	7	2008	BLCU
1082	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
1086	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
1080	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
1085	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
988	Melissodes	H	rivalis	vane trap	na	na	TX	7	2014	OSEC
989	Melissodes	H	rivalis	vane trap	na	na	TX	7	2014	OSEC
1081	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
1084	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
1050	Melissodes	H	rivalis	bluevane	na	na	OR	7	2015	OSAC
986	Melissodes	H	rivalis	vane trap	na	na	TX	6	2014	OSEC
1083	Melissodes	H	rivalis	bluevane	na	na	OR	7	2014	OSAC
496	Melissodes	H	rivalis	na	na	na	ID	7	1972	BLCU
968	Melissodes	H	rivalis	na	na	na	AZ	8	2008	BLCU
492	Melissodes	H	rivalis	na	na	na	AZ	9	2008	BLCU
1048	Melissodes	H	rivalis	bluevane	na	na	OR	7	2015	OSAC
729	Melissodes	H	rivalis	bluevane	na	na	TX	6	2014	OSEC
731	Melissodes	H	rivalis	bluevane	na	na	TX	6	2014	OSEC
732	Melissodes	H	rivalis	bluevane	na	na	TX	6	2014	OSEC
984	Melissodes	H	rivalis	vane trap	na	na	TX	7	2014	OSEC

985	Melissodes	H	rivalis	vane trap	na	na	TX	7	2014	OSEC
1193	Melissodes	M	bimaculatus	multi-pher trap	na	na	PA	8	2009	PennState
1181	Melissodes	M	bimaculatus	bluevane	na	na	PA	8	2014	PennState
1182	Melissodes	M	bimaculatus	bluevane	na	na	PA	8	2014	PennState
1199	Melissodes	M	bimaculatus	bluevane	na	na	PA	7	2013	PennState
1201	Melissodes	M	bimaculatus	pantrap	na	na	PA	7	2011	PennState
1202	Melissodes	M	bimaculatus	pantrap	na	na	PA	7	2011	PennState
1197	Melissodes	M	bimaculatus	bluevane	na	na	PA	7	2013	PennState
1177	Melissodes	M	bimaculatus	Asteraceae	Helianthus	na	PA	8	2013	PennState
1196	Melissodes	M	bimaculatus	pantrap	na	na	PA	7	2007	PennState
245	Melissodes	M	bimaculatus	na	na	na	FL	6	1992	FSCA
249	Melissodes	M	bimaculatus	na	na	na	SD	8	2013	MSBA
1200	Melissodes	M	bimaculatus	pantrap	na	na	PA	8	2013	PennState
1184	Melissodes	M	bimaculatus	bluevane	na	na	PA	7	2014	PennState
1186	Melissodes	M	bimaculatus	bluevane	na	na	PA	8	2012	PennState
1178	Melissodes	M	bimaculatus	Cucurbitaceae	Cucurbita	na	PA	7	2011	PennState
1191	Melissodes	M	bimaculatus	bluevane	na	na	PA	6	2012	PennState
646	Melissodes	M	bimaculatus	na	na	na	GA	8	2013	BIML
259	Melissodes	M	bimaculatus	na	na	na	FL	9	1999	FSCA
1188	Melissodes	M	bimaculatus	bluevane	na	na	PA	8	2012	PennState
1194	Melissodes	M	bimaculatus	multi-pher trap	na	na	PA	8	2009	PennState
1180	Melissodes	M	bimaculatus	bluevane	na	na	PA	8	2014	PennState
1190	Melissodes	M	bimaculatus	bluevane	na	na	PA	8	2012	PennState
1012	Melissodes	M	bimaculatus	vane trap	na	n	NE	8	2014	OSEC
645	Melissodes	M	bimaculatus	Convolvulaceae	Ipomoea	pandurata	GA	8	2013	BIML
255	Melissodes	M	bimaculatus	Portulacaceae	Portulaca	grandiflora	MO	7	1991	FSCA
1011	Melissodes	M	bimaculatus	vane trap	na	n	NE	8	2014	OSEC
264	Melissodes	M	colliciatus	Convolvulaceae	Ipomoea	na	MEX	9	2007	MSBA
1404	Melissodes	M	colliciatus	na	na	na	AZ	8	2003	BLCU
681	Melissodes	M	colliciatus	na	na	na	MEX	10	2014	CEET
772	Melissodes	M	colliciatus	Fabaceae	Hoffmanseggia	glauca	NM	8	2014	MSBA
265	Melissodes	M	colliciatus	na	na	na	AZ	9	2009	BLCU
739	Melissodes	M	communis	bluevane	na	na	TX	8	2014	OSEC

740	Melissodes	M	communis	bluevane	na	na	TX	8	2014	OSEC
281	Melissodes	M	communis	na	na	na	FL	8	2007	FSCA
811	Melissodes	M	communis	na	na	na	FL	8	1997	SHSU
1065	Melissodes	M	communis	bluevane	na	na	OR	7	2015	OSAC
616	Melissodes	M	communis	Asteraceae	Carduus	nutans	CO	7	2012	UCMC
738	Melissodes	M	communis	bluevane	na	na	TX	6	2014	OSEC
271	Melissodes	M	communis	Asteraceae	Thelesperma	na	NM	8	2011	BLCU
617	Melissodes	M	communis	na	na	na	CO	7	2013	UCMC
274	Melissodes	M	communis	Fabaceae	Dalea	leporina	NM	7	2004	MSBA
273	Melissodes	M	communis	na	na	na	NM	8	2002	MSBA
615	Melissodes	M	communis	bowl	na	na	CO	7	2013	UCMC
270	Melissodes	M	communis	Fabaceae	Dalea	lanata	NM	7	2007	MSBA
272	Melissodes	M	communis	na	na	na	NM	8	2002	MSBA
268	Melissodes	M	communis	Asteraceae	Cirsium	coahuilense	MEX	6	2011	MSBA
269	Melissodes	M	communis	pantrap	na	na	NM	7	2004	NMSU
267	Melissodes	M	communis	na	na	na	KS	7	2012	UCRC
745	Melissodes	M	communis	bluevane	na	na	TX	8	2014	OSEC
286	Melissodes	M	communis	Rosaceae	Fallugia	paradoxa	AZ	8	2012	MSBA
764	Melissodes	M	communis	Convolvulaceae	Ipomoea	pandurata	GA	5	2013	BIML
809	Melissodes	M	communis	Zygophyllaceae	Tribulus	cistoides	FL	8	1997	SHSU
742	Melissodes	M	communis	bluevane	na	na	TX	7	2014	OSEC
743	Melissodes	M	communis	bluevane	na	na	TX	7	2014	OSEC
601	Melissodes	M	comptoides	Lamiaceae	Ocimum	basilicum	IA	8	2010	SUI
1008	Melissodes	M	comptoides	vane trap	na	n	NE	8	2014	OSEC
1009	Melissodes	M	comptoides	vane trap	na	n	NE	9	2014	OSEC
1235	Melissodes	M	comptoides	Euphorbiaceae	Euphorbea	marginata	CO	8	1974	UCMC
1236	Melissodes	M	comptoides	Euphorbiaceae	Euphorbea	marginata	CO	8	1977	UCMC
1006	Melissodes	M	comptoides	vane trap	na	n	NE	7	2014	OSEC
733	Melissodes	M	comptoides	bluevane	na	na	TX	8	2014	OSEC
1405	Melissodes	M	gilensis	na	na	na	NM	9	2012	MSBA
722	Melissodes	M	gilensis	na	na	na	NM	8	2009	BLCU
1407	Melissodes	M	gilensis	Cactaceae	Opuntia	na	MEX	5	1997	BLCU
298	Melissodes	M	gilensis	Bignoniaceae	Tecoma	stans	MEX	5	1997	BLCU

1240	Melissodes	M	gilensis	Plantaginaceae	Penstemon	degeneri	CO	6	2008	UCMC
302	Melissodes	M	gilensis	na	na	na	MEX	10	2012	CEET
299	Melissodes	M	gilensis	Bignoniaceae	Tecoma	stans	MEX	5	1997	BLCU
306	Melissodes	M	gilensis	Fabaceae	Phaseolus	grayana	AZ	9	2008	BLCU
303	Melissodes	M	gilensis	na	na	na	AZ	9	2012	AMNH
304	Melissodes	M	gilensis	na	na	na	AZ	8	2011	AMNH
1241	Melissodes	M	gilensis	Malvaceae	Alcea	na	NM	8	2015	MSBA
300	Melissodes	M	gilensis	na	na	na	NM	6	2002	MSBA
296	Melissodes	M	gilensis	Malvaceae	Sphaeralcea	angustifolia	MEX	9	2011	MSBA
301	Melissodes	M	gilensis	Asteraceae	Cirsium	parryi	AZ	8	2012	MSBA
903	Melissodes	M	gilensis	pantrap	na	na	AZ	8	2013	BLCU
307	Melissodes	M	gilensis	na	na	na	MEX	5	1997	BLCU
902	Melissodes	M	gilensis	Asteraceae	Grindelia	na	NM	8	2014	BLCU
1418	Melissodes	M	paroselae	Asteraceae	Helianthus	annuus	NM	7	2013	MSBA
901	Melissodes	M	paroselae	pantrap	na	na	AZ	8	2013	BLCU
317	Melissodes	M	paroselae	Brassicaceae	Lepidium	na	AZ	8	2001	BLCU
311	Melissodes	M	paroselae	na	na	na	AZ	8	1958	SEMC
314	Melissodes	M	paroselae	na	na	na	AZ	8	2004	BLCU
1413	Melissodes	M	paroselae	na	na	na	AZ	7	2005	UCRC
318	Melissodes	M	paroselae	Fabaceae	Psorothamnus	na	AZ	9	2008	BLCU
641	Melissodes	M	paroselae	na	na	na	AZ	8	2014	AMNH
322	Melissodes	M	paroselae	Hydrophyllaceae	Phacelia	robusta	NM	6	2004	MSBA
652	Melissodes	M	paroselae	na	na	na	MEX	10	2014	CEET
640	Melissodes	M	paroselae	na	na	na	NM	8	2014	AMNH
1415	Melissodes	M	paroselae	Rhamnaceae	Condalia	na	AZ	7	2010	UCRC
1417	Melissodes	M	paroselae	Zygophyllaceae	Kallstroemia	grandiflora	AZ	8	2000	SEMC
1033	Melissodes	M	paroselae	na	na	na	NM	8	2000	MSBA
315	Melissodes	M	paroselae	Zygophyllaceae	Kallstroemia	grandiflora	NM	8	2004	BLCU
1416	Melissodes	M	paroselae	Zygophyllaceae	Kallstroemia	grandiflora	NM	8	2000	SEMC
316	Melissodes	M	paroselae	Aizoaceae	Thrianthema	portulacastrum	NM	8	2004	BLCU
735	Melissodes	M	tepaneca	bluevane	na	na	TX	8	2014	OSEC
334	Melissodes	M	tepaneca	na	na	na	MEX	4	2010	CEET
327	Melissodes	M	tepaneca	Malvaceae	Callirhoe	involucrata	TX	5	2013	MSBA

336	Melissodes	M	tepaneca	na	na	na	MEX	12	2010	CEET
655	Melissodes	M	tepaneca	na	na	na	MEX	9	2014	CEET
1428	Melissodes	M	tepaneca	na	na	na	MEX	10	1965	BLCU
1427	Melissodes	M	tepaneca	Gentianaceae	Eustoma	exaltatum	MEX	6	2011	MSBA
737	Melissodes	M	tepaneca	bluevane	na	na	TX	6	2014	OSEC
659	Melissodes	M	tepaneca	na	na	na	MEX	10	2014	CEET
332	Melissodes	M	tepaneca	na	na	na	MEX		2011	CEET
326	Melissodes	M	tepaneca	Cactaceae	Opuntia	na	TX	5	2013	MSBA
734	Melissodes	M	thelypodii	bluevane	na	na	TX	8	2014	OSEC
996	Melissodes	M	thelypodii	vane trap	na	na	TX	7	2014	OSEC
1437	Melissodes	M	thelypodii	Asteraceae	Cirsium	na	TX	7	2012	MSBA
355	Melissodes	M	thelypodii	na	na	na	AZ	8	2001	BLCU
994	Melissodes	M	thelypodii	vane trap	na	na	TX	8	2014	OSEC
997	Melissodes	M	thelypodii	vane trap	na	na	TX	7	2014	OSEC
356	Melissodes	M	thelypodii	Solanaceae	Solanum	elaeagnifolium	NM	7	2008	MSBA
770	Melissodes	M	thelypodii	Solanaceae	Solanum	elaeagnifolium	NM	7	2008	MSBA
1439	Melissodes	M	thelypodii	Solanaceae	Solanum	elaeagnifolium	NM	7	2008	MSBA
1438	Melissodes	M	thelypodii	Fabaceae	Melilotus	officinalis	NM	7	2003	MSBA
358	Melissodes	M	thelypodii	Fabaceae	Melilotus	albus	NM	7	2003	MSBA
359	Melissodes	M	thelypodii	na	na	na	AZ	9	2009	AMNH
771	Melissodes	M	thelypodii	Malvaceae	Sphaeralcea	polychroma	NM	8	2014	MSBA
360	Melissodes	M	thelypodii	na	na	na	NM	9	2011	AMNH
995	Melissodes	M	thelypodii	vane trap	na	na	TX	7	2014	OSEC

APPENDIX D: Pollen sample numbers and BLAST results

number	blast_family	blast_subfamily	HA	NAC	blast_tribe	blast_genus	blast_species (+ means more than one species in genus)	correct_state
739	Alismataceae					Sagittaria	latifolia	yes
740	Alismataceae					Sagittaria	latifolia	yes
735	Alismataceae					Sagittaria	latifolia	yes
734	Alismataceae					Sagittaria	latifolia	yes
1193	Amaranthaceae					Amaranthus	palmeri	yes
601	Amaranthaceae					Amaranthus	arenicola	yes
1095	Apiaceae					Daucus	carota	yes
1001	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1121	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1123	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1125	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
370	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
372	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	yes
911	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
910	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
1293	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
376	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
388	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
382	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
383	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
380	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
387	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	bigelovii	yes
384	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	yes
389	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tagetina	yes
375	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tagetina	yes
400	Asteraceae	Asteroideae	no	yes	Astereae	Dieteria	canescens	yes
395	Asteraceae	Asteroideae	no	yes	Astereae	Dieteria	canescens	yes
1107	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1218	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1220	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
399	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes

773	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
774	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
396	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
397	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
390	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
908	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1226	Asteraceae	Asteroideae	yes	no	Madieae	Calycadenia	hooveri	yes
1222	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	solstitialis	yes
964	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arvense	yes
965	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arvense	yes
411	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	sp	
721	Asteraceae	Asteroideae	yes	no	Heliantheae	Encelia	californica	yes
1223	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	camporum	yes
418	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
730	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
416	Asteraceae	Asteroideae	yes	no	Madieae	Hemizonia	congesta	yes
1224	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
417	Asteraceae	Asteroideae	yes	no	Madieae	Holocarpha	heermannii	yes
424	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
423	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	camporum	yes
1126	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
720	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	menziesii	yes
1047	Asteraceae	Asteroideae	no	no	Gnaphalieae	Anaphalis	margaritaceae	yes
1108	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1110	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
1090	Asteraceae	Cichorioideae	no	no	Cichorieae	Hypochaeris	radicata	yes
1093	Asteraceae	Cichorioideae	no	no	Cichorieae	Hypochaeris	radicata	yes
1094	Asteraceae	Cichorioideae	no	no	Cichorieae	Hypochaeris	radicata	yes
1028	Asteraceae	Asteroideae	no	no	Anthemideae	Tanacetum	vulgare	yes
1310	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	solstitialis	yes
369	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	nuda	yes
367	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	canescens	yes
447	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes

728	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1230	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
777	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
778	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
779	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1327	Asteraceae	Asteroideae	no	yes	Astereae	Conyza	canadensis	yes
153	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
532	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
1324	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
154	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
152	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1325	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1326	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
960	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
959	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
975	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
619	Asteraceae	Asteroideae	yes	no	Heliantheae	Chromolepis	heterophylla	no
1331	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
618	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1128	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1017	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
748	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
31	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
33	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
38	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
35	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
36	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
34	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	anomalus	
667	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
1328	Asteraceae	Cichorioideae	no	no	Cichorieae	Sonchus	arvensis	yes
1332	Asteraceae	Asteroideae	yes	no	Heliantheae	Verbesina	enceliodes	yes
963	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
1333	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes

723	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	acrodenia	yes
724	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	menziesii	yes
1334	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	greenii	yes
43	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	canescens	
45	Asteraceae	Cichorioideae	no	no	Cichorieae	Stephanomeria	exigua	
44	Asteraceae	Cichorioideae	no	no	Cichorieae	Stephanomeria	exigua	
1336	Asteraceae	Asteroideae	no	no	Senecioneae	Tetradymia	canescens	yes
53	Asteraceae	Asteroideae	no	yes	Astereae	Dieteria	canescens	
900	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
50	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
897	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
898	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
899	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
94	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
52	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	
58	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	
57	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	
1338	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosus	yes
895	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
56	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
719	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	acrodenia	yes
54	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	tenuisecta	
726	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
761	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	acradenia	yes
1119	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	niveus	yes
1118	Asteraceae	Asteroideae	yes	no	Bahieae	Palafoxia	arida	yes
542	Asteraceae	Asteroideae	yes	no	Bahieae	Palafoxia	arida	yes
682	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	
79	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
889	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	depressus	yes
67	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	neomexicanum	
683	Asteraceae	Asteroideae	yes	no	Coreopsideae	Cosmos	bipinnatus	yes
643	Asteraceae	Asteroideae	yes	no	Coreopsideae	Cosmos	bipinnatus	

644	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	neomexicanus	yes
68	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	subtrinervis	
884	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
75	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	sp	yes
883	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
642	Asteraceae	Asteroideae	no	yes	Astereae	Gymnosperma	glutinosa	yes
885	Asteraceae	Asteroideae	no	yes	Astereae	Gymnosperma	glutinosa	yes
882	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
881	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
65	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	
62	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	ambigens	
66	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	
76	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	
81	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	
64	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	
69	Asteraceae	Asteroideae	yes	no	Perityleae	Pericome	caudata	yes
63	Asteraceae	Asteroideae	no	yes	Astereae	Pyrrocoma	clementis	
886	Asteraceae	Asteroideae	yes	no	Heliantheae	Rudbeckia	hirta	yes
887	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartoides	yes
671	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
687	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
611	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
610	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
606	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
1003	Asteraceae	Asteroideae	yes	no	Coreopsideae	Coreopsis	tinctoria	yes
1018	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	formosissimus	yes
547	Asteraceae	Asteroideae	yes	no	Helenieae	Gaillardia	pulchella	yes
605	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
782	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
781	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
783	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
608	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
545	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes

543	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
980	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
607	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	petiolaris	yes
634	Asteraceae	Asteroideae	no	no	Anthemideae	Leucanthemum	vulgare	yes
1252	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tanacetifolia	yes
609	Asteraceae	Asteroideae	yes	no	Heliantheae	Ratibida	columnifera	yes
784	Asteraceae	Asteroideae	yes	no	Heliantheae	Ratibida	columnifera	yes
1250	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	canadensis	yes
1257	Asteraceae	Asteroideae	yes	no	Eupatorieae	Eutrochium	fistulosum	
1151	Asteraceae	Asteroideae	yes	no	Helenieae	Helenium	autumnale	yes
1152	Asteraceae	Asteroideae	yes	no	Helenieae	Helenium	autumnale	yes
766	Asteraceae	Asteroideae	no	yes	Astereae	Pityopsis	graminifolia	yes
650	Asteraceae	Asteroideae	no	yes	Astereae	Pityopsis	grminifolia	yes
628	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
1344	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
85	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
1348	Asteraceae	Asteroideae	no	yes	Astereae	Guteirrezia	sarothrae	yes
1345	Asteraceae	Asteroideae	no	yes	Astereae	Guteirrezia	sarothrae	yes
1353	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1349	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
1350	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
1352	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
86	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	
84	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	
87	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
1351	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
83	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	menziesii	
1347	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	rusbyi	yes
904	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	yes
1354	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
1260	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	uliginoso	yes
504	Asteraceae	Asteroideae	yes	no	Coreopsideae	Coreopsis	tinctoria	yes
505	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	subtrinervis	yes

970	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
891	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	fulcrata	yes
971	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
890	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
1356	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	ambigens_floribunda	yes
892	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	yes
1267	Asteraceae	Asteroideae	yes	no	Heliantheae	Ratibida	tagetina	yes
507	Asteraceae	Asteroideae	no	yes	Astereae	Petradoria	pumila	yes
506	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartoides	yes
1361	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
511	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1362	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	fulcrata	yes
509	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	pluriflora	yes
510	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	pluriflora	yes
1364	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	plurifolia	yes
1363	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	canescens	yes
508	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartoides	yes
948	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	depressus	yes
516	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1027	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	formosissimus	yes
1026	Asteraceae	Asteroideae	yes	no	Helenieae	Gaillardia	aristat	yes
1269	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
1366	Asteraceae	Asteroideae	no	yes	Astereae	Pyrrocoma	clementis	yes
517	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	gigantea	yes
518	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1367	Asteraceae	Asteroideae	yes	no	Eupatorieae	Liatris	spicata	yes
706	Asteraceae	Asteroideae	yes	no	Tageteae	Adenopappus	persicifolius	yes
692	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
695	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
699	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
702	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
691	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	ferulifolia	yes
675	Asteraceae	Asteroideae	yes	no	Coreopsideae	Cosmos	bipinnatus	yes

697	Asteraceae	Asteroideae	yes	no	Coreopsideae	Cosmos	bipinnatus	yes
698	Asteraceae	Asteroideae	yes	no	Coreopsideae	Cosmos	bipinnatus	yes
140	Asteraceae	Asteroideae	yes	no	Heliantheae	Perymenium	macrocephalum	yes
696	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
700	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
701	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
694	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	foetida	yes
677	Asteraceae	Asteroideae	yes	no	Eupatorieae	Stevia	pelophila	yes
703	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
523	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
528	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
1276	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
1279	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
930	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	pleniradiata	yes
973	Asteraceae	Asteroideae	yes	no	Heliantheae	Echinacea	angustifolia	yes
776	Asteraceae	Asteroideae	yes	no	Tageteae	Flaveria	chlorifolia	yes
522	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
950	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
760	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
524	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	lemmonii	yes
520	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	acradenia	yes
527	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	angustifolia	yes
951	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	angustifolia	yes
521	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	filipes	yes
635	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	filipes	yes
529	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	papposa	yes
531	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	gigantea	yes
775	Asteraceae	Asteroideae	yes	no	Heliantheae	Xanthium	strumarium	yes
534	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	linifolius	yes
535	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
96	Asteraceae	Asteroideae	no	yes	Astereae	Dieteria	canescens	
1284	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1374	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	subtrinervis	yes

755	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	nuda	yes
1375	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	nuda	yes
92	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	
1005	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
622	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	petiolaris	yes
1037	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
906	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
93	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	
1282	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	plurifolia	yes
89	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	bigelovii	
90	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	bigelovii	
95	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	bigelovii	
1372	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tanacetifolia	yes
1373	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
1370	Asteraceae	Asteroideae	yes	no	Heliantheae	Verbesina	sp	yes
907	Asteraceae	Asteroideae	yes	no	Heliantheae	Viguiera	dentata	yes
537	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	canadensis	yes
540	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	gigantea	yes
967	Asteraceae	Asteroideae	no	no	Anthemideae	Achillea	millefolium	yes
1061	Asteraceae	Asteroideae	no	no	Gnaphalieae	Anaphalis	margaritaceae	yes
1023	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
1102	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	stoebe	yes
1024	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	stoebe	yes
1072	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	pendulum	?
1113	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
102	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	zionis	
1025	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	formosissimus	yes
101	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	
100	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica or oxylepis	no
1114	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	nana	yes
1103	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
1115	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
104	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes

866	Asteraceae	Asteroideae	no	yes	Astereae	Hazardia	whitneyi	yes
861	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	fulcrata	yes
1022	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
865	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	triangularis	yes
868	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	multiradiata	yes
1116	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	boreale	yes
867	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
869	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
863	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
864	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
103	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	
860	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
859	Asteraceae	Asteroideae	yes	no	Helenieae	Helenium	bigelovii	yes
118	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
942	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	depressus	yes
116	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	scopulinus	
638	Asteraceae	Asteroideae	no	yes	Astereae	Gymnosperma	glutinosa	yes
637	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	t
106	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
612	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
110	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	
109	Asteraceae	Asteroideae	yes	no	Heliantheae	Heliomeris	multiflora	yes
111	Asteraceae	Asteroideae	yes	no	Heliantheae	Heliomeris	multiflora	yes
113	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	yes
613	Asteraceae	Asteroideae	yes	no	Millerieae	Melampodium	perfoliatum	n
108	Asteraceae	Asteroideae	yes	no	Tageteae	Porophyllum	scoparium	yes
662	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
712	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	amplexicaulus	yes
107	Asteraceae	Asteroideae	yes	no	Coreopsideae	Thelesperma	longipes	yes
660	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
112	Asteraceae	Asteroideae	yes	no	Heliantheae	Viguiera	dentata	yes
709	Asteraceae	Asteroideae	no	yes	Astereae	Xanthocephalum	gymnospermoides	yes
661	Asteraceae	Asteroideae	no	yes	Astereae	Xylothamia	pseudobaccharis	yes

117	Asteraceae	Asteroideae	yes	no	Heliantheae	Zaluzania	megacephala	yes
120	Asteraceae	Asteroideae	no	yes	Astereae	Corethrogyne	filaginifolia	
1289	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	neomexicanus	yes
1290	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	neomexicanus	yes
1292	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	neomexicanus	yes
1285	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
961	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
1288	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	plurifolia	yes
123	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	pluriflora	
122	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	tenuisecta	
937	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	solsitialis	yes
1105	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	stoebe	yes
129	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	viscidiflorus	yes
1154	Asteraceae	Asteroideae	yes	no	Coreopsideae	Coreopsis	tinctoria	yes
939	Asteraceae	Asteroideae	yes	no	Heliantheae	Engelmannia	peristenia	yes
133	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1106	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	subtrinervis	yes
128	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
1100	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	oxylepis	yes
940	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	stricta	yes
938	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
124	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	
131	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tanacetifolia	yes
1104	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	canadensis	yes
127	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	velutina	yes
1029	Asteraceae	Asteroideae	no	no	Anthemideae	Tanacetum	vulgare	yes
135	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
725	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	menziesii	yes
947	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
136	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
944	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
946	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
945	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes

713	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
672	Asteraceae	Asteroideae	yes	no	Coreopsideae	Cosmos	sulphureus	yes
147	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
148	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
149	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
150	Asteraceae	Asteroideae	yes	no	Tageteae	Porophyllum	scoparium	yes
714	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
715	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
716	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
717	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
718	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
151	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	menziesii	yes
1377	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1034	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1099	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	na	yes
513	Asteraceae	Asteroideae	no	yes	Astereae	Pyrrocoma	lanceolata	yes
526	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	yes
155	Asteraceae	Asteroideae	no	yes	Astereae	Rayjacksonia	phyllocephala	yes
1038	Asteraceae	Asteroideae	no	yes	Astereae	Rayjacksonia	phyllocephala	yes
1039	Asteraceae	Asteroideae	no	yes	Astereae	Rayjacksonia	phyllocephala	yes
1040	Asteraceae	Asteroideae	no	yes	Astereae	Rayjacksonia	phyllocephala	yes
156	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	bigelovii	yes
157	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
159	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
1378	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosus	yes
163	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1379	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
160	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	bigelovii	yes
164	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	canescens	yes
161	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartioides	yes
1384	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	pleniradiata	yes
1382	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	sp	yes
1299	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes

1385	Asteraceae	Asteroideae	no	yes	Astereae	Euthamia	graminifolia	yes
1389	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
1388	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
1391	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	anomolus	yes
991	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	petiolaris	yes
167	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
1320	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	plurifolia	yes
168	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	canescens	yes
169	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	pinnatifida	yes
170	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartioides	yes
172	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartioides	
175	Asteraceae	Cichorioideae			Cichorieae	Hieracium	nauseosa	
1112	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
176	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
788	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
789	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
790	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
952	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
754	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1392	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	fulcrata	yes
179	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	subaxillaris	yes
753	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
177	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
178	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	rusbyi	yes
1300	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	rusbyi	yes
182	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	canescens	
180	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	yes
679	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arvense	yes
185	Asteraceae	Asteroideae	yes	no	Coreopsideae	Coreopsis	lanceolata	
1393	Asteraceae	Asteroideae	no	yes	Astereae	Erigeron	annuus	yes
1303	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1304	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
680	Asteraceae	Asteroideae	no	no	Anthemideae	Leucanthemum	vulgare	yes

575	Asteraceae	Asteroideae	yes	no	Heliantheae	Ratibida	pinnata	yes
184	Asteraceae	Asteroideae	yes	no	Heliantheae	Rudbeckia	hirta	yes
563	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	rigida	yes
578	Asteraceae	Cichorioideae	no	no	Cichorieae	Sonchus	arvensis	yes
192	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
193	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
191	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1395	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1396	Asteraceae	Asteroideae	yes	no	Heliantheae	Verbesina	sp	yes
195	Asteraceae	Asteroideae	yes	no	Eupatorieae	Ageratina	altissima	yes
1397	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	gigantea	yes
201	Asteraceae	Asteroideae	yes	no	Eupatorieae	Ageratum	conyzoides	no
1159	Asteraceae	Cichorioideae	no	no	Cichorieae	Cichorium	intybus	yes
1176	Asteraceae	Asteroideae	yes	no	Coreopsideae	Coreopsis	tinctoria	yes
596	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
199	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	squarrosa	yes
1015	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1016	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1175	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1161	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1164	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1165	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1166	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1167	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1169	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1170	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1171	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1168	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	decapetalus	yes
1158	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	divaricatus	yes
594	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	paucifloris	yes
568	Asteraceae	Asteroideae	yes	no	Heliantheae	Heliopsis	helianthoides	yes
592	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	gigantea	yes
198	Asteraceae	Asteroideae	no	yes	Astereae	Solidago	gigantea	yes

591	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	ciliolatum	yes
590	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	cordifolium	yes
831	Asteraceae	Asteroideae	no	yes	Astereae	Chaetopappa	ericoides	
836	Asteraceae	Asteroideae	yes	no	Heliantheae	Encelia	virginensis	yes
767	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
837	Asteraceae	Asteroideae	yes	no	Heliantheae	Geraea	canescens	yes
826	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	tenuisecta	yes
838	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tanacetifolia	yes
21	Asteraceae	Asteroideae	yes	no	Helenieae	Plummera	floribunda	
823	Asteraceae	Asteroideae	no	no	Senecioneae	Senecio	spartoides	yes
27	Asteraceae	Asteroideae	yes	no	Heliantheae	Verbesina	encelioides	
145	Asteraceae	Asteroideae	yes	no	Heliantheae	Tithonia	tubaeformis	yes
935	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	menziesii	yes
842	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	viscidiflorus	yes
844	Asteraceae	Asteroideae	no	yes	Astereae	Chrysothamnus	viscidiflorus	yes
846	Asteraceae	Asteroideae	no	yes	Astereae	Dieteria	canescens	yes
845	Asteraceae	Asteroideae	no	yes	Astereae	Ericameria	nauseosa	yes
630	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
203	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
843	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
847	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
205	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
218	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
850	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
858	Asteraceae	Asteroideae	no	yes	Astereae	Chaetopappa	ericoides	yes
853	Asteraceae	Asteroideae	yes	no	Heliantheae	Encelia	virginensis	yes
633	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
632	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
857	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
222	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
223	Asteraceae	Asteroideae	yes	no	Helenieae	Hymenoxys	hoopesii	yes
213	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	pluriflora	yes
219	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	pluriflora	yes

849	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	tenuisecta	yes
59	Asteraceae	Asteroideae	no	yes	Astereae	Isocoma	tenuisecta	
212	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	pinnatifida	yes
228	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	pinnatifida	yes
227	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	pinnatifida	yes
229	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	tanacetifolia	yes
216	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	angustifolia	yes
226	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	filipes	yes
639	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	filipes	yes
217	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	papposa	yes
215	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	papposa	yes
854	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	frondosum	yes
856	Asteraceae	Asteroideae	no	yes	Astereae	Symphyotrichum	spathulatum	yes
1314	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
875	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
1401	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	pleniradiata	yes
873	Asteraceae	Asteroideae	yes	no	Heliantheae	Encelia	virginensis	yes
874	Asteraceae	Asteroideae	yes	no	Heliantheae	Encelia	virginensis	yes
871	Asteraceae	Asteroideae	yes	no	Millerieae	Galinsoga	parviflora	yes
872	Asteraceae	Asteroideae	yes	no	Chaenactideae	Orochaenactis	thysanocarpha	yes
870	Asteraceae	Asteroideae	yes	no	Helenieae	Psilostrophe	cooperi	yes
879	Asteraceae	Asteroideae	yes	no	Helenieae	Psilostrophe	cooperi	yes
880	Asteraceae	Cichorioideae	no	no	Cichorieae	Stephanomeria	exigua	yes
625	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1156	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1317	Asteraceae	Asteroideae	yes	no	Helenieae	Baileya	multiradiata	yes
239	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
186	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
758	Asteraceae	Cichorioideae	no	no	Cichorieae	Lactuca	serriola	
235	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	angustifolia	yes
236	Asteraceae	Asteroideae	yes	no	Heliantheae	Rudbeckia	hirta	yes
240	Asteraceae	Asteroideae	yes	no	Heliantheae	Rudbeckia	hirta	yes
1136	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	vulgare	yes

1231	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
1232	Asteraceae	Carduoideae	no	no	Cardueae	Carduus	nutans	yes
983	Asteraceae	Asteroideae	yes	no	Eupatorieae	Brickellia	veronicifolia	yes
491	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	americana	yes
555	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arizonicum	yes
493	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arizonicum	yes
494	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arizonicum	yes
1082	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arvense	yes
1086	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arvense	yes
1080	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	brevistylum	yes
1085	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	vulgare	yes
988	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	ciliaris	yes
989	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	ciliaris	yes
1081	Asteraceae	Cichorioideae	no	no	Cichorieae	Hypochaeris	radicata	yes
1084	Asteraceae	Cichorioideae	no	no	Cichorieae	Hypochaeris	radicata	yes
1050	Asteraceae	Cichorioideae	no	no	Cichorieae	Hypochaeris	radicata	yes
1181	Asteraceae	Cichorioideae	no	no	Cichorieae	Cichorium	intybus	yes
1182	Asteraceae	Cichorioideae	no	no	Cichorieae	Cichorium	intybus	yes
1199	Asteraceae	Cichorioideae	no	no	Cichorieae	Cichorium	intybus	yes
1201	Asteraceae	Cichorioideae	no	no	Cichorieae	Cichorium	intybus	yes
1202	Asteraceae	Cichorioideae	no	no	Cichorieae	Cichorium	intybus	yes
1197	Asteraceae	Asteroideae	no	yes	Astereae	Guterrezia	sarothrae	no
1177	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1196	Asteraceae	Cichorioideae	no	no	Cichorieae	Lactuca	serriola	yes
245	Asteraceae	Asteroideae	yes	no	Heliantheae	Synedrella	nodiflora	yes
281	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	alba	yes
811	Asteraceae	Asteroideae	yes	no	Coreopsideae	Bidens	pilosa	yes
1065	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	arvense	yes
616	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
738	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
271	Asteraceae	Asteroideae	yes	no	Tageteae	Porophyllum	scoparium	yes
1008	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1009	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes

1405	Asteraceae	Asteroideae	no	yes	Astereae	Grindelia	arizonica	yes
722	Asteraceae	Asteroideae	no	yes	Astereae	Heterotheca	villosa	yes
1407	Asteraceae	Cichorioideae	no	no	Cichorieae	Pinaropappus	spathulatus	yes
1418	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
901	Asteraceae	Asteroideae	yes	no	Tageteae	Pectis	filipes	yes
334	Asteraceae	Asteroideae	yes	no	Eupatorieae	Ageratum	conyzoides	yes
327	Asteraceae	Asteroideae	yes	no	Heliantheae	Simsia	calva	yes
336	Asteraceae	Asteroideae	yes	no	Helenieae	Tetraneuris	acaulis	yes
1432	Asteraceae	Carduoideae	no	no	Cardueae	Centaurea	solstitialis	yes
1433	Asteraceae	Asteroideae	yes	no	Chaenactideae	Chaenactis	douglasii	yes
1431	Asteraceae	Asteroideae	no	yes	Astereae	Gutierrezia	sarothrae	yes
996	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	ciliaris	yes
1437	Asteraceae	Asteroideae	yes	no	Coreopsideae	Thelesperma	megapotamicum	yes
475	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
476	Asteraceae	Asteroideae	no	yes	Astereae	Machaeranthera	gracilis	yes
9	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
1	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus(+)	yes
3	Asteraceae	Asteroideae	yes	no	Bahieae	Hymenopappus	tenuifolius(+)	yes
7	Asteraceae	Carduoideae	no	no	Cardueae	Cirsium	undulatum	yes
8	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus	yes
2	Asteraceae	Asteroideae	yes	no	Heliantheae	Helianthus	annuus(+)	yes
4	Asteraceae	Asteroideae	yes	no	Heliantheae	Ratibida	pinnata	yes
5	Asteraceae	Asteroideae	yes	no	Tageteae	Sartwellia	mexicana(+1)	yes
636	Asteraceae	Asteroideae	yes	no	Millerieae	Melampodium	longicorne	yes
828	Bignoniaceae					Chilopsis	linearis	yes
249	Boraginaceae					Borago	officinalis	no
473	Boraginaceae					Cryptantha	flavoculata	yes
924	Brassicaceae					Hirschfeldia	incana	yes
922	Brassicaceae					Hirschfeldia	incana	yes
929	Brassicaceae					Hirschfeldia	incana	yes
459	Brassicaceae					Brassica	tournefortii	????
1383	Brassicaceae					Draba	helleriana	yes
824	Brassicaceae					Lepidium	montanum	yes

317	Brassicaceae					Lepidium	montanum	yes
311	Brassicaceae					Lepidium	thurberi	yes
314	Brassicaceae					Lepidium	thurberi	yes
1413	Capparaceae					Wislizenia	refracta	yes
747	Chenopodiaceae					Salsola	tragus	yes
264	Chenopodiaceae					Salsola	kali	yes
355	Chenopodiaceae					Bassia	scoparia	yes
1270	Convolvulaceae					Cuscuta	cephalanthi	no
932	Convolvulaceae					Convolvulus	arvensis	yes
626	Convolvulaceae					Calystegia	silvatica	yes
986	Convolvulaceae					Convolvulus	arvensis	yes
1200	Convolvulaceae					Calystegia	sepium	yes
617	Convolvulaceae					Convolvulus	arvense	yes
994	Convolvulaceae					Convolvulus	Arvensis	yes
997	Convolvulaceae					Convolvulus	arvensis	yes
1184	Cucurbitaceae					Cucurbita	pepo	yes
1186	Cucurbitaceae					Cucurbita	pepo	yes
1178	Cucurbitaceae					Cucurbita	pepo	yes
298	Cucurbitaceae					Cucurbita	ficifolia	yes
926	Cuscutaceae					Cuscuta	californica	yes
445	Cuscutaceae					Cuscuta	californica	yes
918	Cuscutaceae					Cuscuta	californica	yes
923	Cuscutaceae					Cuscuta	californica	yes
600	Elaeagnaceae					Elaeangus	angustifolia	yes
1404	Euphorbiaceae					Croton	pottsii	yes
1235	Euphorbiaceae					Euphorbia	bicolor	no
1236	Euphorbiaceae					Euphorbia	bicolor	no
99	Fabaceae					Psorothamnus	scoparius	
1387	Fabaceae					Dalea	purpurea	yes
1394	Fabaceae					Amorpha	canescens	yes
15	Fabaceae					Dalea	candida	yes
24	Fabaceae					Dalea	candida	yes
14	Fabaceae					Dalea	candida(+1)	yes

26	Fabaceae					Dalea	melantha or pulchra	
20	Fabaceae					Melilotus	officinalis	yes
19	Fabaceae					Psorothamnus	scoparius	yes
28	Fabaceae					Psorothamnus	scoparius	
681	Fabaceae					Dalea	purpusii	yes
274	Fabaceae					Dalea	candida	yes
273	Fabaceae					Dalea	purpurea	yes
615	Fabaceae					Medicago	sativa	yes
270	Fabaceae					Medicago	sativa	yes
272	Fabaceae					Medicago	sativa	yes
1006	Fabaceae					Melilotus	officionale	yes
1240	Fabaceae					Melilotus	officinalis	yes
302	Fabaceae					Robinia	neomexicana	yes
299	Fabaceae					Senna	corymbosa	?
318	Fabaceae					Psorothamnus	scoparius	yes
641	Fabaceae					Psorothamnus	scoparius	yes
322	Fabaceae					Psorothamnus	scoparius	yes
655	Fabaceae					Dalea	candida	yes
1428	Fabaceae					Desmodium	intortum	yes
356	Fabaceae					Medicago	sativa	yes
770	Fabaceae					Medicago	sativa	yes
1439	Fabaceae					Medicago	sativa	yes
1438	Fabaceae					Melilotus	officinales	yes
358	Fabaceae					Melilotus	officinalis	yes
268	Gentianaceae					Eustoma	exaltatum	yes
1427	Gentianaceae					Eustoma	exaltatum	yes
1191	Goodeniaceae					Coopernookia	strophiolata	no
377	Liliaceae					Allium	sativum	no
143	Loasaceae					Cevallia	sinuata	yes
1380	Loasaceae					Mentzelia	multiflora	yes
827	Loasaceae					Mentzelia	longiloba	
737	Lythraceae					Lythrum	lineare	yes
958	Malvaceae					Sphaeralcea	angustifolia	yes

768	Malvaceae					Sphaeralcea	ambigua	yes
22	Malvaceae					Sphaeralcea	ambigua	yes
25	Malvaceae					Sphaeralcea	ambigua	
30	Malvaceae					Sphaeralcea	ambigua	
646	Malvaceae					Gossypium	hirsutum	yes
259	Malvaceae					Hibiscus	cannabinus	yes
1188	Malvaceae					Hibiscus	syriacus	yes
1194	Malvaceae					Sphaeralcea	ambigua	no
772	Malvaceae					Sphaeralcea	wrightii	yes
306	Malvaceae					Sphaeralcea	ambigua	yes
303	Malvaceae					Sphaeralcea	ambigua	yes
304	Malvaceae					Sphaeralcea	ambigua	yes
1241	Malvaceae					Sphaeralcea	incana	yes
652	Malvaceae					Sida	cordifolia	yes
640	Malvaceae					Sphaeralcea	wrightii	yes
659	Malvaceae					Periptera	punicea	yes
359	Malvaceae					Sphaeralcea	ambigua	yes
771	Malvaceae					Sphaeralcea	ambigua	yes
1245	Malvaceae					Sphaeralcea	incana	yes
1246	Malvaceae					Sphaeralcea	incana	yes
1415	Oleaceae					Fraxinus	velutina	yes
379	Onagraceae					Oenothera	pallida	yes
835	Onagraceae					Oenothera	primiveris	yes
833	Onagraceae					Oenothera	primiveris	yes
1180	Onagraceae					Oenothera	nutans	yes
1190	Onagraceae					Oenothera	nutans	yes
269	Onagraceae					Calylophus	hartwegii	yes
267	Onagraceae					Calylophus	serrulatus	yes
745	Onagraceae					Oenothera	canescens	yes
300	Onagraceae					Oenothera	speciosa	yes
1083	Plantaginaceae					Digitalis	purpurea	yes
496	Poaceae					Agrostis	gigantea	yes
209	Polemoniaceae					Eriastrum	densifolium	yes

211	Polemoniaceae					Eriastrum	densifolium	yes
678	Polemoniaceae					Eriastrum	signatum	yes
913	Polygonaceae					Eriogonum	cinereum	yes
925	Polygonaceae					Eriogonum	fasciculatum	yes
920	Polygonaceae					Eriogonum	fasciculatum	yes
1129	Polygonaceae					Polygonum	pensylvanicum	yes
839	Polygonaceae					Eriogonum	deflexum	yes
1012	Polygonaceae					Polygonum	pensylvanicus	yes
296	Ranunculaceae					Clematis	ligusticifolia	yes
444	Rosaceae					Adenostoma	fasciculatum	yes
132	Rosaceae					Potentilla	norvegica	yes
16	Rosaceae					Fallugia	paradoxa	yes
286	Rosaceae					Fallugia	paradoxa	yes
764	Rosaceae					Rubus	allegheniensis	
809	Rubiaceae					Richardia	grandiflora	yes
742	Rubiaceae					Stenaria	nigricans	yes
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1092	Scrophulariaceae					Digitalis	purpurea	yes
822	Scrophulariaceae					Cordylanthus	tenuis	yes
968	Scrophulariaceae					Linaria	vulgaris	yes
1429	Scrophulariaceae					Leucophyllum	frutescens	no
46	Tamaraceae					Tamarix	chinensis	
23	Tamaraceae					Tamarix	ramosissima	yes
1306	Zygophyllaceae					Kallstroemia	parviflora	yes
29	Zygophyllaceae					Kallstroemia	parviflora	
18	Zygophyllaceae					Larrea	tridentata	yes
265	Zygophyllaceae					Kallstroemia	parviflora	yes
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360	Zygophyllaceae					Kallstroemia	parviflora	yes
468	Zygophyllaceae					Kallstroemia	parviflora	yes

472	Zygophyllaceae					Kallstroemia	parviflora	yes

APPENDIX E: Metabarcoding results by sample number.

num	genus 1	identity	%OTUs	genus 2	identity	%OTUs	genus 3	identity	%OTUs
582	Liatris	99.34	94.52						
1002	Helianthus	98.03	55.45	Solanum	100	11.77			
769	Symphyotrichum	100	62.77	Symphyotrichum	100	32.22			
398	Senecio	98.03	69.14	Symphyotrichum	100	11.59			
419	Helianthus	98.03	67.37	Helianthus	98.68	16.95			
413	Symphyotrichum	100	87.54	Symphyotrichum	100	10.92			
428	Symphyotrichum	100	67.3	Symphyotrichum	100	21.67			
1041	Hypericum	100	51.21	Cirsium	100	12.68			
1043	Chamerion	100	43	Chamerion	98.04	15.11	Festuca	98.03	10.14
1045	Helianthus	98.03	31.18	Verbascum	100	18.28			
927	Adenostoma	97.3	62.78	Adenostoma	99.32	25.92			
928	Ocimum	97.2	85.78						
921	Eriogonum	100	62.52	Adenostema-Rosaceae	97.3	17.93			
780	Senecio	98.03	67.48	Symphyotrichum	100	15.51			
1014	Helianthus	98.03	83.41						
32	Cirsium	100	85.91						
896	Helianthus	98.03	61.52	Symphyotrichum	100	13.88			
669	Symphyotrichum	100	82.37						
544	Cirsium	100	25.72	Symphyotrichum	100	22.76	Helianthus	98.03	17.49
905	Taraxacum	98.68	57.83	Symphyotrichum	100	17.21			
972	Taraxacum	98.03	81.55						
673	Tragopogon	98.03	40.95	Trogapogon	97.99	16.08	Helianthus	98.03	11.93
530	Helianthus	100	79.08						
949	Symphyotrichum	100	54.83	Symphyotrichum	100	39.3			
859	Antennaria	99.35	28.29	Helianthus	98.68	17.67			
862	Tripleurospermum	98.03	39.2	Senecio	98.01	18.76	Bidens	98.63	12.44
1056	Helianthus	98.03	90.35						
1059	Helianthus	98.03	26.78	Hypericum	100	26.63	Cirsium	100	22.08
936	Symphyotrichum	100	39.1	Taraxacum	98.69	28.39			
130	Symphyotrichum	100	64.84	Symphyotrichum	98.68	27.11			

126	Senecio	100	84.26						
231	Cylindropuntia	99.17	91.3						
232	Cylindropuntia	99.17	69.59	Acacia	100	10.46			
146	Helianthus	98.05	45.3	Helianthus	98.03	27.56	Chaenactis	98.68	11.51
931	Malva	99.39	39.58	Mentzelia	100	23.83	Symphiotrichum	100	17.88
162	Senecio	98.03	46.29	Symphyotrichum	100	28.23			
166	Senecio	98.03	41.01	Symphytrichum	100	20.51	Helianthus	98.68	13.86
158	Symphyotrichum	98.03	68.78	Sympyotrichum	100	16.39			
171	Helianthus	98.03	78.63						
173	Symphyotrichum	100	48.73	Symphyotrichum	100	24.19			
787	Symphyotrichum	100	51.98	Symphiotrichum	100	30.66			
579	Helianthus	98.03	76.52						
197	Symphyotrichum	100	83.44						
627	Helianthus	98.03	55.73	Medicago	100	19.91			
848	Symphyotrichum	100	74.61						
876	Helianthus	98.03	54.28	Helianthus	98.05	13.4			
878	Helianthus	98.05	40.91	Malva	99.39	25.39			
877	Helianthus	98.05	63.11	Malva	99.39	15.63			
624	Medicago	100	52.34	Solanum	100	13.63	Liatris	1	12.68
237	Helianthus	98.03	72.88						
492	Cirsium	100	99.96						
1048	Cirsium	100	83.23						
729	Cirsium	100	74.54						
731	Cirsium	100	89.44						
732	Cirsium	100	68.72						
984	Cirsium	100	60.69	Malva	99.39	10.9			
985	Beta-Chenopodiaceae	98	31.13	Gossypium	100	26.15	Acacia	100	10.27
645	Ipomoea	100	43.46	Sorghum-poaceae	98	28.46			
255	Tsuga-conifer	100	100						
1011	Melilotus	100	47.3	Medicago	100	20.5			
733	Gossypium	100	78.11						
301	Cirsium	100	93.97						

903	Desmodium	100	72.8	Helianthus	98.03	12.6			
307	Acacia	99.35	70.71	Acacia	100	16.6			
902	Malva	99.39	74.91	Symphyotrichum	100	15.5			
316	Acacia	100	71.78						
332	Pachira-Malvaceae	100	50.72	Sida	97	38.66			
326	Prosopis	97.32	71.25						
995	Gossypium	100	71.29						
10	Taraxacum	98.63	59.7	Chaenactis	98.68	30.2			

APPENDIX F: Pollen sample sequences.

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