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(Hymenoptera: Apoidea: Anthophila)

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

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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.

Resumen. Se revisan los orígenes de la fauna de abejas de Cuba. Esta fauna comenzó a formarse hace 40 millones de años, durante el periodo de Proto Antillas, a través de los ancestros que arribaron en invasiones sucesivas desde las áreas continentales adyacentes. La composición de la fauna Antillana ha evolucionado continuamente desde hace millones de años hasta el presente. La fauna de abejas nativas de Cuba estuvo representada por 89 especies, contenidas en 29 géneros y cuatro familias. El número de géneros por familias fue como sigue: Colletidae (3), Halictidae (8), Megachilidae (4) y Apidae (14). La apifauna cubana contiene cuatro grupos principales con historias biogeográficas definidas: especies endémicas de Cuba (43.8 %), especies endémicas de las Antillas compartidas por varias islas (33.1 %), especies continentales cuya distribución incluye las Antillas (16.8 %) y especies introducidas por la actividad humana (6.3 %). Un análisis de la distribución de las especies en Cuba reveló que las áreas con mayor endemismo coincidieron con los principales núcleos montañosos del Este, Centro y Oeste. Estos fueron: Sierra Maestra (con 25 especies), Nipe-Sagua-Baracoa (15), Cordillera de Guaniguanico (14) y Macizo de Guamuaya (14). La distribución de las abejas en el archipiélago cubano no fue uniforme, posiblemente debido a condiciones ecológicas de los hábitats, la diversidad y presencia de determinadas plantas melíferas y la competición interespecífica. El endemismo de las especies de abejas en las Antillas es considerado alto, a pesar de ser un grupo de gran movilidad, como se observó no sólo en Cuba (43.8 %) sino también en Jamaica (50 %) y la Hispaniola (45.6%). En Puerto Rico e islas adyacentes es de 26.5 %.

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 (*Melissoptila* Holmberg); F. Silveira (*Exomalopsis* Spinola).

The geographic range of species was obtained from data in collections and from the following papers: FLORIDA: Graenicher (1927, 1930), Krombein et al. (1979), Mitchell (1960, 1962). THE BAHAMAS: Ashmead (1896), Krombein (1953), Elliott (1984). CUBA: Alayo (1973, 1976). ISLA DE LA JUVENTUD: Alayo (1976), Rohwer and Holland (1917), Genaro (2004). JAMAICA: Fox (1891), Gowdey (1926, 1928), Raw (1985). HISPANIOLA: Genaro (2007). PUERTO RICO and adjacent islands: Dewitz (1881), Wolcott (1948), Miskimen and Bond (1970), Genaro and Franz (2008). MONA ISLAND: Ramos (1946); Torres and Snelling (1992). LESSER ANTILLES Leeward and Windward: Crawford (1914); Cockerell (1938), BARBADOS: Cockerell (1937), Tucker (1963), Bennett and Alam (1985). YUCATAN: Roubik et al. (1991). CENTRAL AMERICA and NORTHERN SOUTH AMERICA: Michener (1954), Griswold et al. (1995). SEVERAL AREAS (works that mention the distributions of species from more than one area): Dalla Torre (1896), Ashmead (1900), Cockerell (1906), Cheesman (1929), Eickwort (1988), Friese (1902, 1908), Krombein et al. (1979), Michener (2000), Moure (1960), Moure et al. (2007).

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), *Sphecodes* 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

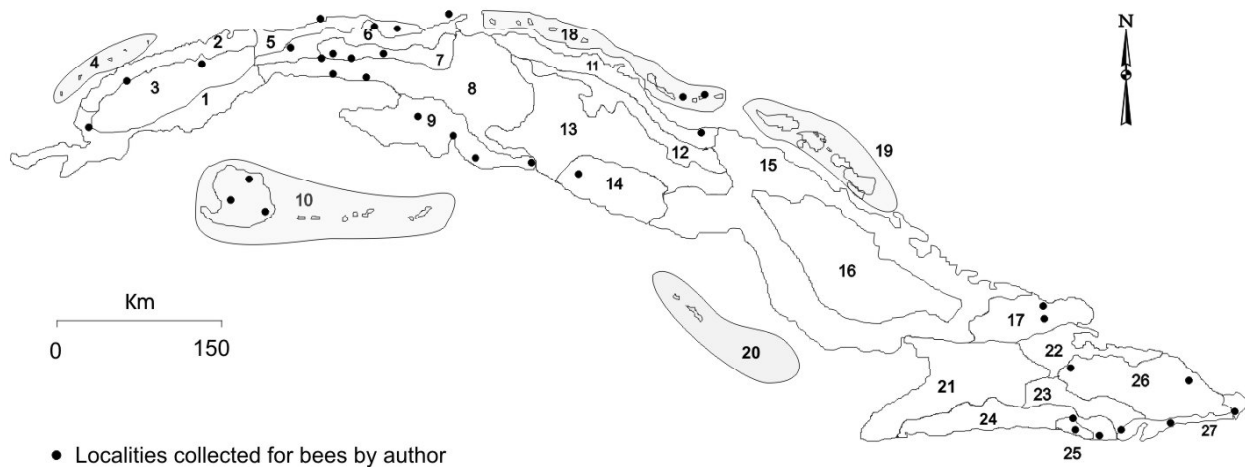


Figure 1. Geographic areas adopted for analysis of bee distribution on the Cuban archipelago. Adapted from Acevedo (1989). Areas: 1. Southern Plain of Pinar del Río. 2. Northern Plain of Pinar del Río. 3. Guaniguanico Mountains Range. 4. Archipelago of Los Colorados. 5. Northern Hills of Habana-Matanzas. 6. Ariguanabo-San Juan Plain. 7. Habana-Matanzas Central Hills. 8. Southern and Eastern Plains of Habana-Matanzas. 9. Zapata Plains. 10. Archipelago of Los Canarreos. 11. Corralillo-Yaguajay Plain. 12. Cubanacán Hills. 13. Cubanacán. 14. Massif of Guamuaya. 15. Outlying Plains of Camagüey-Maniabón. 16. Central Plains and Hills of Camagüey. 17. Maniabón. 18. Archipelago of Sabana. 19. Archipelago of Camaguey. 20. Archipelago of Jardines de La Reina. 21. Eastern Hills of Cauto-Guacanayabo. 22. Nipe Plain-Baguanos Hills-Sagua de Tánamo Plain. 23. Central Valley. 24. Sierra Maestra. 25. Santiago de Cuba. 26. Northeastern Mountains of Nipe-Cristal-Sagua-Baracoa. 27. Maisi-Guantánamo Coast.

1994), *Exomalopsis* (Timberlake 1980), *Xeromelecta* Linsley (Michener 1988a), *Triepeolus* Robertson (Genaro 1999, Rightmyer 2008), *Ceratina* Latreille (Genaro 1998), *Xylocopa* Latreille (Hurd 1978, Ospina 2000), *Melipona* Illiger (Ayala 1999, Schwarz 1932, 1944). Bees introduced by humans were not included in the analyses.

The biogeographic study included an analysis of the patterns of distribution of the bees in the Cuban archipelago. A database was constructed with 3214 entries for the species of bees and their localities, according to the system of geomorphological regionalizations proposed by Acevedo (1989) (Fig. 1), with the following modifications: a smaller number of areas was used, because the subregions and marine areas were omitted. Isla de La Juventud was taken as one unit and was included as part of the Archipelago of the Los Canarreos. A cluster analysis was used to identify homogeneous subgroups of bees in the sample, in order to associate areas of Cuba (shown in Fig. 1); the linkage rules used were weighted pair-group average and Euclidean distances as distance measures. This technique encompasses several algorithms and methods for grouping objects of similar kind into respective categories. It is an exploratory data analysis tool which aims at sorting different objects into groups in a way that the degree of association between two objects is maximal if they belong to the same group and minimal otherwise.

Results

Origins

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,

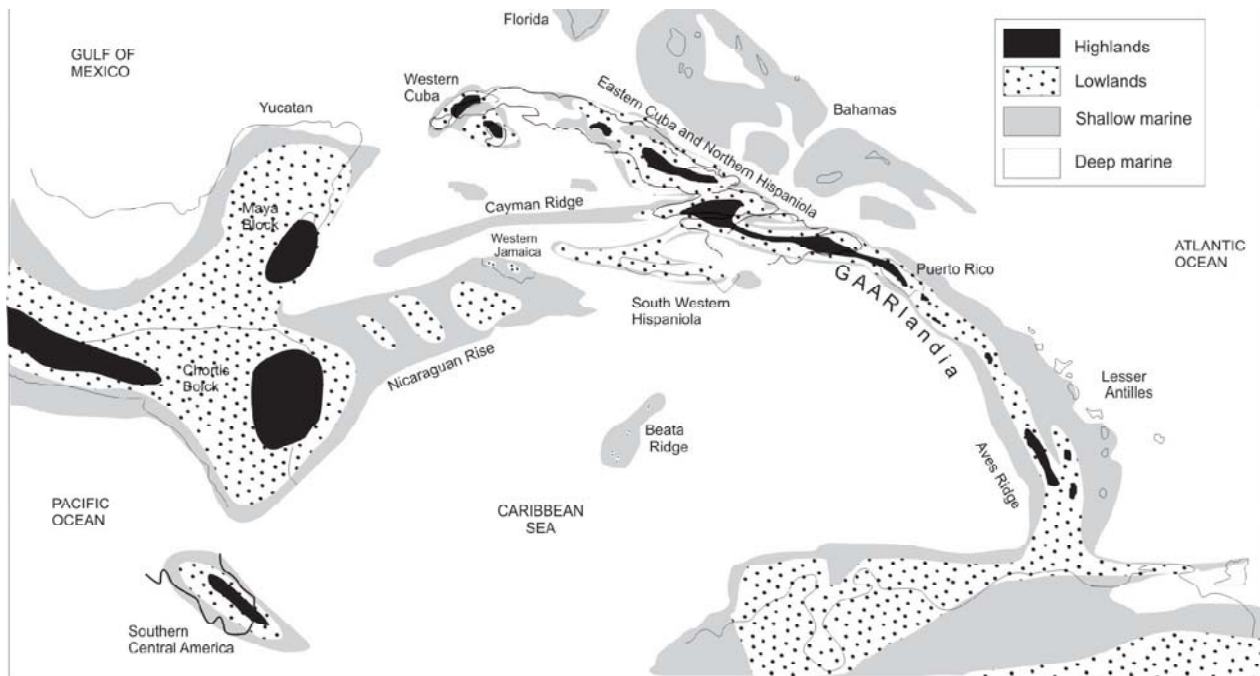


Figure 2. Paleogeographic reconstruction of the Caribbean region for the late Eocene-Early Oligocene (35-33 mya) (after Iturralde-Vinent 2005). The period of most concentrated dispersal of bees from continents to the Proto-Antilles likely took place at this juncture, with its proximity or connections with older landmasses and their populations of bees.

~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

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

Family	Genera	Number of species
Colletidae		
	<i>Colletes</i> Latreille, 1802	3
	<i>Caupolicana</i> Spinola, 1851	2
	<i>Hylaeus</i> Fabricius, 1793	6
Halictidae		
	<i>Halictus</i> Latreille, 1804	1
	<i>Lasioglossum</i> Curtis, 1833	18
	<i>Sphecodes</i> Latreille, 1804	3
	<i>Nesosphecodes</i> Engel, 2006	1
	<i>Temnosoma</i> Smith, 1853	1
	<i>Agapostemon</i> Guérin Méneville, 1844	3
	<i>Augochlora</i> Smith, 1853	5
	<i>Nomia</i> Latreille, 1804	1
Megachilidae		
	<i>Lithurgus</i> Berthold, 1827	1
	<i>Heriades</i> Spinola, 1808	1
	<i>Megachile</i> * Latreille, 1802	10 (4)
	<i>Coelioxys</i> Latreille, 1809	6
Apidae		
	<i>Exomalopsis</i> Spinola, 1853	3
	<i>Nomada</i> Scopoli, 1770	4
	<i>Epeolus</i> Latreille, 1802	1
	<i>Triepeolus</i> Robertson, 1901	4
	<i>Melissodes</i> Latreille, 1829	4
	<i>Florilegus</i> Robertson, 1900	1
	<i>Melissoptila</i> Holmberg, 1884	1
	<i>Anthophora</i> Latreille, 1803	2
	<i>Centris</i> Fabricius, 1804	5
	<i>Xeromelecta</i> Linsley, 1939	1
	<i>Mesocheira</i> Lepeletier & Serville, 1825	1
	<i>Mesoplia</i> Lepeletier, 1841	1
	<i>Ceratina</i> Latreille, 1802	2
	<i>Xylocopa</i> Latreille, 1802	1
	<i>Melipona</i> * Illiger, 1806	(1)
	<i>Apis</i> * Linnaeus, 1758	(1)
Total: 4	31(2)	95(6)

Early Miocene through early Middle Miocene (Iturralde-Vinent and MacPhee 1996, Iturralde-Vinent 2001). Knowledge of the bee fauna in amber from the 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.

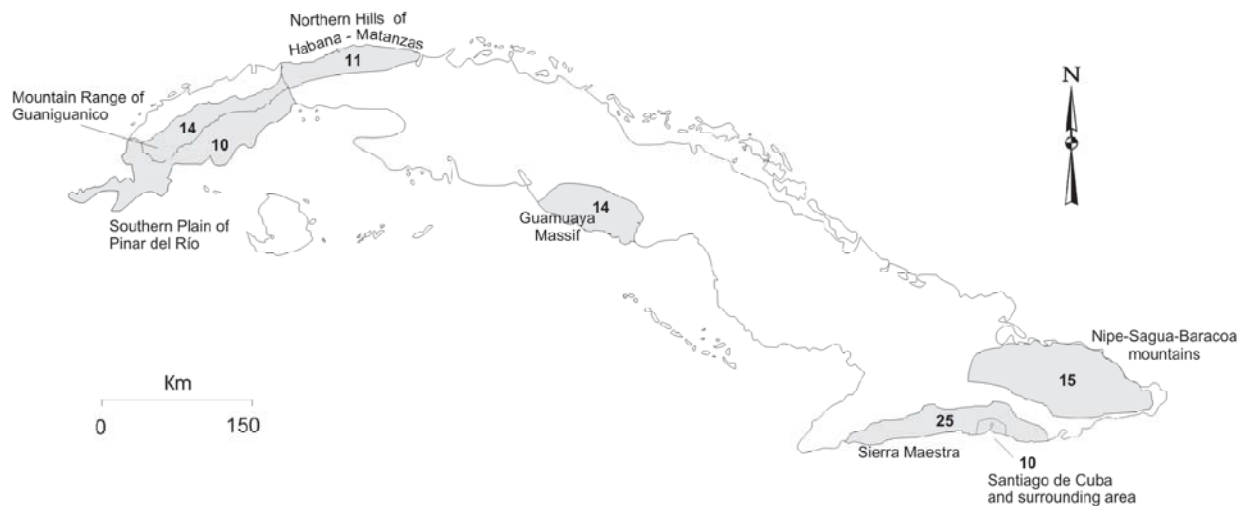


Figure 3. Areas of endemicism of Cuban bees. The numbers of endemic species are indicated inside the area.

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

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 habits 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

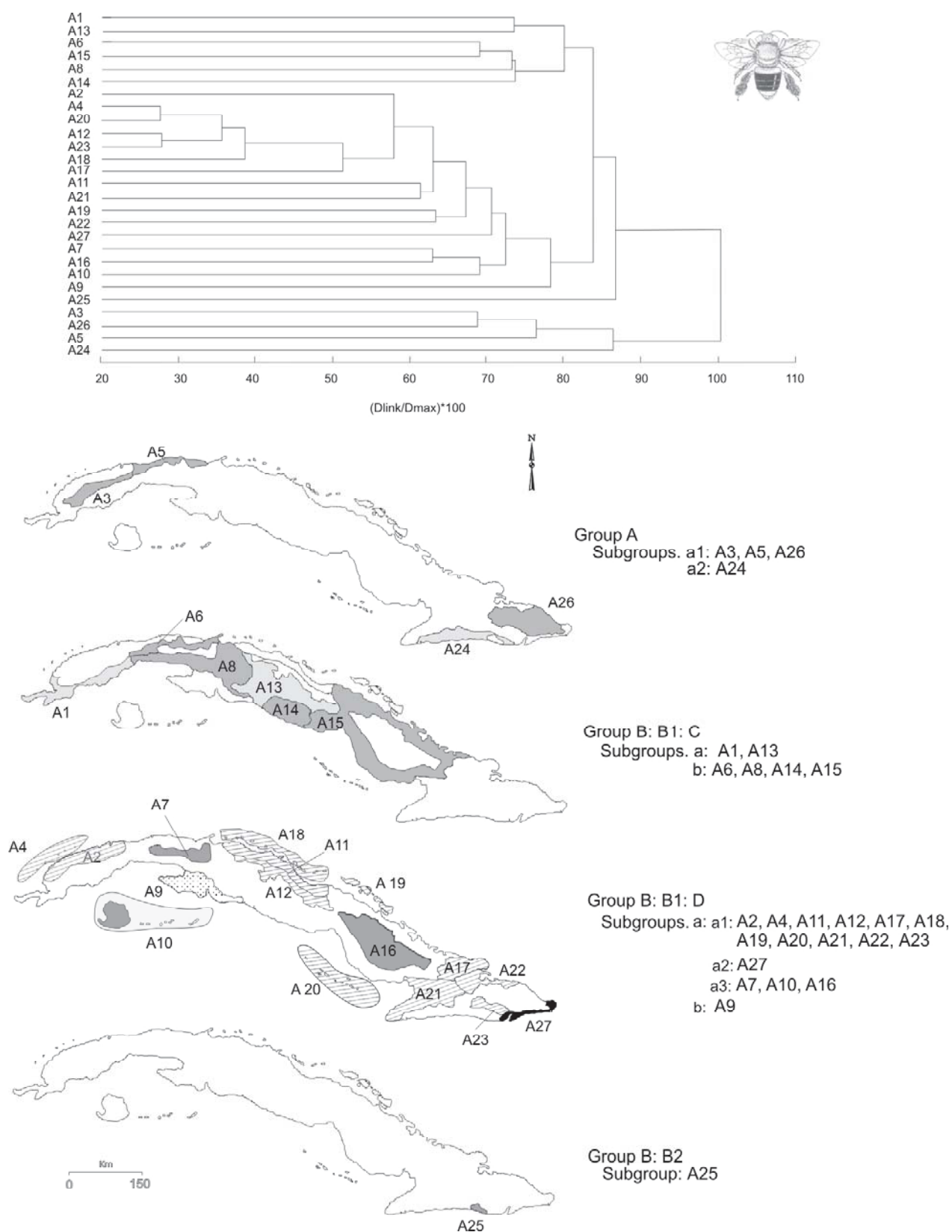


Figure 4. Dendrogram reflecting the clustering between bee species and biogeographic areas of the Cuban archipelago. Additional detail maps show areas according to the groups and subgroups formed.

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: *Triepeolus cuabitisensis* Genaro and *Coelioxys alayoi* Genaro, and species of limited distribution in Cuba such as *Lithurgus antilleorum* Michener, *Megachile armaticeps* Cresson, *Melissoptila 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 *Lasioglossum*, group *Habralictellus*, is in the Sierra Maestra and Nipe-Sagua-Baracoa mountainous regions. *Lithurgus antilleorum* occur only in the xerofitic habitats of the South coast of Santiago de Cuba and Guantanamo; *Triepeolus cuabitisensis* 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*, *Lasioglossum*, *Nesosphecodes*, *Epeolus*, *Triepeolus*, *Caupolicana*, *Megachile*, *Coelioxys*, *Melissoptila*, *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; *Lasioglossum* spp., *Halictus poeyi* Say, *Sphecodes* spp., *Nomia robinsoni* Cresson, *Ceratina cyaniventris* Cresson, *Centris poecila*,

Xylocopa cubaecola, *Megachile poeyi* Guérin-Ménéville, *Coelioxys rufipes* Guérin-Ménéville, *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.

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Appendix 1. Endemic bee species from Cuban Archipelago and areas where they occur. Areas of greater endemism are highlighted.

Bee species	Geographic areas (according to Fig. 1)																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Colletes granpiedrensis</i> Genaro, 2001																									x		
<i>Colletes bicaco</i> Genaro, 2003						x																					
<i>Caupolicana nigrescens</i> (Cresson, 1869)			x																					x		x	
<i>Caupolicana subaurata</i> (Cresson, 1869)			x							x			x											x		x	
<i>Hylaenus limbifrons</i> (Cresson, 1869)	x					x		x																			
<i>Hylaenus</i> n. sp.													x														
<i>Hylaenus near formosus</i> Krombein																						x					
<i>Lasioglossum magdalena</i> (Baker, 1906)														x													
<i>Lasioglossum normalis</i> (Baker, 1906)														x													
<i>Lasioglossum adriani</i> Genaro, 2001			x																								
<i>Lasioglossum engeli</i> Genaro, 2001																								x			
<i>Lasioglossum sierramaestrensis</i> Genaro, 2001																								x			
<i>Lasioglossum</i> n. sp. 1											x													x	x		
<i>Lasioglossum</i> n. sp. 2																								x		x	
<i>Lasioglossum</i> n. sp. 3																								x			
<i>Lasioglossum</i> n. sp. 4																								x			
<i>Sphecodes genaro</i> Engel, 2006b	x							x																x	x		
<i>Sphecodes tainoi</i> Engel, 2006b					x																						
<i>Sphecodes</i> n. sp.																								x			
<i>Nesosphecodes cubicola</i> Engel, 2006a																								x			
<i>Agapostemon viridulus</i> (Fabr., 1793)	x		x		x					x			x	x		x								x	x	x	
<i>Agapostemon cubensis</i> Roberts, 1972	x																										
<i>Megachile singularis</i> Cresson, 1865	x		x		x			x	x	x	x		x	x					x					x		x	
<i>Megachile armaticeps</i> Cresson, 1869	x										x		x	x							x			x	x	x	x
<i>Coelioxys tridentata</i> (Fabr., 1775)																								x		x	x
<i>Coelioxys alayoi</i> Genaro, 2001																									x		
<i>Coelioxys tegularis</i> Cresson, 1869								x							x												
<i>Coelioxys sannicolarensis</i> Genaro, 2001								x	x							x											
<i>Nomada flaviceps</i> Cresson, 1865			x								x			x												x	
<i>Nomada cruralis</i> Moure, 1960					x			x		x											x			x		x	
<i>Epeolus pulchellus</i> Cresson, 1865			x		x				x					x		x								x	x	x	
<i>Triepeolus wilsoni</i> (Cresson, 1865)			x		x						x			x		x					x			x		x	
<i>Triepeolus cuabitisensis</i> Genaro, 1999																									x		
<i>Melissodes cubensis</i> La Berge, 1956	x	x	x		x		x	x		x			x	x		x								x			
<i>Melissodes leprieuri</i> Blanchard, 1849	x		x		x	x	x	x					x	x	x						x			x	x	x	x
<i>Melissodes pullata</i> Cresson, 1865	x	x	x		x		x	x					x	x										x	x	x	
<i>Anthophora atrata</i> Cresson, 1865			x		x			x		x				x		x								x		x	
<i>Xeromelecta alayoi</i> Michener, 1988			x											x										x			
<i>Ceratina cyaniventris</i> Cresson, 1865	x	x	x		x					x			x	x							x			x	x	x	x