Origins, composition and distribution of the bees of Cuba (Hymenoptera: Apoidea: Anthophila)

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Date of Issue: December 5, 2008
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Insecta Mundi 0052: 1-16

Published in 2008 by
Center for Systematic Entomology, Inc.
P. O. Box 141874
Gainesville, FL 32614-1874 U. S. A.
http://www.centerforsystematicentomology.org/

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As of 2007, Insecta Mundi is published irregularly throughout the year, not as quarterly issues. As manuscripts are completed they are published and given an individual number. Manuscripts must be peer reviewed prior to submission, after which they are again reviewed by the editorial board to insure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

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Printed Copy ISSN 0749-6737
On-Line ISSN 1942-1354
CD-ROM ISSN 1942-1362
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Abstract. The origins of the Cuban bee fauna are reviewed. This fauna began to form 40 million years ago during the Proto Antilles period, through ancestors that arrived in successive invasions from adjacent continental areas. The composition of the Antillean fauna has evolved continuously over millions of years until the present time. The native bee fauna of Cuba is represented by 89 species, contained in 29 genera and 4 families. The number of genera represented per family is as follows: Colletidae (3), Halictidae (8), Megachilidae (4), and Apidae (14). The Cuban apifauna contains four principal groups with distinct biogeographic histories: endemic species of Cuba (43.8%); endemic species of the Antilles shared among multiple islands (33.1%); continental species whose distribution includes the Antilles (16.8%); and species introduced through human activity (6.3%). An analysis of the distributions of Cuban bee species reveals that areas of highest species endemism coincide with the main mountainous nuclei of the East, Center and West. These were: the Sierra Maestra mountain range (with 25 species), Nipe-Sagua-Baracoa (15), the Mountain range of Guaniguanico (14) and the Massif of Guamuaya (14). The distribution of the bees in the Cuban Archipelago was not uniform, possibly due to the ecological conditions of the respective habitats, the diversity and presence of specific food plants, and interspecific competition. The endemism of bees in Greater Antilles is considered high keeping in mind the mobility of the group, as observed not only in Cuba (43.8%) but also Jamaica (50%), Hispaniola (45.6%), and in Puerto Rico and adjacent islands (26.5%).

Key words. Hymenoptera, Apoidea, Anthophila, bees, origins, taxonomic composition, distribution, Cuba.

Introduction

Bees are among the world’s dominant pollinators and interact with most species of angiosperms (Michener 2000, Stubbs and Drummond 2001). Bee conservation is therefore vital for the functioning of plant communities. Recent studies have pointed out that bee population declines and extirpations have occurred in many parts of the world (Buchmann and Ascher 2005, Larsson and Franzén 2007), resulting in what has become known as the pollination crisis (Buchmann and Nabhan 1995, Zayed et al. 2004, Vamosi et al. 2006). In this paper I discuss the origin, taxonomic composition and patterns of distribution of the Cuban bee fauna.
The present taxonomic knowledge of Cuban bees is adequate mainly because of the collecting efforts of the Cuban entomologist Pastor Alayo who sent material for identification to Charles D. Michener and George Eickwort. This allowed him to publish two comprehensive catalogs (Alayo 1973, 1976). Nevertheless, updates regarding the systematic positions of many Cuban bees are necessary because of recent taxonomic changes. Genaro (2006, 2007) published accounts of the history of systematic studies on Cuban bees and Hispaniolan bees including records from Cuba.

Very little is known about the distribution of bees from the Cuban archipelago. Some authors have written about the biogeographical aspects of Antillean bees, including Cuban species, viz. Michener (1979), Roberts (1972), and Janjic and Packer (2003). Eickwort’s (1988) study on the distribution patterns of West Indian sweat bees remains the most comprehensive analysis of this topic for the Caribbean region even though it included only halictids. A synthetic study of the biogeography of the extant bee fauna of the Caribbean area is lacking from a historical, ecological or cladistic perspective. On the other hand, the origins of the amber fossil bee fauna of the Dominican Republic have been treated in many publications (Engel 1995, 1997, 1999, 2000, 2001; Michener and Poinar 1997, Camargo et al. 2000).

Materials and Methods

Specimens studied for this work came from several sources; including personal collections, donations by colleagues, or depositions in institutional collections. The following institutional collections were visited: CANADA: York University (YU), Toronto; The Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa. UNITED STATES: Academy of Natural Sciences of Philadelphia; American Museum of Natural History, New York; Florida State Collection of Arthropods, Gainesville; United States National Museum, Washington; the University of Kansas Natural History Museum and Biodiversity Research Center; Museum of Comparative Zoology, Harvard University, Cambridge. CUBA: Museo Nacional de Historia Natural de Cuba, Ciudad de La Habana; Instituto de Ecología y Sistemática; Charles Ramsden Museum, University of Oriente; Tomás Romay Museum, Santiago de Cuba; Fernando de Zayas private collection; Faculty of Biology, University of Havana. DOMINICAN REPUBLIC: Museo Nacional de Historia Natural de Santo Domingo; collection E. de Jesús Marcano at Instituto de Investigación Zoológica y Botánica Rafael M. Moscoso, Universidad Autónoma de Santo Domingo. PUERTO RICO: Museo de Entomología y Biodiversidad Tropical of the Agricultural Experiment Station, and University of Puerto Rico at, Mayagüez, Mayagüez, Puerto Rico (UPRM).

The taxonomic arrangement is in accordance with Michener (2000). Personal communications with the following specialists have validated the distributions of many taxa: R. Snelling (Centris Fabricius, Hylaeus Fabricius); M. Engel (Halictidae); J. Asher (several families); T. Griswold (Megachilidae); C. D. Michener (several families); D. Urban (Melissopitla Holmberg); F. Silveira (Exomalopsis Spinola).


The following papers also treated the distributions of specific Cuban bee taxa: Colletes Latreille (Stephen 1954, Genaro 2003), Caupolicana Spinola (Michener 1966), Agapostemon Guérin-Méneville (Roberts 1972, Janjic and Packer 2003), Lithurgus Berthold (Michener 1988b), Nomia Latreille (Cockerell 1910, Cross 1958), Halictidae (Moure and Hurd 1987), Nesosphecodes Engel (Engel 2006a), Sphedodes Latreille (Engel 2006b), Megachile Latreille (Mitchell 1930, Raw 2007), Megachile group Chalicodoma Lepeletier (Snelling 1990, Genaro 1997), Euglossines (Moure 1967), Melissodes Latreille (LaBerge 1956, 1961), Anthophora Latreille (Brooks 1988, 1999), Florilegus Robertson (Urban 1970), Nomada Scopoli (Alexander and Schwarz...
The islands of the Greater Antilles, as habitats with conditions to support terrestrial life, are not older than the Middle Eocene (~40 mya) (Iturralde-Vinent and MacPhee 1999, MacPhee and Iturralde-Vinent 2000, Iturralde-Vinent 2005, 2006). From the Eocene-Oligocene transition (35-33 mya) to the Middle Miocene (16-14 mya) the emerged land within the Caribbean basin may have been extensive. According to Iturralde-Vinent and MacPhee (1999) and MacPhee et al. (2003) a subaerial connection (whether continuous or punctuated by water gaps) called GAARlandia (Greater Antilles Ridge+Aves Ridge), connected northwestern South America with larger landmasses emergent on these ridges [the presence was brief,
~1 my (MacPhee et al. 2003)]. Also the area of the Nicaraguan rise had emerged (and shallow marine) lands penetrating close to the Proto-Antilles. There were favorable conditions to allow many species of bees to colonize the Proto-Antilles (Fig. 2).

It was probably during this proposed time of larger land connections and closer proximity to continental areas (Fig. 2) that the highest number of social species crossed over the emerged lands to reach the Proto-Antilles (as seen from records of Dominican amber). It is known that social species are poor dispersers across the sea. Thereafter, Caribbean neotectonism resulted in the subdivision of existing land areas and the subsidence of others (Iturralde-Vinent and MacPhee 1999). But never was it as extensive as before and no subsequent land connections existed with the continents.

Many species may have become extinct mainly due to climatic changes and geographic configuration changes (insularization) that have isolated the Proto-Antilles from the continental landmasses. After that, it was more difficult for social species to reach the Antilles. For that reason social species of bees are few in the present fauna.

Antilles bees have been adapting to changing geological and climatological conditions. It was the late Quaternary climatological changes (mean temperature and humidity, rainfall and variations in mean sea level) (Curtis et al. 2001, Iturralde-Vinent 2003) that most affected the islands and likely also the bee fauna (Engel 2004).

Later, other groups of bees may have dispersed and occupied the areas and niches left by the species exterminated mainly by climatic change, as evidenced by the amber fossil record of the Dominican Republic. Amber deposits (resin-produced by the tree Hymenaea protera Poinar, Leguminosae) contain insect fossils of high quality where many bees were preserved (Poinar and Poinar 1999, Grimaldi and Engel 2005). Unfortunately there is no bee fossil record from Cuba. Because of their similar geological history (Iturralde-Vinent and MacPhee 1999), we can extrapolate from that known for Hispaniola to envision that living elsewhere in the Antilles at that time.

The Dominican fossil bee fauna includes 10 genera with 17 species in five families (Engel 2001), indicating that there were significant extinctions. The amber is estimated to be 15-20 million years of age. The main amberiferous deposits in Hispaniola were formed in a single sedimentary basin during the late
Early Miocene through early Middle Miocene (Iturralde-Vinent and MacPhee 1996; Iturralde-Vinent 2001). Knowledge of the bee fauna in amber from the of Dominican Republic is biased because we only know species collected in tree resins or whose behavior let them be associated with resin, enhancing the chances for them to come into contact with the resin (Engel 1995, 1997).

Studies of the amber bees, ants, and wasps suggest that the faunal representation is very similar to today’s Neotropical fauna and assignable to modern genera or to extinct ones closely related to present day ones (Wilson 1985, 1988; Manley and Poinar 1991, 1999; Prentice and Poinar 1993; Engel 1995, 1997, 1999, 2000, 2001; Darling 1996; Michener and Poinar 1997; Andrade 1998, 2003; Poinar and Poinar 1999). The Antillean fauna of bees found in amber is young (Engel 2001), having modern aspects compared to the fauna of Baltic amber (Michener and Poinar 1997, Engel 2001). The following genera of bees are not known in the present fauna: *Oligochlora* Engel, *Eickwortapis* Michener and Poinar, and *Proplebeia* Michener but they are related to present-day genera.

### Table 1. Taxonomic composition of the Cuban fauna of bees (* genera with introduced species; number of introduced species in brackets)

<table>
<thead>
<tr>
<th>Family</th>
<th>Genera</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colletidae</td>
<td><em>Colletes</em> Latreille, 1802</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><em>Caupolicana</em> Spinola, 1851</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Hylaeus</em> Fabricius, 1793</td>
<td>6</td>
</tr>
<tr>
<td>Halictidae</td>
<td><em>Halictus</em> Latreille, 1804</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Lasiglossum</em> Curtis, 1833</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td><em>Sphecodes</em> Latreille, 1804</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><em>Nesosphecodes</em> Engel, 2006</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Temnosoma</em> Smith, 1853</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Agapostemon</em> Guérin Ménéville, 1844</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><em>Augochlora</em> Smith, 1853</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td><em>Nomia</em> Latreille, 1804</td>
<td>1</td>
</tr>
<tr>
<td>Megachilidae</td>
<td><em>Lithurgus</em> Berthold, 1827</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Heriades</em> Spinola, 1808</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Megachile</em> Latreille, 1802</td>
<td>10 (4)</td>
</tr>
<tr>
<td></td>
<td><em>Coelioxys</em> Latreille, 1809</td>
<td>6</td>
</tr>
<tr>
<td>Apidae</td>
<td><em>Exomalopsis</em> Spinola, 1853</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><em>Nomada</em> Scopoli, 1770</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>Epeolus</em> Latreille, 1802</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Tripeolus</em> Robertson, 1901</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>Melissodes</em> Latreille, 1829</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>Florilegus</em> Robertson, 1900</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Melissopita</em> Holmberg, 1884</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Anthophora</em> Latreille, 1803</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Centris</em> Fabricius, 1804</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td><em>Xeromelecta</em> Linsley, 1939</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Mesocheira</em> Lepeletier &amp; Serville, 1825</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Mesopia</em> Lepeletier, 1841</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Ceratina</em> Latreille, 1802</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Xylocopa</em> Latreille, 1802</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Melipona</em> Illiger, 1806</td>
<td>(1)</td>
</tr>
<tr>
<td></td>
<td><em>Apis</em> Linnaeus, 1758</td>
<td>(1)</td>
</tr>
<tr>
<td><strong>Total:</strong></td>
<td><strong>4</strong></td>
<td><strong>31 (2)</strong></td>
</tr>
</tbody>
</table>

**Note:** The number in brackets indicates the number of introduced species.
Genera or species of spiders, butterflies, ants, wasps and bees have become extinct and were substituted by others in later colonizations (Wilson 1985, 1988; Carpenter and Grimaldi 1997; Michener and Poinar 1997; Engel 1995, 1999, 2000; Penney and Pérez-Gelabert 2002; Jason et al. 2004; Penney 2005; Peñalver and Grimaldi 2006).

During the history of Antilles colonization, bees arrived by flight crossing stepping-stone islands or land bridges that connected them, as is true for mammals. According to the GAARlandia geographic scenario there were corridors for faunal movement along the Arc. Rafting, strong winds or hurricanes must have been played a role in dispersion as well. After dispersing from the continent and colonizing habitats with suitable conditions for life, the processes of within-island vicariance likely aided evolution of the biota.

Dispersal (both continent to islands and island to island) is a phenomenon always possible, even today. Cuba and Florida never were connected (Donnelly 1988, Iturralde-Vinent and MacPhee 1999); nevertheless Cuba has elements of the Nearctic bee fauna such as *Nomia*, some *Lasioglossum* spp. and *Hylaeus* spp.

A South American origin has been postulated for augochlorines in amber (Engel 1995, 2000), and a Central American one for orchid bees (Engel 1999) and stingless bees (Camargo et al. 2000). Janjic and Packer (2003) suggested a Central American origin for *Agapostemon*, with one invasion of North America and multiple invasions of South America and the Caribbean.

**Faunal composition**

The insular bee fauna of Cuba is well studied (Cresson 1865, Gundlach 1886, Alayo 1973, 1976), with more than 90 recorded species (Table 1). New species are expected mainly in the genera *Hylaeus*, *Lasioglossum*, *Ceratina*, *Sphecodes* s.l., or new records of species known from other islands such as Bahamas, Jamaica, or Hispaniola.

*Centris (Centris) decolorata* Lepeletier has not been collected in Cuba in spite of its presence along coastal sand dunes of Jamaica, Hispaniola, and all Caribbean Islands as well as northern South America and the Caribbean coast of Central America north to Texas (R. R. Snelling, personal communication 1999).

**Introduced bees**

Six species (6.3% of the bees) were introduced directly or indirectly by man. Of these, *Apis mellifera* L. and *Melipona beecheii* Bennett have been manipulated genetically and ecologically, since they are used in

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**Figure 3.** Areas of endemism of Cuban bees. The numbers of endemic species are indicated inside the area.
the production of honey and to a lesser extent, for pollination. *Apis m. mellifera* (German or black race) was introduced to Cuba in 1768 from hives from Florida in order to obtain wax, which was an important product at that time (Díaz 1985a). In 1904 the Italian race (*A. mellifera ligustica* Spinola) was introduced and both were crossbred. Other races have been introduced in more recent times, among them Caucasian honeybees (*A. mellifera caucasica* Pollmann) and Carniolan honeybees (*A. mellifera carnica* Pollmann). With the increase of beekeeping many bees escaped to natural areas and crossbred so that *A. mellifera* became a common element of the fauna (Díaz 1985b). According to Díaz (1985a) in 1902 there were 82 thousand hives, growing to 215 thousand in 1946, with 33% of them in the eastern provinces (Holguín, Santiago de Cuba and Guantánamo, where Cuban biodiversity is higher). Beekeeping has spread and can now be found throughout Cuba. To date, the Africanized honeybee (*A. mellifera scutellata* Lepeletier) has not arrived in Cuba.

It is not clear if *Melipona beecheii* was introduced into the Antilles by pre-Columbian man, or by Spanish colonists, or if it dispersed naturally from original areas of Central America. Michener (1979; personal communication, 1996) speculated that (1) transport by whatever means must have been recent since Antillean (Jamaica and Cuba) and Central American populations belong to the same species; (2) if *Melipona* arrived in a floating tree trunk, then one would expect other more common meliponines to arrive in the same way, but they have not. It may be significant that the species in the Greater Antilles is, among all Meliponinae, the one most used (the principal honey source of native peoples, certainly in the Yucatan, was hives of *Melipona*) and given sacred status by pre-Columbian peoples of the Yucatan and probably Central America. Therefore, native people might well have carried it if they traveled to Cuba or Jamaica from continental areas. (3) Because of their mode of establishing new colonies, meliponine bees are extremely poor at crossing water barriers (Michener 1979, Camargo et al. 1988). This is supported by their abundance around the continental shores of the Caribbean; yet only one species of *Melipona* has reached the Greater Antilles. Camargo et al. (1988) agree with Michener’s scenario.

I was unable to find references of pre-Columbian people as beekeepers in Cuba. However, when the Spanish settled in Cuba to establish supply headquarters for the conquest of Mexico, this might have been the appropriate moment for the possible introduction of *M. beecheii* due to commercial exchange, supposing that they had not entered the Antilles in a natural way.

Several *Megachile* representing Old World groups were introduced to the Antilles during the slave-trade period (1511-1867). These were *M. rufipennis* (Fabr.), *Megachile lanata* (Fabr.) (although originally an Indian species, it had spread to Africa), *M. concinna* F. Smith and *M. torrida* F. Smith (Eickwort 1970, Krombein et al. 1979, Mitchell 1980). Megachilid bees frequently disperse across long distances because of their habits of constructing nests in stems or crevices of plants or articles of commerce (Eickwort 1970). In Cuba, *M. lanata* is the most ecologically successful species and has occupied a great diversity of habitats whereas the other species were only observed in wooded areas (Genaro 1997). *Megachile rufipennis* and *M. torrida* were more frequently observed in Hispaniola than in Cuba.

### Endemism

Almost half of the fauna, 43.8% of the species, are endemic to the Cuban Archipelago (Appendix 1). All Cuban species of the genera *Caupolicana* (N=2), *Sphecodes* (N=3), *Nesosphecodes* (N=1), *Epeolus* (N=1) and *Xeromelecta* (N=1) are endemic; *Melissodes* has 75%, *Colletes* and *Coelioxys* 66.7%, and *Nomada* 50% endemics.

The most significant endemics at a higher taxonomic level are: the genus *Nesosphecodes* with one endemic species on each island (Cuba, Hispaniola and Puerto Rico) (Engel 2006a); the subgenus *Alayoapis* of the genus *Caupolicana* (found in Cuba and Hispaniola) (Michener 1966), and the group *Habralictellus* (treated as a genus by some authors) of the genus *Lasioglossum* (occurs only in Antilles although one species *Lasioglossum eleutherensis* Engel now occurs in Florida and possibly arrived via the Bahamas or Cuba).

Higher areas of endemism in the Cuban archipelago occur in the mountainous nuclei of Eastern, Central and Western Cuba. The Sierra Maestra mountain range has the highest number of endemic species, with 25 (Fig. 3). These mountain areas also have a high endemism for other animal groups (Alayón and Platnick 1993, Rodríguez 1993, Fontenla 1995, Fernández-Triana 2005). Areas around Habana
Figure 4. Dendrogram reflecting the clustering between bee species and biogeographic areas of the Cuban archipelago. Additional detail maps show areas according the groups and subgroups formed.
city and Santiago de Cuba (the biggest cities) have a high number of endemic species perhaps because of the greater number of entomologist living there resulting in increased inventory activities.

An analysis of the endemic bees in the Antilles shows that Jamaica, Hispaniola and Cuba have the highest ratios of endemism with 50.0%, 45.6% and 43.8%, respectively. Puerto Rico and adjacent islands have 26.5% and Bahamas 23.7% endemism. These values are considered high in light of the high dispersal powers of these bees. It is interesting to highlight the fact that Isla de La Juventud does not have endemics (Genaro 2004). Ecological conditions (great habitat diversity and altitudinal variation) in Hispaniola, Jamaica and Cuba favor evolutionary processes that lead to speciation. On the other hand, societal expansion and agriculture present threats to bee habitats and led to a loss of bee diversity.

Distribution in the Cuban archipelago

Integrating the bee species distributions into a cluster analysis yielded two main groups of areas (A and B), which were also supported by the formation of additional subgroups (Fig. 4).

Group A is characterized by areas of highest endemism (Fig. 4). Except for the area North of Havana city, La Habana and Matanzas (A5), the other areas correspond to mountainous regions with montane forest habitats isolated by a complex topography. This area includes the Sierra Maestra mountain range (A24), the Nipe-Sagua-Baracoa Mountains (A26) and the Guaniguanico Mountain range (A3), although A5 include some highland areas as well. The Sierra Maestra, with the largest number of endemics (Fig. 3), formed a subgroup on its own.

Group B was more diverse and it includes the remaining areas (Fig. 4). It is form by a diverse subgroup (B1), and B2 with single area (A25). B1 is form by two subgroups (C and D). Subgroup C is constitute by a and b subgroups where a represent low elevation areas, with generally alter and cultivate areas (A1, A13), and b include some heights and areas better preserve, with more forests as Massif of Guamuaya (A14).

Subgroup D is form by two subgroups a and b. In the first one, a1 contain the largest number of areas, characterize by contiguous low elevation regions and four archipelagos (that contain the poorest known bee fauna) that surround the island of Cuba. The subgroup a2 is made up exclusively by the area South of Guantánamo (A27). This place is very xerophytic and presents ecological elements with distinguishing characteristics that have favor the occurrence of bees like Lithurgus antilleorum, living only in these coasts. The subgroup a3 includes the fauna of bees of the Isla de La Juventud (A10), with two localities of the Island of Cuba (A7 and A16), demonstrating that the little island does not possess its own fauna since it lacks local endemics. The second subgroup of D, denominate b only include Zapata swamp (A9), the biggest wetland in Cuba, with very particular ecological conditions, is not suitable for the successful establishment and persistence of many ground nesting bees species because of the humidity affecting their nest cells.

In the B2 group, A25 correspond to the flat lands around the Santiago de Cuba bay. In this area there are two local endemic species: Tripeolus cuabitensis Genaro and Coelioxys alayoi Genaro, and species of limited distribution in Cuba such as Lithurgus antilleorum Michener, Megachile armaticeps Cresson, Melissopilia micheneri Genaro, Anthophora hilaris F. Smith and Centris aethiops Cresson.

Bees do not show a uniform distribution across the Cuban archipelago. The species of wider distribution include Xylocopa cubaecola Lucas, frequently appearing in habitats ranging from well-conserved mountain habitats to city gardens. Other species are only known from local areas. For example, the highest diversity of species of the genus Lasio glossum, group Habralictellus, is in the Sierra Maestra and Nipe-Sagua-Baracoa mountainous regions. Lithurgus antilleorum occur only in the xerotic habitats of the South coast of Santiago de Cuba and Guanitamo; Tripeolus cuabitensis is restrict to the north of Santiago de Cuba city and Colletes granpiedrensis and Centris cornuta Cresson inhabit the mountainous areas of the Sierra Maestra and Nipe-Sagua-Baracoa.

A diverse fauna of bees inhabits the higher regions, including species of Centris, Lasio glossum, Nesospecodes, Epeolus, Tripeolus, Caupolicana, Megachile, Coelioxys, Melissopila, Xeromelecta and Sphecodes. Another group of species appears in the low areas, such as valleys and savannas (frequently disturbed). This apifauna is characterized by the presence of Exomalopsis spp; Lasio glossum spp., Halictus poeyi Say, Sphecodes spp., Nomia robinsoni Cresson, Ceratina cyaniventris Cresson, Centris poecila,
Xylocopa cubaecola, Megachile poeyi Guérin-Méneville, Coelioxys rufipes Guérin-Méneville, Nomada cubensis Cresson and N. pilipes (Cresson).

Ecological factors were decisive in the formation of the clusters according to the presence of the species of bees. The limited collections of bees in many areas, mainly in the central region of Cuba, likely affected the present results.

Acknowledgments

Grants from 1994 to 2005 by RARE Center Tropical for Conservation, Philadelphia, American Museum Natural of History (AMNH), United States National Museum (USNM), Natural History Museum, University of Kansas (NHMUK), Florida State Collection of Arthropods (FSCA), Group of Work on Cuba of the ACLS/SSRC, with funds of the Foundations MacArthur and Reynolds, and Canadian National Collection of Insects, Arachnids and Nematodes, Biosystematics Research Institute Ottawa (CNC) allowed me to study collections in several museums of United States, Puerto Rico and Canada. Idea Wild (www.idealwild.org) provided me with equipment such as a microscope and a digital camera that facilitated and improved my work. Víctor González (Puerto Rico Land and Fruit Company) kindly financed the fieldwork (1994-2008) in Puerto Rico, Mona Island and Hispaniola. Grupo Jaragua and specially Ivonne Arias provide support during field trips to Dominican Republic. Among them, thanks to C. Michener, M. Engel, J. Rozen, R. McGinley, R. Snelling and J. Asher (who also shared the information of his data base of the WI bees with me). Thanks to the following curators for the attention they offered me, in their institutions, during my stay for study of collections; loan of specimens and access to bibliographical sources: E. Reyes (IES); E. Portuondo (Centro Oriental de Ecosistemas y Biodiversidad, Santiago de Cuba); C. D. Michener, M. Engel and R. Brooks (NHMUK); R. McGinley and M. Mello (formerly USNM); J. G. Rozen Jr. and E. Quinter (AMNH); S. Cover (Museum of Comparative Zoology, Harvard); J. Wiley, P. Skelley, L. Stange, R. Woodruff and J. Kingsolver (FSCA); L. Masner and J. T. Huber (CNC), the late J. Torres (University of Puerto Rico), R. Franqui (Agricultural Experiment Station, University of Puerto Rico), and K. Guerrero and I. Arias (Grupo Jaragua, Dominican Republic). I appreciate loans of Navassa bees from W. E. Steiner (USNM) and M. A. García (Departamento de Recursos Naturales y Ambientales, Puerto Rico). Cristina Juarrero graciously digitalized figures. Daniel Pérez-Gelabert (USNM) sent to me the bees collected by him during his project in Dominican Republic which allowed me to study fresh material. Preparation of the manuscript was supported by Discovery Grants from the Natural Sciences and Engineering Research Council of Canada to L. Packer, NSERC postdoctoral fellowship (PDF 314411-2005) and from special awards from Stan M. Shapson, the Vice President for Research and Innovation at York University. I thank C. D. Michener for his comments on an early version of the manuscript. Also, I thank L. Packer (YU) and N. Franz (UPRM) for reviewing the manuscript.

Literature cited


Received June 10, 2008; accepted October 17, 2008.
### Appendix 1. Endemic bee species from Cuban Archipelago and areas where they occur. Areas of greater endemism are highlighted.

<table>
<thead>
<tr>
<th>Bee species</th>
<th>Geographic areas (according to Fig. 1)</th>
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<tr>
<td><strong>Colletes granipeculis</strong> Genaro, 2001</td>
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<td><strong>Colletes bijac</strong> Genaro, 2003</td>
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<tr>
<td><strong>Canopicana nigrescens</strong> (Cresson, 1869)</td>
<td>x</td>
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<tr>
<td><strong>Canopicana subaurata</strong> (Cresson, 1869)</td>
<td>x</td>
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<tr>
<td><strong>Hylaena limbifrons</strong> (Cresson, 1869)</td>
<td>x</td>
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<tr>
<td><strong>Hylaena n. sp.</strong></td>
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<tr>
<td><strong>Hylaena near formosa</strong> Krombein</td>
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<tr>
<td><strong>Lasiosomus magdalenus</strong> (Baker, 1906)</td>
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<td><strong>Lasiosomus normalis</strong> (Baker, 1906)</td>
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<td><strong>Lasiosomus adriani</strong> Genaro, 2001</td>
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<td><strong>Lasiosomus engeli</strong> Genaro, 2001</td>
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<td><strong>Lasiosomus sieramacostris</strong> Genaro, 2001</td>
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<td><strong>Lasiosomus n. sp. 1</strong></td>
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<td><strong>Sphexodes genarai</strong> Engel, 2006b</td>
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<td><strong>Sphexodes taiini</strong> Engel, 2006b</td>
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<td><strong>Sphexodes n. sp.</strong></td>
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<td><strong>Nesosphexodes cabiola</strong> Engel, 2006a</td>
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<td><strong>Agapostemon viridulus</strong> (Fabr., 1793)</td>
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<td><strong>Agapostemon calensis</strong> Roberts, 1972</td>
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<td><strong>Megachile singularis</strong> Cresson, 1865</td>
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<td><strong>Megachile armaticeps</strong> Cresson, 1869</td>
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<tr>
<td><strong>Collocey cinctata</strong> (Fabr., 1775)</td>
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<td><strong>Collocey alyoi</strong> Genaro, 2001</td>
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<td><strong>Collocey tegularis</strong> Cresson, 1869</td>
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<td><strong>Collocey zannichenkoi</strong> Genaro, 2001</td>
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<td><strong>Nomada filicita</strong> Cresson, 1865</td>
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<td><strong>Nomada cruralis</strong> Moure, 1960</td>
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<td><strong>Epeolus palchela</strong> Cresson, 1865</td>
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<td><strong>Tribeolus wilsoni</strong> (Cresson, 1865)</td>
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<td><strong>Tribeolus cintastris</strong> Genaro, 1999</td>
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<td><strong>Melissodes calenensis</strong> La Berge, 1956</td>
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<td><strong>Melissodes leprieuri</strong> Blanchard, 1849</td>
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<td><strong>Melissodes pollaens</strong> Cresson, 1865</td>
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<td><strong>Aethlopsora strato</strong> Cresson, 1865</td>
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<tr>
<td><strong>Xeromelecta alempi</strong> Michener, 1988</td>
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| **Ceratina cyaniventris** Cresson, 1865            | x x x x x x x x x x x x x x x x x x