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Mitogenomic phylogeny of bee families confirms the basal position and monophyly of Melittidae

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Abstract

Bees (Anthophila) represent a critical taxon for the ecosystem service of pollination and hence have received great scientific attention. The more than 20,000 known species of bees are grouped in seven families. Yet, the relationships between bee families are not entirely clear, and specifically, the position of Melittidae and their monophyly has been discussed in the past. Here, we present the most comprehensive mitogenomic phylogeny of bees including five members of Melittidae from two subfamilies and three tribes. Our results suggest monophyly of the family Melittidae and further support their basal position. The data also support the two subfamilies, but are not in line with current assignment of tribes. Our results show, despite advancement with transcriptomic and whole genomic data, the value of mitochondrial data for the reconstruction of phylogenies.

KEYWORDS

Anthophila, Apidae, Megachilidae, Melittidae, mitochondrial genome

1 | INTRODUCTION

As important pollinators, bees (Anthophila) have received much attention in recent years. Their diversity goes much beyond the well-known honey bee *Apis mellifera* and includes more than 20,000 species in the seven families Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae and Stenotritidae (Michener 2007). Besides the Stenotritidae, all families are species-rich and have a diverse range of morphological variation. While the monophyletic status of most families has been confirmed for a relatively long time (e.g. Danforth et al., 2006), monophyly of the Melittidae has been widely discussed, because of their high phenotypic diversity and ambiguous molecular results (Michez et al., 2009).

The phylogeny of the Anthophila more generally has been explored in a variety of studies employing morphological data (Alexander & Michener, 1995; Engel, 2001; Michener, 1944), diverse molecular markers (e.g. Branstetter et al., 2017; Peters et al., 2017; Sann et al., 2018), or a combination of both (Danforth et al., 2006; Michez et al., 2009), delivering divergent results. Especially, the status and phylogenetic position of the Melittidae have frequently changed. While earlier studies often grouped Melittidae as the sister group of Megachilidae and Apidae and suggested a derived status of the family, more recently the family was thought to be paraphyletic and consisting of multiple families (Danforth et al., 2006; Michez et al., 2010). This has been revoked by Danforth et al. (2013) who concluded that

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the family is monophyletic, but also stated that it requires further revision. This study already suggested a basal position of the Melittidae within the Anthophila. Finally, studies based on transcriptomic data, genomic ultraconserved elements, and combined transcriptomic and target enrichment data (Branstetter et al., 2017; Peters et al., 2017; Sann et al., 2018) supported the basal position on the Melittidae and their monophyletic status, yet with limited sampling for the family.

A first mitogenomic study by Kahnt et al. (2015) suggested a close relationship of Melittidae with Colletidae, yet with limited sampling across all Anthophila families. A more comprehensive study of mitogenomes was performed by He et al. (2018) which placed the Melittidae at the basis of all bees, yet, again, only the mitogenome sequence of a single species, *Rediviva intermixta*, was included. While the analyses of mitogenomes for phylogenetics may appear basic in times of genomics, mitogenomes remain useful as a source of data for phylogenetic analyses, but also represent an interesting marker system for larger scale community studies as shown by Tang et al. (2015). Surprisingly, even charismatic taxa, such as bees, are not yet fully understood from a mitogenomic standpoint. Hence, we here include four additional species, belonging to four genera, two subfamilies and three tribes of Melittidae, into a mitogenomic phylogeny to test whether Melittidae remain monophyletic based on mitogenomic data and whether the basal position within the Anthophila is further supported.

2 | MATERIALS AND METHODS

2.1 | Sampling

In this study, we included four new mitogenomes of Melittidae (*Dasypoda hirtipes* (Dasypodainae: Dasypodaini) – MT985326, *Melitta schultzei* (Melittinae: Melittini) – MT985327, *Capicola nanula* (Dasypodainae: Hesperaspini) – MT985325 and *Samba griseonigra* (Dasypodainae: Dasypodaini) – MT985328) (Nickel et al. in press) together with the previously published sequence of *R. intermixta* (Melittinae: Melittini; Kahnt et al., 2015) raising the number to five mitogenomes available for the family. Material of *D. hirtipes* was collected during a field trip to Pevestorf (Lower Saxony, Germany) in July 2017. Material of *M. schultzei* (Farm Kanolfontein, 20 km W Sutherland, road side, 1,385 m, S32°24′43″, E20°27′28″, 17.IX.2017, leg. MK), *C. nanula* (1 km NW Vioolsdrif, Orange River Valley, 310 m, S28°42′02″, E17°30′22″, 9.IX.2016, leg. MK) and *S. griseonigra* (8 km WNW Leliefontein, Fynbos, road side, S30°15′58″, E18°03′17″, 14.IX.2017, leg. MK) was collected in South Africa by MK in 2016 and 2017 and was conserved pinned and dried, or in ethanol.

2.2 | Molecular analyses

Genomic DNA was extracted from *D. hirtipes* using a salt-extraction protocol as described in Aljanabi and Martinez (1997). Subsequently, genomic DNA was fragmented and libraries were prepared using NEBNext® Ultra™ II DNA Library Prep Kit for Illumina® (New England Biolabs). Genomic DNA was extracted from *M. schultzei*, *C. nanula* and *S. griseonigra* using EchoLUTION Blood DNA HiYield Kit (BioEcho), and libraries were prepared using Nextera DNA Flex Library Prep Kit (Illumina). Sequencing was performed on the Illumina MiSeq platform producing 250 bp paired-end reads for *M. schultzei*, *C. nanula* and *S. griseonigra* and 250 bp single-end reads for *D. hirtipes* yielding at least 1.1 million reads per species.

Adapter trimming and quality filtering were performed using Trimmomatic v. 0.38 (Bolger et al., 2014) for paired-end and single-end reads. Initially, the bases at the end of the read were cut if the Phred score, indicating the quality of each base, fell below 15. The Trimmomatic sliding window function was used to remove fragments of 4 bases once the average quality within the window fell below the Phred score 15. Reads shorter than 70 bp after trimming were discarded. Finally, the quality of the trimmed reads was checked using FastQC v. 0.11.7 (Andrews, 2010) to evaluate if previous steps were successful.

All remaining reads were then used to produce mitochondrial genome assemblies using the "de novo assembly" and "find mitochondrial scaffold" modules provided in MitoZ v2.4 with default settings (Meng et al., 2019). For *D. hirtipes* and *M. schultzei*, this was not sufficient to recover a complete mitogenome. The multi-kmer mode in MitoZ to identify missing PCGs was used with a kmer size of 99 for *D. hirtipes* and 31 for *M. schultzei* to achieve the longest continuous mitochondrial contig. The preliminary mitogenomes (~13,000 bp) were then used as the respective reference genome for the mitochondrial baiting and iterative mapping implemented in MITObim v1.9.1 (Hahn et al., 2013). Finished mitogenomes were annotated using the MITOS2 webserver (Bernt et al., 2013). The gene boundaries were checked manually, and start and stop codons were corrected when necessary using Geneious v10 (Kearse et al., 2013). Protein-coding and rRNA genes were extracted for phylogenetic analysis.

2.3 | Sequence alignment and phylogenetic analyses

Published data for the 13 mitochondrial protein-coding genes and the mitochondrial large and small subunit ribosomal RNA genes were downloaded from GenBank and incorporated into the datasets containing the newly generated sequences. Protein coding sequences were aligned with MUSCLE (Edgar, 2004) as implemented in MEGA X

(Kumar et al., 2018) using default settings. Sequences of the small and large subunit ribosomal RNA genes were aligned with MAFFT (Katoh & Standley, 2013) as implemented in the MAFFT online service (Katoh et al., 2019) using the Q-INS-i iterative refinement algorithm and otherwise default settings. Alignments were concatenated and ambiguously aligned positions were then excluded with Gblocks (Castresana, 2000) as implemented at the Gblocks Server (http://molevol.cmima.csic.es/castresana/Gblocks_server.html), with options chosen to allow for smaller final blocks, gap positions within the final blocks and less strict flanking positions.

PartitionFinder 2.1.1 (Lanfear et al., 2017) was used to select the best-fitting evolutionary models for the maximum likelihood (ML) analysis of phylogenetic relationships, conducting exhaustive searches with separate estimation of branch lengths for each partition and with the Bayesian information criterion to select among models. The dataset was initially divided into five partitions corresponding to the three codon positions of the mitochondrial protein-coding genes as well as the stem and loop regions of the mitochondrial ribosomal genes determined based on the secondary structure models published by Gillespie et al. (2006).

The ML analysis was performed using Garli (Zwickl, 2006) with evolutionary models and data partitions as suggested by the PartitionFinder analysis and otherwise default settings. Support values were calculated by bootstrapping with 1,000 replications.

Heuristic maximum parsimony (MP) searches were conducted with PAUP* 4.0a166 (Swofford, 2002) with unordered characters, 100 random sequence addition replicates, tree bisection reconnection (TBR) branch-swapping, and gaps treated as missing data. Support for internal branches was assessed in PAUP* by bootstrapping with 1,000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition.

Bootstrap support (BS) values from the ML and MP analyses were mapped onto the ML tree with Sumtrees 3.3.1, which is part of the DendroPy 3.8.0 package (Sukumaran & Holder, 2010). BS values with $70 \leq BS < 80$ and Bayesian posterior probability (PP) values with $0.95 \leq PP < 0.97$ were interpreted as moderate support for a node, nodes with $80 \leq BS < 90$ and $0.97 \leq PP < 0.99$ as well supported, and $BS \geq 90$ and $PP \geq 0.99$ as highly supported.

3 | RESULTS

3.1 | Alignments and evolutionary models

The mitochondrial genomes of *D. hirtipes*, *M. schultzei*, *C. nanula* and *S. griseonigra* are 18,594, 20,324, 15,884 and 16,978 bp in length, respectively. All consist of 13 protein-coding genes (PCGs), 22 tRNA genes, two rRNA genes and the non-coding mitochondrial control region. The final alignment of the 13 mitochondrial protein-coding genes and the two mitochondrial rRNA genes had a length of 15,468 base pairs (bp), with 2,821 bp excluded by Gblocks (see Table 1).

TABLE 1 Length of genes included in phylogenetic analyses and positions excluded by Gblocks

Gene	Length (bp)	Positions excluded (bp)
COXI	1,611	76
COXII	705	27
COXIII	885	103
CYTB	1,254	109
ATP6	783	117
ATP8	270	123
NAD1	1,011	84
NAD2	1,263	367
NAD3	375	21
NAD4	1,482	194
NAD4L	324	57
NAD5	1,815	207
NAD6	678	189
12S	1,232	569
16S	1,780	578
Total	15,468	2,821

The PartitionFinder analysis suggested to use four partitions corresponding to the 1st codon positions (GTR + G), 2nd codon positions (GTR + G) and 3rd codon positions (GTR + G) of the protein-coding genes and the combined stem and loop regions of the rRNA genes (GTR + G).

3.2 | Phylogenetic analyses

Anthophila were recovered as monophyletic clade with maximal support (Figure 1). The Melittidae, represented by the genera *Capicola*, *Dasypoda*, *Melitta*, *Rediviva* and *Samba*, formed a monophyletic clade with maximum support in all analyses (Figure 1). Similarly, all other bee families were monphyletic with high support values in most analyses. The Melittidae were placed as the sister group of an unsupported clade including all other families. The short-tongued bees (Andrenidae, Halictidae and Colletidae, BS [ML]: 100, BS [MP]: 87) and the long-tongued bees (Apidae and Megachilidae, with maximum support) were both recovered as monophyletic groups with high support. However, the relationships between the three short-tongued bee families were not resolved (Figure 1).

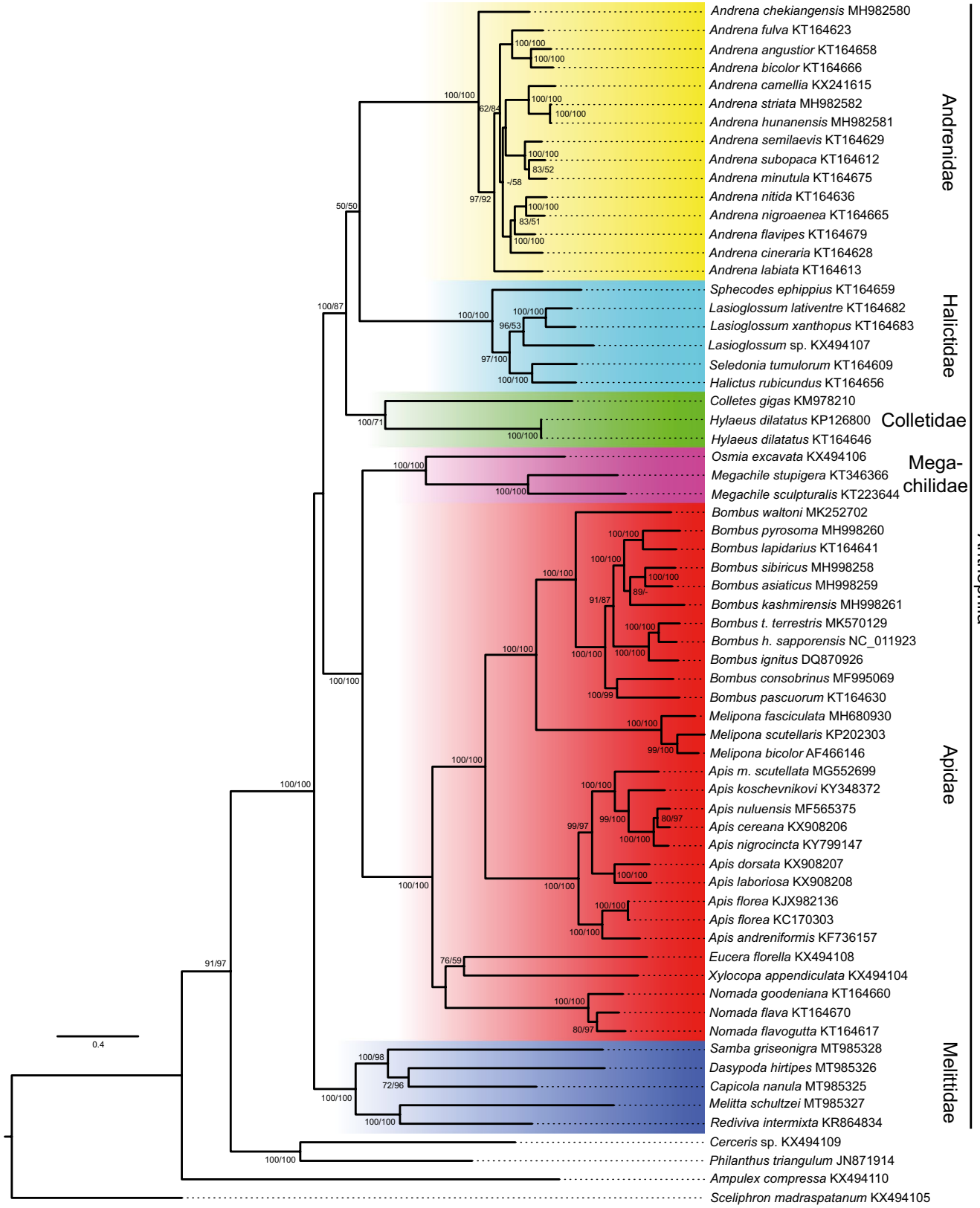

FIGURE 1 Maximum likelihood tree showing the relationships of bees based on the analysis of 13 mitochondrial protein-coding genes and two mitochondrial ribosomal RNA genes. Values at nodes represent maximum likelihood (left) and maximum parsimony (right) bootstrap values. Only nodes with bootstrap values ≥50 are annotated

4 | DISCUSSION

In this study, we provide the so far most comprehensive mitogenomic phylogeny of bees, which for the first time includes more than a single member of the family Melittidae; our sampling represents five genera of two subfamilies (Melittinae, Dasypodainae) and three tribes (Melittini, Hesperaspini, Dasypodaini). The length of the newly generated mitochondrial genomes varies between 15,884 bp in *C. nanula* and 20,324 bp in *M. schultzei*. The structure matches that of other bees and contains the typical set of genes and RNAs (Nickel et al. in press). Our analyses confirm the monophyly of all studied bee families, including the Melittidae and further support the position of the Melittidae as sister group to all other bees. We also confirm the monophyly of the long-tongued bees (Apidae and Megachilidae), which are nested within the short-tongued bees rendering them paraphyletic. We further find Andrenidae and Halictidae to be sister groups with Colletidae at their base.

Our results largely agree with the relationships found by He et al. (2018) which also constructed a phylogeny based on mitogenomic sequences with a large overlap with our data set, albeit with a less comprehensive sampling for Melittidae. Yet, theirs and our results are divergent in the sister group relationships within the last-mentioned group. He et al. (2018) found a closer relationship between Halictidae and Colletidae, with Andrenidae at their base with high support. However, the relationship between Andrenidae and Halictidae is not well-supported in our phylogeny, leaving this question to further investigations. A sister group relationship between Colletidae, Halictidae and the here not included Stenotritidae is, however, also supported by a combined multi-gene approach (Danforth et al., 2006), a supertree analysis (Hedke et al., 2013), and ultraconserved elements (Branstetter et al., 2017). Analysis of transcriptomes yielded different results depending on the inclusion of the Stenotrididae (Peters et al., 2017; Sann et al., 2018). Hence, the inclusion of the Stenotritidae may be a crucial factor in the phylogenetic reconstruction of the Anthophila. Yet, it is surprising that we did not recover this relationship in our phylogeny. The divergent results may be due to slightly different sampling of Halictidae of which we included less samples, as many of the mitogenomes were rather incomplete. Sampling, especially of Stenotritidae, but also for Colletidae needs therefore to be expanded in the future.

The basal position of Melittidae can be seen as confirmed as all recent analyses with various types of data supported this relationship (e.g. Branstetter et al., 2017; Hedke et al., 2013; Peters et al., 2017; Sann et al., 2018); only the multigene analysis by Danforth et al. (2006) suggested paraphyly for the family.

We can say only little about the intra-family relationships within Melittidae with only five species representing five genera included. However, we recovered two well-supported groups: the first group includes the genera *Melitta* and *Rediviva*, consistent with the tribe Melittini within the subfamily Melittinae (e.g. Michez et al., 2009), and the second group contains *Dasypoda* and *Capicola* (yet, only with medium support) as sister taxa with *Samba* as basal taxon. *Capicola* represents the tribe Hesperapini, whereas *Dasypoda* and *Samba* belong to the Dasypodaini, both within the Dasypodainae (Michez et al., 2010). Our phylogeny does not reflect the currently recognized tribes, but matches with subfamilies. These suggest that tribes will have to be reevaluated based on a larger sampling in the future.

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