APPENDIX A

Diversity and Origins of Fijian Leaf-Cutter Bees (Megachilidae)

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Abstract:

Bees are key pollinators in almost all terrestrial ecosystems and can have major roles in agricultural production. Records of bees in the Southwest Pacific indicate a very low diversity, with the Fijian bee fauna one of the least diverse, despite an otherwise rich biota. Megachilid bees represent a large proportion of the bee fauna for almost all island groups in the Southwest Pacific and, because they are wood and stem-nesting, their wide distribution is likely to have been influenced by rafting and anthropogenic maritime trade. Our study is the first to apply molecular techniques to the study of megachilid bees in this region and indicates between four and five recent introductions to Fiji, likely from Southeast Asia. The study also provides the first record of *Heriades* (*Michenerella*) in the Southwest Pacific and the first record of the subgenus *Megachile* (*Callomegachile*) in Fiji. These results indicate that a large proportion of the Fijian bee fauna is likely to have been introduced only very recently and, therefore, has had only a very recent role in Fijian ecosystems, despite their current abundance. This has very wide implications for understanding Fijian plant-pollinator relationships. We argue that there is a strong need to understand ancient plant-pollinator relationships that may have evolved in Fiji before the mid–late Pleistocene and Holocene and whether these could be disrupted by recent bee introductions.

Introduction

Bees compose one of the most important groups of pollinators (Michener 2007) and have coevolved with angiosperms since the mid-Cretaceous (Crepet and Nixon 1998, Engel 2000). They play a critical role in most terrestrial ecosystems, yet recent studies suggest a variety of threats to both their abundance and diversity (Memmott et al. 2007, Kaiser-Bunbury et al. 2010, Potts et al. 2010). Understanding these threats is important in maintaining pollination networks that have evolved over long periods of evolutionary time. However, it is also possible that some terrestrial ecosystems have evolved in the absence of bees, or where bee abundances and diversities were very different before human activities. Identifying these circumstances is also important for conservation and for understanding the genesis of plant-pollinator ecosystems.

The ecosystems of continental landmasses, such as those associated with tectonic plates originating from early Gondwanan and Laurasian supercontinents, have seen bees and angiosperms share very long evolutionary histories, and we might therefore expect a range of both broad and narrow pollinator suites for different plant groups (Danforth et al. 2006, Thien et al. 2009). However, many island ecosystems are characterized by recent and relatively complex geological histories, where plant-pollinator relationships are likely to have been heavily influenced by patterns of colonization from older continental regions.

Previous studies have suggested that the bee fauna in the Southwest Pacific is depauperate (Perkins and Cheesman 1928, Michener 1965). This is unexpected, considering the otherwise complex geographical and biotic history of the region

(Groom and Schwarz 2011). For Fiji, a total of only 14 non-*Apis* bee species have been listed (Evenhuis 2007) and summarized by Groom and Schwarz (2011), but this figure is more likely only 12 species. It has been suggested that *Hylaeus fijiensis* was collected elsewhere (Michener 1965), and the record of the Samoan *Lasioglossum* (*Homalictus*) *perpessicius* in Fiji is also doubtful (Perkins and Cheesman 1928). Five of the 12 definite bee species from Fiji are from the large and cosmopolitan family Megachilidae. Another three species are from the family Apidae: a *Ceratina* species (tribe Ceratinini), a *Braunsapis* species (tribe Allodapini), and an *Amegilla* species (tribe Anthophorini) that are likely to represent anthropogenic dispersals (S.V.C.G., unpubl. data). The remaining four species are from the family Halictidae, subgenus *Homalictus* (genus *Lasioglossum*), which composes a major bee element in the Southwest Pacific. *Homalictus* appears to have shown major radiations within and between the principal Southwest Pacific archipelagos (Groom and Schwarz 2011), and its presence in Fiji is relatively recent, dating back to the late Pliocene or early Pleistocene (Groom et al. 2013).

Current estimates of bee diversity in the Southwest Pacific may be inaccurate. Falsely high diversity estimates could result from taxonomic studies using species descriptions that do not adequately consider within-species morphological variations. Conversely, falsely low diversity estimates could result from inadequate sampling or the inability to identify cryptic species. There is a further problem in that earlier studies of Southwest Pacific bee faunas have been regionally piecemeal, with the possibility that some species may be the result of unrecognized anthropogenic dispersal events from other regions that were not considered in taxonomic surveys.

It is interesting that *Homalictus* is the only non-introduced bee group in the Southwest Pacific that is ground-nesting, and all other endemics nest in stems or wood. The dispersal of stem and wood-nesting bee species could be aided by rafting following severe monsoonal rainfalls or tsunamis. However, distances between the major Southwest Pacific archipelagos are considerable, so it is more likely that many of these stem and wood-nesting species were spread by human maritime traffic (Pauly and Villemant 2009), a situation that has been reported from other regions in the Southern Hemisphere. For example, the only known Mauritian allodapine bee, *Braunsapis dentipes,* is identical in mtDNA (COI) sequence to specimens from Malaysia and was probably introduced to Mauritius by people using the trade route connecting these two distant regions (Rehan et al. 2010). A number of other stem-nesting bees have widespread distributions covering remote islands in the southern Indian Ocean and are also likely to have been spread by human maritime activity (Pauly et al. 2001). Wind transport could be another explanation for the distribution of various bee groups in the Southwest Pacific, especially in the case of smaller bee species (Pauly and Munzinger 2003). Distinguishing between anthropogenic and natural agents that influenced current bee faunas in the Southwest Pacific is important because the recency of humans in the Southwest Pacific indicates that anthropogenic dispersals have resulted in bee elements that are unlikely to have coevolved with indigenous flowering plants.

Here we use the mitochondrial cytochrome oxidase subunit I (COI) gene to investigate species diversity, number of dispersal events, and the likely origins of Megachilidae in Fiji.

Materials and methods

Sampling occurred over a 4-week period during the dry season (July–August 2010) when bee diversity was expected to be at its highest, because drier conditions promote activity in the vast majority of bee species. Flowers of both native and introduced plant species were sampled using sweeping nets. The four major Fijian islands (Vanua Levu, Taveuni, Viti Levu, and Kadavu) were selected, and sampling occurred at 77 sites across an altitudinal range of 0 to 906 m above sea level within a 2.6° latitude/longitude square. Megachilidae were searched for on all four main islands but only collected from the two main islands of Vanua Levu and Viti Levu, with additional specimens provided from opportunistic sampling by our collaborators from Vatoa in the southern Lau group and Lomaiviti.

We obtained DNA sequences for ca. 650 bp (base pairs) of COI mtDNA from the International Barcode of Life project, at the University of Guelph, for a total of 29 Fijian megachilid specimens. Bidirectional sequencing was used for the universal primer pair of LepF1/LepR2 (Hebert et al. 2004). Trace files for forward and reverse sequences were compared using Geneious v.5.6.4 (Drummond et al. 2012). We also included 36 COI sequences of megachilids obtained from GenBank and BOLD (accessed from http://www .boldsystems.org/), including a specimen from Thailand and 13 from Vietnam to help resolve phylogenetic relationships and identify possible relationships between our Fijian samples and taxa from other regions. Outgroup taxa comprised three Apidae representatives: *Apis mellifera, Braunsapis* sp., and *Nomada pygmaea*. GenBank and BOLD accession numbers, along with locality data are given in Table 1.

We used a Bayesian MCMC technique for inferring phylogenetic relationships implemented in MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001). Data were partitioned into first, second, and third codon positions, and we used a GTR + I + G model following a test for most appropriate substitution model using ModelTest 3.06 (Posada and Crandall 1998). We ran the analysis for 50 million generations, sampling every 10,000th generation and with six chains. Stationarity in model parameters was assessed by plotting LnL and parameter estimates against iteration number using Tracer v.1.5 (Rambaut and Drummond 2007). We used a burn-in of 30 million generations, well beyond stationarity as indicated by plotting indicator values.

An amino acid translation of the DNA data set implemented using MacClade was used to examine the impact of any within-clade substitutions of the Fijian representatives on the topology of the clades. This process also provides us with an estimate of the level of intraspecific genetic variability and allows us to compare this with the results of other studies on Fijian bee fauna (Groom et al. 2013).

The results of our analyses were able to address whether two Fijian clades in the subgenus *Eutricharea* were monophyletic or not. For this we compared an unconstrained analysis with an analysis where the two clades were constrained to be monophyletic and compared the two scenarios using a variant of the Bayes Factor test (Suchard et al. 2001), implemented in Tracer v.1.5. For this analysis, we used the same priors as for generating the phylogeny (methods described earlier), running the analysis for 50 million generations and sampling every 10,000th iteration.

Results

The consensus phylogram from our MrBayes analysis is given in Figure 1. Posterior probability (PP) values are given for all nodes except those where branch lengths and associated genetic differences are so small that resulting clades clearly represent intraspecific variation. In Figure 1, clades are colored by corresponding collection location, with Fijian representative labels black and in bold, Vietnam black, Thailand dark gray, and all other localities light gray, as indicated in the included key. Key nodes supporting the segregation of the Fijian clades are indicated as *i–iv*.

Using morphological traits outlined in Michener (2007), we were able to identify the five Fijian clades as one belonging to the *Heriades* subgenus *Michenerella,* with the other four all being contained in the genus *Megachile,* three clades of which were in the subgenus *Eutricharea* and one in the subgenus *Callomegachile.* These latter subgenera will herein be referred to without their corresponding genus name as only *Eutricharea* and *Callomegachile*.

The Fijian clades (Figure 1 *A–E*) were identified to species level with moderate confidence based on the limited dichotomous keys available and supporting descriptions (Cockerell 1924, Perkins and Cheesman 1928, Cheesman 1936, Krombein 1950, Michener 2007) or images (Pauly and Munzinger 2003).

Clade A in Figure 1 comprised a species of *Heriades* (*Michenerella*), and this was recovered as sister clade to *Heriades* species from GenBank with a high PP value. The subgenus has been previously recorded in Micronesia (Krombein 1950), but the specimens here do not fit the descriptions of either *H.* (*M.*) *paganensis* or *H.* (*M.*) *plumosa* from that region. A moderately large number of undescribed *Heriades* species are known to occur in Southeast Asia (Michener 2007), so identifying the Fijian species is problematic at this time.

The remaining four clades all belonged to the genus *Megachile* and were interspersed amongst Southeast Asian representatives throughout our phylogenetic tree. For two of these species, *Megachile* (*Callomegachile*) *umbripenne* and *M.* (*Eutricharea*) *scutellata,* sister clades were clearly Asian (see PP values for nodes *ii* and *iii*). However, the low PP values for nodes separating *M.* (*E.*) *laticeps* and *M.* (*E.*) *albomarginata* allow the possibility that these two species comprise sister clades (Figure 1, node *iv* and more distal nodes). However, it is unlikely that these two species represent a speciation event that occurred within Fiji, as we now explain.

Megachile (*Eutracharea*) *laticeps* has a distribution from the Maldives and India through Thailand, Malaysia, and the Philippines to New Caledonia and as far east as Tahiti (Pauly and Munzinger 2003). In contrast, *M.* (*E.*) *albomarginata* has been reported previously only from New Caledonia (Michener 1965). A common origin for these two species in Fiji followed by speciation and then wide dispersal into other regions of Asia and the Solomon Islands seems extremely unlikely.

Megachile (*Callomegachile*) *umbripenne* was originally recorded from Nepal and was thought to have a distribution throughout India (Smith 1853) but also occurs in New Caledonia and Tahiti within the Pacific (Pauly and Munzinger 2003). The phylogenetic position of our Fijian clade suggests an affinity to specimens from Vietnam.

Our single specimen of *Megachile* (*Eutricharea*) *scutellata* is the only species recovered from our collection previously known from Fiji. Our phylogeny places this species in a well-supported clade that also contains species from the subgenus *Xanthosarus,* as well as *Megachile* (*Eutricharea*) *rotundata.* We note that the subgeneric taxonomy of *Megachile* is well known to be problematic (Michener 2007), and our results suggest that current taxonomy may not reflect phylogeny.

For four of the five Fijian clades in our analyses, we had sequences from multiple specimens, ranging from four specimens of *H.* (*Michenerella*) (Clade A) to 11 for *M.* (*E.*) *albomarginata* (Clade E). Across all Fijian clades we found only two specimens whose haplotypes were different from their clade members. Specimen MSAPB122 *Heriades* (*Michenerella*) sp. differed from its clade members in two nucleotide sites, but in each case the sequence trace files did not indicate firm differences. Instead, the ambiguity caused by small-scale background noise in the sequencing process is concordant with this specimen having an identical sequence to the other *H.* (*Michenerella*) specimens. Specimen MSAPB100 *M.* (*E.*) *albomarginata* (Clade E) differed from its clade members by only a single nucleotide, and this was a synonymous substitution at a third codon position. Consequently, each Fijian clade shows either no, or remarkably little, haplotype diversity.

Clades A to C are all separated from each intervening non-Fijian clades by at least one highly supported node (>0.93 PP) in each case (*i–iii*). However, the low PP values separating the two Fijian *Eutricharea* clades from each other by intervening non-Fijian clades allows the possibility that these two clades are monophyletic. We used a Bayes Factor test to confirm this monophyly, which returned a BF value of 1.506, indicating that we cannot reject monophyly although distinct morphological characters suggest that it is unlikely.

Discussion

Previous studies of megachilids suggested that this family represented a considerable proportion of the bee fauna in Fiji (Perkins and Cheesman 1928, Michener 1979). However, those studies did not indicate whether that bee fauna involved multiple dispersals of megachilids into Fiji, whether those dispersals were followed by subsequent speciation, or the possible timings of such events. Our DNA sequence data allows those issues to be explored for the first time.

Our data strongly suggest up to five dispersals of megachilids into Fiji but a minimum of four pending resolution of the relationship between clades D [*M.* (*E.*) *laticeps*] and E [*M.* (*E.*) *albomarginata*]. We also have evidence of four new species records for the archipelago, including one record of a subgenus new to Fiji. It is unknown how long Fijian megachilid clades have been present in Fiji. We cannot reject the possibility that the two *Eutricharea* clades are monophyletic and therefore represent speciation even after an early dispersal into Fiji. More thorough taxon sampling of Asian and Southwest Pacific megachilids could resolve this if, for example, the Fijian clades were found to have sequences identical to those of other Asian taxa, or if further intervening non-Fijian clades were found. Currently, very few of the Asian and IndoMalayan megachilid fauna have been sequenced, and there is a need for major taxonomic revision of this fauna.

The most recent available checklist of Fijian megachilids reported the presence of the Pacific-wide *Lithurgus scabrosus* (Evenhuis 2007), but that species was not recovered in our samples. This indicates that despite conducting the most intensive bee-collecting protocol in Fiji to date, we were not able to recover all recorded megachilid species. By contrast, our samples of *Heriades* uncovered the first record of this genus from Fiji. Around the Pacific Rim, the distribution of this genus is entirely limited to the Northern Hemisphere, with the closest records occurring in the islands of Micronesia (Krombein 1950). Therefore, it is likely that the presence of *Heriades* is the result of an anthropogenic introduction, rather than an over-water dispersal. Our samples also uncovered the first record of *Callomegachile* for Fiji; however, unlike *Heriades* this subgenus has been recorded in New Caledonia (Pauly and Munzinger 2003), Vanuatu (Pauly and Villemant 2009), and, surprisingly, the Cook Islands (Kuhlmann 2006). Its wide distribution suggests a likely influence of human-aided dispersal. The three *Eutricharea* clades of our samples likely represent only one species previously recorded for Fiji, the Southwest Pacific–wide distributed *M.* (*E.*) *scutellata,* also found in Tonga and Samoa (Perkins and Cheesman 1928). The other two species, *M.* (*E.*) *laticeps* and *M.* (*E.*) *albomarginata,* are also new records for Fiji. Our results suggest, at the very least, that the recorded diversity in the Megachilidae of Fiji was an underestimate, but there may be cause for concern regarding the impact of nonnative introductions on ecosystem functioning.

The extremely low haplotype diversity in the Fijian *Eutricharea* clades strongly suggests that these species represent recent introductions to Fiji. Groom et al. (2013) found very high haplotype diversity in Fijian *Homa lictus* samples, despite a single dispersal to Fiji in the middle–late Pleistocene. In fact, for one Fijian *Homalictus* species with a crown age in the late Holocene, nearly 40 haplotypes were found for a 650 bp fragment of COI, involving up to three consecutive substitutions within lineages. This provides a very strong contrast with our megachilid Clades D and E, where there was no haplotype diversity in Clade D and only a single specimen with one differing base pair in Clade E. Lack of mitochondrial haplotype diversity can result from very small population size, where genetic drift can remove variation (Kimura and Ohta 1971), or from genetic sweeps (Bazin et al. 2006) where a favorable mutation in one mitochondrion can drag the entire genome with it to fixation. We argue that although such events may be likely for any one species, it is unlikely that they could affect all of our clades where we sequenced more than one specimen. Our samples also indicated large and widespread populations for the *Eutricharea* and *Callomegachile* species, making severe genetic drift also very unlikely.

The considerations discussed here strongly support the possibility that the establishment of Fijian megachilid fauna is very recent and perhaps largely or even entirely due to anthropogenic dispersal. This is also likely to be the case for the *Braunsapis* and *Ceratina* species we have collected in Fiji (S.V.C.G., unpubl. data). From the bee species recorded from Fiji, it is possible that the oldest bee presence, which comprises *Homalictus,* dates back only to the Pleistocene. If so, then bees have been absent for the majority of time during which Fijian plant-pollinator suites have been evolving. This situation may have important conservation implications. The presence of abundant bees on flowering plants in Fiji may indicate that there was potential displacement of original Fijian pollinators. Bees may alter pollen dispersal patterns that have evolved under older plant-pollinator relationships. We believe that both possibilities require attention.

Given the possibly far-reaching consequences of a very recent but now pervasive presence of bees in Fiji, we argue that future research needs to concentrate on four objectives:

1. More extensive sampling of bees is needed for both the Fijian fauna as well as the bee faunas of potential source populations, especially those in the Asian and Indo-Malayan regions. Extensive intraspecific sampling of bees in Fiji is required because resulting data allow the ages of these clades to be estimated with coalescent analyses (e.g., Groom et al. 2013).
2. Species-level revisionary studies to delimit species boundaries and clarify the taxonomy of the group.
3. To identify nonbee pollinators of Fijian angiosperms and assess whether older plant-pollinator relationships may be disrupted by recently-arrived bee species.
4. The establishment of systematic longitudinal sampling regimes to track changes in the distribution and abundance of recently established bee species in Fiji.

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Literature Cited

Bazin, E., S. Glemin, and N. Galtier. 2006. Population size does not influence mitochondrial genetic diversity in animals. Science (Washington, D.C.) 312:570–572.

Cheesman, L. E. 1936. Hymenoptera of the New Hebrides and Banks Islands. Trans. R. Entomol. Soc. Lond. 85:169–195.

Cockerell, T. D. A. 1924. Bees from the Tonga and Samoa Islands. Ann. Entomol. Soc. Am. 17:392–394.

Crepet, W. L., and K. C. Nixon. 1998. Fossil Clusiaceae from the Late Cretaceous (Turonian) of New Jersey and implications regarding the history of bee pollination. Am. J. Bot. 85:1122–1133.

Danforth, B. N., S. Sipes, J. Fang, and S. G. Brady. 2006. The history of early bee diversification based on five genes plus morphology, Proc. Natl. Acad. Sci. U.S.A. 103:15118–15123.

Drummond, A., B. Ashton, S. Buxton, M. Cheung, A. Cooper, C. Duran, M. Field, J. Heled, M. Kearse, S. Markowitz, R. Moir, S. Stones-Havas, S. Sturrock, T. Thierer, and A. Wilson. 2012. Geneious 5.6.4. Biomatters. http://www.geneious.com/.

Engel, M. S. 2000. Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). Bull. Am. Mus. Nat. Hist. 250:1–89.

Evenhuis, N. L. 2007. Checklist of Fiji Hymenoptera. Bishop Mus. Tech. Rep. 38.
Groom, S. V. C., and M. P. Schwarz. 2011. Bees in the Southwest Pacific: Origins, diversity and conservation. Apidologie 42:759–770.

Groom, S. V. C., M. I. Stevens, and M. P. Schwarz. 2013. Diversification of Fijian halictine bees: Insights into a recent island radiation. Mol. Phylogenet. Evol. doi:10.1016/j.ympev.2013.04.015.

Hebert, P. D. N., E. H. Penton, J. M. Burns, D. H. Janzen, and W. Hallwachs. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator.* Proc. Natl. Acad. Sci. U.S.A. 101:14812–14817.

Huelsenbeck, J. P., and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17:754–755.

Kaiser-Bunbury, C. N., A. Traveset, and D. M. Hansen. 2010. Conservation and restoration of plant-animal mutualisms on oceanic islands. Perspect. Plant Ecol. 12:131–143.

Kimura, M., and T. Ohta. 1971. On the rate of molecular evolution. J. Mol. Evol. 1:1–17.

Krombein, K. V. 1950. The aculeate Hymenoptera of Micronesia. II. Colletidae, Halictidae, Megachilidae, and Apidae. Proc. Hawaii. Entomol. Soc. 14:101–142.

Kuhlmann, M. 2006. Fauna and biogeography of the bees and wasps of the Cook Islands (Hymenoptera Aculeata). J. Hymenopt. Res. 15 (1): 26–37.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant-pollinator interactions. Ecol. Lett. 10:710–717.

Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific Regions. Bull. Am. Mus. Nat. Hist. 130:1– 362.

———. 1979. Biogeography of the bees. Ann. Mo. Bot. Gard. 66:277–347.

———. 2007. The bees of the world. 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

Pauly, A., W. Brooks, A. L. Nilsson, Y. A. Persenko, C. D. Eardley, M. Terzo, T.

Griswold, M. P. Schwarz, S. Patiny, J. Munzinger, and Y. Barbier. 2001. Hymenoptera Apoidea de Madagascar. Ann. Zool. Wetenschappen 128:1–390.

Pauly, A., and J. Munzinger. 2003. Contribution à la connaissance des Hymenoptera Apoidea de Nouvelle-Calédonie et de leurs relations avec la flore butinée. Ann. Soc. Entomol. Fr. 39:153–166.

Pauly, A., and C. Villemant. 2009. Hyménoptères Apoidea (Insecta) de l'archipel du Vanuatu. Zoosystema 31:719–730.

Perkins, R. C. L., and L. E. Cheesman. 1928. Hymenoptera: Apoidea, Sphecoidea, and Vespoidea. Insects of Samoa, Part V, 1–32.

Posada, D., and K. A. Crandall. 1998. Modeltest: Testing the model of DNA substitution. Bioinformatics 14:817–818.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25:345–353.

Rambaut, A., and A. J. Drummond. 2007. Tracer, v. 1.5. http://beast.bio.ed.ac.uk/Tracer.

Rehan, S. M., T. W. Chapman, A. I. Craigie, M. H. Richards, S. J. B. Cooper, and M. P. Schwarz. 2010. Molecular phylogeny of the small carpenter bees (Hymenoptera: Apidae: Ceratinini) indicates early and rapid global dispersal. Mol. Phylogenet. Evol. 55:1042–1054.

Smith, F. 1853. Catalogue of hymenopterous insects in the collection of the British Museum. Part 1. Adrenidae and Apidae. Taylor and Francis, London. doi:http://dx.doi.org/10.5962/bhi.title.20999.

Suchard, M. A., R. E. Weiss, and J. S. Sinsheimer. 2001. Bayesian selection of continuous-time Markov chain evolutionary models. Mol. Biol. Evol. 18:1001–1013.

Thien, L. B., P. Bernhardt, M. S. Devall, Z. D. Chen, Y. B. Luo, J. H. Fan, L. C. Yuan, and J. H. Williams. 2009. Pollination biology of basal angiosperms (Anita Grade). Am. J. Bot. 96:166–182.

TABLE 1

Collection Information of Included Taxa

Specimen ID	Species	Lat.	Long.	State/Region	Country	GenBank Acc.	BOLD ID
Outgroup							
	Apis (*Apis*) *mellifera**			Maryland	United States		GTENK024-11
	*Nomada pygmaea**	45.12	−64.2	Nova Scotia	Canada	FJ582398	HDBNS127-03
ACV012	*Braunsapis* sp.	−17.3957	178.013	Viti Levu	Fiji		MSAPB179-11
Ingroup							
	Ashmeadiella (*Ashmeadiella*) *bucconis**	32.7339	−116.951	San Diego	United States		SDBEE225-12
	Coelioxys (*Boreocoelioxys*) *moesta**	45.12	−64.273	Nova Scotia	Canada	FJ582189	HCBNS149-03
	Coelioxys (*Coelioxys*) *sodalis**	45.119	−64.263	Nova Scotia	Canada	FJ582196	HCBNS221-03
	Heriades (*Heriades*) *truncorum**	45.16	19.648	Frusca Gora NP	Serbia	GU708143	BWONE002-09
AAL015	*Heriades* (*Michenerella*) sp.	−18.247	178.08	Viti Levu	Fiji		MSAPB117-11
AAZ001	*Heriades* (*Michenerella*) sp.	−18.247	178.08	Viti Levu	Fiji		MSAPB118-11
ABD001	*Heriades* (*Michenerella*) sp.	−18.247	178.08	Viti Levu	Fiji		MSAPB122-11
ACN002	*Heriades* (*Michenerella*) sp.	−18.2331	178.073	Viti Levu	Fiji		MSAPB142-11
	Heriades (*Neotrypetes*) *carinatus**	45.12	−64.273	Nova Scotia	Canada	FJ582230	HCBNS144-03
	Heriades (*Neotrypetes*) *carinatus**	45.085	−64.234	Nova Scotia	Canada	FJ582231	HCBNS219-03
	Heriades (*Neotrypetes*) *carinatus**	45.085	−64.234	Nova Scotia	Canada	FJ582232	HCBNS220-03
	Heriades (*Neotrypetes*) *leavitti**	43.158	−79.247	Ontario	Canada	GU707684	BEECD363-09
	Heriades sp.*	32.7329	−116.955	San Diego	United States		SDBEE254-12
	Hoplitis (*Monumetha*) *fulgida platyura**	32.7201	−117.078	San Diego	United States		SDBEE265-12
	Hoplitis (*Monumetha*) *spoliata**	45.087	−64.668	Nova Scotia	Canada	FJ582243	HCBNS147-03
ACK002	*Megachile* (*Callomegachile*) *umbripenne*	−18.247	178.08	Viti Levu	Fiji		MSAPB130-11
ACK003	*Megachile* (*Callomegachile*) *umbripenne*	−18.247	178.08	Viti Levu	Fiji		MSAPB131-11
ACM006	*Megachile* (*Callomegachile*) *umbripenne*	−18.247	178.08	Viti Levu	Fiji		MSAPB140-11
ACM007	*Megachile* (*Callomegachile*) *umbripenne*	−17.4216	177.996	Viti Levu	Fiji		MSAPB187-11
	Megachile (*Eutricharaea*) *rotundata**			Saskatchewan	Canada	FJ582326	HCBNS225-03
AAA001	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB100-11
AAK003	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB106-11
AAL010	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB110-11
AAL011	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB111-11
AAL012	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB115-11
AAL013	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB116-11
AAL018	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB112-11
AAL019	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB113-11
AAL020	*Megachile* (*Eutricharea*) *albomarginata*	−18.247	178.08	Viti Levu	Fiji		MSAPB114-11
ACR001	*Megachile* (*Eutricharea*) *albomarginata*	−17.3823	178.158	Viti Levu	Fiji		MSAPB166-11
ACS001	*Megachile* (*Eutricharea*) *albomarginata*	−17.3823	178.158	Viti Levu	Fiji		MSAPB167-11
AAK001	*Megachile* (*Eutricharea*) *laticeps*	−18.247	178.08	Viti Levu	Fiji		MSAPB104-11

AAK002	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB105-11
AAL016	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB107-11
AAL021	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB108-11
AAL022	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB109-11
ACM002	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB136-11
ACM003	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB137-11
ACM004	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB138-11
ACM005	*Megachile* (*Eutricharea*) *laticeps*	–18.247	178.08	Viti Levu	Fiji		MSAPB139-11
ABC001	*Megachile* (*Eutricharea*) *scutellata*	–18.247	178.08	Viti Levu	Fiji		MSAPB121-11
	Megachile (*Megachile*) *centuncularis**	45.187	–64.403	Nova Scotia	Canada	FJ582307	HCBNS133-03
	Megachile (*Megachile*) *inermis**	45.079	–64.483	Nova Scotia	Canada	FJ582315	HCBNS158-03
	Megachile (*Sayapis*) *pugnata**	44.966	–65.058	Nova Scotia	Canada	FJ582324	HCBNS156-03
	Megachile (*Xanthosarus*) *frigida**	44.319	–64.016	Nova Scotia	Canada	FJ582308	HCBNS216-03
	Megachile (*Xanthosarus*) *gemula**	43.876	–66.101	Nova Scotia	Canada	FJ582312	HCBNS140-03
	Megachile (*Xanthosarus*) *latimanus**	45.119	–64.263	Nova Scotia	Canada	FJ582319	HCBNS218-03
	Megachile (*Xanthosarus*) *melanophaea**			Nova Scotia	Canada	FJ582320	HCBNS166-03
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708090	BOWGF319-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708086	BOWGF322-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708087	BOWGF320-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708088	BOWGF321-09
	Megachile sp.			Dak Lak – Chu Lang Sin NP	Vietnam	GU708079	BOWGF333-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708085	BOWGF326-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708083	BOWGF328-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708081	BOWGF330-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708082	BOWGF331-09
	Megachile sp.	16.6598	101.136	Phetchabun	Thailand	GU707848	BOWGF524-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708091	BOWGF317-09
	Megachile sp.			Dak Lak – Easo NP	Vietnam	GU708089	BOWGF318-09
	Megachile sp.			Dak Lak – Krong Bong	Vietnam	GU708084	BOWGF325-09
	Megachile sp.			Dak Lak – Chu Lang Sin NP	Vietnam	GU708080	BOWGF334-09
	Osmia (*Melanosmia*) *atriventris**	45.135	–64.489	Nova Scotia	Canada	FJ582411	HCBNS172-03
	Osmia (*Melanosmia*) *virga**	44.319	–64.016	Nova Scotia	Canada	FJ582447	HDBNS216-04
	Osmia (*Osmia*) *cornifrons**			Milyang	South Korea	EU726578	GBAH3929-08

Note: Specimen locality data, GenBank Accession numbers and BOLD Process IDs provided for sequences of Cytochrome Oxidase I (COI) mtDNA. *, GenBank sequence data were acquired from a previous study.

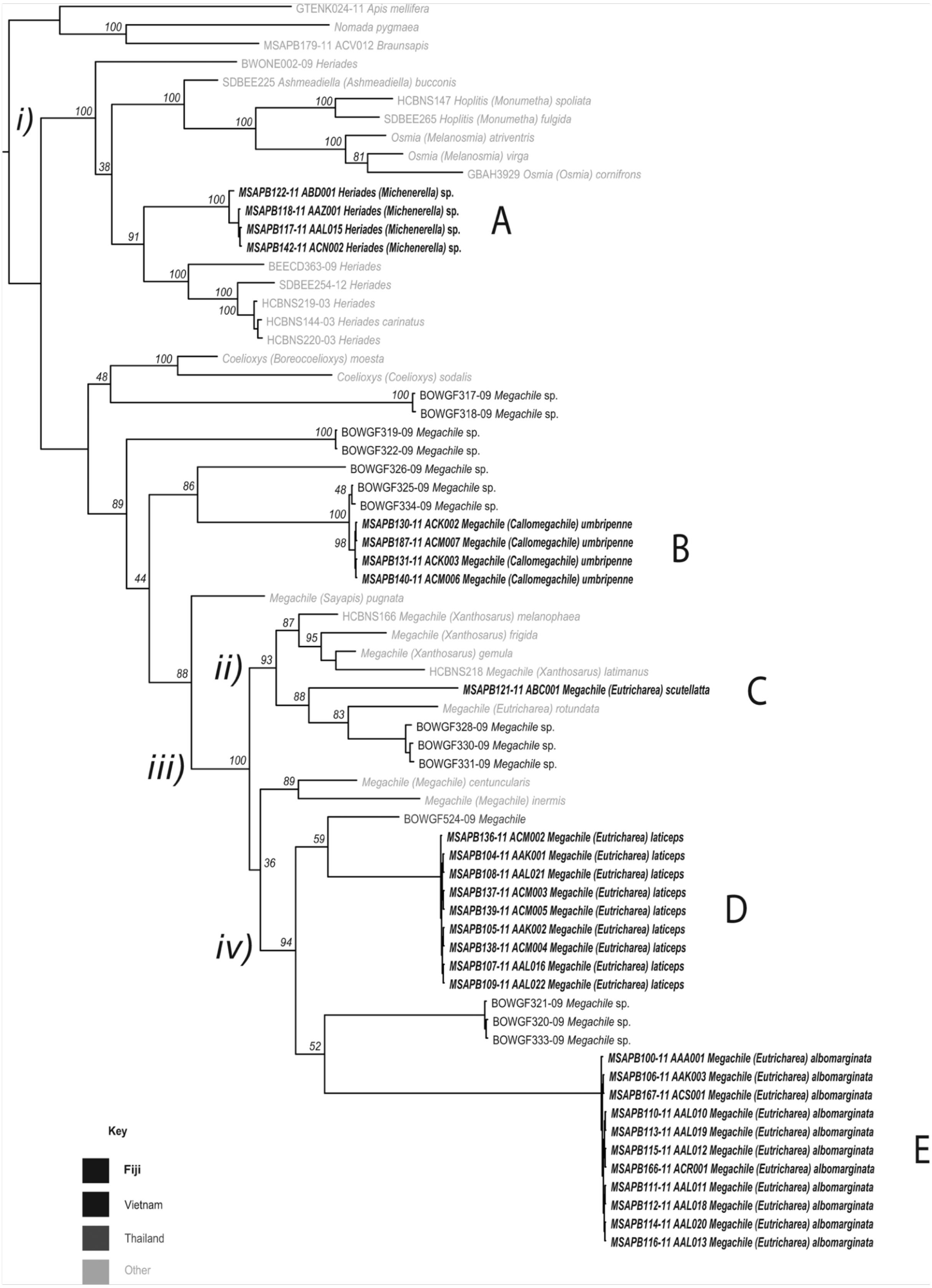

FIGURE 1. Bayesian phylogeny based on mtDNA (COI) data set. Phylogeny estimated via MrBayes with GTR + I + Γ substitution prior for a data set partitioned by codon position. Clades labeled A–E indicate Fijian haplotypes referred to in the text. Collection locality of key regional groups as indicated by color in the included key, with Fijian representative labels black and in bold; Vietnam black; Thailand dark gray; all other localities light gray. Posterior probability values are given above all nodes outside of haplotype clades. Key nodes for Fijian topological arrangement are indicated by *i–iv* as referred to in the text.