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The bees of Greater Puerto Rico
(Hymenoptera: Apoidea: Anthophila)

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Abstract. The bee fauna of the Greater Puerto Rico area was studied. A review of the previous relevant studies is presented. An annotated catalog and information about the origin and distributional patterns are also provided. Thirty-nine species of bees occur in Puerto Rico and adjacent islands. This fauna is composed of four elements: exclusive Puerto Rican endemics (26.5%); Antillean endemics occurring on multiple islands (76.5%); continental species that have also colonized the Antilles (23.5%); and species introduced through human activity (12.8%). The bee fauna was both low in its diversity and showed the highest level of disharmony in relation to other faunas of the Greater Antilles. A lectotype is here designated for *Agapostemon krugii* Wolcott, 1936.

Resumen. La fauna de abejas del área del Gran Puerto Rico fue estudiada. Se revisaron los primeros estudios relevantes sobre este tema. Se presenta un catálogo anotado e información sobre el origen y los patrones de distribución. En Puerto Rico y sus islas adyacentes viven 39 especies de abejas. Esta fauna está compuesta por cuatro elementos: especies endémicas de esta área (26.5%); endémicas antillanas que aparecen en varias islas (76.5%); especies continentales que han colonizado las Antillas (23.5%); y especies introducidas por la actividad antrópica (12.8%). La fauna de abejas tuvo poca diversidad y mostró el mayor grado de desarmonía, en relación con las otras faunas de las Grandes Antillas. El lectótipo de *Agapostemon krugii* Wolcott, 1936 es designado en este trabajo.

Key words. Apoidea, bees, biodiversity, origin, pattern of distribution, annotated catalog, Puerto Rico, adjacent islands.

Introduction

Bees are the most important pollinators on the planet and without them terrestrial ecosystems, agricultural or otherwise, would be severely affected (Ascher and Buchmann 2005). In addition to their role in pollination, bees have been shown to be highly susceptible to extinction in comparison to other organisms (Zayed et al. 2004; Zayed and Packer 2005). A high responsiveness to habitat alterations makes them an ideal indicator taxon for the preservation of terrestrial environments.

Wolcott (1923, 1936, 1948) included bees in his important works reviewing the insects of Puerto Rico, and thereby contributed significantly to our knowledge of this fauna. However, these historical reports now require updating to account for erroneous identifications, new records and new species that were described subsequent to his studies.

Here we analyze the origin, composition and distribution of the bee fauna of Puerto Rico and adjacent islands. We provide a review of the relevant authors and publications on this fauna and present a new annotated catalog, including new records and nomenclatural emendations.

Materials and methods

The taxonomic arrangement at higher and lower levels is in accordance with Michener (2000). In some cases we were unable to ascertain information related to the sex or repository institution of the holotypes of the treated bee species.

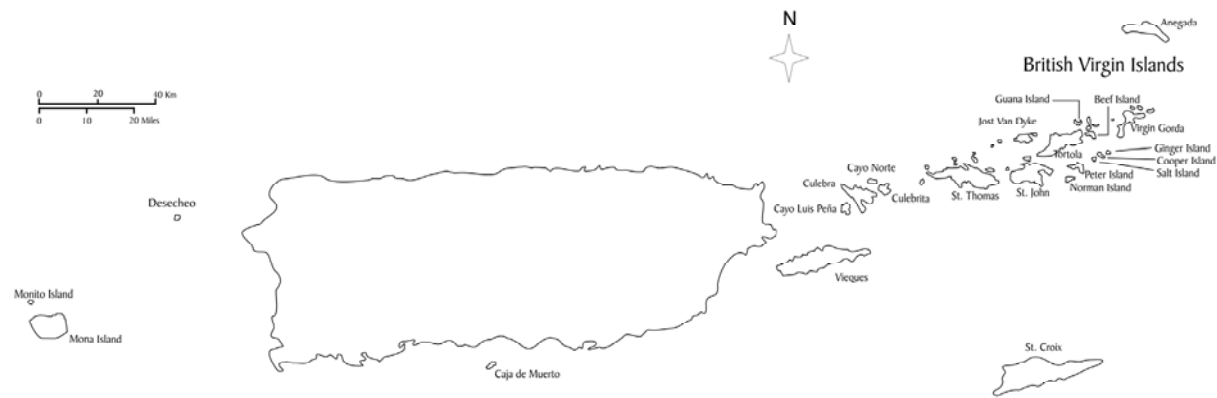


Figure 1. Map of Greater Puerto Rico showing the islands included in this study.

For the purpose of this review we refer to Greater Puerto Rico in the sense of Thomas and Joglar (1996); including (1) the adjacent Puerto Rican islands Culebra, Desecheo, Mona, Monito, and Vieques; (2) the British Virgin Islands Anegada, Guana, Jost van Dyke, Tortola, and Virgin Gorda (etc.); and (3) the United States Virgin Islands St. Croix, St. John, and St. Thomas (Fig. 1).

The following Puerto Rican insect repositories were studied: the collection located in the Museum of Entomology and Tropical Biodiversity (collection coden MEBT-MC) of the Agricultural Experiment Station, University of Puerto Rico at Mayagüez (located in Río Piedras; see Franqui-Rivera et al. 1997); the insect collection of the Department of Biology, University of Puerto Rico at Mayagüez (UPRM; located in Mayagüez); and the Juan Torres personal collection, now transferred to the MEBT-MC.

Additional specimen material was examined in numerous collections that are listed here according to country, institution (with collection coden), and city. **Austria:** Naturhistorisches Museum (NMV), Vienna. **Canada:** Canadian National Collection, Ottawa (CNC); York University, Toronto (YU); Julio A. Genaro personal collection (JAG), Toronto. **Cuba:** Gundlach's collection, located in the Instituto de Ecología y Sistemática (CG-IES), Havana; Museo Nacional de Historia Natural de Cuba (MNHNCu), Havana. **Denmark:** Zoological Museum of University of Copenhagen (ZMUC), Copenhagen. **Dominican Republic:** Museo Nacional de Historia Natural, Santo Domingo (MNHNSD) and Marcano Collection at Universidad Autónoma de Santo Domingo. **France:** Muséum National d'Histoire Naturelle (MNHN), Paris. **Germany:** Museum für Naturkunde der Humboldt-Universität (ZMB), Berlin; Zoologisches Museum der Universität Kiel (ZMK), Kiel; Zoologische Staatssammlung München (ZSM), Munich. **Great Britain:** Natural History Museum, London (BMNH). **Italy:** Museo Civico di Storia Naturale (MCSNG), Genoa; Museo Regionale di Scienze Naturali (MSNT), Turin. **The Netherlands:** Nationaal Natuurhistorisch Museum (Naturalis, NNM), Leiden. **United States:** Academy of Natural Science of Philadelphia (ANSP), Philadelphia; American Museum of Natural History (AMNH), New York; Cornell University Insect Collection (CUIC), Ithaca; Museum of Comparative Zoology at Harvard University (MCZ), Boston; National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; Natural History Museum of Los Angeles County (NHMLAC), Los Angeles; Natural History Museum, University of Kansas (NHMUK), Lawrence.

A complete synonymy list is not presented for non-natives bees. We only list synonyms of interest for Greater Puerto Rico.

Review of previous relevant studies

Cresson (1878b) listed the species of bees from North America and Caribbean area. Ashmead (1900) and Friese (1902) presented annotated lists of the Antillean Hymenoptera in early efforts to review the fauna known at that time. Several bee species reported in these works were incorrectly assigned to particular Caribbean islands due to misidentifications.

Friese's (1899) monograph of *Exomalopsis* Spinola was a first step to resolving its taxonomy. He later presented descriptions and keys to the species of Megachilinae (Friese 1911) and also published on *Coelioxys*

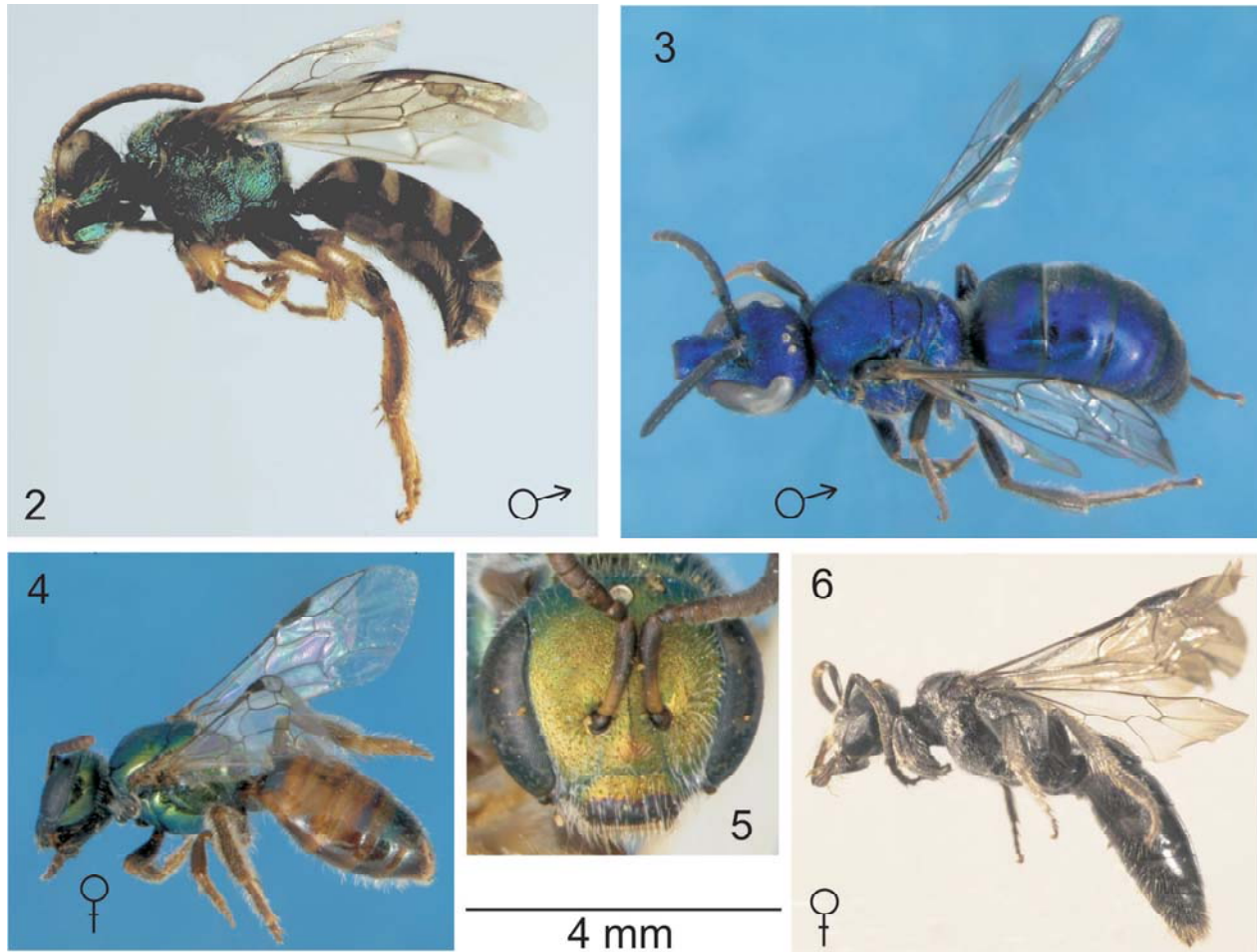


Figure 2-6. Halictidae. **2)** *Agapostemon viequesensis* Cockerell. **3)** *Augochlora buscki* Cockerell. **4)** *Lasioglossum rufopanticis* (Engel). **5)** *L. rufopanticis*, face of female. **6)** *Nesosphecodes anthracinus* Engel. Scale (4 mm) for all figures except close-ups.

Latreille from the Antilles (Friese 1921). Cockerell (1910) studied the West Indian species of *Augochlora* Smith, providing a key and describing *A. buscki* Cockerell from Puerto Rico.

Many specialists included material from Greater Puerto Rico in their contributions treating lineages across larger geographic areas. LaBerge (1956, 1961) studied the genus *Melissodes* Latreille in North and Central America. Moure (1960a), after reviewing the type material of Fabricius deposited in European collections, clarified numerous nomenclatural problems. Roberts (1972) revised the genus *Agapostemon* Guérin-Méneville and offered a key to the species. Hurd (1978) reclassified the species of *Xylocopa* Latreille of the Western Hemisphere. Timberlake (1980) revised the American and West Indian species of *Exomalopsis*. Moure and Hurd (1987) published an annotated catalogue of the halictids of the Western Hemisphere. Eickwort's (1988) work on the distributional patterns of halictids from the West Indies is a remarkable contribution, and furthermore provides valuable notes on the nesting behaviors of some species. Alexander and Schwarz (1994) published a catalogue of the species of *Nomada* Scopoli. Brooks (1999) published the first revision of *Anthophora* Latreille occurring in the Antilles. Engel (2001a, 2006) described new species of West Indian halictids. Raw (2007) published an annotated catalogue of the leafcutter bees of the Neotropics but in some cases information regarding Antillean bees is inaccurate.

Regarding studies of the hymenopteran fauna focused specifically on Puerto Rico and adjacent islands, Wolcott's (1923, 1936, 1948) accounts of reported species and their life histories constitute the foundational entomological work. Ramos (1946) treated the insects of Mona Island; Medina Gaud and Martorell (1974) those of the key Caja de Muerto; Torres and Snelling (1992) reviewed the Hymenoptera of Mona Island; and Snelling (1992, 1993, 1994, 2005) studied the respective faunas of Guana Island and

Mona Island. No bees have been reported from Desecheo Island (García et al. 1974). Maldonado Capriles (1996) summarized the status of the alpha taxonomy for Puerto Rico insects, but noted that information on bees was incomplete. Torres and Medina-Gaud (1998) recorded 29 species of bees from Puerto Rico. Torres et al. (2000) list the parasitoids of *Lasioglossum* sp. and *Xylocopa mordax* Smith. Moure et al. (2007) published a catalogue of the bees of the Neotropical region, but at least for the Antilles, the catalogue is not fully updated, nor does it cite all relevant papers, nor is all information about distribution therein accurate.

Annotated catalogue of the bees of Greater Puerto Rico

The following abbreviations and symbols are used: “GD” for geographic distribution, “=” to indicate synonymy, and “~” to refer to informal names used in other works.

Family Colletidae Lepeletier de Saint Fargeau

Hylaeus (Paraprosopis) wootoni (Cockerell)

Prosopis wootoni Cockerell, 1896: 26. Holotype male in USNM.

GD: Introduced into the British Virgin Islands (Guana Island) (Snelling 1994).

Native to the southwestern United States and adjacent Mexico, extending from Colorado and Coahuila to California (Hurd 1979; Snelling 1994).

Hylaeus (Hylaeana) sp. nov.

GD: British Virgin Islands (Guana Island).

Snelling (1993) found a new species of *Hylaeus* Fabricius which is not yet described. This constitutes the first native record of the genus for Greater Puerto Rico. In the Greater Antilles the subgenus is now known from Jamaica (4 species; Snelling 1982; Raw 1984), Cuba (1 species; R. R. Snelling, personal communication, 1995) and Hispaniola (1 species; Genaro 2007).

Family Halictidae Thomson

Agapostemon (Agapostemon) viequesensis Cockerell (Fig. 2)

Agapostemon viequesensis Cockerell, 1918: 419. Holotype female in USNM.

= *Agapostemon radiatus portoricensis* Cockerell, 1919: 209. Holotype male in USNM.

= *Agapostemon krugii* Wolcott, 1936: 569. Syntypes male and female in MEBT-MC. **New synonymy.**

GD: Bahamas (New Providence and Cat Island), and Puerto Rico (including Mona and Vieques Islands) (Roberts 1972; Janjic and Packer 2003).

Wolcott (1923, 1936, 1948) stated that *A. krugii* was a manuscript name proposed by Cresson. Cresson never published such a name. Wolcott's (1936) description of *A. krugii*, however brief, is sufficient to validate the name and so it must be attributed to Wolcott (1936). The *A. krugii* specimens examined by Wolcott were likely never labeled as primary types; no specialist has succeeded in locating such labeled types, including Juan A. Torres (personal communication, ca. 1997). For that reason all specimens available to Wolcott (1936) have the status of syntypes.

To maintain nomenclatural stability, we here designate a **lectotype** from the syntypes for *A. krugii*, located at MEBT-MC, with the following label data: “Pt. [Punta] Cangrejos, P.R., June 10, 1920/ G.N. Wolcott, collector”. To this specimen a red label was added reading: “*Agapostemon krugii* Wolcott, 1936, Lectotype, male, Genaro & Franz, 2008”. We furthermore designate the following **paralectotypes**: (1) “1-28/ Pt. Cangrejos, P.R., June 28, 1920/ G.N. Wolcott, Collector/ *Agapostemon viequesensis* Ckll., det. Snelling ‘98”; and (2) “Isabela, P.R., May 22-31, Acc # 146-31/ col: Wolcott”. To each of these two specimens a yellow label was added reading: “*Agapostemon krugii* Wolcott, 1936, Paralectotype, male, Genaro & Franz, 2008”.

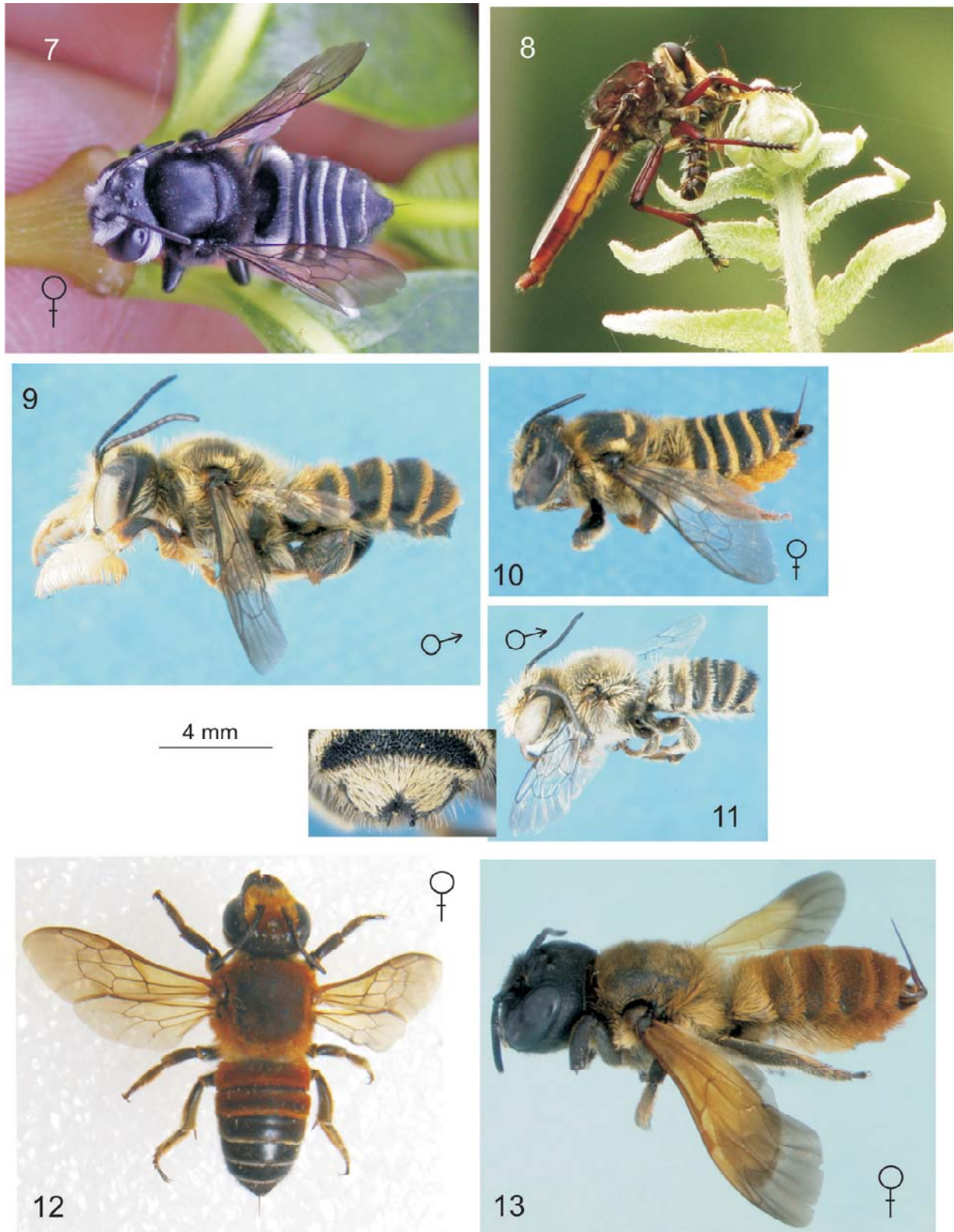


Figure 7-13. Megachilidae. 7) *Megachile luctifera* Spinola. 8) *Proctacanthus danforthi* (Diptera: Asilidae) eating a male of *M. holosericea* (Fabr.). 9) *M. holosericea*, male. 10) *M. holosericea*, female. 11) *M. concinna* F. Smith, male with detail of tergum VI, with small teeth. 12) *M. lanata* (Fabr.). 13) *M. rufipennis* (Fabr.).

Augochlora (Augochlora) buscki Cockerell (Fig. 3)*Augochlora buscki* Cockerell, 1910: 493. Holotype female in USNM.

GD: British Virgin Islands (Guana and Virgin Gorda Islands) and Puerto Rico.

Lasioglossum (Dialictus) buschiellum (Cockerell)*Halictus buschiellus* Cockerell, 1915: 9. Holotype female in USNM.

GD: Hispaniola and Puerto Rico (Moure and Hurd 1987; Genaro 2007).

Lasioglossum (Dialictus) ferrerii (Baker)*Chloralictus ferrerii* Baker, 1906: 263. Syntype females in AMNH and USNM.= *Halictus proangularis* Ellis, 1914: 155. Holotype female in USNM. Synonymy established by George C. Eickwort (in letter of 21. Febr. 1980 to P. Alayo).

GD: Cuba (including Isla de La Juventud), Hispaniola, Jamaica, and Puerto Rico (Genaro 2007).

Baker (1906) did not designate holotypes in his original description of the Cuban species of *Lasioglossum* Curtis; therefore all specimens which bear his handwriting and were labeled at the time of the description should be considered syntypes. Baker deposited this material in his own collection which was later sent to the USNM. Other specimens with his handwriting are deposited at AMNH and may perhaps be found in other collections.***Lasioglossum (Dialictus) gundlachii*** (Baker)*Chloralictus gundlachii* Baker, 1906: 268. Syntypes females in USNM.

GD: Cuba (including Isla de La Juventud), Hispaniola, and Puerto Rico (Eickwort 1988; Moure and Hurd 1987; Genaro 2007).

Lasioglossum (Dialictus) mestrei (Baker)*Chloralictus mestrei* Baker, 1906: 267. Male and female syntypes in USNM.= *Augochlora parva* Cresson, 1865: 171. Preoccupied due to secondary homonymy with *Panurgus parvus* Cresson [now also placed in *Lasioglossum (Dialictus)*]. Female holotype in ANSP.

GD: Cuba, Hispaniola, Jamaica, and Puerto Rico (Moure and Hurd 1987; Genaro 2007).

Lasioglossum (Dialictus) parvum (Cresson)*Panurgus parvus* Cresson, 1865: 175. Holotype male in ANSP.

GD: Bahamas (North and South Bimini, San Salvador), British Virgin Islands, Cuba (including Key Coco, Key Paredón Grande, Key Sabinal), Hispaniola, and Puerto Rico (Moure and Hurd 1987; Genaro 2007).

Lasioglossum (Dialictus) eickwortellum (Engel). *Habralictellus* group*Habralictellus eickwortellus* Engel, 2001a: 35. Holotype female in CUIC.

GD: Puerto Rico. Only known from the holotype collected at Cerro de Punta, Toro Negro State Forest, Cordillera Central.

Lasioglossum (Dialictus) rufopantex (Engel) (Figs. 4 and 5)*Habralictellus rufopanticis* Engel, 2001a: 33. Holotype female in NHMLAC.

GD: British Virgin Islands (Guana Island), Puerto Rico (including Mona Island), and United States Virgin Islands (St. John; new record).

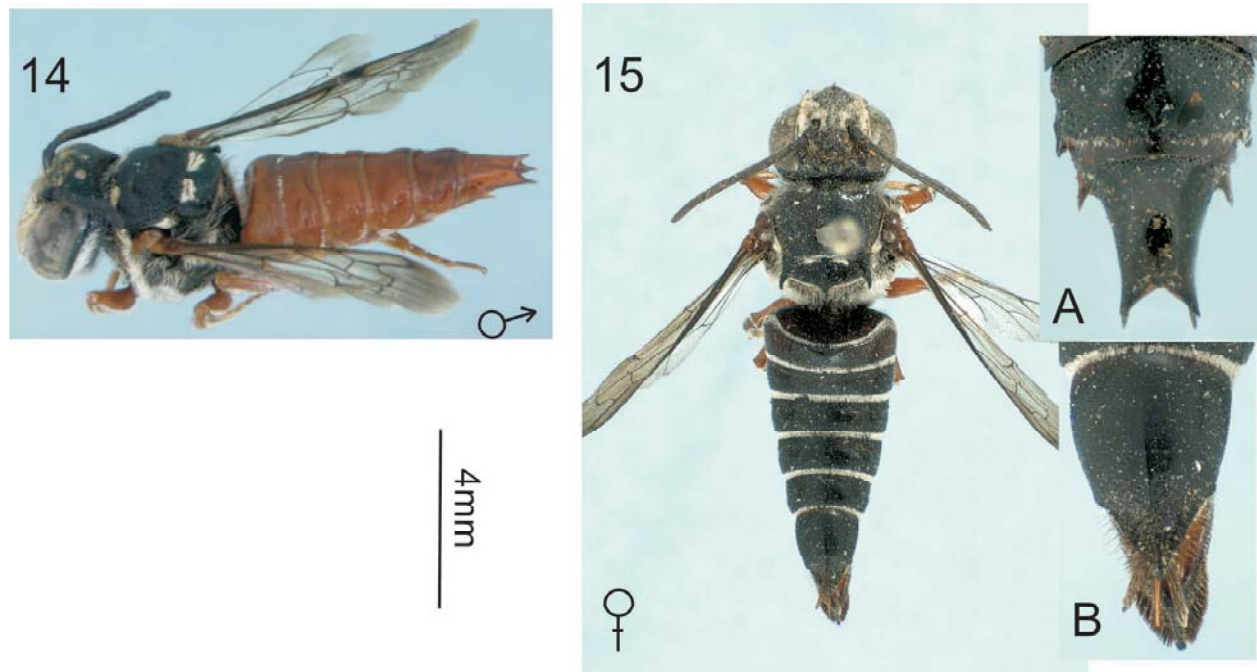


Figure 14-15. *Coelioxys* species. 14) *C. abdominalis* Guérin-Méneville. 15) *C. spinosa* Dewitz holotype, and sixth metasomal tergum (magnified): A) male; B) female. Photo by Stephanie Krause.

New record: ST JOHN, Leinstern bay, 13-16.ii.1969, col. H. E. Evans"; and "ST JOHN, Coral Harbor, 12-14.ii.1969, coll. H. E. Evans" (5 females in USNM).

The senior author (JAG) observed females in Puerto Rico nesting in vertical banks at Guánica and El Túnel de Guajataca, Quebradillas. This is a widespread species occurring throughout the Greater Puerto Rican islands.

***Nesosphecodes anthracinus* Engel**

Nesosphecodes anthracinus Engel, 2006: 3. Holotype female in NHMLAC.

GD: Puerto Rico. Only known from the holotype collected at Toro Negro Forest, Cordillera Central (Fig. 6). It is remarkable that this is now the only known cleptoparasitic halictid in the Greater Puerto Rico area.

Family Megachilidae Latreille

***Megachile (Pseudocentron) luctifera* Spinola (Fig. 7)**

Megachile luctifera Spinola, 1841: 142. Holotype female in MSNT.

= *Megachile binotata* Guérin-Méneville, 1844: 450. Holotype female in MCSNG.

= *Megachile flavitarsata* F. Smith, 1853: 183. Holotype male in BMNH.

= *Megachile barbadensis* Cockerell, 1937b: 111. Holotype male in USNM.

GD: Barbados, Colombia, Dominica, Grenada, Grenadines, Martinique, and United States Virgin Islands (St. Croix and St. Thomas) (Cockerell 1938, as *M. binotata*; Genaro 1998).

***Megachile (Pseudocentron) holosericea* (Fabricius) (Figs. 8 to 10)**

Apis holosericea Fabricius, 1793: 336. Lectotype female in ZMUC, designated by Moure (1960a).

~ *Megachile* sp. Snelling, 1992: 14; Torres and Snelling, 1992: 88.

~ *Megachile* undescr. sp. near *poyei* Guérin-Méneville in Snelling, 1993: 6.

GD: British Virgin Islands (Guana Island), and Puerto Rico (including Mona Island) (Moure 1960a; Snelling 1992, 1993).

The species placed in the subgenus *Pseudocentron* Mitchell are very similar in their morphology; and this has led to some misidentifications. The senior author (JAG) and Moure (1960a) have repeatedly come across specimens of *M. holosericea* identified as *M. vitracii* Pérez in United States museum collections. Moure (1960a) reviewed the types of these species and clarified the taxonomic status of each. Ashmead (1900) and Moure et al. (2007) recorded *Megachile poeyi* Guérin-Méneville from Puerto Rico. We have seen no corresponding specimens in the material available to us. It is likely that Ashmead's specimens pertain to the very similar *M. holosericea*. *Megachile singularis* Cresson (1865) is another misidentification from Puerto Rico by Ashmead (1900; see also above). Cresson (1865) described this species based on males from Cuba. We have seen no specimens matching that description among the Puerto Rican material studied, and therefore suspect that this record is based on misidentified specimens - possibly males of *M. holosericea*.

A male of *M. holosericea* was preyed on by the asilid fly *Proctacanthus danforthi* Curran in Humacao, Puerto Rico (1.vi.2006) (Fig. 8).

Megachile (Eutricharaea) concinna F. Smith (Fig. 11).

Megachile concinna F. Smith, 1879: 79. Holotype female in BMNH.

= *Megachile multidentis* Fox, 1891: 345. Syntype female in ANSP.

~ *Megachile* sp. F. of Alayo, 1976: 24. Males.

~ *Megachile* sp. F. of Alayo, 1976: 24. Females.

GD (in the neotropics): Cuba, Dominica, Guana Island, Hispaniola, Jamaica, Mexico, Puerto Rico (including Mona Island), and United States (Crawford 1914 [as *M. multidentis*]; Hurd 1979; Snelling 1992; Genaro 2007).

Megachile concinna was introduced into the West Indies from Africa in the early 19th century, and presumably reached the United States from the West Indies after World War II (Eickwort 1971; Parker 1978; Mitchell 1980; Hurd 1979).

This species was originally described from material collected from the Dominican Republic, however all species placed in the subgenus *Eutricharaea* Thomson are of Old World origin. Perhaps *M. concinna* was introduced into Hispaniola during the slave period.

We examined the specimens recorded by Wolcott (1948) as "*M. insularis* Cresson" that were identified by Karl V. Krombein (located in MEBT-MC and UPRM), these are actually *M. concinna*. Wolcott (1936) apparently misunderstood the name *Megachile singularis* Cresson mentioned in Ashmead (1900) interpreting it to be *Megachile insularis* Cresson. Since then, the erroneous name has remained in use; e.g. Krombein (personal communication, 1997) merely copied the name *M. insularis* as listed in Wolcott's (1948) *Insects of Puerto Rico*. A different and valid species described as *M. insularis* F. Smith, 1859 is from Aru, one of the southern Indonesian islands. This latter species was described by F. Smith in 1859. Incidentally, it also belongs to the subgenus *Eutricharaea* (Michener 1965).

Megachile (Pseudomegachile) lanata (Fabricius) (Fig. 12)

Apis lanata Fabricius, 1775: 385. Lectotype female in ZMUC.

= *Apis purpurea* Christ, 1791: 168.

= *Megachile martindalei* Fox, 1891: 344. Holotype male in ANSP.

GD (in the neotropics): Barbados, Cuba (including Isla de la Juventud), Grenada, Guadeloupe, Hispaniola, Jamaica, Montserrat, Puerto Rico (including key Caja de Muerto), St. Vincent, Trinidad, and United States (Florida) (Cockerell 1938; Eickwort 1971; Genaro 2007). Introduced into the West Indies from Africa, via the slave trade (Eickwort 1971; Mitchell 1980).

Megachile (Callomegachile) rufipennis (Fabricius) (Fig. 13)

Apis rufipennis Fabricius, 1793: 335. Lectotype female in ZMK, designated by Moure (1960a).

= *Megachile atriceps* Cresson, 1865: 176. Lectotype female in ANSP, designated by Cresson (1916).

= *Megachile atriceps phenacosoma* Cockerell, 1937a: 146. Holotype female.

= *Megachile atriceps rukuruensis* Cockerell, 1937a: 146. Holotype male.

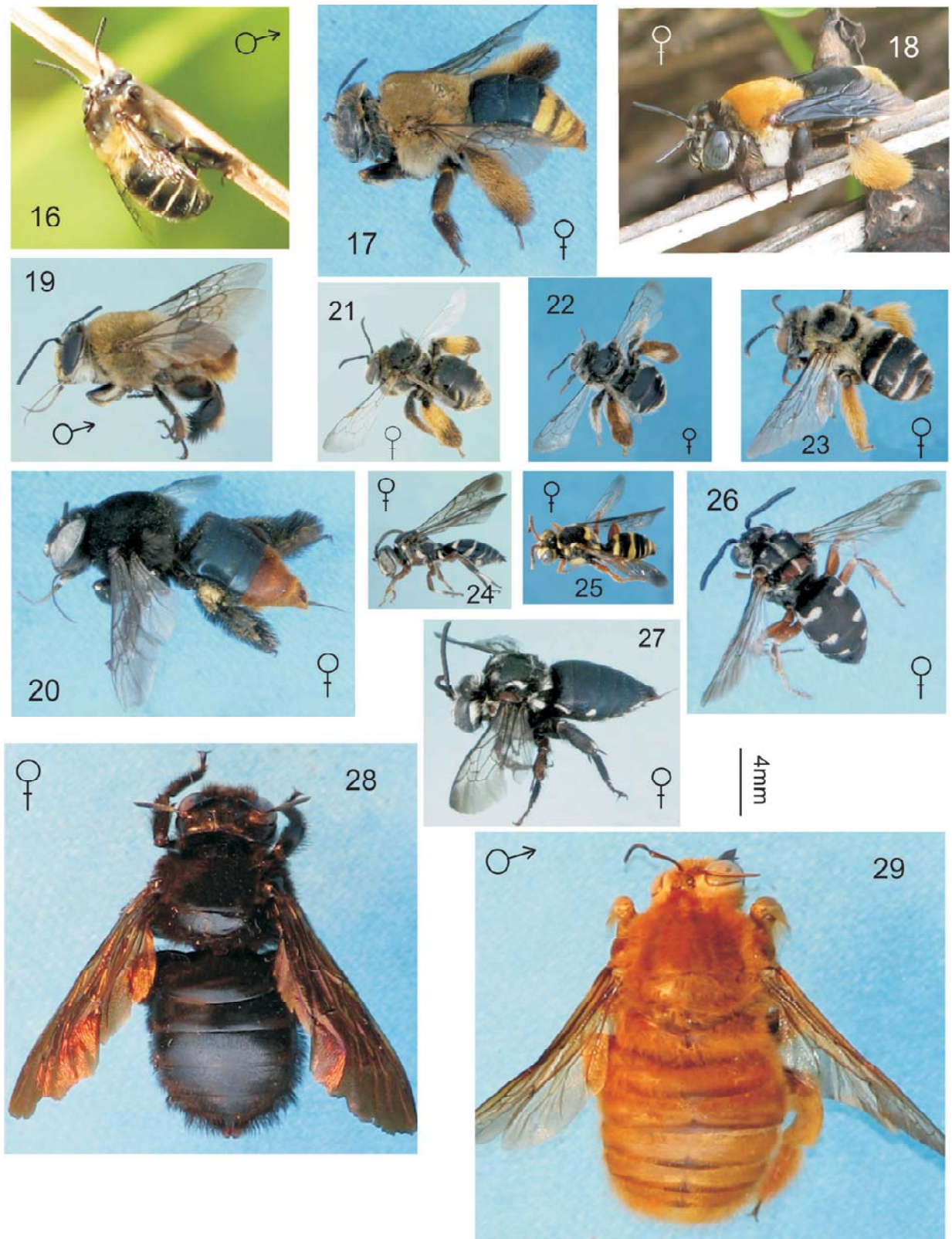


Figure 16-29. Apidae. 16) *Anthophora tricolor* (Fabr.). 17) *Centris smithii* Cresson. 18) *C. decolorata* Lepeletier. 19) *C. lanipes* (Fabr.). 20) *C. haemorrhoidalis* (Fabr.). 21) *Exomalopsis analis* Spinola. 22) *Exomalopsis bahamica* Timberlake. 23) *Melissodes trifasciata* Cresson. 24) *Nomada pilipes* (Cresson). 25) *N. krugii* Cresson. 26) *Xeromelecta tibialis* (Fabr.). 27) *Mesoplia rufipes* (Perty). 28-29) *Xylocopa mordax* F. Smith.

GD (in the neotropics): Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Montserrat, Puerto Rico (new record), and St. Croix (Moure 1960a; Genaro 2007). Introduced into the West Indies from Africa (Zaire, East Africa) (Pasteels 1965; Mitchell 1980).

New record: PUERTO RICO, Aguada, 6.ix.1979, coll. I. Bello (female, UPRM).

Coelioxys (Neocoelioxys) abdominalis Guérin-Méneville (Fig. 14)

Coelioxys abdominalis Guérin-Méneville 1844: 453. Male and female holotype in MCSNG, and apparently a syntype in NNM.

GD: Barbados, British Virgin Islands (Guana Island), Colombia, Curacao, Dominica, Grenada, Grenadines, Panama, Puerto Rico, Trinidad, United States Virgin Islands (St. Thomas), and Venezuela (Ashmead 1900; Crawford 1914; Cockerell 1937b, 1938; Michener 1954; Snelling 1993; Star and Hook 2003).

The records from Cuba (Sagra 1856; Ashmead 1900; Friese 1902, 1921) are erroneous. Gundlach (1886) noted that this species occurs in Puerto Rico yet not in Cuba.

Coelioxys (Cyrtocoelioxys) apicata F. Smith

Coelioxys apicata F. Smith, 1854: 267. Holotype female in BMNH.

Two females are deposited in the USNM collection with the label data: “acerca via Borinquen, Puerto Rico, 17.viii.1944, plane 12405, no. 2185, lot. no. 44 23/36”. This Palearctic species (Pasteels 1968) was likely introduced by a similar means as the host bees it may parasitize (*Megachile* spp). It remains to be verified whether it has become established in Puerto Rico.

Coelioxys (Cyrtocoelioxys) spinosa Dewitz

Coelioxys spinosa Dewitz, 1881: 197. Male and female types in ZMB (Figs. 15A and 15B).

GD: Puerto Rico.

An additional female was collected by the senior author at Guánica, Ponce (viii.2005).

Coelioxys (Cyrtocoelioxys) sp. nov.

GD: Puerto Rico.

One female housed in the USNM collection and with the following label data seems to have been temporarily misplaced: Borinquen, Puerto Rico, 18.vi.1944, plane 5978, #1918, lo. no. 44 19590. This specimen was studied by the senior author (JAG) in 1999 while visiting the collection. The reddish-brown color on metasomal tergum I is more extensively present in the basal area (in *C. spinosa* this coloration occurs only laterally), the apical process of metasomal sternum VI is short (versus elongate in *C. spinosa*; Fig. 15B), and the apical margin of tergum VI is tridentate. Drawings of the female’s scutellum, axillae and apex of the metasoma were published by Genaro (2001) as erroneously pertaining to *C. spinosa*.

Family Apidae Latreille

Anthophora (Mystacanthophora) tricolor (Fabricius) (Fig. 16).

Andrena tricolor Fabricius, 1775: 377. Lectotype male in ZMK, designated by Moure (1960a).

= *Andrena nigrita* Fabricius, 1775: 377. Holotype female in ZMK. Synonymy established by Brooks (1999).

= *Anthophora krugii* Cresson, 1878a: 188. Lectotype female in ANSP, designated by Cresson (1916).

GD: Antigua, British Virgin Islands (Guana and Tortola Island), Dominica, Hispaniola, Montserrat, Puerto Rico (including Mona Island), Saba Island, United States Virgin Islands (St. Croix, St. John, and St. Thomas). (Brooks 1999; Genaro 2007).

Centris (Centris) smithii Cresson (Fig. 17).

Centris smithii Cresson, 1878b: 229. New name for *C. apicalis* F. Smith, 1874a, not *C. apicalis* (Guérin-Méneville 1845).

= *Centris apicalis* F. Smith, 1874a: 367. Holotype female in BMNH. Preoccupied name, established by Cresson (1878b).

GD: British Virgin Islands (Guana Island), Lesser Antilles, Puerto Rico (including Culebra, Desecheo, and Mona Islands), and United States Virgin Islands (St. Thomas).

Centris (Centris) decolorata Lepeletier (Fig. 18)

Centris decolorata Lepeletier, 1841: 160. Holotype male in MNHN.

GD: Caribbean coast from southern Texas to Guianas, British Virgin Islands (Guana Island), Hispaniola, Jamaica, Lesser Antilles, and Puerto Rico (including key Caja de Muerto and Mona Island).

It is common to observe *C. decolorata* in sandy areas along coasts, where females nest and males are involved in perching (Torres and Snelling 1992; personal observations of authors; see Fig. 18). The MEBT-MC and UPRM collections contain specimens of this species identified by K. V. Krombein as *C. versicolor* (Fabricius). Wolcott (1923, 1936, 1948) erroneously reported this species from Puerto Rico (cf. Torres and Snelling 1992). Additional misidentifications of this kind appear in Dewitz (1881), Ståhl (1882), and Maldonado Capriles and Navarro (1967). According to R. R. Snelling (personal communication, 1999), *C. versicolor* is limited to the Lesser Antilles; however several Greater Antillean species have been misidentified as *C. versicolor*.

Centris (Centris) haemorrhoidalis (Fabricius) (Fig. 20)

Apis haemorrhoidalis Fabricius, 1775: 386. Lectotype female in ZMK, designated by Moure (1960a).

= *Centris tabaniformis* Fabricius, 1804: 358. Lectotype male in ZMUC.

= *Centris lepeletieri* Cockerell, 1912c: 140. Location of holotype female unknown. Considered a **nomen nudum** by R. R. Snelling.

GD: British Virgin Islands (Guana Island and Virgin Gorda Island), Hispaniola, , Puerto Rico (including Mona Island), and United States Virgin Islands (St. John).

Snelling (personal communication, 1999) rightly considers Cockerell's *C. lepeletieri* as a *nomen nudum* because the original description only provided remarks on how specimens of *C. haemorrhoidalis* from Hispaniola differ from those of a putative Jamaican species for which he proposed the name *C. lepeletieri*. There are no statements describing features of *C. lepeletieri*.

Centris (Heterocentris) lanipes (Fabricius) (Fig. 19).

Apis lanipes Fabricius, 1775: 386. Lectotype female in ZMK, designated by Moure (1960a).

GD: British Virgin Islands (Guana Island), Hispaniola, Lesser Antilles (Guadeloupe), Puerto Rico (including Culebra and Mona Islands), and United States Virgin Islands (St. Thomas) (Crawford 1914; Moure 1960a; Genaro 2007).

Gribodo (1892) mentioned this species' distribution. It is common to observe *C. lanipes* gathering sand for nest construction along trails of the Guánica dry forest reserve in southwestern Puerto Rico. This species may also use preexisting cavities located in various substrates, as occurs in other species of the subgenus *Heterocentris* (Snelling 1984; Vinson et al. 1996).

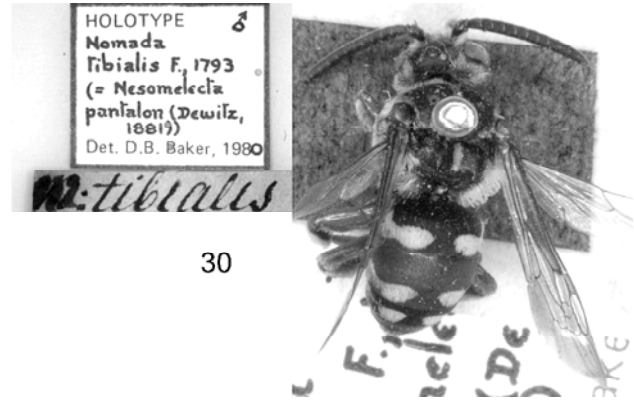


Figure 30. Holotype male of *Nomada tibialis* Fabricius, a senior synonym of *Xeromelecta pantalon* Dewitz, deposited at the Zoological Museum of the University of Copenhagen in Denmark. Photo by Lars Vilhelmsen.

Exomalopsis (Exomalopsis) analis Spinola (Fig. 21)

- Exomalopsis (Exomalopsis) analis* Spinola, 1853: 91. Holotype female in MSNT.
 = *Exomalopsis villipes* F. Smith, 1854: 365. Holotype female in BMNH.
 = *Exomalopsis mexicana* Cresson, 1878c: 133. Lectotype female in ANSP, designated by Cresson (1916).
 = *Exomalopsis tarsata* F. Smith, 1879: 125. Holotype female in BMNH.
 = *Epimonispractor gratiosus* Holmberg, 1903: 427. Location of holotype female unknown.
 = *Exomalopsis hiberna* Schrottky, 1908: 238. Location of holotype female unknown.
 = *Exomalopsis paraguayensis manni* Cockerell, 1912a: 56. Holotype female possibly in USNM (location not provided in original description and not further verified).
 = *Exomalopsis zexmeniae* Cockerell, 1912b: 447. Holotype female in USNM.
 = *Exomalopsis azulensis* Cockerell, 1949: 451. Holotype female in USNM.

GD: Hispaniola and Puerto Rico (Genaro 2007), and Argentina north to the United States (Texas) (Moure et al. 2007); therefore with perhaps the widest distribution of all species in the genus (F. Silveira, personal communication, 2006).

Exomalopsis (Exomalopsis) bahamica Timberlake (Fig. 22)

Exomalopsis bahamica Timberlake, 1980: 126. Holotype female in USNM.

GD: Bahamas (New Providence Island), Cuba, Hispaniola, and Puerto Rico (Genaro 2007).

Exomalopsis (Exomalopsis) pubescens Cresson

Exomalopsis pubescens Cresson, 1865: 192. Holotype male in CG-IES.

GD: Grenada, Grenadines, St. Kitts (first record) St. Vincent, Trinidad, and United States Virgin Islands (St. Croix; first record) (Timberlake 1980).

Although the type locality is Cuba this species has never been collected on that island. Perhaps there is a mistake in the type specimens's locality data. **New records:** ST KITTs, South Friars bay, 5 km 17°16.5'N, 62°40.7'W, 15.ii.2002, coll. D. Brzoska, det. R. W. Brooks, 2002 (female, NHMUK); ST CROIX, WI, F.5024, 6.iii.1925, det. J. A. Genaro, 2006 (female, NHMUK).

Exomalopsis (Exomalopsis) pulchella Cresson

Exomalopsis pulchella Cresson, 1865: 191. Lectotype female in ANSP, designated by Cresson (1916).

GD: Bahamas, Costa Rica, Cuba (including Isla de La Juventud), Jamaica, Mexico (Veracruz), Guatemala, Puerto Rico, United States (Florida), and United States Virgin Islands (St. Thomas) [Friese 1899, as *E. globosa* (Fabr.) in part; Mitchell 1962; Timberlake 1980, as *E. globosa*; Genaro 2004, 2007; Moure et al. 2007].

In his studies of the Jamaican fauna, Raw (1976, 1977; reiterated in Rozen 1984) referred to this species as *E. globosa* (Fabr.).

Exomalopsis (Exomalopsis) similis Cresson

- Exomalopsis similis* Cresson, 1865: 191. Holotype female in ANSP.
 = *Apis globosa* Fabricius, 1793: 333. Lectotype female in ZMUC, designated by Moure (1960a). Junior homonym of *Apis globosa* Scopoli, 1763, established by Moure et al. (2007).
 = *Exomalopsis penelope* Cockerell, 1897: 161. Holotype female in USNM.
 = *Exomalopsis ogilviei* Cockerell, 1938: 281. Holotype female in USNM. Synonymy by Moure et al. (2007). Moure (1960a) considered it as a separate species.

GD: Bahamas (New Providence Island), Cayman Islands, Central America, Cuba (including Isla de La Juventud), Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Montserrat, Puerto Rico, St. Vincent, United States (Florida), and United States Virgin Islands (St. Thomas) (Cockerell 1938, as *E. ogilviei*; Michener 1954; Mitchell 1962; Timberlake 1980; Genaro 2004, 2007; Moure et al. 2007).

Timberlake (1980) treated *Apis globosa* Fabricius as a senior synonym of *E. pulchella* Cresson, without explanation.

Exomalopsis (Exomalopsis) sp. near bahamica Timberlake

A female (PUERTO RICO, Guaynabo, Barrio Soñadora, 16.xi.1992, coll. J. A. Torres, #121, deposited at coll. JAG) differs from the reported species from the Great Puerto Rico area. It is closely related to *E. bahamica* but punctures on the second tergum are larger than in *E. bahamica*. Also, hairs on the posterior margin of the scutellum and outer surface of the hind leg are fuscous (some dark hairs are mixed with pale ones on tibiae) whereas in *E. bahamica* they are darker.

Melissodes (Eplectica) trifasciata (F. Smith) (Fig. 23).

Melissodes trifasciata Cresson, 1878d: 208. Holotype female in ANSP.
= *Melissodes insularis* Crawford, 1914: 132. Holotype male in USNM.

GD: Dominica, Puerto Rico (including Mona Island), and United States Virgin Islands (St. Croix and St. Thomas) (LaBerge 1956).

LaBerge and Moure (1962) synonymized *M. trifasciata* with *M. nigroaenea* F. Smith, 1854, an older name for a species from Brazil, without offering additional comments. These authors furthermore designated a lectotype female for *M. nigroaenea* deposited in the Hope Department of Entomology, Oxford University. However, both species seem to be distinct (D. Urban, personal communication 2007), and are treated separately by Moure et al. (2007). On the other hand, LaBerge communicated to Snelling (R. R. Snelling, personal communication 1997) that "*M. nigroaenea* seems to be limited to South America". It would be useful to learn why these authors amended their earlier perspective. LaBerge and Moure (1962) offered descriptive notes on the lectotype and paratype females of *M. nigroaenea*. Therein they mentioned some differences in hair coloration between that species and *M. trifasciata*. The authors offered little information on surface sculpturing which tends to be more reliable characters for species recognition. Here we treat both species as distinct.

Florilegus (Florilegus) lanierii (Guérin-Méneville).

Macrocera lanierii Guérin-Méneville, 1844: 455. Holotype male in MCSNG.
= *Melissodes condigna* Cresson, 1878d: 207. Holotype female in ANSP.
= *Melissodes palustris* Robertson, 1892: 273. Syntypes females in ANSP.
Refer to Moure et al. (2007) for complete synonymy of *F. condigna*.

GD: Eastern United States, Cuba, Puerto Rico (first record), Central and South America (LaBerge and Ribble, 1966; Urban, 1970).

New record: PUERTO RICO, Toa Baja, 2.viii.1984, coll. J. A. Torres (1 female, MNHNCu); Real Anón, Coto Laurel, Ponce, v.1994, coll. J. A. Genaro (1 female, MNHNCu).

Cockerell (1906), LaBerge and Ribble (1966), and Moure and Michener (1955) considered *F. condignus* and *F. lanierii* as the same species, but Urban (1970) and Moure et al. (2007) treated them as separate species without explanation.

This species is variable according to pubescence color (LaBerge and Ribble, 1966). The female specimens from Puerto Rico have white hairs at the base of first metasomal tergum while Cuban females have black and white hairs.

Nomada pilipes (Cresson) (Fig. 24)

Pasites pilipes Cresson, 1865: 183. Holotype female in ANSP.

GD: Cuba (including Isla de La Juventud), Hispaniola, Jamaica, and Puerto Rico (Genaro 2007).

Nomada krugii Cresson (Fig. 25)

Nomada krugii Cresson, 1878c: 75. Syntype female in ANSP.

GD: Hispaniola and Puerto Rico (Genaro 2007).

Misidentifications of this species as *N. cubensis* Cresson were made by Dewitz (1881), Ashmead (1900), Friese (1902), and Gundlach (1887).

Xeromelecta (Nesomelecta) tibialis (Fabricius) (Fig. 26)

Nomada tibialis Fabricius, 1793: 346. Holotype male in ZMUC.

= *Crocisa pantalon* Dewitz, 1881: 198. Holotype male in ZMUC (Fig. 30). Synonymy established by D. B. Baker in Michener (2000).

GD: Puerto Rico.

Linsley (1943) described the female as *Melecta (Melectomorpha) pantalon* [sic] based on one specimen collected at Lares (3.xi.1922, coll. F. Seín). After examining this specimen at MEBT-MC, we concluded that it is actually a male. The specimen was identified as *Melecta* sp. by K. Krombein before he sent it to E. G. Linsley for identification (Linsley 1943). Subsequently, R. Snelling identified the specimen as *X. pantalon*. Neither of these specialists placed a gender label on the specimen.

We have examined two additional Puerto Rican specimens deposited in UPRM, with the following label data: “Aguada, Cerro Gordo, 23.viii.1987, coll. Douglas II”, a female; and Orocovis, 3.x.1979, coll. AEQ”, a male.

Mesoplia (Mesoplia) aff. rufipes (Perty) (Fig. 27)

Crocisa rufipes Perty, 1833: 149. Male holotype in ZSM.

GD: British Virgin Islands (Guana Island), Greater and Lesser Antilles, Mexico to Brazil (Moure 1960b; Snelling 1994).

The taxonomy of species placed in the genus *Mesoplia* Lepeletier is in an unsatisfactory state, hampered by inaccurate information on distributions and unresolved problems of synonymy. The usage of names for Antillean species is therefore compromised. Snelling and Brooks (1985) reviewed the genera of cleptoparasitic bees in the tribe Ericrocini (misspelled as Ericrocini by these authors: refer to Engel 2005), including the genus *Mesoplia*, however that work did not extend to the species level. Moure (1960b) studied the holotype of *M. rufipes*, commenting on issues of synonymy, and established three species groups within the genus. He placed *M. rufipes* and *M. azurea* (Lepeletier and Serville, 1828) in the same group. Several authors have treated *M. rufipes* and *M. azurea* as synonyms without providing additional comments (i.e.; Cresson 1865; Gundlach 1886; Dalla Torre 1896; Friese 1902; Ducke 1912). According to G. Melo (personal communication, 2007), *M. rufipes* is restricted to the continental mainland; a revision of the species is in preparation and will clarify the proper names and distributions of the Antillean species, not clarified in Moure et al. (2007).

Xylocopa (Neoxylocopa) mordax F. Smith (Figs. 28 and 29)

Xylocopa mordax F. Smith, 1874b: 294. Holotype female in BMNH.

GD: British Virgin Islands (Guana Island), Hispaniola, Jamaica, Lesser Antilles, and Puerto Rico (including key Caja de Muerto and Mona Island) (Hurd 1978).

This species has been misidentified throughout the Caribbean as either *X. brasiliatorum* (Linnaeus, 1767) or, less frequently, as *X. morio* (Fabricius, 1793). Both misidentifications refer to Brazilian species not present in the West Indies (Hurd 1978). Moure (2003) provided taxonomic notes on *X. mordax*. The common name of this species in Puerto Rico is “cigarrón” (large cigar). Martorell (1976) and O’Farril-Nieves and Medina-Gaud (2007) mention that this species drills into dry branches and tree trunks. Jackson and Woodbury (1976) and Jackson (1986) studied the nectar and pollen-gathering activities and nesting sites of *X. mordax*. Rivera-Marchand and Ackerman (2006) determined that this species was the only effective pollinator of the cactus *Pilosocereus royerii* (L.) Byles and Rowley.

Apis (Apis) mellifera Linnaeus

Apis mellifera Linnaeus, 1758: 576.

Refer to Engel (1999a) for complete synonymy.

GD: Cosmopolitan; present on most or all of the islands of Greater Puerto Rico, except Mona Island.

The domestic honey bee, introduced from Europe by colonists in the 17th century (Engel 1999a), has colonized Puerto Rico for a long time. According to Ledru (1863) and Gundlach (1887), the species was already well established in the island's non-cultivated habitats.

Species excluded from the Greater Puerto Rican catalogue

Several reports by previous authors indicating the presence of bee species in Puerto Rico are likely based on misidentifications. In the absence of any verifiable records we have excluded these species from the above list.

Agapostemon (Agapostemon) poeyi (Lucas, 1856)

GD: Bahamas, Cuba, and Hispaniola (Roberts 1972).

Moure and Hurd (1987) cited *A. poeyi* from Puerto Rico and Genaro (2007), following these authors, did the same. However, there is no reliable evidence that this species occurs in Puerto Rico. The specimens cited by Dewitz (1881) as *A. festivus* Cresson, 1865 (a synonym of *A. poeyi*), and as *A. poeyi* were in all likelihood misidentifications.

Centris ornatifrons "Cresson"

This name, used in Wolcott (1936), is a *nomen nudum* because Cresson never described such a species (R. Snelling, personal communication 1999). We were unable to locate specimens under this name in the Wolcott collection located at MEBT-MC, and therefore cannot ascertain which species he may have seen.

Halictus (Odontalisctus) ligatus Say *sensu lato*

GD: Bahamas, Canada, Central America south to Colombia, Cuba, Jamaica, Trinidad, and United States (Moure and Hurd 1987).

This species was previously regarded as the most widespread halictine species in the New World, however recent electrophoretic and molecular analyses have shown that two species are involved (Carman and Packer 1997; Danforth et al., 1998). The Caribbean species is *Halictus poeyi* Lepeletier (Carman and Packer 1997; Genaro 2007; L. Packer and J. A. Genaro, unpublished data). Ashmead (1900) recorded *H. ligatus* as occurring in Puerto Rico, under the synonym *H. poeyi* Lepeletier. However, Wolcott (1948) expressed the view that *H. poeyi* as listed by Ashmead is actually one of the *Lasioglossum (Dialictus)* species listed above. In absence of evidence to the contrary, we accept Wolcott's conclusions.

Melissodes (Eumelissodes) mimica (Cresson, 1869)

GD: Cuba and Hispaniola.

Recorded from Puerto Rico by Ståhl (1882), Gundlach (1887), and Friese (1902). These records are apparently misidentifications of *M. trifasciata*.

Paleogeography and origin of bee fauna

The Greater Antilles have existed as emerging land masses since the middle Eocene (ca. 45 mya), thus presenting favorable conditions for biota that would arrive from neighboring continental habitats (Iturralde-Vinent and MacPhee 1999; MacPhee and Iturralde-Vinent 2000). The constantly changing geographic scenario of the Caribbean region provided either barriers or highways for faunal exchanges and the evolution of ecosystems (Iturralde-Vinent 2006). The transition from Late Eocene to Early Oligocene (37-33 mya) was one of the most important periods of significant land connection, as this period was characterized by a "landspan", i.e. a subaerial connection from the northern South America to the proto-Antillean zone including central Cuba (Iturralde-Vinent and MacPhee 1999; MacPhee and Iturralde-

Vinent 2000; Iturralde-Vinent 2006). This landspan, named GAARlandia (Greater Antilles + Aves Ridge), facilitated the dispersal of biota including the bee fauna.

On the other hand, the area of the Nicaragua Rise included lowlands and shallow marine habitats which reduced the distance between Central America and parts of the land masses that would eventually make up Jamaica and Hispaniola (Iturralde-Vinent 2006), thus further promoting the passage of biota towards the proto-Antilles. Subsequently, and in the course of many millenia, these connections were interrupted while other parts of land masses emerged or submerged until the present geographic configuration became established (Iturralde-Vinent and MacPhee 1999).

The successive climatic changes over the past three million years have impacted the biota (Curtis et al. 2001). These temporally and regionally restricted effects may explain why the bee fauna documented in Dominican Amber (Michener and Poinar 1997; Camargo et al. 2000; Engel 1995, 1999b, 1999c, 2001b), which would be expected to also inhabit nearby islands such as Puerto Rico, differs from the actual fauna, suggesting past events of massive extinction. A similar pattern is seen in a variety of other insect lineages documented in Dominican amber (e.g., Grimaldi and Engel 2005; Engel and Grimaldi 2007). The present-day bee fauna of Puerto Rico is most likely the result of multiple succeeding colonizations from the continent, entering the islands and dispersing among them, even though island/island vicariance events were significant during the region's earlier geological periods. Martorell (1945) examined the origins of the Puerto Rican insect fauna, concluding that most elements came from South and Central America. This conclusion is also valid for the bee fauna.

Faunal composition

The Greater Puerto Rican bee fauna is composed of four elements: exclusive Greater Puerto Rico area endemics (26.5%); Antillean endemics occurring on multiple islands (76.5%); continental species that have also colonized the Antilles (23.5%); and species introduced through human activity (12.8%). Among the native species, 21.6% have parasitic life habits.

With a total of 39 documented species, including those introduced by man, the bee fauna of Greater Puerto Rico is both low in its diversity and shows the highest level of disharmony in relation to other faunas of the Greater Antilles. Other authors reviewing the fauna of Puerto Rican invertebrates have been similarly surprised by a lower biodiversity in relation to the remaining Antillean islands, including Aguayo (1961; land snails); and A. Pérez-Asso (personal communication 2007; diplopods).

The absence of such typical Antillean bee genera as *Ceratina* Latreille, *Sphecodes* Latreille, *Microsphecodes* Eickwort and Stage, *Triepeolus* Robertson and *Colletes* Latreille is remarkable. *Hylaeus* is represented only by one undescribed species occurring on Guana Island (R. R. Snelling, personal communication 1998).

Over the past 100 years Greater Puerto Rico has experienced a massive degradation of primary natural ecosystems (e.g., Wadsworth 1950), with as little as 6% of the main island's area covered by forest in the late 1940s (Birdsey and Weaver 1967). This period was followed by an increasing awareness of the importance and fragile nature of the native plant and animal communities (e.g., Ewel and Whitmore 1973). In the early 1990s the forest cover had returned to 42% (Helmer et al. 2002), yet urban sprawl has increased concomitantly and continues to put pressure on the reforested areas (Helmer 2004).

Deforestation and other human-induced activities have undoubtedly led to a significant imbalance in the ecological conditions required for many insect species to survive. Because of that, we will never know how many species of insects once inhabited the Island and were never recorded by early scientists (cf. Martorell 1945).

Many of the reported Puerto Rican endemics seem to have very low population levels and highly restricted distributions; e.g. *Coelioxys spinosa*, *Coelioxys* n. sp., *Lasioglossum eickwortellus*, *Nesosphecodes anthracinus*, and *Xeromelecta tibialis*. This inference is supported by the scarcity of collection records as well as direct lack of observations in the field. These small populations are susceptible to habitat changes and thus endangered in light of an increasing fragmentation and loss of natural habitats.

The Guánica Dry Forest of southwestern Puerto Rico has the highest diversity of bee species within the region, which may be explained by its xerophytic conditions that favor the development of the brood

and tend to produce a high diversity of flowers. Guánica is a well preserved habitat with an appropriately high conservation status.

Bee fauna of Mona island

Among all islands adjacent to Puerto Rico, Mona Island is of greatest interest in light of its size, geographic location, conservation state, and geological trajectory. The Island has a recent origin - emerging in the Pliocene or early Pleistocene - and has never been connected to the nearby landmasses of Hispaniola or Puerto Rico (see Peck and Kukalova-Peck 1981; Smith et al. 1994; Frank et al. 1998; MacPhee et al. 2003). Thus Mona's bee species necessarily arrived on the Island via dispersal, mainly through active flight or by being swept there by winds. The genus *Centris* has the highest number of species, with four species presently reported. Several of these are ground nesting (e.g., *C. smithii*, *C. decolorata*, *C. haemorrhoidalis*) and occur along coasts. These habits may frequently lead to dispersal, as evidenced by their wide distributions spanning many Caribbean islands. At present 13 bee species have been documented on Mona, yet none of them are endemics. The main directionality of dispersal is probably from east to west, given that Puerto Rican and Lesser Antillean species dominate the Island's fauna. From the west, Hispaniola has contributed to a lesser extent to the overall species composition.

Females and males of *Lasioglossum (Dialictus)* sp. were very common at flowers of *Mamillaria nivosa* Link. (Cactaceae) in the high plateau around Caigo y no Caigo locality, perhaps playing an important role in pollination of the snowy cactus.

Three males of *Exomalopsis* sp. were examined; these were collected in January and February of 2002 and are located in the Miguel A. García personal collection. They constitute the first record of *Exomalopsis* from Mona Island.

Interestingly, *Apis mellifera* has not been introduced, which means that this island is a suitable laboratory for ecological studies of native Caribbean bee assemblages.

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