

## 15. Geological History of the Stingless Bees (Apidae: Meliponini)

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### Abstract

A brief overview of the fossil record of stingless bees is provided. The eleven fossil species of Meliponini are discussed in order of descending geological age and placed within the paleoecological and paleogeographical context of their period. The earliest fossil meliponine is *Cretotrigona prisca* from the Late Cretaceous of New Jersey, USA, while the youngest are various species preserved in relatively modern copals. The implications of these species for understanding the evolutionary history of Meliponini are briefly discussed.

### Keywords:

Anthophila, Apoidea, biogeography, climate change, Meliponini, paleontology

### Introduction

Stingless bees (Apinae: Meliponini) are abundant in the tropical parts of the world and are particularly frequent and diverse in the New World. Like their sister tribe, the Apini or true honey bees, meliponines are highly eusocial, living in often large, perennial colonies consisting of a worker caste, a queen, and sometimes males. Nests are constructed of wax, secreted from dorsal metasomal glands, as well as resin or propolis collected from the vegetation, and are frequently in hollows within trees or among branches and lianas, although sometimes within the walls of human buildings, or in limestone cliffs or even in the ground (Wille and Michener, 1973; Wille, 1983; Roubik, 2006; Michener, 2007, 2013; Bänziger et al., 2011). Fossils of stingless bees are the most abundant of all fossilized Apoidea, with specimens of *Proplebeia dominicana* (Wille and Chandler) in amber numbering into the thousands and being common enough to be sold as novelties in gem and

fossil shops. It is similarly not difficult to find stingless bees in copal (see below) from many tropical regions of the world, sometimes with large numbers of individuals in a single piece. Despite this abundance, most of such material represents very few species, while the remaining fossil Meliponini are documented from only one or a few known specimens. To date, 11 extinct species have been recorded from amber and copal (Table 1). Among the stingless bees there are only five extinct genera presently recognized, although at least one additional group is pending. In order of increasing age, those now known are *Melipononrytes* Tosi, *Proplebeia* Michener, *Kelneriapis* Sakagami, *Liotrigonopsis* Engel, and *Cretotrigona* Engel. Although resembling stingless bees, the extinct tribe Melikertini consisted of a series of genera and species that were early relatives of the Meliponini but retained complete wing venation, a single metatibial spur, a supraalar

**Table 1. Currently described extinct species of stingless bees**

Taxon	Age	Locality	Refs.
<i>Cretotrigona prisca</i> (Michener and Grimaldi)	Cretaceous (Maastrichtian)	New Jersey, USA	2, 8
<i>Liotrignopsis rozeni</i> Engel	Eocene (Lutetian)	Baltic region	3
<i>Kelneriapis eocenica</i> (Kelner-Pillault)	Eocene (Lutetian)	Baltic region	3, 6
<i>Nogueirapis silacea</i> (Wille)	Miocene (Burdigalian)	Chiapas, Mexico	12, 4
<i>Proplebeia abdita</i> Greco and Engel	Miocene (Burdigalian)	Dominican Republic	5
<i>Proplebeia dominicana</i> (Wille and Chandler)	Miocene (Burdigalian)	Dominican Republic	1, 7, 13
<i>Proplebeia tantilla</i> Camargo, Pedro, and Grimaldi	Miocene (Burdigalian)	Dominican Republic	1
<i>Proplebeia vetusta</i> Camargo, Pedro, and Grimaldi	Miocene (Burdigalian)	Dominican Republic	1
<i>Meliponorytes sicula</i> Tosi	Miocene (Langhian?)	Sicily	11
<i>Meliponorytes succini</i> Tosi	Miocene (Langhian?)	Sicily	11
<i>Liotrigona vetula</i> Moure and Camargo	Pleistocene-Holocene	East African copal	9

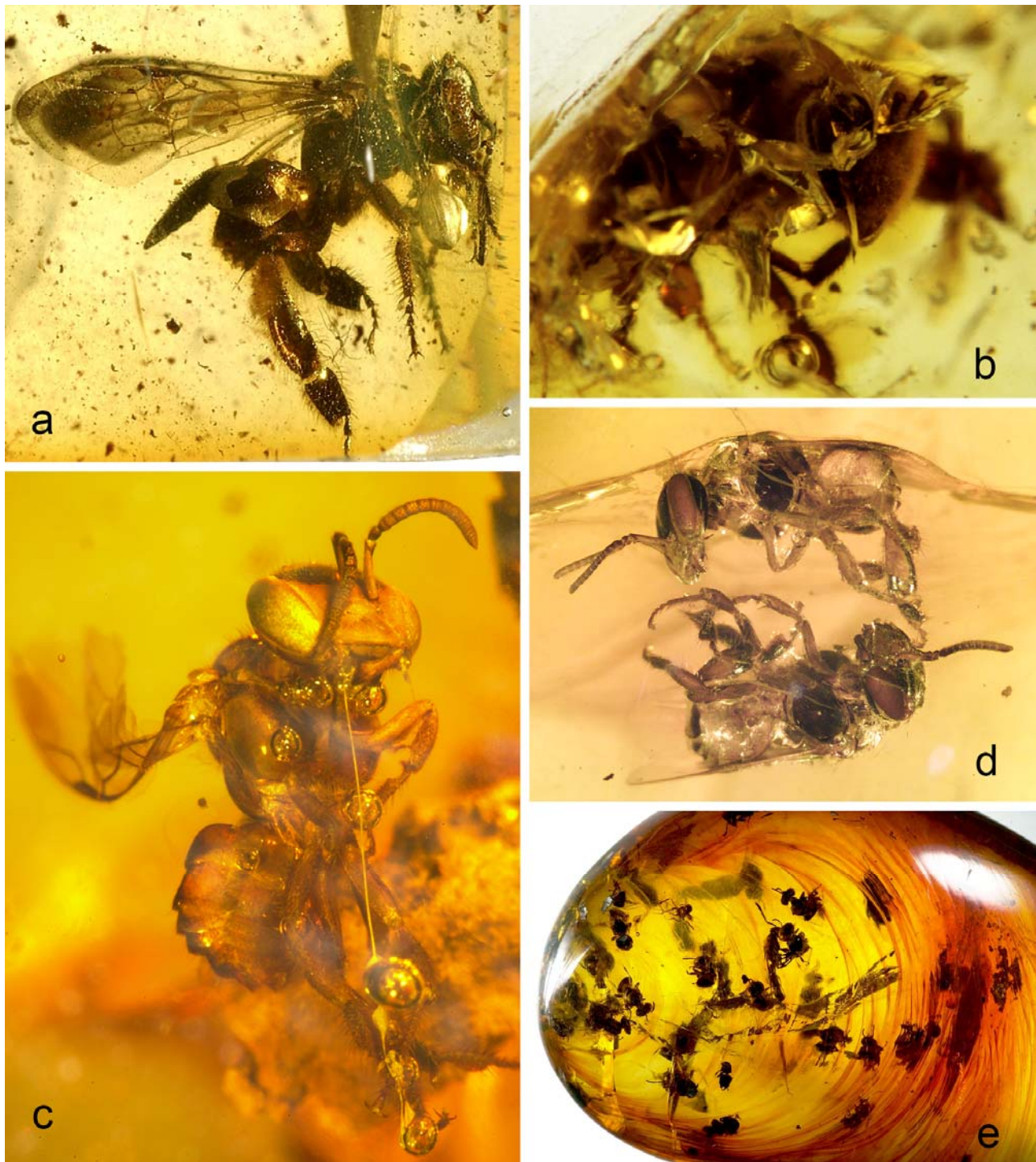
1= Camargo et al. 2000; 2= Engel 2000; 3= Engel 2001a; 4= Engel unpubl. data; 5= Greco et al. 2011; 6= Kelner-Pillault 1969; 7= Michener 1982; 8= Michener and Grimaldi 1988a; 9= Moure and Camargo 1978; 10= Sakagami 1978; 11= Tosi 1896; 12= Wille 1959; 13= Wille and Chandler 1964.

carina, toothed pretarsal claws, a distinct auricle (pollen press) at the metatibia-metabasitarsal articulation, and a well-developed sting, among other traits (Engel, 2001a) (Figure 1a). Melikertine bees appear to have become extinct around the time of the Eocene-Oligocene transition (Engel 2001a).

General accounts of the geological history of bees as a whole have been provided by Engel (2001a, 2004a), Ohl and Engel (2007), and Michez et al., (2012). The following is a brief review of the fossil record of Meliponini, progressing from oldest to youngest and through the geological periods of the Cretaceous, Paleogene (Paleocene, Eocene, and Oligocene epochs), and Neogene (Miocene, Pliocene, Pleistocene, and modern epochs). In our brief review the abbreviations Ma, mya, and myo are used for mega annum, million years ago, and million years old, respectively. The review covers only the record as revealed by amber and copal, because stingless bees are not presently known as compression or impression fossils (*i.e.*, those in sedimentary rock deposits). Amber is fossilized resin, exuded from ancient trees and having undergone significant molecular polymerization as part of its diagenesis, this process resulting from the pressure and temperature produced by surrounding sediments, usually lignite. Copal is essentially ‘young amber’, and represents one of the first stages in this diagenetic transformation from the exuded resin to amber. Copals are typically a few hundred to thousand years old and have undergone only partial polymerization. Both amber and copal are capable of preserving within them organic remains with life-like fidelity, making them ideal for paleobiological investigation.

### 15.1 Cretaceous (145–65.5 mya)

The Cretaceous period spanned nearly 80 million years and bore witness to some of the most dramatic episodes of biotic diversification and change, particularly the origin and rise of flowering plants and the numerous lineages and suites of animals that arose to take advantage of either the new flora or those creatures associated with it. It was within this context that bees first diverged from among the apoid wasps, perhaps at least 125 mya (Engel, 2001a, 2004a, 2011; Ohl and Engel, 2007). Bee diversification was likely rapid, with the earliest roots and stem members of the principal families arising during the mid-Cretaceous and subsequently radiating through the latter part of the period (Engel, 2001a, 2004a; Ohl and Engel, 2007). The earliest evidence of stingless bees comes from the latest stage of the Cretaceous. From Maastrichtian-aged deposits, approximately 70 myo, in New Jersey, a single worker has been recovered in amber produced by extinct species of Taxodiaceae (Michener and Grimaldi, 1988a, 1988b; Engel, 2000). *Cretotrigona prisca* (Michener and Grimaldi) (Figure 1b), comprises the sole Mesozoic record of the Meliponini, and indeed the only definitive apid from the great middle age of Earth. The species exhibits remarkable superficial similarity to modern species of *Trigona* s.str. (Michener and Grimaldi, 1988), although detailed examination has suggested that its phylogenetic affinities are more closely tied to some Old World lineages (Engel, 2000). *Cretotrigona* demonstrates that stingless bees once occupied what are today higher latitudes in the New World, but were likely dramatically impacted by the globally disruptive events that occurred during the mass extinction event around the K-T boundary, 65.5 mya (*e.g.*, Renne et al., 2013; Pálíke, 2013).



**Figure 1. Photomicrographs of amber-entombed workers of melikertine and meliponine bees.**

**a.** *Melissites trigona* Engel (Melikertini) in mid-Eocene Baltic amber. **b.** *Cretotrigona prisca* (Michener and Grimaldi) (Meliponini) in Late Cretaceous New Jersey amber. **c.** *Nogueirapis silacea* (Wille) (Meliponini) in Early Miocene Mexican amber. **d.** Two individuals of *Proplebeia dominicana* (Wille and Chandler) in Early Miocene Dominican amber. **e.** 'Swarm' of *P. dominicana* in Dominican amber. All rights to the images are retained by M.S. Engel, and may not be reproduced without explicit permission.

The extraterrestrial impact of a bolide colliding with the earth, off of the Yucatan Peninsula, along with a series of smaller impacts around the globe (some perhaps part of the initial break-up of the Chicxulub asteroid), set into motion a chain of events which led to a significant reshuffling of the flora and fauna. This was particularly dramatic across Central and North America because these were the sites of impact as well as, given the incident angle at which the asteroid struck (a 20°–30° angle from the southeast to northwest), primary ejecta (Schultz and D'Hondt, 1996). Northern Hemisphere effects were perhaps most catastrophic at this time, particularly in the New World, and certainly *C. prisca* and any of its relatives would have been devastated by such an event. In addition to its biogeographic implications, *C. prisca* demonstrates that highly eusocial bees were already well developed and present in the later epochs of the Mesozoic (Michener and Grimaldi, 1998b). This is perhaps not surprising given that many eusocial insect lineages (*e.g.*, termites, ants) had their origins during the Cretaceous, albeit much earlier, during the earlier or middle stages of the Early Cretaceous (Grimaldi and Engel, 2005; Engel et al., 2009).

### 15.2 Paleogene (65.5–23 mya)

The Paleogene period (Paleocene through Oligocene epochs) marked the beginning of the Cenozoic (commonly known as the Age of Mammals, but just as much a mere fragment in an overarching Age of Insects). Non-avian dinosaurs were gone, along with countless other ecologically important lineages, and the flora and fauna had to contend with massive climatic changes, particularly a rapid spike at the Paleocene-Eocene Thermal Maximum (PETM). Although the PETM was a formidable upsurge in global temperatures, overall the Cenozoic experienced a trend toward cooling and drying relative to the Cretaceous (particularly after the Eocene and continuing through the Neogene), a shift partially driven by the formation of the Antarctic Circumpolar Current which also led to the ultimate freezing of Antarctica. It was also during the Paleogene that the 'Grand Coupure' took place, also known as the Eocene-Oligocene extinction event. It was tied to another drop in global temperatures (apparently tied to lowered atmospheric carbon dioxide) as well as the beginning of ice sheet formation on Antarctica. It was at the Eocene-Oligocene boundary that there appears to have been a shift in the composition of bee faunas. Many primitive forms relative to lineages we recognize as extant tribes became extinct. Those more primitive

forms coexisted with more modern taxa but were clearly in greater abundance during the Eocene, and likely earlier epochs as well. That turnover included the loss of various, probably highly eusocial, bee lineages, most notably the Melikertini, understood to be the closest relatives of the stingless bees (Engel, 2001a, 2001b).

Although the Paleogene record of bees is significantly stronger than that of the Mesozoic (*e.g.*, Engel, 2001a; Michez et al., 2012), there are presently only two definitive stingless bees documented from the Paleogene. Both are preserved in middle Eocene amber of the Baltic region. *Liotrigonopsis rozeni* Engel and *Kelneriapis eocenica* (Kelner-Pillault) are both known from a single worker, and both appear similar to genera today living in sub-Saharan Africa and Southeast Asia (Engel 2001a). The botanical origin of Baltic amber is greatly debated, with the most likely contenders being extinct species of *Sciadopityaceae* or *Pinaceae* (Schubert 1961; Langenheim 2003; Wolfe et al. 2009). Both of the Baltic amber species highlight the once more global distribution of stingless bees. Like *Cretotrigona*, *Liotrigonopsis* and *Kelneriapis* push the historical bounds of meliponine distribution well northward, encompassing what are today cool temperate regions of northern Europe and northeastern North America. While we today discuss stingless bee biogeography in terms of a pantropical distribution and within the context of what this means at the present moment, we must remain cognizant that tropical zones have not remained static. Climates have changed (and continue to change!) considerably, even over relatively recent spans of time, and any consideration of meliponine historical biogeography must take this into account, particularly given that the tribe is of such great antiquity. Prior to the Eocene-Oligocene boundary the planet's higher latitudes were subtropical or paratropical, permitting more thermophilic lineages to have much broadened ranges. Such was the case with the stingless bees, and *Liotrigonopsis* and *Kelneriapis* both are indicative of these paratropical conditions within the middle Eocene of Europe. Present day occurrences of stingless bees in what could be called temperate climates, such as along the eastern coast of Australia or at higher elevations in the tropics (*e.g.*, Ayala et al., 2013; Halcroft et al., 2013), are invasions by tropical lineages.

### 15.3 Neogene (23 mya–today)

During the Neogene period (Miocene epoch through today) the global cooling and drying trend continued,

with development of distinct seasonalities, and continental positions largely approximated those of today, particularly with the formation of the Isthmus of Panama and the connection of North and South America. It is from the Neogene that we have the richest sources of fossil stingless bees, albeit representing relatively few species (*e.g.*, Michez et al., 2012).

It is from the Early Miocene (19–17 myo) amber mines of the Dominican Republic that the greatest wealth of stingless bee fossils has been recovered. Dominican amber is likely of an extinct species of *Hymenaea* (Fabaceae). While West Indian stingless bees are today only found in Jamaica, the Lesser Antilles, and putatively adventive in Cuba, they were a diverse and abundant component of the native fauna of ancient Hispaniola. When first discovered, Wille and Chandler (1964) placed the Dominican amber species known to them in *Liotrigona* Moure, a group otherwise known from Africa and Madagascar, but Moure and Camargo (1978) subsequently considered the Dominican taxa to belong to *Plebeia* Schwarz s.str. Michener (1982) later confirmed that the Dominican amber species was indeed more closely related to *Plebeia* but noted significant differences and therefore established the genus *Proplebeia*. *Proplebeia dominicana* remains the single most common fossil bee anywhere in the world, although subsequent research has added additional species to the genus (Camargo et al. 2000; Greco et al. 2011: Table 1). Multiple individuals of *Proplebeia* are often found together and these clusters can even be quite numerous (Figures 1d, e). The various species of *Proplebeia*, as well as many other Dominican amber bees (*e.g.*, Engel, 1996, 1999a, 1999b; Engel et al., 2012), highlight the changes to the composition of the West Indian melittofauna that have taken place during the last 19 million years.

The contemporaneous amber deposits of southern Mexico are another rich source of Early Miocene flora and fauna, and this fossil resin was perhaps also produced by an extinct species of *Hymenaea* much like Dominican amber (Engel, 2004b; Solórzano-Kramer, 2007). Unfortunately, unlike the Dominican amber, those fossil resins from Mexico have far fewer bee inclusions, although all presently recorded individuals are stingless bees. The first bees discovered from these deposits were described as an extinct species of *Nogueirapis* Moure (Wille, 1959). *Nogueirapis silacea* Wille (Figure 1c) is not as abundant as *P. dominicana*, but is certainly not a rarity in the Mexican amber fauna. In fact, there are

multiple stingless bee species in the Mexican amber fauna and some of these should be reclassified (Engel, 2004b, unpublished data), and work on the Mexican amber melittofauna is presently underway (Strelow et al., in preparation). Indeed, a detailed geometric morphometric study of a large series of stingless bees from various Mexican amber deposits reveals that perhaps at least two species are present in the fauna, and that these, including *N. silacea*, are best classified elsewhere outside of *Nogueirapis*. This work is ongoing but is already highlighting that there remains much to be discovered about Mexico's fossil meliponines.

Pleistocene and younger copals harbor numerous stingless bee individuals and come from a wide diversity of botanical sources. Indeed, some of the young copals from Colombia, Tanzania, Madagascar, the Philippines, and elsewhere are known to contain workers of a variety of living meliponine species, and these can sometimes be quite common or come in large numbers within individual pieces. Pieces with large numbers of individuals likely represent the tree resins exuding in large quantities near nesting sites. Given that meliponines regularly harvest such resins for nest construction, it is not surprising that many workers would become ensnared and preserved. In the past, these copal sources were confused with true amber and even some historical works purportedly based on samples of amber insects (*e.g.*, Hope, 1836), were largely comprised of records from modern copals (*e.g.*, Engel, 2001a). Although copal-preserved stingless bees provide little information about phylogeny or global biogeography, they can perhaps provide more regional insights into shifts in distributions or, if the copals are sufficiently old, recent localized extinctions.

#### 15.4 Concluding remarks

Stingless bees are not only morphologically and biologically diverse (Michener, 2013), but simultaneously ancient. Any serious consideration of their evolution must take into account their expansive history, extending back over the entire Tertiary period and eclipsing an episode otherwise famed for the explosive diversification of mammals. While tectonic plates and climates have gradually shifted, the stingless bees have borne witness to dramatic biotic changes all through at least the last 70 million years. Meliponine distribution in the past encompassed regions otherwise foreign to any modern genus of stingless bees, and certainly there must have once been an even greater and as yet unrevealed biological and ethological diversity. Yet,

all of this unseen history has shaped every aspect of meliponines. As discussed herein, we are only beginning to get small glimpses into this veiled history but already the insights have enriched our understanding of the Meliponini. Continued paleomelittological inquiry will undoubtedly bring forth new revelations.

One must remember that most of the ideas about stingless bee evolution have been based on our knowledge of hundreds of species of living stingless bees. At each moment during the evolution of stingless bees, there must have been several, and later hundreds, of species. If the total picture were known since the origin of the Meliponini, it would have involved many thousands of species, mostly extinct. The approximately 500 living species are a mere fraction of the total historical diversity of stingless bees. Our account above concerns a mere eleven fossil species, interpreted in the light of information on changing climates and biotas. Of course new findings and new interpretations should be expected to change, or perhaps strengthen, current interpretations.

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