Acta Zoológica Mexicana (n.s.) 20(1): 99-117 (2004)

DISTRIBUTIONAL PATTERNS OF THE NEOTROPICAL AND ANDEAN SPECIES OF THE GENUS *BOMBUS* (HYMENOPTERA: APIDAE)

Alberto H. ABRAHAMOVICH[1], Norma B. DÍAZ[1] and Juan J. MORRONE[2]
[1] División Entomología, Museo de La Plata,
Paseo del Bosque, 1900 La Plata, ARGENTINA
[2] Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias,
Universidad Nacional Autónoma de México (UNAM),
Apdo. Postal 70-399, 04510 Mexico D.F., MEXICO

RESUMEN

Se analizaron los patrones de distribución de especies neotropicales y andinas del género *Bombus* Latreille, comparando los trazos individuales de 36 especies. Se hallaron ocho trazos generalizados: (1) Mexicano de Montaña (*B. [Fv.] fervidus* [Fabricius], *B. [Br.] haueri* Handlirsch, *B. [Pr.] hunti* Greene y *B. [Cu.] rufocinctus* Cresson); (2) Mesoamericano Septentrional (*B. [Br.] brachycephalus* Handlirsch, *B. [Fv.] diligens* Smith, *B. [Ds.] macgregori* Labougle & Ayala y *B. [Fv.] steindachneri* Handlirsch); (3) Mesoamericano Meridional (*B. [Fv.] digressus* [Milliron] y *B. [Ps.] variabilis* [Cresson]); (4) Mesoamericano Amplio (*B. [Pr.] ephippiatus* Say, *B. [Fv.] medius* Cresson, *B. [Fv.] mexicanus* Cresson, *B. [Fv.] pennsylvanicus* [DeGeer] y *B. [Fv.] weisi* Friese); (5) Andino Septentrional (*B. [Cc.] coccineus* Friese, *B. [Rb.] ecuadorius* Meunier, *B. [Fv.] excellens* Smith, *B. [Fr.] funebris* Smith, *B. [Ds.] handlirschi* Friese, *B. [Rb.] hortulanus* Friese, *B. [Rb.] melaleucus* Handlirsch, *B. [Fv.] pullatus* Franklin, *B. [Rb.] robustus* Friese, *B. [Fr.] rohweri* Frison y *B. [Rc.] rubicundus* Smith); (6) Yungas (*B. [Cc.] baeri* Vachal y *B. [Rb.] tucumanus* Vachal); (7) Brasileño Austral (*B. [Fv.] bellicosus* Smith y *B. [Fv.] brasiliensis* Lepeletier); y (8) Sudamericano Amplio (*B. [Fv.] atratus* Franklin, *B. [Fv.] morio* [Swederus], *B. [Fv.] opifex* Smith y *B. [Fv.] transversalis* [Olivier]). Se determinaron tres nodos panbiogeográficos: (A) Istmo de Tehuantepec, en la intersección de los trazos generalizados Mesoamericano Septentrional y Mesoamericano Meridional; (B) Panamá, en la intersección de los trazos generalizados Mesoamericano Austral y Andino Septentrional, y (C) Puna, en la intersección de los trazos generalizados Andino Septentrional y Yungas. Estos patrones refelejan la compleja historia biogeográfica de las regiones Neotropical y Andina.
Palabras Clave: Apidae, región Neotropical, región Andina, panbiogeografía.

ABSTRACT

Distributional patterns of the Neotropical and Andean species of the genus *Bombus* Latreille were analyzed, by comparing individual tracks of 36 species. Eight generalized tracks were found: (1) Mexican Mountain (*B. [Fv.] fervidus* [Fabricius], *B. [Br.] haueri* Handlirsch, *B. [Pr.] hunti* Greene, and *B. [Cu.] rufocinctus* Cresson); (2) Northern Mesoamerican (*B. [Br.] brachycephalus* Handlirsch, *B. [Fv.] diligens* Smith, *B. [Ds.] macgregori* Labougle & Ayala, and *B. [Fv.] steindachneri* Handlirsch); (3) Southern Mesoamerican (*B. [Fv.] digressus* [Milliron] and *B. [Ps.] variabilis* [Cresson]); (4) Widespread Mesoamerican (*B. [Pr.] ephippiatus* Say, *B. [Fv.] medius* Cresson, *B. [Fv.] mexicanus* Cresson, *B. [Fv.] pennsylvanicus* [DeGeer], and *B. [Fv.] weisi* Friese); (5) Northern Andean (*B. [Cc.] coccineus* Friese, *B. [Rb.] ecuadorius* Meunier, *B. [Fv.] excellens* Smith, *B. [Fr.] funebris* Smith, *B. [Ds.] handlirschi* Friese, *B. [Rb.] hortulanus* Friese, *B. [Rb.] melaleucus* Handlirsch, *B. [Fv.] pullatus* Franklin, *B. [Rb.] robustus* Friese, *B. [Fr.] rohweri* Frison, *and B. [Rc.] rubicundus* Smith); (6) Yungas (*B. [Cc.] baeri* Vachal and *B. [Rb.] tucumanus* Vachal); (7) Southern Brazilian (*B. [Fv.] bellicosus* Smith and *B. [Fv.] brasiliensis* Lepeletier) and (8) Widespread South American (*B. [Fv.] atratus* Franklin, *B. [Fv.] morio* [Swederus], *B. [Fv.] opifex* Smith, and *B. [Fv.] transversalis* [Olivier]). Three panbiogeographic nodes were determined: (A) Isthmus of Tehuantepec, in the intersection of the Northern and Southern Mesoamerican generalized tracks; (B) Panama, in the intersection of the Southern Mesoamerican and Northern Andean generalized tracks, and (C) Puna, in the

intersection of the Northern Andean and Yungas generalized tracks. These patterns reflect the complex biogeographic history of the Neotropical and Andean regions.
Key Words: Apidae, Neotropical region, Andean region, panbiogeography.

INTRODUCTION

The genus *Bombus* Latreille belongs to the monotypic tribe Bombini (Hymenoptera: Apidae), comprising 239 known species (Williams 1985, 1998). The majority of these species are distributed in the temperate areas of North America and Eurasia (Lievano *et al*. 1991). In the Neotropical and Andean regions, 42 species have been recorded in a great variety of habitats, from sea level up to about 4400 m in the Andes. In spite of broad interest in the group, their large-scale distribution has received little attention, but promise to contribute with some interesting patterns.

In order to elucidate the biogeographic history of the genus *Bombus* in the Neotropical and Andean regions, we analyze herein the geographical distribution of the species assigned to it, applying a track analysis.

MATERIAL AND METHODS

Distributional data for this study were obtained from the literature (Franklin 1913, Frison 1925, Moure & Sakagami 1962, Milliron 1971, 1973a,b, Labougle 1990, Lievano *et al*. 1991, Williams 1998, Michener 2000, Abrahamovich & Díaz 2001, Silveira *et al*. 2002) and from the labels of specimens from the collections of the Museo Argentino de Ciencias Naturales, Buenos Aires; Museo de La Plata, La Plata; and Instituto y Fundación Miguel Lillo, San Miguel de Tucumán. Imprecise localities were not considered. We excluded from the analysis six species known from a single locality (*B. [Cr.] crotchii* Cresson, *B. [Fr.] fraternus* [Smith], *B. [Bi.] nevadensis* Cresson and *B. [Fv.] rubriventris* Lepeletier), from few close localities (*B. [Fv.] trinominatus* Dalla Torre) or introduced (*B. [Mg.] ruderatus* [Fabricius]). Classification and subgenus acronyms follow Williams (1998). The area basically corresponds to the Neotropical and Andean regions (Morrone 2001a).

The panbiogeographic approach basically consists of plotting distributions of different taxa on maps, connecting their localities together with lines called individual tracks. When individual tracks for different taxa coincide, the resulting summary lines are considered generalized tracks, which indicate the preexistence of ancestral biotas that become fragmented by tectonic and/or climatic changes. If two or more generalized tracks intersect, they determine a node, which indicates that different ancestral biotic and geological fragments interrelate in space/time, constituting a composite area. For details of the track methodology see Morrone & Crisci (1995) and Craw *et al*. (1999).

RESULTS

Individual tracks. Individual tracks corresponding to the species of *Bombus* are represented in the maps of figures 1-13.

Bombus (Br.) brachycephalus Handlirsch (Fig. 1) is distributed from central Mexico to northern Central America (Mexico: Chiapas, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosí, and Veracruz; Guatemala: Chimaltenango, Guatemala, San Marcos, and Zacapa; Honduras: Tegucigalpa; El Salvador: Chalatenango).

Figure 1
Individual tracks of species of *Bombus (Br.) brachycephalus* Handlirch and *B. (Fv.) atratus* Franklin.

Bombus (Fv.) atratus Franklin (Fig. 1) is distributed from northwestern South America to southeastern Brazil, Uruguay, and central Argentina (Colombia: Antioquia, Bolívar, Boyacá, Cundinamarca, Distrito Capital, Magdalena, Nariño, Quindío, Santander, and Valle del Cauca; Venezuela: Carabobo, Distrito Capital, and Mérida; Ecuador: Azuay and Guayas; Peru: Cuzco and San Martín; Bolivia: Beni, Cochabamba, La Paz, and Santa Cruz; Paraguay: Alto Paraná, Caaguazú, Caazapá, Central, Concepción, Cordillera, Guairá, Itapúa, San Pedro, and Villa Hayes; Brazil: Bahía,

Espirito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Rondônia, and Santa Catarina; Uruguay: Artigas, Canelones, Colonia, Durazno, Florida, Maldonado, Montevideo, Paysandú, Rivera, San José, and Tacuarembó; Argentina: Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, La Rioja, Neuquén, Mendoza, Misiones, Río Negro, Salta, Santa Fe, Santiago del Estero, and Tucumán).

Bombus (Fv.) digressus (Milliron) (Fig. 2) is distributed in Central America: Guatemala (Escuintla) and Costa Rica (Puerto Limón and Cartago).

Bombus (Fv.) brevivillus Franklin (Fig. 2) is distributed from northern Guyana to northeastern and central Brazil (Alagoas, Amapá, Bahía, Ceará, Espírito Santo, Goiás, Mato Grosso, Matto Grosso do Sul, Minas Gerais, Pará, Paraíba, Pernambuco, Rio de Janeiro, and Rio Grande do Norte).

Figure 2
Individual tracks of species of *Bombus (Fv.) digressus* (Milliron), *B. (Fv.) brevivillus* Franklin, *B. (Cc.) baeri* Vachal and *B. (Fv.) bellicosus* Smith.

Bombus (Cc.) baeri Vachal (Fig. 2) is distributed from southern Peru to northwestern Argentina (Peru: Arequipa, Cuzco, and Puno; Bolivia: La Paz and Potosí; Argentina: Catarmarca, Jujuy, La Rioja, Salta, and Tucumán).

Bombus (Fv.) bellicosus Smith (Fig. 2) is distributed from southern Brazil to central Patagonia, Argentina (Brazil: Paraná and Rio Grande do Sul; Uruguay: Artigas, Colonia, Durazno, Flores, Florida, Lavalleja, Maldonado, Montevideo, Paysandú, San José, and Soriano; Argentina: Buenos Aires, Córdoba, Corrientes, Chubut, Entre Ríos, La Pampa, Misiones, Río Negro, San Luis, Santa Fe, and Santiago del Estero).

Bombus (Fv.) diligens Smith (Fig. 3) is distributed from northwestern Mexico (Distrito Federal, Mexico, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, San Luís Potosí, Sinaloa, and Veracruz) to southwestern Guatemala (Guatemala and Sololá).

Bombus (Rc.) rubicundus Smith (Fig. 3) is distributed from northern Venezuela to western Bolivia (Venezuela: Amazonas and Trujillo; Colombia: Bolivar, Boyacá, Cundinamarca, and Nariño; Ecuador: Azuay, Pichincha, and Tungurahua; Peru: Ancash and La Libertad; Bolivia: Cochabamba).

Figure 3
Individual tracks of species of *Bombus (Fv.) diligens* Smith, *B. (Rc.) rubicundus* Smith, *B. (Fv.) brasiliensis* Lepeletier and *B. (Fv.) dahlbomii* Guérin.

Bombus (Fv.) brasiliensis Lepeletier (Fig. 3) is distributed from central and southern Brazil to southern Uruguay (Brazil: Espirito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, and São Paulo; Paraguay: Alto Paraná, Caaguazú, Central, Cordillera, Guairá, Itapúa, Paraguari, and San Pedro; Argentina: Misiones; Uruguay: Maldonado).

Bombus (Fv.) dahlbomii Guérin (Fig. 3) is distributed from central Chile and Argentina to the south of both countries (Chile: Región Metropolitana, Maule, Bío-Bío, Valparaíso, Magallanes, Los Lagos, Araucanía, and Aisén; Argentina: Buenos Aires, Chubut, Mendoza, Neuquén, Río Negro, and Santa Cruz).

Bombus (Pr.) ephippiatus Say (Fig. 4) is distributed from northern Mexico to northwestern South America (Mexico: Chiapas, Chihuahua, Distrito Federal, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Tabasco, Veracruz, and Zacatecas; Guatemala: Alta Verapaz, Chimaltenango, Chiqué, Escuitla, Guatemala, Huehuetenango, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, and Sololá; El Salvador: Ahuachapán, La Libertad, and Morazán; Honduras; Costa Rica: Alajuela, Cartago, Guanacaste, Heredia, Irazú, Puerto Limón, Puntarenas, and San José; Panama: Chiriquí).

Figure 4
Individual tracks of species of *Bombus (Pr.) ephippiatus* Say and *B. (Rb.) ecuadorius* Meunier.

Bombus (Rb.) ecuadorius Meunier (Fig. 4) is distributed from northern Ecuador to central Bolivia (Ecuador: Bolívar, Chimborazo, and Pichincha; Peru: Arequipa, Ayacucho, Cuzco, and Piura; Bolivia: Cochabamba and La Paz).

Bombus (Fv.) fervidus (Fabricius) (Fig. 5) is only found in northern and central Mexico (Chihuahua, Distrito Federal, Durango, Guanajuato, Mexico, Morelos, and Puebla).

Bombus (Ds.) macgregori Labougle & Ayala (Fig. 5) is distributed from Jalisco and Guerrero in Mexico to Quetzaltenango in Guatemala.

Bombus (Fv.) excellens Smith (Fig. 5) is distributed from northern Colombia and Venezuela to central Bolivia (Venezuela: Mérida, Distrito Capital, and Falcón; Colombia: Cauca and Magdalena; Peru: Piura, Junín, and Huánuco; Bolivia: Cochabamba and La Paz).

Figure 5
Individual tracks of species of *Bombus (Fv.) fervidus* (Fabricius), *B. (Ds.) macgregori* Labougle & Ayala and *B. (Fv.) excellens* Smith.

Bombus (Br.) haueri Handlirsch (Fig. 6) is distributed in northern and central Mexico (Coahuila, Chihuahua, Distrito Federal, Durango, Mexico, Guanajuato, Jalisco, Michoacán, Morelos, and Nuevo León).

Bombus (Fn.) rohweri Frison (Fig. 6) is distributed from northwestern Venezuela to central Peru (Venezuela: Mérida and Trujillo; Colombia: Distrito Capital; Peru: Ancash).

Bombus (Fn.) funebris Smith (Fig. 6) is distributed from western Colombia to western Bolivia (Colombia: Cundinamarca and Nariño; Ecuador: Azuay, Guayas, Loja, Los Ríos, Pastaza, Pichincha, and Tungurahua; Peru: Ancash, Arequipa, Ayacucho, Cajamarca, Cuzco, Junín, Lima, Piura, and Puno; Bolivia: Cochabamba and La Paz).

Figure 6
Individual tracks of species of *Bombus (Br.) haueri* Handlirsch, *B. (Fr.) rohweri* Frison and *B. (Fr.) funebris* Smith.

Bombus (Pr.) huntii Greene (Fig. 7) is distributed in northern and central Mexico (Coahuila, Chihuahua, Mexico, Jalisco, Michoacán, Nuevo León, and Veracruz).

Bombus (Rb.) hortulanus Friese (Fig. 7) is distributed from northern Colombia to west of Ecuador (Colombia: Bolívar, Cundinamarca, and Magdalena; Venezuela: Mérida; Ecuador: Guayas and Tungurahua).

Bombus (Ds.) handlirschi Friese (Fig. 7) is distributed in southern Venezuela, Ecuador, Peru and western Bolivia (Venezuela: Amazonas; Ecuador; Peru: Ayacucho, Cuzco, Junín, Piura, and Puno; Bolivia: La Paz).

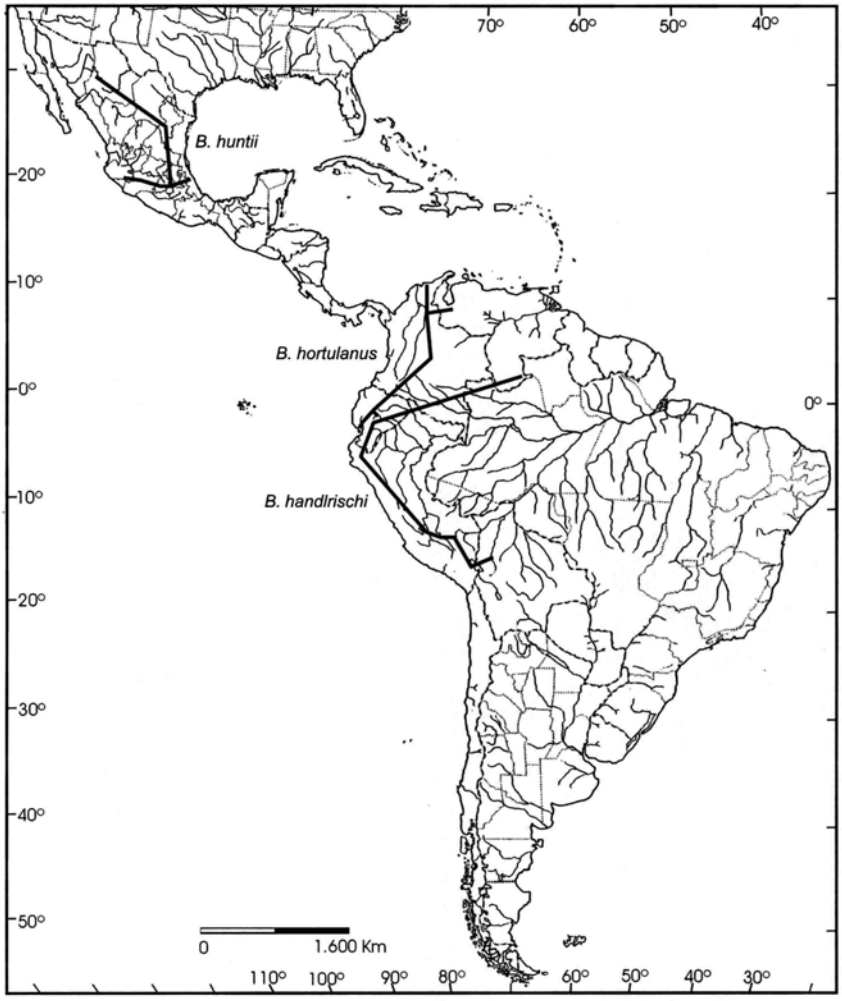

Figure 7
Individual tracks of species of *Bombus (Pr.) huntii* Greene, *B. (Rb.) hortulanus* Friese and *B. (Ds.) handlrischi* Friese.

Bombus (Fv.) medius Cresson (Fig. 8) is distributed from central Mexico to southern Central America (Mexico: Campeche, Chiapas, Durango, Mexico, Hidalgo, Oaxaca, Puebla, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, Veracruz, and Yucatán; Guatemala: Guatemala and San Marcos; El Salvador: San Salvador; Honduras: Comayagua, Cortés, El Paraíso, Morazán, and Yoro; Nicaragua: Nueva Segovia; Panama: Chiriquí).

Bombus (Fv.) morio (Swederus) (Fig. 8) is distributed from northwestern South America to southeastern Brazil, Uruguay and northern Argentina (Venezuela: Carabobo; Colombia: Santander; Ecuador: Pichincha and Tungurahua; Peru: Cuzco, Lima, and San Martín; Bolivia: Beni, Cochabamba, La Paz, Potosí, Santa Cruz, and Tarija; Paraguay: Alto Paraná, Caaguazú, Caazapá, Central, Cordillera, Guairá, Itapúa, and Paraguari; Brazil: Bahía, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo, and Spirito Santo, Uruguay: Montevideo; Argentina: Catamarca, Chaco, Corrientes, Formosa, Jujuy, Misiones, Salta, Santa Fe, Santiago del Estero, and Tucumán).

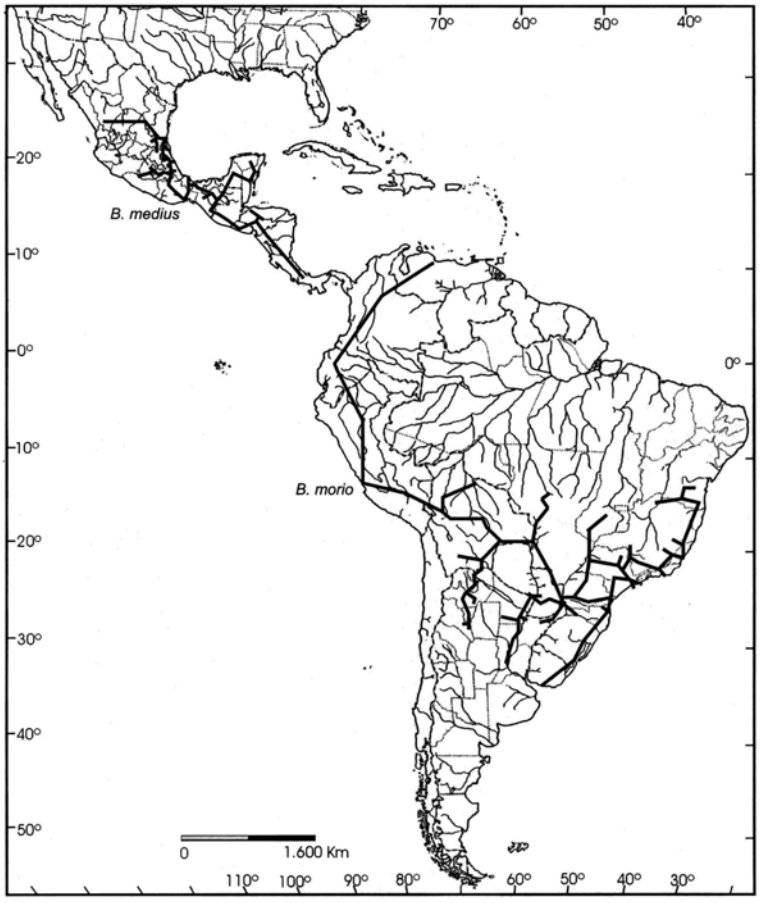

Figure 8
Individual tracks of species of *Bombus (Fv.) medius* Cresson and *B. (Fv.) morio* (Swederus).

Bombus (Fv.) pennsylvanicus (DeGeer) (Fig. 9) is distributed from northern Mexico to northern Central America (Mexico: Aguascalientes, Baja California, Baja California Sur, Chiapas, Chihuahua, Coahuila, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, Mexico, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Veracruz, and Zacatecas; Guatemala: Izabal).

Bombus (Rb.) melaleucus Handlirsch (Fig. 9) is distributed from southern Central America (Costa Rica: Alajuela, Cartago, Puntarenas, and San José; Panama: Chiriquí) to northwestern South America (Colombia: Cauca, Magdalena, and Meta; Venezuela: Amazonas; Ecuador: Esmeraldas and Tungurahua; Peru: Ancash, Ayacucho, Cuzco, Huanuco, Ica, Lima, and Piura; Bolivia: Cochabamba and La Paz).

Figure 9
Individual tracks of species of *Bombus (Fv.) pennsylvanicus* (DeGeer) and *B. (Rb.) melaleucus* Handlirsch.

Bombus (Fv.) mexicanus Cresson (Fig. 10) is distributed from central Mexico to Colombia and Ecuador in South America (Mexico: Chiapas, Jalisco, Michoacán, Oaxaca, Puebla, San Luis Potosí, and Veracruz; Guatemala: Chimaltenango, Escuintla, Guatemala, Quetzaltenango, Retalhuleu, San Marcos, Sololá, and Suchitepéquez; El Salvador: La Libertad, La Paz, and Morazán, San Salvador; Honduras: Choluteca and Francisco Morazán; Nicaragua: Carazo, Jinotega, Managua, and Rivas; Costa Rica: Cartago, Guanacaste, Heredia, Puerto Limón, Puntarenas, and San José; Panama: Chiriquí; Colombia; Ecuador).

Bombus (Fv.) opifex Smith (Fig. 10) is distributed from central Ecuador to central Argentina (Ecuador: Tungurahua; Peru: Arequipa and Puno; Bolivia: Cochabamba and La Paz; Paraguay: Cordillera and Guairá; Argentina: Catamarca, Córdoba, Jujuy, La Rioja, Mendoza, Misiones, Salta, San Juan, San Luis, Santiago del Estero, Tucumán, and Formosa).

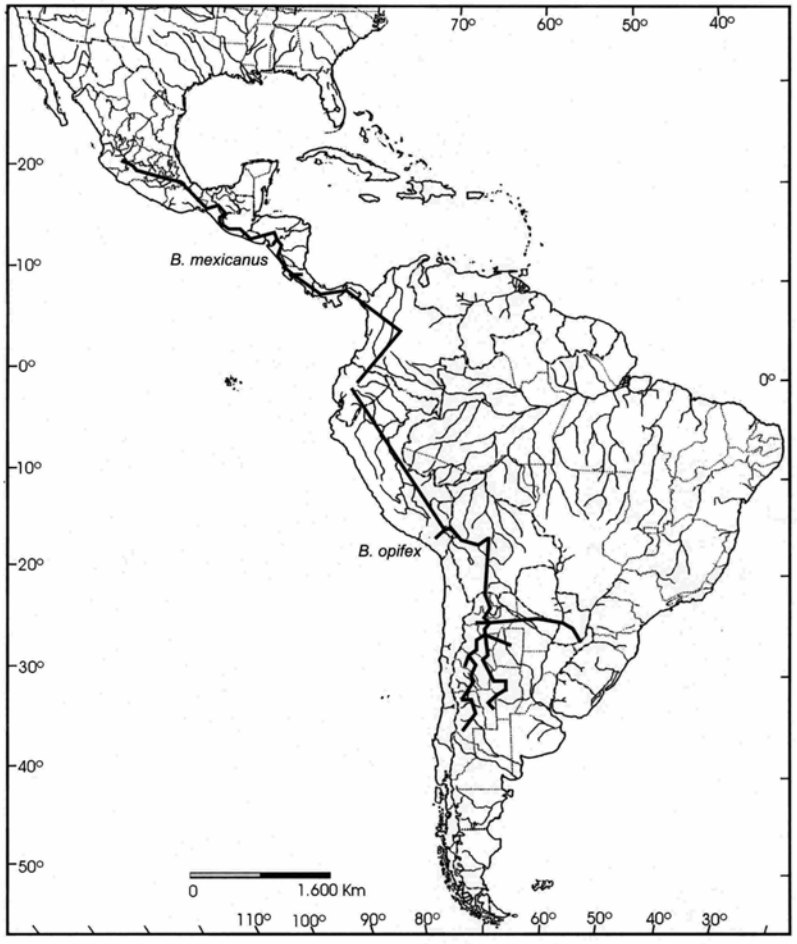

Figure 10
Individual tracks of species of *Bombus (Fv.) mexicanus* Cresson and *B. (Fv.) opifex* Smith.

Bombus (Cu.) rufocinctus Cresson (Fig. 11) is distributed in northern and central Mexico (Distrito Federal, Hidalgo, Mexico, Michoacán, Morelos, and Sonora).

Bombus (Ps.) variabilis (Cresson) (Fig. 11) is distributed from central Mexico (Puebla, Oaxaca) to Guatemala (Sololá, Guatemala) and Honduras.

Bombus (Fv.) pullatus Franklin (Fig. 11) is distributed from northern Central America to northwestern South America (Honduras: Atlántida, Cortés, and Santa Bárbara; Nicaragua: Atlántico Norte and Atlántico Sur; Costa Rica: Alajuela, Cartago, Guanacaste, Heredia, Puerto Limón, Puntarenas, and San José; Panama: Bocas del Toro, Chiriquí, Coclé, and Panama; Colombia: Boyacá, Caldas, Chocó, Cundinamarca, Distrito Capital, Huila, Magdalena, Meta, Santander, Tolima, and Valle del Cauca; Venezuela: Aragua, Carabobo, Miranda, Sucre, Mérida, and Zulia; Ecuador: Guaya).

Figure 11
Individual tracks of species of *Bombus (Cu.) rufocinctus* Cresson, *B. (Ps.) variabilis* (Cresson), *B. (Fv.) pullatus* Franklin, *B. (Cc.) coccineus* Friese and *B. (Rb.) tucumanus* Vachal.

Bombus (Cc.) coccineus Friese (Fig. 11) is distributed in central and southern Peru (Ancash, Apurimac, Cuzco, Junin, Lima, and Pasco).

Bombus (Rb.) tucumanus Vachal (Fig. 11) is distributed from western Bolivia (Cochabamba and La Paz) to northwestern Argentina (Catamarca, Jujuy, Salta, and Tucumán).

Bombus (Fv.) steindachneri Handlirsch (Fig. 12) is distributed in northwestern and central Mexico (Colima, Chihuahua, Distrito Federal, Durango, Mexico, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Sonora, and Veracruz).

Bombus (Rb.) robustus Friese (Fig. 12) is distributed from northern Colombia and Venezuela to central Ecuador (Colombia: Distrito Capital, Magdalena, Meta, Nariño, and Putumayo; Venezuela: Mérida; Ecuador: Azuay, Manabí, Pichincha, and Tungurahua).

Figure 12
Individual tracks of species of *Bombus (Fv.) steindachneri* Handlirsch and *B. (Rb.) robustus* Friese.

Bombus (Fv.) weisi Friese (Fig. 13) is distributed from northern Mexico to Costa Rica in Central America (Mexico: Chiapas, Chihuahua, Distrito Federal, Durango, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Morelos, Oaxaca, Puebla, San Luis Potosí, Sinaloa, and Tlaxcala; Guatemala: Chimaltenalgo, Escuntla, Huchuetenango, Jutiapa, Quezaltenango, Quiché, and San Marcos; Costa Rica: Cartago and San José).

Bombus (Fv.) transversalis (Olivier) (Fig. 13) is distributed from northern South America to central Bolivia (Colombia: Amazonas and Distrito Capital; Venezuela: Bolívar; Guyana; Surinam: Marowijne; French Guiana: Saint-Laurent-du-Maroni; Brazil: Acre, Amapá, Amazonas, Mato Grosso, Pará, and Rondônia; Peru: Huánuco, Junín, Loreto, Madre de Dios, Pasco, and Ucayali; Bolivia: Beni, Cochabamba, La Paz, and Santa Cruz).

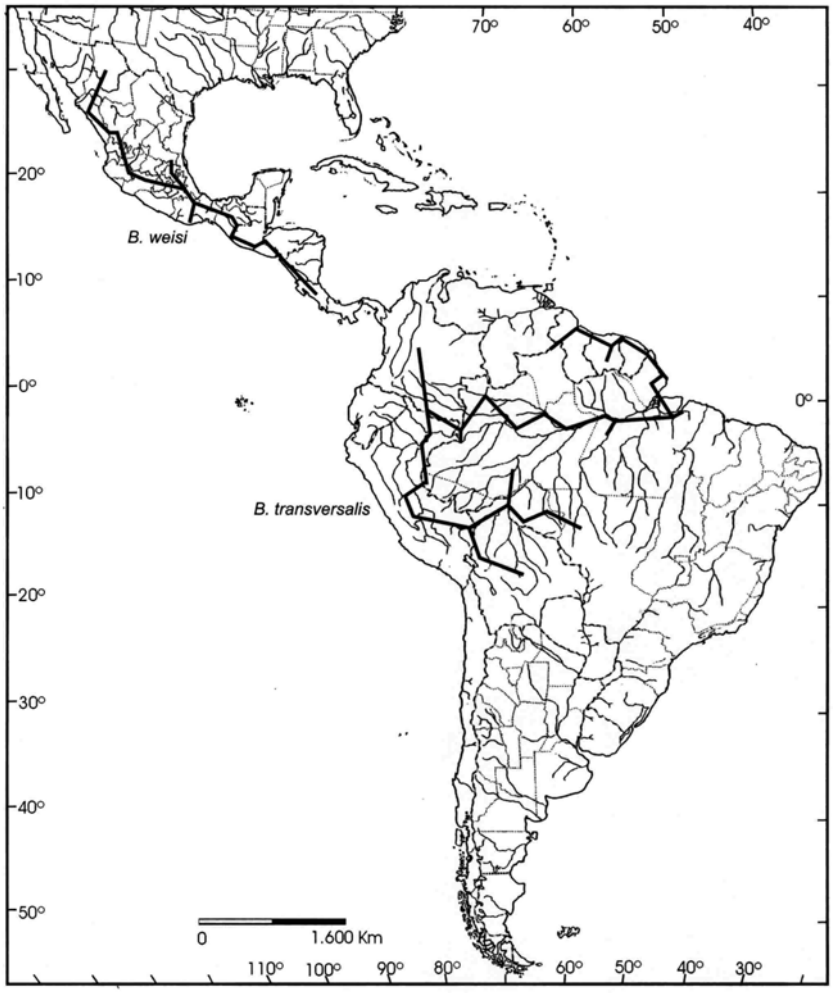

Figure 13
Individual tracks of species of *Bombus (Fv.) weisi* Friese and *B. (Fv.) transversalis* (Olivier).

Some common features of these individual tracks can be summarized as follows:
1. The geographical distribution of the majority of the species of *Bombus* is relatively restricted, with the exception of the widespread species *B. ephippiatus* (Fig. 4), *B. medius* (Fig. 8), *B. pennssylvanicus* (Fig. 9), *B. mexicanus* (Fig. 10), and *B. weisi* (Fig. 13) in Mesoamerica; and *B. (Fv.) atratus* (Fig. 1) and *B. (Fv.) morio* (Fig. 8) in South America.
2. Sixteen species are distributed in Mesoamerica (Neotropical region, Caribbean subregion), the remaining species being exclusively South American (Neotropical and Andean regions). Among the former, only *B. (Pr.) ephippiatus* (Fig. 4), *B. (Fv.) mexicanus* (Fig. 10), and *B. (Fv.) pullatus* (Fig. 11) reach northwestern South America.
3. Within the South American species, 10 (Figs. 1-3, 5, 7, 8, 10, 11, 13) are distributed in the Amazonian, Chacoan and Parana subregions of the Neotropical region, and 11 (2-4, 6, 7, 9, 11, 12) in the Andean region.

Generalized tracks and nodes. Comparison among the individual tracks revealed the existence of eight generalized tracks (Fig. 14):
Mexican mountain: determined by *B. (Fv.) fervidus, B. (Br.) haueri, B. (Pr.) hunti* and *B. (Cu.) rufocinctus.*
Northern Mesoamerican: determined by *B. (Br.) brachycephalus, B. (Fv.) diligens, B. (Ds.) macgregori*, and *B. (Fv.) steindachneri.*
Southern Mesoamerican: determined by *B. (Fv.) digressus* and *B. (Ps.) variabilis.*
Widespread Mesoamerican (1 + 2 + 3): determined by *B. (Pr.) ephippiatus, B. (Fv.) medius, B. (Fv.) mexicanus, B. (Fv.) pennsylvanicus*, and *B. (Fv.) weisi.*
Northern Andean: determined by *B. (Cc.) coccineus, B. (Rb.) ecuadorius, B. (Fv.) excellens, B. (Fv.) funebris, B. (Ds.) handlrischi, B. (Rb.) hortulanus, B. (Rb.) melaleucus, B. (Fv.) pullatus, B. (Rb.) robustus, B. (Fr) rohweri*,and *B. (Rc.) rubicundus.*
Yungas: determined by *B. (Cc.) baeri* and *B. (Rb.) tucumanus.*
Southern Brazilian: determined by *B. (Fv.) bellicosus* and *B. (Fv.) brasiliensis.*
Widespread South American (5 + 6 + 7): determined by *B. (Fv.) atratus, B. (Fv.) morio, B. (Fv.) opifex*, and *B. (Fv.) transversalis.*

Species *B. (Fv.) brevivillus* (Fig. 2) and *B. (Fv.) dahlbomii* (Fig. 3) are not assigned to any of the generalized tracks, because they do not show substantial overlap with other species.

Three panbiogeographic nodes were determined (Fig. 14):
(A) Isthmus of Tehuantepec: intersection of the Northern and Southern Mesoamerican generalized tracks.
(B) Panama: intersection of the Southern Mesoamerican and Northern Andean generalized tracks.
(C) Puna: intersection of the Northern Andean and Yungas generalized tracks.

DISCUSSION

Results of our analysis coincide with other studies, that have previously addressed the complex historical biogeography of the Neotropical and Andean regions. The Mexican

mountain generalized track is similar to the Northern generalized track from Morrone & Márquez (2001) and to the Transmexican Volcanic Belt and Sierra Madre Oriental generalized tracks from Márquez & Morrone (2003), based on beetle taxa (Coleoptera). The Southern Mesoamerican generalized track was also identified by Márquez & Morrone (2003). The Northern Andean generalized track was also recognized by Posadas *et al.* (1997) and Márquez & Morrone (2003), based on vascular plant and beetle taxa, respectively. Two of the nodes were also identified previously, the Isthmus of Tehuantepec node by Márquez & Morrone (2003) and the Puna node by Katinas *et al.* (1999).

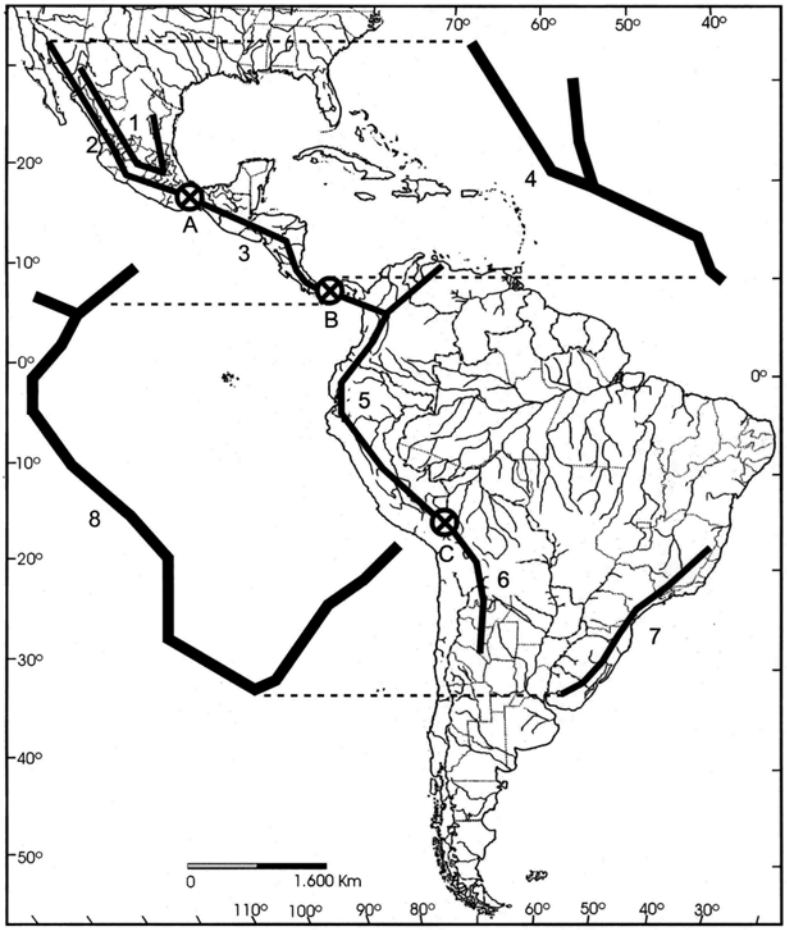

Figure 14

Generalized tracks and nodes of the genus *Bombus* in the Neotropical and Andean regions. 1, Mexican mountain generalized track; 2, Northern Mesoamerican generalized track; 3, Southern Mesoamerican generalized track; 4, Widespread Mesoamerican (1+2+3) generalized track; 5, Northern Andean generalized track; 6, Yungas generalized track; 7, Southern Brazilian generalized track; 8, Widespread South American (5+6+7) generalized track; A, Isthmus of Tehuantepec node; B, Panama node; C, Puna node.

On the other hand, some of the generalized tracks found in this study are coincident with subregions or provinces delimited in other studies. The Widespread Mesoamerican generalized track is coincident with the Mexican-Central American portion of the Caribbean subregion (Morrone 2001a, b). The Northern Andean generalized track is coincident with the Paramo Punan subregion of the Andean region, particularly with the Northern Andean Paramo and Puna provinces (Morrone 2001a, c). The Southern Brazilian generalized track is coincident with the Parana subregion of the Neotropical region (Morrone 2001a, 2002).

ACKNOWLEDGMENTS

Economic support to JJM by CONACyT grant 36488 is gratefully acknowledged.

LITERATURE CITED

Abrahamovich, A. H. & N. B. Díaz. 2001. Distribución geográfica de las especies del género *Bombus* Latreille (Hymenoptera, Apidae) en Argentina. *Revta. Bras. Entomol.*, 45: 23-36.

Craw, R. C., J. R. Grehan & M. J. Heads, M. J. 1999. *Panbiogeography: Tracking the history of life*. Oxford Biogeography Series 11, Oxford University Press, New York.

Franklin, H. J. 1913. The Bombidae of the New World. *Trans. Amer. Entomol. Soc.* 38: 177-486.

Frison, T. H. 1925. Contribution to the classification of the Bremidae (bumble-bees) of Central and South America. *Trans. Amer. Entomol. Soc.* 51: 137-165.

Katinas, L., J.J. Morrone & J. V. Crisci. 1999. Track analysis reveals the composite nature of the Andean biota. *Austr. Syst. Bot.* 47: 111-130.

Labougle, J. M. 1990. *Bombus* of Mexico and Central America (Hymenoptera, Apidae). *Kansas Univ. Sci. Bull.* 54: 35-73.

Lievano A., R. Ospina & G. Nates. 1991. Distribución altitudinal del género *Bombus* en Colombia. *Trianea* 4: 541-550.

Márquez, J. & J. J. Morrone. 2003. Análisis panbiogeográfico de las especies de *Homalolinus* y *Heterolinus* (Coleoptera: Staphylinidae: Xantholinini). *Acta Zool. Mex. (n.s.)* 90: 15-25.

Michener, C. D. 2000. *The bees of the world*. The John Hopkins University Press, Baltimore and London.

Milliron, H. E. 1971. A monograph of the western hemisphere bumblebees (Hymenoptera: Apidae: Bombinae) I. The genera *Bombus* and *Megabombus* subgenus *Bombias*. *Mem. Entomol. Soc. Canada* 82: 1-80.

_____. 1973a. A monograph of the western hemisphere bumblebees (Hymenoptera: Apidae: Bombinae) II. The genus *Megabombus* subgenus *Megabombus*. *Mem. Entomol. Soc. Canada* 89: 81-237.

_____. 1973b. A monograph of the western hemisphere bumblebees (Hymenoptera: Apidae: Bombinae) III. The genus *Pyrobombus* subgenus *Cullumanobombus*. *Mem. Entomol. Soc. Canada* 91: 238-333.

Moure, J. S. & S. F. Sakagami. 1962. As mamangabas sociais do Brasil (*Bombus* Latreille) (Hymenoptera, Apoidea). *Studia Entomol.* 5: 65-194.

Morrone, J. J. 2001a. *Biogeografía de América Latina y el Caribe*. Manuales y Tesis SEA, nro. 3. 148. Zaragoza.

_____. 2001b. Toward a cladistic model for the Caribbean subregion: Delimitation of areas of endemism. *Caldasia* 23: 43-76.

_____. 2001c. A formal definition of the Paramo-Punan biogeographic subregion and its provinces, based mainly on animal taxa. *Rev. Mus. Argent. Cienc. Nats., n. s.* 3:1-12.

_____. 2001. The Parana subregion and its provinces. *Physis,* 58 :1-7.

Morrone, J. J. & J. V. Crisci. 1995. Historical biogeography: Introduction to methods. *Annu. Rev. Ecol. Syst.* 26: 373-401.

Morrone, J. J. & J. Márquez. 2001. Halffter's Mexican Transition Zone, beetle generalised tracks, and geographical homology. *J. Biogeogr.* 28: 635-650.

Posadas, P. E., J. M. Estévez & J. J. Morrone. 1997. Distributional patterns and endemism areas of vascular plants in the Andean subregion. *Fontqueria* 48: 1-10.

Silveira F. A., G. A. R. Melo & E. A. B. Almeida. 2002. *Abelhas brasileiras: Sistemática e identificaçao.* Fernando A. Silveira, Belo Horizonte.

Williams, P. H. 1985. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Syst. Ent.* 10: 239-255.

_____. 1998. An annotated checklist of bumblebees with an analysis of patterns of description. *Bull. Nat. Hist. Mus., London (Entomol.)* 67: 79-152.

Recibido: 11 de diciembre 2002
Aceptado: 20 de julio 2003.