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SPECIAL ISSUE: BEES AND POLLINATORS IN THE FACE OF CLIMATE CHANGE

REVIEW

Bee Systematics and Conservation

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Abstract

Diversity can be examined and interpreted from various perspectives, including species richness, genetic and phenotypic differences, variation in behaviors and natural history, and phylogenetic history. Centuries of taxonomic research have revealed approximately 21,000 bee species worldwide. These can be subdivided into a hierarchy of subgroups that reflects their evolutionary history, thanks to the increasingly more comprehensive phylogenetic hypotheses available. Advances in bee systematics have enhanced our understanding of how their diversity has evolved, including their origin in the Cretaceous, shifts in their geographical distribution, the evolution of social and parasitic behaviors, and changes in relationships between bees and the plants they visit throughout a 120-million-year shared evolutionary history. An important outcome of the enduring relationship with flowering plants is the vital role bees play in pollination in both natural and agricultural ecosystems. Habitat loss, climate change, and other anthropogenic environmental alterations have led to declines in bee populations, which have sparked concerns about bee conservation and highlighted the importance of understanding the complementary aspects of diversity, including the evolutionary and geographical components of this variation. The availability of increasingly reliable and comprehensive phylogenetic hypotheses has led to significant advancements, enabling assessments of the phylogenetic diversity of bee communities and predictions regarding their vulnerability to habitat change and their ecological functions. This review explores perspectives of documenting and interpreting bee diversity in a changing world and summarizes the current bee classification while discussing the phylogenetic advances in contemporary research.

1. Biological systematics and the interpretation of bee diversity

Systematics conveys the primordial need to understand the diversity of life, providing a meaningful organization of living beings by categorizing them into species and those species into higher taxa (Wheeler, 2001). It is both an ancient and a very modern scientific field that has integrated the most up-to-date advances in several biological fields, including evolutionary biology, genetics, genomics, bioinformatics, and comparative morphology (as well as other comparative phenomics disciplines). In modern systematics, biological taxa are expected to reflect natural affinities among their

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constituent species and be monophyletic. The natural connections are most precisely expressed by the phylogenetic relationships that connect all living and extinct species into a unifying nexus, thus providing a universal system upon which biodiversity can be interpreted (Hennig, 1966).

The number of described bee species has grown since the beginning of the modern stage of taxonomic accounting of animal diversity, marked by the publication of the 10th edition of Linnaeus' Systema Naturae over 250 years ago. Specifically for bees, we now recognize nearly 21,000 species worldwide (Ascher & Pickering, 2020), and thousands more will likely be formally recognized and described in the coming decades. In parallel to the expansion of known species-level diversity, classifications have been proposed to accommodate this diversity in an ever-changing number of bee genera, tribes, subfamilies, and families (e.g., Michener, 2007; Plant & Paulus, 2016; Engel et al., 2020). In recent years, there has been a growing consensus in bee classification, driven by an increasing number and the reliability of the phylogenetic hypotheses available for them.

A solid taxonomic framework is essential to promote and guide the exploration of bee diversity (Danforth et al., 2013, 2019), serving as a general reference system and fostering initiatives to conserve them (e.g., by allowing the identification of mechanisms underlying declines, e.g., Haas et al. 2022), especially in the face of climate change . Bees are remarkable not only for their sheer number of species but also for their varied natural histories that have made them attractive models to interpret the evolution of cleptoparasitic behaviors (e.g., Litman, 2019; Sless et al., 2023), variation in nesting biology and food sources (e.g., Michener, 1964; Wcislo & Cane, 1996; Danforth, 2007; Danforth et al., 2019; Engel et al., 2020), transitions to life in societies and reversals from social to solitary behaviors (e.g., Lin & Michener, 1972; Michener, 1974; Packer, 1991; Wcislo & Danforth, 1997; Danforth, 2002; Schwarz et al., 2007), among other aspects of their biology. A significant transition in bee evolution is their origin from apoid wasp ancestors in the Early Cretaceous (Cardinal & Danforth, 2013; Sann et al., 2018; Almeida, Bossert et al., 2023), marked by the shift from an animal host/prey to a vegetal protein source (e.g., Danforth, 2007; Michener, 2007; Murray et al., 2018; Sann et al., 2018; Danforth et al., 2019).

Bees, through their active collection of floral resources, are considered the most dominant pollinators worldwide (Ollerton, 2017; Roubik, 2020), and their behavioral and morphological adaptations associated with efficient pollen harvesting are noteworthy (Danforth, 2007). Throughout their diversification history, bees changed how they interact with flowers and other sources of nutrition for their offspring (Camargo & Roubik, 1991; Steffan et al., 2024).

2. Bee systematics and biogeography

The history of bee classifications underscores a recurring theme in biological taxonomy: the transition from classifications based on superficial similarities to those that reflect the underlying evolutionary relationships (Michener, 1944, 2007; Plant & Paulus, 2016). The discovery of new species has accompanied this shift, the development of increasingly sophisticated analytical methods, and the investigation of novel morphological, behavioral, and genetic data. Early efforts to systematize bee diversity relied mainly on simple and few observable phenotypic characteristics, such as body shape, social behaviors, and mouthpart morphology (Plant & Paulus, 2016). Throughout the 20th century, our understanding of species-level diversity expanded following the description of new genus and family-level taxa (e.g., Plant & Paulus, 2016; Engel et al., 2020) as we approach a stable and natural classification.

2.1. Bee phylogeny

The effort to systematize bee diversity reached a new milestone by adopting phylogenetic methods, particularly from the 1990s onward. This development is well illustrated by two landmark publications: Roig-Alsina and Michener (1993) and Alexander and Michener (1995). These two important studies represent a hallmark of sophistication in contemporary bee systematics and set the foundation of modern bee classifications (Michener, 2007).

In recent years, molecular data, especially DNA sequences, have gained prominence in studies of bee phylogeny (Danforth et al., 2006b, 2013), facilitating a more nuanced understanding of evolutionary relationships and occasionally challenged conclusions derived solely from morphological data (e.g., Roig-Alsina & Michener, 1993; Alexander & Michener, 1995; Pesenko, 1999; Gonzalez et al., 2012; Porto & Almeida, 2021). The use of different kinds of high-throughput sequence data has recently enabled the investigation of bee phylogenomics at an unprecedented scale and resolution, particularly for generating transcriptomic and genomic data (e.g., Romiguier et al., 2016; Branstetter et al., 2017, 2021; Peters et al., 2017; Bossert et al., 2017, 2019, 2020, 2022, 2024; Sann et al., 2018; Freitas et al., 2021, 2023; Orr et al., 2022, 2024; Pisanty et al., 2022; Sless et al., 2022, 2024; Almeida, Bossert et al., 2023; Lepeco et al., 2024; Straka et al., 2024).

Molecular data have reshaped our understanding of bee evolution, particularly at higher levels (i.e., phylogenetic relationships of families, subfamilies, and tribes). The transformative power of genetic evidence for the reconstruction of historical patterns has been recognized, and molecular phylogenetics has revolutionized our understanding of bee evolutionary relationships (Danforth et al., 2013; Engel et al., 2020), as summarized in Figure 1. Throughout the recent history of bee phylogenetics, some challenging puzzles have hampered a more accurate understanding of the bee tree of life. Particularly noticeable challenges are described below family-by-family and indicated in Figure 1 and further detailed in Appendix:

(A) Andrenidae: delimitation of tribes of Panurginae and resolution of their phylogenetic relationships (Ascher, 2003; Bossert et al., 2022; Pisanty et al., 2022; Ramos et al., 2022);

(B) Apidae: insights into the relationships among parasitic groups (Cardinal et al., 2010; Litman et al., 2013; Martins et al., 2018; Bossert et al., 2019, 2020; Sless et al., 2022), resolution of the relationships among corbiculate bee tribes and their relationships with the centridine oil-collecting bees (e.g., Cameron, 1993; Kawakita et al., 2008; Martins et al., 2014; Romiguier et al., 2016; Bossert et al., 2017, 2019), reclassification of Anthophorinae (Bossert et al., 2019; Orr et al., 2022), Xylocopinae with the inclusion of Ctenoplectrini and Tetrapediini (Bossert et al., 2019), the recognition of the Eucerinae and changes to the tribes and genera in this subfamily (Bossert et al., 2019, Freitas et al., 2021, 2023).

(C) Colletidae: resolution of relationships within the family and the reclassification of a broadly defined tribe "Paracolletini" (sensu Moure et al., 1999; Michener, 2007) into Callomelittinae, Neopasiphaeinae, Scrapterinae, and a narrowly defined Paracolletini now part of Diphaglossinae (Almeida & Danforth, 2009; Almeida et al., 2012, 2019; Almeida, Bossert et al., 2023);

(D) Halictidae: support for the classification of Halictinae into five tribes: Augochlorini, Caenohalictini, Halictini, Sphecodini, and Thrinchostomini (Danforth et al., 2004, 2006, 2008), and resolution of genus-level relationships within Augochlorini (Gonçalves, 2016; Gonçalves et al. 2022) and Halictini (Danforth et al., 2003; Gibbs et al., 2012) as well as tribal and generic resolution of Nomiinae (Bossert et al., 2020, 2024), and Rophitinae (Patiny et al., 2008);

(E) Megachilidae: reevaluation of the traditional subdivision of the family into two subfamilies: Fideliinae and Megachilinae (sensu, e.g., Michener, 2007) based on comprehensive phylogenetic analyses of the family (Gonzalez et al., 2012; Litman et al., 2011; Packer et al., 2017), resulting in recognition of five subfamilies and seven megachiline tribes (Appendix);

(F) Melittidae: resolution of relationships within, which supported improvements in the classification of their subfamilies and tribes (Michez et al., 2009), increasing evidence for the monophyly of the family and their placement as the sister group of all other bee families (Husemann et al., 2021; Almeida, Bossert et al., 2023; Henríquez-Piskulich et al., 2024); and

(G) Stenotritidae: the well-supported placement of Stenotritidae as a family-level lineage closely related to Colletidae (Danforth et al., 2006a,b; Almeida & Danforth, 2009; Almeida, Bossert et al., 2023).

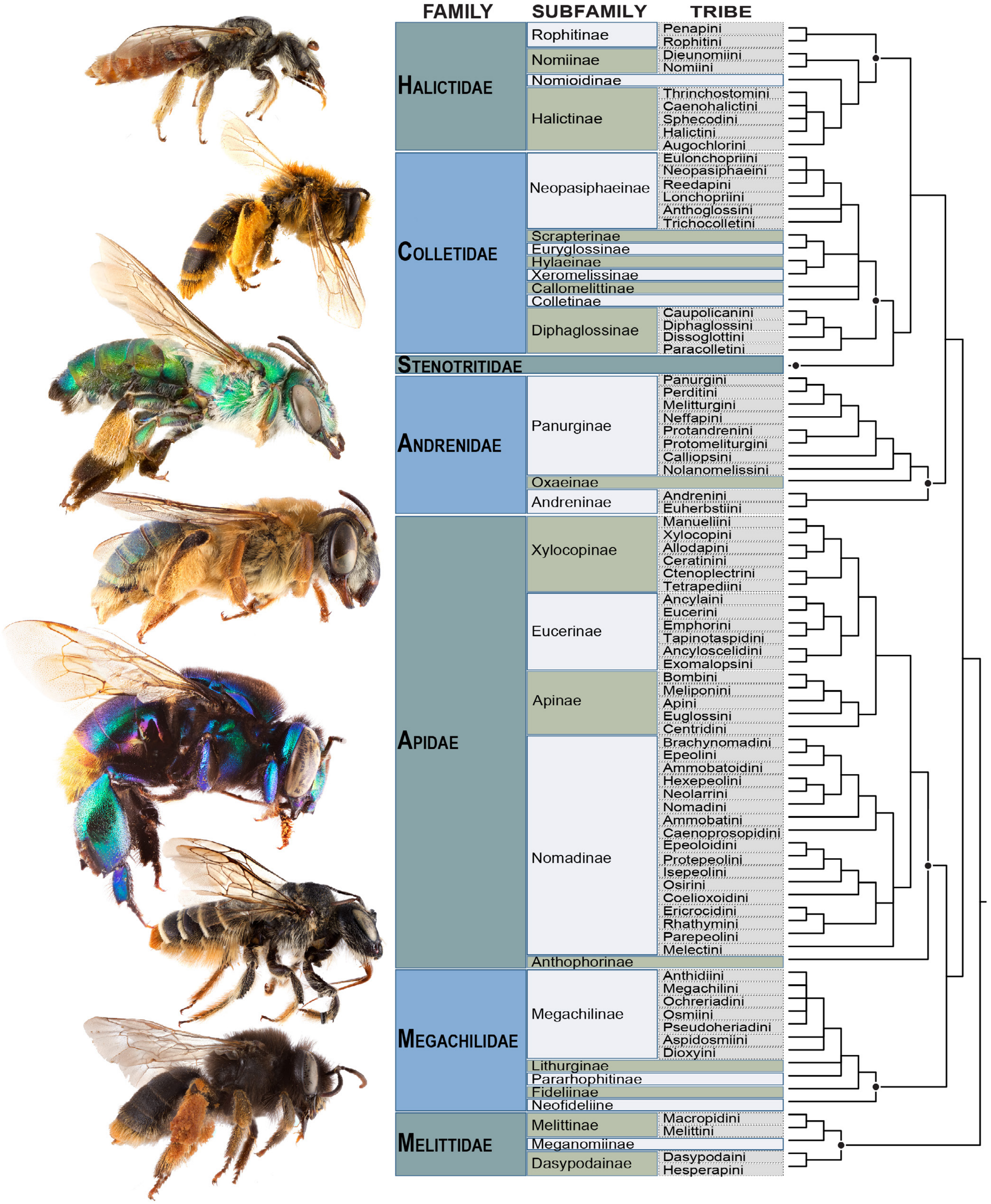
We appear to have reached a stage of enhanced stability in higher-level classifications, as all major lineages of bees have undergone phylogenetic investigation, with most family-level taxa (i.e., families, subfamilies, and tribes) supported by hypotheses of monophyly (Figure 1). In contrast to significant strides in understanding higher-level relationships, research at lower taxonomic levels remains limited to a small fraction of bee diversity, hindering valuable insights into bee evolution and diversification and highlighting the pressing need for more investigations focusing on groups of closely related species. The expansion of species-level phylogenetic research will continue to provide a framework for understanding evolutionary relationships in the context of revisionary taxonomic work (Gonzalez et al., 2013).

2.2. A temporal framework for bee evolution and biogeography

The known fossil record of bees is extensive during some periods but virtually absent (or unknown) for the first 60 million years of their evolutionary history (Engel, 2001; Michez et al., 2012; Almeida, Bossert et al., 2023; Engel & Xie, 2024). The undoubtedly oldest fossil record of a bee is *Cretotrigona prisca* Michener and Grimaldi from the Upper Cretaceous (~65 Ma: Engel, 2000), substantially more recent than the estimated age for the origin of bees (~124 Ma: Almeida, Bossert et al., 2023). The fossil record is, therefore, insufficient to illuminate the origin and timing of the early evolution of bees. In contrast, when knowledge of the fossil record, phylogenetic relationships (of bees and other taxa of Apoidea), biogeography, and natural history are combined, we can confidently confirm Michener's hypothesis that bees arose in western Gondwana before the breakup of Africa and South America in the Cretaceous period (Michener, 1979; Almeida, Bossert et al., 2023), most likely in arid areas of that supercontinent. This timeframe coincides with the origin of the main lineages of angiosperms, further cementing our understanding of the close evolutionary relationship between the histories of the diffuse co-diversification of bees and flowering plants (Michener, 1979; Engel, 2001; Cardinal & Danforth, 2013; Almeida, Bossert et al., 2023).

The exploration of bee biogeography in various time frames and for diverse groups of taxa has been significantly propelled by expanding the availability of increasingly more reliable phylogenetic hypotheses. When opening his monographic treatment of bee biogeography over four decades ago, Charles Michener stated, "The time may seem premature for a paper on distributional history of bees in the sense that studies now under way on the cladistic relationships among bees will probably add to what can be said" (Michener, 1979: p. 279). This time for biogeographic interpretations has come.

The present-day diversity of bees is not evenly distributed worldwide, reflected by the species richness in different continents and climatic zones (Michener, 1979; Orr et al., 2021) and the uneven distribution of lineages across biogeographic realms (Figure 2). The timing and the paleogeological setting in which each major group of bees arose and evolved shaped the diversity patterns we currently observe for these taxa (additional references are listed in the Appendix for biogeographic studies of various taxa).



FAMILY	SUBFAMILY	TRIBE
HALICTIDAE	Rophitinae	Penapini
		Rophitini
	Nomiinae	Dieunomiini
		Nomiini
	Nomioidinae	
	Halictinae	Thrinchostomini
		Caenohalictini
		Sphecodini
		Halictini
		Augochlorini
COLLETIDAE	Neopasiphaeinae	Eulonchopriini
		Neopasiphaeini
		Reedapini
		Lonchopriini
		Anthoglossini
		Trichocolletini
	Scrapterinae	
	Euryglossinae	
	Hylaeinae	
	Xeromelissinae	
	Callomelittinae	
	Colletinae	
	Diphaglossinae	Caupolicanini
		Diphaglossini
		Dissoglottini
		Paracolletini
STENOTRITIDAE		
ANDRENIDAE	Panurginae	Panurgini
		Perditini
		Melitturgini
		Neffapini
		Protandrenini
		Protomeliturgini
		Calliopsini
		Nolanomelissini
	Oxaeinae	
	Andreninae	Andrenini
		Euherbstiini
APIDAE	Xylocopinae	Manueliini
		Xylocopini
		Allodapini
		Ceratinini
		Ctenoplectrini
		Tetrapediini
	Eucerinae	Ancylaini
		Eucerini
		Emphorini
		Tapinotaspidini
		Ancyloscelidini
		Exomalopsini
	Apinae	Bombini
		Meliponini
		Apini
		Euglossini
		Centridini
	Nomadinae	Brachynomadini
		Epeolini
		Ammobatoidini
		Hexepeolini
		Neolarrini
		Nomadini
		Ammobatini
		Caenoprosopidini
		Epeoloidini
		Protepeolini
		Isepeolini
		Osirini
		Coelioxoidini
		Ericrocidini
		Rhathymini
		Parepeolini
		Melectini
	Anthophorinae	
MEGACHILIDAE	Megachilinae	Anthidiini
		Megachilini
		Ochreriadini
		Osmiini
		Pseudoheriadini
		Aspidosmiini
		Dioxyini
	Lithurginae	
	Pararhophitinae	
	Fideliinae	
	Neofideliine	
MELITTIDAE	Melittinae	Macropidini
		Melittini
	Meganomiinae	
	Dasypodainae	Dasypodaini
		Hesperapini

Fig 1. Synopsis of the family-level classification for the bees followed in this review: the central table lists the families and their corresponding subfamilies and tribes, when applicable; the cladogram on the right summarizes the phylogenetic relationships among the taxa outlined in the table based on the results of Almeida, Bossert et al. (2023), complemented by research on particular groups (Litman et al., 2011; Almeida et al., 2012, 2019; Bossert et al., 2019, 2022; Freitas et al., 2021; Orr et al., 2022; Sless et al., 2022). The photographs on the left depict a sample of bee morphological diversity, with one exemplar selected to represent each of the seven families, from top to bottom: *Xeralictus bicuspidariae* Snelling & Stage ♀ [Halictidae: Rophitini], *Nesocolletes fulvescens* (Smith) ♀ [Colletidae: Neopasiphaeini], *Ctenocolletes smaragdinus* (Smith) ♀ [Stenotritidae], *Oxaea flavescens* Klug ♀ [Andrenidae: Oxaeinae], *Eufriesea anisochlora* (Kimsey) ♂ [Apidae: Euglossini], *Lithurgopsis apicalis* (Cresson) ♀ [Megachilidae: Lithurginae], *Melitta haemorrhoidalis* (Fabricius) ♀ [Melittidae: Melittini]; photos not to scale.

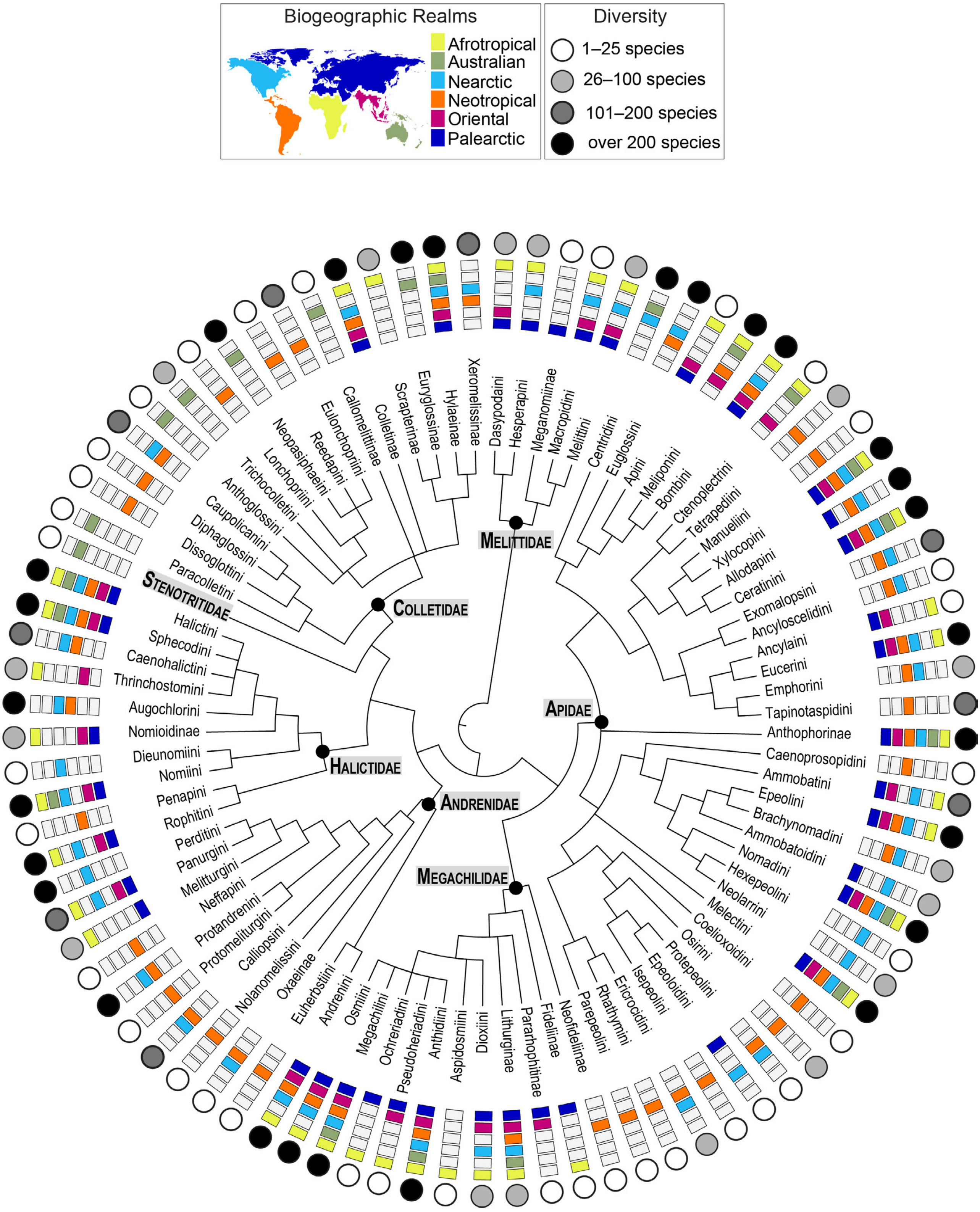


Fig 2. Geographic distribution of the major lineages of bees in six terrestrial biogeographic realms (modified from Holt et al., 2013), their species richness, and a summary of phylogenetic relationships among these taxa. Current species-level diversity and occurrence of taxa were compiled from the Discover Life world checklist (Ascher & Pickering, 2020) and complemented by Almeida, Bossert et al. (2023: Data S1C); non-native distributional ranges are disregarded.

We can now infer that some groups had an initial diversification history intimately associated with Africa, such as Melittidae (Michener, 1979; Almeida, Bossert et al., 2023), while others diversified in the portion of Gondwana that now corresponds with South America, such as Andrenidae (Bossert et al., 2022; Ramos et al., 2022). In contrast, the stage of the early history of some taxa involved two continents before their breakup during the Cenozoic: the first offshoots of both Apidae and Megachilidae are represented by descendants that later diversified in Africa and South America (Litman et al., 2011; Almeida, Bossert et al., 2023), whereas most of the evolutionary history of Colletidae and Stenotritidae took place in a southern province connecting Antarctica, Australia, and South America that persisted roughly until the end of the Eocene (Almeida et al., 2012).

3. Threats, conservation, and the future of bee diversity

Human-induced changes have negatively affected biodiversity across the globe (e.g., Pereira et al., 2010), also creating challenges for bee species (e.g., Mayer et al., 2011; Goulson et al., 2015; Ollerton, 2017; Harrison et al., 2018; Kevan & Silva, 2020; Dicks et al., 2021; Hrncir, 2022; Ostwald et al., 2024; Payne et al., 2024). The main drivers associated with bee declines have mainly been driven by reductions in suitable habitat, including lower abundance and richness of floral resources (Scheper et al., 2014), exposure to toxic insecticides and fungicides (McArt et al., 2017), exposure to novel pests and pathogens (Dobelmann et al., 2024), and rising temperatures, as well as increases in the frequency of extreme weather events (Soroye et al., 2020). While the impacts of these different stressors have been extensively investigated in isolation, more empirical data are needed to understand better the interaction among these factors and the relative magnitude of their effects.

Evidence of bee decline has prompted efforts to enhance pollinator populations through habitat augmentations, particularly in the surroundings of agricultural areas where they provide pollination services that carry significant economic value (Blaauw & Isaacs, 2014). These initiatives often focus on creating pollinator habitats through targeted plantings, which have positively impacted the abundance of bee species that persist in agricultural areas (Lowe et al., 2021; Majewska & Altizer, 2020). However, only a limited number of bee species thrive in human-modified environments, meaning these plantings may only support a fraction of overall bee biodiversity (Scheper et al., 2014). For instance, in eastern North America, only three out of 10 bumble bee species (genus *Bombus*) are associated with anthropogenic environments. In contrast, 30% of the species prefer forested habitats and are considered habitat specialists (Gratton et al., 2023). Therefore, the selection of plant species and the creation of pollinator habitats may disproportionately favor certain groups within the native pollinator community. Generalist species, which can use a wider array of floral resources, may benefit more from these plantings. At the same time, pollen specialists, which depend on specific host plants, may not be supported (Müller et al., 2024). These findings highlight the need for a careful understanding of the degree of variability in habitat specialization and floral niche breadth across bees to work on establishing pollinator habitat that prioritizes the conservation of less abundant species.

Numerous bee pollinator monitoring programs exist worldwide, which have primarily focused on collecting long-term data about bee presence across different spatial and temporal scales (e.g., Flaminio et al., 2021; Best et al., 2022; Turley et al., 2022, 2024). The methods implemented for such monitoring efforts are varied and range from community science-based approaches that can cover large geographic areas with lots of observations with low taxonomic resolution to localized studies that implement highly standardized methodologies with high taxonomic resolution data (Turley et al., 2024). Many of these initiatives address gaps in long-term datasets, providing valuable insights into changes in community composition and species distribution over time. However, community-based monitoring often falls short of delivering demographic information that reflects population size changes at the species level. To address this limitation, occupancy models – designed to estimate the likelihood of a species occupying a specific area based on presence-absence data while factoring in detection probability – should be employed once species of conservation concern are identified (e.g., MacIvor & Packer, 2016; Boone et al., 2023; Otto et al., 2023). Despite the pressing need for immediate conservation actions to protect bees, the field of bee monitoring remains relatively nascent, lacking a solid framework with standardized protocols that can effectively generate the necessary data to guide practitioners in bee conservation efforts (Woodard et al., 2020).

Significant barriers to bee conservation persist, including the limited knowledge of species diversity worldwide. Except for a few areas in North America and Europe, most parts of the world remain understudied, especially in tropical and temperate areas of South America, Africa, and Asia (Orr et al., 2021). Effective conservation of bee biodiversity is impossible without first discovering and characterizing this diversity (Hortal et al., 2015; Marshall et al., 2024). Moreover, many groups of bees are taxonomically challenging based on morphological traits alone (e.g., *Lasioglossum* [Gibbs, 2018]), complicating the development of monitoring programs and conservation strategies. Taxonomic investigations of the Chilean fauna applying DNA barcoding data revealed that the number of known bee species is predicted to grow from 436 to about 559, considering that more than 100 species await to be formally described for the country based on the estimates of Packer and Ruz (2017). There is an urgent need for the bee systematics community to focus on revisionary taxonomy, address species delimitation issues, and develop molecular tools that can aid and enhance the speed and accuracy of identification across all bee groups (Packer et al., 2009; Gonzalez et al., 2012).

4. Bridging diversity patterns and phylogenetic relationships

The main biogeographic hypotheses for bees examine species' spatial and temporal distribution and the factors shaping these patterns, providing insights into population trends, evolutionary history, and ecosystem functions (Almeida, Bossert et al., 2023). Recent advances have extended beyond taxonomic distribution to consider evolutionary and functional dimensions, especially important for understanding the role of bees in pollination, including crop production, where functional diversity may be overshadowed by managed species introduced in agroecosystems (Leclercq et al., 2023). With the ability to generate increasingly more reliable and comprehensive phylogenies, it has become common practice in conservation to evaluate phylogenetic diversity (or lineage diversity) alongside species taxonomic richness when discussing alpha diversity (Harrison et al., 2018; Marshall et al., 2023; Leclercq et al., 2023; de Pedro et al., 2023). Mapping these patterns and comparing them with environmental conditions allows for the identification of bee species that serve as indicators of habitat quality and conservation status (Corrêa-Neto et al., 2024), as well as a more accurate assessment of the impacts of global changes on these patterns and the species they encompass (Kammerer et al., 2021; Zattara & Aizen, 2021).

Phylogenetic diversity is a widely used measure to represent the evolutionary diversity of a given area. Additionally, by considering how patterns of alpha and phylogenetic diversity are represented across geographical space, it is also possible to understand how anthropogenic habitat changes affect biodiversity measures in an evolutionary context (Turley et al., 2022; Villalta et al., 2022). Although generally correlated with spatial patterns of species richness, geographic patterns of phylogenetic diversity can be especially informative when they diverge from species richness, signaling potential changes in speciation and extinction rates or a legacy of the region's biogeographical history (Leclercq et al., 2023a,b; Marshall et al., 2023). Thus, phylogenetic diversity has been established as an important metric for conservation, given the amount of information it carries about the historical processes underlying diversity patterns and because it informs us about the evolutionary potential of a community (Davies & Buckley, 2011; Voskamp et al., 2017). This is important because closely related species are more likely to share similar traits, including those that affect their response to environmental change. Grab et al. (2019) found that agriculturally dominated landscapes have lower bee phylogenetic diversity, associated with reduced crop yield and quality. Such decreased diversity is because the loss of specific bee lineages can reduce the diversity of functional traits present in the bee community, such as body size, plant fidelity, and visitation rate, which are essential for effective pollination (Grab et al., 2019; Odanaka & Rehan, 2019). Loss of phylogenetic diversity can significantly affect ecosystem function, including pollination services.

Functional traits like nesting biology and behavior may be phylogenetically conserved (Odanaka & Rehan, 2019), meaning that closely related bee species are more likely to share them. This understanding can help predict how different bee lineages might respond to future environmental changes and inform conservation strategies that also account for ecosystem functioning (Vereecken, 2017). By identifying areas with high phylogenetic diversity and unique lineages, conservation efforts can be targeted at protecting a more comprehensive range of evolutionary history and its ecosystem services (de Pedro et al., 2023; Vereecken, 2017). Phylogenetic diversity can also provide clues on how bee assemblies might respond to changes in climate and other natural conditions (Vereecken, 2017).

5. Concluding remarks

This review highlights some of the progress made in understanding bee diversity. Phylogenetic research has helped clarify aspects of bees' evolutionary history and provided an increasingly solid basis for recent advances in their classification. Their origin in western Gondwana and subsequent diversification across continents parallel with the history of flowering plants paint a compelling picture of the progress in understanding Cretaceous-old history. On the present-day front, the ongoing threats to bee diversity, stemming from habitat loss, pesticide use, climate change, and the introduction of novel pests and pathogens, urge for effective conservation strategies. The expansion of standardized bee monitoring programs will provide reliable hallmarks to account for the conservation status of bee species and populations. Integrating data on species richness, life-history traits, and phylogenetic diversity can show what bee diversity means and how it is geographically distributed. It is worth remarking that despite progress in higher-level relationships of bees, key gaps remain in our knowledge of species-level diversity and distribution. By adopting integrated approaches to interpreting and monitoring bee diversity, we can support the long-term persistence of these ecologically crucial insects.

Authors' Contributions

All authors: writing-original draft and review.
EABA: conceptualization and visualization

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Appendix. Taxonomic summary of the family-level classification followed in this review (see Michener, 1986, 2007; Engel, 2005; Engel et al., 2020; Melo & Gonçalves, 2005; Moure et al., 2023 for additional information and references).

- 1. Andrenidae Latreille
  - 1.1. Andreninae Latreille
    - 1.1.1. Andrenini Latreille
    - 1.1.2. Euherbstiini Moure
  - 1.2. Oxaeinae Ashmead
  - 1.3. Panurginae Leach
    - 1.3.1. Calliopsini Robertson
    - 1.3.2. Melitturgini Newman
    - 1.3.3. Neffapini Ascher
    - 1.3.4. Nolanomelissini Rozen & Ascher
    - 1.3.5. Panurgini Leach
    - 1.3.6. Perditini Robertson
    - 1.3.7. Protandrenini Robertson
    - 1.3.8. Protomeliturgini Ruz[1]
- 2. Apidae Latreille
  - 2.1. Anthophorinae Dahlbom
  - 2.2. Apinae Latreille
    - 2.2.1. Apini Latreille
    - 2.2.2. Bombini Latreille
    - 2.2.3. Centridini Cockerell & Cockerell
    - 2.2.4. Euglossini Latreille
    - 2.2.5. Meliponini Lepeletier
  - 2.3. Eucerinae Latreille
    - 2.3.1. Ancylaini Michener
    - 2.3.2. Ancyloscelidini Roig-Alsina & Michener[2]
    - 2.3.3. Emphorini Robertson
    - 2.3.4. Eucerini Latreille
    - 2.3.5. Exomalopsini Vachal
    - 2.3.6. Tapinotaspidini Roig-Alsina & Michener
  - 2.4. Nomadinae Latreille
    - 2.4.1. Ammobatini Handlirsch
    - 2.4.2. Ammobatoidini Michener
    - 2.4.3. Brachynomadini Roig-Alsina & Michener
    - 2.4.4. Caenoprosopidini Michener
    - 2.4.5. Coelioxoidini Nates-Parra & Fernandez
    - 2.4.6. Epeolini Robertson
    - 2.4.7. Epeoloidini Linsley and Michener
    - 2.4.8. Ericrocidini Cockerell & Atkins
    - 2.4.9. Hexepeolini Rozen
    - 2.4.10. Isepeolini Rozen, Eickwort & Eickwort
    - 2.4.11. Melectini Westwood
    - 2.4.12. Neolarrini Fox[3]
    - 2.4.13. Nomadini Latreille
    - 2.4.14. Osirini Handlirsch
    - 2.4.15. Parepeolini Linsley & Michener
    - 2.4.16. Protepeolini Linsley & Michener
    - 2.4.17. Rhathymini Lepeletier
  - 2.5. Xylocopinae Latreille
    - 2.5.1. Allodapini Cockerell
    - 2.5.2. Ceratinini Latreille
    - 2.5.3. Ctenoplectrini Cockerell
    - 2.5.4. Manueliini Sakagami & Michener
    - 2.5.5. Tetrapediini Michener & Moure
    - 2.5.6. Xylocopini Latreille
- 3. Colletidae Lepeletier
  - 3.1. Callomelittinae Almeida
  - 3.2. Colletinae Lepeletier
  - 3.3. Diphaglossinae Vachal
    - 3.3.1. Caupolicanini Michener
    - 3.3.2. Diphaglossini Vachal
    - 3.3.3. Dissoglottini Moure
    - 3.3.4. Paracolletini Cockerell
  - 3.4. Euryglossinae Michener
  - 3.5. Hylaeinae Viereck
  - 3.6. Neopasiphaeinae Cockerell
    - 3.6.1. Anthoglossini Engel
    - 3.6.2. Eulonchopriini Moure
    - 3.6.3. Lonchopriini Moure
    - 3.6.4. Neopasiphaeini Cockerell
    - 3.6.5. Reedapini Engel
    - 3.6.6. Trichocolletini Plant
  - 3.7. Scrapterinae Melo & Gonçalves[4]
  - 3.8. Xeromelissinae Cockerell
- 4. Halictidae Thomson
  - 4.1. Halictinae Thomson
    - 4.1.1. Augochlorini Beebe
    - 4.1.2. Caenohalictini Michener
    - 4.1.3. Halictini Thomson
    - 4.1.4. Sphecodini Schenck
    - 4.1.5. Thrinchostomini Sakagami
  - 4.2. Nomiinae Robertson
    - 4.2.1. Dieunomiini Engel
    - 4.2.2. Nomiini Robertson
  - 4.3. Nomioidinae Börner
  - 4.4. Rophitinae Schenck[5]
    - 4.4.1. Penapini Engel
    - 4.4.2. Rophitini Schenck
- 5. Megachilidae Latreille
  - 5.1. Fideliinae Cockerell
  - 5.2. Lithurginae Newman
  - 5.3. Megachilinae Latreille
    - 5.3.1. Anthidiini Ashmead
    - 5.3.2. Aspidosmiini Gonzalez, Griswold, Praz & Danforth
    - 5.3.3. Dioxyini Cockerell
    - 5.3.4. Megachilini Latreille
    - 5.3.5. Ochreriadini Gonzalez & Engel
    - 5.3.6. Osmiini Newman
    - 5.3.7. Pseudoheriadini Gonzalez & Engel
  - 5.4. Neofideliinae Engel
  - 5.5. Pararhophitinae Popov
- 6. Melittidae Schenck
  - 6.1. Dasypodainae Börner
    - 6.1.1. Dasypodaini Börner
    - 6.1.2. Hesperapini Ascher & Engel
  - 6.2. Meganomiinae Michener
  - 6.3. Melittinae Schenck
    - 6.3.1. Macropidini Robertson
    - 6.3.2. Melittini Schenck
- 7. Stenotritidae Cockerell

Notas

[1] Bossert et al. (2022) treated Protomeliturgini as part of Protandrenini; therefore, as a junior synonym of the latter. Both the inclusion of *Protomeliturga* as Protandrenini or as its separate tribe are justifiable in light of phylogenetic evidence (Bossert et al., 2022; Ramos et al., 2022) because this genus is placed as the sister-group of the remaining protandrenines. Here, we recognize them as separate tribes to highlight the biogeographic and morphological distinctiveness of *Protomeliturga*, as done by Ramos et al. (2022) and Almeida, Bossert et al. (2023).

[2] This tribe includes the following genera: *Ancyloscelis*, *Chilimalopsis*, *Eremapis,* and *Teratognatha*, as circunscribed by Freitas et al. (2021). Sheffield and Yanega (2024) argued for the priority of Teratognathini Silveira, 1995 over Ancyloscelidini Roig-Alsina & Michener, 1993 because the latter name would not have complied with Article 13(a) (i) of the third edition of the Code (ICZN – International Commission on Zoological Nomenclature, 1985). We disagree with Sheffield & Yanega's interpretation because Roig-Alsina and Michener (1993: p. 159) stated that Ancyloscelidini "is different enough from other Emphorini" when they described Ancyloscelidini as a new taxon – their Fig. 1a (p. 148) shows 13 apomorphies that make these two lineages morphologically distinct, therefore complying with the International Code of Zoological Nomenclature and making the name Ancyloscelidini available.

[3] Interpreted in its expanded sense, including Biastini and Townsendiellini as junior synonyms of Neolarrini (Bossert et al., 2020).

[4] Two family-group names were proposed based on the genus *Scrapter*: Scrapterinae and Scraptrini. The latter was published about two months later than the former. Based on the interpretation of Article 13.1.2 of the fourth edition of the Code (ICZN – International Commission on Zoological Nomenclature, 1999), we prefer to remain neutral on this and adhere to the Principle of Priority, which favors the name by Melo and Gonçalves, thus making Scraptrinae the junior synonym, as done by Almeida et al. (2008: Appendix). In contrast with this interpretation, Ascher and Engel (2006) claimed that the name based on the stem "Scrapter-" is not valid because Melo and Gonçalves did not comply with article 13.1 (ICZN, 1999) for not providing an explicit diagnosis for the group. Nonetheless, Melo and Gonçalves (2005) listed various references that indirectly serve for the diagnosis of the group and, therefore, comply with Article 13.1.2 of the Code (ICZN, 1999).

[5] Patiny et al. (2009) recognized two additional tribes in Rophitinae: Conanthalictini and Xeralictini (herein, both are interpreted as part of Rophitini). Although we agree that these may be distinctive lineages deserving recognition, we choose to be conservative in only accepting the South American clade represented by Penapini (*Ceblurgus*, *Goeletapis,* and *Penapis)* and the bulk of the subfamily as classified into Rophitini until further phylogenetic analyses are available for Rophitinae.