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Phylogenetic relationships and the evolution of host preferences in the largest clade of brood parasitic bees (Apidae: Nomadinae)

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ABSTRACT

Brood parasites (also known as cleptoparasites) represent a substantial fraction of global bee diversity. Rather than constructing their own nests, these species instead invade those of host bees to lay their eggs. Larvae then hatch and consume the food provisions intended for the host's offspring. While this life history strategy has evolved numerous times across the phylogeny of bees, the oldest and most speciose parasitic clade is the subfamily Nomadinae (Apidae). However, the phylogenetic relationships among brood parasitic apids both within and outside the Nomadinae have not been fully resolved. Here, we present new findings on the phylogeny of this diverse group of brood parasites based on ultraconserved element (UCE) sequence data and extensive taxon sampling with 114 nomadine species representing all tribes. We suggest a broader definition of the subfamily Nomadinae to describe a clade that includes almost all parasitic members of the family Apidae. The tribe Melectini forms the sister group to all other Nomadinae, while the remainder of the subfamily is composed of two sister clades: a "nomadine line" representing the former Nomadinae *sensu stricto*, and an "ericrocidine line" that unites several mostly Neotropical lineages. We find the tribe Osirini Handlirsch to be polyphyletic, and divide it into three lineages, including the newly described Parepeolini *trib. nov*. In addition to our taxonomic findings, we use our phylogeny to explore the evolution of different modes of parasitism, detecting two independent transitions from closed-cell to open-cell parasitism. Finally, we examine how nomadine host-parasite associations have evolved over time. In support of Emery's rule, which suggests close relationships between hosts and parasites, we confirm that the earliest nomadines were parasites of their close free-living relatives within the family Apidae, but that over time their host range broadened to include more distantly related hosts spanning the diversity of bees. This expanded breadth of host taxa may also be associated with the transition to open-cell parasitism.

1. Introduction

Bees are known to display a wide variety of life history strategies, including diverse plant associations, ways of collecting food and building nests, and varying levels of sociality. The evolution of eusociality in particular has been the focus of much research attention in bees, in part due to the close association between some social species and human agriculture. Brood parasitism is another fascinating life history

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which has received substantially less research attention than eusociality despite being taxonomically more frequent, with about one in eight of the 20,000 species of bee adopting this strategy compared with fewer than one in ten for eusociality (Danforth et al., 2019). Brood parasitic bees have important ecological consequences for their bee hosts, in some cases causing greater brood loss than any other group of nest predators/parasites, including beetles, flies, and other hymenopterans (Minckley and Danforth, 2019). The prevalence of both brood parasitic (also known as "cuckoo") species and eusocial species within bees is higher than almost all other animal lineages, which may partially be explained by the early evolution of food provisioning in bees - something that may reasonably be considered a prerequisite for both strategies (at least insofar as brood parasites must target a host that exhibits such behavior).

The exact number of origins of brood parasitism within bees is unclear. Michener (2007) posited as many as thirty independent transitions from solitary species to brood parasites, although more recent studies reduce this number while still recognizing several convergent transition events (Cardinal et al., 2010; Litman et al., 2013). One thing that is broadly agreed, however, is that there is no evidence for a reversal from brood parasitism back to pollen provisioning. Additionally, it is clear that there is a high degree of variation in species richness across brood parasitic groups, with some being much more species-rich than others. The reasons for this variation in species diversity have been the subject of some previous work (Litman et al., 2013; Policarová et al., 2019) but are still not fully understood. The oldest and most diverse brood parasitic group is the subfamily Nomadinae Latreille (1802) within the family Apidae. As traditionally defined, this group contains approximately 1,200 species – nearly half of all brood parasitic bees – and has a cosmopolitan distribution (Michener, 2007; Danforth et al., 2019).

In addition to the tribes that make up the Nomadinae *sensu stricto* as described by Latreille, various studies over the past decade (Cardinal et al., 2010, 2018; Litman et al., 2013; Policarová et al., 2019; Bossert et al., 2019) have indicated that several other brood parasitic lineages within the Apidae are closely related to this group. The expanded Nomadinae *sensu* Bossert et al. (2019), including these taxa, is itself a monophyletic group of brood parasites containing closer to 1,600 species (Ascher and Pickering, 2020). We will henceforth use this broader definition of Nomadinae and refer to Nomadinae *sensu stricto* as the "nomadine line" within this clade. As a whole, this newly defined Nomadinae contains approximately 60% of all brood parasitic bees and has a crown age of 77.2–109.7 million years (Litman et al., 2013). Though the monophyly of Nomadinae is supported by all other recent studies, the relationships within this group are more contentious. Previous studies into the phylogenetic relationships of the Nomadinae have either relied on relatively little molecular data (Cardinal et al., 2010; Litman et al., 2013; Policarová et al., 2019) or a limited number of taxa (Bossert et al., 2019).

As a group, parasites in the subfamily Nomadinae attack a wide range of hosts across the phylogeny of bees. These include other subfamilies of Apidae, as well as hosts in the families Andrenidae, Halictidae, Colletidae, and Melittidae. As of yet, no members of the Nomadinae are known to parasitize members of family Megachilidae. This may be due to differences in nesting biology; most megachilids nest in above-ground cavities, while almost all hosts attacked by nomadines are ground-nesting (Danforth et al., 2019). Additionally, there are no known associations between nomadines and members of the depauperate Australian family Stenotritidae. Most likely, this is a result of the low abundance and high endemism of this family, as well as the relative paucity of apid brood parasites in Australia, being represented on the continent by just one species of *Nomada* and about ten species of *Thyreus* (Houston, 2018).

At the level of individual genera and species, it is difficult to ascertain to what extent nomadines have specialized on their hosts. Most nomadine genera are consistent in parasitizing a set of closely related hosts or a single host genus, but reliable host association data are rare or absent in the literature for many species. In some cases, such as a few of the better-studied *Nomada*, a single species has been recorded attacking hosts from multiple bee families, though their most common host by far appears to be the genus *Andrena* (Snelling, 1986; Alexander, 1991). Within-species size variation has in some cases been interpreted as evidence of multiple hosts, though this may also represent cryptic diversity or simply environmental effects (Michener, 2007). It is, however, clear that apid brood parasites like the Nomadinae are more specialized than some other cuckoo bees, such as the generalist genus *Sphecodes* in the family Halictidae (Habermannová et al., 2013).

While all members of the Nomadinae are obligate brood parasites, they differ in the details of how they exploit their hosts. Some species wait for the host to finish building, provisioning, and sealing up a nest before invading. Females of these "closed-cell" parasites will then break into the brood cell, lay their own eggs, and reseal it. In contrast, others are "open-cell" parasites. Females of these species invade a nest while it is still under construction or being provisioned and then lay their eggs in brood chambers, but do not seal up the nest afterwards. Exceptions to this dichotomy do exist, such as the genus *Epeoloides*, which has been observed invading unfinished cells but closing them off afterwards, combining aspects of both strategies (Straka and Bogusch, 2007). The discovery of up to four *Epeoloides* eggs/larvae of different ages within a single cell indicates that this strategy also allows females to attack nests that have already been parasitized by other individuals. Different modes of parasitism have resulted in corresponding differences in behavior and morphology in the Nomadinae. For example, open-cell parasites lay smaller eggs than non-parasitic species of similar body size (Iwata and Sakagami, 1966; Rozen, 2003). These eggs often have conspicuous tubercules, flanges, or other modifications, and are typically hidden against the brood cell wall, presumably to avoid detection and removal by hosts (Rozen and Özbek, 2003). Closed-cell parasites, meanwhile, have average-sized eggs, likely because hosts will not return to investigate a finished nest. In some brood parasitic bees, adult females will kill or remove host eggs/larvae. However, in all members of the Nomadinae regardless of the mode of parasitism, host eggs or larvae are killed directly by the parasitic larva instead. These so-called "hospicidal" larvae typically have enormous mandibles during their first instar which are used for this purpose but lost after molting (Michener, 2007).

Over a century ago, Carlo Emery suggested that in socially parasitic or brood parasitic insect species, hosts are typically closely related to the parasites themselves (Emery, 1909). The rationale behind this idea stems largely from the possibility that these types of parasites may at first evolve intraspecifically, as suggested by some models (Zink, 2000) and observed cases in both parasitic birds and ants (Petrie and Møller, 1991; Rabeling et al., 2014). Additionally, the possibility of shared chemical signals for mimicry, as is sometimes seen with parasitic ants (Lenoir et al., 2001), as well as the higher likelihood of sharing other aspects of life history (e.g. diet, habitat, seasonality) represent plausible factors which may create an expectation of close relationships between parasites and hosts. Within some literature, "Emery's rule", as it has come to be known, is often divided into a "strict" form (requiring that a parasitic lineage be sister to its host) and a "loose" form, which merely suggests that parasites and hosts are generally closely related (Ward, 1989; Huang and Dornhaus, 2008). In either sense, Emery's rule suggests that the earliest brood parasites within a group were likely associated with their close relatives, which raises an interesting question: can the signal of these ancestral host-parasite relationships still be detected in a group as diverse as the Nomadinae, which transitioned to brood parasitism tens of millions of years ago?

In this study, we present the most comprehensive exploration of the nomadine phylogeny to date, including an unprecedented level of taxon sampling and a wealth of molecular data provided by ultraconserved element (UCE) sequencing. The resulting phylogenetic tree is subsequently used as a framework to analyze traits of interest, including the evolution of host preferences (providing an opportunity to examine the applicability of Emery's rule) and transitions between open- and closed-

cell modes of parasitism.

2. Materials and methods

2.1. Sample collection

A total of 114 samples of brood parasites from within the family Apidae were obtained, including several species that have not been included in previous phylogenetic studies. Collectively, these represent 55 of the 61 total genera that comprise the Nomadinae, and original collection localities ranged across all six continents where this subfamily can be found. An additional five outgroup taxa representing other major groups of Apidae (*Apis mellifera*, *Bombus nevadensis*, *Centris hoffmanseggiae*, *Eufriesea surinamensis*, and *Habropoda laboriosa*) were also included, bringing the total number of samples used in phylogenetic analyses up to 119.

Samples were assembled from a combination of museum and laboratory collections. DNA was extracted from pinned or ethanol-preserved voucher specimens (n = 40), or in some cases was already available as a result of previously conducted extractions (n = 68). Additionally, data for some samples (including outgroup taxa) were obtained in the form of already processed sequence data from published or in-preparation datasets (Bossert et al., 2019 (n = 5), Grab et al., 2019 (n = 4), Freitas et al., 2021 (n = 2)). Collection methods varied by specimen and are unknown in some cases, but most were caught by hand-netting. See Appendix A for full details on voucher specimen sources, collection dates, and localities.

2.2. DNA extraction

For samples in which DNA extraction had not already been carried out (n = 40), a phenol–chloroform based protocol was used (Danforth et al., 2011). First, tissue samples were placed into a 2x CTAB solution and ground with a pestle for 30 s. When possible, a single leg was taken from pinned or ethanol-preserved specimens for DNA extraction, though in some cases multiple legs were used. For a few exceptionally small individuals, the entire body was destructively sampled. After grinding, proteinase K was added, and samples were incubated at 55 °C overnight.

DNA extraction continued the next day with the addition of chloroform:isoamyl alcohol (24:1), followed by centrifugation and aspiration of the supernatant. This was followed with a phenol:chloroform:isoamyl alcohol (25:24:1) treatment, and then a final chloroform:isoamyl alcohol treatment to wash out any remaining phenol. DNA pellets were precipitated in 100% ethanol with sodium acetate, then washed in 80% ethanol again before final resuspension in Tris-EDTA buffer.

For the samples obtained in the form of previously extracted DNA, extraction methods varied, but most were obtained by either the same phenol–chloroform extraction as detailed above, or with the use of either a DNeasy Blood and Tissue kit (Qiagen) or a Quick-DNA Miniprep Plus kit (Zymo Research).

All samples were subsequently measured on a Nanodrop 2000 and Qubit 3 or 4 Fluorometer, both Thermo Fisher Scientific, to estimate DNA quantity and quality. A subset of samples was further analyzed on an Agilent 2200 TapeStation machine with D1000 HS tapes (Agilent Technologies) to estimate the size distribution of DNA samples based on age.

2.3. UCE library preparation and enrichment

We used a targeted UCE approach to generate sequence data following previous literature (Faircloth et al., 2012, 2015). The protocols used followed those outlined in Branstetter et al. (2017) and were carried out at the USDA-ARS Pollinating Insects Research Unit in Logan, Utah, USA.

We targeted a set of 2,527 UCE loci and additional "legacy" loci using baits based on the Hymenoptera v2 probe set outlined by Branstetter et al. (2017), with ant-bee specific probes as described in Grab et al. (2019). Probes were synthesized by Arbor Biosciences, previously MYcroarray.

First, extracted DNA samples were sheared to reduce the average fragment size to a target of ~400–600 bp. Older or more degraded samples were not sheared, while other samples were sheared in a Q800R3 sonicator (Qsonica) for 30, 60, or 90 s depending on sample quality and predicted size distribution. Mean final DNA input mass for all samples was 102 ng but ranged from less than 1 ng – 1,630 ng.

Library preparation involved the use of a KAPA HyperPrep kit (Roche Sequencing Systems) for enzymatic steps including repair of fragment ends and addition of A-tails, and Illumina TruSeq-style adapters (Glenn et al., 2019) for dual-indexing with redundantly unique sequences. DNA-binding magnetic beads were made following an in-house protocol based on Rohland and Reich (2012) and were used to clean and concentrate samples at various steps in the process. After the final bead cleaning, samples were measured for DNA concentration with a Qubit 3 fluorometer and pooled in groups of 8–10 at equimolar concentrations.

These pooled samples were enriched following a protocol from Arbor Biosciences (v4) for the first day of UCE enrichment, and a standard UCE protocol for the second day (enrichment protocol v1.5 available at ultraconserved.org, based on Blumenstiel et al. (2010)). Post-enrichment samples were measured on a TapeStation machine for fragment size distributions and size selected with a Blue Pippin machine (Sage Science) for a range of 200–700 base pairs, if necessary. Finally, pooled libraries were quantified with an Applied Biosystems qPCR machine and KAPA reagents, pooled together, and sent off for sequencing.

2.4. Sequencing

After library preparation and enrichment, a final total of 97 samples were sent to Novogene inc. for multiplexed sequencing on a single lane of an Illumina HiSeq X instrument (paired-end 150 bp). A total of approximately 360 Gb of sequencing data was received. Of these, 3 samples were ultimately not used due to the presence of redundant taxa. The remaining 94 UCE assemblies were combined with 20 previously generated datasets as well as UCE sequences for 5 outgroup taxa from Bossert et al. (2019), as mentioned above.

2.5. In silico processing

Sequence data were demultiplexed to sort reads to their respective samples using BBMap (accessed from https://sourceforge.net/projects/bbmap/). Most processing was done through the PHYLUCE pipeline (Faircloth, 2016). First, reads were trimmed and adapters were removed using illumiprocessor (Faircloth, 2013), which is a wrapper software based on Trimmomatic (Bolger et al., 2014). Removal of adapters was assessed using FastQC (Andrews, 2010) for quality control. Reads for each sample were then assembled into contigs using SPAdes (Bankevich et al., 2012). The software LastZ (Harris, 2007) was then used to identify contigs containing UCE sequences which matched the probes from the Hymenoptera v2 "ant-bee" probe set, with "min-identity" and "min-coverage" parameters set to 80.

These contigs were then aligned using MAFFT v7.31 (Katoh and Standley, 2013), followed by internal trimming using Gblocks (Talavera and Castresana, 2007) as recommended by Faircloth (2019), in both cases using default parameters. Data matrices were then created to test different levels of taxon completeness. Separate alignments were made which included all UCE loci present in greater than or equal to 75%, 85%, and 95% of samples, respectively.

2.6. Phylogenetic trees

Concatenated data matrices for the three different levels of taxon completeness were used to generate unpartitioned phylogenies in IQ-

TREE v1.6.9 (Nguyen et al., 2015). In each case, ModelFinder (Kalyaanamoorthy et al., 2017) was first used to select an appropriate model, and then a phylogeny was created with 1,000 replicates for approximate maximum likelihood ratio tests (Guindon et al., 2010) and ultra-fast bootstraps (Hoang et al., 2018). Further analyses were conducted only on the 95% taxon-completeness matrix, which was selected due to the minimal amount of missing data. First, gene trees were generated for all 1,247 UCE loci in this matrix using IQ-TREE v2.1.2 (Minh et al., 2020a). These were subsequently used to calculate gene and site concordance factors in IQ-TREE (Minh et al., 2020b), and also to create a coalescent species tree with ASTRAL v5.7.4 (Zhang et al., 2018) on default settings (including calculation of local posterior probabilities). Finally, a partitioning analysis of loci in the 95% taxon-completeness matrix was conducted using the sliding-window site characteristics method (SWSC; Tagliacollo and Lanfear, 2018). The resulting partitioning scheme by entropy (SWSC-EN), along with a separate by-locus partitioning scheme, were both fed into IQ-TREE v2.1.2 using the "testmerge" option (Chernomor et al., 2016) and a GTR + G model to generate partitioned trees. All phylogenies were then edited for clarity in FigTree v1.4.4 (Rambaut, 2014).

2.7. Trait evolution analysis

To reconstruct the ancestral hosts parasitized by Nomadinae, each brood parasitic species' host preferences were identified at the family level through a literature search (see Appendix B for character state data). Additionally, mode of parasitism was analyzed as a character, distinguishing open- and closed-cell parasites. Ancestral state reconstructions were conducted on the SWSC-EN partitioned 95% taxon-completeness matrix phylogeny in Mesquite v3.61 (Maddison and Maddison, 2019). The "trace characters over trees" option was used after inputting relevant phylogenies and character data, using a maximum likelihood reconstruction method with the Markov k-state 1 parameter model ("Mk1"). Since Mesquite is not able to work with polymorphic states at tips, a few species that have been recorded attacking multiple host families were coded according to the most commonly recorded host (if clear), or as "unknown" otherwise.

2.8. Nomenclature

Names of the tribes were adopted from Michener (2007), Engel (2005), a subsequent revision of Neolarrini (Bossert et al., 2020), and the tribe Coelioxoidini (Martins et al., 2018; Bossert et al., 2019; Engel et al., 2020). For the new names, including lineages called "lines", we applied family group name rules (ICZN, 1999). The "nomadine line" used herein is identical to the *sensu stricto* definition of Nomadinae Latreille 1802, and the "ericrocidine line" corresponds to the group of the same name first used by Litman et al. (2013).

3. Results

3.1. Topologies of generated phylogenetic trees

We created three data matrices consisting of loci that were recovered from 75%, 85%, and 95% of sampled taxa. These resulted in final datasets of 2,048, 1,833, and 1,247 UCE loci respectively. The latter of these, with a total alignment length of 366,640 bp and the lowest proportion of missing data at approximately 4.96%, was then used to generate two partitioning schemes: one by locus, and one using the SWSC-EN method (Tagliacollo and Lanfear, 2018). Within-locus partitioning has been shown to improve phylogenetic inference in similar datasets (e.g. Freitas et al., 2021), and so for this reason we used the SWSC-EN partitioned phylogeny for the ancestral state reconstructions discussed below, but the overall conclusions of these analyses are consistent with all generated topologies. This final phylogeny consisted of 114 nomadine species as tips, as well as five outgroup species (Fig. 1). A majority of nodes in the tree were recovered with 100/100 support values according to SH-aLRT (Guindon et al., 2010) and ultra-fast bootstrap (Hoang et al., 2018) metrics respectively, though six nodes had less than 100/100 support.

The unpartitioned phylogenies (Supp. Figs. 1–3), locus-partitioned phylogeny (Supp. Fig. 4), and ASTRAL coalescent phylogeny (Supp. Fig. 5) were all topologically similar to the concatenated SWSC-EN partitioned tree, differing at only a few nodes. While the tribe Coelioxoidini was recovered as the sister group to the clade consisting of Osirini, Epeoloidini, Protepeolini, and Isepeolini in the SWSC-EN partitioned phylogeny, the unpartitioned 75% and 85% taxon-completeness matrix trees, as well as the ASTRAL coalescent phylogeny, recovered it instead as the sister group to all other members of the ericrocidine line. The tribe Epeoloidini was typically recovered as the sister to Protepeolini, but instead appeared as the sister to Protepeolini + Isepeolini in the unpartitioned 95% matrix and ASTRAL trees. The relationship among *Townsendiella*, *Rhopalolemma*, and the clade consisting of *Biastes* and *Schwarzia* also varied. While both partitioned phylogenies recovered *Townsendiella* and *Rhopalolemma* as successive sister groups to this latter clade, the unpartitioned phylogenies reversed their positions, and the ASTRAL phylogeny recovered a sister relationship between *Townsendiella* and *Rhopalolemma* instead. Within the tribe Ammobatini, the SWSC-EN partitioned and all unpartitioned phylogenies recovered a weakly-supported paraphyletic *Ammobates* with respect to *Oreopasites*, but this was not recovered in either the locus-partitioned or ASTRAL phylogenies. Finally, the ASTRAL phylogeny uniquely recovered *Epeolus scutellaris* as the sister group to *E. caffer*, *E. tarsalis*, and *E. variegatus*, while all other analyses instead recovered a sister relationship between *E. scutellaris* and *E. compactus*. Unsurprisingly, these nodes had lower gene and site concordance factors than most other parts of the phylogeny (Supp. Fig. 6).

3.1.1. Monophyletic Nomadinae includes almost all brood parasites within Apidae

As suggested by other recent molecular studies, the subfamily Nomadinae in the broad sense forms a monophyletic clade consisting of almost all the brood parasitic species within Apidae (Fig. 1). The tribes Melectini, Isepeolini, Protepeolini, Ericrocidini, Osirini, Rhathymini, and Coelioxoidini are descendants of a single parasitic common ancestor shared with the Nomadinae *sensu stricto* (henceforth "nomadine line"). Though this study does not have as broad a selection of outgroup taxa as some previous analyses (e.g. Cardinal et al., 2010; Bossert et al., 2019; Policarová et al., 2019), our recovered topology is consistent with suggestions that the subfamily Anthophorinae *sensu* Bossert et al. (2019) is the sister group to Nomadinae.

3.1.2. Melectini is the sister group to all other Nomadinae

All phylogenies generated as part of this study place the tribe Melectini as the sister group to all other members of Nomadinae (Fig. 1). This result is consistent with one previous study (Litman et al., 2013) but differs from others which found Melectini to be the sister group to the nomadine line (Cardinal et al., 2010; Policarová et al., 2019) or to Caenoprosopidini (Cardinal et al., 2018).

3.1.3. Other apid parasites form a predominantly Neotropical "ericrocidine line"

Besides Melectini, the other parasitic tribes not included within the nomadine line form a monophyletic group (Fig. 1). This "ericrocidine line" (including the tribes Osirini, Rhathymini, Ericrocidini, Coelioxoidini, Protepeolini, and Isepeolini, as well as the revived Epeoloidini and Parepeolini *trib. nov.*) is also suggested by Cardinal et al. (2010), Litman et al. (2013), and Policarová et al. (2019). This clade is almost entirely Neotropical, with the exceptions of *Ericrocis*, which extends north to the southern Nearctic, and *Epeoloides*, which is found in the Nearctic and Palearctic. The tribes in this ericrocidine line mainly consist of parasites on oil-collecting bees and may represent a radiation

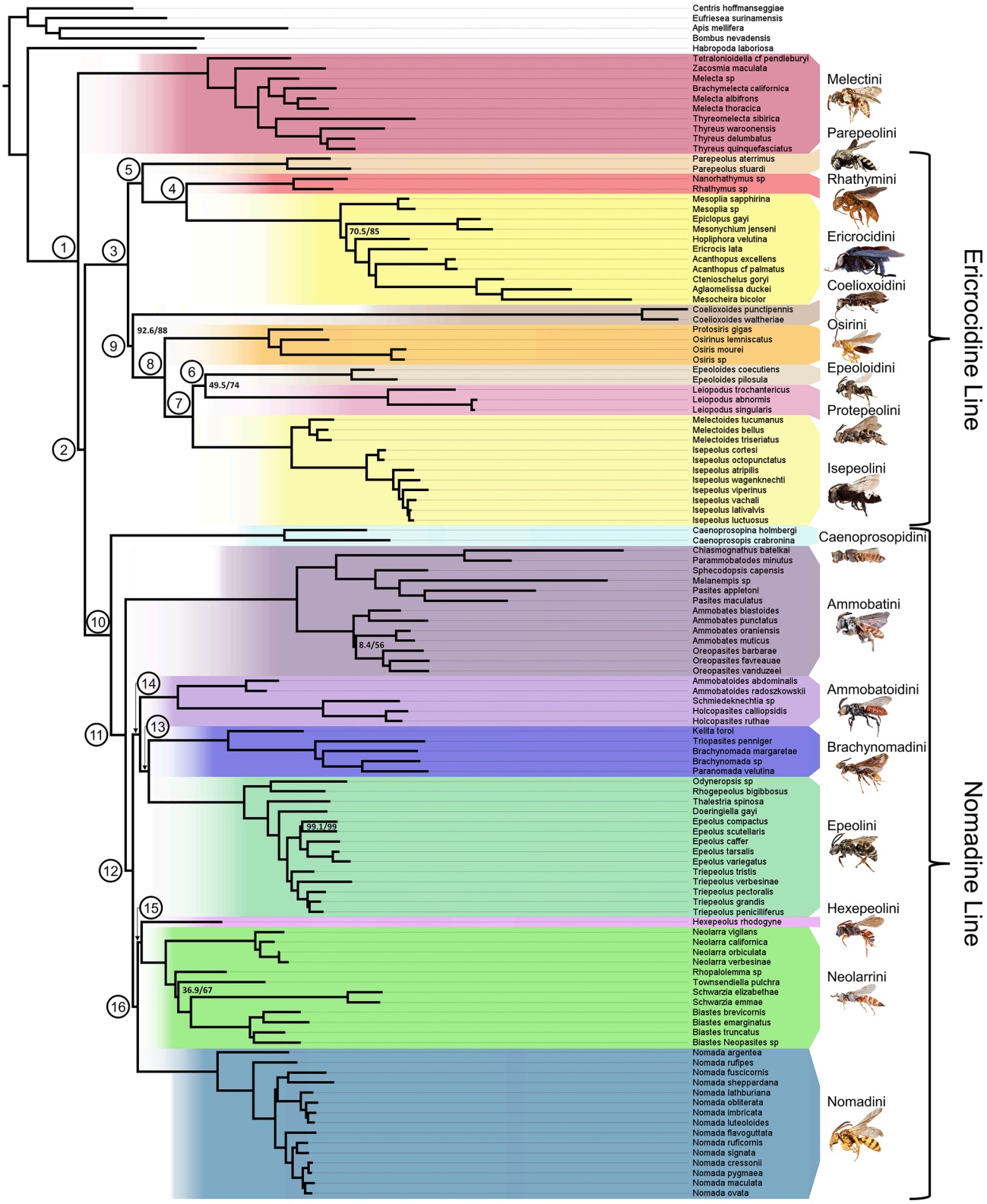

Fig. 1. Phylogeny of Nomadinae based on concatenated, SWSC-EN partitioned phylogeny (with partitions merged) generated with IQ-TREE2 using the 95% taxon-completeness matrix of 1,247 UCE loci. SH-aLRT and ultra-fast bootstrap values are indicated for some nodes; all unlabeled nodes have 100/100 support. All tribes are highlighted for clarity; members of the nomadine line are highlighted in cool colors, while the ericrocidine line and tribe Melectini are shown in warm colors. Numbered circles at some nodes correspond to clades listed in Table 1. From top to bottom, images depict *Zacosmia maculata* ♀, *Parepeolus stuardi* ♀, *Rhathymus* sp. ♀, *Acanthopus* sp. ♂, *Coelioxoides waltheriae* ♀, *Osiris* sp. ♀, *Epeoloides pilosula* ♀, *Leiopodus singularis* ♀, *Isepeolus wagenknechti* ♀, *Caenoprosopina holmbergi* ♀, *Oreopasites favreauae* ♀, *Holcopasites calliopsidis* ♀, *Paranomada velutina* ♀, *Triepeolus pectoralis* ♀, *Hexepeolus rhodogyne* ♀, *Neolarra verbesinae* ♀, and *Nomada luteoloides* ♀. Images courtesy of Laurence Packer and USGS Bee Inventory and Monitoring Lab.

associated with these hosts as discussed by Policarová et al. (2019).

3.1.4. Internal relationships among nomadine tribes

To the extent that individual tribes within the subfamily Nomadinae have been studied, our phylogeny generally supports previously suggested topologies. Within the tribe Melectini, the finding of *Brachymelecta* (*sensu* Onuferko et al., 2021) nested within the genus *Melecta* is somewhat unexpected, though there have been some preliminary suggestions that the latter genus may be paraphyletic (M. Orr, personal communication).

Our phylogeny also identified the tribe Osirini as polyphyletic, with the genera *Epeoloides* and *Parepeolus* individually appearing distinct from the type genus *Osiris*, which clusters with *Osirinus* and *Protosiris*. For this reason, we propose the elevation of the genus *Epeoloides* to the tribe Epeoloidini Linsley and Michener (1939), and the elevation of *Parepeolus* to the new tribe Parepeolini (see below).

Within the nomadine line, the tribe Epeolini shows similar genus-level relationships to those recovered by Onuferko et al. (2019), with the additional recovery of a sister relationship between the genera *Odyneropsis* and *Rhogepeolus*. The monophyly of the tribe Neolarrini *sensu* Bossert et al. (2020) is also recovered in this study, subsuming the former tribes Biastini and Townsendiellini. Our topology for the tribe Ericrocidini differs slightly from that of Martins et al. (2018), which recovered *Ericrocis* as the sister genus to all other ericrocidines, instead of *Mesoplia* as in the present study.

Finally, two genera (*Brachynomada* and *Ammobates*) are recovered as paraphyletic in our phylogeny due to nested members of the genera *Paranomada* and *Oreopasites* respectively, though in the latter case the node in question is poorly supported, and *Ammobates* was recovered as monophyletic in some analyses.

3.2. Nomadinae followed Emery's rule during initial origins of brood parasitism

The question of how host preferences of the Nomadinae have evolved over time has not been examined in detail previously, and the application of ancestral state reconstruction techniques to the phylogeny generated here provides some interesting new insights in this respect. The rule suggested by Emery (1909) holds that certain types of parasitic insects should be closely related (or even sister clades) to their host taxa. In the case of the Nomadinae, at least the "loose" form of this rule does appear to hold true when considering the context in which parasitism first evolved. The reconstructed ancestral hosts for Nomadinae are other members of family Apidae, with a calculated proportional likelihood of 86.2% (Fig. 2), and it was not until long after the initial transition to parasitism that nomadines began branching out to more distantly related hosts.

Similarly to the Nomadinae as a whole, both the tribe Melectini and the ericrocidine line are recovered as ancestrally attacking other members of Apidae. The former does not contain any transitions away from this state, but within the ericrocidine line, there are host switching events in the genus *Epeoloides* to attacking Melittidae, and in the tribe Isepeolini, which predominantly attacks members of Colletidae. The nomadine line as a whole experienced a transition in host preference at its origin, with members of the family Andrenidae recovered as its ancestral hosts (prop. likelihood 83.3%). Within the nomadine line, the initial host preferences of some clades are unclear; both the tribes Ammobatini and Epeolini are somewhat equivocal at their ancestral nodes and experience multiple transition events internally (variously to hosts of the families Halictidae, Colletidae, Andrenidae, or Apidae, with some reversals likely). There is also a clear transition from parasitism of Andrenidae to Halictidae within the tribe Neolarrini (*sensu* Bossert et al., 2020).

3.3. Closed-cell parasitism ancestral, with two transitions to open-cell parasitism

We recovered closed-cell parasitism as the most likely ancestral mode which was adopted during the initial transition to brood parasitism (proportional likelihood 99.4%; Fig. 3). This was subsequently followed by two transitions to open-cell parasitism: one in the subsection of the nomadine line that forms the sister group to the tribe Caenoprosopidini (prop. likelihood 98.6%), and another ancestral to the tribes Isepeolini, Protepeolini, and Epeoloidini (prop. likelihood 90.7%). The somewhat ambiguous mode of parasitism exhibited by *Epeoloides* may represent a partial reversion to a strategy employing some characteristics of closed-cell parasitism, however the uncertainty of this node complicates the reconstruction of this trait. Some of our other phylogenetic analyses instead recovered Epeoloidini as the sister group to both Isepeolini and Protepeolini, in which case the strategy observed in *Epeoloides* may be a transitional state between closed-cell parasitism and the "fully" open-cell mode of parasitism suggested for the latter two tribes.

3.4. Nomenclature of Nomadinae

In light of the polyphyletic status of the tribe Osirini Handlirsch, we divide the five genera represented therein into three tribes. The tribe Osirini is reduced to the three genera *Osiris*, *Osirinus*, and *Protosiris*. Additionally, we reinstate the tribe Epeoloidini Linsley and Michener (1939) containing the genus *Epeoloides*, and describe the following new tribe:

Parepeolini, Straka and Sless, *trib. nov.*

Type genus: *Parepeolus* Ducke (1912))

Diagnosis: This tribe includes epeoliform cuckoo bees with three submarginal cells from the former Osirini tribe. As in Osirini and Epeoloidini, they have a ventral neck sclerite, a carina along the inner and basal margins of the forecoxa, a very large stigma (several times larger than prestigma), and a marginal cell distinctly separated from the wing margin. They also share mouthparts typical for most Apidae, but absent in the nomadine line, including a ridge on the outer surface of the stipes and a more or less anteroventrally emarginated stipes with comb. The posterior margin of the metasternum is translucent and impunctate. The tribe is differentiated from other Nomadinae by the additional combination of the following characters. Jugal lobe of the hind wing is rounded. Parocular carina is reduced to completely missing. Labrum with paired tubercules. Sternum 6 of female with longitudinal ridge medially. Gonostyli of male genitalia large and complex in structure, ventral gonostylus bifid, and dorsal gonostylus large and flattened.

4. Discussion

4.1. Comparison to other phylogenies

Several previous phylogenetic studies have included at least some nomadine representatives, though most of these used datasets consisting of a small number of highly conserved protein-coding or ribosomal genes. Specifically, Cardinal et al. (2010, 2018), and Policarová et al. (2019) used wingless (wg), RNA polymerase II (pol II), long-wavelength rhodopsin (LWR), sodium–potassium ATPase (NaK), elongation factor 1 alpha (EF-1α), and both 18S and 28S rRNAs, resulting in a total alignment length of approximately 7,500 bp. Litman et al. (2013) also used NaK, LWR, EF-1α, and 28S rRNA, but added carbamoyl phosphate synthetase 2 (CAD) in place of the other genes, giving an alignment length of approximately 6,000 bp. Meanwhile, Bossert et al. (2019) used two UCE datasets with 129 and 561 loci respectively, resulting in alignments of about 79,293 and 302,379 bp. In contrast, the 95% taxon-completeness UCE dataset in the present study consists of 1,247 loci and a final alignment length of 366,640 bp. The difference in average UCE locus length between Bossert et al.'s study and ours may be due in part to

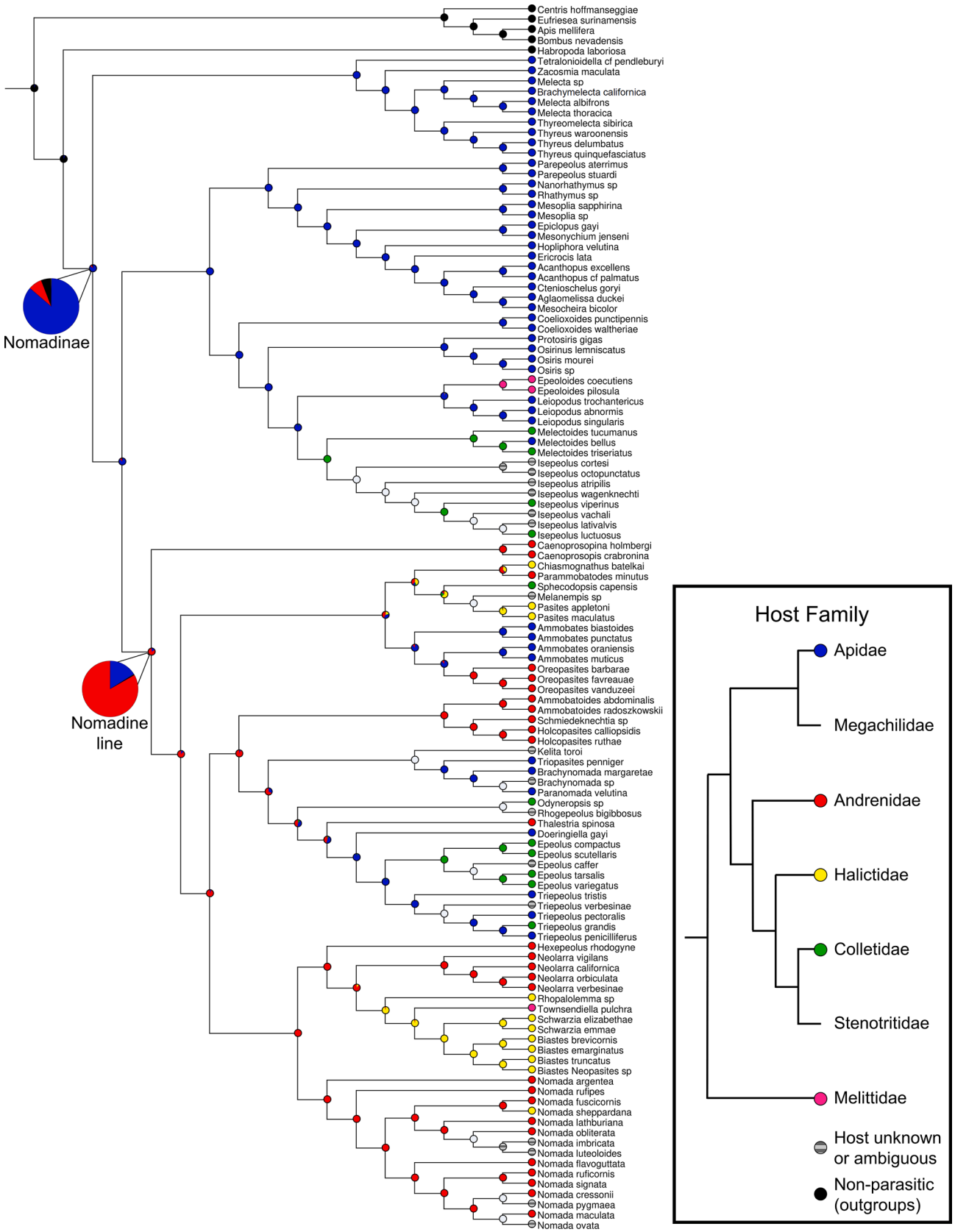

Fig. 2. Cladogram showing ancestral state reconstruction of nomadine host preferences based on the concatenated, SWSC-EN partitioned phylogeny. Tips are colored according to known host families. Blue = Apidae, green = Colletidae, red = Andrenidae, yellow = Halictidae, pink = Melittidae, black = non-parasitic (outgroups), gray = unknown/polymorphic. Ancestral states at each node are shown by pie charts of proportional likelihood value for each state. Two of these, at the nodes ancestral to all Nomadinae and the nomadine line respectively, are enlarged for clarity. Inset: phylogeny of host bee families, following Danforth et al. (2013). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

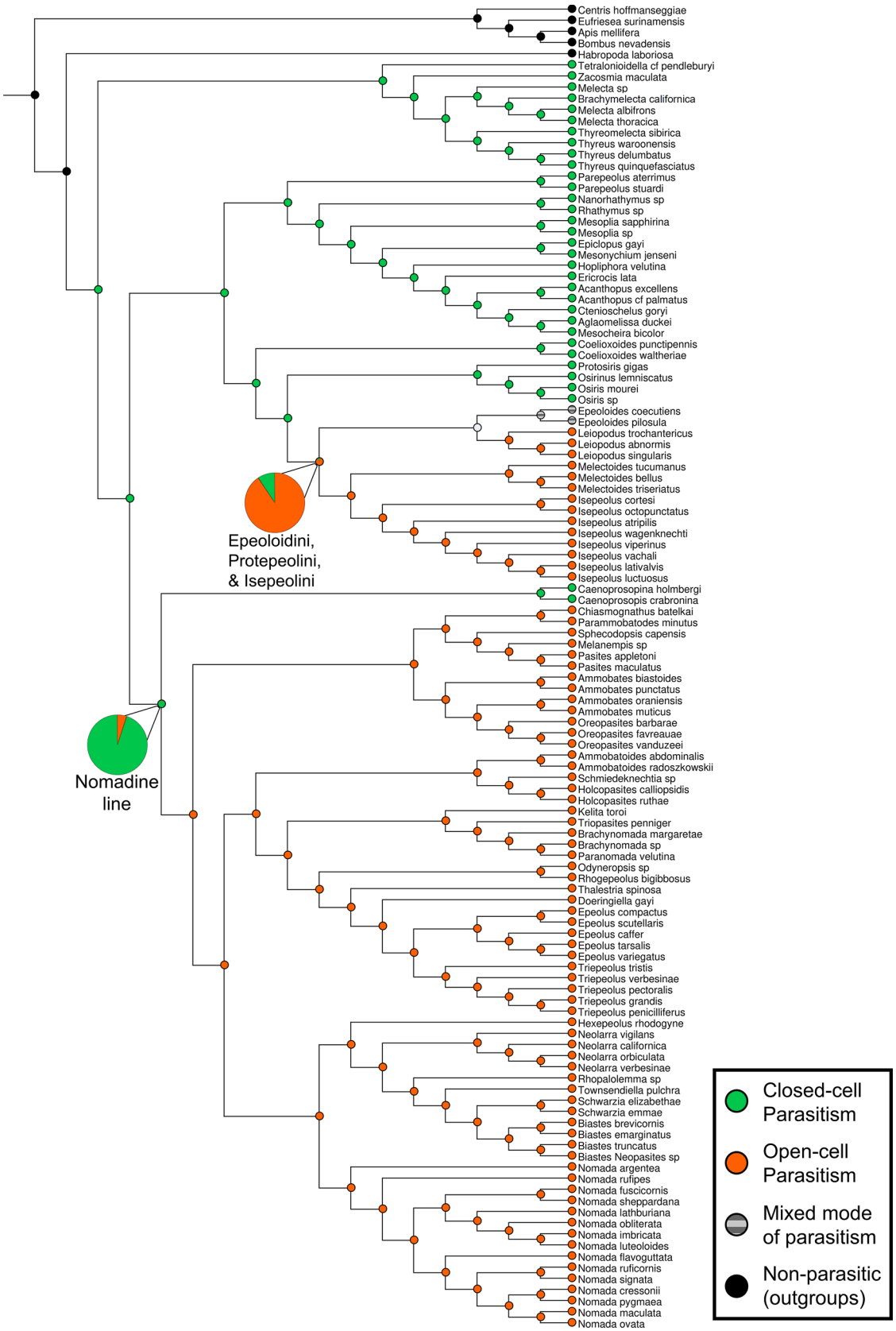

Fig. 3. Cladogram showing ancestral state reconstruction of mode of parasitism based on the concatenated, SWSC-EN partitioned phylogeny. Tips are colored according to known or suspected mode of parasitism. Light green = closed-cell parasitism, orange = open-cell parasitism, white = non-parasitic (outgroups), gray = ambiguous mode of parasitism. Ancestral states at each node are shown by pie charts of likelihood value for each state. Two of these, at the nodes ancestral to the nomadine line and to the clade consisting of Epeoloidini, Protepeolini, and Isepeolini, are enlarged for clarity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the extraction of UCEs from genomes with large (up to 3,200 bp) flanking regions and more relaxed parameters during trimming with Gblocks by Bossert et al., or simply a consequence of older average specimen age in the present study. In terms of taxon sampling, these previous studies included 63 (Cardinal et al., 2010), 32 (Litman et al., 2013), 44 (Cardinal et al., 2018), 35 (Policarová et al., 2019), and 12 (Bossert et al., 2019) representative species from the broader Nomadinae respectively, compared to the 114 species included in the present study. We believe that our substantially greater taxon sampling provides more reliability to our data and gives us confidence with respect to instances of variance in our taxonomy in relation to previous studies (see below).

Overall, the topology recovered in the present study has many similarities with these earlier ones, though it is not identical to any of them (Table 1). For example, Cardinal et al. (2010) and Policarová et al. (2019) recovered the tribe Melectini as the sister group to the nomadine line, rather than the sister to all other Nomadinae (Table 1, row 2). The tribe Protepeolini is placed as the sister group to Epeoloidini in our main analysis (Table 1, row 6), in agreement with Cardinal et al. (2010, 2018) and Litman et al. (2013), but contrary to its position as the sister to Isepeolini in Policarová et al. (2019). However, some of our other analyses did recover a sister relationship between Protepeolini and Isepeolini to the exclusion of Epeoloidini (Supp. Figs. 1, 5), making the placement of this group somewhat problematic. Another part of the former Osirini, the tribe Parepeolini newly described herein, is uniquely recovered in our analysis as sister to Rhathymini + Ericrocidini, whereas previous studies (Cardinal et al., 2010, 2018; Litman et al., 2013) have often recovered it as the sister group to Coelioxoidini (Table 1, row 5). This latter group is itself inconsistently placed across past studies, and also appears to be of uncertain placement in our analyses, appearing as by far the longest branch in our phylogeny and changing position with different methodologies (Supp. Figs. 2, 3, and 5).

We recover the enigmatic tribe Caenoprosopidini (Table 1, row 11) as the sister group to the rest of the nomadine line, similarly to Policarová et al. (2019), while other studies have instead considered it the sister to Ammobatini (Cardinal et al., 2010) or Melectini (Cardinal et al., 2018). Additionally, the present study is the only one so far to recover the tribe Ammobatoidini as the sister group to Epeolini + Brachynomadini, while other studies have more commonly recovered Ammobatini as the sister to the Neolarrini (*sensu* Bossert et al., 2020) + Hexepeolini group (Table 1, row 14). This Neolarrini + Hexepeolini clade also includes some of the lowest gene and site concordance factors across the phylogeny (Supp. Fig. 6), which may be a result of the short internode lengths separating these species, but the broader topology of this tree is generally supported by these metrics.

4.2. Taxonomic implications

The findings of this study have several important implications for the classification of the subfamily Nomadinae and its component subclades. As has been suggested by previous literature, there is a clear signal of a large, entirely parasitic clade consisting of both the Nomadinae *sensu stricto* (our nomadine line) and several other tribes of apid brood parasites. Previously referred to as the "large cleptoparasitic clade" by Cardinal et al. (2010), this group contains all brood parasitic members of the family Apidae with the exceptions of the orchid bee genera *Aglae* and *Exaerete* (Euglossini) and the genus *Ctenoplectrina* (Ctenoplectrini). Due to the inclusion of several lineages traditionally classified in the subfamily Apinae, viz. the tribes Melectini, Rhathymini, Ericrocidini, Coelioxoidini, Osirini, Protepeolini, and Isepeolini as well as the resurrected Epeoloidini and newly named Parepeolini, this large parasitic clade thus renders the Apinae paraphyletic. For this reason, we support the recommendation by Bossert et al. (2019) to revise the definition of the subfamily Nomadinae such that it includes all of the above-mentioned tribes in addition to those that currently form the nomadine line (Nomadinae *s.s.*). Correspondingly, Apinae should be redefined to exclude these taxa and should therefore only include the tribes Centridini, Euglossini, Apini, Bombini, and Meliponini, again following Bossert et al. (2019). We also find support for the reclassification of Neolarrini proposed by Bossert et al. (2020) to include Biastini and Townsendiellini, though that study shares some data with the present one and thus these findings are not fully independent.

Considering the broader internal classification of the Nomadinae, we recover three major lineages which make up the group. The tribe Melectini on its own is one descendant of the earliest branching event within Nomadinae. The other branch then further splits into the "ericrocidine" and "nomadine" lines. The ericrocidine line includes the tribes Rhathymini, Ericrocidini, Isepeolini, Protepeolini, Coelioxoidini,

Table 1
Comparison of clades recovered in this and previous phylogenetic studies. Presence of a monophyletic group composed of the listed clades is indicated with a "Y", absence with an "N". Cases where a study had insufficient taxon sampling to identify a clade as present or absent are indicated with "n/a". Clades labelled with an asterisk were recovered in our primary SWSC-EN partitioned phylogeny but were absent from at least one other analysis in the present study.

	Group recovered as monophyletic?	This study	Cardinal et al. (2010)	Litman et al. (2013)	Cardinal et al. (2018)	Policarová et al. (2019)	Bossert et al. (2019)
	Total # nomadine species	114	63	32	44	35	12
	Dataset type	UCEs	7 genes	5 genes	7 genes	7 genes/ morphology	UCEs/ transcriptomes
1	Single large parasitic clade [2–16]	Y	Y	Y	Y	Y	Y
2	All Nomadinae excluding Melectini [3–16]	Y	N	Y	N	N	Y
3	"Ericrocidine line" [4–9]	Y	Y	Y	Y	Y	Y
4	Rhathymini + Ericrocidini	Y	Y	Y	Y	Y	Y
5	Parepeolini + [4]	Y	N	N	N	N	n/a
6	Protepeolini + Epeoloidini	Y*	Y	Y	Y	N	n/a
7	Isepeolini + [6]	Y*	Y	Y	Y	N	n/a
8	Osirini + [7]	Y	Y	Y	Y	Y	n/a
9	Coelioxoidini + [8]	Y*	N	N	N	N	n/a
10	"Nomadine line" [Nomadinae *sensu stricto*; 11–16]	Y	Y	Y	Y	Y	Y
11	Nomadine line excluding Caenoprosopidini [12–16]	Y	N	n/a	N	Y	n/a
12	Remaining Nomadine line excluding Ammobatini [13–16]	Y	N	Y	Y	Y	N
13	Epeolini + Brachynomadini	Y	Y	Y	Y	Y	Y
14	Ammobatoidini + [13]	Y	N	N	N	N	n/a
15	Neolarrini *sensu* Bossert et al. (2020) + Hexepeolini	Y	Y	Y	Y	Y	n/a
16	Nomadini + [15]	Y	Y	N	N	N	n/a

and all lineages previously included in Osirini (see below: Osirini, Epeoloidini, and Parepeolini *trib. nov.*). Such a grouping has also been suggested by previous studies (Litman et al., 2013; Martins et al., 2018). This group is tentatively united by the absence of the epistomal suture past the anterior tentorial pits in adult bees (Martins et al., 2018). Meanwhile, the nomadine line (former Nomadinae *sensu stricto*) includes the tribes Ammobatini, Ammobatoidini, Epeolini, Brachynomadini, Caenoprosopidini, Hexepeolini, Nomadini, and Neolarrini *sensu* Bossert et al. (2020) (i.e., Neolarrini along with the former tribes Biastini and Townsendiellini). From a biogeographic perspective, the ericrocidine line is almost entirely Neotropical in distribution, with the exception of a few species that reach the extreme southern Nearctic and the genus *Epeoloides*, found in both the Palearctic and Nearctic realms. The nomadine line, in contrast, is cosmopolitan in distribution but generally most diverse in the Holarctic region, with only a few *Nomada* species reaching the Australasian realm (Michener, 2007).

Additionally, the continued recognition of one of the tribes is not supported by our analyses. Our phylogeny, the first to include representatives of all five genera traditionally included in the tribe Osirini Handlirsch, finds the relationship among these to be polyphyletic. To clarify the nomenclature of this group, we propose to include within the tribe Osirini only the three genera which do form a clade in our analyses, namely *Osiris*, *Protosiris*, and *Osirinus*. Representatives of the tribe Osirini *sensu stricto* are described in detail by Roig-Alsina (1989). Meanwhile, the genus *Parepeolus* is recovered as the sister group to Ericrocidini + Rhathymini. Due to a lack of morphological characters uniting *Parepeolus* with Ericrocidini and Rhathymini, we diagnose the new tribe Parepeolini. The erstwhile osirine genus *Epeoloides* is recovered with a weakly-supported sister relationship to Protepeolini, but similarly could not be included with this tribe. Thus, we suggest that the previously proposed tribe Epeoloidini Linsley and Michener (1939) should be used for this genus. Our analyses also support previous suggestions that the enigmatic genus *Coelioxoides* should not be considered a close relative of its host *Tetrapedia*, but rather should be placed into its own tribe of Coelioxoidini (Martins et al., 2018; Engel et al., 2020). While it might be optimal to include these newly recognized small tribes within larger clades, this solution is problematic due to the divergent morphology of the aforementioned genera from their sister groups, and so we propose the above solution as a more stable one.

4.3. Host preferences and Emery's rule

The ability to map traits associated with parasitism onto a phylogenetic tree of the Nomadinae with unprecedented resolution in turn allows for more detailed investigation of the evolutionary dynamics which drive the evolution and diversification of such brood parasitic groups. Perhaps the most interesting question of this type relates to how host preferences are determined, and how they change over time. In his 1909 paper, Carlo Emery noted that social and brood parasites have a tendency to attack closely related species, and this principle has come to be known as Emery's rule. Other parasitic bees, such as those in the families Halictidae and Megachilidae as well as the apine tribe Euglossini, typically follow this rule (Michener, 2007). However, the age and diversity of the Nomadinae compared to other brood parasitic clades has been a complicating factor in evaluating their adherence to this concept. The use of ancestral state reconstruction techniques, combined with the broad taxon sampling utilized in this study, provide the first chance to look back in time to the origins of parasitism in the Nomadinae, estimated to have occurred approximately 100 million years ago (Litman et al., 2013).

As these analyses show, it appears that nomadine bees do follow Emery's rule when considering their initial transition to parasitism. The ancestral hosts for the earliest nomadines are indeed recovered to be other members of the family Apidae. Furthermore, the tribe Melectini, which forms the sister group to all other Nomadinae, are entirely parasitic on members of the apid subfamily Anthophorinae, which is recovered as the sister group to Nomadinae as a whole in both this and other studies (Cardinal et al., 2010; Policarová et al., 2019; Bossert et al., 2019). This suggests the possibility that not only the loose but also the strict form of Emery's rule (requiring a direct sister relationship between host and parasite) may have been the case during the origins of this group. As time went on and the Nomadinae diversified and grew more speciose, they evolved to attack a more diverse range of hosts, which at present span five families of bees. Unfortunately, sufficiently detailed phylogenies for all of these host groups do not exist, so that a comprehensive co-evolutionary analysis is not currently possible. Though difficult to quantify, there does appear to be a general trend towards increased host diversity demonstrated by more recent parasitic clades. However, it is still unclear whether this trend may be due to an increased number of host-switching events, or simply increased generalization in host use at the level of particular parasitic groups.

The applicability of Emery's rule to the Nomadinae presents an important contrast with some other brood parasitic and social parasitic insects, where the rule has been considered in relation to much more recent origins of parasitism in smaller taxonomic groups. For example, Smith et al. (2013) and Sumner et al. (2004) both report that Emery's rule in the loose sense is broadly observed in socially parasitic allodapine bees and leafcutter ants respectively, though the exact sister relationships expected under the strict form of the rule are not always seen. Conversely, Lopez-Osorio et al. (2015) fail to find support for this principle at all in socially parasitic vespine wasps. As for other lineages of bees outside the Apidae, there are several examples of apparently recent origins of brood parasitism with a close relationship between parasite and host, sometimes within a single genus. The family Halictidae in particular features several examples, including certain species of *Lasioglossum* (*Dialictus*), *Megalopta* (*Noctoraptor*), and *Megommation* (*Cleptommation*) all parasitic on congeneric species, as well as parasitic representatives of *Parathrincostoma* and *Temnosoma* which attack other members of their respective tribes (*Thrincostoma* and other Augochlorini; Michener, 2007).

Some nomadines have remained fairly specialized on a narrow range of hosts. In some cases, there are clear biological factors which may account for this, such as parasites in the tribes Ericrocidini, Rhathymini, and Osirini which target hosts that are themselves specialized in collecting floral oils as food resources (Martins et al., 2018; Policarová et al., 2019). Other genera of brood parasites have become much wider generalists, attacking diverse host groups. For example, while the genus *Nomada* is most commonly associated with mining bee hosts in the genus *Andrena*, it has been recorded parasitizing members of five different families of bees (Michener, 2007; Westrich, 1989). However, this level of generalization is not necessarily unique among brood parasitic bees; outside the Nomadinae, brood parasites of the genus *Sphecodes* have even been shown to display individual differences among their preferred hosts (Bogusch et al., 2006) as well as flexible host switches over evolutionary time (Habermannová et al., 2013).

It is interesting to note that, while the five families of bees attacked by nomadines represent a substantial diversity of hosts, there is a large group of species which remain as a potential, yet unused, resource. To our knowledge, no records exist of any nomadine species attacking a member of the family Megachilidae as a host, despite the fact that this group contains over 4,000 species and is widely distributed. The reasons for this can only be speculated on, though the existence of several brood parasitic megachilids which attack other members of their family (including *Coelioxys*, *Radoszkowskiana*, the *Stelis* group, the tribe Dioxyini, and certain species of *Hoplitis*; Litman et al., 2013) rules out any advanced defenses that make these bees immune to parasitism entirely. The most obvious potential explanation seems to be the diversity of nesting strategies employed by members of the Megachilidae, which includes the use of cavities in wood, stone, or even snail shells as well as a variety of structures created from mud or plant material (Danforth et al., 2019). In contrast, almost all hosts of Nomadinae are ground-nesting, though the existence of several ground-nesting megachilids

leaves the question somewhat open.

4.4. Mode of parasitism

In addition to studying the historical patterns in changing host preferences, the phylogeny presented in this study also allows for research into changes in different strategies and forms of brood parasitism. Michener (2007) outlines some general modes of parasitism, which were further expanded by Litman et al. (2013). In some parasites, the host larvae or eggs are killed by the adult female parasite before her own eggs are laid, though this strategy is not found in any members of the Nomadinae, where parasitic larvae kill their nestmates instead. The main dichotomy in this group exists between so-called "closed-cell" parasites – those which invade a nest after it has been completed and close the cell themselves – and "open-cell" parasites, which infiltrate a nest that is still under construction and leave it open for the host to complete.

In line with the findings of Litman et al. (2013), we recover the closed-cell mode of brood parasitism as ancestral for Nomadinae, with two transitions to open-cell parasitism. However, in contrast to this study, we recover the tribe Caenoprosopidini as the sister group to all other members of the nomadine line. Though the tribe is poorly studied, the description of possible egg insertion holes by Rozen and Roig-Alsina (1991) suggests that they are closed-cell parasites. Thus, this origin of open-cell parasitism in our study is detected at a slightly later date, and in fewer taxa, than in Litman et al. (2013).

The other transition to open-cell parasitism in both the present study and Litman et al. occurs in the common ancestor of the tribes Isepeolini, Protepeolini, and Epeoloidini. However, the genus *Epeoloides* has been observed to use a strategy that does not neatly fit either the open-cell or closed-cell modes. As described by Straka and Bogusch (2007), *Epeoloides coecutiens* females were observed entering nests of their *Macropis* hosts that were still being provisioned, like open-cell parasites, yet closing them afterwards in the same way as closed-cell parasites. This combination of behaviors may represent a partial reversion to closed-cell parasitism, or perhaps a derived but transitional state between obligate open- and closed-cell modes. The somewhat poorly resolved location of Epeoloidini in our phylogenetic analyses further complicates the interpretation of this trait. Such cases demonstrate the importance of field observations of the invasion behaviors of brood parasites to further verify and record the strategies used by lesser-studied groups.

Comparisons of host preference in concert with mode of parasitism also reveal some noteworthy patterns. Both transitions from closed-cell to open-cell parasitism in our phylogeny occur within one node of inferred shifts in host preference: from Apidae to Colletidae in the Isepeolini, and from Apidae to Andrenidae in the nomadine line. Indeed, with the exception of the poorly known tribe Caenoprosopidini, all closed-cell parasites in our phylogeny appear restricted to the use of confamilial hosts (i.e., other species of Apidae). This suggests that the open-cell strategy allows for greater evolutionary lability in host preferences and could in part account for the much greater diversity of hosts utilized by the nomadine line in contrast to the ericrocidine line and tribe Melectini, though it is difficult to speculate as to the exact mechanism by which this might be achieved. The existence of many open-cell parasites within the nomadine line which have reverted to attacking apids would seem to preclude the possibility that these hosts are simply better at defending against this mode of parasitism. Perhaps the open-cell strategy instead allows for the circumvention of host defenses used by some non-apids that only become effective upon completion of nest cells, such as the complex glandular secretions of many colletids (Almeida, 2008). This pattern may also relate to Emery's rule in the sense that the ability to locate, enter, and reseal a finished nest as in closed-cell parasitism is potentially a more straightforward strategy against close relatives with similar nest architecture to a brood parasite's most recent free-living ancestors. As already expressed, however, further investigation into the nesting biology of brood parasites and their hosts is essential to the continued exploration of such questions.

5. Conclusions

This study provides the first comprehensive analysis of the phylogeny of the oldest and largest clade of brood parasitic bees, the subfamily Nomadinae in the broad sense. While the specific relationships among most of the members of this group are consistent with findings from previous research, there are some notable differences. Additionally, the unprecedented level of taxon sampling included herein has allowed us to explore novel questions related to the evolution of brood parasitism. Emery's rule is supported, at least in the loose sense, by ancestral state reconstruction of other members of the family Apidae as the earliest hosts of nomadine parasites. Similarly, these techniques shed light on the most likely behavioral strategies used by the first brood parasitic bees over 100 million years ago, with closed-cell parasitism inferred to be ancestral, followed by the independent evolution of open-cell parasitism in two lineages. Finally, this study also amends the nomenclature of subgroups within the Nomadinae to remove poly- and paraphyletic taxa by partitioning the tribe Osirini into three tribes.

CRediT authorship contribution statement

Trevor J.L. Sless: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Michael G. Branstetter:** Methodology, Formal analysis, Investigation, Resources, Data curation, Funding acquisition. **Jessica P. Gillung:** Investigation. **Erin A. Krichilsky:** Investigation. **Kerrigan B. Tobin:** Investigation. **Jakub Straka:** Resources, Writing – review & editing. **Jerome G. Rozen Jr.:** Resources. **Felipe V. Freitas:** Resources. **Aline C. Martins:** Resources. **Silas Bossert:** Resources. **Jeremy B. Searle:** Conceptualization, Writing – review & editing, Supervision. **Bryan N. Danforth:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data Accessibility

The appendices for this article include information on all voucher specimens used in the study. Unprocessed Illumina reads are deposited

in the NCBI Sequence Read Archive under project number PRJNA694187, and UCE sequences are available through GenBank's Targeted Locus Study (accessions KFBX00000000-KFFM00000000). Assembled UCE contigs, alignments, and phylogenetic trees are available from the following Figshare repository: 10.6084/m9.figshare.c.5556573.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2021.107326.

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