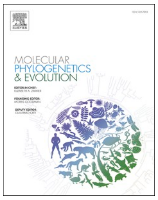
Molecular Phylogenetics and Evolution 204 (2025) 108273

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

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



Phylogeny, antiquity, and niche occupancy of *Trinomia* (Hymenoptera: Halictidae), an Afrotropical endemic genus of Nomiinae

Silas Bossert [a,b,*], Felipe V. Freitas [a], Alain Pauly [c], Gengping Zhu [a], David W. Crowder [a], Michael C. Orr [d], James B. Dorey [e], Elizabeth A. Murray [a,b]

[a] *Department of Entomology, Washington State University, Pullman, WA, USA*
[b] *Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA*
[c] *Royal Belgian Institute of Natural Sciences, O.D. Taxonomy and Phylogeny, Rue Vautier 29, 1000 Brussels, Belgium*
[d] *Entomologie, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany*
[e] *Faculty of Science, Medicine and Health, University of Wollongong, Wollongong, New South Wales, Australia*

ABSTRACT

The Afrotropical region is home to many endemic bee groups, yet almost none have been studied from an integrated, holistic perspective. Among them, the halictid subfamily Nomiinae contains exceptional African diversity with variable distributions and life histories. Here, we combine phylogenomics, molecular dating, and distributional modelling to explore the evolutionary ecology of the genus *Trinomia*. We analyzed a matrix of 59 species of Nomiinae using ultraconserved element (UCE) and whole genome data, including all six species of *Trinomia*, and estimated divergence times for the subfamily. We then generated distribution models for all six species of *Trinomia* using Maximum Entropy models (MaxEnt) and 671 spatial data points. From these methods, we discovered a monophyletic *Trinomia* with an unexpected sister group relationship to the Asian-endemic genus *Gnathonomia*, as well as a recent origin of *Trinomia* in the late Miocene (~5.8 million years ago). From our results, we found hints of phylogenetic conservatism in distribution among sister-groups of *Trinomia*, however, our results also highlight the need for additional efforts inventorying, identifying, and sharing data on African bees. This study represents an exemplary first step into studying bee spatial phylogenomics of African endemic bees.

1. Introduction

We are moving toward a cohesive picture of global bee biodiversity through space and time (Almeida et al., 2023), but much work remains in some regions of the globe (Warrit et al., 2023). Africa is home to several hotspots of bee biodiversity (Orr et al., 2021), but its fauna is understudied compared to other parts of the world (Eardley et al., 2010; Kuhlmann, 2005; Kuhlmann, 2009; Kuhlmann et al., 2012). Given hypotheses of Gondwanan bee origins (Almeida et al., 2023), investigating the contemporary and historical dynamics of the bee fauna there is paramount for understanding the drivers governing bee ecology and evolution. However, given taxonomic challenges and the various difficulties of acquiring verified specimens for many species, intensive efforts at comprehensive views of bee biodiversity in the region are only now possible on a case-by-case basis for specific bee groups.

The sweat bee subfamily Nomiinae has its center of diversity in tropical realms of the Old World and half of the 620 recognized species occur in sub-Saharan Africa (Michener, 2007; Pauly, 2009). Several lineages are endemic to the Afrotropics and 9 of the 32 genera recognized by Pauly (2009) are restricted to the Afrotropics. Recent work established phylogenetic relationships of the genera comprising *Pseudapis* s. l. and the distinct phylogenetic position of *Clavinomia* Warncke, 1980 (Bossert et al., 2024). However, higher-level relationships of the Nomiinae remain poorly understood, and none of the African-endemic groups, including *Trinomia* Pauly, 1980, have been phylogenetically revised using molecular data. This limits our understanding of the natural history of African endemics, the evolutionary relationships among lineages, and their antiquity.

To better assess the natural history of these groups, we developed a fully-sampled, species-level phylogeny of the genus *Trinomia* using whole genome sequencing. This phylogenetic framework enabled us to achieve three objectives. First, we addressed prior taxonomic uncertainties as Michener (2007) treated *Trinomia* as a subgenus of *Lipotriches* Gerstäcker, 1858, but cautioned *Lipotriches* “may turn out to be a paraphyletic unit”. In contrast to Pauly (e.g., Pauly (1990, 2014a, 2014b), Michener (2007) urged further study and used *Lipotriches* in a wider sense. This included several lineages that Pauly (1990) and the DiscoverLife.org global checklist (Ascher and Pickering, 2024)

---

* Corresponding author at: Department of Entomology, Washington State University, Pullman, Washington, USA.
E-mail address: silas.bossert@wsu.edu (S. Bossert).

https://doi.org/10.1016/j.ympev.2024.108273
Received 14 April 2024; Received in revised form 21 November 2024; Accepted 9 December 2024

recognize as genera, including *Trinomia* and *Afronomia* Pauly, 1990. However, neither classification was developed when genome-scale phylogenetic inference could address taxonomic problems, and clarification could be achieved by establishing a sound molecular-phylogenetic framework. Such a phylogenetic framework could further help to understand the phylogenetic pattern of the morphological similarities between *Trinomia* and the genus *Austronomia* Michener, 1965, like the entirely carinate basitibial plate of the females or the lack of integumental bands that are characteristic for certain Nomiinae (Pauly, 1999).

Second, a well-sampled molecular phylogeny will enable the estimation of the temporal origin of *Trinomia*. Recent work indicated an origin in the late Neogene (Bossert et al., 2024), but with the limited sampling of just one representative individual, only stem age estimates could be inferred. Furthermore, Bossert et al. (2024) found a surprising Miocene-split of the most recent common ancestor (MRCA) of present-day *Trinomia* with *Gnathonomia* Pauly, 2009, an Asian-endemic lineage, and a sister-group relationship of this clade to *Afronomia*: ((*Trinomia* + *Gnathonomia*) + *Afronomia*). Revisiting this pattern with additional data and denser sampling would help test this unexpected finding, given the disjunct present-day distribution of the genera.

Lastly, a modern phylogeny would aid in understanding the spatial distribution of *Trinomia* from an evolutionary perspective. *Trinomia* are Afrotropical bees, and all six species occur in continental Africa with the range of one species, *Trinomia triodonta* (Kohl, 1906), expanding into the southern Arabian Peninsula. The Global Biodiversity Information Facility (GBIF) hosts about 800 records for the genus, yet most of this information comprises records of two commonly collected species, *Trinomia tridentata* (Smith, 1875) (~170 records) and *Trinomia orientalis* (Friese, 1909) (~450 records). Georeferenced records for other species are sparse (e.g., 12 entries for *Trinomia digitata* (Friese, 1909)) or unavailable (*Trinomia triodonta*). Also, *Trinomia tridentata* and *Trinomia natalensis* (Cockerell, 1916) can only be separated by examining male genitalia, and records identified as '*Trinomia tridentata*' prior to 1999 most likely correspond to *Trinomia natalensis* because of problematic synonymies clarified by Pauly (1999). This limits the basis for our understanding on the spatial distribution of *Trinomia* and warrants a modern reassessment using newly georeferenced records and distributional modeling. Our study addresses these knowledge gaps by using both phylogenetic analysis of a genome-wide dataset and species distribution models. In doing so, we provide an important starting point into future investigations on not just Nomiinae, but also the wealth of other African endemic bee groups.

2. Material and methods

2.1. Taxon sampling

We obtained recently collected, pinned specimens for all six described species of *Trinomia* and from two closely related genera, *Afronomia* and *Gnathonomia* (Bossert et al., 2024), for sequencing. Voucher specimens were deposited in the Washington State University Insect Collection (WSUC) and the Cornell University Insect Collection (CUIC). A total of seven new samples were processed, sequenced, and embedded in the molecular-phylogenetic framework of Nomiinae (Bossert et al., 2024), resulting in 59 studied taxa. This dataset comprises 22 out of the 32 genera sensu Pauly (2009), including all major genera (> 25 species), and provides a framework for assessing the relationships within *Trinomia* and the relationships of *Trinomia* to other Nomiinae. We included all nomiine taxa from Bossert et al. (2024) except duplicate species of *Dieunomia* Cockerell, 1899, and two samples of *Dieunomia* with relatively low sequencing success, *D. boharti* (Cross, 1958) and *D. bolliana* (Cockerell, 1910). As outgroups, we chose the two samples with greatest UCE capture success for the subfamilies Nomioidinae and Halictinae from Bossert et al. (2024). Eleven of the 26 included genera are represented by their respective type species. The taxon sampling is detailed in Table S1, including information on voucher repositories and their respective NCBI BioProject IDs.

2.2. Molecular methods

For the five samples used for whole-genome sequencing, DNA was extracted from three legs of one side of each specimen using a Zymo Quick-DNA Miniprep Plus Kit. Voucher specimens were given a unique DNA extraction label and were deposited according to Table S1. After quantifying DNA concentration using a Qubit 3.0 fluorometer (Thermo Fisher Scientific, Inc.), we assessed fragmentation of each sample by running screen tapes on a 4150 TapeStation (Agilent Technologies, Inc.). We sheared up to 50 ng of total DNA to a target size range of 300–600 bp using a BioRuptor 300 (Diagenode, Inc.). After sonication, we purified DNA using magnetic beads (manufactured by Sergi Lab Supplies) at a 3:1 (3.0 × SPRI) beads to product ratio. We prepared Illumina sequencing libraries using KAPA HyperPrep Kits (F. Hoffmann-La Roche, Ltd.) following Branstetter et al. (2021). We prepared dual-indexed libraries (Glenn et al., 2019) and replaced the KAPA PCR mastermix with 2 × TaKaRa Ex Premier DNA Polymerase mastermix (Takara Bio USA, Inc.). We ran between 14 and 18 PCR cycles, purified each product with magnetic beads at a 1:1 ratio (1.0 × SPRI), and measured DNA concentration using Qubit assays. We pooled samples at equal concentrations and size selected the pool using a BluePippin device (Sage Science, Inc.) for a size distribution of 250–650 bp. Sequencing was carried out by Novogene Co, Ltd. using an Illumina NovaSeq X Plus sequencer and a 10B flow cell, targeting a coverage of 10 ×. The two samples sequenced for UCEs (Table S1), were processed according to Bossert et al. (2024), as they were generated with data contained in this paper.

2.3. Bioinformatic processing

A detailed account of the bioinformatic approach is in the supplementary material. After raw multiplexed Illumina reads were generated by the sequencing facilities, the read data were demultiplexed using the program *demuxbyname* of the *BBtools* package (https://sourceforge.net/projects/bbmap/). We allowed for one mismatch in index sequences (hdist = 1). The reads in each sample were then reordered and duplicated reads were removed (= dedupe) using the *BBtools* function *Clumpfy*. Adapters were trimmed using *fastp* (Chen et al., 2018), again dropping duplicated reads. *BBnorm*, also part of *BBtools*, was used to normalize the reads targeting a coverage of 20× and a minimum coverage of 2×. The normalized reads were assembled using *SPAdes* (Bankevich et al., 2012) using a coverage cutoff of 5 with the parameters '–careful' and '–sc'.

After assembling read data into contigs, we used the *Phyluce* pipeline (Faircloth, 2016) to identify and extract UCE loci from the genomes. To this end, we first converted the fasta assembly files into 2bit files using *faToTwoBit*, a tool provided through the UCSC genome browser (Kuhn et al., 2013). We required 80 % overlap and 80 % identity for extracting UCEs corresponding to the UCE probes of the 'bee-ant-specific hym-v2 bait set' (Grab et al., 2019). Ultraconserved elements were extracted with 1,000 bp of flanking regions. The extracted sequences were treated as UCE contigs and combined with published UCE contigs (see Bossert et al., 2024) and the new UCE sequences for *T. cirrita* and *A. sjostedti* (Friese, 1909). Using the Phyluce pipeline, we identified, extracted, and processed UCE data using an 80 % sequence overlap and 80 % identity for UCE identification. After aligning the sequences with *MAFFT* and the L-INS-i method (Katoh and Standley, 2013), we trimmed alignments with *Gblocks* (Castresana, 2000) and the 'relaxed' settings (Talavera and Castresana, 2007). Our final concatenated sequence matrix comprised all UCE loci with 80 % or more of the analyzed samples present (= 80 % completeness matrix).

2.4. Molecular phylogeny

Phylogenetic analyses were conducted using Bayesian inference and maximum likelihood approaches on the concatenated sequence matrix. We partitioned the matrix using *CURE* (Freitas et al., 2023) and the UCERegion strategy, which is based on a sliding-window site characteristics (SWSC) partitioning workflow (Tagliacollo and Lanfear, 2018). This strategy divides individual UCEs into three partitions, representing the left and right flanking regions as well as the core region. Implementing this strategy led to a total of 4,320 separate partitions. Using *ModelFinder* as implemented in *IQ-Tree2* (Minh et al., 2020), we selected the best fitting partition scheme by testing model fit for merged partitioning schemes (‘MFP + MERGE’). To lower computational effort, we used the clustering algorithm (Lanfear et al., 2014) ‘–rcluster’ at 20 %, meaning we examined only the top 20 % of schemes. This resulted in 203 total partitions.

We used *IQ-Tree2* to calculate a maximum likelihood tree and assessed node support with 1,000 bootstrap replicates for Shimodaira-Hasegawa-like approximate likelihood ratio tests (SH-aLRT; Guindon et al., 2010) and 1,000 ultrafast bootstrap approximations (UFBoot2; Hoang et al., 2018). We designated the 203 partitions and used the best fitting substitution models from *ModelFinder*. To corroborate the maximum likelihood phylogeny with another method, we inferred Bayesian trees using *ExaBayes* (Aberer et al., 2014) by performing three runs, each with four Metropolis-coupled Markov chain Monte Carlo simulations. We executed the runs for 500,000 generations, sampled every 100th generation and used a relative burn-in of 0.2, leading to 4,000 examined trees. We linked branch lengths among the 203 partitions and used a generalised time reversible model of nucleotide substitution (GTR). We used the *consense* and *postProcParam* programs of the *ExaBayes* package for post-processing. After 500,000 generations, we confirmed sufficient sampling by ensuring effective sample size values of >100 for all parameters and potential scale reduction factors ranging very close to 1. To this end, effective sample size values for the vast majority of parameters, including the likelihood, exceeded 1,000. Topological convergence was deemed adequate once average standard deviations of split frequencies fell to 0.0 %.

2.5. Divergence times estimation

To assess the evolution of *Trinomia* from a temporal perspective, we estimated divergence times using the *RelTime* approach (Tamura et al., 2012), as implemented in *MEGA 11* (Tamura et al., 2021). We chose our *IQ-Tree2* phylogeny as input tree for *RelTime* analysis. Because of the lack of known nomiine fossil specimens, we used a single secondary calibration to inform the analysis by calibrating the crown age of all Nomiinae based on a recent comprehensive dating analysis of all bees, which included 25 Nomiinae species (Almeida et al., 2023; their 20 most clock-like analysis). The present study includes all but one nomiine species of Almeida et al. (2023). Specifically, we secondarily calibrated the crown of Nomiinae in the present study with the crown age estimate of Nomiinae from Almeida et al. (2023). Given their median crown age estimate of all Nomiinae of 38.66 mya (29.60–50.724; 95 % highest posterior density), we applied a normal distribution with a mean of 38.7 and a standard deviation of 5.0, which covers ~90 % of their 95 % highest posterior density age interval. We applied GTR (generalized time reversible) as substitution model and designated the Halictinae and Nomioidinae as outgroups.

2.6. Distributional modeling

For modeling habitat suitability of *Trinomia* species and comparing distributions across species, we gathered distributional records from three sources. First, we obtained records from the *BeeBDC* dataset (Dorey et al., 2023a; Dorey et al., 2023b). Records in *BeeBDC* are standardized for synonyms, duplicate records, and questionable data points. Using the ‘cleaned’ version of the *BeeBDC* dataset, we obtained 148 records (47 for *T. cirrita*, 12 for *T. digitata*, 8 for *T. natalensis*, 35 for *T. orientalis*, 46 for *T. tridentata*, 0 for *T. triodonta*). Given the problematic synonymy of *T. tridentata* and *T. natalensis* before 1999 (Pauly, 1999), we discarded 38 records prior to this year. Second, we georeferenced the material that was identified by Pauly (1999) using the *GEOLocate* Web Application (https://geo-locate.org/web/WebGeoref.aspx). Using this source, we were able to georeference 378 additional occurrences, including records of *T. triodonta.* Lastly, we digitized 180 newly identified records of *Trinomia* that we identified from the collections of the South African National Collection of Insects (SANC, South Africa), the Oberösterreichisches Landesmuseum (OLM, Austria), and the California Academy of Sciences (CAS, USA), leading to a total of 671 records (142 for *T. cirrita*, 28 for *T. digitata*, 137 for *T. natalensis*, 221 for *T. orientalis*, 96 for *T. tridentata*, 40 for *T. triodonta*). We did not exclude records other than *T. tridentata* and *T. natalensis* identified prior to 1999 (see above). The digitized information can be found in the FigShare article associated with this article (https://doi.org/10.6084/m9.figshare.26863411).

Habitat suitability models were built for each species separately (Araújo et al. 2019, Soley-Guardia et al. 2024). Before modeling, assembled occurrence records were thinned to reduce sample bias using the *spThin* package in R (Aiello-Lammens et al., 2015; R Core Team, 2024). The trimmed occurrence records were used to fit Maximum Entropy (MaxEnt) models for each species; MaxEnt is a common approach to build habitat suitability models based on occurrence data (Warren and Siefert, 2011; Vignali et al., 2020). We considered a variety of bioclimate variables as inputs for habitat suitability models based on a priori expectations of what variables might be important and prior research on distributional drivers for bees (Orr et al., 2021): (i) annual mean temperature, (ii) maximum temperature of the warmest month, (iii) minimum temperature of the coldest month, (iv) annual precipitation, and (v, vi) precipitation of wettest and driest months. The source of this climatic data is the Worldclim version 2 database (Fick and Hijmans, 2017). Rather than using default settings, the fine-tuned MaxEnt model was used to minimize model complexity and overfitting (Warren and Seifert, 2011) using the AIC criteria in the *SDMtune* package in R (Vignali et al., 2020). Individual MaxEnt models for each species were calibrated on the accessible areas, which were delimited by buffering minimum convex polygons of observed points and using a “random” method to select 10,000 pseudo-absence records from the “accessible” areas (Barve et al., 2011). Seventy percent of the trimmed records were used for model training and 30 % were used for evaluation. Final models for displaying model predictions were fitted with all trimmed occurrence records. Details of model parameters and performances are provided in the supporting materials.

3. Results

3.1. Phylogeny and antiquity of Trinomia

We analyzed 1,536 concatenated UCE loci from 59 species, corresponding to a 1,021,016 bp long DNA matrix, using maximum likelihood and Bayesian inference. Results of both ML and BI methods showed topologically congruent, well-supported phylogenies for the examined species, including for the genus *Trinomia* (Fig. 1A). Both species phylogenies recovered the three halictid subfamilies Halictinae, Nomioidinae, and Nomiinae as monophyletic and further recovered a monophyletic genus *Trinomia* (Supplementary Fig. S1). While the Bayesian consensus tree is perfectly supported with posterior probabilities of 1.0 for every node, the maximum likelihood phylogeny recovered four nodes with less than perfect support. Three of these nodes are still well-supported ($\geq$ 94.9 UFBoot2 and $\geq$ 95 SH-aLRT) but the position of *Dieunomia micheneri* (Cross, 1958) within the genus *Dieunomia* is rather uncertain (60.7; 80; Fig. 1A).

Our phylogenies recovered the genus *Trinomia* as sister group to the Southeast Asian-endemic genus *Gnathonomia*, represented by two

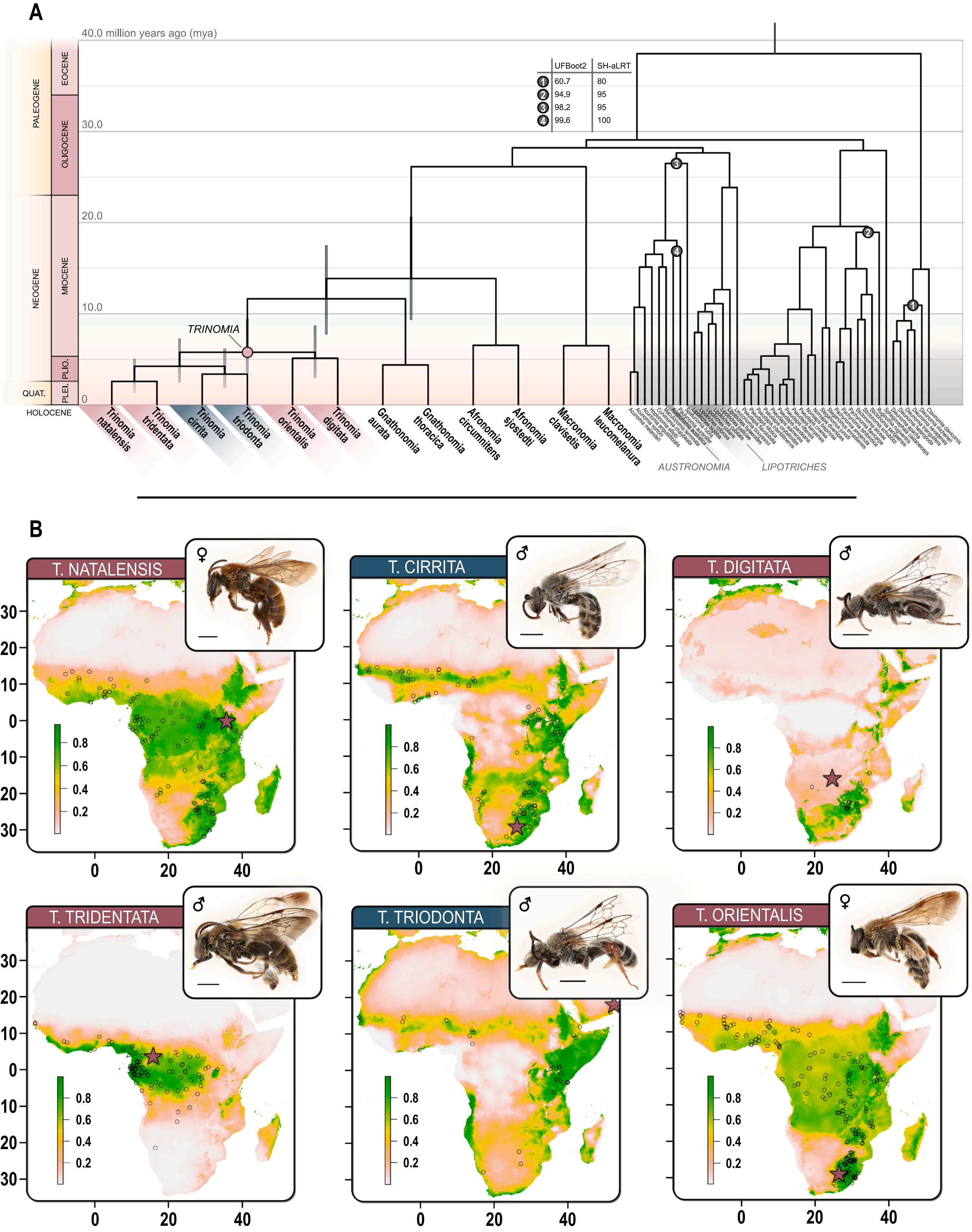


Fig. 1. Phylogeny, antiquity, and modeled habitat suitability of *Trinomia*. (A) Phylogeny of *Trinomia* and related Nomiinae based on analysis of 1,536 UCE loci. Nodes show divergences in absolute time and node bars show 95 % confidence intervals. Node support was 1 posterior probability (pp) and 100 for ultrafast bootstrap approximations and SH-aLRT replicates unless shown otherwise. (B) Model-based spatial predictions for the six described species of *Trinomia*. The colored scale bars show MaxEnt suitability predictions (cloglog format) with greater estimated habitat suitability shaded in green. Circular points are the assembled records for distributional modeling. Red stars show the collecting locality of the samples used for whole genome or UCE sequencing. Scale bars next to specimens correspond to 2 mm length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species in our tree. The clade comprising *Trinomia* and *Gnathonomia*, in turn, is sister group to another African-endemic lineage, the genus *Afronomia*. The phylogeny within *Trinomia* reveals three pairs of species with different node heights, with the divergence of *T. natalensis* and *T. tridentata* being most recent. For the genus *Trinomia*, we show a crown age of 5.76 mya (3.51–9.42 mya, 95 % CI) and a split from *Gnathonomia* of ~11.63 mya (7.73–17.5 mya, 95 % CI). Lineages within *Trinomia* split much more recently, with *T. digitata* and *T. orientalis* at ~5.09 mya (2.99–8.67 mya, 95 % CI), *T. triodonta* and *T. cirrita* at ~3.36 mya (1.83–6.16 mya, 95 % CI) and most recently, *T. tridentata* and *T. natalensis* at ~2.56 mya (1.32–4.97 mya, 95 % CI). The subfamily Nomiinae as a whole was recovered with a crown age of 38.56 mya (31.65–45.47 mya, 95 % CI).

3.2. *Spatial distribution of Trinomia*

MaxEnt models calibrated with 70 % of observed records for each *Trinomia* species had strong performance in predicting the remaining 30 % of records during model validation (see supplementary material). The most important variables identified in the fine-tuned MaxEnt models were annual precipitation for *T. cirrita*, *T. natalensis*, *T. tridentata*, and *T. triodonta*, maximum temperature of the hottest month for *T. orientalis*, and precipitation of the driest month for *T. digitata*. The habitat suitability models identified considerable variability in the potential distributions of the six known *Trinomia* species (Fig. 1B). Models indicate *T. triodonta* may be able to persist across most of the continent, although the scant distributional records make these predictions the most unreliable. Our models suggest broad overlap in the ecological niches for *T. cirrita*, *T. orientalis*, and *T. natalensis*, with all three having suitable habitat throughout most of central, eastern, and southern Africa (Fig. 1B). *Trinomia tridentata* had a predicted niche that comprised only a small region of south-central Africa, while the predicted region of suitable habitat for *T. digitata* was limited to southern Africa and parts of the coasts (Fig. 1B).

4. Discussion

4.1. *Improving our understanding of nomiine phylogeny and taxonomy*

Our study represents the first molecular-informed attempt to characterize the phylogeny and antiquity of *Trinomia*. Our phylogenetic framework enabled us to (1) reevaluate the taxonomy of *Trinomia* and its status as a genus, (2) discuss the phylogenetic relationships to other Nomiinae and its sister group, and (3) understand the species-level relationships within the genus. Bees of the subfamily Nomiinae are morphologically diverse. In contrast to their halictine relatives, which are often referred to as "morphologically monotonous" (Michener, 1974; Michener, 2007; with respect to *Lasioglossum* Curtis, 1833), Nomiinae frequently possess distinct structural characters, such as enlarged tegulae; various kinds of spines on their legs, scutellum or head; and a diversity of shapes and sizes of femur, tibia, and tarsus morphology. While these morphological features are easy to recognize, it has been difficult to establish a sound genus-level classification for the subfamily. This is because these morphological features are frequently not unique for particular groups, but a result of convergent evolutionary processes. For example, the conspicuously enlarged tegulae of *Pseudapis* Kirby, 1900 appear near identical to those of the distantly related bees in the genus *Lipotriches*, subgenus *Tegumelissa* Pauly, 2014. Similarly, males in numerous distinct lineages of Nomiinae have strongly projecting apical structures on the hind tibia, indicating that such morphological characteristics have great evolutionary lability and limited phylogenetic utility. In fact, they exemplify the particular challenge of separating homologous modifications from convergently evolved, analogous structures.

This conflicting situation is present in the morphology of *Trinomia*. For example, all males of *Trinomia* possess a pronounced apical process on the hind tibia, a character shared with other genera of Nomiinae, including, but not limited to *Acunomia* Cockerell, 1930, *Afronomia* Pauly, 1990, *Austronomia* Michener, 1965, certain *Lipotriches* s. str., *Crocisaspidia* Ashmead, 1899, *Curvinomia* Michener, 1944, *Dieunomia* Cockerell, 1899, *Macronomia* Cockerell, 1917, *Nomia* Latreille, 1804, *Nomiapis* Cockerell, 1919, and *Pseudapis*. Characteristic for *Trinomia* males is also the enlarged hind femur, which bears the three ("Tri") name-giving, ventrally oriented spines. However, swollen femora are not uncommon across Nomiinae and similarly produced spines can be found in certain species of *Afronomia* (*A. picardii* species group) and some species of *Macronomia*, itself almost certainly a paraphyletic group (Almeida et al., 2023) (Fig. 2A–D). Unique for *Trinomia* is the tesselate, dull, hexagonal honeycomb-shaped surface punctation on the terga, especially on the first tergum, in both sexes. However, this feature is not present in every species because it is lacking in *T. digitata* (Fig. 2E–G).

By assessing the morphology of *Trinomia*, Pauly (1980, 1990, 1999) hypothesized a close relationship to the genus *Austronomia*, specifically because of the entirely carinate basitibial plate in females, the absence of integumental bands, and the unmodified tegula. He further noted similarities to the genus *Afronomia*, which also possess femoral spines in the males, but lack the tesselate surface sculpturing on T1 (Fig. 2G). Michener (2007) also indicated a close relationship to *Austronomia*. Besides these similar assessments, they treated the taxonomic rank of *Trinomia* differently: Pauly (1980, 1990, 1999) recognized it as a genus, while Michener (2007) used it as a subgenus of a much more broadly defined genus *Lipotriches*.

The phylogeny presented here (Fig. 1) enabled us to reevaluate these hypotheses. The inferred tree is strongly supported and all but four nodes received the highest possible bootstrap and approximate likelihood ratio test values. The phylogeny is congruent with Bossert et al. (2024; their Fig. 4) except for one weakly supported node in the outgroups, specifically *Dieunomia micheneri* (Cross, 1958). This is to be expected as 52 out 59 samples are shared between the two studies; the present study expands on this existing dataset by providing a species-level phylogeny of the genus *Trinomia*. Examining the placements of *Austronomia*, and *Lipotriches*, we found that these genera are not very closely related to *Trinomia*, as their most recent common ancestor dates back ~28.22 mya (95 % CI 21.99–35.97 mya) and several other lineages (*Gnathonomia*, *Afronomia*, *Macronomia*, and potentially more) are more closely related to *Trinomia*. This renders a close relationship of *Trinomia* to *Austronomia* sensu Michener (1965) as highly unlikely, as the included species *Austronomia australica* (Smith, 1875) is the type species of the genus *Austronomia*. Similarly, a close relationship of *Trinomia* to *Lipotriches* sensu Pauly (1990, 2014a) was not supported, and the included representative *Lipotriches cribrosa* (Spinola, 1843) is the type species. Given that neither initial hypothesis pertaining the sister group of *Trinomia* is supported by our phylogeny, but that *Trinomia* is most closely related to the genus *Gnathonomia*, we retained *Trinomia* as a separate genus. This phylogenetic pattern further underlines that certain morphological similarities are inadequate characters to infer close phylogenetic relationships, at least not exclusively. For example, the entirely carinate basitibal plate in females is present in the fairly distantly related lineages *Austronomia* (Fig. 3B), the North American *Acunomia* (Fig. 3C), *Pseudapis*, *Nomiapis*, *Steganomus* Ritsema, 1873, and several other lineages of Nomiinae. These lineages likely separated up to 30 million years ago (Fig. 1), indicating long separate evolutionary histories between some lineages with this trait.

The close phylogenetic relationship between *Trinomia* and *Gnathonomia* is unexpected but well supported. While geographically disjunct, morphological support for this close relationship comes from the sternal hair patches that males of both *Gnathonomia* and *Trinomia* possess on the fifth and six sternum (Fig. 3D-E). While these patches may not be strictly identical, they are undoubtedly highly similar and present a potential shared, derived morphological feature (= synapomorphy). However, it remains to be established if this holds up for every species *Trinomia* and *Gnathonomia*.

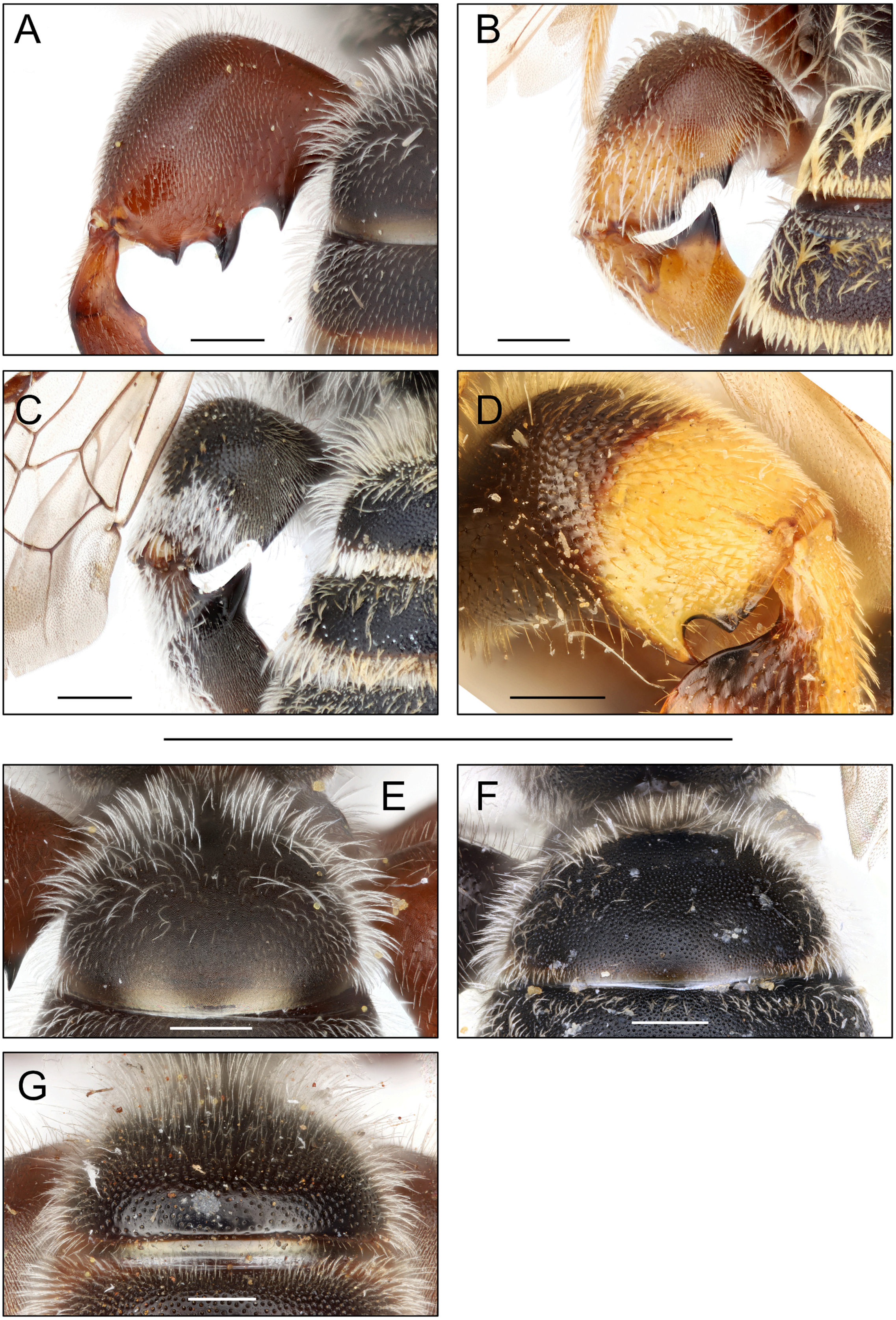


Fig. 2. Hind femur and first tergum morphology of select species of Nomiinae. (A) Femur of male *Trinomia triodonta* (Kohl, 1906), (B) male *Macronomia* sp. from the '*trochanterica*-group', (C) a different male *Macronomia* sp. from the same group, and (D) male *Nomia (Nomia) crassipes* (Fabricius, 1798). First tergum of (E) *Trinomia triodonta*, (F) *Trinomia digitata* (Friese, 1909), and (G) *Afronomia sjostedti* (Friese, 1909). Scale bars correspond to 2 mm length.

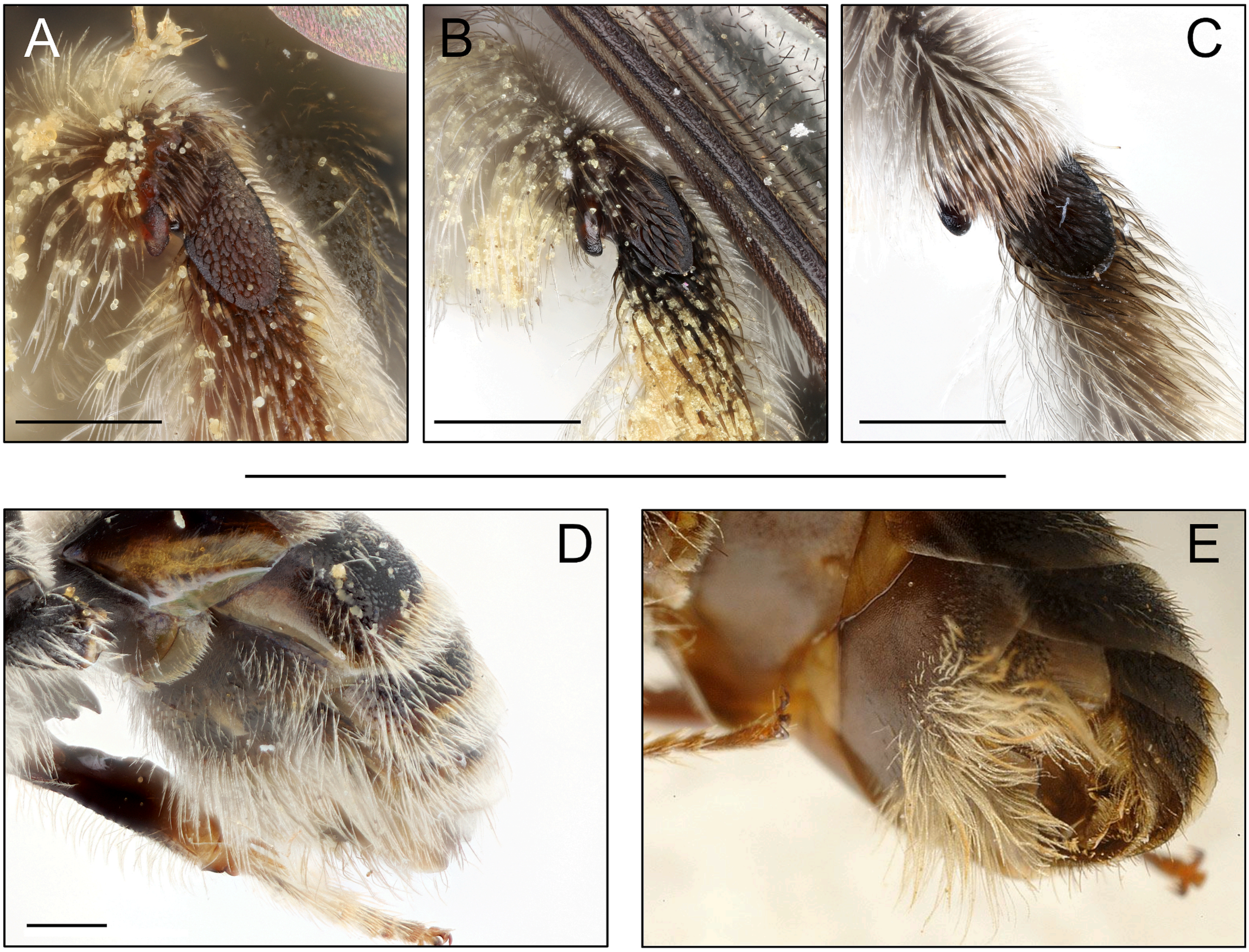


Fig. 3. Hind tibia and sternum morphology of select species of Nomiinae. (A) Basitibial plate of female *Trinomia orientalis* (Friese, 1909), (B) female *Austronomia australica* (Smith, 1875), and (C) female *Acunomia melanderi* (Cockerell, 1906). Characteristic hairbrush on male sterna of (D) male *Trinomia digitata*, and (E) *Gnathonomia radiata* Pauly, 2009. Scale bars, when available, correspond to 500 µm length.

4.2. Divergence times and natural history of *Trinomia*

Divergence time estimations in the present study were carried out using the non-Bayesian approach RelTime (Tamura et al., 2012; Tamura et al., 2018), which is less computationally demanding than more commonly used Bayesian methods. To this end, we informed the RelTime analysis using a secondary calibration derived from a recently published, comprehensive dating analysis of all bees (Almeida et al., 2023), which employed a Bayesian tip-dating approach. Comparing the results of the two studies, we found highly similar crown age estimates for the subfamily Nomiinae as a whole, as well as for individual clades.

The crown age of Nomiinae in the present study was inferred to be ~38.56 mya (31.65–45.47 mya, 95 % CI) and ~39.1 mya (29.60–50.72 mya; 95 % HPD) in Almeida et al. (2023). Similarly, crown age estimates for the clade comprising *Pseudapis* s. l. (~22.2 mya in Almeida et al. (2023) vs. ~19.58 mya herein), *Dieunomia* (~10.38 mya in Almeida et al. (2023) vs. ~10.93 mya herein) and any major clade are highly similar, despite the much greater taxon sampling in the present study. This supports previous research that found RelTime and Bayesian estimates and confidence intervals to be comparable (Tao et al., 2020), despite much lower computational effort of RelTime estimates over their Bayesian counterparts.

Our divergence times recovered *Trinomia* as a comparatively young lineage, with a crown age of just 5.76 mya (3.5–9.4 mya; 95 % CI). Further, the fairly recent divergence of *Trinomia* with its closest relatives in the genus *Gnathonomia* around 11.6 mya provides an interesting spatiotemporal pattern. *Trinomia* is restricted to the Afrotropics and southern Arabian Peninsula, whereas *Gnathonomia* is a Southeast Asian endemic lineage, occurring from India eastwards to Indonesia. Their distributions are geographically disjunct without spatial overlap. However, considering that the distribution of *Trinomia triodonta* extends eastwards into Oman, the southeasternmost country of the Arabian Peninsula, and the presence of *Gnathonomia* in Western India (Pannure and Belavadi, 2017), the distributional gap is not very extensive and provides a potential dispersal route. That the potential distribution of several species extends into the Arabian Peninsula also narrows the disjunction between these groups.

As far as is known, all species of *Trinomia* are polylectic (females collect pollen from many flowering plant species; Pauly, 1999). Albeit not explicitly specified for pollen gathering, documented flower visits include plants from over 40 genera and 30 families. To the best of our knowledge, there is no account describing *Trinomia* nesting behavior, underlining the knowledge gaps that persist when studying Afrotropical-endemic bee genera. However, given that all previous accounts of nomiine nesting biology described ground-dwelling species (e.g., Hirashima, 1961; Pauly, 2014a; Udayakumar and Shivalingaswamy, 2018; Wcislo and Engel, 1996; Westrich, 2018), species of *Trinomia* are likely ground-nesting bees.

4.3. Distribution of *Trinomia* species

Our study links a molecular-phylogeny of the genus *Trinomia* with habitat suitability models that provide insight into the ecological requirements of each species and whether niches are conserved over time. For example, the sister group with the most recent estimated divergence time had two species with broadly similarly niches (*T. tridentata* and *T. natalensis*), although both the observed and predicted distributions of *T. tridentata* were concentrated in a smaller area of south-western Africa (Fig. 1B). Another sister group, *T. cirrita* and *T. triodonta*, also had similar predicted distributions, suggesting that ecological niches are conserved over evolutionary time (Fig. 1B). While the potential range for *T. triodonta* was predicted to be slightly larger than *T. cirrita*, this may be an artifact of building a model with scant data for the species (Fig. 1B).

While the ecological niche models developed here identify climatically-suitable niches for each species across space, they do not necessarily correspond to the realized distribution of each species. This is because species may not establish in all potentially suitable habitats due to geographic barriers, biotic interactions, or other barriers to gene flow (Peterson et al., 2011). For example, while ecological niche models suggested that Madagascar may be suitable for all six species, none are known to occur there. Similarly, none of the species have been observed along the northern African coast despite the appearance of climatically suitable habitat there and some substantial recent faunistic work there (e.g., Lhomme et al., 2020), and only one species has been observed in the Middle-East countries of Yemen and Oman (*T. triodonta*). These results suggest that large geographic barriers, such as the Mozambique channel and the Sahara Desert, may have limited further geographic expansion of several of the species.

5. Conclusion

The present study presents the first account to systematically assess the distribution of an entire bee genus using distributional modeling in a phylogenomic framework. We confirm the status of this genus and better account for the unusual disjunction of *Trinomia* with its sister-group *Gnathonomia*. From our results, we also see hints of phylogenetic conservatism in distribution among sister-groups. However, the apparent absence of some species within areas of predicted high suitability suggests that the full dynamics shaping their distributions cannot be entirely accounted for in our present models. This highlights the need for further efforts inventorying, identifying, and sharing data on African bees. We here present and make accessible new sequence data on African bees as well as hundreds of new spatial records, but our results also build on pre-existing information. To better understand the evolution, biology and natural history of the African bee fauna, we highlight the value of publicly sharing information and collaboration, and show great potential for future advances in our knowledge on African bees.

CRediT authorship contribution statement

Silas Bossert: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Felipe V. Freitas:** Writing – review & editing, Methodology, Investigation, Data curation. **Alain Pauly:** Writing – review & editing, Investigation, Data curation. **Gengping Zhu:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **David W. Crowder:** Writing – review & editing, Writing – original draft, Investigation. **Michael C. Orr:** Writing – review & editing, Methodology, Investigation. **James B. Dorey:** Writing – review & editing, Software, Resources, Data curation. **Elizabeth A. Murray:** Writing – review & editing, Investigation, Funding acquisition, 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.

Acknowledgements

This work was supported by U.S. National Science Foundation grant DEB-2127744.

Research Data

Newly generated Illumina reads are available under Sequence Read Archive (SRA) BioProject ID PRJNA1154266 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1154266). Extensive supplementary information, including supplementary methods and figures, is available in supplementary material 1. Newly generated genome and UCE assembly files, DNA alignments, tree files and the occurrence data are available from the FigShare archive associated with this research under https://doi.org/10.6084/m9.figshare.26863411.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2024.108273.

References

Aberer, A.J., Kobert, K., Stamatakis, A., 2014. ExaBayes: massively parallel bayesian tree inference for the whole-genome era. Mol. Biol. Evol. 31, 2553–2556.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545.

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, 3409–3422.e3406.

Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E., Rahbek, C., 2019. Standards for distribution models in biodiversity assessments. Science Advances 5, 4858–4874.

Ascher, J.S., Pickering, J., 2024. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V.M., Nikolenko, S.I., Pham, S., Prjibelski, A.D., 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. J. Comput. Biol. 19, 455–477.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling 222, 1810–1819.

Bossert, S., Pauly, A., Danforth, B.N., Orr, M.C., Murray, E.A., 2024. Lessons from assembling UCEs: A comparison of common methods and the case of *Clavinomia* (Halictidae). Mol. Ecol. Resour. 24, e13925.

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, 453–472.

Castresana, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol. Biol. Evol. 17, 540–552.

Chen, S., Zhou, Y., Chen, Y., Gu, J., 2018. fastp: an ultra-fast all-in-one FASTQ preprocessor. Bioinformatics 34, i884–i890.

Dorey, J.B., O'Reilly, R.L., Bossert, S., Fischer, E.E., 2023b. BeeBDC: an occurrence data cleaning package. R package version 1.0.1, https://github.com/jbdorey/BeeBDC.

Dorey, J.B., Fischer, E.E., Chesshire, P.R., Nava-Bolaños, A., O'Reilly, R.L., Bossert, S., Collins, S.M., Lichtenberg, E.M., Tucker, E.M., Smith-Pardo, A., Falcon-Brindis, A., Guevara, D.A., Ribeiro, B., de Pedro, D., Pickering, J., Hung, K.-L.J., Parys, K.A., McCabe, L.M., Rogan, M.S., Minckley, R.L., Velazco, S.J.E., Griswold, T., Zarrillo, T.A., Jetz, W., Sica, Y.V., Orr, M.C., Guzman, L.M., Ascher, J.S., Hughes, A.C., Cobb, N.S., 2023. A globally synthesised and flagged bee occurrence dataset and cleaning workflow. Scientific Data 10 (1), 747. https://doi.org/10.1038/s41597-023-02626-w.

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

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

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climat. 37, 4302–4315.

Freitas, F.V., Branstetter, M.G., Franceschini-Santos, V.H., Dorchin, A., Wright, K.W., López-Uribe, M.M., Griswold, T., Silveira, F.A., Almeida, E.A.B., 2023. UCE phylogenomics, biogeography, and classification of long-horned bees (Hymenoptera: Apidae: Eucerini), with insights on using specimens with extremely degraded DNA. Insect Syst. Div. 7, 3.

Glenn, T.C., Nilsen, R.A., Kieran, T.J., Sanders, J.G., Bayona-Vásquez, N.J., Finger, J.W., Pierson, T.W., Bentley, K.E., Hoffberg, S.L., Louha, S., Garcia-De Leon, F.J., del Rio Portilla, M.A., Reed, K.D., Anderson, J.L., Meece, J.K., Aggrey, S.E., Rekaya, R., Alabady, M., Belanger, M., Winker, K., 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 7, 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, 282–284.

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst. Biol. 59, 307–321.

Hirashima, Y., 1961. Monographic Study of the Subfamily Nomiinae of Japan (Hymenoptera, Apoidea). Acta Hymenopterologica 1, 241–303.

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, 518–522.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30, 772–780.

Kuhlmann, M., 2005. Diversity, Distribution Patterns and Endemism of Southern African Bees (Hymenoptera: Apoidea). In: Huber, B.A., Sinclair, B.J., Lampe, K.-H. (Eds.), African Biodiversity. Springer, US, Boston, MA, pp. 167–172.

Kuhlmann, M., 2009. Patterns of diversity, endemism and distribution of bees (Insecta: Hymenoptera: Anthophila) in southern Africa. South African J. Botany 75, 726–738.

Kuhlmann, M., Guo, D., Veldtman, R., Donaldson, J., 2012. Consequences of warming up a hotspot: species range shifts within a centre of bee diversity. Diver. Distrib. 18, 885–897.

Kuhn, R.M., Haussler, D., Kent, W.J., 2013. The UCSC genome browser and associated tools. Brief. Bioinform. 14, 144–161.

Lanfear, R., Calcott, B., Kainer, D., Mayer, C., Stamatakis, A., 2014. Selecting optimal partitioning schemes for phylogenomic datasets. BMC Evol. Biol. 14, 82.

Lhomme, P., Michez, D., Christmann, S., Scheuchl, E., El Abdouni, I., Hamroud, L., Ihsane, O., Sentil, A., Smaili, M.C., Schwarz, M., 2020. The wild bees (Hymenoptera: Apoidea) of Morocco. Zootaxa 4892, 1–159.

Michener, C.D., 1965. A classification of the bees of the Australian and South Pacific Regions. Bull. Am. Mus. Nat. Hist. 130, 1–362.

Michener, C.D., 1974. The Social Behavior of the Bees: A Comparative Study. Harvard University Press, Cambridge, MA.

Michener, C.D., 2007. The Bees of the World. The Johns Hopkins University Press, Baltimore, Maryland.

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, 1530–1534.

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. https://doi.org/10.1016/j.cub.2020.10.053.

Pannure, A., Belavadi, V.V., 2017. An updated distributional checklist of Bees of the subfamily Nomiinae (Hymenoptera: Apoidea: Halictidae) with new records from south India. Entomon 42, 311–328.

Pauly, A., 1980. Descriptions préliminaires de quelque sous-genres afrotropicaux nouveaux dans la famille des Halictidae. Revue De Zoologie Africaine 94, 119–125.

Pauly, A., 1990. Classification des Nomiinae Africains (Hymenoptera Apoidea Halictidae). Musée Royal De L'afrique Centrale Tervuren, Belgique 261, 1–206.

Pauly, A., 1999. Classification des Nomiinae africains. Le genre *Trinomia* Pauly (Hymenoptera Apoidea Halictidae). Belg. J. Entomol. 1, 101–136.

Pauly, A., 2009. Classification des Nomiinae de la Région Orientale, de Nouvelle-Guinée et des îles de l'Océan Pacifique (Hymenoptera: Apoidea: Halictidae). Bull. Inst. Roy. Sci. Nat. Belgique 79, 151–229.

Pauly, A., 2014a. Les Abeilles des Graminées ou *Lipotriches* Gerstaecker, 1858, sensu stricto (Hymenoptera : Apoidea : Halictidae : Nomiinae) de l'Afrique subsaharienne. Belg. J. Entomol. 20, 1–393.

Pauly, A., 2014b. Les Abeilles des Graminées ou *Lipotriches* Gerstaecker, 1858, sensu stricto (Hymenoptera : Apoidea : Halictidae : Nomiinae) de la Région Orientale. Belg. J. Entomol. 21, 1–94.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. Ecological niches and geographic distributions. Princeton University Press, New Jersey, USA.

R Core Team (2024) R: A language and environment for statistical computing. Vienna, Austria. Available from: http://www.r-project.org/.

Soley-Guardia, M., Alvarado-Serrano, D.F., Anderson, R.P., 2024. Top ten hazards to avoid when modeling species distributions: a didactic guide of assumptions, problems, and recommendations. Ecography 2024, e06852.

Tagliacollo, V.A., Lanfear, R., 2018. Estimating improved partitioning schemes for ultraconserved elements. Mol. Biol. Evol. 35, 1798–1811.

Talavera, G., Castresana, J., 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56, 564–577.

Tamura, K., Battistuzzi, F.U., Billing-Ross, P., Murillo, O., Filipski, A., Kumar, S., 2012. Estimating divergence times in large molecular phylogenies. Proc. Natl. Acad. Sci. U. S.A. 109, 19333–19338.

Tamura, K., Tao, Q., Kumar, S., 2018. Theoretical foundation of the reltime method for estimating divergence times from variable evolutionary rates. Mol. Biol. Evol. 35, 1770–1782.

Tamura, K., Stecher, G., Kumar, S., 2021. MEGA11: molecular evolutionary genetics analysis version 11. Mol. Biol. Evol. 38, 3022–3027.

Tao, Q., Tamura, K., Mello, B., Kumar, S., 2020. Reliable confidence intervals for reltime estimates of evolutionary divergence times. Mol. Biol. Evol. 37, 280–290.

Udayakumar, A., Shivalingaswamy, T.M., 2018. Nesting biology, seasonality and host range of sweat bee, Hoplonomia westwoodi (Gribodo)(Hymenoptera: Halictidae: Nomiinae). Sociobiology 65, 491–496.

Vignali, S., Barras, A.G., Arlettaz, R., Braunisch, V., 2020. SDMtune: an R package to tune and evaluate species distribution models. Ecology and Evolution 10, 11488–11506.

Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological Applications 21, 335–342.

Warrit, N., Ascher, J., Basu, P., Belavadi, V., Brockmann, A., Buchori, D., Dorey, J.B., Hughes, A., Krishnan, S., Ngo, H.T., Williams, P., Zhu, C.-D., Abrol, D., Bawa, K., Bhatta, C., Borges, R.M., Bossert, S., Cervancia, C., Chatthanabun, N., Chesters, D., Chinh, P.H., Devkota, K., Duc, H.P., Ferrari, R., Garibaldi, L., Ge, J., Ghosh, D., Huang, D., Jung, C., Klein, A.-M., Koch, J.B.U., Krichilsky, E., Kunte, K., Ling, T.C., Liu, S., Liu, X., Luo, A., Luo, S., Mu, J., Nidup, T., Niu, Z., Nur-Zati, A.M., Olsson, S. B., Otis, G.W., Ouyang, F., Peng, Y.-Q., Priawandiputra, W., Proshchalykin, M., Raffiudin, R., Rameshkumar, A., Ren, Z., Suruliraj, A., Sane, S., Shi, X., Sinu, P.A., Smith, D.R., Soh, Z.W.W., Somananthan, H., Sritongchuay, T., Stewart, A.B., Sun, C., Tang, M., Thanoosing, C., Tscharntke, T., Vereecken, N., Wang, S., Wayo, K., Wongsiri, S., Zhou, X., Xie, Z., Zhang, D., Zou, Y., Zu, P., Orr, M., 2023. Opportunities and challenges in Asian bee research and conservation. Biol. Conserv. 285, 110173.

Wcislo, W.T., Engel, M.S., 1996. Social behavior and nest architecture of nomiine bees (hymenoptera: halictidae; nomiinae). J. Kans. Entomol. Soc. 69, 158–167.

Westrich, P., 2018. Die Wildbienen Deutschlands. Eugen Ulmer KG, Stuttgart, Germany.