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

Published By: American Museum of Natural History

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

AMERICAN MUSEUM NOVITATES

Number 3758, 16 pp. September 14, 2012

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

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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 *Thaumatosoma* (*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-

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ISSN 0003-0082

lissine, halictine, panurgine, megachiline, euglossine, and further meliponine bees documented (table 1).[5] 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

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[5] 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[1] Latreille
      Genus *Thaumatosoma* Smith, 1865
        Subgenus †*Chalicodomopsis* Engel, 1999b
          †*Thaumatosoma* (*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*[2] 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

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[1] The generic classification of Megachilini adopted here follows the multigeneric system proposed by Gonzalez (2008).

[2] 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 *Chilimalopsis* Toro	2	SA
Genus *Teratognatha* Ogloblin	1	SA
Subtribe Exomalopsina Vachal		
Genus *Anthophorula* Cockerell		
Subgenus *Anthophorisca* Michener and Moure	30	NA
Subgenus *Anthophorula* Cockerell	29	NA
Subgenus *Isomalopsis* Michener and Moure	4	SA
Genus *Eremapis* Ogloblin	1	SA
Genus *Exomalopsis* Spinola		
Subgenus *Diomalopsis* Michener and Moure	2	SA
Subgenus *Exomalopsis* Spinola	55	CA*, SA
Subgenus *Phanomalopsis* Michener and Moure	15	NA, CA, SA
Subgenus *Stilbomalopsis* 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

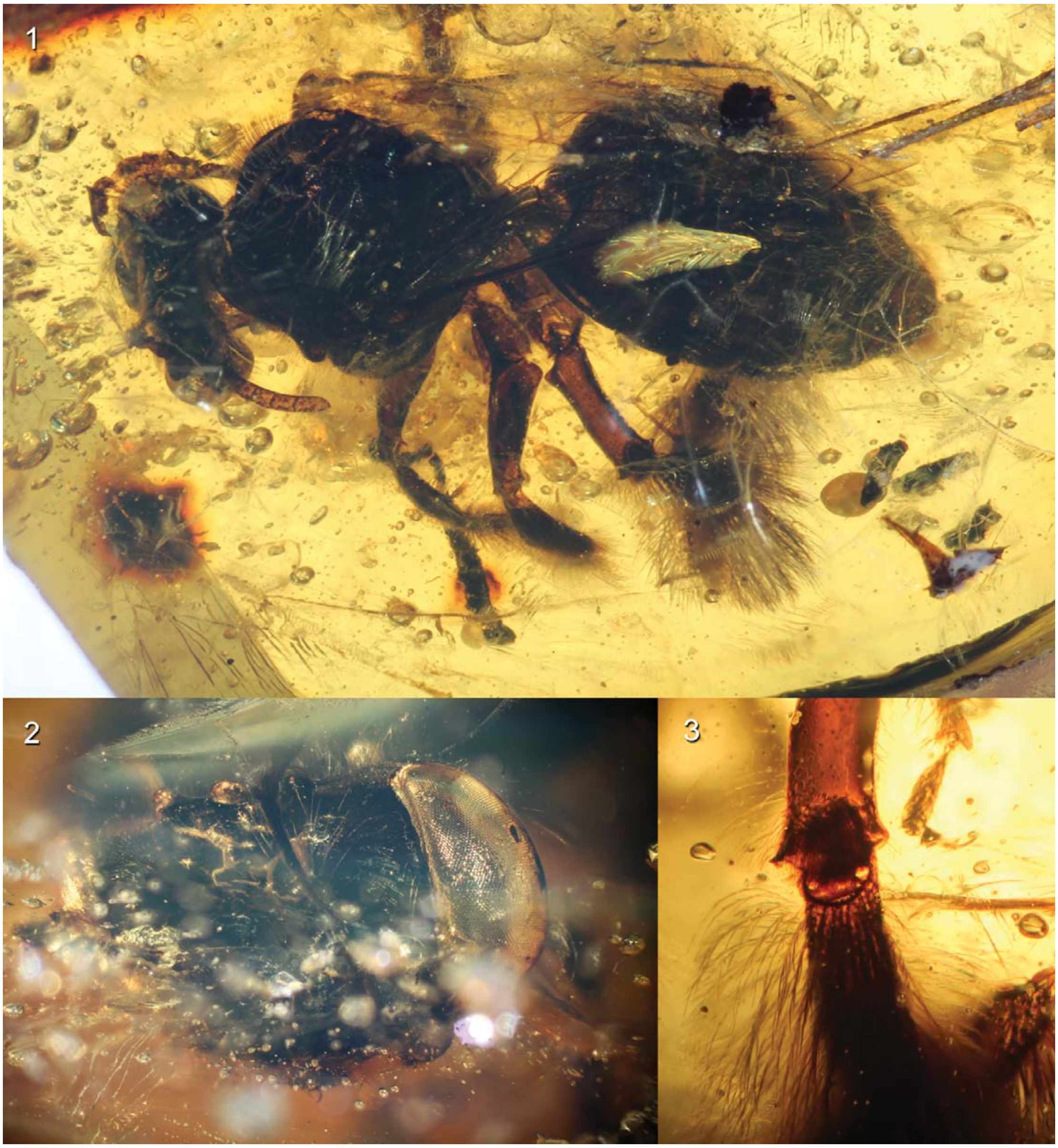
Anthophorula (*Anthophorula*) ***persephone*** Engel, new species

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. Intertegular 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),

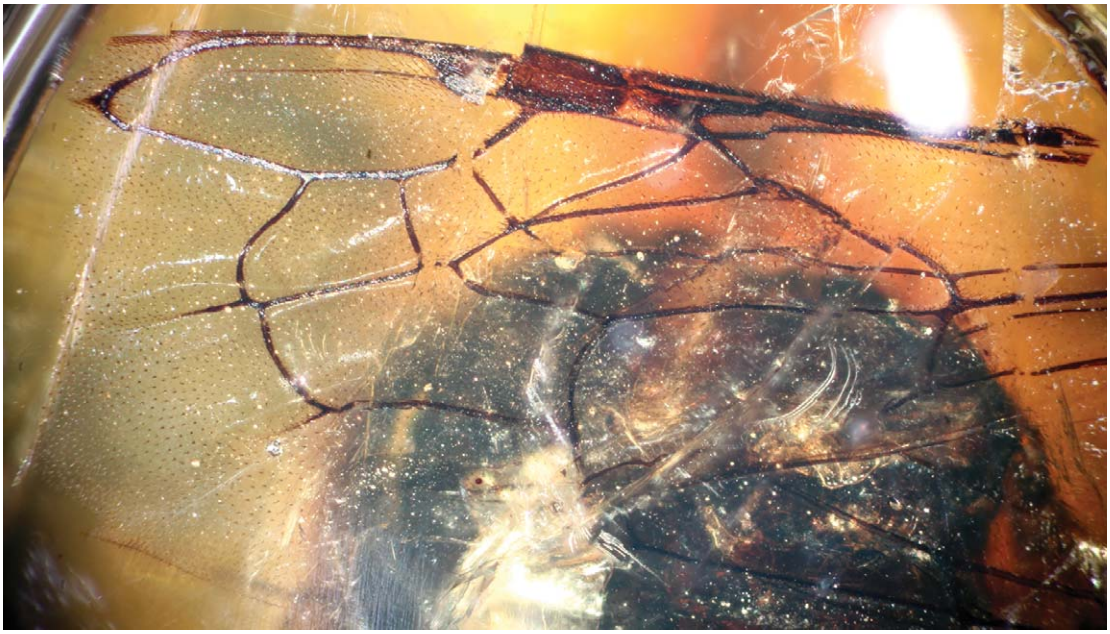


FIGURE 4. Apical forewing venation of fragmentary female of *Anthophorula* (*Anthophorula*) *persephone* Engel, new species (AMNH DR-KL1); note that fracturing in wing as preserved distorts some proportions (holotype is preserved completely [fig. 1], but detailed images of the venation appear dark and 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
E. analis Spinola, 1853	Hispaniola, Puerto Rico throughout SA
E. bahamica Timberlake, 1980	Bahamas, Cuba, Hispaniola, Puerto Rico
E. bartschi Timberlake, 1980	Guadeloupe
E. nr. *bahamica*	Puerto Rico
E. pubescens Cresson, 1865	Grenada, Grenadines, St. Kitts, St. Vincent, Trinidad, U.S. Virgin Islands (St. Croix)
E. pulchella Cresson, 1865	Bahamas, Costa Rica, Cuba, Jamaica, Mexico, Guatemala, Puerto Rico, US (Florida), U.S. Virgin Islands (St. Thomas)
E. rufitarsis Smith, 1879	Jamaica
E. similis 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)
E. vincentana 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)**		
			Colletidae		
Diphaglossinae					
	Caupolicanini				
		Caupolicana (*Alayoapis*)			
Hylaeinae					
		Hylaeus (*Prosopis*, *Hylaeana*)			
			Xeromelissinae		
					Chilicola (*Hylaeosoma*)
			Andrenidae		
Panurginae			Panurginae		
	Perditini				
		Perdita (*Perdita*)			
	Protandrenini			Protandrenini	
		Heterosarus			*Heterosarus*
			Halictidae		
Halictinae			Halictinae		
	Halictini				
		Halictus (*Odontalictus*)			
		Lasioglossum (*Dialictus*)			

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

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

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.

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