ORIGINAL ARTICLE

Systematic Entomology · Royal Entomological Society

Phylogeny, biogeography and diversification of the mining bee family Andrenidae

Silas Bossert[1,2] | Thomas J. Wood[3] | Sébastien Patiny[3] | Denis Michez[3] | Eduardo A. B. Almeida[4] | Robert L. Minckley[5] | Laurence Packer[6] | John L. Neff[7] | Robert S. Copeland[2,8] | Jakub Straka[9] | Alain Pauly[10] | Terry Griswold[11] | Seán G. Brady[2] | Bryan N. Danforth[12] | Elizabeth A. Murray[1,2]

[1]Department of Entomology, Washington State University, Pullman, Washington, USA

[2]Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA

[3]Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Mons, Belgium

[4]Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo, Brazil

[5]Department of Biology, University of Rochester, Rochester, New York, USA

[6]Department of Biology, York University, Toronto, Ontario, Canada

[7]Central Texas Melittological Institute, Austin, Texas, USA

[8]ICIPE, International Centre of Insect Physiology and Ecology, Nairobi, Kenya

[9]Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic

[10]Royal Belgian Institute of Natural Sciences, O.D. Taxonomy and Phylogeny, Brussels, Belgium

[11]U.S. Department of Agriculture, Agricultural Research Service, Pollinating Insects Research Unit, Utah State University, Logan, Utah, USA

[12]Department of Entomology, Cornell University, Ithaca, New York, USA

Correspondence
Silas Bossert, Department of Entomology, Washington State University, Pullman, WA, USA.
Email: silas.bossert@wsu.edu

Abstract

The mining bees (Andrenidae) are a major bee family of over 3000 described species with a nearly global distribution. They are a particularly significant component of northern temperate ecosystems and are critical pollinators in natural and agricultural settings. Despite their ecological and evolutionary significance, our knowledge of the evolutionary history of Andrenidae is sparse and insufficient to characterize their spatiotemporal origin and phylogenetic relationships. This limits our ability to understand the diversification dynamics that led to the second most species-rich genus of all bees, *Andrena* Fabricius, and the most species-rich North American genus, *Perdita* Smith. Here, we develop a comprehensive genomic dataset of 195 species of Andrenidae, including all major lineages, to illuminate the evolutionary history of the family. Using fossil-informed divergence time estimates, we characterize macroevolutionary dynamics, incorporate paleoclimatic information, and present our findings in the context of diversification rate estimates for all other bee tribes. We found that diversification rates of Andrenidae steeply increased over the past 15 million years, particularly in the genera *Andrena* and *Perdita*. This suggests that these two groups and the brood parasites of the genus *Nomada* Scopoli (Apidae), which are the primary cleptoparasitic counterparts of *Andrena*, are similar in age and represent the fastest diversifying lineages of all bees. Using our

newly developed time frame of andrenid evolution, we estimate a late Cretaceous origin in South America for the family and reconstruct the past dispersal events that led to its present-day distribution.

KEYWORDS

Andrena, divergence times, *Nomada*, paleoclimate, Panurginae, ultraconserved elements

INTRODUCTION

One universal feature of the Tree of Life is that diversification rates vary widely among lineages and over time (Alfaro et al., 2009; Jetz et al., 2012; Morlon, 2014; Raup et al., 1973; Stanley, 1975). If diversification and extinction rates were constant across clades, then clade age alone would be a reasonable predictor of species richness. However, species richness and age of clades have been shown to be decoupled across the Tree of Life (Rabosky et al., 2012), suggesting that other factors determine clade-specific diversification rates. Key innovations, such as changes in life history and ecological traits, may impact diversification rates (Hunter, 1998; Mayhew, 2007; Rabosky, 2017). Environmental factors, such as changes in climate, seasonality and shifting continental plates, may also drive shifts in diversification (Botero et al., 2014; Claramunt & Cracraft, 2015; Kergoat et al., 2018; Toussaint et al., 2012). Phylogenies, combined with the fossil record, paleoclimatic and geological information and the biogeographic distribution of organisms, can provide insights into the impact of environmental change on diversification rate shifts. Linking macroevolutionary dynamics to environmental factors, however, requires densely sampled and reliable phylogenetic estimates, which remain a persistent challenge for studies on hyperdiverse taxa such as insects.

With ~20,500 described species (Ascher & Pickering, 2021), bees are the most species-rich group of pollinivorous insects and the most important pollinators in natural and agricultural ecosystems (Ballantyne et al., 2017; Klein et al., 2007; Ollerton, 2017). Bees exhibit exceptionally diverse life-history strategies, which include various social behaviours, diverse nesting habits, brood parasitism, and various diet specialization on particular host plants ('oligolecty'; Danforth et al., 2019; Michener, 2007; Mikát et al., 2021; Westrich, 2018). The repeated independent evolution of these traits in bees makes them an excellent group for studying fundamental questions in basic and applied science.

Understanding the past diversification dynamics of bees is hampered by our insufficient knowledge of the phylogeny of one of the major families, the mining bees (Andrenidae). Andrenidae comprises 3019 described species in three morphologically disparate subfamilies, all of which are ground-nesting and either solitary or communal. The family is distributed globally except for Australasia and Antarctica (Danforth et al., 2019; Michener, 2007). Andrenidae includes the second largest genus of bees, *Andrena* Fabricius (~1600 spp.), with a wide distribution mainly throughout the Holarctic. It also includes *Perdita* Smith (~640 spp.), a large group of morphologically similar, mostly minute bees with narrow host plant preferences and restricted Nearctic distribution, with its centre of diversity in the xeric regions of southwestern North America. Species of *Andrena* are critical pollinators for a range of important tree fruit crops, such as apple (*Malus* Mill. spp. [Rosaceae]) (Pardo & Borges, 2020; Park et al., 2016; Russo et al., 2017). Remarkably, Andrenidae is the only bee family for which no comprehensive molecular phylogeny is available, although some representatives have been included in previous studies of bee family-level relationships (Branstetter et al., 2017; Cardinal et al., 2018; Cardinal & Danforth, 2013; Danforth, Fang, & Sipes, 2006; Danforth, Sipes, et al., 2006; Hedtke et al., 2013; Peters et al., 2017; Sann et al., 2018) and in a recent study on the subfamily Andreninae Latreille (Pisanty et al., 2021). This limits our ability to characterize the spatiotemporal origin of Andrenidae and its major lineages, as well as to understand diversification and range expansion in light of changes in climate, drifting intercontinental connections and other significant geological events. Accordingly, robust estimates of phylogenetic relationships and divergence times are key for characterizing the mode and timing of diversification in Andrenidae and for illuminating patterns of diversification across bees.

We analysed ultraconserved genomic data from nearly 2000 loci to establish the first densely sampled, molecular-phylogenetic framework for all major extant lineages of the bee family Andrenidae. Using fossil-informed divergence time estimates, we calculated lineage-specific diversification rates for the major lineages of Andrenidae and placed our findings in the context of crown age-based diversification rates for all other bee tribes and specifically for the largest bee genera (>600 spp.) outside of Andrenidae: *Megachile* Latreille (Megachilidae), *Lasioglossum* Curtis (Halictidae), *Hylaeus* Fabricius (Colletidae) and *Nomada* Scopoli (Apidae). Our estimates strongly indicate that *Perdita*, *Andrena* and the brood parasites in the genus *Nomada* (Apidae), which primarily attack *Andrena*, are similar in age and may be the fastest diversifying lineages of all bees. Finally, we use our phylogenetic framework to investigate the biogeographic history of Andrenidae through time and space.

MATERIALS AND METHODS

Taxon selection and molecular methods

A detailed version of the materials and methods, including taxon sampling and details on molecular methods and bioinformatic processing, can be found in the Appendix S1. We developed a densely sampled, diversified taxon representation of Andrenidae, including 37 out of the 41 genera recognized by Michener's classification (2007). The four

missing genera of this classification comprise no more than two species each and are either only known from the type material or are extremely rare, and together account for less than 0.17% of all species of the family. Additionally, we included several lineages as genera that Michener (2007) treated as subgeneric groups. We were unable to acquire material for the small genera described subsequent to Michener's taxonomy (2007), such as *Psaenythisca*, Ramos and Rozen (2014) or *Incasarus* Gonzalez et al. (2013). We included all 29 samples of andrenid ultraconserved sequence data (ultra-conserved elements [UCEs]) that were publicly available as of February 2021 (Branstetter et al., 2017; Grab et al., 2019) and used 31 DNA extracts generated in the course of a dissertation in the lab of B.N.D. at Cornell University (Ascher, 2004). Including the 140 samples that we chose exclusively for this study, our taxon sampling comprises 200 samples from 195 different species throughout Andrenidae. We sequenced UCEs for most samples following the methods described in Bossert et al. (2021). This workflow follows the principal methods of earlier studies using UCEs (Faircloth et al., 2015) and includes subsequent modifications (Blaimer, LaPolla, et al., 2016; Blaimer, Lloyd, et al., 2016). For the 10 samples vouchered at the Universidade de São Paulo, Brazil (RPSP; see Table S1), library preparation was conducted by Rapid Genomics LLC following an older workflow using the initial version of the Hymenoptera probe set (Faircloth et al., 2015).

Phylogenetic reconstruction

We primarily used the Phyluce pipeline (Faircloth, 2016) for processing of UCE sequence data but conducted a number of steps with different programs (see Appendix S1). After filtering loci for taxon completeness, we discarded alignments with less than 160 terminals (= 80% completeness). This trimmed, concatenated alignment was used for subsequent analyses. We used IQ-Tree 2 (Minh et al., 2020) to calculate a maximum likelihood (ML) tree and used ModelFinder (Kalyaanamoorthy et al., 2017) with the greedy strategy (Lanfear et al., 2012) to merge partitions with similar patterns of substitution (MFP + MERGE option). To lower the computational demand, we used the relaxed hierarchical clustering algorithm (Lanfear et al., 2014) to assess only the top 30% of all schemes (rcluster 30). We calculated node support with 1000 ultrafast bootstrap approximations (UFBoot2; Hoang et al., 2018). To compare phylogenetic results from concatenation analyses, we estimated a species tree under the multispecies coalescent model (Rannala & Yang, 2003). To this end, we split the concatenated supermatrix by locus (using AMAS; Borowiec, 2016), estimated species trees with IQ-Tree and automated model search (MFP), and summarized the gene trees with ASTRAL-III (Zhang et al., 2018).

Divergence time estimates

Due to the large size of our sequence matrix, Bayesian divergence time estimates using the entire matrix were computationally impractical. Instead, we designed four separate subsets of loci. First, we tested the molecular clock hypothesis for the individual gene trees using an R script (modified from Borowiec et al., 2015). According to their similarity to an ultrametric tree ('clocklikeness'), we identified the 100 most clocklike loci and concatenated their respective alignments. Similarly, for the second subset, we identified the 100 most informative UCEs according to their number of parsimony-informative sites (assessed with AMAS). Finally, we generated two matrices each of 100 randomly chosen loci (without replacement). For each of these four matrices, we used PartitionFinder2 (Lanfear et al., 2017) to designate subsets of nucleotides using all models implemented in MrBayes, the Bayesian information criterion and a rcluster search scheme, while providing the locus partitions as data blocks.

The fossil record for Andrenidae is sparse and the phylogenetic placement of most fossils is largely uncertain (Michez et al., 2012). These circumstances render fossil-calibrated node dating (the strategy for which the oldest available fossil is assigned to serve as a minimum age constraint for a specified node) questionable. The newer tip-dating approaches under the FBD model (Heath et al., 2014; Stadler, 2010) eliminate the need to assign age constraints to internal nodes by including the fossils as tips in the phylogeny (e.g., Luo et al., 2020; Ronquist, Klopfstein, et al., 2012; Zhang et al., 2016). This allows us to include 13 fossils that were associated with Andrenidae as taxa in our phylogeny, by using a set of constraints specifying the fossils to be members of certain clades. This effectively circumvents the need to designate the fossil taxa as stem- or crown-group fossils. For example, wing morphometric analyses revealed that *Andrenopteryx willardi* Cockerell, a compression fossil from the Florissant Fossil Beds (Colorado, USA), is most similar to modern-day Andreninae, but does not fit in any of the present-day genera, including *Andrena* (Dewulf et al., 2014). We therefore constrained this fossil to be a tip of Andreninae (excluding *Andrena*) but did not specify an affinity with any particular lineage of this group. In contrast, *Andrena antoinei* Michez & De Meulemeester, a compression fossil from the late Oligocene, is probably a member of the genus *Andrena* (Dehon et al., 2014). We therefore constrained it to be part of a monophyletic *Andrena* and not with the remaining Andreninae. While appreciating the great uncertainty for the actual phylogenetic placement of most of these fossils and the clear need for modern revision (Dewulf et al., 2014; Michez et al., 2012), we followed some of Cockerell's assessments (Cockerell, 1906, 1908, 1911, 1914) and assumed four additional Florissant fossils to be likely part of *Andrena* or stem lineages thereof (*Andrena grandipes* Cockerell, *Andrena hypolitha* Cockerell, *Andrena percontusa* Cockerell, *Andrena sepulta* Cockerell). We assigned four additional fossils as part of Andreninae (*Andrena*(?) *clavula* Cockerell, *Andrena*(?) *primaeva* Cockerell, *Lithandrena saxorum* Cockerell, *Pelandrena reducta* Cockerell). All these fossil deposits are younger than previous age estimates of the origin of Andreninae using molecular data (e.g., Cardinal et al., 2018; Cardinal & Danforth, 2013), so we did not expect their inclusion to inflate age estimates for the group, but future study to reevaluate these fossils and their phylogenetic affinity is needed.

Three additional fossils were used as tips for Panurginae Leach. Both species of *Libellulapis* Cockerell (*L. antiquorum* Cockerell, *L. wilmattae* Cockerell) were described as Panurginae by Cockerell (Cockerell, 1913; Rozen, 1996), but we did not assign them to an extant group. Instead, we constrained them to be part of this subfamily without specifying a particular clade. Finally, we considered *Heterosarus eickworti* Rozen, the sole hitherto andrenid fossil from Dominican amber (Rozen, 1996). Given the unclear monophyly of present-day *Heterosarus* Robertson, we treated this fossil as a tip of *Protandrena* Cockerell in its broader sense as detailed below. Details on the fossils used can be found in Table S2.

We included fossils as samples with missing data in four different analyses in MrBayes (Ronquist, Teslenko, et al., 2012), each using one of the four matrices outlined above. For all fossils, we treated the age of their respective formation as a uniform age prior and calibrated the root with a truncated normal distribution with a *mean* = 95.5 and σ = 8. This is based on previously published estimates: a recent phylogenomic study on Hymenoptera found the split of Andrenidae and Colletidae + Halictidae to be at most 126 Ma and at least 65.5 Ma old (Peters et al., 2017). Based on our underlying normal distribution, this ensures that 99.9% of the area under the curve falls into this time interval. We used the continuous uncorrelated mode (Independent Gamma Rate, IGR; Lepage et al., 2007) for the clock model and let reversible jump Markov chain Monte Carlo (rjMCMC; Huelsenbeck et al., 2004) sample the parameter space across all models implemented in MrBayes, given the partitions designated via PartitionFinder2. We used a set of 22 partial and hard constraints to associate fossils and constrain a set of groups to resemble the IQ-Tree ML and ASTRAL summary analyses. These constraints are detailed in the MrBayes input files, which are deposited in the online data repository. For each data matrix, we executed six runs each with four chains, sampled every 1000 generations, and ran between 120 and 185 million generations when convergence was achieved. Using a 20% burn-in, we considered convergence to be sufficient once the average standard deviation of split frequencies fell below 0.01 and all parameters, including the clock rate, reached combined effective sample size (ESS) values of ≥200.

Assessments of diversification dynamics

We assessed the past diversification dynamics of Andrenidae with four different approaches. For all four diversification analyses, we modified the previously estimated chronogram of Andrenidae from the 100 most clocklike loci. To this end, we removed duplicate species and grafted an additional three taxa onto the clade comprising Andrenini Latreille. Pisanty et al.'s (2021) comprehensive recent study on *Andrena* included three early-branching taxa of Andrenini that we were unable to obtain: *Cubiandrena cubiceps* (Friese), species of *A.* (*Melittoides*) other than the type species (the subgenus was found paraphyletic by Pisanty et al. (2021)), and *Andrena bytinskii* Warncke. Since our crown age estimate of *Andrena* is nearly identical with that of their analysis excluding these three specified lineages (21.38 and

20.13 Ma, respectively), we grafted the three tips onto the tree according to the divergence times found in their study. This led to a phylogeny with 197 total species.

Environment-dependent speciation

First, we estimated speciation rates using episodic birth–death models (Höhna, 2015) as implemented in RevBayes (Höhna et al., 2016). We used the same chronogram as for the biogeographic analysis, employed an empirical taxon strategy and accounted for incomplete taxon representation by assigning missing taxa for individual clades. The estimates for missing taxa are based on species numbers from the Discover Life database (Ascher & Pickering, 2021) and our own estimates for the subgenera of *Andrena*, which were assigned in conjunction with the taxon-dense phylogeny developed by Pisanty et al. (2021). To understand if speciation of Andrenidae may be correlated with paleoclimatic change, we assessed correlations between environmental variables and speciation rates. To this end, we used reversible jump MCMC in our RevBayes analyses to estimate posterior probabilities for two models: a model of environmentally dependent speciation and an episodic birth–death that does not account for any paleoclimatic variables. We designated 5 Ma time intervals and quantified the support for the models using Bayes factors (BFs), effectively assessing if environmental variables may have played a particular role in the diversification of Andrenidae. Specifically, we separately examined two paleoclimatic factors from the K-Pg boundary to the Holocene: temperature and CO_2. We obtained recently published $\delta^{18}O$ measurements for the Cenozoic (Westerhold et al., 2020; their ISOBENd18oLOESSsmoothLongTerm dataset) and calculated surface air temperature values using the formulas provided in Hansen et al. (2013), assuming a Holocene mean temperature of 14.15°C. CO_2 values correspond to the pCO_2 probability maximum from Foster et al. (2017). For all analyses, we used a burn-in of 25% and assured sufficiently high ESS values by inspecting the MCMC results with Tracer (Rambaut et al., 2018).

Diversification rate shifts

We used Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Rabosky, 2014) to sample from a posterior distribution of macroevolutionary scenarios, in order to identify areas of the phylogeny where significant changes in net diversification rates appear likely. The BAMM input consisted of the previously used chronogram, priors inferred through BAMMtools (Rabosky et al., 2014), and estimates accounting for missing taxa in our phylogeny. These sampling fractions correspond to those used for the RevBayes analyses, albeit in a different format, and were assigned as closely as possible. However, for certain groups with a limited phylogenetic resolution, we evenly dispersed the number of described species across the included tips (see BAMM configuration file in the data repository). We used a 50% burn-in and assessed convergence and sufficient sampling of the parameter space with BAMMtools (Rabosky et al., 2014).

Tip rates

To compare the model-based Bayesian approaches with a model-free alternative, we estimated tip rates of our phylogeny using the *DR* statistic (Jetz et al., 2012). This statistic measures the amount of splits from the root to individual tips ('splitting rate'; Jetz et al., 2012) and is best interpreted as a measure of tip speciation rate (Title & Rabosky, 2019). As such, this measure cannot account for incomplete taxon representation, which presents a challenging requirement for studies on species-rich groups such as insects. To overcome this, we simulated fully resolved species trees of Andrenidae using Taxonomic Addition for Complete Trees (Chang et al., 2020), a stochastic polytomy resolver that computes local birth–death rates. We generated a taxonomy file that specifies numbers of missing taxa for the clades identified for the RevBayes and BAMM analyses and stochastically added 2601 species of Andrenidae to the previously used chronogram. We replicated this for a total of 200 simulations and calculated tip rates for all nonsimulated taxa using the R package Picante (Kembel et al., 2010).

Comparison of diversification across bees

Because we were interested in knowing how diversification rates of Andrenidae compare to those of other bee lineages, we used method-of-moments (MoM) estimators (Magallón & Sanderson, 2001) to calculate diversification rates for all major lineages of bees. We calculated net diversification rates using both the crown and stem ages and with four different relative extinction fractions ($\varepsilon = 0$, 0.1, 0.5 and 0.9). These estimates rely on two inputs: an age estimate for a clade of interest and the species richness of the respective clade. To this end, we obtained published crown and stem age estimates for all tribes of bees and all major genera (≥600 described species). We included age estimates from 10 studies with different focal taxa: Andrenidae (present study), Colletidae and Stenotritidae (Almeida et al., 2012), *Lasioglossum* (Gibbs et al., 2012), Megachilini Latreille (Trunz et al., 2016), Neolarrini Fox (Bossert et al., 2020), Bombini Latreille (Hines, 2008), Xylocopini Latreille (Blaimer et al., 2018), *Hylaeus* (Kayaalp et al., 2013) and different tribes of Eucerinae Latreille (Praz & Packer, 2014). Age estimates for all remaining tribes were taken from Cardinal (2018). Tribes that were found paraphyletic in Cardinal et al. (2018) were split into genera and coded accordingly. We were unable to obtain crown age estimates for 14 species-poor lineages and calculated diversification rates only using their stem ages. We used species richness numbers from the Discover Life database (Ascher & Pickering, 2021). Age estimates, species richness and the respective studies can be found in Table S3.

Biogeographic reconstruction

To understand the historical biogeography of Andrenidae, we considered four global regions: North America (N), South America (S),

sub-Saharan Africa (A) and the Palearctic (P). Our interpretation of the regions of the Old World follows Olson et al. (2001), which considers the Middle East as largely Palearctic, except for the southern coastal region of the Arabian Peninsula. The term Holarctic is used to describe the Palearctic plus North America. For the biogeographic reconstruction, we used the same modified chronogram as for the diversification analyses and coded the species' biogeographic distributions as shown in Figures 1 and 2. Subsequently, we used the R (R Core Team, 2021) package BioGeoBEARS (Matzke, 2018) to test the model fit of three biogeographic models. Disregarding the founder-event speciation parameter ($+j$; see Ree & Sanmartín, 2018), we tested the Dispersal-Extinction-Cladogenesis (DEC) model (Ree & Smith, 2008), and the ML adaptations of the Dispersal-Vicariance Analysis (DIVA; Ronquist, 1997) and BayArea (Landis et al., 2013) models. We allow species to be distributed in up to two areas but excluded the possibility of species concurrently occurring in sub-Saharan Africa and North America, and in the Palearctic and South America. Given the continental distances in the examined time frame, we lowered the dispersal multiplier for direct dispersals from North America to Africa (and reverse) to 0.5, and those from and to North America from the Palearctic to 0.8. The dispersal multiplier for South America to Africa was lowered to 0.8 and to the Palearctic to 0.5 and vice versa. We picked the best-fitting model according to the weighted corrected Akaike's information criterion (AICc) score. Biogeographic maps were generated with Paleomap Maker (portal.gplates.org/map/) using the Muller 2016 model.

RESULTS AND DISCUSSION

Phylogeny and systematics of Andrenidae

We sequenced UCEs of 172 Andrenidae and obtained an average of 1891 single-copy loci per sample. Combining these sequences with published UCEs of Andrenidae resulted in an 80% completeness matrix of 1388 loci with an average alignment length of 429.8 bp after trimming and 195 species. The final concatenated sequence matrix comprises 595,217 bp with 15.8% nongap missing data.

The comprehensive taxon sampling of this study allowed us to reevaluate subfamilial, tribal and generic concepts across Andrenidae. Concatenation and gene tree summary analyses found unambiguous support for monophyletic groups that correspond to the three previously recognized subfamilies: Andreninae, Oxaeinae Ashmead and Panurginae (Figures 1 and 2, S1 and S2). Attributing subfamily status to the monotypic *Alocandrena* Michener (Alocandreninae) (sensu Engel, 2001; Michener, 2007) renders Andreninae paraphyletic and should be avoided. As in previous studies involving molecular data (Ascher, 2003; Ascher, 2004; Cardinal et al., 2018; Cardinal & Danforth, 2013; Danforth, Fang, & Sipes, 2006; Danforth, Sipes, et al., 2006; Hedtke et al., 2013), Oxaeinae was found nested within Andrenidae as sister to Panurginae, thereby refuting family status for Oxaeinae as suggested using morphology (Hurd & Linsley, 1976; Plant & Paulus, 2016; Rozen, 1964; Rozen, 1965; but see Ascher, 2004).
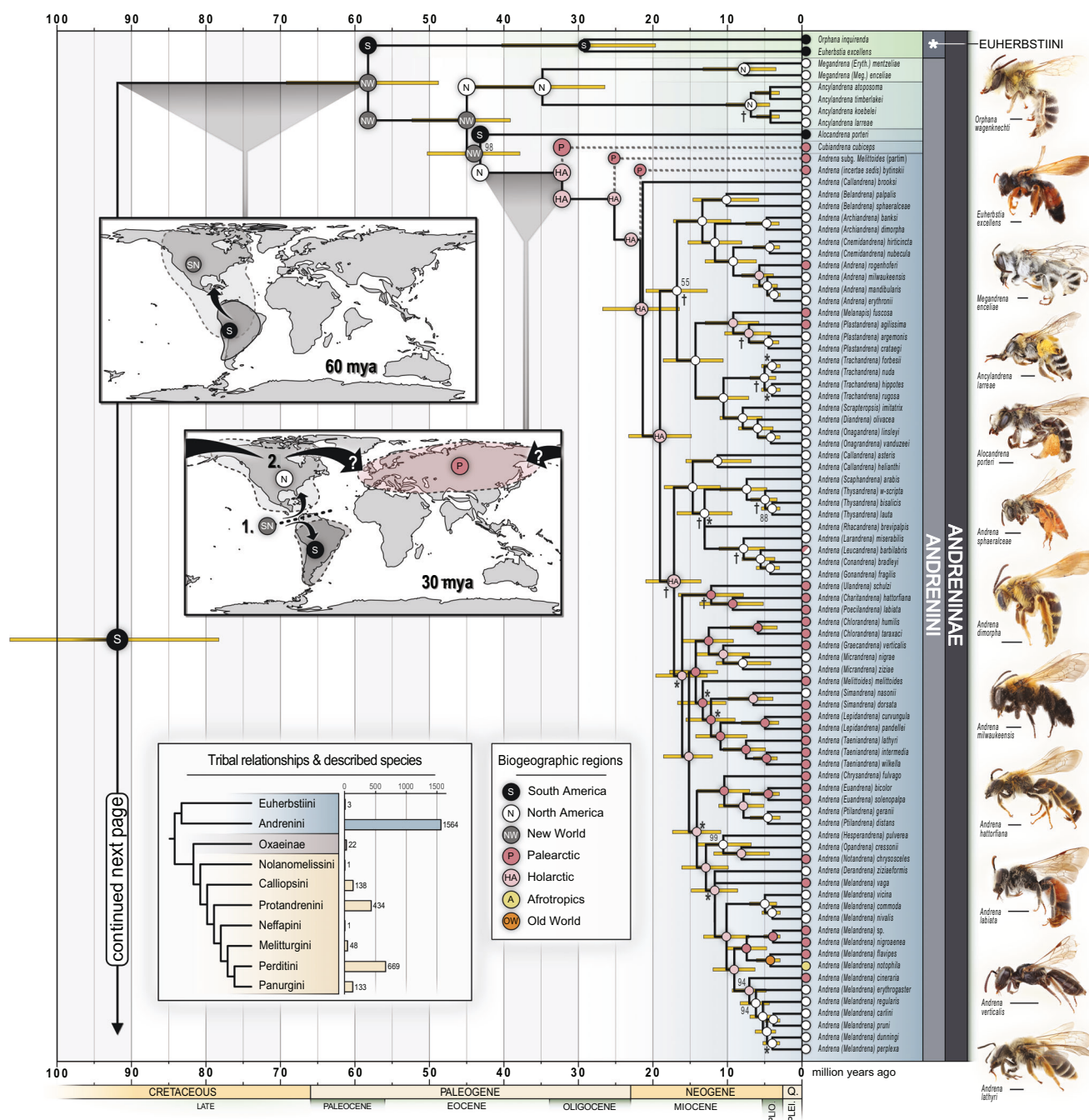
FIGURE 1 Bayesian chronogram of Andrenidae, part 1: The subfamily Andreninae. Divergence time estimates are based on the 100 most clocklike UCE loci. We used 22 phylogenetic constraints for the chronogram to align the topology with the maximum likelihood (ML) and coalescent-based summary tree (Figures S1 and S2). Bars show the 95% highest posterior density and node support values show ultrafast bootstrap approximations for the respective ML tree and were omitted when support was 100. Asterisks show nodes with differing phylogenetic placements between the Bayesian and ML analysis, and daggers indicate topological differences to the ASTRAL summary tree. Tips with dashed branches were not part of our original sampling but were grafted onto the phylogeny based on published topologies (Pisanty et al., 2021). Genus and species names follow the taxonomy of the Discover Life database (Ascher & Pickering, 2021), except for names changed in this study and for *Andrena* (which follows Pisanty et al., 2021). Ancestral geographic ranges were estimated under the DEC model and only the single most likely ancestral range is displayed at each node. The lower histogram inset summarizes the higher-level relationships found in this study and the respective species richness for the tribes of Andrenidae. Scale bars next to specimen photographs show 2 mm in length

For the largest subfamily Andreninae, both coalescent and concatenation analyses produced congruent results for the relationships among genera. Both Euherbstiini Moure and Andrenini, as previously used (e.g., Pisanty et al., 2021), were found monophyletic (Figure 1). Our recovered relationships are in-line with Pisanty et al. (2021), except for the placement of *Alocandrena*, an enigmatic,
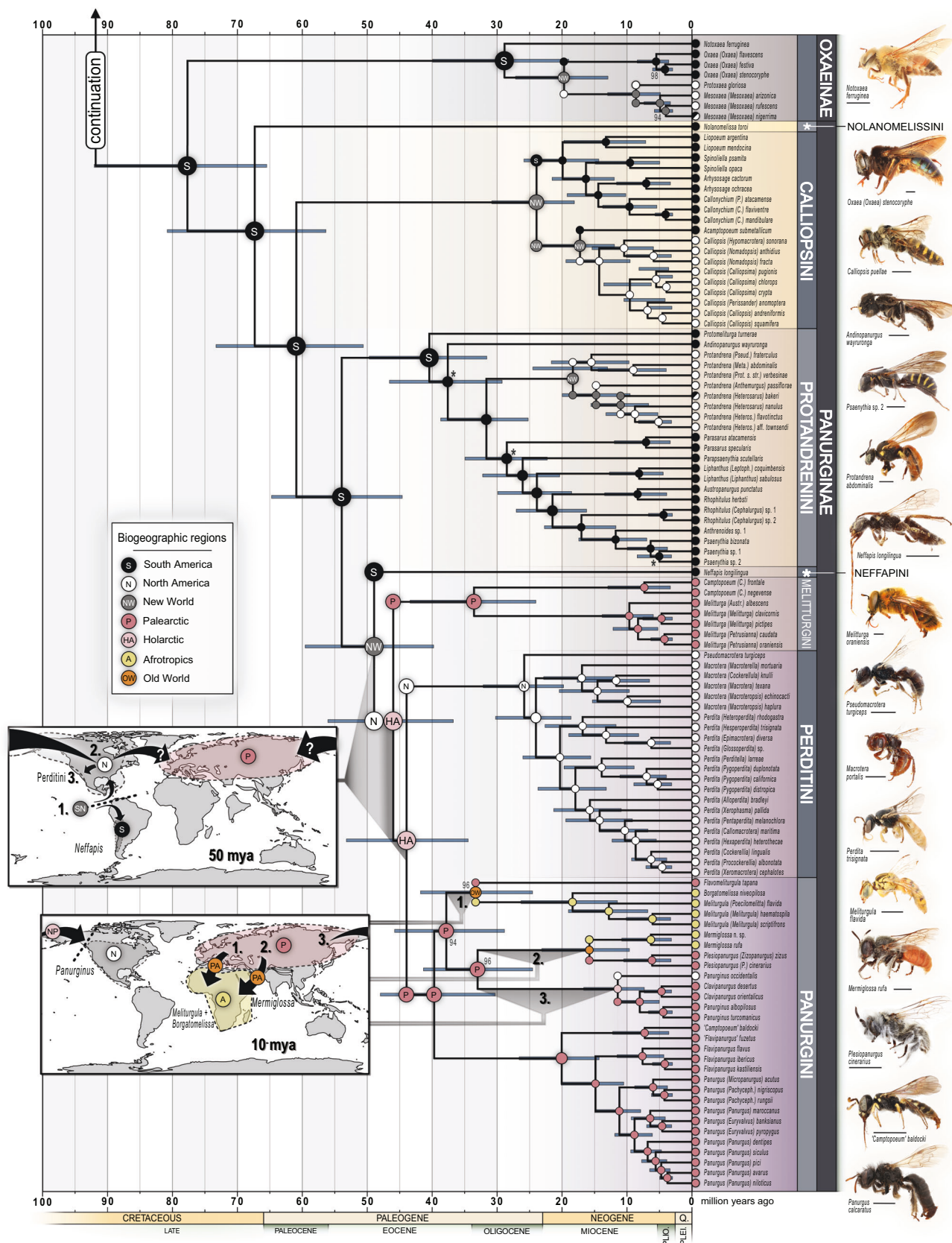
FIGURE 2 Chronogram of Andrenidae, part 2: Oxaeinae and Panurginae. We found strong support for seven tribes of Panurginae, including the two monotypic tribes Nolanomelissini and Neffapini. Specimen scale bars are 2 mm

monotypic genus (Michener, 1986), whose phylogenetic position has remained unclear in the decades since its description (see Ascher, 2004; Plant & Paulus, 2016). This endemic to the Andes of Peru (Michener, 2007) has features of both Panurginae and Andreninae. As such, its phylogenetic position is significant for understanding the spatiotemporal origin of the tribe Andrenini and the species-rich genus *Andrena*. Both our ML and ASTRAL analyses found *Alocandrena* as a sister group to *Andrena* + *Cubiandrena* Warncke (Figures S1 and S2), a finding in-line with previous studies (Cardinal et al., 2018). Interestingly, Pisanty et al. (2021) used UCE sequence data obtained with the same probe set as in the present study, yet they found a sister group relationship of *Alocandrena* to *Megandrena* Cockerell + *Ancylandrena* Cockerell with their concatenation analyses, but our configuration in their coalescent-based species tree. These topological differences and the very short coalescent times in both studies clearly highlight the need for additional study of *Alocandrena* and its phylogenetic affinities.

We found strong support for the oxaeine genera described in Hurd and Linsley (1976), with the monotypic genus *Notoxaea* Hurd & Linsley from southern South America as the earliest branching lineage of this subfamily (Figures S1 and S2). Molecular sequence data confirm the previously assumed close relationship between *Protoxaea* Cockerell & Porter and *Mesoxaea* Hurd & Linsley (Hurd & Linsley, 1976; Michener, 2007), but raises doubt over a recently published classification with an additional subgenus of *Mesoxaea* (Engel, 2015): we found *Mesoxaea nigerrima* (Friese), the type species, to be more closely related to the type species of the subgenus *Heteroxaea* Engel (*Mesoxaea rufescens* Hurd and Linsley) than to other *Mesoxaea*, rendering the subgenus paraphyletic. Since the diagnosis of the subgenus *Heteroxaea* is almost exclusively based on pile colouration (Engel, 2015), we regard the subgenus *Heteroxaea* as a junior synonym of *Mesoxaea*. The phylogenetic positions of the *Oxaea* Klug subgenera *Alloxaea* Ascher et al. (2006), *Rhodoxaea* Engel and *Percnoxaea* Engel remain to be studied with molecular data.

Reconciliation of our species tree estimates allows us to stabilize the tribal classification of Panurginae. While most higher-level lineages of Panurginae are well characterized by morphological features (e.g., Ascher, 2004; Michener, 2007; Patiny, 1999; Ruz, 1986), their relationships to each other remained unclear. This is evident by the numerous alternative classifications, ranging from four to nine different tribes and up to nine subtribes (reviewed by Ascher, 2004; Plant & Paulus, 2016). Our congruent and well-supported phylogenetic estimates of relationships among Panurginae support recognition of seven tribes without the need for subtribes (Figure 2). The monophyly of these groupings is strongly supported and congruent across methods, with all lineages recognizable based on morphology. Remarkably, these relationships are nearly identical to those found with a single gene analysis by Ascher (2003), except that our data allow us to delineate the exact phylogenetic relationships among Panurgini Leach, Melitturgini Newman and Perditini Robertson.

Taxonomy

Family Andrenidae Latreille.

Subfamily Oxaeinae Ashmead.

Genus *Mesoxaea* Hurd & Linsley.

Subgenus *Mesoxaea* Hurd & Linsley.

= *Heteroxaea* Engel, 2015. Type species *Mesoxaea rufescens* Hurd & Linsley, 1976. **syn.n.**

Comment: *Heteroxaea* is a junior synonym of *Mesoxaea*: we found that *Mesoxaea nigerrima* (Friese), the type species of *Mesoxaea*, is more closely related to the type species of the subgenus *Heteroxaea* (*M. rufescens* Hurd & Linsley) than to other *Mesoxaea* (*M. arizonica* [Cockerell]). To avoid paraphyly of *Mesoxaea*, we synonymize the subgenus *Heteroxaea* with *Mesoxaea*.

Genera included in Oxaeinae: *Alloxaea* Ascher, Engel, & Griswold (1 sp.), *Mesoxaea* (7 spp.), *Notoxaea* Hurd & Linsley (1 sp.), *Oxaea* Klug (10 spp.), *Protoxaea* Cockerell & Porter (3 spp.).

Subfamily Panurginae Leach.

Tribe Calliopsini Robertson.

Genus *Liopoeum* Friese. **stat.n.**

= *Camptopoeum* (*Liopoeum*) Friese, 1906. Type species: *Camptopoeum hirsutulum* Spinola, by designation of Sandhouse (1943). [raised to genus rank].

Comment: *Liopoeum* is usually treated as a subgenus of *Calliopsis* Smith (Ascher & Pickering, 2021; Michener, 2007), but we found strong support for a sister-group relationship to a clade comprising *Spinoliella* Ashmead, *Arhysosage* Brèthes, and *Callonychium* Brèthes. To avoid a paraphyletic genus *Calliopsis*, we raise *Liopoeum* to genus and include the following five species: *Liopoeum argentinum* (Jörgensen) **comb.n.**, *L. hirsutulum* (Spinola), *L. mendocinum* Jörgensen, *L. rigormortis* (Dumesh & Packer) **comb.n.**, *L. trifasciatum* (Spinola) **comb.n**.

Genera included in Calliopsini: *Acamptopoeum* Cockerell (11 spp.), *Arhysosage* (8 spp.), *Calliopsis* (81 spp.), *Callonychium* (13 spp.), *Liopoeum* (5 spp.) **stat.n.**, *Liopoeodes* Ruz (1 sp.), *Litocalliopsis* Roig-Alsina & Compagnucci (1 sp.), *Spinoliella* (17 spp.), *Xeranthrena* Gonzalez & Engel (1 sp.). The phylogenetic positions of *Liopoeodes*, *Litocalliopsis* and *Xeranthrena* are uncertain and need to be further studied.

PHYLOGENY AND DIVERSIFICATION OF ANDRENIDAE

Systematic
Entomology

Royal
Entomological
Society

291

Tribe Melitturgini Newman. Type genus: *Melitturga* Latreille.

= Camptopoeini Patiny, 1999 [originally as Camptopoeumini, corrected by Engel, 2005]. Type genus: *Camptopoeum* Spinola, 1843. **syn.n.**

Comment: Our concatenation and coalescent-based phylogenetic analyses found strong support for a sister-group relationship of *Camptopoeum* (excluding 'Camptopoeum' baldocki Wood & Cross) to *Melitturga*, which is the type genus of Melitturgini. This relationship has been found in previous studies using molecular data (Cardinal et al., 2018; Hedtke et al., 2013). Since none of the other genera of Melitturgini sensu Michener (2007) is closely related to this group, but instead are closely related to Panurgini (Figure 2), we consolidate *Camptopoeum* and *Melitturga* in the tribe Melitturgini and formally synonymize Camptopoeini.

Genera included in Melitturgini: *Melitturga* (17 spp.), *Camptopoeum* (31 spp.)

Tribe Panurgini Leach. Type genus: *Panurgus* Panzer.

= Meliturgulini Engel, 2001. Replacement name for Paramelitturgini Patiny, 1999. Type genus *Meliturgula* Friese, 1903. **syn.n.**
= Mermiglossini Patiny, 1999. Type genus: *Mermiglossa* Friese, 1912. **syn.n.**
= Panurginini Patiny, 1999. Type genus: *Panurginus* Nylander, 1848. **syn.n.**

Comment: To avoid excessive splitting at the tribal level, we consolidate the four small tribes Panurgini, Meliturgulini, Mermiglossini and Panurginini in one tribal concept, Panurgini.

Genera included in Panurgini: *Avpanurgus* Warncke (1 sp.), *Borgatomelissa* Patiny (3 spp.), *Clavipanurgus* Warncke (11 spp.), *Flavipanurgus* Warncke (7 spp.), *Flavomeliturgula* Patiny (5 spp.), *Gasparinahla* Patiny (1 sp.), *Meliturgula* Friese (13 spp.), *Mermiglossa* Friese (2 spp.), *Panurginus* Nylander (52 spp.), *Panurgus* Panzer (35 spp.), *Plesiopanurgus* Cameron (4 spp.), *Simpanurgus* Warncke (1 sp.). The phylogenetic positions of *Avpanurgus*, *Gasparinahla* and *Simpanurgus* are uncertain and need further study.

Tribe Neffapini Ascher. Type genus: *Neffapis* Ruz.

Genus included in Neffapini: *Neffapis* Ruz (1 sp.).

Tribe Nolanomelissini Rozen. Type genus: *Nolanomelissa* Rozen.

Genus included in Nolanomelissini: *Nolanomelissa* (1 sp.).

Tribe Perditini Robertson.

Genus *Pseudomacrotera* Timberlake, 1954. **stat.n.**

= *Perdita* (*Pseudomacrotera*) Timberlake, 1954. Type species: *Perdita turgiceps* Timberlake, 1954. [raised to genus rank].

Comment: This lineage only comprises *Pseudomacrotera turgiceps* and was previously recognized as a subgenus of *Perdita*. We found *Pseudomacrotera* as a sister group to *Macrotera* Smith + *Perdita*, requiring a taxonomic change to reflect its phylogenetic position. Interestingly, *Pseudomacrotera* has morphological features of both *Perdita* and *Macrotera*, and further has males with bimodal head size (Michener, 2007), as frequently observed in these genera. This suggests the possibility that varying head size in males is an ancestral condition for Perditini.

Genera included in Perditini: *Macrotera* (31 spp.), *Perdita* (637 spp.), *Pseudomacrotera* (1 sp.) **stat.n.**

Tribe Protandrenini Robertson. Type genus: *Protandrena* Cockerell.

= Protomeliturgini Ruz, 1991. Type genus: *Protomeliturga* Ducke, 1912. **syn.n.**

Comment: The previously recognized tribe Protomeliturgini includes only the genus *Protomeliturga* with two described species. Our ML analyses found *Protomeliturga* closely related to Protandrenini (Figure S1) and the coalescent-based ASTRAL tree found it even within this tribe (Figure S2). To avoid potential paraphyly and oversplitting at the tribal level, we propose to include *Protomeliturga* in Protandrenini and formally synonymize the tribe Protomeliturgini. To date, the phylogeny of Protandrenini is not well understood and deserves further investigation with denser taxon sampling. Several of the genera listed below require revision and their taxonomic status and circumscriptions will need to be reevaluated, which will affect future interpretations of the systematics of the tribe. Specifically, we consider the genus *Protandrena* in a larger sense that includes the subgenera *Anthemurgus* Robertson **stat.n.**, *Heterosarus* Robertson, *Metapsaenythia* Timberlake, *Protandrena* s. str., *Pseudopanurgus* Cockerell **stat.n.**, and *Pterosarus* Timberlake. The monophyly of *Heterosarus* and *Pterosarus* remains to be established. *Rhophitulus* Ducke, paraphyletic in the present study, needs further study with more extensive sampling.

Genera included in Protandrenini: *Andinopanurgus* Gonzalez & Engel (12 spp.), *Anthrenoides* Ducke (63 spp.), *Austropanurgus* Toro (2 spp.), *Chaeturginus* Lucas de Oliveira & Moure (2 spp.), *Incasarus* Gonzalez, Rasmussen & Engel (1 sp.), *Liphanthus* Reed (49 spp.), *Parapsaenythia* Friese (7 spp.), *Parasarus* Ruz (3 spp.), *Protandrena* (186 spp.), *Protomeliturga* (2 spp.), *Psaenythia* Gerstaecker (72 spp.), *Psaenythisca* Ramos (3 spp.), *Pseudosarus* Ruz (1 sp.), *Rhophitulus* (38 spp.).

Future directions of panurgine taxonomy

The taxon sampling used in this study covers all major lineages of Andrenidae. However, it is not sufficient to ultimately address all phylogenetic relationships at the genus and species levels. In particular, the following panurgine lineages require further systematic work:

1. The phylogeny of the species-rich Protandrenini needs to be revised. *Pseudopanurgus*, as currently used (Ascher & Pickering, 2021), is not monophyletic, and *Pterosarus* as well as *Pseudosarus*, '*Protandrena*' *avulsa* Ramos & Melo, and '*Protandrena*' *evansi* Ruz & Chiappa need to be included in future studies. We were unable to incorporate them into our analyses, and their phylogenetic relationships are uncertain. Our analyses indicate that recognition of the monotypic genus *Anthemurgus* renders *Protandrena* paraphyletic and it should be recognized instead as a subgenus. Additionally, the South American *Rhophitulus*, as used on the Discover Life database (Ascher & Pickering, 2021), intergrade into the species-rich genera *Anthrenoides* and *Psaenythia*. However, both *Anthrenoides* and *Psaenythia* are well-recognizable groups, whereas *Rhophitulus* is problematic and needs to be revised. For example, '*Rhophitulus*' *herbsti* (Friese), as included in our tree, is likely not a member of this genus (Ramos, 2011) and both other included *Rhophitulus* are from the *Cephalurgus* group. This means that we likely did not include a true representative of *Rhophitulus* in the present study. This situation warrants further investigation with comprehensive taxon sampling of South American Protandrenini.

2. '*Camptopoeum*' *baldocki* is a recently described species of Panurginae from Portugal (Wood & Cross, 2017). Despite the morphological resemblance to other species of *Camptopoeum*, this species is rather distantly related to this genus, with an estimated age of their most recent common ancestor (MRCA) of ~46 Ma. Instead, it is closely related to '*Flavipanurgus*' *fuzetus* Patiny, with which it shares a series of morphological features as shown in Wood & Cross (2017). The two species co-occur and are similar in their ecology and distribution, as both species are only known from saltmarshes in southern Portugal (Wood & Cross, 2017). Since this sister-group relationship renders *Flavipanurgus* paraphyletic, these two species will need to be combined in a new taxon.

3. *Clavipanurgus*, a genus with primary distribution in the Eastern Mediterranean, is sister group to the two species of Old World *Panurginus* included in the present study. The status of *Clavipanurgus* is uncertain; since its original description as a subgenus of *Panurginus* (Warncke, 1972), it has been viewed as a subgenus, synonym of *Panurginus* and a separate genus (Michener, 2000, 2007; Patiny, 2003). The only sample included in this study of *Panurginus* from North America, where the genus is present with at least 18 species, was recovered as sister to this Old World clade and renders *Panurginus* paraphyletic. Certain North American *Panurginus* were treated under the now-synonymized name *Greeleyella* Cockerell (Cockerell, 1904) and our included species *Panurginus occidentalis* (Crawford) was described in *Greeleyella* (Crawford, 1916). Resolving the paraphyly of *Panurginus* could be achieved by either synonymizing *Clavipanurgus* with *Panurginus*, as done by Michener (2007), or by resurrecting *Greeleyella*. In any case, we found our taxon sampling too sparse to confidently delineate the species groups and argue that any such name changes should be accompanied by a thorough revisionary study with broad taxonomic coverage from both the Palearctic and Nearctic. Such revisionary work must include East Asian material including the type species of the genus *Panurginus* (*P. niger* Nylander) to fully resolve this issue.

4. The subgenus *Panurgus* s. str. Panzer was rendered paraphyletic by the subgenus *Euryvalvus* Patiny. We refrain from synonymizing these subgenera until this group can be reevaluated with denser taxon sampling.

5. For the purpose of this study, we diversified our taxon sampling to include the greatest phylogenetic breadth of Perditini as possible. For *Perdita* and *Macrotera*, we included 19 out of the 21 subgenera recognized by Michener (2007). Several of these subgenera are likely not monophyletic groups, such as *Glossoperdita* Cockerell, *Epimacrotera* Timberlake, and the species-rich *Perdita* (*Perdita*) Smith, (>400 described spp.; Danforth, 1996). Resolving these groups is not possible with our limited taxon sampling and considerable future research is needed to better understand the evolutionary relationships within Perditini.

6. While phylogenetic relationships among panurgine tribes are stable throughout our analyses, we identified two rogue taxa that changed position within their respective tribes when using different methods: *Flavomeliturgula tapana* (Warncke) and *Andinopanurgus wayruronga* (Gonzalez & Ruz). Specifically, both their phylogenetic positions changed from being nested within their tribes in the concatenation analyses to being sister group to all remaining taxa of their tribes in the gene tree analyses (Figures S1 and S2). This warrants further study, ideally by including additional species of these genera in future research.

Antiquity of Andrenidae

Fossil-informed divergence time estimates under the fossilized birth–death model revealed a late Cretaceous (~90 Ma) origin for the family Andrenidae (Figure 1). With a crown age of ~67 Ma, Panurginae likely originated in close temporal proximity to the K–T boundary (~66 Ma, Figure 2) and the associated mass extinction of marine and terrestrial life (e.g., Keller, 2001; Labandeira et al., 2002; Longrich et al., 2012), including some bees (Rehan et al., 2013). Andreninae has a crown age that is slightly younger (~58 Ma) and originated in the early Paleogene, while the morphologically derived Oxaeinae is likely relatively young (~29 Ma). Replicating our dating analysis with four different subsets of 100 UCEs produced highly consistent age estimates for all subfamilies (Figure 3a). This consistency shows that using different subsets of loci has a limited effect on our age estimates and that our results are robust to different locus selection criteria.

While our crown ages overlap with previous estimates of andrenid divergence times (Cardinal et al., 2018; Cardinal & Danforth, 2013; Pisanty et al., 2021), they tend to be slightly older (Figure 3a). This can be explained in two ways. First, our taxon
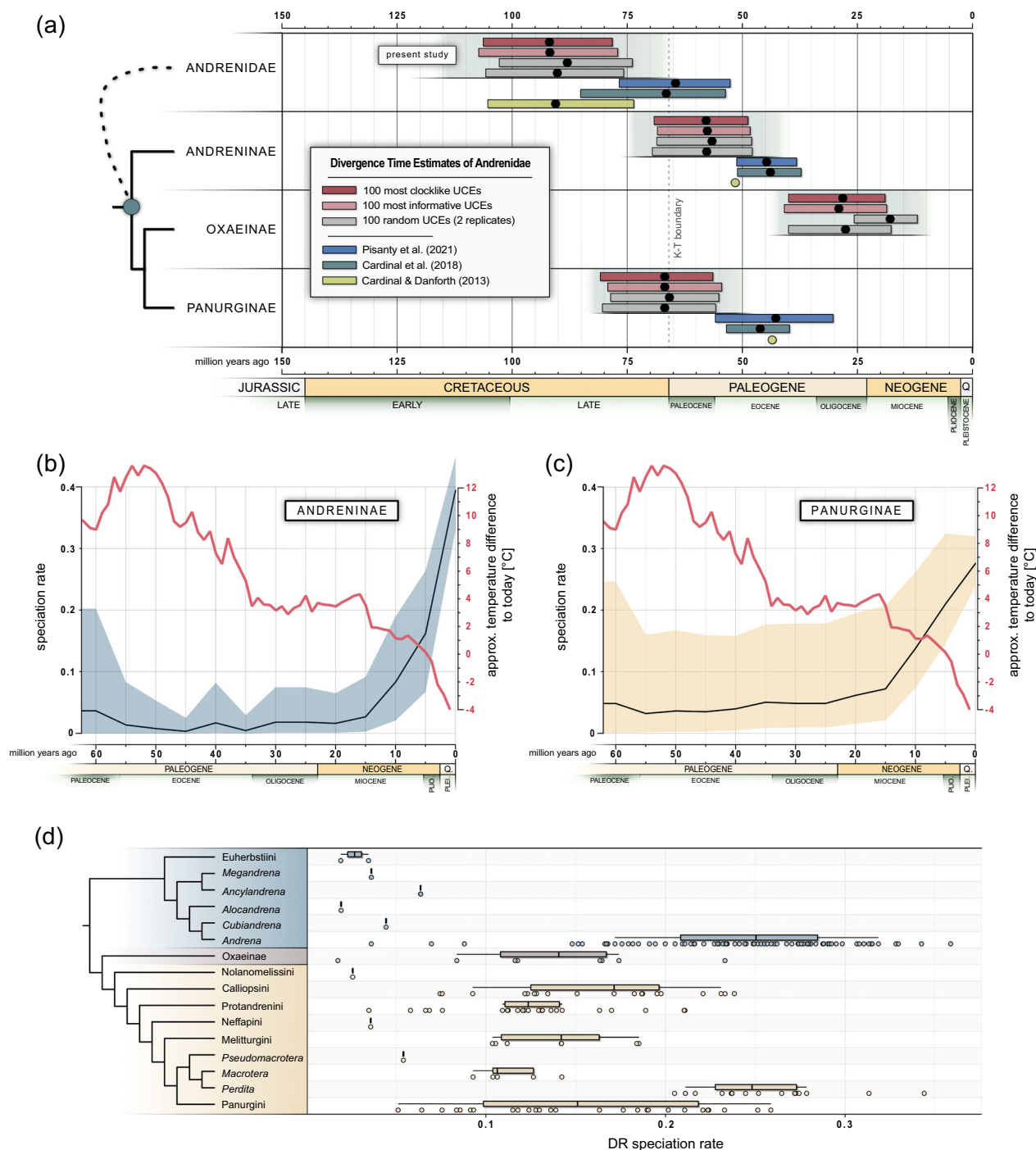
PHYLOGENY AND DIVERSIFICATION OF ANDRENIDAE

Systematic
Entomology

Royal
Entomological
Society

293

FIGURE 3 Antiquity and speciation rates of Andrenidae. (a) Comparison of age estimates for different groups of Andrenidae, with a 95% highest posterior density (HPD) range when provided. (b) Speciation rates of Andreninae inferred with the episodic birth–death model and time intervals of 5 Ma. (c) Speciation rates of Panurginae using the same approach. Estimates for the approximate annual air temperature difference to the present-day are derived from Westerhold et al. (2020). (d) Diversification rate (DR) values for the tribes of Andrenidae and the genera of Andrenini and Perditini. Each point shows the median DR tip rate for an individual species of Andrenidae calculated from 200 simulated, fully resolved phylogenies. The full range of DR values for each species is shown in Figure S9

sampling is more comprehensive and includes nearly every described, currently accepted genus of Andrenidae. This ensures the inclusion of early-branching lineages, which necessarily leads to older crown ages. For example, Cardinal and Danforth (2013) estimated a crown age of

Panurginae of ~45 Ma based on four species that did not include *Nolanomelissa*, the earliest branching lineage in the present study. Although our crown age estimate is significantly older (67.4 Ma, Figure 2), the stem age estimates are very similar to theirs (~76 vs. 77.8

Ma, respectively). Furthermore, the age estimates for the family Andrenidae as a whole are very similar between these two studies: ~91 Ma from Cardinal and Danforth (2013) versus our estimated mean of 91.9 Ma. Given the differences in taxon sampling, tree prior choice, fossil usage and DNA sequence data (5 protein-coding genes vs. 100 UCEs), these estimates are remarkably similar. Second, our study did not specifically calibrate nodes with ages of fossil specimens ('node dating'). Instead, we included fossils as tips ('tip dating') under the FBD model, thereby eliminating the need to assign age constraints to internal nodes (e.g., Luo et al., 2020; Ronquist, Klopfstein, et al., 2012; Zhang et al., 2016). This means that, while we incorporated the same four putative andrenid fossils as in Cardinal et al. (2018) (with one exception), we did not constrain the node ages for Andreninae and Panurginae with the same prior distribution, effectively letting the Bayesian MCMC infer ages more freely. The exception is *Andrenopteryx willardi*, a compression fossil from the Florissant fossil beds, which was associated with Andreninae using wing morphometric analyses (Dewulf et al., 2014). This fossil is the oldest 'andrenid' fossil in Cardinal et al. (2018) but was used by them to calibrate the unrelated genus *Melitta* (Melittidae), likely because of its placement in the original description (Cockerell, 1909). Consequently, all four UCE subset replicates in our study clearly favour an older origin of Andreninae and Panurginae. Pisanty et al. (2021) used node ages from Cardinal et al. (2018) as secondary calibrations, and hence our differences to these two studies are similar.

The spatiotemporal origin and the phylogenetic position of *Nolanomelissa* are of particular interest. The single extant species of this genus, *Nolanomelissa toroi* Rozen, is a sister group to all the remaining ~1400 species of Panurginae and diverged at around 67.4 Ma (56.4–80.9 Ma, 95% highest posterior density). It occurs only in a restricted area in the southern part of the Atacama Desert, where it has been found to forage pollen only from *Nolana* L.f. (Solanaceae) (Rozen, 2003). *Nolana* as a genus is thought to have a stem age of ~10.9 Ma and a crown age of ~6.3 Ma (Särkinen et al., 2013). Therefore, the crown age of *Nolanomelissa* predates the age of its host plant lineage by ~61.1 million years, meaning that the lineage leading to present-day *Nolanomelissa* must have foraged on other plants in this time frame.

Diversification dynamics

Diversification across Andrenidae

Our analyses identified *Andrena* and *Perdita* as the fastest diversifying lineages of Andrenidae, with rapid radiations continuing into the Holocene (Figures 3 and 4). Speciation estimates under episodic birth–death models of RevBayes (Höhna et al., 2016) show sharp increases for both Andreninae and Panurginae in the Neogene, starting in the episodes of 20–15 Ma and 25–20 Ma, respectively (Figure 3b,c). This time frame is comparable with the rate shifts identified through BAMM. The most probable rate shift regime found three

upward shifts in diversification rates: (1) an increase early in the evolution of *Andrena* (~18 Ma), (2) a shift coincident with the origin of *Perdita* (~21 Ma), and (3) a rate increase involving all Panurginae except the monotypic Nolanomelissini (~70 Ma, Figure 4a). Extremely similar dynamics were captured estimating only speciation rates (Figure S3) in BAMM. Following the most commonly observed scenario of rate shifts ($f = 0.084$, Figure S4), the eight most frequently recovered configurations are similar but differ as follows: the exact positions of the shift within *Andrena*, a slight increase in the branch leading to the common ancestor of Panurginae and Oxaeinae, the presence of rate decreases along the branches of Neffapini, Nolanomelissini, and *Andrena bytinskii*, or a combination thereof (Figure S4). Strikingly, every shift configuration recovered diversification/speciation increases for *Andrena* and *Perdita*, clearly reflecting their extraordinary contemporary species richness. However, while a rate increase with the origin of *Perdita* was unequivocally recovered in every regime, its exact timing should be interpreted with caution. We used a diversified taxon sampling to include the greatest phylogenetic breadth of Perditini by including 19 out of the 21 recognized subgenera (Michener, 2007). However, several subgenera, such as the very species-rich *Perdita* s. str. (>400 spp.), are almost certainly paraphyletic (Danforth, 1996) and the phylogenetic relationships among the many species groups remain inadequately resolved. This precluded us from precise designations of missing species for individual clades and required an even distribution of missing species across all branches of *Perdita*. This means that, while a rate increase within *Perdita* can be expected with certainty, it may in fact have taken place at a node or branch that was not phylogenetically characterized in our study.

While the sharp increases of speciation for *Perdita* and *Andrena* temporally coincide with declining global air surface temperature (Westerhold et al., 2020), we did not find a direct correlation with this environmental variable in our analyses: correlation probability between global temperature and speciation rates is only 0.38 (Andreninae) and 0.28 (Panurginae). A model without environmentally correlated speciation is favoured but BFs are low (0.61 and 0.40, respectively). We found a slightly greater probability of correlation with paleoclimatic CO_2 with 0.52 for both Andreninae and Panurginae (Figure S5), but negligible BFs (1.07 and 1.1, respectively). This confirms that neither of the environmental factors we examined fully explain the present-day species richness of Andrenidae. While correlations with individual paleoclimatic factors have been shown in the past for groups of plants (Lagomarsino et al., 2016; Sun et al., 2020; Thompson et al., 2021), other insects (Sahoo et al., 2017; Toussaint et al., 2012), vertebrates (Botero et al., 2014; Claramunt & Cracraft, 2015), or a combination thereof (Kergoat et al., 2018), diversification dynamics are best understood by considering both abiotic and biotic factors (Condamine et al., 2018; Ezard et al., 2011). Accordingly, the term 'confluence' was introduced (Donoghue & Sanderson, 2015) to better capture scenarios in which biotic factors (e.g., innovations) and environmental change (e.g., climate and geographic range) sequentially assemble, moving away from the simplified concept of single key innovations. For the evolution of Andrenidae,
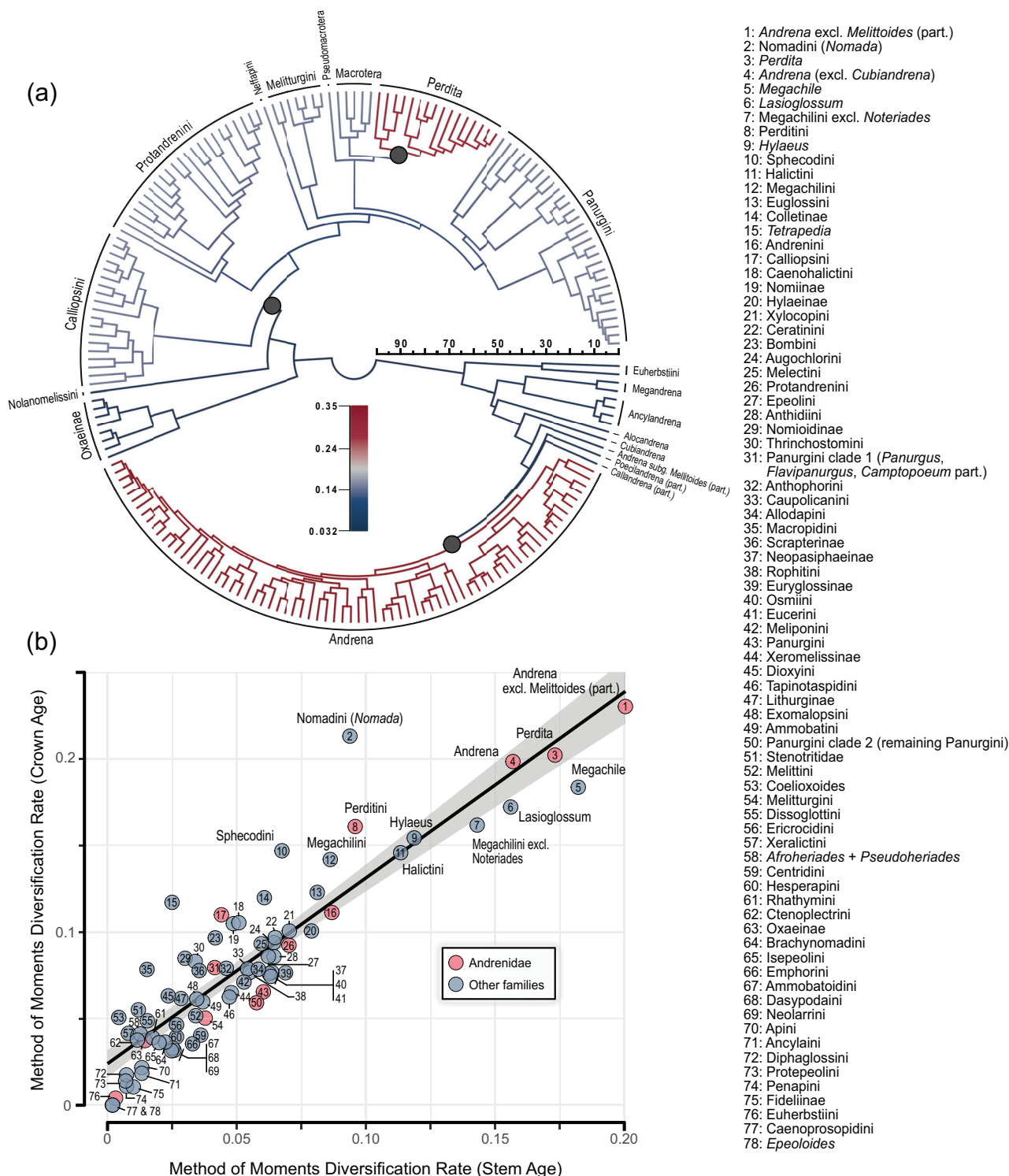
1: *Andrena* excl. *Melittoides* (part.)
2: Nomadini (*Nomada*)
3: *Perdita*
4: *Andrena* (excl. *Cubiandrena*)
5: *Megachile*
6: *Lasioglossum*
7: Megachilini excl. *Noteriades*
8: Perditini
9: *Hylaeus*
10: Sphecodini
11: Halictini
12: Megachilini
13: Euglossini
14: Colletinae
15: *Tetrapedia*
16: Andrenini
17: Calliopsini
18: Caenohalictini
19: Nomiinae
20: Hylaeinae
21: Xylocopini
22: Ceratinini
23: Bombini
24: Augochlorini
25: Melectini
26: Protandrenini
27: Epeolini
28: Anthidiini
29: Nomioidinae
30: Thrinchostomini
31: Panurgini clade 1 (*Panurgus*, *Flavipanurgus*, *Camptopoeum* part.)
32: Anthophorini
33: Caupolicanini
34: Allodapini
35: Macropidini
36: Scrapterinae
37: Neopasiphaeinae
38: Rophitini
39: Euryglossinae
40: Osmiini
41: Eucerini
42: Meliponini
43: Panurgini
44: Xeromelissinae
45: Dioxyini
46: Tapinotaspidini
47: Lithurginae
48: Exomalopsini
49: Ammobatini
50: Panurgini clade 2 (remaining Panurgini)
51: Stenotritidae
52: Melittini
53: Coelioxoides
54: Melitturgini
55: Dissoglottini
56: Ericrocidini
57: Xeralictini
58: *Afroheriades + Pseudoheriades*
59: Centridini
60: Hesperapini
61: Rhathymini
62: Ctenoplectrini
63: Oxaeinae
64: Brachynomadini
65: Isepeolini
66: Emphorini
67: Ammobatoidini
68: Dasypodaini
69: Neolarrini
70: Apini
71: Ancylaini
72: Diphaglossini
73: Protepeolini
74: Penapini
75: Fideliinae
76: Euherbstiini
77: Caenoprosopidini
78: *Epeoloides*

FIGURE 4 Diversification dynamics of Andrenidae and other major lineages of bees. (a) Dated phylogeny of Andrenidae with branches coloured according to their net diversification rates from the BAMM analysis. The most frequently recovered configuration ($f = 0.084$) has three rate shifts (grey circles), all of which are rate increases. This involves an early branching within *Andrena* (*Andrena* excluding the early branching subgenera *Melittoides* [partial], *Poecilandrena* [partial], and *Callandrena* [partial]), an upshift coincident with the origin of *Perdita*, and an increase at the earliest branch of Panurginae excluding *Nolanomelissa*. (b) Diversification rate estimates for the tribes of all seven bee families and major bee genera (i.e., those over ≥600 described spp.). Net diversification is calculated using method-of-moments estimators and an extinction fraction (ϵ) of 0.9 (see Figure S6 for estimates with alternative ϵ values) and with stem and crown ages. The grey area shows the 95% CI of the linear regression. Twelve species-poor or monotypic tribes or genera were omitted from the plot due to the lack of crown age estimates. BAMM, Bayesian Analysis of Macroevolutionary Mixtures; CI, confidence interval

this process-oriented view suggests that a cooling, changing climate with stronger seasonality elicited biotic factors to contribute to an environment well suited to lineages of primarily solitary, univoltine, host-plant specialists, such as many species of *Andrena* and *Perdita*.

One obvious biotic factor is the marked evolutionary success of the most important lineage of host plants of *Andrena* and *Perdita* over the past 30 million years. Asteraceae, the single most important host plant lineage for Andrenidae (TJW, unpublished data), underwent increased diversification in the Oligocene and Miocene (Panero & Crozier, 2016). Specifically, Panero and Crozier (2016) identified a diversification rate increase involving the Helianthodae around 24 Ma, which is largely coincident with our crown age estimates of *Andrena* and Perditini. This Asteraceae lineage of over 3000 North American species includes the sunflowers (*Helianthus* L.) and several other genera (e.g., *Bidens* L., *Ericameria* Nutt., *Rudbeckia* L.) that are host to numerous andrenid pollen specialists (Krombein et al., 1979). Similarly, several other major host-plant lineages experienced increased diversification in the Neogene, such as Rosaceae (Zhang et al., 2017), Brassicaceae (Huang et al., 2020) and the large rosid clades Fabales, Geraniales, and, to a lesser extent, Malvales (Sun et al., 2020). Strikingly, the disproportionate diversification of rosids overlaps both temporally and geographically with the diversification of *Andrena* and *Perdita* in the Northern Hemisphere, including arid southwestern North America (Sun et al., 2020). Given the tight, present-day host plant associations of Andrenidae with the above-mentioned lineages, it is reasonable to assume that these biotic factors contributed to the diversification process of Andrenidae, but its extent and the possibility of codiversification remain to be tested statistically in a more extensive phylogenetic framework.

Finally, despite the temporal overlap of speciation increases in *Andrena* and *Perdita*, the underlying factors that contributed to their diversification are not necessarily the same. *Perdita* is geographically restricted to North America with unmatched species-richness in the xeric regions of the American Southwest. Nearly all species are narrowly oligolectic and highly seasonal. *Andrena*, in contrast, comprises a mix of generalist and specialist species, some of which are highly seasonal, whereas other species are multivoltine. The genus is most species-rich in the Holarctic, but are also found in Central America, Africa and southern Asia, and its rapid speciation involves lineages in both North America and Eurasia (see Historical Biogeography section). Interestingly, the pollen-collecting behaviour of *Andrena* and *Perdita* is different as well. All species of *Andrena* transport collected pollen dry, without applying nectar or floral oils to moisten the pollen load. With the exception of a few derived lineages, *Perdita* females transport moistened pollen (Portman & Tepedino, 2017).

Corroboration of estimates and comparison to other bees

We corroborated our estimates of diversification and speciation with MoM estimators (Magallón & Sanderson, 2001). MoM is a phylogeny-independent approach to calculate rates using clade-specific ages and species richness. Our estimates of andrenid diversification rates from this approach corroborate very high rates for *Andrena* and *Perdita* (Figures 4b and S6). MoM rate estimates for other andrenid groups are similar to those from BAMM (Table S4) and are, as expected, strongly correlated to these (Figure S7).

We also used MoM to calculate diversification rates across all bee tribes and large genera using previously published age estimates and data on species richness. Using crown ages under four scenarios of relative extinction, including a pure-birth process ($\varepsilon = 0$), we found *Andrena* and *Perdita* among the three lineages with the highest diversification rates across all ~20,500 species of bees (Figures 4b and S6): *Andrena*, *Perdita* and *Nomada*. The two other very species-rich bee genera *Lasioglossum* (>1850 spp.; crown age of ~30 Ma according to Gibbs et al., 2012) and *Megachile* (>1450 spp.; sensu Ascher & Pickering, 2021; crown age of ~27 Ma according to Trunz et al., 2016) are both slightly older than *Andrena* and hence have slightly lower crown age-based clade diversification. Interestingly, we consistently recovered *Nomada* (the sole genus of Nomadini, Apidae) as a third lineage with a very high diversification rate. *Nomada* is a genus of brood parasitic bees comprised of more than 700 described species in the family Apidae that primarily attack *Andrena*, although a few species also attack bees from other families. For example, in Central Europe, the majority of *Andrena* species are parasitized by at least one species of *Nomada*, except for a few species for which no parasite is known (Amiet & Krebs, 2012; Gusenleitner et al., 2012; Westrich, 2018). Strikingly, most *Nomada*, for which host information is available, have been associated with one species of *Andrena*, even to the extent that they are bivoltine if their hosts have two generations a year as well (Scheuchl, 1995; Westrich, 2006; Westrich, 2018). They even mirror the spatial richness patterns of *Andrena*: *Nomada* is species-poor where *Andrena* is rare, such as in tropical Africa (Eardley & Schwarz, 1991), and only a single species of *Nomada* is known from Australia (Alexander, 1994), where *Andrena* is absent (the Australian species parasitizes *Lasioglossum* (*Homalictus*), Halictidae (Walker et al., 2020).

Our findings strongly indicate that the parasitic *Nomada* has codiversified along with their principal host lineage *Andrena*: *Nomada* seemingly diversified at similar rates to their principal host lineage. However, the stem age-based rates of *Nomada* diversification are comparatively small and the estimates significantly deviate from the 95% confidence interval of the linear regression (Figure 4b). This indicates that even though *Nomada* diversification is certainly very high, its crown age-based diversification rate estimates may be overestimated, which would be expected if the crown age has been underestimated due to incomplete sampling.

Historical biogeography

Our time frame of andrenid evolution provides an unprecedented opportunity to study the biogeography of Andrenidae. Andrenid biogeography has been studied previously: in his major 1979 study on the biogeography of bees, Michener (1979) discussed a probable Laurasian origin for the family and emphasized the Western

Hemisphere because of its diversity of genera. At the time, he considered Oxaeinae as a separate family and assumed its origin was Neotropical. Ascher's (2004) thesis provides an in-depth discussion on andrenid biogeography, including several potential dispersal routes that were also recovered in our analysis. Finally, Hedtke et al. (2013) estimated ancestral ranges for all subfamilies of bees, including those of Andrenidae. As such, their work does not capture dispersal or vicariance events at lower taxonomic levels (Hedtke et al., 2013). Although all these studies are geographically comprehensive, they lack the temporal context of divergence time estimates, which are critical to understand the timing and direction of geographic range changes and hence to trace back the historical biogeography of Andrenidae as a whole.

By testing the model fit of the three biogeographic models with AICc scores, we found the DEC model (Ree & Smith, 2008) as the best fit for our data. Using this model, our results indicate a South American origin of Andrenidae and all three subfamilies, with the exception that Andreninae also includes North America in its ancestral range (Figures 1, 2 and S8). We recovered similar dispersal routes explaining the present-day distributions of the two subfamilies Andreninae and Panurginae, but the timing of their respective range expansions is different and detailed below.

Andreninae

The MRCA of Andreninae most likely originated in South America, from where it would have traversed over the Central American Seaway to North America between ~90 and ~60 Ma (Figure 1). Aside from a slightly older time frame, this finding matches Pisanty et al.'s (2021) biogeographic assessment of the subfamily. While it seems unlikely that one species simultaneously occupied two regions over a significant water barrier at the time, dispersal from the Neotropics to the Nearctic region must have occurred in some form (Figure 1, upper inset). As previously suggested (Pisanty et al., 2021), dispersal may have occurred in a stepwise manner over islands in the Central American Seaway, which at times only required the crossing of relatively short stretches of water. Our results indicate that a series of cladogenetic events in the mid-Paleogene split this trans-American lineage into (1) the present-day Euherbstiini, which is endemic to Chile; (2) the clade comprising *Megandrena* and *Ancylandrena*, which is restricted to xeric southwestern North America; (3) the Peruvian-endemic *Alocandrena*; and (4) the lineage that led to the present-day *Andrena*. The last lineage likely first traversed from the Nearctic to the Palearctic between ~42 and ~33 Ma, forming a Holarctic distribution (Figure 1, lower inset). This clearly shows that even though *Andrena* is among the most species-rich bee genera in the Palearctic today, all early branching, relictual lineages of Andreninae originated in the Western Hemisphere. However, the direction of this first Nearctic-Palearctic dispersal is difficult to reconcile with today's understanding of geological history, as it coincides with the disappearance of the North Atlantic Land Bridges (NALBs) in the Eocene (Milne, 2006; Tiffney, 1985). The range expansion towards the Palearctic could have taken this transatlantic route or alternatively gone over the Bering

Land Bridge (BLB), which formed an alternative land bridge at the time. The Bering route appears more obvious given the xeric habitats found in western North America and the current presence of early-branching lineage of Andreninae. Our analysis shows that the MRCA of *Andrena* + *Cubiandrena* and the descending lineage that gave rise to present-day *Andrena* likely held Holarctic distributions for extensive periods of time (Figure 1). This likely led to numerous subsequent cladogenetic events in Eurasia and North America. While we also found evidence for geodispersal between the Palearctic and the Nearctic, they are less numerous than predicted based on previous treatment of andrenine biogeography (Pisanty et al., 2021). This can be explained by a smaller set of *Andrena* species included in the present study. Finally, our results indicate that the Afrotropical region was populated recently with a geodispersal from the Palearctic to Africa around 4 Ma. Today there are five subgenera of *Andrena* reported from Africa (Eardley et al., 2010), none of which are African endemics, suggesting that additional dispersal events occurred which our analysis was not able to capture because of limited taxon sampling of Afrotropical *Andrena*.

Panurginae

The historical biogeography of Panurginae is characterized by a South American origin, three separate range expansions to the Nearctic and one exchange between North America and Eurasia (*Panurginus*, Figure 2). The earliest range expansion from the Neotropics to the Nearctic likely occurred ~50 Ma, when both the BLB and the NALBs were available, and was followed by fast vicariant cladogenesis (Figure 2, upper inset). One descendant lineage is monotypic today and only represented by *Neffapis longilingua* from the southern Atacama Desert. The other descendant lineage expanded its range from the Nearctic to the Palearctic in the mid-Paleogene, forming a Holarctic distribution. Subsequent cladogenetic events split this widespread MRCA into the present-day Melitturgini, Perditini, and Panurgini as defined herein (Figure 2, upper inset). At present, Melitturgini and Perditini occur primarily in xeric habitats of the Palearctic and Nearctic, respectively, in contrast to Panurgini which underwent additional range expansion in a wider range of habitats. We found evidence for at least two separate geodispersals of panurgine lineages from the Palearctic to the Afrotropics, around 35 and 25 Ma (Figure 2, lower inset). Presumably, these events gave rise to the genus *Mermiglossa* with at least three species (with one undescribed species included here), *Borgatomelissa* (3 spp.) and *Meliturgula* (13 spp.). *Panurginus* represents the only recovered panurgine lineage for which we found a return to North America around 12 Ma, when the BLB would have been available.

For the New World Panurginae, we recovered the MRCA of Protandrenini to be of South American origin. Within Protandrenini, we found a monophyletic group comprising the North American species, which indicates a single geodispersal event from the Neotropics to the Nearctic in the Oligocene. This clade's extended, trans-American range in Figure 2 is explained by the lenient coding of *Protandrena bakeri* as being present in the Neotropics, because this taxon extends

south into montane habitats of Mexico (Timberlake, 1975). However, it is primarily a North American species. Similarly, we found a clade of North American *Calliopsis*, which indicates a single dispersal from the Neotropics to the Nearctic in this group.

Oxaeinae

This small subfamily of 22 species was estimated to have originated in the Neotropical region and dispersed to North America between 29 and 20 Ma. This view differs from a previous assessment because of the position of the monotypic *Notoxaea*. Ascher (2004) inferred *Protoxaea*, which occurs in the southwestern Nearctic, to be the earliest branching oxaeine lineage, thereby suggesting the possibility of a North American origin for the subfamily. In contrast, we found strong support for *Notoxaea* being the sister group to all other Oxaeinae. Aside from *Notoxaea*, this subfamily is principally divided into a Nearctic clade comprising *Protoxaea* and *Mesoxaea*, and a Neotropical clade with *Oxaea* and most likely *Alloxaea*. However, both clades have individual species that extend into Central America, blurring this distinct pattern in the present day.

Global patterns

From a South American origin, Andrenidae likely expanded to inhabit diverse habitats across the globe, with the greatest species diversity in the northern temperate zone, particularly in xeric regions (Danforth et al., 2019; Michener, 2007; Orr et al., 2021; Ruz, 1986). Our results show that all but one dispersal route that led to the present-day distribution of Andrenidae temporally coincide with the existence of land bridges. Presumably, only the initial expansion from South America to North America must have occurred over relatively short stretches of water. Since modern-day Andrenidae are absent from many major islands like Sri Lanka, New Guinea, and most of the Caribbean Islands, it appears that they rarely traverse over water. This provides an explanation for the absence of Andrenidae in Australia: at no time since their origin was Australia connected to a continent inhabited by Andrenidae. The only major landmass that remained connected to both Australia and South America through most of the Paleogene was Antarctica, but we speculate that Antarctica likely did not harbour an andrenid bee fauna, even during times when its climate was warmer. Trans-Antarctic interchanges between Australia and South America have been shown for other groups of bees and are most evident for the bee family Colletidae (Almeida et al., 2012, 2019). According to our results, Andrenidae was present on the South American landmass since the late Cretaceous or early Palaeocene. However, this does not mean that andrenids occupied Antarctica or even the southern portion of South America—areas assumed to have hosted cool temperate rainforests during much of the Cenozoic (Cantrill & Poole, 2012; Klages et al., 2020), similar to Valdivian rainforests of southern South America today. In-line with this, the few bee surveys conducted in southern South America record little or no Andrenidae diversity in comparison to surveys from northern areas (e.g., Smith-Ramírez et al., 2005; Spagarino et al., 2001; Vázquez & Simberloff, 2002).

CONCLUSIONS

Our study comprises the first comprehensive phylogenomic treatment of Andrenidae including all major lineages and provides significant, basic knowledge on a near-globally distributed lineage of pollinating insects. We establish the family's spatiotemporal origin and characterize their rapid diversification, which includes two of the fastest radiations across all bees. Nonetheless, significant questions on the mechanisms of their diversification, as well as on phylogenetic relationships at the genus level remain to be answered. Our results have broad implications for understanding the tempo and mode of bee diversification and, more broadly, bee-angiosperm coevolution.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw Illumina sequence reads are available in the Sequence Read Archive (SRA) under BioProject PRJNA767669 or under the specifier in Table S1. SPAdes assembly files, alignments, tree files, high-resolution figures, and various scripts and config/input files used for this project are available on FigShare (https://doi.org/10.6084/m9.figshare.14593629.v3).

ORCID

Silas Bossert https://orcid.org/0000-0002-3620-5468

Thomas J. Wood https://orcid.org/0000-0001-5653-224X

Denis Michez https://orcid.org/0000-0001-8880-1838

Eduardo A. B. Almeida https://orcid.org/0000-0001-6017-6364

Robert L. Minckley https://orcid.org/0000-0002-1217-7693

Laurence Packer https://orcid.org/0000-0002-1711-8203

John L. Neff https://orcid.org/0000-0002-4767-2053

Robert S. Copeland https://orcid.org/0000-0003-4865-5412

Jakub Straka https://orcid.org/0000-0002-8987-1245

Terry Griswold https://orcid.org/0000-0003-3952-9393

Bryan N. Danforth https://orcid.org/0000-0002-6495-428X

Elizabeth A. Murray https://orcid.org/0000-0001-9300-3419

REFERENCES

Alexander, B.A. (1994) Species-groups and cladisitic analysis of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apoidea). *University of Kansas Science Bulletin*, 55, 175–238.

Alfaro, M.E., Brock, C.D., Banbury, B.L. & Wainwright, P.C. (2009) Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? *BMC Evolutionary Biology*, 9, 255.

Almeida, E.A.B., Pie, M.R., Brady, S.G. & Danforth, B.N. (2012) Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): emerging patterns from the southern end of the world. *Journal of Biogeography*, 39, 526–544.

Almeida, E.A.B., Packer, L., Melo, G.A.R., Danforth, B.N., Cardinal, S.C., Quinteiro, F.B. et al. (2019) The diversification of neopasiphaeine bees during the Cenozoic (Hymenoptera: Colletidae). *Zoologica Scripta*, 48, 226–242.

Amiet, F. & Krebs, A. (2012) *Bienen Mitteleuropas - Gattungen, Lebensweise, Beobachtung*. Bern: Haupt Verlag.

Ascher, J.S. (2003) Evidence for the phylogenetic position of *Nolanomelissa* from nuclear EF-1a sequence data. In: Melo, G.A.R. & Alves-dos-Santos, I. (Eds.) *Apoidea Neotropica: Homenagem aos 90 Anos de Jesus Santiago Moure*. Criciúma: UNESC, pp. 17–19.

Ascher, J.S. (2004) *Systematics of the bee family Andrenidae (Hymenoptera: Apoidea)*. PhD Thesis, Cornell University, 333 pp.

Ascher, J.S. & Pickering, J. (2021) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available at: http://www.discoverlife.org/mp/20q?guide=Apoidea_species. Accessed January 2021

Ascher, J.S., Engel, M.S. & Griswold, T.L. (2006) A new subgenus and species of *Oxaea* from Ecuador (Hymenoptera: Andrenidae). *Polskie Pismo Entomologiczne*, 75, 539–552.

Ballantyne, G., Baldock, K.C.R., Rendell, L. & Willmer, P.G. (2017) Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Scientific Reports*, 7, 8389.

Blaimer, B.B., LaPolla, J.S., Branstetter, M.G., Lloyd, M.W. & Brady, S.G. (2016) Phylogenomics, biogeography and diversification of obligate mealybug-tending ants in the genus *Acropyga*. *Molecular Phylogenetics and Evolution*, 102, 20–29.

Blaimer, B.B., Lloyd, M.W., Guillory, W.X. & Brady, S.G. (2016) Sequence capture and phylogenetic utility of genomic ultraconserved elements obtained from pinned insect specimens. *PLoS One*, 11, e0161531.

Blaimer, B.B., Mawdsley, J.R. & Brady, S.G. (2018) Multiple origins of sexual dichromatism and aposematism within large carpenter bees. *Evolution*, 72, 1874–1889.

Borowiec, M.L. (2016) AMAS: a fast tool for alignment manipulation and computing of summary statistics. *PeerJ*, 4, e1660.

Borowiec, M.L., Lee, E.K., Chiu, J.C. & Plachetzki, D.C. (2015) Extracting phylogenetic signal and accounting for bias in whole-genome data

sets supports the Ctenophora as sister to remaining Metazoa. *BMC Genomics*, 16, 1–15.

Bossert, S., Copeland, R.S., Sless, T.J.L., Branstetter, M.G., Gillung, J.P., Brady, S.G. et al. (2020) Phylogenomic and morphological reevaluation of the bee tribes Biastini, Neolarrini, and Townsendiellini (Hymenoptera: Apidae) with description of three new species of *Schwarzia*. *Insect Systematics and Diversity*, 4, 1–29.

Bossert, S., Murray, E.A., Pauly, A., Chernyshov, K., Brady, S.G. & Danforth, B.N. (2021) Gene tree estimation error with ultraconserved elements: an empirical study on *Pseudapis* bees. *Systematic Biology*, 70, 803–821.

Botero, C.A., Dor, R., McCain, C.M. & Safran, R.J. (2014) Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Molecular Ecology*, 23, 259–268.

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L. et al. (2017) Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. *Current Biology*, 27, 1019–1025.

Cantrill, D.J. & Poole, I. (2012) *The vegetation of Antarctica through geological time*. Cambridge: Cambridge University Press.

Cardinal, S. (2018) Bee (Hymenoptera: Apoidea: Anthophila) diversity through time. In: Foottit, R.G. & Adler, P.H. (Eds.) *Insect biodiversity: science and society*, Vol. 2. Oxford, UK: John Wiley & Sons Ltd., pp. 851–867.

Cardinal, S. & Danforth, B.N. (2013) Bees diversified in the age of eudicots. *Proceedings of the Royal Society B: Biological Sciences*, 280, 1–9.

Cardinal, S., Buchmann, S.L. & Russell, A.L. (2018) The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution*, 72, 590–600.

Chang, J., Rabosky, D.L. & Alfaro, M.E. (2020) Estimating diversification rates on incompletely sampled phylogenies: theoretical concerns and practical solutions. *Systematic Biology*, 69, 602–611.

Claramunt, S. & Cracraft, J. (2015) A new time tree reveals earth history's imprint on the evolution of modern birds. *Science Advances*, 1, e1501005.

Cockerell, T.D.A. (1904) New records of bees. *The Entomologist*, 37, 231–236.

Cockerell, T.D.A. (1906) Fossil Hymenoptera from Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 50, 33–58.

Cockerell, T.D.A. (1908) Descriptions and records of bees. XX. *Annals and Magazine of Natural History*, 8, 323–334.

Cockerell, T.D.A. (1909) Two fossil bees. *Entomological News*, 20, 159–161.

Cockerell, T.D.A. (1911) Fossil insects from Florissant, Colorado. *Bulletin of the American Museum of Natural History*, 30, 71–82.

Cockerell, T.D.A. (1913) Some fossil insects from Florissant, Colorado. *Proceedings of the United States National Museum*, 44, 341–346.

Cockerell, T.D.A. (1914) Miocene fossil insects. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 66, 634–648.

Condamine, F.L., Rolland, J., Höhna, S., Sperling, F.A.H. & Sanmartín, I. (2018) Testing the role of the red queen and court jester as drivers of the macroevolution of *Apollo* butterflies. *Systematic Biology*, 67, 940–964.

Crawford, J.C. (1916) Nine new species of Hymenoptera. *Insecutor Inscitiae Menstruus*, 4, 101.

Danforth, B.N. (1996) Phylogenetic analysis and taxonomic revision of the *Perdita* subgenera *Macrotera*, *Macroteropsis*, *Macroterella* and *Cockerellula* (Hymenoptera: Andrenidae). *The University of Kansas Science Bulletin*, 55, 635.

Danforth, B.N., Fang, J. & Sipes, S. (2006) Analysis of family-level relationships in bees (Hymenoptera: Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. *Molecular Phylogenetics and Evolution*, 39, 358–373.

Danforth, B.N., Sipes, S., Fang, J. & Brady, S.G. (2006) The history of early bee diversification based on five genes plus morphology.

Proceedings of the National Academy of Sciences, 103, 15118–15123.

Danforth, B.N., Minckley, R.L. & Neff, J.L. (2019) *The solitary bees: biology, evolution, conservation*. Princeton: Princeton University Press.

Dehon, M., Michez, D., Nel, A., Engel, M.S. & De Meulemeester, T. (2014) Wing shape of four new bee fossils (Hymenoptera: Anthophila) provides insights to bee evolution. *PLoS One*, 9, e108865.

Dewulf, A., De Meulemeester, T., Dehon, M., Engel, M.S. & Michez, D. (2014) A new interpretation of the bee fossil *Melitta willardi* Cockerell (Hymenoptera, Melittidae) based on geometric morphometrics of the wing. *ZooKeys*, 389, 35–48.

Donoghue, M.J. & Sanderson, M.J. (2015) Confluence, synnovation, and depauperons in plant diversification. *New Phytologist*, 207, 260–274.

Eardley, C.D. & Schwarz, M. (1991) The Afrotropical species of *Nomada* Scopoli (Hymenoptera: Anthophoridae). *Phytophylactica*, 23, 17–28.

Eardley, C.D., Kuhlmann, M. & Pauly, A. (2010) The bee genera and subgenera of sub-Saharan Africa. *Abc Taxa*, 7, 1–139.

Engel, M.S. (2001) A monography of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 1–192.

Engel, M.S. (2015) A review of the genera and subgenera of Oxaeinae (Hymenoptera: Andrenidae). *Journal of Melittology*, 52, 1–18.

Ezard, T.H.G., Aze, T., Pearson, P.N. & Purvis, A. (2011) Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, 332, 349–351.

Faircloth, B.C. (2016) PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics*, 32, 786–788.

Faircloth, B.C., Branstetter, M.G., White, N.D. & Brady, S.G. (2015) Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among Hymenoptera. *Molecular Ecology Resources*, 15, 489–501.

Foster, G.L., Royer, D.L. & Lunt, D.J. (2017) Future climate forcing potentially without precedent in the last 420 million years. *Nature Communications*, 8, 14845.

Gibbs, J., Brady, S.G., Kanda, K. & Danforth, B.N. (2012) Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). *Molecular Phylogenetics and Evolution*, 65, 926–939.

Gonzalez, V.H., Rasmussen, C. & Engel, M.S. (2013) *Incasarus garciai*, a new genus and species of panurgine bees from the Peruvian Andes (Hymenoptera: Andrenidae). *Journal of Melittology*, 8, 1–9.

Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J. et al. (2019) Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science*, 363, 282–284.

Gusenleitner, F., Schwarz, M. & Mazzucco, K. (2012) Apidae (Insecta: Hymenoptera). In: Schuster, R. (Ed.) 162 pp. *Checklisten der Fauna Österreichs, No. 6*. Wien: Österreichische Akademie der Wissenschaften.

Hansen, J., Sato, M., Russell, G. & Kharecha, P. (2013) Climate sensitivity, sea level and atmospheric carbon dioxide. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 371, 20120294.

Heath, T.A., Huelsenbeck, J.P. & Stadler, T. (2014) The fossilized birth-death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences of the United States of America*, 111, E2957–E2966.

Hedtke, S.M., Patiny, S. & Danforth, B.N. (2013) The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC Evolutionary Biology*, 13, 1–13.

Hines, H.M. (2008) Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*). *Systematic Biology*, 57, 58–75.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518–522.

Höhna, S. (2015) The time-dependent reconstructed evolutionary process with a key-role for mass-extinction events. *Journal of Theoretical Biology*, 380, 321–331.

Höhna, S., Landis, M.J., Heath, T.A., Boussau, B., Lartillot, N., Moore, B.R. et al. (2016) RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology*, 65, 726–736.

Huang, X.-C., German, D.A. & Koch, M.A. (2020) Temporal patterns of diversification in Brassicaceae demonstrate decoupling of rate shifts and mesopolyploidization events. *Annals of Botany*, 125, 29–47.

Huelsenbeck, J.P., Larget, B. & Alfaro, M.E. (2004) Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. *Molecular Biology and Evolution*, 21, 1123–1133.

Hunter, J.P. (1998) Key innovations and the ecology of macroevolution. *Trends in Ecology & Evolution*, 13, 31–36.

Hurd, P.D.J. & Linsley, E.G. (1976) The bee family Oxaeidae with a revision of the north American species (Hymenoptera, Apoidea). *Smithsonian Contributions to Zoology*, 220, 1–75.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, 491, 444–448.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587.

Kayaalp, P., Schwarz, M.P. & Stevens, M.I. (2013) Rapid diversification in Australia and two dispersals out of Australia in the globally distributed bee genus, *Hylaeus* (Colletidae: Hylaeinae). *Molecular Phylogenetics and Evolution*, 66, 668–678.

Keller, G. (2001) The end-cretaceous mass extinction in the marine realm: year 2000 assessment. *Planetary and Space Science*, 49, 817–830.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

Kergoat, G.J., Condamine, F.L., Toussaint, E.F.A., Capdevielle-Dulac, C., Clamens, A.-L., Barbut, J. et al. (2018) Opposite macroevolutionary responses to environmental changes in grasses and insects during the Neogene grassland expansion. *Nature Communications*, 9, 5089.

Klages, J.P., Salzmann, U., Bickert, T., Hillenbrand, C.D., Gohl, K., Kuhn, G. et al. (2020) Temperate rainforests near the south pole during peak cretaceous warmth. *Nature*, 580, 81–86.

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. et al. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274, 303–313.

Krombein, K.V., Hurd, P.D., Smith, D.R. & Burks, B.D. (1979) *Catalog of Hymenoptera in America north of Mexico*. Washington, DC: Smithsonian Institution Press.

Labandeira, C.C., Johnson, K.R. & Wilf, P. (2002) Impact of the terminal cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences*, 99, 2061–2066.

Lagomarsino, L.P., Condamine, F.L., Antonelli, A., Mulch, A. & Davis, C.C. (2016) The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New Phytologist*, 210, 1430–1442.

Landis, M.J., Matzke, N.J., Moore, B.R. & Huelsenbeck, J.P. (2013) Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, 62, 789–804.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.

Lanfear, R., Calcott, B., Kainer, D., Mayer, C. & Stamatakis, A. (2014) Selecting optimal partitioning schemes for phylogenomic datasets. *BMC Evolutionary Biology*, 14, 82.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: new methods for selecting partitioned models of

PHYLOGENY AND DIVERSIFICATION OF ANDRENIDAE

Systematic
Entomology

Royal
Entomological
Society

301

evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34, 772–773.

Lepage, T., Bryant, D., Philippe, H. & Lartillot, N. (2007) A general comparison of relaxed molecular clock models. *Molecular Biology and Evolution*, 24, 2669–2680.

Longrich, N.R., Bhullar, B.-A.S. & Gauthier, J.A. (2012) Mass extinction of lizards and snakes at the cretaceous-Paleogene boundary. *Proceedings of the National Academy of Sciences*, 109, 21396–21401.

Luo, A., Duchêne, D.A., Zhang, C., Zhu, C.-D. & Ho, S.Y.W. (2020) A simulation-based evaluation of tip-dating under the fossilized birth-death process. *Systematic Biology*, 69, 325–344.

Magallón, S. & Sanderson, M.J. (2001) Absolute diversification rates in angiosperm clades. *Evolution*, 55, 1762–1780.

Matzke, N.J. (2018, November 6) *BioGeoBEARS: BioGeography with Bayesian (and likelihood) evolutionary analysis with R scripts. version 1.1.1*, published on GitHub.

Mayhew, P.J. (2007) Why are there so many insect species? Perspectives from fossils and phylogenies. *Biological Reviews*, 82, 425–454.

Michener, C.D. (1979) Biogeography of the bees. *Annals of the Missouri Botanical Garden*, 66, 277–347.

Michener, C.D. (1986) New Peruvian genus and a generic review of Andreninae (Hymenoptera: Apoidea: Andrenidae). *Annals of the Entomological Society of America*, 79, 62–72.

Michener, C.D. (2000) *The bees of the world*. Baltimore: The Johns Hopkins University Press.

Michener, C.D. (2007) *The bees of the world*. Baltimore: The Johns Hopkins University Press.

Michez, D., Vanderplanck, M. & Engel, M.S. (2012) Fossil bees and their plant associates. In: Patiny, S. (Ed.) *Evolution of plant-pollinator relationships*. Cambridge: Cambridge University Press, pp. 103–164.

Mikát, M., Matoušková, E. & Straka, J. (2021) Nesting of *Ceratina nigrolabiata*, a biparental bee. *Scientific Reports*, 11, 5026.

Milne, R.I. (2006) Northern hemisphere plant disjunctions: a window on tertiary land bridges and climate change? *Annals of Botany*, 98, 465–472.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. et al. (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, 37, 1530–1534.

Morlon, H. (2014) Phylogenetic approaches for studying diversification. *Ecology Letters*, 17, 508–525.

Ollerton, J. (2017) Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48, 353–376.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C. et al. (2001) Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience*, 51, 933–938.

Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.-D. & Ascher, J.S. (2021) Global patterns and drivers of bee distribution. *Current Biology*, 31, 451–458.

Panero, J.L. & Crozier, B.S. (2016) Macroevolutionary dynamics in the early diversification of Asteraceae. *Molecular Phylogenetics and Evolution*, 99, 116–132.

Pardo, A. & Borges, P.A.V. (2020) Worldwide importance of insect pollination in apple orchards: a review. *Agriculture, Ecosystems & Environment*, 293, 106839.

Park, M.G., Raguso, R.A., Losey, J.E. & Danforth, B.N. (2016) Per-visit pollinator performance and regional importance of wild *Bombus* and *Andrena* (*Melandrena*) compared to the managed honey bee in New York apple orchards. *Apidologie*, 47, 145–160.

Patiny, S. (1999) Etude phylogénétique des Panurginae de l'Ancien Monde (Hymenoptera, Andrenidae). *Linzer Biologische Beiträge*, 31, 249–275.

Patiny, S. (2003) Phylogénie des espèces de *Clavipanurgus* Warncke, 1972 (Hymenoptera, Apoidea: Andrenidae). *Annales de la Société Entomologique de France*, 39, 229–234.

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K. et al. (2017) Evolutionary history of the Hymenoptera. *Current Biology*, 27, 1013–1018.

Pisanty, G., Richter, R., Martin, T., Dettman, J. & Cardinal, S. (2021) Molecular phylogeny and historical biogeography of andrenine bees (Hymenoptera: Andrenidae). *Molecular Phylogenetics and Evolution*, 107151. https://doi.org/10.1016/j.ympev.2021.107151

Plant, J.D. & Paulus, H.F. (2016) Evolution and phylogeny of bees - a review and a cladistic analysis in light of morphological evidence (Hymenoptera, Apoidea). *Zoologica*, 161, 1–364.

Portman, Z.M. & Tepedino, V.J. (2017) Convergent evolution of pollen transport mode in two distantly related bee genera (Hymenoptera: Andrenidae and Melittidae). *Apidologie*, 48, 461–472.

Praz, C.J. & Packer, L. (2014) Phylogenetic position of the bee genera *Ancyla* and *Tarsalia* (Hymenoptera: Apidae): a remarkable base compositional bias and an early Paleogene geodispersal from North America to the Old World. *Molecular Phylogenetics and Evolution*, 81, 258–270.

R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna: R Core Team. Available at: http://www.r-project.org/

Rabosky, D.L. (2014) Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One*, 9, e89543.

Rabosky, D.L. (2017) Phylogenetic tests for evolutionary innovation: the problematic link between key innovations and exceptional diversification. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 372, 20160417.

Rabosky, D.L., Slater, G.J. & Alfaro, M.E. (2012) Clade age and species richness are decoupled across the eukaryotic tree of life. *PLoS Biology*, 10, e1001381.

Rabosky, D.L., Grundler, M., Anderson, C., Title, P., Shi, J.J., Brown, J.W. et al. (2014) BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*, 5, 701–707.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Systematic Biology*, 67, 901–904.

Ramos, K.S. (2011) *Relações filogenéticas entre as abelhas da subfamília Andreninae com ênfase nas tribos Calliopsini, Protandrenini e Protomelitturgini (Hymenoptera, Apidae)*. PhD Thesis, Universidade Federal do Paraná, Brazil, 156 pp.

Ramos, K.S. & Rozen, J.G. (2014) *Psaenythisca*, a new genus of bees from South America (Apoidea: Andrenidae: Protandrenini) with a description of the nesting biology and immature stages of one species. *American Museum Novitates*, 2014, 1–32.

Rannala, B. & Yang, Z. (2003) Bayes estimation of species divergence times and ancestral population sizes using DNA sequences from multiple loci. *Genetics*, 164, 1645–1656.

Raup, D.M., Gould, S.J., Schopf, T.J.M. & Simberloff, D.S. (1973) Stochastic models of phylogeny and the evolution of diversity. *The Journal of Geology*, 81, 525–542.

Ree, R.H. & Sanmartín, I. (2018) Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *Journal of Biogeography*, 45, 741–749.

Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57, 4–14.

Rehan, S.M., Leys, R. & Schwarz, M.P. (2013) First evidence for a massive extinction event affecting bees close to the K-T boundary. *PLoS One*, 8, e76683.

Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, 46, 195–203.

Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D.L. & Rasnitsyn, A.P. (2012a) A total-evidence approach to dating with

fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology*, 61, 973–999.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S. et al. (2012b) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.

Rozen, J.G. (1964) Phylogenetic-taxonomic significance of last instar of *Protoxaea gloriosa* fox, with descriptions of first and last instars (Hymenoptera: Apoidea). *Journal of the New York Entomological Society*, 72, 223–230.

Rozen, J.G. (1965) The biology and immature stages of *Melitturga clavicornis* (Latreille) and of *Sphecodes albilabris* (Kirby) and the recognition of the Oxaeidae at the family level (Hymenoptera, Apoidea). *American Museum Novitates*, 2224, 1–18.

Rozen, J.G. (1996) A new species of the bee *Heterosarus* from Dominican Amber (Hymenoptera: Andrenidae; Panurginae). *Journal of the Kansas Entomological Society*, 69, 346–352.

Rozen, J.G. (2003) A new tribe, genus, and species of south American panurgine bee (Andrenidae, Panurginae), oligolectic on *Nolana* (Nolanaceae). In: Melo, G.A.R. & Alves-dos-Santos, I. (Eds.) *Apoidea Neotropica: Homenagem aos 90 Anos de Jesus Santiago Moure*, pp. Criciúma, Brazil: Editora da UNESC, 93–108.

Russo, L., Park, M.G., Blitzer, E.J. & Danforth, B.N. (2017) Flower handling behavior and abundance determine the relative contribution of pollinators to seed set in apple orchards. *Agriculture, Ecosystems & Environment*, 246, 102–108.

Ruz, L. (1986) Classification and phylogenetic relationships of the panurgine bees. PhD Thesis, University of Kansas, 312 pp.

Sahoo, R.K., Warren, A.D., Collins, S.C. & Kodandaramaiah, U. (2017) Hostplant change and paleoclimatic events explain diversification shifts in skipper butterflies (family: Hesperiidae). *BMC Evolutionary Biology*, 17, 1–9.

Sann, M., Niehuis, O., Peters, R.S., Mayer, C., Kozlov, A., Podsiadlowski, L. et al. (2018) Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. *BMC Evolutionary Biology*, 18, 71.

Särkinen, T., Bohs, L., Olmstead, R.G. & Knapp, S. (2013) A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evolutionary Biology*, 13, 214.

Scheuchl, E. (1995) *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band I: Anthophoridae*. Velden: Eigenverlag.

Smith-Ramírez, C., Martinez, P., Nuñez, M., González, C. & Armesto, J.J. (2005) Diversity, flower visitation frequency and generalism of pollinators in temperate rain forests of Chiloé Island, Chile. *Botanical Journal of the Linnean Society*, 147, 399–416.

Spagarino, C., Martínez Pastur, G. & Peri, P. (2001) Changes in *Nothofagus pumilio* forest biodiversity during the forest management cycle. 1. Insects. *Biodiversity & Conservation*, 10, 2077–2092.

Stadler, T. (2010) Sampling-through-time in birth-death trees. *Journal of Theoretical Biology*, 267, 396–404.

Stanley, S.M. (1975) A theory of evolution above the species level. *Proceedings of the National Academy of Sciences*, 72, 646–650.

Sun, M., Folk, R.A., Gitzendanner, M.A., Soltis, P.S., Chen, Z., Soltis, D.E. et al. (2020) Recent accelerated diversification in rosids occurred outside the tropics. *Nature Communications*, 11, 3333.

Thompson, J.B., Dodd, H.O., Wills, M.A., & Priest, N.K. (2021) Speciation across the earth driven by global cooling in orchidoid orchids. *bioRxiv [Preprint]*. https://doi.org/10.1101/2021.02.06.430029. Accessed January 2021

Tiffney, B.H. (1985) The Eocene North Atlantic land bridge: its importance in tertiary and modern phytogeography of the northern hemisphere. *Journal of the Arnold Arboretum*, 66, 243–273.

Timberlake, P.H. (1975) The north American species of *Heterosarus* Robertson (Hymenoptera, Apoidea). *University of California Publications in Entomology*, 77, 1–57.

Title, P.O. & Rabosky, D.L. (2019) Tip rates, phylogenies and diversification: what are we estimating, and how good are the estimates? *Methods in Ecology and Evolution*, 10, 821–834.

Toussaint, E.F.A., Condamine, F.L., Kergoat, G.J., Capdevielle-Dulac, C., Barbut, J., Silvain, J.-F. et al. (2012) Palaeoenvironmental shifts drove the adaptive radiation of a noctuid stemborer tribe (Lepidoptera, Noctuidae, Apameini) in the Miocene. *PLoS One*, 7, e41377.

Trunz, V., Packer, L., Vieu, J., Arrigo, N. & Praz, C.J. (2016) Comprehensive phylogeny, biogeography and new classification of the diverse bee tribe Megachilini: can we use DNA barcodes in phylogenies of large genera? *Molecular Phylogenetics and Evolution*, 103, 245–259.

Vázquez, D.P. & Simberloff, D. (2002) Ecological specialization and susceptibility to disturbance: conjectures and refutations. *The American Naturalist*, 159, 606–623.

Walker, K.L., Tattersall, M. & Houston, T.F. (2020) First host record for the Australian kleptoparasitic bee *Nomada australensis* (Perkins) (Hymenoptera: Apidae) and a new synonymy. *The Australian Entomologist*, 47, 285–300.

Warncke, K. (1972) Westpaläarktische Bienen der Unterfamilie Panurginae (Hym., Apidae). *Polskie Pismo Entomologiczne*, XLII, 53–108.

Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E. et al. (2020) An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science*, 369, 1383.

Westrich, P. (2006) Ein weiterer Beleg für den Bivoltinismus und das Wirt-Parasit-Verhältnis von *Andrena bicolor* (Fabricius 1804) und *Nomada fabriciana* (Kirby 1802)(Hym. Apidae). *Linzer Biologische Beiträge*, 38, 919–923.

Westrich, P. (2018) *Die Wildbienen Deutschlands*. Stuttgart: Eugen Ulmer KG.

Wood, T.J. & Cross, I. (2017) *Camptopoeum* (*Camptopoeum*) *baldocki* spec. Nov., a new panurgine bee species from Portugal and a description of the male of *Flavipanurgus fuzetus* Patiny (Andrenidae: Panurginae). *Zootaxa*, 4254, 285–293.

Zhang, C., Stadler, T., Klopfstein, S., Heath, T.A. & Ronquist, F. (2016) Total-evidence dating under the fossilized birth-death process. *Systematic Biology*, 65, 228–249.

Zhang, S.D., Jin, J.J., Chen, S.Y., Chase, M.W., Soltis, D.E., Li, H.T. et al. (2017) Diversification of Rosaceae since the late cretaceous based on plastid phylogenomics. *New Phytologist*, 214, 1355–1367.

Zhang, C., Rabiee, M., Sayyari, E. & Mirarab, S. (2018) ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*, 19, 153.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Supporting information