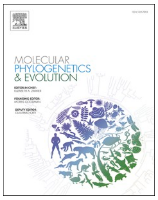
Molecular Phylogenetics and Evolution 198 (2024) 108133

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev



Phylogenomics and biogeography of the small carpenter bees (Apidae: Xylocopinae: *Ceratina*)

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ARTICLE INFO

Keywords:
Historical biogeography
Wild bee dispersal
Ultraconserved elements
Molecular phylogeny
Hymenoptera
Ceratinini

ABSTRACT

Small carpenter bees in the genus *Ceratina* are behaviourally diverse, species-rich, and cosmopolitan, with over 370 species and a range including all continents except Antarctica. Here, we present the first comprehensive phylogeny of the genus based on ultraconserved element (UCE) phylogenomic data, covering a total of 185 ingroup specimens representing 22 of the 25 current subgenera. Our results support most recognized subgenera as natural groups, but we also highlight several groups in need of taxonomic revision – particularly the nominate subgenus *Ceratina sensu stricto* – and several clades that likely need to be described as new subgenera. In addition to phylogeny, we explore the evolutionary history of *Ceratina* through divergence time estimation and biogeographic reconstruction. Our findings suggest that Ceratinini split from its sister tribe Allodapini about 72 million years ago. The common ancestor of *Ceratina* emerged in the Afrotropical realm approximately 42 million years ago, near the Middle Eocene Climatic Optimum. Multiple subsequent dispersal events led to the present cosmopolitan distribution of *Ceratina*, with the majority of transitions occurring between the Afrotropics, Indomalaya, and the Palearctic. Additional movements also led to the arrival of *Ceratina* in Madagascar, Australasia, and a single colonization of the Americas. Dispersal events were asymmetrical overall, with temperate regions primarily acting as destinations for migrations from tropical source regions.

1. Introduction

Many recent studies have made use of novel approaches in phylogenetics to gain new insights into the commonalities and patterns of biogeography throughout the tree of life, with a range of taxa including birds (Batista et al., 2020), spiders (Ledford et al., 2021), snakes (Esquerré et al., 2020), trees (Wang et al., 2022) and recently bees (Almeida et al., 2023). Early work such as Michener's identification of the "amphitropical" distribution of bee species richness (Michener, 1979) has led to large, occurrence data-driven projects including detailed characterization of global hotspots of diversity (Orr et al., 2021). Other publications have focused on elucidating biogeographic patterns for particular bee lineages of interest, such as the apid subfamilies Eucerinae (Freitas et al., 2022), Anthophorinae (Orr et al., 2022), and particularly diverse genera such as *Nomada* (Odanaka et al., 2022).

The genus *Ceratina*, commonly known as the small carpenter bees, consists of approximately 370 species divided into 25 subgenera and can be found on all continents except Antarctica (Ascher & Pickering, 2020; Engel, 2023). They are typically polylectic or generalist foragers, and as with other members of the carpenter bee subfamily Xylocopinae, all species excavate nests in plant material (Eardley & Daly, 2007; Michener, 2007; Sakagami & Laroca, 1971). Like many other species of Xylocopinae, members of *Ceratina* exhibit a range of social organization, including completely solitary species, subsocial species with extended maternal (or biparental) care of adult young, and some facultatively eusocial species in which multiple females contribute to brooding (Mikát et al., 2019; Sakagami and Maeta, 1977; Sless & Rehan, 2023).

The phylogeny and biogeography of *Ceratina* have previously been explored by Rehan et al. (2010) and Rehan & Schwarz (2015), including

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https://doi.org/10.1016/j.ympev.2024.108133
Received 3 April 2024; Received in revised form 31 May 2024; Accepted 15 June 2024

about 70 and 99 species respectively. Subsequent analysis by Groom & Rehan (2018) emphasized the important role of climate in the evolution of *Ceratina* and the relationship between tropical regions and the maintenance of social behaviour. However, the availability of previously unstudied taxa, including six newly added subgenera, as well as new molecular methods allowing for broad, genome-wide sampling of genetic material both present a timely opportunity for an updated study of this genus. In this paper, we present the most complete phylogeny of *Ceratina* to date, based on the enrichment and sequencing of ultraconserved element (UCE) data for over 140 species representing nearly all recognized subgenera. This extensive phylogenetic framework allows for the evolutionary history of small carpenter bees to be investigated in an unprecedented level of detail, which we conducted with divergence time estimates and biogeographic reconstruction of the genus to explore its origins and diversification.

2. Materials and methods

2.1. Taxon sampling

We obtained data from a broad taxonomic sampling of the genus *Ceratina*, including a total of 185 ingroup specimens in addition to 29 outgroup members representing all other major clades within the family Apidae (Table S1). These specimens comprise at least 140 distinct species of *Ceratina*, representing more than a third of the currently described species, and include 22 out of the 25 currently described subgenera (Ascher & Pickering, 2020; Engel, 2023). Newly sequenced specimens were obtained from a variety of personal and museum collections and included both pinned and ethanol-stored material. In addition, some previously published UCE sequences were also used, primarily for outgroups (Blaimer et al., 2018; Bossert et al., 2019; Freitas et al., 2021; Grab et al., 2019; Sless et al., 2022).

2.2. DNA extraction and UCE library preparation

DNA was non-destructively extracted from specimens with a Zymo Quick-DNA Miniprep Plus Kit (Zymo Research, catalog #D4068) following protocols described in Branstetter et al. (2021). Whole specimens were removed from pins and digested in proteinase-K overnight before being washed in ethanol and remounted. The concentration and size distribution of extracted DNA was quantified with a Qubit 3.0 fluorometer (Thermo Fisher Scientific) and TapeStation 4150 system (Agilent).

Library preparation and enrichment steps were then conducted to target ultraconserved elements following previously established protocols (Faircloth et al., 2012; Branstetter et al., 2017,2019). We used the “ant-bee” subset of the Hymenoptera V2 probe set (Grab et al., 2019) targeting a total of 2,545 UCE loci. DNA samples were first sheared to fragment sizes of 400–600 bp using a Q800R2 sonicator (Qsonica) for 30 or 60 s according to specimen age and DNA volume. Older samples were not sheared, since in these cases DNA is typically already fragmented due to age-related degradation, and any samples that were already sufficiently fragmented. Illumina libraries were made using Kapa HyperPrep kits (Roche Sequencing) along with custom 8 bp, dual-indexed adapters (Glenn et al., 2019). DNA fragments were cleaned and concentrated with paramagnetic beads (Rohland & Reich, 2012) before the enrichment steps, which followed a combination of protocols from Arbor Biosciences and Blumenstiel et al. (2010). Samples were then quantified with qPCR and pooled before being sent for sequencing with Novogene Inc. (Sacramento, CA, USA) on the HiSeq X platform (Illumina).

2.3. Phylogenetic tree construction

After demultiplexing with BBTools (Bushnell, 2014), sequence data were processed using the Phyluce v1.7.1 package (Faircloth, 2016). Reads were first trimmed using Illumiprocessor v2.0 (Faircloth, 2013), which is a wrapper for Trimmomatic (Bolger et al., 2014), and then assembled with SPAdes (Bankevich et al., 2012). Within Phyluce, contigs that matched target UCE loci were identified by LastZ v1.0 (Harris, 2007), using 70 and 75 for the min-identity and min-coverage settings in Phyluce, and aligned using MAFFT v7.130b (Katoh & Standley, 2013). Following alignment, the data were trimmed using Gblocks (Talavera & Castresana, 2007), with reduced stringency settings (0.5, 0.5, 12, 7, for b1-b4), and then further trimmed with Spruceup (Borowiec, 2019). The Spruceup analysis was run using uncorrected distances, a guide tree, a lognormal cutoff of 0.9 and several manual cutoffs (Ceratina_saundersi_BLX2339, 0.04; Ceratina_sp_BLX2972, 0.04; Ceratina_callosa_BLX2337, 0.04; Ceratina_zwakhalsi_BLX2338, 0.04). Finally, the alignment was filtered for 75 % taxon occupancy using a Phyluce script.

Each UCE locus was separated into three regions (right flank, core, left flank) using the Sliding Window Site Characteristics by Entropy method (SWSC-EN; Tagliacollo & Lanfear, 2018). We then merged the subsets into fewer data partitions using ModelFinder2 (Kalyaanamoorthy et al., 2017), which is included within IQ-TREE v2.2 (Chenomor et al., 2016; Minh et al., 2020). Merging was performed using the rclusterf and AICc options for model selection, and GTR + F + G4 for the model of sequence evolution. Following selection of the best partitioning scheme, we estimated a phylogenetic tree with IQ-Tree2 using the MFP option for model selection and with 1000 replicates of ultrafast bootstraps (UFB; Hoang et al., 2018) and the SH-like approximate likelihood ratio (SH-alrt; Guindon et al., 2010) calculated for support. We used the BNNI option in the analysis to reduce the risk of overestimating bootstrap support values. This option further optimizes each bootstrap replicate by performing an additional hill-climbing nearest neighbor interchange search.

2.4. Divergence time estimation and biogeographic reconstruction

Divergence time estimation on the resulting phylogeny was conducted with BEAST2 v2.7.3 (Bouckaert et al., 2019) without partitioning and using the GTR + F + G4 model for sequence evolution and the optimized relaxed model for the clock (Douglas et al., 2021). Due to the large size of the dataset, using the full alignment with all loci was not computationally feasible. Instead, a subset of 200 randomly selected UCE loci was used along with a fixed tree based on the topology of the IQ-TREE phylogeny. To improve the initialization efficiency of the analysis, the input tree was made ultrametric by estimating a quick, dated tree using the function chronos, which is part of the R package ape (Paradis & Schliep, 2018). Five independent runs of BEAST were conducted in parallel for 200 million generations, sampling every 5 thousand generations, each before merging results from all five. Run convergence and ESA values were assessed in Tracer v1.7.1 (Rambaut et al., 2018).

For calibrating the divergence analysis, a secondary calibration based on Almeida et al. (2023) was used as a prior for the root of Apidae (normal distribution, M = 101.2, S = 7.5). In addition, five fossil calibrations were used as priors with minimum ages based on their respective deposits and maximum ages estimated from Almeida et al. (2023) (Table S2). Specifically, *Paleohabropoda oudardi* (Michez et al., 2009) was used for the node uniting *Anthophora* and *Habropoda* (59.2–96.8 Ma); *Cretotrigona prisca* (Michener & Grimaldi, 1988) for *Melipona* + *Bombus* (66.0–88.3 Ma); *Paleoepeolus micheneri* (Dehon et al., 2017) for *Epeolus* + *Brachynomada* (59.2–85.1 Ma); *Tetralonia berlandi* (Zeuner & Manning, 1976) for *Tetralonia* + *Diadasia* (33.9–89.5 Ma); and finally *Boreallodape baltica* (Engel 2001a) for the split between *Ceratina* and Allodapini (33.9–84.9 Ma).

Once the dated phylogeny was obtained, biogeographic reconstruction was completed in R v4.2.1 (R Core Team, 2022) using the packages phytools v1.5–1 (Revell, 2012) and BioGeoBEARS v1.1.2 (Matzke, 2013). Each tip in the phylogeny was coded by presence/absence across seven biogeographic realms: Afrotropics, Australasia, Indomalaya, Madagascar, Nearctic, Neotropics, and Palearctic (Table S3). Distribution data for all species was based on range maps from DiscoverLife (Ascher & Pickering, 2020) and GBIF (GBIF: The Global Biodiversity Information Facility, 2023). Specimens which could not be conclusively assigned to a species (those labelled "cf", "near", or "sp") were coded based on their collection locality. Realm boundaries were defined following the Ecoregions 2017 project (Dinerstein et al., 2017), with the exception that Madagascar was considered its own region distinct from the Afrotropical realm. In general, any occupancy of a realm was included in coding, though a few cases with dubious records or species present near the boundary of two biogeographic realms were not counted – such as some Indomalayan species recorded in Sulawesi but nowhere else in Australasia. Two specimens of *C. dentipes* in our dataset were collected in Oceania (Hawaii and the Cook Islands respectively), but these represent recent human-mediated introductions (Shell & Rehan, 2019) and as such were still coded according to the species' native range. *C. guarnacciana* from the Dominican Republic is also almost certainly a recent introduction and part of the *C. dentipes* species complex, but since this species is only recorded from the Caribbean and the ancestral range is not clear we coded it as Neotropical (Genaro, 1998).

In BioGeoBEARS, the maximum number of states was set to four, and dispersal and adjacency matrices were not used to alter rates of migration between different pairs of biogeographic realms. We separately tested three models, each with and without the "+J" jump parameter (Matzke, 2014): DEC (Ree & Smith, 2008), DIVALIKE (based on Ronquist, 1997), and BAYAREALIKE (Landis et al., 2013). Although some have criticized the use of the + J parameter for potentially overemphasizing the role of founder events (Ree & Sanmartín, 2018), we chose to consider it in part because stem-nesting bees such as *Ceratina* may in fact have the potential for significant long-range dispersal by rafting (Poulsen & Rasmussen, 2020).

3. Results

3.1. Sequence data and alignment statistics

UCE loci were successfully extracted from all samples, with a mean of 1,986 loci recovered (Table S4). After filtering to 75 % taxon occupancy, the final alignment consisted of 215 taxa and 1,818 UCE loci with a total length of 1,134,208 bp. This included 593,893 bp of informative sites and 26.8 % missing data. The best partitioning scheme identified by ModelFinder used a total of 1,619 partitions after merging SWSC-EN regions.

3.2. Phylogeny of the genus Ceratina

We recovered a robust phylogeny of *Ceratina* which includes an ingroup of 185 specimens representing 22 of 25 previously recognized subgenera, as well as 29 outgroup species (Fig. 1, S1). Branch support values were high throughout, with nearly all nodes receiving 100/100 support besides a small number of shallow nodes. The tribe Allodapini forms the immediate sister group to *Ceratina*, followed by *Xylocopa* + *Manuelia* and *Ctenoplectra* representing the rest of the subfamily Xylocopinae. The apid subfamilies Eucerinae, Apinae, Nomadinae, and Anthophorinae each independently appear as progressively more distant sister groups to Xylocopinae.

The genus *Ceratina* itself is split into two subclades of approximately equal size. One group ("Clade A") includes a mix of Old World subgenera: *Megaceratina*, *Catoceratina*, *Lioceratina*, *Xanthoceratina*, *Ceratinidia*; and New World subgenera: *Ceratinula*, *Neoclavicera*, *Rhysoceratina*, *Crewella*, *Calloceratina*, and *Zadontomerus*. The second group ("Clade B") includes only Old World subgenera: *Protopithitis*, *Pithitis*, *Neoceratina*, *Malgatina*, *Copoceratina*, *Dalyatina*, *Simioceratina*, *Ctenoceratina*, *Hirashima*, and *Euceratina*. The nominate subgenus *Ceratina sensu stricto* is highly polyphyletic and includes members divided between both major clades.

The results of our combined BEAST analyses suggest that the lineages leading to Allodapini and Ceratinini separated approximately 72 million years ago (95 % HPD 60.07–84.46 Ma; Fig. 1, S2), with the crown age of *Ceratina* placed at 41.87 Ma (95 % HPD 31.47–52.76 Ma). Clade A described above has a crown age of 28.92 Ma (95 % HPD 20.64–37.78 Ma), while clade B has a relatively short internode before *Pithitis* and *Protopithitis* split from the remaining subgenera around 39.87 Ma (95 % HPD 29.94–50.31 Ma).

3.3. Subgeneric classification

Most currently recognized subgenera of *Ceratina* were recovered as monophyletic and represent clear natural groups (Fig. 1). However, there are several exceptions with varying degrees of significance for the future of *Ceratina* systematics. Within clade A, the subgenus *Lioceratina* is polyphyletic due to the relatively distant placement of *C.* (*L.*) *canarensis*. Similarly, *Xanthoceratina* is rendered paraphyletic with respect to *Ceratinidia* due to the placement of *C.* (*X.*) *picta* as well as the inclusion of *C. unicolor* which is nominally part of *Ceratina sensu stricto*. *Ceratinula* is also polyphyletic, with three other small subgenera nested within the main group of *Ceratinula* species (*Neoclavicera*, *Rhysoceratina*, and *Crewella*). Another small group of *Ceratinula* (with distinctive green colouration in contrast to the rest of the subgenus) is recovered as the sister clade to *C.* (*Zadontomerus*) *marginata*, which also renders *Zadontomerus* paraphyletic.

Within clade B, the three representatives of the relatively newly described subgenus *Dalyatina* (Terzo et al., 2007) in our tree also do not form a natural group, and in fact none of them is the immediate sister species to any other. However, the nominate subgenus is by far the most problematic group from a taxonomic perspective. Species which are presently counted as part of *C.* (*Ceratina*) are spread throughout the tree either singly or in small groups and disrupt the monophyly of several other subgenera – most notably within clade G. To retain monophyly, some of these may simply be reclassified into other subgenera, but at least two new subgenera consisting of former *Ceratina s.s.* would also need to be described.

3.4. Biogeographic reconstruction

Of the six models assessed within BioGeoBEARS, BAYAREALIKE + J was selected as our preferred model based on the resulting likelihood and AIC scores (Table 1) and is therefore the primary reference for the remainder of our findings. Based on this model, the common ancestor of *Ceratina* is suggested to have inhabited the Afrotropical realm (post. prob. = 0.87) during the middle Eocene. The next most likely ancestral ranges were Indomalayan (0.07) and Afrotropical + Palearctic (0.03), while all other area combinations had posterior probabilities below one percent.

From this starting point, many subsequent dispersal events lead to the present-day cosmopolitan distribution of the genus (Fig. 2; Table S5). Clade A underwent a dispersal event from the ancestral Afrotropical realm to the Indomalayan realm approximately 25–29 Ma, where the subset of this group which gave rise to *Lioceratina*, *Xanthoceratina*, *Ceratinidia*, and some *Ceratina s.s.* (clade C) primarily remains today. However, clade C includes four recent migrations from the Indomalayan to the Palearctic, as well as another back to the Afrotropics. In contrast, all members of clade D descend from a single dispersal event from Asia to the Americas about 20–24 Ma. Clade D is reconstructed as being ancestrally Neotropical, though a group of species within *Zadontomerus* later crossed into the Nearctic approximately 4–5 Ma before rapidly diversifying.

Clade E, consisting of the subgenera *Protopithitis* and *Pithitis* remains ancestrally Afrotropical, but underwent range expansion to the Palearctic between 13–19 Ma. The subgenus *Pithitis* then split into two lineages, one Afrotropical and the other Indomalayan (though both groups

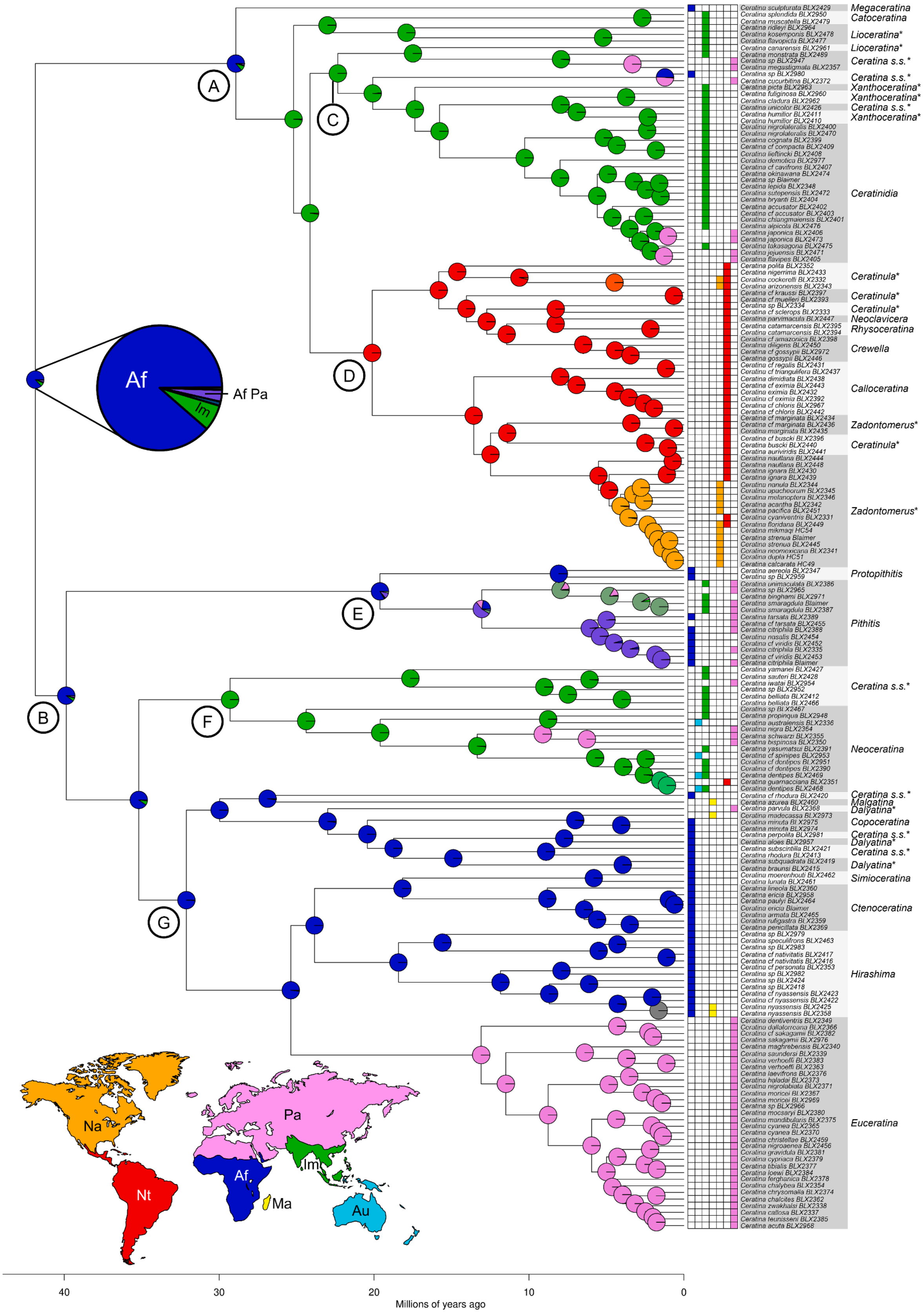

Fig. 1. Results of biogeographic reconstruction using BAYAREALIKE + J model with outgroups omitted. Colour-coding follows map legend in bottom left. Pie charts at nodes indicate estimated probabilities of each state or combination of states. The chart representing crown *Ceratina* is magnified for clarity. Coloured squares next to tips indicate present distributions of all included species. Boxes around tip labels correspond are monophyletic groups corresponding to entire or partial subgenera. Subgenera labelled with asterisks are found to be non-monophyletic.

Table 1

Statistical comparison of six tested BioGeoBears models. The model shown in bold was selected as the best model for the purposes of our results based on comparison of AIC scores. LnL = log likelihood; d = dispersal parameter; e = extinction parameter; j = jump parameter; AIC = Akaike Information Criterion (based on paired test of model with and without + J parameter); AICc = sample size corrected AIC; p-value = results of paired one-tailed X^2 tests of alternative model (+J) against null model (no J parameter).

Model	LnL	d	e	j	AIC	AICc	p-value
DEC	−202.9483	0.003018518	1.00E-12	0	409.8967	409.9623	7.60E-06
DEC + J	−192.9281	0.001923682	6.05E-10	0.006542924	389.8563	389.9219	
DIVALIKE	−207.7326	0.003905245	1.00E-12	0	419.4652	419.5308	1.00E-04
DIVALIKE + J	−200.3636	0.002568938	1.00E-12	0.006476698	404.7273	404.7928	
BAYAREALIKE	−229.056	0.001398958	3.25E-02	0	462.1121	462.1777	7.00E-21
BAYAREALIKE + J	−185.1245	0.001234228	5.18E-03	0.010403056	374.2491	374.3146	

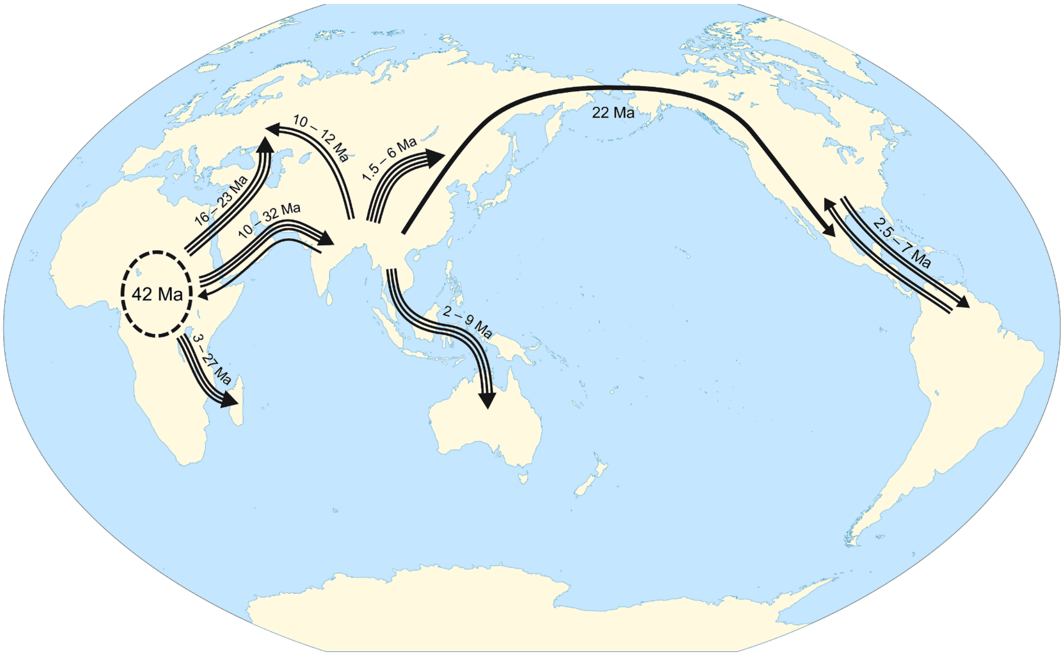

Fig. 2. Map of inferred biogeographical transitions within *Ceratina*. Arrow width indicates number of independent dispersal and range expansion events in the given direction. Numbers above arrows show approximate range of dates for events in millions of years before present, given as the average of mean ages for nodes above and below the branch on which the inferred transition occurred. Dashed circle and date indicate origins of *Ceratina*. World map modified from https://t.ly/uLZeF, CC-BY-3.0 Ding Zhiren.

include species with ranges extending to the western or eastern Palearctic respectively). Clade F migrated from Africa to Indomalaya about 29–35 Ma – a similar or slightly earlier time frame to Clade C. From there, members of *Neoceratina* went on to separately colonize the Palearctic once (9–13 Ma) and Australasia at least twice (both times likely in the range of 3–6 Ma). The presence of *Ceratina* (*Neoceratina*) *guarnacciana* in the Neotropics (Hispaniola) is almost certainly the result of human-mediated introduction from the Asia, as has already occurred with other members of the *dentipes* species complex (Shell & Rehan 2018), and its position in the tree suggests that *C. guarnacciana* may be synonymized with *C. dentipes* in any case.

Clade G retains the ancestral Afrotropical distribution, but also includes two independent colonizations of Madagascar by *C.* (*Malgatina*) *azurea* and *C.* (*Copoceratina*) *madecassa* (as well as a more recent range expansion to include Madagascar in *C.* (*Hirashima*) *nyassensis*). Also within this group, the ancestors of subgenus *Euceratina* transitioned from Africa to the western Palearctic about 13–25 Ma, where they still make up the majority of *Ceratina* diversity in Europe and West Asia with about 35 species (Ascher & Pickering, 2020; Terzo & Rasmont, 2011).

4. Discussion

4.1. Subgeneric relationships

The relationships in our main phylogeny differ to some degree from previous studies. Most notably, both Rehan et al. (2010) and Rehan & Schwarz (2015) recover *Neoceratina* as the sister group to all other *Ceratina*, while in our tree the first split within the genus occurs between two groups of similar size (clades A and B), with *Neoceratina* as the sister group to part of *Ceratina sensu stricto* (clade F). As in Rehan & Schwarz (2015), we recover a large clade consisting of *Euceratina* as the sister group to *Hirashima* + *Ctenoceratina* + *Simioceratina* (clade G). The position of *Pithitis* is another significant difference. In this study, *Pithitis* (along with *Protopithitis* in clade E) is recovered as the sister to the rest of our clade B, while former studies reported *Pithitis* as sister to a large group consisting of *Lioceratina* + *Ceratinidia* + *Zadontomerus* and other Neotropical species (Rehan et al., 2010; Rehan & Schwarz, 2015). The position of the sole representative of *Megaceratina*, *C.* (*M.*) *sculpturata*, also differs in our tree, being the sister to all other members of clade A rather than nested within *Ceratina s.s.* as in Rehan & Schwarz (2015). Due to the present study's greater taxon sampling and significantly larger dataset (hundreds of UCE loci in contrast to three genes), we suggest that our results are likely to be more strongly supported where the topology differs from these previous studies. The subgenus *Chloroceratina* (Philippines) as well as the recently described *Alloceratina* and *Xestoceratina* (Afrotropics; Engel, 2023) are not represented in our tree, and as such are of uncertain phylogenetic position.

There are several *Ceratina* subgenera which merit some form of systematic revision. The placement of *C. canarensis* and *C. picta* within *Lioceratina* and *Xanthoceratina* respectively may need to be reconsidered given their positions in the tree. *Ceratinula* should likely be reduced in size, with some species moved to other Neotropical subgenera or erected as new subgenera themselves. For example, *C. buscki* and *auriviridis* could be grouped with *C. marginata* to create a new subgenus while also restoring the monophyly of *Zadontomerus*. A monophyletic group could be made by uniting the recently described subgenera *Copoceratina* and *Dalyatina* (Pauly et al., 2001; Terzo et al., 2007) with a few stray species of *Ceratina sensu stricto*. While the description of novel subgenera is important for resolving issues of paraphyly, this section of clade G exemplifies that new taxa should be carefully evaluated for monophyly themselves to avoid oversplitting.

The nominate subgenus remains the most problematic due to its highly polyphyletic nature, however. Of particular concern is the fact that the type species of *Ceratina*, *C. cucurbita* (Rossi 1792) is effectively orphaned as the sister to *Xanthoceratina* + *Ceratinidia*, rather than other members of the nominate subgenus. Though this situation is difficult to rectify, it seems most desirable that this subgenus be reduced in size significantly to the type species and its close relatives, allowing for many of the other current members to be reassigned into more natural groupings with related subgenera. Where needed, novel subgenera could also be described for former members of *Ceratina s.s.* to preserve monophyly, as has already been done in some cases (Terzo et al., 2007). Some potential candidates are a new subgenus including *Ceratina monstrata* and *megastigmata*, and possibly another including the five species we recover as the sister clade of *Neoceratina*.

4.2. Evolutionary history of Ceratina

The recovered dates in our main phylogeny are broadly in agreement with previous findings. In particular, our mean crown age for *Ceratina* of 41.87 Ma is somewhat younger than the dates 55.6 Ma suggested by Rehan & Schwarz (2015) and slightly younger than the 47 Ma, 51.3 Ma, or 50.2 Ma dates recovered by Rehan et al., (2010,2012) and Smith et al. (2013) respectively. However, other studies have recovered still younger ages as well (e.g., Martins & Melo, 2016; 38.3 Ma). There is little fossil evidence to directly corroborate these dates, besides the extinct *Boreoallodape* which imposes a lower limit of roughly 40 million years on the split between Ceratinini and Allodapini (Engel 2001a). The single fossil attributed to *Ceratina*, that of *C. disrupta* from the Eocene of Colorado (Cockerell, 1906), is not well preserved and its affinity has previously been brought into question (Engel 2001b). It is noteworthy that our mean estimate for the crown age of *Ceratina* of 41.87 Ma corresponds very closely to the estimated start of the Middle Eocene Climatic Optimum (MECO) around 41.5 Ma, as evidenced by shifts in oxygen isotope ratios (Bohaty & Zachos, 2003; Jovane et al., 2007). This event, characterized by a relatively sudden (though short-lived) increase in temperature, may have played a role in facilitating early dispersal or range expansion of *Ceratina*, as has been suggested for other bee taxa such as the Ancylaini (Freitas et al., 2022). Future analyses of *Ceratina* and other groups of bees may further support this hypothesis if a more consistent pattern of increased dispersal during such warming events can be identified.

The evolutionary history of *Ceratina* includes several clear-cut instances of dispersal between biogeographic realms, often leading to diversification in new territories. The early dispersal events from the ancestral Afrotropics to Indomalaya would have been plausible in the given time frame (~25–35 Ma) due to the absence of some barriers to dispersal between Africa and Western Asia. In particular, by this time the Neo-Tethys Ocean separating Arabia from Eurasia was in the process of closing (Zhu et al., 2022), while the Red Sea did not begin opening until approximately 25 Ma (Ghebreab, 1998). The absence of any known Palearctic taxa from these early lineages could potentially be the result of fairly direct dispersal from Arabia to India without any northward expansion, or this could simply be due to the extinction of all early Palearctic groups. Similar distributions and inferred patterns of dispersal between the Afrotropics and Indomalaya have also been noted in the bee tribes Meliponini (Rasmussen & Cameron, 2009) and Ctenoplectrini (Schaefer & Renner, 2008). Another noteworthy biogeographic question concerns the low diversity of *Ceratina* in Australia. Though there are several species known from other islands around the Australasian realm, only one (*C. australensis*) is found in Australia itself, having arrived from Indomalaya at some time during the past nine million years. Competition for nesting substrate could serve as a potential explanation for this observation, since Australia was already home to a diverse group of small stem- and cavity-nesting bees (e.g. Allodapini, Euryglossinae, and Hylaeinae; Michener, 1979).

The arrival of *Ceratina* in the Americas was another important event in the history of the genus. Except for *C. guarnacciana* as discussed above, all Neotropical and Nearctic species form a monophyletic group (clade D) which has two successive sister groups of Indomalayan taxa. The recent timing of this inferred dispersal (~20–25 Ma) likely places it after the formation of the Antarctic Circumpolar Current (Siegert et al., 2008), making a southern dispersal route through Antarctica (as has been suggested for some Colletidae; Kayaalp et al., 2017) impossible. Similarly, the vast distance between the Indomalayan and Neotropic realms seems to make an oceanic dispersal highly unlikely. The northern land-based dispersal route, as described by Rehan et al. (2010) and Rehan & Schwarz (2015), thus remains the most parsimonious method of dispersal. Our estimated date for this biogeographic transition during the early Miocene corresponds well with similar dispersals towards the end of the first major phase of the Bering Land Bridge by other groups of bees (Dorchin et al., 2018; Ferrari et al., 2020; Hines, 2008) as well as several lineages of plants (Wen et al., 2016). The absence of any Palearctic taxa within this clade, as well as its apparent Neotropical origins, may suggest the existence of previous Nearctic lineages which were wiped out during glaciation events – of which the fossil *C. disrupta* could be a member, if it is indeed within *Ceratina* at all. However, all current Nearctic species clearly arrived more recently from the Neotropics, presumably by island hopping during the early phases of the Great American Biotic Interchange prior to the completion of the Isthmus of Panama as has been inferred for some vertebrate taxa (Woodburne, 2010).

As previously discussed by Groom & Rehan (2018), our results highlight the importance of the tropics in the origin and evolution of *Ceratina*. In contrast to the amphitropical distribution for most bees suggested by Michener (1979), the origins and much of the present diversity of *Ceratina* can be found in the tropics, including over half of the specimens included in our tree. When considering the overall pattern of biogeographic transitions suggested by our reconstruction, the majority of dispersal events originate in the Paleotropics. Interestingly, while at least nine independent lineages of *Ceratina* are inferred to have migrated to the Palearctic, we identify no known instances of dispersal in the other direction (i.e., Palearctic back to tropics). Dispersal rates from Africa to Madagascar, Indomalaya to Australasia, and the Neotropics to Nearctic are similarly asymmetrical, though these events tend to be more recent and so there may not have been enough time for migrations in the opposite direction to occur. As such, tropical regions were not only the ancestral homeland for *Ceratina*, but also continued to serve as major points of origin for repeated dispersal events over the course of the evolution of the genus and tribe Ceratinini.

5. Conclusions

The expansion in the number of included taxa as well as the use of ultraconserved element phylogenomic data for a large, genome-wide sequence dataset has allowed us to gain further insights into the phylogeny and evolutionary history of *Ceratina* than ever before. The relationships recovered in our tree are generally consistent with current subgeneric classification but highlight the need for additional taxonomic focus on some groups – none more so than the highly polyphyletic *Ceratina sensu stricto*. Our reconstructed crown age of 41.87 Ma for crown *Ceratina* is slightly younger than previous estimates but is still generally consistent with inferred biogeographic history. In line with previous work, our favoured model suggests an ancestral distribution for *Ceratina* in Africa during the mid Eocene. Subsequent dispersal events, beginning with two migrations to Indomalaya, carried the genus throughout the rest of the world. In contrast to many other groups of bees, most of these biogeographical transitions occurred within or from the tropics, which also served as the cradle for the early evolution of *Ceratina* and remain significant sources of small carpenter bee diversity. This apparent inversion of the trend for bees more generally may be related to the interaction between *Ceratina*'s nesting biology and the increased niche heterogeneity of the tropics, though this topic merits further investigation.

CRediT authorship contribution statement

Trevor J.L. Sless: Writing – original draft, Visualization, Methodology, Formal analysis. **Michael G. Branstetterb:** Writing – review & editing, Visualization, Software, Resources, Methodology, Formal analysis, Data curation. **Michael Mikát:** Writing – review & editing, Visualization, Software, Resources, Methodology, Formal analysis, Data curation. **Katherine A. Odanaka:** Writing – review & editing, Validation, Investigation, Data curation. **Kerrigan B. Tobin:** Writing – review & editing, Methodology, Investigation, Data curation. **Sandra M. Rehan:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Read data for all newly sequenced species included in this study are available through the NCBI SRA under BioProject PRJNA966956. Additional supplementary files including sequence alignments, phylogenetic trees, and R scripts can be found in the DataDryad repository [TBD].

Acknowledgements

We thank several individuals and institutions who loaned specimens for this study, namely Daniel Benda, Michael Kuhlman, Laurence Packer, Valerie Peters, Jakub Straka, Michael Terzo, Jitka Waldhauserová, Wen-Chi Yeh, and the Linz Museum (Austria). Funding was provided by NSERC Discovery Grants, Supplement and EWR Steacie Memorial Fellowship (Canada, to SMR); Marie Curie Postdoctoral Fellowship (European Union, to MM; N 893244, Project Ceratina); Ontario Graduate Scholarship and Mitacs Research and Training Award (Canada, to KAO); the U.S. Department of Agriculture, Agricultural Research Service (United States, to MGB, KBT; Project#2080-21000-019-000-D); and the U.S. National Science Foundation (United States, to MGB; DEB#2127744). USDA is an equal opportunity provider and employer. We also thank the two anonymous reviewers who provided constructive feedback and helped to improve the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2024.108133.

References

Almeida, E.A.B., Bossert, S., Danforth, B.N., Porto, D.S., Freitas, F.V., Davis, C.C., Murray, E.A., Blaimer, B.B., Spasojevic, T., Ströher, P.R., Orr, M.C., Packer, L., Brady, S.G., Kuhlmann, M., Branstetter, M.G., Pie, M.R., 2023. The evolutionary history of bees in time and space. Curr. Biol. 33 (16), 3409–3422. https://doi.org/10.1016/j.cub.2023.07.005.

Ascher JS, Pickering J. (2020). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available from http://www.discoverlife.org/mp/20q?guide=Apoidea_species.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Pevzner, P.A., 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. J. Comput. Biol. 19 (5), 455–477. https://doi.org/10.1089/cmb.2012.0021.

Batista, R., Olsson, U., Andermann, T., Aleixo, A., Ribas, C.C., Antonelli, A. (2020). Phylogenomics and biogeography of the world's thrushes (Aves, *Turdus*): new evidence for a more parsimonious evolutionary history. *Proceedings of the Royal Society B: Biological Sciences* 287(1919): 20192400. doi: 10.1098/rspb.2019.2400.

Blaimer, B.B., Mawdsley, J.R., Brady, S.G., 2018. Multiple origins of sexual dichromatism and aposematism within large carpenter bees. Evolution 72 (9), 1874–1889. https://doi.org/10.1111/evo.13558.

Blumenstiel, B., Cibulskis, K., Fisher, S., DeFelice, M., Barry, A., Fennell, T., Gabriel, S., 2010. Targeted exon sequencing by in-solution hybrid selection. Curr. Protoc. Hum. Genet. 66 (1), 18–24. https://doi.org/10.1002/0471142905.hg1804s66.

Bohaty, S.M., Zachos, J.C., 2003. Significant Southern Ocean warming event in the late middle Eocene. Geology 31 (11), 1017–1020. https://doi.org/10.1130/G19800.1.

Bolger, A.M., Lohse, M., Usadel, B., 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30 (15), 2114–2120. https://doi.org/10.1093/bioinformatics/btu170.

Borowiec, M.L., 2019. Spruceup: fast and flexible identification, visualization, and removal of outliers from large multiple sequence alignments. Journal of Open Source Software 4 (42), 1635. https://doi.org/10.21105/joss.01635.

Bossert, S., Murray, E.A., Almeida, E.A.B., Brady, S.G., Blaimer, B.B., Danforth, B.N., 2019. Combining transcriptomes and ultraconserved elements to illuminate the phylogeny of Apidae. Mol. Phylogenet. Evol. 130, 121–131. https://doi.org/10.1016/j.ympev.2018.10.012.

Bouckaert, R., Vaughan, T.G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F., Ogilvie, H.A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C.-H., Xie, D., Zhang, C., Stadler, T., Drummond, A.J., 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 15 (4), e1006650.

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L., Brady, S.G., 2017. Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. Curr. Biol. 27 (7), 1019–1025. https://doi.org/10.1016/j.cub.2017.03.027.

Branstetter, M.G., Longino, J.T., 2019. Ultra-conserved element phylogenomics of New World *Ponera* (Hymenoptera: Formicidae) illuminates the origin and phylogeographic history of the endemic exotic ant *Ponera exotica*. Insect Systematics and Diversity 3 (2). https://doi.org/10.1093/isd/ixz001.

Branstetter, M.G., Müller, A., Griswold, T.L., Orr, M.C., Zhu, C.-D., 2021. Ultraconserved element phylogenomics and biogeography of the agriculturally important mason bee subgenus *Osmia* (*Osmia*). Syst. Entomol. 46 (2), 453–472. https://doi.org/10.1111/syen.12470.

Bushnell B. (2014). BBTools software package. Available from https://sourceforge.net/projects/bbmap/.

Chenomor, O., von Haeseler, A., Minh, B.Q., 2016. Terrace aware data structure for phylogenomic inference from supermatrices. Syst. Biol. 65 (6), 997–1008. https://doi.org/10.1093/sysbio/syw037.

Cockerell, T.D.A., 1906. Fossil hymenoptera from florissant, colorado. Bulletin of the Museum of Comparative Zoology, Harvard College 50 (2), 33–58.

Dehon, M., Perrard, A., Engel, M.S., Nel, A., Michez, D., 2017. Antiquity of cleptoparasitism among bees revealed by morphometric and phylogenetic analysis of a Paleocene fossil nomadine (Hymenoptera: Apidae). Syst. Entomol. 42, 543–554. https://doi.org/10.1111/syen.12230.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.-B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. Bioscience 67 (6), 534–545. https://doi.org/10.1093/biosci/bix014.

Dorchin, A., López-Uribe, M.M., Praz, C.J., Griswold, T., Danforth, B.N., 2018. Phylogeny, new generic-level classification, and historical biogeography of the *Eucera* complex (Hymenoptera: Apidae). Mol. Phylogenet. Evol. 119, 81–92. https://doi.org/10.1016/j.ympev.2017.10.007.

Douglas, J., Zhang, R., Bouckaert, R., 2021. Adaptive dating and fast proposals: revisiting the phylogenetic relaxed clock model. PLoS Comput. Biol. 17 (2), e1008322.

Eardley, C.D., Daly, H.V., 2007. Bees of the genus *Ceratina* Latreille in southern Africa (Hymenoptera, Apoidea). Entomofauna 13, 1–96.

Engel, M.S., 2001. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). Bull. Am. Mus. Nat. Hist. 2001 (259), 1–192. https://doi.org/10.1206/0003-0090(2001)259%3C0001:AMOTBA%3E2.0.CO;2.

Engel, M.S., 2023. On the subgeneric placements of *Ceratina foveifera* Strand and *C. labrosa* Friese from Africa (Hymenoptera: Apidae). Entomologist's Monthly Magazine 159 (4), 48–52. https://doi.org/10.31184/M00138908.1594.4211.

Engel, M.S (2001b). The first large carpenter bee from the Tertiary of North America, with a consideration of the geological history of Xylocopinae (Hymenoptera: Apidae). *Transactions of the American Entomological Society (1890-)* 127(2): 245-254. https://www.jstor.org/stable/25078743.

Esquerré, D., Donnellan, S., Brennan, I.G., Lemmon, A.R., Lemmon, E.M., Zaher, H., Grazziotin, F.G., Keogh, J.S., 2020. Phylogenomics, biogeography, and morphometrics reveal rapid phenotypic evolution in pythons after crossing Wallace's line. Syst. Biol. 69 (6), 1039–1051. https://doi.org/10.1093/sysbio/syaa024.

Faircloth, B.C., 2016. PHYLUCE is a software package for the analysis of conserved genomic loci. Bioinformatics 32 (5), 786–788. https://doi.org/10.1093/bioinformatics/btv646.

Faircloth, B.C., McCormack, J.E., Crawford, N.G., Harvey, M.G., Brumfield, R.T., Glenn, T.C., 2012. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. Syst. Biol. 61 (5), 717–726. https://doi.org/10.1093/sysbio/sys004.

Faircloth, B.C (2013). Illumiprocessor: a trimmomatic wrapper for parallel adapter and quality trimming. Available from https://doi.org/10.6079/J9ILL.

Ferrari, R.R., Onuferko, T.M., Monckton, S.K., Packer, L., 2020. The evolutionary history of the cellophane bee genus *Colletes* Latreille (Hymenoptera: Colletidae): Molecular phylogeny, biogeography and implications for a global infrageneric classification. Mol. Phylogenet. Evol. 146, 106750 https://doi.org/10.1016/j.ympev.2020.106750.

Freitas, F.V., Branstetter, M.G., Griswold, T., Almeida, E.A.B., 2021. Partitioned gene-tree analyses and gene-based topology testing help resolve incongruence in a phylogenomic study of host-specialist bees (Apidae: Eucerinae). Mol. Biol. Evol. 38 (3), 1090–1100. https://doi.org/10.1093/molbev/msaa277.

Freitas, F.V., Branstetter, M.G., Casali, D.M., Aguiar, A.J.C., Griswold, T., Almeida, E.A.B., 2022. Phylogenomic dating and Bayesian biogeography illuminate an antitropical pattern for eucerine bees. J. Biogeogr. 49 (6), 1034–1047. https://doi.org/10.1111/jbi.14359.

GBIF: The Global Biodiversity Information Facility. (2023). Available from https://www.gbif.org.

Genaro, J.A., 1998. El Género *Ceratina* en Cuba y La Española (Hymenoptera: Apidae). Carib. J. Sci. 34 (1–2), 95–98.

Ghebreab, W., 1998. Tectonics of the Red Sea region reassessed. Earth Sci. Rev. 45 (1–2), 1–44. https://doi.org/10.1016/S0012-8252(98)00036-1.

Glenn, T.C., Nilsen, R.A., Kieran, T.J., Sanders, J.G., Bayona-Vásquez, N.J., Finger, J.W., Faircloth, B.C., 2019. Adapterama I: Universal stubs and primers for 384 unique dual-indexed or 147,456 combinatorially-indexed Illumina libraries (iTru & iNext). PeerJ 2019 (10), e7755.

Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., Blitzer, E.J., Poveda, K., Loeb, G., Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science 363 (6424), 282–284. https://doi.org/10.1126/science.aat6016.

Groom, S.V.C., Rehan, S.M., 2018. Climate-mediated behavioural variability in facultatively social bees. Biol. J. Linn. Soc. 125 (1), 165–170. https://doi.org/10.1093/biolinnean/bly101.

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O., 2010. New algorithms methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst. Biol. 59 (3), 307–321. https://doi.org/10.1093/sysbio/syq010.

Harris, R.S., 2007. Improved pairwise alignment of genomic DNA. The Pennsylvania State University. Ph.D. Thesis,.

Hines, H., 2008. Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*). Syst. Biol. 57 (1), 58–75. https://doi.org/10.1080/10635150801898912.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q., Vinh, L.S., 2018. UFBoot2: improving the ultrafast bootstrap approximation. Mol. Biol. Evol. 35 (2), 518: 522. https://doi.org/10.1093/molbev/msx281.

Jovane, L., Florindo, F., Coccioni, R., Dinarès-Turell, J., Marsili, A., Monechi, S., Roberts, A.P., Sprovieri, M., 2007. The middle Eocene climatic optimum event in the Contessa Highway section, Umbrian Apennines Italy. GSA Bulletin 119 (3–4), 413–427. https://doi.org/10.1130/B25917.1.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A., Jermiin, L.S., 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nat. Methods 14, 587–589. https://doi.org/10.1038/nmeth.4285.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30 (4), 772–780. https://doi.org/10.1093/molbev/mst010.

Kayaalp, P., Stevens, M.I., Schwarz, M.P., 2017. 'Back to Africa': increased taxon sampling confirms a problematic Australia-to-Africa bee dispersal event in the Eocene. Syst. Entomol. 42, 724–733. https://doi.org/10.1111/syen.12241.

Landis, M.J., Matzke, N.J., Moore, B.R., Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. Syst. Biol. 62 (6), 789–804. https://doi.org/10.1093/sysbio/syt040.

Ledford, J., Derkarabetian, S., Ribera, C., Starrett, J., Bond, J.E., Griswold, C., Hedin, M., 2021. Phylogenomics and biogeography of leptonetid spiders (Araneae : Leptonetidae). Invertebr. Syst. 35, 332–349. https://doi.org/10.1071/IS20065.

Martins, A.C., Melo, G.A.R., 2016. The New World oil-collecting bees *Centris* and *Epicharis* (Hymenoptera, Apidae): molecular phylogeny and biogeographic history. Zool. Scr. 45 (1), 22–33. https://doi.org/10.1111/zsc.12133.

Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Frontiers of Biogeography 5 (4). https://doi.org/10.21425/F5FBG19694.

Matzke, N.J., 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Syst. Biol. 63 (6), 951–970. https://doi.org/10.1093/sysbio/syu056.

Michener, C.D., 1979. Biogeography of the bees. Ann. Mo. Bot. Gard. 66 (3), 277–347. https://doi.org/10.2307/2398833.

Michener, C.D., 2007. The Bees of the World, 2nd Edition. John Hopkins University Press, Baltimore.

Michener, C.D., Grimaldi, D.A. (1988). The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proceedings of the National Academy of Sciences of the United States of America* 85(17): 6424-6426. doi: 10.1073/pnas.85.17.6424.

Michez, D., De Meulemeester, T., Rasmont, P., Nel, A., Patiny, S., 2009. New fossil evidence of the early diversification of bees: *Paleohabropoda oudardi* from the French Paleocene (Hymenoptera, Apidae, Anthophorini). Zool. Scr. 38 (2), 171–181. https://doi.org/10.1111/j.1463-6409.2008.00362.x.

Mikát, M., Janošík, L., Černá, K., Straka, S. (2019). Polyandrous bee provides extended offspring care biparentally as an alternative to monandry based eusociality. *Proceedings of the National Academy of Sciences of the United States of America* 116(13): 6238-6243. doi: 10.1073/pnas.1810092116.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A., Lanfear, R., 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Mol. Biol. Evol. 37 (5), 1530–1534. https://doi.org/10.1093/molbev/msaa015.

Odanaka, K.A., Branstetter, M.G., Tobin, K.B., Rehan, S.M., 2022. Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements. Mol. Phylogenet. Evol. 170, 107453 https://doi.org/10.1016/j.ympev.2022.107453.

Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.-D., Ascher, J.S., 2021. Global patterns and drivers of bee distribution. Curr. Biol. 31 (3), 451–458. https://doi.org/10.1016/j.cub.2020.10.053.

Orr, M.C., Branstetter, M.B., Straka, J., Yuan, F., Leijs, R., Zhang, D., Zhou, Q., Zhu, C.-D., 2022. Phylogenomic interrogation revives an overlooked hypothesis for the early evolution of the bee family Apidae (Hymenoptera: Apoidea), with a focus on the subfamily Anthophorinae. Insect Systematics and Diversity 6 (4). https://doi.org/10.1093/isd/ixac022.

Paradis, E., Schliep, K., 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35 (3), 526–528. https://doi.org/10.1093/bioinformatics/bty633.

Pauly, A., Brooks, R.W., Nilsson, L.A., Pesenko, Y.A., Eardley, C.D., Terzo, M., Griswold, T., Schwarz, M., Patiny, S., Munzinger, J., Barbier, Y., 2001. Hymenoptera Apoidea de Madagascar et des îles voisines. *Annales du Musée royal de l'Afrique centrale (Sciences Zoologiques)*. Tervuren (Belgique) 286, 1–406.

Poulsen, N.R., Rasmussen, C., 2020. Island bees: do wood nesting bees have better island dispersal abilities? Apidologie 51, 1006–1017. https://doi.org/10.1007/s13592-020-00778-x.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst. Biol. 67 (5), 901–904. https://doi.org/10.1093/sysbio/syy032.

Rasmussen, C., Cameron, S.A., 2009. Global stingless bee phylogeny supports ancient divergence, vicariance, and long distance dispersal. Biol. J. Linn. Soc. 99 (1), 206–232. https://doi.org/10.1111/j.1095-8312.2009.01341.x.

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. J. Biogeogr. 45 (4), 741–749. https://doi.org/10.1111/jbi.13173.

Ree, R.H., Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Syst. Biol. 57 (1), 4–14. https://doi.org/10.1080/10635150701883881.

Rehan, S.M., Schwarz, M.P., 2015. A few steps forward and no steps back: long-distance dispersal patterns in small carpenter bees suggest major barriers to back-dispersal. J. Biogeogr. 42, 485–494. https://doi.org/10.1111/jbi.12439.

Rehan, S.M., Chapman, T.W., Craigie, A.I., Richards, M.H., Cooper, S.J.B., Schwarz, M.P., 2010. Molecular phylogeny of the small carpenter bees (Hymenoptera: Apidae: Ceratinini) indicates early and rapid global dispersal. Mol. Phylogenet. Evol. 55 (3), 1042–1054. https://doi.org/10.1016/j.ympev.2010.01.011.

Rehan, S.M., Leys, R., Schwarz, M.P., 2012. A mid-cretaceous origin of sociality in xylocopine bees with only two origins of true worker castes indicates severe barriers to eusociality. PLoS One 7 (4), e34690.

Revell, L.J., 2012. Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3 (2), 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x.

Rohland, N., Reich, D., 2012. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. Genome Res. 22 (5), 939–946. https://doi.org/10.1101/gr.128124.111.

Ronquist, F., 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Syst. Biol. 46 (1), 195–203. https://doi.org/10.1093/sysbio/46.1.195.

Sakagami, S.F., Laroca, S., 1971. Observations of the bionomics of some neotropical xylocopine bees, with comparative and biofaunistic notes (Hymenoptera, Anthophoridae). Journal of the Faculty of Science Hokkaido University 18 (1), 57–127.

Sakagami, S.F., Maeta, Y., 1977. Some presumably presocial habits of Japanese *Ceratina* bees, with notes on various social types in Hymenoptera. Insect. Soc. 24, 319–343. https://doi.org/10.1007/BF02223784.

Schaefer, H., Renner, S.S., 2008. A phylogeny of the oil bee tribe Ctenoplectrini (Hymenoptera: Anthophila) based on mitochondrial and nuclear data: evidence for early Eocene divergence and repeated out-of-Africa dispersal. Mol. Phylogenet. Evol. 47 (2), 799–811. https://doi.org/10.1016/j.ympev.2008.01.030.

Shell, W.A., Rehan, S.M., 2019. Invasive range expansion of the small carpenter bee, *Ceratina dentipes* (Hymenoptera: Apidae) into Hawaii with implications for native endangered species displacement. Biol. Invasions 21, 1155–1166. https://doi.org/10.1007/s10530-018-1892-z.

Siegert, M.J., Barrett, P., Deconto, R.M., Dunbar, R., Cofaigh, C.O., Passchier, S., Naish, T., 2008. Recent advances in understanding Antarctic climate evolution. Antarct. Sci. 20 (4), 313–325. https://doi.org/10.1017/S0954102008000941.

Sless, T.J.L., Branstetter, M.G., Gillung, J.P., Krichilsky, E.A., Tobin, K.B., Straka, J., Rozen, J.G., Freitas, F.V., Martins, A.C., Bossert, S., Searle, J.B., Danforth, B.N., 2022. Phylogenetic relationships and the evolution of host preferences in the largest clade of brood parasitic bees (Apidae: Nomadinae). Mol. Phylogenet. Evol. 166, 107326 https://doi.org/10.1016/j.ympev.2021.107326.

Sless, T.J.L., Rehan, S.M., 2023. Phylogeny of the carpenter bees (Apidae: Xylocopinae) highlights repeated evolution of sociality. Biol. Lett. 19 (8), 20230252. https://doi.org/10.1098/rsbl.2023.0252.

Smith, J., Chenoweth, L., Tierney, S., Schwarz, M., 2013. Repeated origins of social parasitism in allodapine bees indicate that the weak form of Emery's rule is widespread, yet sympatric speciation remains highly problematic. Biol. J. Linn. Soc. 109 (2), 320–331. https://doi.org/10.1111/bij.12043.

Tagliacollo, V.A., Lanfear, R., 2018. Estimating improved partitioning schemes for ultraconserved elements. Mol. Biol. Evol. 35 (7), 1798–1811. https://doi.org/10.1093/molbev/msy069.

Talavera, G., Castresana, J., 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56 (4), 564–577. https://doi.org/10.1080/10635150701472164.

Terzo, M., Iserbyt, S., Rasmont, P., 2007. Révision des Xylocopinae (Hymenoptera: Apidae) de France et de Belgique. Annales De La Société Entomologique De France 43 (4), 445–491. https://doi.org/10.1080/00379271.2007.10697537.

Terzo, M., Rasmont, P., 2011. Atlas of the European bees: genus *Ceratina*. STEP Project, Atlas Hymenoptera, Mons, Gembloux. Available from http://www.atlashymenoptera.net/page.aspx?id=192.

Wang, Y., Huang, J., Li, E., Xu, S., Zhan, Z., Zhang, X., Yang, Z., Guo, F., Liu, K., Liu, D., Shen, X., Shang, C., Zhang, Z., 2022. Phylogenomics and biogeography of *Populus* based on comprehensive sampling reveal deep-level relationships and multiple intercontinental dispersals. Front. Plant Sci. 13, 813177 https://doi.org/10.3389/fpls.2022.813177.

Wen, J., Nie, Z.-L., Ickert-Bond, S.M., 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. J. Syst. Evol. 54 (5), 469–490. https://doi.org/10.1111/jse.12222.

Woodburne, M.O. (2010). The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* 17(4): 245-264. doi: 10.1007%2Fs10914-010-9144-8.

Zeuner, F.E., Manning, F.J., 1976. A monograph on fossil bees: Apoidea. Bulletin of the British Museum of Natural History (geology) 27 (3), 151–264.

Zhu, R., Zhao, P., Zhao, L., 2022. Tectonic evolution and geodynamics of the Neo-Tethys Ocean. Sci. China Earth Sci. 65, 1–24. https://doi.org/10.1007/s11430-021-9845-7.