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Combining transcriptomes and ultraconserved elements to illuminate the phylogeny of Apidae

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ABSTRACT

Two increasingly popular approaches to reconstruct the Tree of Life involve whole transcriptome sequencing and the target capture of ultraconserved elements (UCEs). Both methods can be used to generate large, multigene datasets for analysis of phylogenetic relationships in non-model organisms. While targeted exon sequencing across divergent lineages is now a standard method, it is still not clear if UCE data can be readily combined with published transcriptomes. In this study, we evaluate the combination of UCEs and transcriptomes in a single analysis using genome-, transcriptome-, and UCE data for 79 bees in the largest and most biologically diverse bee family, Apidae. Using existing tools, we first developed a workflow to assemble phylogenomic data from different sources and produced two large nucleotide matrices of combined data. We then reconstructed the phylogeny of the Apidae using concatenation- and coalescent-based methods, and critically evaluated the resulting phylogenies in the context of previously published genetic, genomic, and morphological data sets. Our estimated phylogenetic trees are robustly supported and largely congruent with previous molecular hypotheses, from deep nodes to shallow species-level phylogenies. Moreover, the combined approach allows us to resolve controversial nodes of the apid Tree of Life, by clarifying the relationships among the genera of orchid bees (Euglossini) and the monophyly of the Centridini. Additionally, we present novel phylogenetic evidence supporting the monophyly of the diverse clade of cleptoparasitic Apidae and the placement of two enigmatic, oil-collecting genera (*Ctenoplectra* and *Tetrapedia*). Lastly, we propose a revised classification of the family Apidae that reflects our improved understanding of apid higher-level relationships.

1. Introduction

Phylogenomics, the use of genome-scale data to reconstruct evolutionary relationships among orders, families, genera, and species, is currently conducted primarily with two different *reduced representation* sequencing strategies: (1) transcriptome sequencing (=RNA-seq; e.g., Bank et al., 2017; Bazinet et al., 2017; Misof et al., 2014; Peters et al., 2018), and (2) target enrichment methods, such as the use of *ultraconserved elements* (UCEs; e.g., Blaimer et al., 2016a; Branstetter et al., 2017b; Faircloth et al., 2012) or *anchored hybrid enrichment* (AHE; e.g., Espeland et al., 2018; Lemmon et al., 2012; Young et al., 2016).

There are distinct advantages and disadvantages to both approaches. Transcriptomic data can be generated in the absence of prior genomic resources for the group under study (i.e., one does not need previously published genomes of related taxa). However, the generation of transcriptomic data also has some drawbacks. Extraction of high quality RNA requires freshly preserved tissue samples (Yeates et al., 2016) and preparation of cDNA libraries can be time-consuming and costly relative to the targeted enrichment approaches. On the other hand, target enrichment methods perform better than transcriptomic methods when tissue samples are poorly preserved and can even be successfully used with pinned, decades-old insect specimens (Blaimer et al., 2016b; McCormack et al., 2016) or specimens fixed in formalin (Ruane and Austin, 2017).

Despite recent attempts to combine both approaches using specifically designed exon baits (Bank et al., 2017; Breinholt et al., 2018; Quattrini et al., 2018; Sann et al., 2018), transcriptome sequencing and target enrichment of UCEs are generally regarded as competing

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methods which generate data sets that are difficult, if not impossible, to combine into a single analysis. The majority of UCE loci were initially described as transcriptionally inactive when originally discovered through comparative analyses of the genomes of human, mouse, and rat (Bejerano et al., 2004), and should therefore *not* be part of the transcriptome. However, the standard UCE workflow targets any genomic region that is highly conserved and does not exclude exons (Faircloth, 2017; Faircloth et al., 2015). In fact, recent examination of invertebrate UCE bait sets indicate that they largely target coding sequences (Branstetter et al., 2017c), and that the most widely shared loci can be exclusively exons or partially exonic regions (Bossert and Danforth, 2018). This implies that exonic UCEs and transcriptome sequence data *should* be combinable, without the need to specifically design UCE baits to target transcriptome sequences.

In this study, we test the hypothesis that UCEs and transcriptomes can be combined into a single analysis using genome-, transcriptome-, and UCE data for 79 bees in the family Apidae. This family provides a model system for this study for several reasons. First, Apidae is the largest and most diverse family of bees with over 5880 species in 205 genera, and 34 tribes. Second, the phylogeny of the Apidae has been the subject of extensive study, which allows us to evaluate our inferred evolutionary relationships in the context of previously published genetic, genomic, and morphological data sets. Third, the apid bees include many of the most thoroughly studied social insect lineages, including carpenter bees (Xylocopinae), stingless bees (Meliponini), bumblebees (Bombini), and honeybees (Apini). There are 11 published, annotated, whole genome sequences available for Apidae, more than for any other family of bees (e.g., Brand et al., 2017; Kapheim et al., 2015; Rehan et al., 2016; Sadd et al., 2015). Finally, in spite of the extensive previous phylogenetic work focused on apid phylogeny, fundamental questions remain about the placement and monophyly of key taxa, including the cleptoparasitic groups (e.g., Cameron, 2004; Cardinal and Danforth, 2013; Litman et al., 2013), the Centridini (Martins and Melo, 2016; Martins et al., 2014), and the placement of two, enigmatic, oil-collecting genera (*Ctenoplectra* and *Tetrapedia*).

2. Material and methods

We developed a comprehensive data matrix of 79 samples of Apidae, representing all 5 subfamilies, 22 tribes, 43 genera, and two outgroup taxa. We included the 11 apid genomes that were publicly available on NCBI in May 2017, as well as the genome of *Megachile rotundata* (Kapheim et al., 2015). We included all 16 transcriptome assemblies of apid bees and one outgroup from a recent phylotranscriptomic study of Hymenoptera (Peters et al., 2017), as well as all 12 samples of Apidae from a UCE phylogeny of this order (Branstetter et al., 2017a). We expanded this taxon sampling by sequencing UCEs of 42 additional species of apid bees. The extensive version of the materials and methods, including the taxon table and a detailed step-by-step documentation of all bioinformatic procedures, is available in the supplementary material.

2.1. Generation of new UCE data

DNA extractions were carried out using a standard phenol/chloroform protocol (modified from Saghai-Maroof et al., 1984). Tissue samples were extracted from the specimens' hind legs or thoracic muscles. We quantified extracted DNA and sheared an average of 215 ng DNA for each sample to a targeted fragment size of 500–600 bp. We followed the library preparation protocol of Faircloth et al. (2015), and included all modifications from Blaimer et al. (2016a, 2016b). We prepared dual-indexed libraries using TruSeq adapters (Faircloth and Glenn, 2012), and amplified the input DNA. The target enrichment was carried out using two different bait sets; the initial set by Faircloth et al. (2015; hereafter 'UCE v1'), and the enhanced HymV2-ant UCE bait set from Branstetter et al. (2017c; hereafter 'UCE v2'). We enriched a total of 42 samples and prepared 21 samples for each bait set. For the UCE v2 samples, enrichment was conducted according to Blaimer et al. (2016a, 2016b) followed by post-enrichment amplifications. We quantified the enrichment success using qPCR and pooled the samples at equimolar concentrations. We selected for fragment sizes between 250 and 800 bp length and carried out the sequencing on an Illumina HiSeq 2500 platform with 150 bp paired ends. Sequencing took place at the Cornell Biotechnology Resource Center. The newly generated UCE sequences that were captured using the initial UCE bait set (hereafter 'UCE v1') were processed by Rapid Genomics LLC., following the workflow outlined in Faircloth et al. (2015). Sequencing for this data was conducted on an Illumina HiSeq 3000 platform with 150 bp paired end reads.

2.2. Assembly of phylogenomic data from different sources

We assembled genomic and transcriptome data using the existing UCE pipeline PHYLUCE (Faircloth, 2016) with adjusted settings. First, we identified genomic sequences that correspond to hymenopteran UCEs in all 12 included genomes. We extracted these UCE core sequences together with 1600 bp long up- and downstream flanking regions, totaling 3320 bp for each locus. These long genomic extracts typically span multiple exons and introns. They provide the alignment backbone for the transcriptome and UCE sequences and are integral to the successful alignment of exons (Fig. 1). We included all apid transcriptomes from a

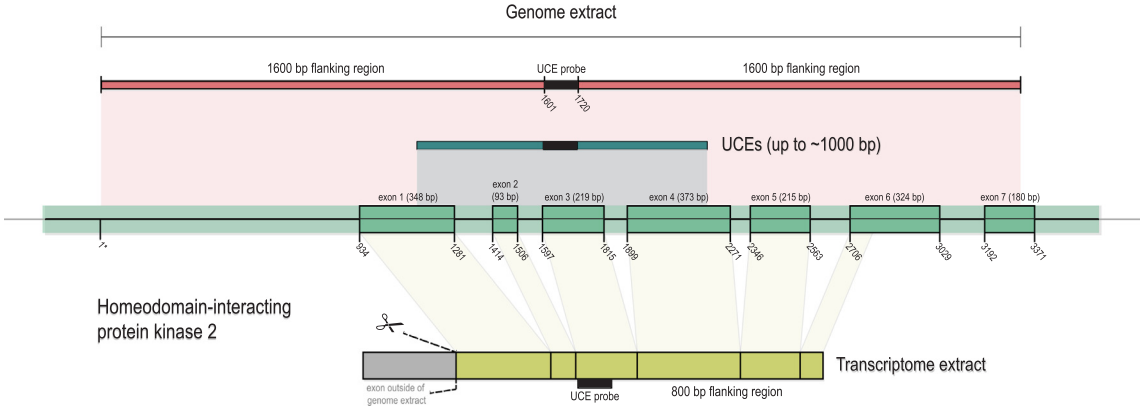

Fig. 1. Graphical summary of the workflow developed for combining genome-, transcriptome-, and UCE data, exemplified for the widely shared HIPK2 gene (Homeodomain-interacting protein kinase 2) of *Apis mellifera*. Displayed is locus GB55411, based on the Amel_4.5 assembly (Elsik et al., 2014) and the EnsemblMetazoa (Kersey et al., 2018) *Apis mellifera* annotation release 39. The locus corresponds to UCE 11,073 of the enhanced Hymenoptera bait set (Branstetter et al., 2017c). The first position (*) corresponds to position 13,682,968 of the second chromosome of the honeybee genome. Exon 1 corresponds to GB55411-RA-E4, exon 2 to GB55411-RA-E5, exon 3 to GB55411-RA-E6, and so forth.

recent comprehensive phylogenomic study (Peters et al., 2017). In principle, transcriptomes were treated as genomes. However, as the Hymenoptera UCE baits can target regions that are at least partially intronic (Bossert and Danforth, 2018), we lowered the overlap threshold to more effectively identify corresponding regions. This significantly increased the capture success for the transcriptome data. The corresponding regions were extracted with 800 bp flanking regions. Subsequently, the extracted genomic and transcriptomic sequences were treated as TRINITY-assemblies (Grabherr et al., 2011). The *in-solution* captured UCE data were demultiplexed and subsequently trimmed with TRIMMOMATIC (Bolger et al., 2014) via ILLUMIPROCESSOR (Faircloth, 2013). Reads were assembled *de-novo* using TRINITY. We used PHYLUCE (Faircloth, 2016) on all assemblies and *in-silico* captured sequences to identify and extract UCEs with different identification stringencies. Sequences were aligned by locus with the accuracy-oriented L-INS-i algorithm of MAFFT v7.13 (Katoh and Standley, 2013). Variable sites were removed according to the relaxed GBLOCKS trimming parameters of Talavera and Castresana (2007). Each alignment was visually inspected, including manual removal of misalignments. We finalized 70% and 80% completeness matrices, ensuring that each included locus is represented by at least 70% or 80% of all taxa, respectively. All UCE searches were conducted using the enhanced principal UCE bait set (Branstetter et al., 2017c).

2.3. Phylogenetic reconstruction

Phylogenetic relationships within Apidae were inferred using both concatenation- and coalescent-based methods. First, we applied a Bayesian approach on the 80% matrix using the scalable implementation of PHYLOBAYES (Lartillot et al., 2013). As the trimmed matrices do not allow for codon-based partitioning, we applied the CAT-GTR model with discrete Γ (Lartillot and Philippe, 2004) to account for site-heterogeneous substitution rates. We ran 3 chains for at least 10,000 cycles. We ensured relative differences between the log likelihood values of < 0.3 and effective sizes of > 300, using the tracecomp program of the PHYLOBAYES package. Convergence was evaluated with bpcomp, and chains were considered converged after the largest discrepancies among the partitions (maxdiff) fell below 0.1. Further we used both the 70% and the 80% matrix to calculate maximum likelihood trees with the ML implementation IQ-TREE (Nguyen et al., 2015). We partitioned the matrices by locus and used the best-fit models as designated by MODELFINDER (Kalyaanamoorthy et al., 2017).

To contrast our concatenation-based relationships of the Apidae, we reconstructed the phylogeny under the multispecies coalescent model (Rannala and Yang, 2003). We applied a two-step approach: Single gene trees were calculated with IQ-TREE, partitioned by locus, and using the best-fit model as inferred with MODELFINDER. We examined each resulting gene tree and collapsed nodes with bootstrap support of less than 50%. Lastly, gene trees were summarized with ASTRAL-II (Mirarab et al., 2014; Mirarab and Warnow, 2015).

3. Results

3.1. Capture and matrix statistics

We captured an average of ~1.75 (0.88–2.75) million Illumina reads for samples that were prepared using the UCE v1 bait set and an average of ~2.03 (0.23–4.86) million reads for samples prepared with the v2 set. The de-novo assemblies with TRINITY produced an average of 42,281 (13,371–109,081) contigs for the v1 set, averaging 295 bp in length. Usage of the v2 set yielded an average of 76,523 (7387–241,919) contigs per sample, averaging 340 bp. Capture success was higher for the improved Hymenoptera bait set (v2; Branstetter et al., 2017c) than for the initial UCE v1 bait set (Faircloth et al., 2015). Nonetheless, UCEs of the v1 set were more widely shared among the samples and are more prevalent in the 80% and 70% matrices (Fig. 2).

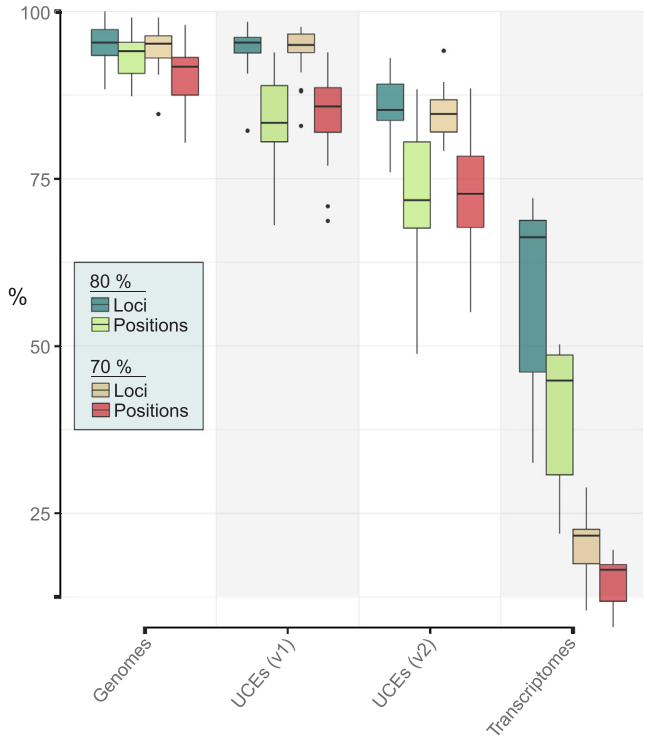

Fig. 2. Prevalence of sequence data in the two final nucleotide matrices (70%, 80%), sorted by sequencing strategy. Displayed is the percentage of present UCE loci and present nucleotide sites. Whiskers show 1.5*IQR.

Table 1
Statistics of capture success and matrix processing. Shown are mean values ± σ, and **n** indicates the number of included taxa.

	Number of loci		
	Identified	in 80% matrix	in 70% matrix
Genomes (n = 12)	2236.5 ± 95.3	123 ± 4.5	529 ± 22.7
Transcriptomes (n = 17)	903.7 ± 227.9	76.6 ± 18.1	112 ± 26
UCE v1 set (n = 31)	951.2 ± 99.7	121.9 ± 3.9	529.5 ± 18.1
UCE v2 set (n = 21)	1592 ± 193.3	110.9 ± 6	477 ± 19.8

In total, we identified and extracted an average of ~900 (458–1179) ultraconserved elements from all included transcriptome samples and ~2200 loci from the 12 included genomes (Table 1). We successfully combined these newly sequenced ultraconserved elements with transcriptome and genome sequence data to generate two large nucleotide supermatrices.

The 80% dataset produced the densest matrix with a total of 129 loci, 79,293 nucleotide positions and 17.4% non-gap missing data (total of 27% undetermined characters). The 70% matrix has 561 loci, 302,379 positions and 26.5% non-gap missing data (total of 32.8% undetermined characters). The transcriptome sequences contained the highest degree of missing data. These statistics were inferred after the exclusion of twelve loci of the 70% matrix that contained major misalignments: UCE #36, 40, 55, 74, 225, 400, 404, 606, 608, 1023, 1342, 1483.

3.2. Phylogeny of Apidae

The Bayesian inferences, maximum likelihood estimates, and gene tree summaries of both the 70% and 80% alignments produced well-resolved phylogenetic trees of the Apidae (Figs. 3–5, Supplementary Figs. 1–4). These phylogenies are strongly supported with nearly identical topologies, despite the differences in applied reconstruction

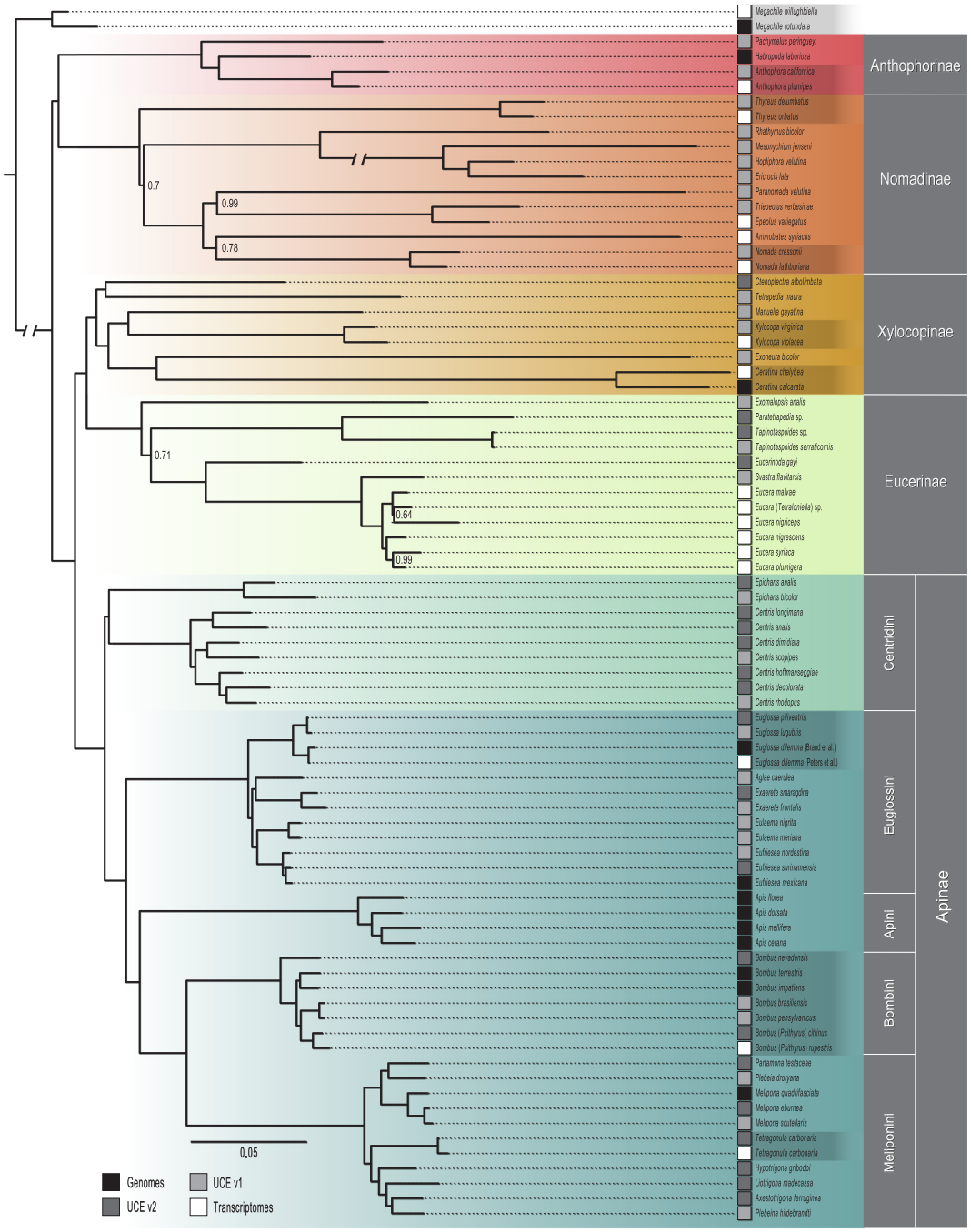

Fig. 3. Bayesian phylogram of the Apidae, based on the concatenated 80% matrix. Highlighted clades show groupings of species within the same genus whose sequence data was generated using differing sequencing approaches. Node support values are Bayesian posterior probabilities and are 1.0 unless otherwise indicated. The scale bar represents the probability of nucleotide substitutions per site.

methods and datasets. On seven occasions, we included multiple samples of species that are classified in the same genus or subgenus, using sequence data generated from both transcriptome and UCE methods. Each of these genera and subgenera are monophyletic with joint groupings of transcriptome and UCE samples. This holds true for the 70% and 80% matrices, and under both concatenation- and coalescent methods (Fig. 3, highlighted groupings). This confirms the feasibility of combining UCE and transcriptome data.

All inferred phylogenies converged on five major clades within Apidae (Fig. 6). Moreover, each phylogeny rendered the subfamily Apinae, as currently recognized, paraphyletic with respect to Xylocopinae and Nomadinae, and both these lineages include taxa that are currently classified as apine bees. We therefore propose a revised classification for the subfamilies of Apidae in order to ensure a rank-based taxonomy of monophyletic groups:

(1) Anthophorinae, *stat. rev*. We raise the tribe Anthophorini, which was previously classified as part of the Apinae (Michener, 2007), to its own subfamily.
(2) Nomadinae, *stat. rev*. Based on the inferred phylogeny and recent molecular studies (Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018), we include all cleptoparasitic Apidae except for *Ctenoplectrina* and the cleptoparasitic Euglossini in the subfamily Nomadinae. The tribes Coelioxoidini, Ericrocidini, Isepeolini,

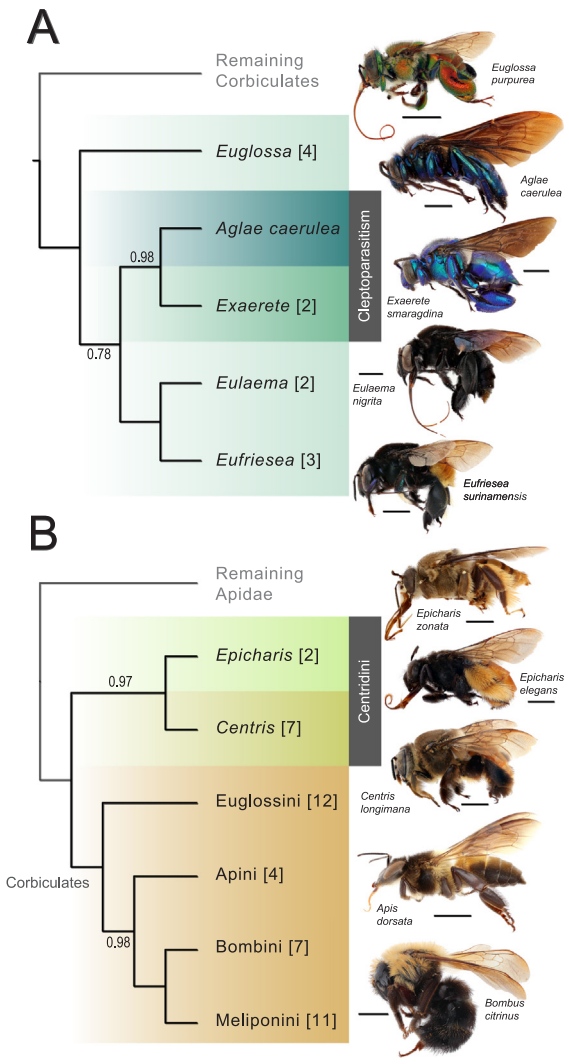

Fig. 4. Details of the ASTRAL summary tree, based on the 80% matrix. Numbers in brackets correspond to the number of included species of the respective groups. Branch support values are local posterior probabilities and are 1.0 unless shown; scale bars next to bee photos correspond to 4 mm. A. The phylogeny of the Euglossini reveals a sister relationship of the only cleptoparasitic genera of orchid bees: *Aglae* and *Exaerete*. This indicates a single origin of cleptoparasitic behaviors in the corbiculate lineage. B. The well-supported sister grouping of *Epicharis* and *Centris* affirms the previously contested tribe Centridini as a monophyletic group.

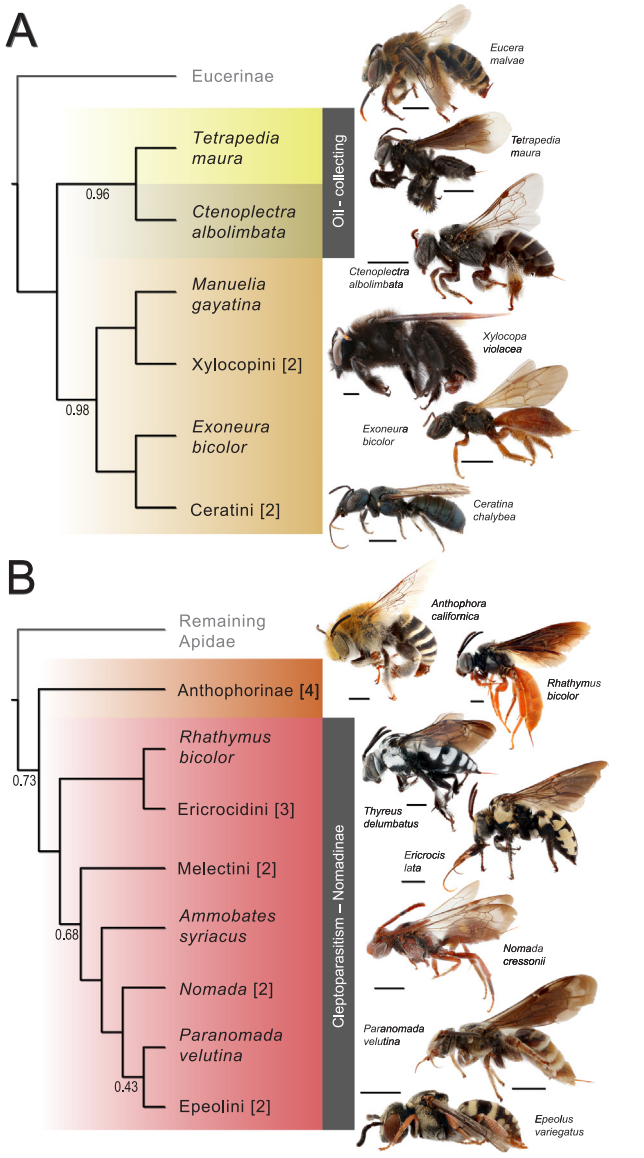

Fig. 5. Details of the ASTRAL summary tree, based on the 80% matrix. Numbers in brackets correspond to the number of included species of the respective groups. Branch support values are local posterior probabilities and are 1.0 unless shown; scale bars next to bee photos correspond to 2 mm. A. The phylogeny shows that the oil-collecting *Ctenoplectra* and *Tetrapedia* are sister to the rest of the subfamily Xylocopinae. This indicates a single origin of oil-collecting behavior in this lineage. B. The cleptoparasitic Nomadinae, as classified in this study, are most closely related to the primarily solitary Anthophorinae. This is in line with a recent transcriptome study (Peters et al., 2017). However, it contradicts a previously inferred phylogeny based on UCEs (Branstetter et al., 2017a).

Melectini, Osirini, Protepeolini, Rhathymini, which were placed in the Apinae in the past, are now placed in Nomadinae.

(3) Xylocopinae, *stat. rev*. Species of *Tetrapedia* and *Ctenoplectra* were previously classified as Apinae (Michener, 2007), but were inferred as a joint sister group to the carpenter bees in this study. To avoid a paraphyletic subfamily Apinae, we include the tribes Ctenoplectrini and Tetrapediini in the subfamily Xylocopinae.

(4) Eucerinae, *stat. rev*. We recovered a clade comprising the tribes Eucerini, Exomalopsini, and Tapinotaspidini, which corresponds to the 'eucerine line' sensu Silveira (1993). This clade was inferred as the sister group to the Xylocopinae, rendering the Apinae paraphyletic. Based on these results and the placement of Ancylaini and Emphorini in recent studies (Cardinal and Danforth, 2013; Praz and Packer, 2014), we raise the eucerine line to subfamily rank. We derive the name from the oldest suprageneric name of the group, *Eucerœ* (Latreille, 1802). The subfamily Eucerinae includes all the five above-mentioned tribes.

(5) Apinae, *stat. rev*. We consistently recovered a clade including the four corbiculate tribes (Apini, Bombini, Meliponini, and Euglossini) plus the tribe Centridini. The latter includes the two genera *Centris* and *Epicharis*, both containing oil-collecting bees that several studies have identified as the likely sister group to the corbiculates (Cardinal and Danforth, 2013; Cardinal et al., 2010). Apinae in this sense represents a more narrowly defined group than in previous classifications.

The detailed revised classification can be found in Appendix A and will be used throughout this article.

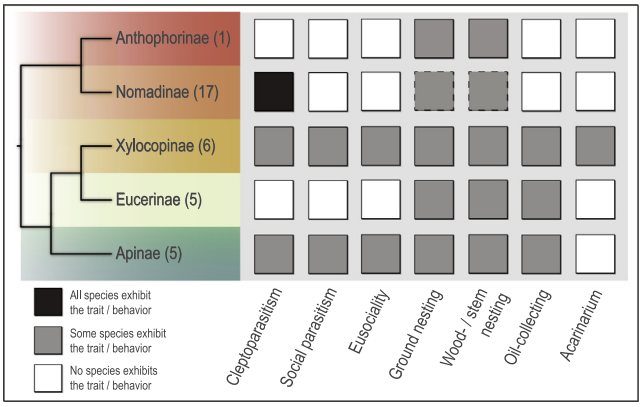

Fig. 6. Summary of the phylogenetic relationships of Apidae. Displayed are the revised subfamilies with selected life-history traits. The numbers following the subfamily names show the number of described tribes. The dashed outlines around the squares indicate that the cleptoparasitic Nomadinae do not construct nests on their own. They primarily attack nests of ground-nesting hosts but a few exceptions of stem-nesting host-parasite pairs have been described (e.g., *Coelioxoides* and *Tetrapedia*; Alves-Dos-Santos et al., 2002).

4. Discussion

4.1. The phylogeny of the Apidae proves the combinability of transcriptomes and UCEs

In order to critically evaluate the performance of our combined transcriptome/UCE dataset, we examined three aspects of our resulting trees. First, we examined whether closely related species (or even the same species) sequenced with the two different methods clustered together on the trees. In all seven cases, each of these groups were unambiguously recovered as monophyletic (highlighted in Fig. 3). This shows that UCE and transcriptome data can be meaningfully combined in the same analysis. This also demonstrates that transcriptomes and UCEs can be combined to infer phylogenies at relatively shallow levels.

Second, we examined how closely our tree matches previously published molecular phylogenies on lower-level relationships of apid bees. The inferred topologies are highly congruent with previous studies, yet with stronger statistical support. The inferred phylogeny of bumblebees (genus *Bombus*) matches the molecular phylogeny published by Cameron et al. (2007), and the phylogeny of *Apis* corresponds to the widely accepted consensus tree from Koeniger et al. (2011). This holds true for both matrices, as well as concatenation- and coalescent based methods. The same applies for the phylogeny of the stingless bees. We inferred the basal split of Old and New World Meliponini, as well as the same generic relationships as the most comprehensive phylogeny of the group based on Sanger sequencing in all probabilistic approaches (Rasmussen and Cameron, 2010). The tribal relationships of the corbiculate bees reflect recent phylogenomic studies (Bossert et al., 2017; Romiguier et al., 2015), in which the Euglossini (orchid bees) are placed as sister to the clade comprising honey bees, stingless bees and bumble bees. Controversies about the phylogeny of the four corbiculate tribes has persisted for more than two decades, evidencing phylogenetic incongruencies between molecular and morphological hypotheses (reviewed by Porto et al., 2016). The reiterated placement of orchid bees as the sister group of the remaining corbiculate bees is highly supported by a wealth of morphological characters (e.g., Porto et al., 2016). Fig. 3 depicts the same relationships among genera of the eucerine clade ('Eucerinae') as in a recent total evidence analyses (Praz and Packer, 2014), and the phylogeny of *Centris* corresponds to a new comprehensive study, except for the sister taxon to the genus (Martins and Melo, 2016).

Finally, the phylogenetic backbone of the tree is consistent with recent studies on the higher-level relationships within Apidae. Previous multi-gene studies (Cardinal and Danforth, 2013; Litman et al., 2013), total evidence analyses (Payne, 2014), and phylogenomic studies (Branstetter et al., 2017a; Peters et al., 2017) differ in one controversial node and the placements of a few lineages (discussed below), but they unambiguously agree on five major clades: the former Anthophorini (here raised to Anthophorinae), the large clade which includes the vast majority of all cleptoparasitic Apidae (herein Nomadinae; 'cleptoclade' sensu Cardinal et al., 2010), the Xylocopinae, the eucerine clade (here raised to Eucerinae), and the four tribes of the corbiculate bees plus Centridini. This shows that transcriptomes and UCEs can be effectively combined to generate large supermatrices of coding and non-coding sequences.

4.2. Methodological aspects of matrix processing

Combining transcriptome sequences with UCEs requires careful inspection of combined alignments, including manual curation if necessary. Despite recent discussions on the feasibility of manual sequence curation of genome-scale datasets (Irisarri et al., 2017; Liu et al., 2017), we strongly advocate a semi-automated approach to identify and remove misaligned sequences. We identified three main sources of misalignments with particular relevance for combined matrices. First, merging exclusively coding transcriptome regions with partially intronic UCE and genome sequences leads to alignments with extensive gaps and substantial missing data for the transcriptome samples. These gaps are distributed non-randomly, with missing data that is shared only among transcriptome or UCE samples. Manual inspection of the alignments is necessary to verify that transcriptome sequence data correctly aligns with the exons of the genome backbone, and not with intronic sequences. Second, depending on the arrangement of exons and introns of each individual target locus, the extracted transcriptome sequences can exceed the length of the genome alignment backbone. This is exemplified in Fig. 1 for the HIPK2 locus (Homeodomain-interacting protein kinase 2) of *Apis mellifera*. The transcriptome sequence includes an exonic region (GB55411-RA-E3), which is located outside the frame of the genome sequence in the downstream direction. Arguably, these data have potential for misalignments and biases, and must be removed manually in the subsequent processing. Third, additional potential for misalignments comes from the unusually long stretches of nucleotides that we extracted from the included genomes. Synteny among genome extracts can be expected to decrease with increasing fragment length. While the applied alignment algorithm can account for indels, it cannot account for differing gene arrangements caused by translocations, gene duplication, or transpositions. Such differing arrangements can lead to 'illogical jumps' of genomic sequences, such as exons, and produce alignments of non-homologous regions (Springer and Gatesy, 2017). Several recent genome-scale studies were shown to be affected by such misalignments (Gatesy and Springer, 2017; Springer and Gatesy, 2017). We therefore argue that manual inspection is necessary even after using stringent trimming algorithms such as GBLOCKS.

Lastly, UCE bait sets are tailored towards certain taxonomic groups of interest (Faircloth, 2017), and hence target unique sets of different loci. The Hymenoptera bait set used here targets primarily exonic or partially exonic regions (Bossert and Danforth, 2018; Branstetter et al., 2017c), but the extent to which other bait sets target exons is largely unknown. As genomic landscapes of different groups of animals differ substantially, the different bait sets should be expected to capture UCEs from transcriptomes with differing efficiency.

4.3. Combined sequence data resolves controversial nodes of apid phylogeny

Our study provides the most comprehensive phylogenomic treatment of the Apidae to date. Two recent phylogenomic studies on higher-level relationships of Hymenoptera included apid species (Branstetter et al., 2017a; Peters et al., 2017); however, the sparse

taxon sampling (not more than 18 species) limits their significance for the apid Tree of Life and does not allow one to resolve controversial nodes. Herein, we included every species from both studies and enhanced these data sets by sequencing additional key lineages of the family.

4.3.1. Cleptoparasitism among the Euglossini

Our analysis includes species from each of the five genera of euglossine bees. Two genera (*Aglae* and *Exaerete*) include obligate cleptoparasitic species that parasitize pollen-collecting hosts in the genera *Eulaema*, and *Eulaema* and *Eufriesea*, respectively (Michener, 2007; Roubik and Hanson, 2004). Previous molecular phylogenies based on multiple genes and Sanger sequencing (Cardinal and Danforth, 2011; Cardinal et al., 2010; Litman et al., 2013; Michel-Salzat et al., 2004), as well as several incongruent morphological results (reviewed in Cameron, 2004), did not group the two cleptoparasitic lineages as monophyletic, suggesting two independent origins of cleptoparasitism in orchid bees. Our results strongly support a sister group relationship between *Aglae* and *Exaerete* (Figs. 3 and 4a), thus suggesting a single origin of cleptoparasitism in orchid bees. Furthermore, we inferred the cleptoparasitic clade as sister group to a branch consisting of both host genera, *Eulaema* and *Eufriesea*. This placement represents an example of *Emery's rule* (named after the Italian entomologist Carlo Emery; Emery, 1909) in a loose interpretation: host and parasite are not sister species but are closely related lineages. In the presented case, the lineage with multiple obligate parasitic species is sister to the host lineage with several taxa.

4.3.2. The monophyly of Centridini

Our resulting phylogenies shed light on the unsettled relationships within Centridini and the evolution of the specialized pollen collecting structures of the corbiculate bees. The tribe Centridini consists of the two genera *Centris* and *Epicharis*, which have a center of diversity in the New World tropics (Martins and Melo, 2016; Michener, 2007; Silveira et al., 2002). These bees are predominantly oil-collecting: females of most species collect fatty floral oils in addition to pollen for provisioning the brood cells with larval food (Buchmann, 1987; Neff and Simpson, 1981; Renner and Schaefer, 2010). Morphological studies support monophyly of Centridini with several synapomorphic characters related to oil-collecting (Roig-Alsina and Michener, 1993; Plant and Paulus, 2016; but see Straka and Bogusch, 2007). However, molecular phylogenies using multiple genes failed to unambiguously corroborate this hypothesis. Some studies recovered a monophyletic Centridini and placed the tribe as sister group to the corbiculate Apinae (Cardinal and Danforth, 2013; Litman et al., 2013). However, more recent studies with much more comprehensive taxon sampling inferred a paraphyletic tribe Centridini with just *Centris* as sister group to the corbiculates (Martins and Melo, 2016; Martins et al., 2014). This would imply that the common ancestor of one of the most successful bee lineages, the corbiculates, was most likely an oil-collecting specialist, and that the corbicula (the so-called pollen basket, a smooth cavity on the hind legs surrounded by long hairs) is derived from the brush-like scopa of an oil-collecting precursor (Martins et al., 2014). Our study strongly supports centridine monophyly with the tribe being the sister group to the corbiculates (Fig. 4b). This result is in line with studies based on morphology and does not indicate that the corbicula is derived from a scopa of an oil-collecting specialist.

4.3.3. The placement of Ctenoplectra and Tetrapedia

The present study clarifies the phylogenetic position of the oil-collecting genera *Ctenoplectra* and *Tetrapedia*, which represent two lineages with traditionally uncertain relationships. Because of their unusual mouthpart morphology, the Ctenoplectrini have been included in various lineages of bees, such as Melittidae (Rozen, 1978), and have even been considered a separate family (Alexander and Michener, 1995; Michener and Greenberg, 1980). The tribe comprises the genus *Ctenoplectra* and the cleptoparasitic sister lineage *Ctenoplectrina* (Schaefer and Renner, 2008). Comprehensive morphology-based phylogenies found the tribe to be an apid lineage, but due to ambiguous results, relationships remained unclear (Plant and Paulus, 2016; Roig-Alsina and Michener, 1993; Silveira, 1993). Studies using molecular sequence data were inconclusive as well. Some indicated a closer relationship to the eucerine lineage (Cardinal and Danforth, 2013; Schaefer and Renner, 2008). Others nested *Ctenoplectra* within Xylocopinae (Hedtke et al., 2013), placed it as sister group to *Centris* (Debevec et al., 2012), or inferred *Ctenoplectra* and *Tetrapedia* as a joint sister group to the Centridini and corbiculates (Martins and Melo, 2016). The phylogenetic position of *Tetrapedia* has been equally uncertain. Two previous studies using morphological and molecular data suggested a closer relationship to the Xylocopinae, most likely as their sister group (Cardinal and Danforth, 2013; Straka and Bogusch, 2007). However, this finding was weakly supported, and also contradicted by other recent studies using morphological (Plant and Paulus, 2016; Praz and Packer, 2014) and molecular data (Martins and Melo, 2016; Martins et al., 2014).

Radchenko (1996) was the first to hypothesize a closer relationship of *Ctenoplectra* and *Tetrapedia* based on nesting strategies, and Alves-Dos-Santos et al. (2002) discussed the same relationship based on nesting behaviors and potential larval synapomorphies: "Although *Ctenoplectra* is quite distinct from *Tetrapedia*, a sister group relationship between the two cannot be totally discarded at this point". Additional larval synapomorphies were discovered by Rozen (2010), but because of their different adult morphology and disjunct allopatric distributions, no decisive conclusion was drawn. Our result provides support for the sister relationship of Ctenoplectrini and Tetrapediini (Fig. 5a). These lineages are widely disjunct: *Ctenoplectra* is primarily restricted to the Palaeotropics and all species of *Tetrapedia* are neotropical, which certainly made hypotheses of a taxonomic and biogeographical connection between them less obvious in the past. Nonetheless, both groups share distinct life history traits, such as specialized oil-collecting behaviors and similar nesting strategies. *Ctenoplectra* and *Tetrapedia* are among the only apid lineages outside the corbiculates that nest in pre-existing wood cavities, such as beetle burrows (Alves-Dos-Santos et al., 2002; Roman'Kova, 1989; Williams, 1928), crevices (Sung et al., 2009), hollow bamboo stems (Camillo, 2005), and abandoned megachilid nests (Alves-Dos-Santos et al., 2002; Rozen, 1978). Intriguingly, both lineages follow a comparable strategy when occupying these pre-existing cavities. According to Radchenko (1996), females collect soil and transport it to the new nest, where they apply floral oils to solidify the 'cement' as cell walls. These shared life history traits, together with the previously described larval synapomorphies and the strong molecular evidence of this study, provide the best justified phylogenetic hypothesis concerning Tetrapediini and Ctenoplectrini to date. Our phylogeny also suggests that the common ancestor of the taxa in these two tribes was an oil-collecting bee. This reduces the instances of known independent origins of oil-collecting behaviors among bees from six (Renner and Schaefer, 2010) to five.

4.3.4. Morphological and life history evidence in support of a close relationship between Tetrapediini, and Xylocopinae sensu stricto

There are a number of life-history traits that corroborate our hypothesis of a close phylogenetic relationship between Xylocopinae (*sensu stricto*) and the tribes Tetrapediini and Ctenoplectrini. Both the small carpenter bees (Ceratinini) and their larger relatives (Xylocopini) produce unusually large eggs, and eggs of *Xylocopa* have been considered the largest of all insects in absolute size (Iwata and Sakagami, 1966). Michener (1973) assumed that such large eggs are an ancestral condition for Xylocopinae. A survey of egg- to body-size ratios of bees revealed only one other species of Apidae that produces eggs of comparable size: the single representative of Tetrapediini, *Tetrapedia maura* (Iwata and Sakagami, 1966). Even if the eggs of *Ctenoplectra* are smaller in relation to their body size (Rozen, 2003; Rozen, 2010), the unusually

large eggs of *Tetrapedia* and the Xylocopinae *s. str.* may constitute a synapomorphy of Xylocopinae in the broader sense used here.

A close relationship of Tetrapediini and the Xylocopinae *s. str.* also sheds new light on our understanding of the co-evolution of bees and phoretic mites. Several lineages of Apidae are host to a diversity of mites, most of which are commensal (Eickwort, 1994). However, some mite-host associations are of mutualistic or parasitic nature (e.g., Cordeiro et al., 2011; Eickwort, 1994). Strong co-evolutionary ties between bees and mites are indicated by bees that possess acarinaria, which are specialized morphological structures that allow the phoretic mites to shelter and disperse with their bee host (Klimov et al., 2007b; OConnor, 1993). Strikingly, such acarinaria are only known from two lineages of Apidae, the Xylocopinae *s. str.* and *Tetrapedia* (Klimov et al., 2007b), which we inferred as much more closely related to each other than previously believed. This placement further simplifies the co-evolutionary pattern of host-associations of chaetodactylid mites. Klimov et al. (2007a) matched the tips of a mite phylogeny to a morphology-based apid phylogeny in which the Tetrapediini are deeply nested within Apinae, and not Xylocopinae. They inferred that recently diverged lineages of apid bees are associated with early diverged lineages of mites and vice versa, contradicting a pattern of co-speciation. Our placement of Tetrapediini as an early branch of Xylocopinae *sensu lato* inverts this pattern, and shows that the early diverging chaetodactylid mite genus *Roubikia* (based on Klimov et al., 2007a) is associated with the early diverging *Tetrapedia*. To the best of our knowledge, no phoretic mites have been reported for Ctenoplectrini.

4.3.5. The phylogeny of the cleptoparasitic Apidae and their sister group

The phylogenetic relationships of the apid cleptoparasites to each other and to their hosts has long been a challenge in reconstructing apid higher-level relationships. The apid cleptoparasites include the subfamily Nomadinae (Michener, 2007; as defined by Roig-Alsina and Michener, 1993) as well as numerous tribes that have historically been placed in the subfamily Apinae (Ericrocidini, Melectini, Rhathymini, Isepeolini, Protepeolini). Morphological studies (Plant and Paulus, 2016; Roig-Alsina and Michener, 1993) have inferred that these cleptoparasitic groups were closely related to their hosts. For example, members of the tribe Ericrocidini attack members of the tribe Centridini (Snelling and Brooks, 1985), members of the tribe Melectini attack members of the tribe Anthophorini, and these host-parasite pairs were thought to form sister groups in the higher-level phylogeny (e.g., Ericrocidini + Centridini, Melectini + Anthophorini). However, more recent molecular studies (e.g., Cardinal and Danforth, 2013; Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018) have consistently recovered a single monophyletic group including all cleptoparasitic Apidae minus *Ctenoplectrina* (which are closely related to *Ctenoplectra*) and the parasitic Euglossini (which are clearly related to their euglossine hosts; see above). This monophyletic lineage of cleptoparasites was initially referred to as the “cleptoclade” by Cardinal et al. (2010). We prefer to recognize this group more formally as the expanded subfamily Nomadinae (see Appendix A). Few unambiguous synapomorphies exist for this group but Rozen et al. (2017) recently described a novel mode of eclosion from the egg that appears to be restricted to Nomadinae, as defined here.

Nomadinae in our revised sense represents an ancient clade of brood parasitic bees (Cardinal et al., 2010). Estimated ages of the nomadine stem group range from ~95 mya (Cardinal et al., 2010) to ~52 mya (Peters et al., 2017). The latter date was estimated using a large transcriptome data set with rather low taxon sampling of Nomadinae, however, both ages are roughly in line with a recently described nomadine fossil from the Paleocene (~60 mya, Dehon et al., 2017). This old age, together with the long branches, reveals extensive evolutionary change in this clade, and could be indicative of a millions of year-old evolutionary arms race between parasites and hosts. We argue that this host-parasite coevolution contributed to the great morphological diversity of the cleptoparasitic Apidae, which consequentially aggravates the phylogenetic reconstruction based on morphological characters (cf., Roig-Alsina and Michener, 1993).

Lastly, our analyses revealed a clade of cleptoparasitic Nomadinae specialized on oil-collecting hosts. This group comprises the Ericrocidini and Rhathymini. Except for the ericrocidine *Hopliphora velutina*, for which the host is unknown, the aforementioned bees are parasites of species of *Centris* and *Epicharis*, respectively (Michener, 2007; Wagenknecht, 1969; Werneck et al., 2012). These results are in line with previous research (Martins et al., 2018) and are indicative of an ancient adaptation of a common cleptoparasitic ancestor towards the oily provisioning mass of an oil-collecting host.

5. Conclusion

We demonstrate that sequence data from ultraconserved elements, transcriptomes and genomes can be effectively combined to provide novel insights into resolving difficult evolutionary relationships. Combining sequence data from different sources enables greater taxon sampling for revisionary taxonomic work and allows the inclusion of old and degraded museum material with target capture of UCEs. Our study provides an example for future use of combined phylogenomic data sets to overcome the needs of fresh tissue material of rarely sampled lineages with uncertain evolutionary relationships.

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Research Data

Research data associated with this study is available from the Mendeley Data platform (doi:10.17632/ynynbc6df6.1). This includes the assemblies of the de-novo sequenced UCEs, the extracted UCE sequence data from the included genomes and transcriptomes, as well as the concatenated nucleotide matrices with their respective partition files. We further provide the inferred phylogenetic trees in newick format. The unprocessed sequence data is deposited in the Sequence Read Archive (accession numbers SAMN10149468-SAMN10149509; BioProject ID PRJNA494160: https://www.ncbi.nlm.nih.gov/bioproject/PRJNA494160).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2018.10.012.

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