

## **An Exomalopsine Bee in Early Miocene Amber from the Dominican Republic (Hymenoptera: Apidae)**

Authors: Engel, Michael S., Grimaldi, David A., Gonzalez, Victor H., Hinojosa-Díaz, Ismael A., and Michener, Charles D.

Source: American Museum Novitates, 2012(3758) : 1-16

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/3758.2>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## An Exomalopsine Bee in Early Miocene Amber from the Dominican Republic (Hymenoptera: Apidae)

MICHAEL S. ENGEL,<sup>1</sup> DAVID A. GRIMALDI,<sup>2</sup> VICTOR H. GONZALEZ,<sup>3</sup>  
ISMAEL A. HINOJOSA-DÍAZ,<sup>3, 4</sup> AND CHARLES D. MICHENER<sup>3</sup>

### ABSTRACT

The first fossil exomalopsine bee is described and figured from two females, one very partially preserved in Early Miocene amber from the Dominican Republic. *Anthophorula* (*Anthophorula*) *persephone* Engel, new species, is distinguished from its modern counterparts mainly by the broader pterostigma in which its inner breadth is greater than that of its marginal veins. This record expands the Dominican amber melittofauna to 21 species. Brief comments are made on the discovery as well as the Dominican amber bees in general. The new combination *Thaumatoma* (*Chalicodomopsis*) *glaesaria* (Engel) is established.

### INTRODUCTION

As recently as 1995 the only species of bee known from the rich amber deposits of the Dominican Republic was the common stingless bee, *Proplebeia dominicana* (Wille and Chandler) (Wille and Chandler, 1964; Michener, 1982). During the intervening years, however, the total diversity and available material has risen significantly, with numerous species of xerome-

<sup>1</sup> Division of Invertebrate Zoology, American Museum of Natural History; and Division of Entomology, Natural History Museum, and Department of Ecology and Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045.

<sup>2</sup> Division of Invertebrate Zoology, American Museum of Natural History.

<sup>3</sup> Division of Entomology, Natural History Museum, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045.

<sup>4</sup> Current address: Department of Environmental Studies, Emory University, Math and Science Center – Suite E510, 400 Dowman Drive, Atlanta, Georgia 30322.

lissine, halictine, panurgine, megachiline, euglossine, and further meliponine bees documented (table 1).<sup>5</sup> Although species have continued to accumulate, not since 1999 have any new tribes been recorded from these deposits. It is therefore of great significance that a new species of Apinae representing the tribe Exomalopsini was recently recognized among new material of Dominican amber.

Exomalopsines are restricted to the Western Hemisphere, ranging from the United States to Argentina, and are particularly abundant and diverse in arid habitats. They are small to moderate-sized anthophoriform bees, densely setose and commonly with pale metasomal bands of setae, and lacking maculation except in some species for the clypeus, labrum, and mandibles. The tribe in its broadest sense (Michener, 2007) comprises five genera (*Anthophorula* Cockerell, *Chilimalopsis* Toro, *Eremapis* Ogloblin, *Exomalopsis* Spinola, and *Teratognatha* Ogloblin) and approximately 150 modern species (table 2). Silveira (1995) developed a phylogenetic hypothesis for the tribe and excluded at that time *Teratognatha* and *Chilimalopsis* in their own tribe. However, given the weakness of some of the characters used by Silveira (1995) to separate Teratognathini, Michener (2007) considered this decision premature and regarded them as a subtribe. Although Exomalopsini are widely distributed in the Americas, all five exomalopsine genera occur in South America, but only a few lineages of the genera *Anthophorula* and *Exomalopsis* have reached and diversified in Central and North America. The two major genera are *Exomalopsis* and *Anthophorula*. The former ranges from the southernmost United States, the Bahamas, and the Antilles south throughout the Neotropical region to Argentina, whereas the latter, whose species have until recently been included in *Exomalopsis*, occurs from the central western United States (Oregon, Nebraska) south to southernmost Mexico, and seems to be especially abundant in xeric or mesic areas. Timberlake (1980), Roig-Alsina (1992), Almeida and Silveira (1999), González-Vaquero and Roig-Alsina (2005), and Silveira and Almeida (2008) have revised most of the groups.

Herein we provide a brief description of the new fossil material as well as a brief discussion on exomalopsines and the Dominican amber melittofauna in general.

## MATERIAL AND METHODS

The age and origin of Dominican amber are discussed by Grimaldi and Engel (2005), while the bee fauna was most recently summarized by Engel (2009), Greco et al. (2011), and Michez et al. (2012). For the descriptions morphological terminology generally follows that of Engel (2001) and Michener (2007). The description and all measurements provided are based on the holotype (figs. 1–4), with supplemental details taken from a second, fragmentary female preserved in the same amber piece. Measurements were prepared using an ocular micrometer on an Olympus SZX-12 stereomicroscope while photomicrographs were made using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens. The amber piece

<sup>5</sup> We have modified the taxonomy of the sole Dominican amber megachiline to reflect the multigeneric classification of Megachilini as proposed by Gonzalez (2008). The resulting new combination is as follows: *Thaumatosoma* (*Chalicodomopsis*) *glaesaria* (Engel), new combination.

TABLE 1. Hierarchical outline of the known Dominican amber bees (Apoidea: Anthophila), updated from Engel (2009). Dates and citations provided only for genus- and species-group taxa. Those for suprageneric taxa provided by Engel (2005).

---

Family **APIDAE** Latreille

Subfamily APINAE Latreille

Tribe Meliponini Lepeletier de Saint Fargeau

Genus †*Proplebeia* Michener, 1982

†*Proplebeia abdita* Greco and Engel in Greco et al., 2011

†*Proplebeia dominicana* (Wille and Chandler, 1964)

†*Proplebeia tantilla* Camargo et al., 2000

†*Proplebeia vetusta* Camargo et al., 2000

Tribe Euglossini Latreille

Genus *Eufriesea* Cockerell, 1908

†*Eufriesea melissiflora* (Poinar, 1998)

Genus *Euglossa* Latreille, 1802

†*Euglossa moronei* Engel, 1999a

Tribe Exomalopsini Vachal

Genus *Anthophorula* Cockerell, 1897

Subgenus *Anthophorula* Cockerell, 1897

†*Anthophorula (Anthophorula) persephone* Engel, n. sp.

Family **MEGACHILIDAE** Latreille

Subfamily MEGACHILINAE Latreille

Tribe Megachilini<sup>1</sup> Latreille

Genus *Thaumatostoma* Smith, 1865

Subgenus †*Chalicodomopsis* Engel, 1999b

†*Thaumatostoma (Chalicodomopsis) glaesaria* (Engel, 1999b), n. comb.

Family **ANDRENIDAE** Latreille

Subfamily PANURGINAE Leach

Tribe Protandrenini Roberston

Genus *Heterosarus* Robertson, 1918

†*Heterosarus eickworti* Rozen, 1996

Family **HALICTIDAE** Thomson

Subfamily HALICTINAE Thomson

Tribe Caenohalictini Michener

Genus †*Eickwortapis* Michener and Poinar, 1996

†*Eickwortapis dominicana* Michener and Poinar, 1996

Genus †*Nesagapostemon* Engel, 2009

†*Nesagapostemon moronei* Engel, 2009

Tribe Augochlorini Beebe

Genus *Augochlora* Smith, 1853

Subgenus †*Electraugochlora* Engel, 2000

†*Augochlora* (*Electraugochlora*) *leptoloba* Engel, 2000

Genus *Neocorynura* Schrottky, 1910

†*Neocorynura* *electra* Engel, 1995

Genus †*Oligochlora*<sup>2</sup> Engel, 1996

†*Oligochlora* *eickworti* Engel, 1996

†*Oligochlora* *grimaldii* Engel, 1997

†*Oligochlora* *marquettorum* Engel and Rightmyer, 2000

†*Oligochlora* *micheneri* Engel, 1996

†*Oligochlora* *rozeni* Engel, 2000

†*Oligochlora* *semirugosa* Engel, 2009

Family **COLLETIDAE** Lepeletier de Saint Fargeau

Subfamily XEROMELISSINAE Cockerell

Genus *Chilicola* Spinola, 1851

Subgenus *Hylaeosoma* Ashmead, 1898

†*Chilicola* (*Hylaeosoma*) *electrodominica* Engel, 1999c

†*Chilicola* (*Hylaeosoma*) *gracilis* Michener and Poinar, 1996

<sup>1</sup> The generic classification of Megachilini adopted here follows the multigeneric system proposed by Gonzalez (2008).

<sup>2</sup> The subgenera of *Oligochlora* recognized by Engel (2000) were synonymized by Engel (2002).

TABLE 2. Summary of generic and subgeneric classification and modern diversity of Exomalopsini. NA = North America; CA = Central America; SA = South America; \* = includes Caribbean Region. Dates and citations for family- and genus-group taxa provided by Engel (2005) and Michener (2007).

Taxa	Species (no.)	Distribution
Subtribe Teratognathina Silveira		
Genus <i>Chilimalopsis</i> Toro	2	SA
Genus <i>Teratognatha</i> Ogloblin	1	SA
Subtribe Exomalopsina Vachal		
Genus <i>Anthophorula</i> Cockerell		
Subgenus <i>Anthophorisca</i> Michener and Moure	30	NA
Subgenus <i>Anthophorula</i> Cockerell	29	NA
Subgenus <i>Isomalopsis</i> Michener and Moure	4	SA
Genus <i>Eremapis</i> Ogloblin	1	SA
Genus <i>Exomalopsis</i> Spinola		
Subgenus <i>Diomalopsis</i> Michener and Moure	2	SA
Subgenus <i>Exomalopsis</i> Spinola	55	CA*, SA
Subgenus <i>Phanomalopsis</i> Michener and Moure	15	NA, CA, SA
Subgenus <i>Stilbomalopsis</i> Silveira	13	NA, CA

is conserved in the amber fossil collection of the Division of Invertebrate Zoology, American Museum of Natural History, New York.

#### SYSTEMATIC PALEONTOLOGY

Tribe Exomalopsini Vachal, 1909

Genus *Anthophorula* Cockerell, 1897

Subgenus *Anthophorula* Cockerell, 1897

*Anthophorula* (*Anthophorula*) ***persephone*** Engel, new species

Figures 1–4

**DIAGNOSIS:** The new species can be most readily distinguished from other *Anthophorula* proper by the broader pterostigma in which its inner breadth is greater than that of its marginal veins (fig. 4). In addition, the species can be characterized by the combination of a uniformly punctate mesoscutum and mesoscutellum, similarly punctate pleura, absence of distinct setal bands on the metanotum, and the pygidial fimbria composed of dense fuscous setae with a reddish tint.

**DESCRIPTION: Female.** Total body length (as preserved) 6.1 mm; forewing length 4.6 mm; integument dark (fig. 1), apparently black throughout except legs dark brown, with spurs and pretarsal claws lighter brown, maculations absent; wing membranes hyaline, veins dark brown. Head broader than long (width as preserved 2.08 mm, length 1.30 mm) (fig. 2), with inner orbits of compound eyes only slightly diverging above; clypeus weakly convex; gena rounded, narrower than compound eye; lateral ocellus separated from occipital margin by approximately 1.5 times its diameter and from compound eye margin by about three times its diameter (values approximate as the ocelli are slightly distorted, making it difficult to determine their proper diameter in life); toruli situated well below midlength of face. Inter-tetragular distance 1.46 mm; mesoscutellum more than twice length metanotum; metabasitibial plate short, broadly rounded, with planar surface, without carinate rim or covering of fine setae (fig. 3); scopa on metatibia and metabasitarsus composed of dense, plumose setae (fig. 3); metabasitarsus with apical process and penicillus. Forewing marginal cell obliquely truncate and bent away from costal margin (fig. 4); marginal cell apex somewhat pointed (fig. 4), length of cell slightly greater than distance from its apex to wing tip; pterostigma three times as long as prestigma, its inner breadth greater than that of bordering marginal veins; second medial cell shorter than second cubital cell; other venational details in figure 4. Anterior-facing surface of first metasomal tergum depressed and apparently only slightly shorter than length of dorsal-facing surface; first metasomal tergum with distinct, transverse carina demarcating anterior- and dorsal-facing surfaces; pygidial plate black, apparently broad basally with relatively straight, apically tapering lateral margins to narrowly rounded apex (very difficult to discern).

Face with small, well-defined punctures separated by a puncture width or less, integument between smooth and shining; frontal line weakly impressed, disappearing approxi-





FIGURES 1–3. Photomicrographs of holotype female of *Anthophorula* (*Anthophorula*) *persephone* Engel, new species (AMNH DR-KL1). 1. Dorsal oblique view of holotype female as preserved. 2. Facial view. 3. Detail of metabasitibial plate and branched scopal setae.

mately two ocellar diameters before median ocellus. Mesoscutum uniformly with punctures separated by a puncture width or less, often only slightly less, integument between punctures smooth and shining; mesoscutellum sculptured as on mesoscutum; pleura sculptured as on mesoscutum. Metasomal terga with ill-defined, coarse, shallow punctures separated by less than a puncture width (except anterior-facing surface of first tergum apparently impunctate),



FIGURE 4. Apical forewing venation of fragmentary female of *Anthophorula* (*Anthophorula*) *persephone* Engel, new species (AMNH DR-KL1); note that fracturing in wing as preserved distorts some proportions (holotype is preserved completely [fig. 1], but detailed images of the venation appear dark and without contrast against the darkened metasoma immediately beneath it).

such punctures slightly more defined along lateral margins, integument between finely imbricate and shining.

Pubescence appearing largely fuscous or lightly fuscous with reddish tint except those setae of face whitish; setae of mesosoma branched and numerous, not dense or obscuring integument. Scopal setae elongate, fuscous, plumose throughout and along entire rachis. Metasomal terga without dense transverse bands of setae, setae most prominent laterally on terga; pygidial fimbria dense, composed of fuscous branched setae with reddish tint.

**Male.** Unknown.

**HOLOTYPE:** Female (fig. 1), DR-KL1; Dominican Republic; Early Miocene amber (Burdigalian?), specific mine unknown (AMNH).

**ADDITIONAL MATERIAL:** Fragmentary female, same amber piece as holotype (AMNH DR-KL1). This individual is largely represented by the metasoma, fragments of the hind and midlegs, a very few fragments of one foreleg, and the wings which are folded over the metasoma and somewhat fractured (fig. 4).

**ETYMOLOGY:** The specific epithet is from Greek mythology. Persephone, daughter of Zeus and Demeter, was abducted by Hades, who was later forced to return her. Before she left, Hades tricked her into eating four pomegranate arils thereby dooming her eternally to the underworld. Persephone was therefore bound to spend four months of each year with Hades as his consort.



## DISCUSSION

It is exciting to record for the first time in many years a tribe new to the Dominican amber fauna. It is greatly hoped that additional tribes and genera, particularly one of the cleptoparasitic lineages that are present today, will be forthcoming from these deposits in time. The new fossil species can be recognized as an exomalopsine by the well-developed and plumose scopa (fig. 1), the clypeus rather flat in profile, the vertex not convex in facial view (fig. 2), the second abscissa of  $M + Cu$  in the hind wing over one-half as long as  $M$ , the lack of a paraocular carina, the presence of a line of fine setae along the inner orbit of the compound eye, and the forewing marginal cell obliquely truncate and bent away from the costal margin, its apex somewhat pointed and the total length of the cell greater than the distance from its apex to the wing tip (observable in the holotype and right forewing of the partial female [left forewing depicted in fig. 4]). Among exomalopsines the fossil most closely resembles the modern species of *Anthophorula* subgenus *Anthophorula* as evidenced by the combination of the second medial cell of the forewing shorter than the second cubital cell, the labrum and clypeus dark, the simple mandible (apparently so; difficult to discern in holotype), the metabasitarsus with an apical process and penicillus, the metabasitibial plate small and with a planar surface, the first metasomal tergum with a distinct transverse carina, a dense scope consisting of strongly plumose setae, and a pterostigma that is just about three times longer than the prestigma. However, it should be noted that *A. persephone* does differ from other species of the subgenus by the broader pterostigma (its inner breadth greater than the breadth of its marginal veins), in this regard resembling the subgenus *Isomalopsis* Michener and Moure (known only from xeric western Argentina) and many *Exomalopsis* Spinola. Indeed, the pterostigma, while shorter than in species of *Isomalopsis* (where it is four times the length of the prestigma), is at the upper end of the range of pterostigmal lengths for other *Anthophorula* s.l. Overall the broader pterostigma likely represents a plesiomorphy for the subgenus or genus as a whole. While a new subgenus could be proposed for this isolated species, to do so would serve no purpose at this time, particularly given that the sole, prominent difference from *Anthophorula* s.str. is such a minor trait, and one for which the polarity, as noted, likely indicates it as simply basal within the subgenus.

It is likely that Exomalopsini arose in semidesertic habitats in South America given that all five genera occur there while only a few lineages have reached and diversified in Central and North America; they are also particularly abundant and diverse in those types of habitats (Michener and Moure, 1957; Silveira, 1995). Although a northward migration was surely facilitated when the Isthmus of Panama was formed during the Pliocene, the presence of *A. persephone* in Dominican amber indicates that such a migration may have occurred much earlier throughout the Antilles, as documented for other taxa (Iturralde-Vinent and MacPhee, 1999; Engel, 1999a, 1999b, 2000). It also indicates that *Anthophorula* was also present in the West Indies and then became extinct with subsequent climatic and geographical changes, a phenomenon recorded in other bee taxa (Engel, 2004; Ohl and Engel, 2007). It is interesting to note that, except for the two South American species placed in the subgenus *Isomalopsis* (known only from xeric western Argentina), all *Anthophorula* are primarily found in North America. Such a distribution of the genus and the distinctive pterostigma of *A. persephone* described

above supports the idea of the basal position of this extinct taxon within the subgenus. While it may seem somewhat peculiar for fossils of a group of largely xeric or mesic species to be discovered alongside or as close relatives of fossils from an otherwise tropical paleofauna, such relationships and patterns are known to exist (e.g., Bennett and Engel, 2006). Furthermore, species of *Diomalopsis* Michener and Moure and several of *Exomalopsis* s.str. are apparently restricted to moist tropical environments (Silveira, 1995), indicating ecological variation among species and the potential to colonize and occupy other environments.

The modern exomalopsine fauna of the West Indies is relatively poor. About six species are known, all of them in *Exomalopsis* s.str. (table 3). It is not known whether such colonization may have been from Central or South America. A species-level phylogenetic analysis, including *A. persephone*, could help explain the relationships as well as to clarify the historical biogeographical patterns of Exomalopsini. However, higher-level analyses are often preferred over species-level studies perhaps because of their apparent greater impact, but the latter are more informative and explanatory for addressing such biological questions. Understanding such patterns, particularly in the present case, requires testing of species circumscriptions (fortunately well established in Exomalopsini) and cladistic analyses at the specific level, and for which such biological and biogeographic transitions are taking place (e.g., Franz and Engel, 2010; Engel, 2011).

It is noteworthy that after more than 15 years of research, we have at this time a moderately robust perspective regarding the bee fauna of ancient Hispaniola. The modern fauna comprises around 75 species, 6.3% of which are introduced (Genaro, 2007), and by comparison the 21 species already recorded from the extinct fauna would appear to be a moderately decent sampling of the presumed total potential paleofauna. What is of interest is that while several elements of these faunas are quite similar, such as the shared presence of many tribes and genera (table 4), there are some just as stark differences. For example, the native corbiculate bee species in ancient Hispaniola, specifically the stingless bees and orchid bees, which today are not only

TABLE 3. List of species of *Exomalopsis* known from the West Indies. All species belong to the nominate subgenus. Distributions based on Genaro (2007, 2008), Genaro and Franz (2008), and Silveira (2007).

Taxa	Distribution
<i>E. analis</i> Spinola, 1853	Hispaniola, Puerto Rico throughout SA
<i>E. bahamica</i> Timberlake, 1980	Bahamas, Cuba, Hispaniola, Puerto Rico
<i>E. bartschi</i> Timberlake, 1980	Guadeloupe
<i>E. nr. bahamica</i>	Puerto Rico
<i>E. pubescens</i> Cresson, 1865	Grenada, Grenadines, St. Kitts, St. Vincent, Trinidad, U.S. Virgin Islands (St. Croix)
<i>E. pulchella</i> Cresson, 1865	Bahamas, Costa Rica, Cuba, Jamaica, Mexico, Guatemala, Puerto Rico, US (Florida), U.S. Virgin Islands (St. Thomas)
<i>E. rufitarsis</i> Smith, 1879	Jamaica
<i>E. similis</i> Cresson, 1865	Bahamas, Cayman Islands, Central America, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Montserrat, Puerto Rico, St. Vincent, U.S. (Florida), U.S. Virgin Islands (St. Thomas)
<i>E. vincentana</i> Cockerell, 1917	St. Vincent

absent in Hispaniola, but are either entirely or largely absent from the West Indies as a whole. During the complex tectonic history of the region over the last 19 million years it is no wonder that there was considerable faunal turnover. Clearly, lineages such as Euglossini, Meliponini, and the other bee tribes in Dominican amber had invaded the West Indies by the Early Miocene, most likely entering via South America. Most were extirpated as islands subsided and were again uplifted later (Donnelly, 1988; Iturralde-Vinent and MacPhee, 1999), and then the same genera or close relatives reinvaded the Caribbean, but this time from a myriad of sources, many coming again via South America, but with others clearly entering from Central and North America (e.g., Eickwort, 1988). Naturally, some may have persisted on one or more landmasses throughout the Miocene, Pliocene, and Quaternary, but evidence of this is lacking. If none managed to persist by moving from island to island as the West Indies adjusted in

TABLE 4. Comparison of the living and extinct faunas of bees from Hispaniola (only native genera and subgenera included: see Genaro, 2007). With about 75 species living on the island today (and at least 6.3% of these are introduced, and only 45.6% of the total are endemic), the 21 species from Dominican amber represents a relatively robust sampling of the potential fossil fauna.

EXTANT		FOSSIL (19 Ma)		
<b>COLLETIDAE</b>				
Diphaglossinae	Caupolicanini	<i>Caupolicana</i> ( <i>Alayoapis</i> )		
Hylaeinae		<i>Hylaeus</i> ( <i>Prosopis</i> , <i>Hylaeana</i> )	Xeromelissinae	<i>Chilicola</i> ( <i>Hylaeosoma</i> )
<b>ANDRENIDAE</b>				
Panurginae	Perditini	<i>Perdita</i> ( <i>Perdita</i> )	Panurginae	
	Protandrenini	<i>Heterosarus</i>	Protandrenini	<i>Heterosarus</i>
<b>HALICTIDAE</b>				
Halictinae	Halictini	<i>Halictus</i> ( <i>Odontalictus</i> )  <i>Lasioglossum</i> ( <i>Dialictus</i> )	Halictinae	

EXTANT		FOSSIL (19 Ma)			
	Caenohalictini	<i>Sphecodes</i> ( <i>Austrosphecodes</i> ) <i>Nesosphecodes</i>		Caenohalictini	
	Augochlorini	<i>Agapostemon</i> ( <i>Agapostemon</i> ) <i>Augochlora</i> ( <i>Augochlora</i> )		Augochlorini	† <i>Eickwortapis</i> † <i>Nesagapostemon</i> <i>Augochlora</i> († <i>Electraugochlora</i> ) † <i>Oligochlora</i> <i>Neocorynura</i>
<b>MEGACHILIDAE</b>					
Lithurginae	Lithurgini	<i>Lithurgus</i> ( <i>Lithurgopsis</i> )			
Megachilinae	Osmiini	<i>Osmia</i> ( <i>Diceratosmia</i> ) <i>Heriades</i> ( <i>Neotrypetes</i> )			
	Megachilini	<i>Megachile</i> ( <i>Leptorachis</i> , <i>Melanosarus</i> , <i>Sayapis</i> , <i>Pseudocentron</i> ) <i>Coelioxys</i> ( <i>Neocoelioxys</i> , <i>Cyrtocoelioxys</i> )		Megachilini	<i>Thaumatostoma</i> († <i>Chalicodomopsis</i> )
<b>APIDAE</b>					
Xylocopinae	Xylocopini	<i>Xylocopa</i> ( <i>Neoxylocopa</i> )			
	Ceratinini	<i>Ceratina</i> ( <i>Ceratinula</i> )			
Nomadinae					

EXTANT		FOSSIL (19 Ma)					
Apinae	Nomadini	<i>Nomada</i>	Apinae	Exomalopsini	<i>Anthophorula</i> ( <i>Anthophorula</i> )		
	Epeolini	<i>Triepeolus</i>					
	Exomalopsini	<i>Exomalopsis</i> ( <i>Exomalopsis</i> )					
	Eucerini	<i>Melissoptila</i> ( <i>Eclectica</i> ) <i>Melissodes</i> ( <i>Ptilomelissa</i> )					
	Anthophorini	<i>Anthophora</i> ( <i>Mystacanthophora</i> )					
	Melectini	<i>Xeromelecta</i> ( <i>Nesomelecta</i> )					
	Ericrocidini	<i>Mesoplia</i> ( <i>Mesoplia</i> ) <i>Mesocheira</i>					
	Centridini	<i>Centris</i> ( <i>Centris</i> , <i>Xanthemisia</i> , <i>Heterocentris</i> , <i>Trachina</i> , <i>Hemisiella</i> )					
						Euglossini	<i>Euglossa</i> ( <i>Glossura</i> ) <i>Eufriesea</i>
						Meliponini	† <i>Proplebeia</i>



composition over the intervening 19 million years, then is interesting to note the similarities, at least at the generic/subgeneric level, between the extinct and modern faunas of Hispaniola (table 4). In order to more fully elucidate the biogeography of the region and the implications of Dominican amber taxa, more cladistic analyses are needed of species within particular genera, including the fossils. Only such treatments will refine hypotheses as to the sources of the particular Dominican amber elements. In addition, it shall be exciting to discover the degree to which similarities between the faunas continue to accumulate as we undoubtedly recover more species from the mines of the Dominican Republic.

#### ACKNOWLEDGMENTS

We are grateful to Keith Luzzi for the donation of this curious new material to the AMNH and for his continued generosity and friendship. We are also thankful to Julio A. Genaro and Claus Rasmussen for valuable critiques of the manuscript. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

#### REFERENCES

- Almeida, E.A.B., and F.A. Silveira. 1999. Revision of the species of the subgenera of *Exomalopsis* Spinola, 1853, occurring in South America. I: *Diomalopsis* Michener & Moure, 1957 (Hymenoptera: Apidae), and a revised key to the subgenera. University of Kansas Natural History Museum Special Publication 24: 167–170.
- Ashmead, W.H. 1898. Some new genera of bees. *Psyche* 8 (271): 282–285.
- Bennett, D.J., and M.S. Engel. 2006. A new moustache wasp in Dominican amber, with an account of apoid wasp evolution emphasizing Crabroninae (Hymenoptera: Crabronidae). *American Museum Novitates* 3529: 1–10.
- Camargo, J.M.F., D.A. Grimaldi, and S.R.M. Pedro. 2000. The extinct fauna of stingless bees (Hymenoptera: Apidae: Meliponini) in Dominican amber: two new species and redescription of the male of *Proplebeia dominicana* (Wille and Chandler). *American Museum Novitates* 3293: 1–24.
- Cockerell, T.D.A. 1897. Life-zones in New Mexico. Agricultural Experiment Station, New Mexico College of Agriculture, Bulletin 24: 1–44.
- Cockerell, T.D.A. 1908. Notes on the bee-genus *Exaerete*. *Psyche* 15 (2): 41–42.
- Cockerell, T.D.A. 1917. Descriptions and records of bees – LXXVII. *Annals and Magazine of Natural History (Series 8)* 20 (118): 298–304.
- Cresson, E.T. 1865. On the Hymenoptera of Cuba. *Proceedings of the Entomological Society of Philadelphia* 4: 1–200.
- Donnelly, T.W. 1988. Geologic constraints on Caribbean biogeography. In J.K. Liebherr (editor), *Zoogeography of Caribbean Insects*: 15–37. Ithaca, NY: Cornell University Press, ix + [i] + 285 pp.
- Eickwort, G.C. 1988. Distribution patterns and biology of West Indian sweat bees (Hymenoptera: Halictidae). In J.K. Liebherr (editor), *Zoogeography of Caribbean Insects*: 231–253. Ithaca: Cornell University Press, ix + [i] + 285 pp.
- Engel, M.S. 1995. *Neocorynura electra*, a new fossil bee species from Dominican amber (Hymenoptera: Halictidae). *Journal of the New York Entomological Society* 103 (3): 317–323.

- Engel, M.S. 1996. New augochlorine bees (Hymenoptera: Halictidae) in Dominican amber, with a brief review of fossil Halictidae. *Journal of the Kansas Entomological Society, Supplement* 69 (4): 334–345.
- Engel, M.S. 1997. A new fossil bee from the Oligo-Miocene Dominican amber (Hymenoptera: Halictidae). *Apidologie* 28 (2): 97–102.
- Engel, M.S. 1999a. The first fossil *Euglossa* and phylogeny of the orchid bees (Hymenoptera: Apidae; Euglossini). *American Museum Novitates* 3272: 1–14.
- Engel, M.S. 1999b. *Megachile glaesaria*, the first megachilid bee fossil from amber (Hymenoptera: Megachilidae). *American Museum Novitates* 3276: 1–13.
- Engel, M.S. 1999c. A new xeromelissine bee in Tertiary amber of the Dominican Republic (Hymenoptera: Colletidae). *Entomologica Scandinavica* 30 (4): 453–458.
- Engel, M.S. 2000. Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). *Bulletin of the American Museum of Natural History* 250: 1–89.
- Engel, M.S. 2001. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.
- Engel, M.S. 2002. Halictine bees from the Eocene-Oligocene boundary of Florissant, Colorado (Hymenoptera: Halictidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 225 (2): 251–273.
- Engel, M.S. 2004. Geological history of the bees (Hymenoptera: Apoidea). *Revista de Tecnologia e Ambiente* 10 (2): 9–33.
- Engel, M.S. 2005. Family-group names for bees (Hymenoptera: Apoidea). *American Museum Novitates* 3476: 1–33.
- Engel, M.S. 2009. Two new halictine bees in Miocene amber from the Dominican Republic (Hymenoptera, Halictidae). *ZooKeys* 29: 1–12.
- Engel, M.S. 2011. Systematic melittology: where to from here? *Systematic Entomology* 36 (1): 2–15.
- Engel, M.S., and M.G. Rightmyer. 2000. A new augochlorine bee species in Tertiary amber from the Dominican Republic (Hymenoptera: Halictidae). *Apidologie* 31 (3): 431–436.
- Franz, N.M., and M.S. Engel. 2010. Can higher-level phylogenies of weevils explain their evolutionary success? A critical review. *Systematic Entomology* 35 (4): 597–606.
- Genaro, J.A. 2007. Las abejas (Hymenoptera: Apoidea: Anthophila) de la Hispaniola, Antillas. *Boletín de la Sociedad Entomológica Aragonesa* 40: 247–254.
- Genaro, J.A. 2008. Origins, composition and distribution of the bees of Cuba (Hymenoptera: Apoidea: Anthophila). *Insecta Mundi* 52: 1–16.
- Genaro, J.A., and N.M. Franz. 2008. The bees of greater Puerto Rico (Hymenoptera: Apoidea: Anthophila). *Insecta Mundi* 44: 1–24.
- Gonzalez, V.H. 2008. Phylogeny and classification of the bee tribe Megachilini (Hymenoptera: Apoidea, Megachilidae), with emphasis on the Genus *Megachile*. Ph.D. dissertation, University of Kansas, Lawrence, 274 pp.
- González-Vaquero, R., and A. Roig-Alsina. 2005. Revisión de las especies sudamericanas de *Anthophorula* Cockerell (Hymenoptera, Apidae, Exomalopsini). *Revista del Museo Argentino de Ciencias Naturales* 7 (1): 67–76.
- Greco, M.K., et al. 2011. Description of an ancient social bee trapped in amber using diagnostic radio-entomology. *Insectes Sociaux* 58 (4): 487–494.
- Grimaldi, D., and M.S. Engel. 2005. *Evolution of the insects*. Cambridge: Cambridge University Press, xv + 755 pp.
- Iturralde-Vinent, M.A., and R.D.E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* 238: 1–95.

- Latreille, P.A. 1802. Histoire naturelle des fourmis, et recueil de memoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes. Paris: Crapelet, xvi + 445 pp.
- Michener, C.D. 1982. A new interpretation of fossil social bees from the Dominican Republic. *Sociobiology* 7 (1): 37–45.
- Michener, C.D. 2007. The bees of the world. 2nd ed. Baltimore: Johns Hopkins University Press, xvi + [i] + 953 pp., +20 pls.
- Michener, C.D., and J.S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). *Bulletin of the American Museum of Natural History* 112 (5): 395–451.
- Michener, C.D., and G.O. Poinar, Jr. 1996. The known bee fauna of the Dominican amber. *Journal of the Kansas Entomological Society, Supplement* 69 (4): 353–361.
- Michez, D., M. Vanderplanck, and M.S. Engel. 2012. Fossil bees and their plant associates. In S. Patiny (editor), *Evolution of plant-pollinator relationships*: 103–164. Cambridge: Cambridge University Press, xv + 477 pp.
- Ohl, M., and M.S. Engel. 2007. Die Fossilgeschichte der Bienen und ihrer nächsten Verwandten (Hymenoptera: Apoidea). *Denisia* 20: 687–700.
- Poinar, G.O., Jr. 1998. *Paleoeglossa melissiflora* gen. n. sp. n. (Euglossinae: Apidae), fossil orchid bees in Dominican amber. *Journal of the Kansas Entomological Society* 71 (1): 29–34.
- Robertson, C. 1918. Some genera of bees (Hym.). *Entomological News* 29: 91–92.
- Roig-Alsina, A. 1992. La presencia de *Chilimalopsis* Toro en la Argentina y descripción de una nueva especie (Hymenoptera, Anthophoridae). *Neotrópica* 38: 149–153.
- Rozen, J.G., Jr. 1996. A new species of the bee *Heterosarus* from Dominican amber (Hymenoptera: Andrenidae; Panurginae). *Journal of the Kansas Entomological Society, Supplement* 69 (4): 346–352.
- Schrottky, C. 1910. Berichtigung (Hym.). *Deutsche Entomologische Zeitschrift* 1910: 540.
- Silveira, F.A. 1995. Phylogenetic relationships and classification of Exomalopsini with a new tribe Teraognathini (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* 55 (12): 425–454.
- Silveira, F.A. 2007. Exomalopsini Michener, 1944 [sic]. In J.S. Moure, D. Urban, and G.A.R. Melo (editors), *Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region*: 255–267. Curitiba: Sociedade Brasileira de Entomologia, xiv + 1058 pp.
- Silveira, F.A., and E.A.B. Almeida. 2008. Revision of the species of the subgenera of *Exomalopsis* Spinola, 1853 occurring in South America. II – *Phanomalopsis* Michener & Moure, 1957 (Hymenoptera, Apidae). *Lundiana* 9 (2): 111–153.
- Smith, F. 1853. Catalogue of the hymenopterous insects in the collection of the British Museum. Part 1. Andrenidae and Apidae. London: British Museum, [i] + 1–198 pp., pls. i–vi.
- Smith, F. 1865. Descriptions of some new species of hymenopterous insects belonging to the families Thynnidae, Masaridae and Apidae. *Transactions of the Royal Entomological Society of London (Series 3)* 2 (5): 389–399, + pl. 21.
- Smith, F. 1879. Descriptions of new species of Hymenoptera in the collection of the British Museum. London: British Museum, xxi + 240 pp.
- Spinola, M. 1851. Hymenópteros. In C. Gay (editor), *Historia física y política de Chile, Zoología*: 6: 153–569. Paris: Casa del autor, 572 pp.
- Spinola, M. 1853. Compte rendu des hyménoptères inédits provenant du voyage entomologique de M. Ghiliani dans le Para en 1846. *Memorie della Reale Accademia delle Scienze di Torino* (2) 13: 19–94.
- Timberlake, P.H. 1980. Review of North American *Exomalopsis* (Hymenoptera, Anthophoridae). *University of California Publications in Entomology* 86: [v–vi], 1–158.

- Vachal, J. 1909. Espèces nouvelles ou litigieuses d'Apidae du haut bassin du Parana et de régions contiguës et délimitation d'une nouvelle sous-famille Diphaglossinae. *Revue d'Entomologie* [Caen] 28: 5–72.
- Wille, A., and L.C. Chandler. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera; Meliponini). *Revista de Biología Tropical* 12 (2): 187–195.

Complete lists of all issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from <http://www.amnhshop.com> or via standard mail from:

American Museum of Natural History—Scientific Publications  
Central Park West at 79th Street  
New York, NY 10024

Ⓒ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).