BIOGEOGRAPHY OF THE AREAS AND CANTHONINI (COLEOPTERA: SCARABAEIDAE) OF DRY TROPICAL FORESTS IN MESOAMERICA AND COLOMBIA

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RESUMEN

Este análisis biogeográfico examina los procesos históricos, geológicos, climáticos y ecológicos que han influido en la formación de los bosques tropicales secos (DTF) de Mesoamérica y Colombia, bosques que son sitios de múltiples historias biogeográficas como la que ilustran los Canthonini. Sometemos a prueba la hipótesis de que la fauna de Canthonini de los bosques tropicales secos tiene una afinidad sudamericana. Para este propósito comparamos las especies que se encuentran en un enclave de bosque tropical seco en México, en un segundo enclave en Costa Rica, en cuatro de la región Caribe de Colombia y finalmente uno más en el norte de Tolima en el valle superior del río Magdalena, Colombia. Las características geomorfológicas de los enclaves son también comparadas, así como la distribución geográfica y las afinidades taxonómicas de cada una de las especies de Canthonini que se encuentran en estos bosques tropicales secos. Los aspectos de historia biogeográfica, geológica y ecológica de los enclaves son evaluados usando un Análisis de Parsimonia de Endemicidad (PAE), utilizando como grupo externo dos lugares de selva siempre verde: Leticia (Amazonas, Colombia) y Los Tuxtlas (Veracruz, México). Este estudio pone de manifiesto que el origen y distribución de los bosques tropicales secos de la región ocurre durante el Pleistoceno, con una acentuación de las características de sequía durante el Holoceno. También revela similitudes entre los Canthonini de los bosques tropicales secos de México, Costa Rica y Colombia, con tres patrones de distribución que corresponden a diferentes grados de expansión hacia el norte y a la diversificación de líneas evolutivas, incluso a la presencia de especies sudamericanas.

La comparación entre el cladograma generado por las especies de Canthonini y el de eventos geológicos, indica que la distribución de los primeros en los bosques tropicales secos comienza en el Plioceno con el restablecimiento de la conexión panameña, sin evidencias de que eventos geomorfológicos previos hayan ejercido influencias. Por otra parte, hay muy pocas especies compartidas con las selvas siempre verdes usadas como grupo externo en los cladogramas.

Palabras Clave: Scarabaeinae, Canthonini, bosque tropical seco, México, Costa Rica, Colombia, patrones biogeográficos.

ABSTRACT

This biogeographical analysis examines the historical, geological, climatic and ecological processes that have influenced the formation of the dry tropical forests (DTF) of Mesoamerica and Colombia, areas that are the setting for multiple biogeographical stories that in this case are illustrated by the patterns and evolutionary processes of Canthonini. In this study we test the hypothesis that the Canthonini fauna of dry tropical forests has a South American affinity. To this end, we compare extant species from a tract of dry tropical forest in Mexico, a second enclave in Costa Rica, four from the Caribbean region of Colombia and finally one from the north of Tolima in the Upper Magdalena River Valley, Colombia. The geomorphological characteristics of the enclaves of DTF are also compared, as are the geographical distribution and

taxonomic affinities of each of the species found in these dry tropical forests. The biogeographical, historical and geological aspects of the enclaves were evaluated using a Parsimony Analysis of Endemicity (PAE), with two tropical rain forests as the outgroup: Leticia (Amazonas, Colombia) and Los Tuxtlas (Veracruz, Mexico).

This study reveals the origin and distribution of Neotropical dry forests in the Pleistocene, and the establishment of its dry conditions during the Holocene. It also reveals apparent similarities among the Canthonini of the dry tropical forests of Mexico, Costa Rica and Colombia, with three geographical distribution patterns that correspond to different degrees of expansion towards the north and the diversification of evolutionary lines, and even species of South American origin.

The comparison of the cladogram generated for species of Canthonini with that of the geological events that have occurred in the study regions indicates that the distribution of Canthonini in dry tropical forests began during the Pliocene with the re-establishment of the Panamanian connection, with no evidence of previous geomorphological events having any influence. On the other hand, there are few species shared with the tropical rain forests used as the outgroup for the cladograms.

Key Words: Scarabaeinae, Canthonini, dry tropical forest, Mexico, Costa Rica, Colombia, biogeographical patterns

INTRODUCTION

It has been suggested that tribe Canthonini (Scarabaeidae: Scarabaeinae) has an ancient Gondwanian distribution with high species richness in South America (Halffter 1974). In the Americas, the genus with the most species is *Canthon*, with 174 according to Halffter & Martínez (1977) that are distributed from Argentina to Canada. The origin of *Canthon* and close genera appears to be northern South America where it reaches its greatest richness in phyletic lines and species, with an expansion of lines toward the periphery of Chile where it is barely represented (Halffter 1974, Rivera-Cervantes & Halffter 1999). From South America, Central and North America were populated by elements of this tribe during two probable great expansion events (Halffter 1964, 1974, 1976, Kohlmann & Halffter 1990). The first could have occurred before or during the Miocene and the second when the connection with South and Central America was re-established from the Pliocene to the Recent. In the phyletic lines that participated in the first expansion, although it is possible to identify the South American affinities at the level of genus, there was notable speciation in Mexico and the United States of America, followed in some cases by secondary expansion. For those phyletic lines that participated in the second expansion event, the affinities with northern South America are much more marked, although there was also *in situ* speciation.

The objective of this study is to test this biogeographical hypothesis. To that end, we chose to use the species of Canthonini that inhabit dry tropical forest (DTF). These were selected because they are the least studied Scarabaeinae fauna compared to their tropical rain forest (TRF) counterparts and also because their distribution, now discontinuous, has been much less interrupted in the recent past.

This hypothesis regarding the biogeographical history of the Canthonini (common for other groups of Scarabaeinae and, in general, for insects) has been tested in various ways. First, by establishing the similarity of the Canthonini present in a series of enclaves found in DTF in Mexico, Costa Rica and Colombia – places for which we have reliable

lists of the fauna. Second, we have analyzed the historical and geological relationships of the regions where these enclaves are located in order to relate the history of the areas with both the phylogeny and the geographical distribution of Canthonini. Finally, the two previous points are integrated in order to recreate the setting of the DTF where the processes of speciation and dispersion of some Canthonini probably took place, and also to explain their geographic distribution. As proposed by Zunino (2005) we intend to compare the distribution and phylogenetic history of the taxa with the geography and geomorphological history of the areas to arrive at a comprehensive interpretation of the entire set of elements.

DTF, also known as tropical deciduous forest is defined as that formation of vegetation with a continuous woody cover distributed from sea level to 1000 m, with mean temperatures above 24 ºC and precipitation ranging from 700 to 2000 mm per year (Espinal 1985; IAvH 1997a). This vegetation has woody species that lose their leaves during the dry season over a variable period of time that lasts around six months (Rzedowski 1978).

According to Rzedowski (1978) DTF is particularly characteristic of the Pacific Slope of Mexico, where it covers extensive areas almost uninterrupted from the south of Sonora and southwest of Chihuahua to Chiapas, continuing southwards in Central America. It penetrates deep into the Balsas and the Santiago River basins, as well as those of the tributaries of these rivers. In the Isthmus of Tehuantepec, DTF passes the watershed and occupies a good part of the Central Depression of Chiapas. On the Atlantic Slope there are at least three large patches of DTF and it is also found on the Yucatan Peninsula (see Trejo 2005).

In Mexico, DTF once covered 6 to 14% (270 000 km^2) of the area in the country that lies between sea level and 1500 m. DTF has been reduced to 27% of its original cover (Trejo & Dirzo 2000). In Costa Rica almost all of the Nicoya Peninsula and Chira Island in the northeast of the country, were covered by this type of forest 100 years ago (Kohlmann *et al*. 2002). In Central America, DTF once covered 7% (33 600 km^2) of the total area between 0 and 1000 m. The remaining tropical dry forest in Central America probably represents less than 2% of the original (Sabogal & Valerio 1998). Colombia has three large regions with DTF and the two largest are the Caribbean Plain, including southern Guajira and the Magdalena River Valley in the Departments of Tolima, Cundinamarca and Huila (IAvH 1997b). In Colombia the status of DTF is critical. It is estimated that only 1% of the original 80 000 km^2 of dry to subhumid forests remains (Etter 1993). Figure 1 summarizes the distribution of DTF in the study area.

The biogeography of the areas of dry tropical forest is undertaken with cladistic analysis, keeping in mind the past and present geological and geomorphological characteristics of the area. In order to understand the biogeographical relationships between the enclaves of DTF and the species of Canthonini, we used a Parsimony Analysis of Endemicity (PAE) that produces a hierarchical set of the species represented in the different areas, and associates it with the geological or ecological factors, or a combination thereof. PAE can provide the grounds for explaining: 1) the effects of geological events on evolution; 2) the effects of ecological factors on evolution; 3) the influence of geological events on ecological conditions and the evolutionary consequences of these; 4) distribution patterns,

i.e. which sets of species can appear in different areas owing solely to events in geological history or the association of the latter with ecological conditions (Rosen 1988).

This study has two purposes, the first is to analyze the biogeographical history of the areas of dry tropical forest in Mesoamerica and Colombia based on their geomorphological characteristics and their geological origin; the second is to establish the relationships between these forests using the Canthonini as an indicator group, comparing their distribution with the geomorphological history of those areas and explaining the presence of Canthonini in dry forest.

First we carry out the biogeographical analysis of the neotropiocal dry forests that are the object of this study, and then the biogeographical analysis of the Canthonini. Some aspects of Canthonini in dry forest are discussed in light of other floristic, faunal, ecological and biogeographical elements that are particularly related to the Canthonini and the geographical limits of some species.

MATERIALS AND METHODS

Study sites:
The DTF sites we selected in Mesoamerica and Colombia are enclaves representative of the current distribution of this type of vegetation (Fig. 1). Chamela (Jalisco, Mexico) and Palo Verde (Guanacaste, Costa Rica) are located on the Pacific coast. In the Caribbean region of Colombia we selected four areas: Neguanje, Tierra Bomba, Los Colorados and Zambrano. In the Magdalena River Valley, we selected the DTF located in the north of the Department of Tolima. Two of the sites selected in the Caribbean region, Los Colorados and Neguanje, have the highest floristic richness, basal area and canopy height of the DTF found in the Caribbean and Tolima region (Mendoza 1999). Another factor which led to the selection of these sites was the availability of information on the Scarabaeinae fauna. There are publications for each of the sites, and there are also databases for Costa Rica (INBio) and Mexico (SNIB-CONABIO). The sites are described below together with the most relevant features associated to geological and geomorphologic characters (see Tables 1 and 2).

Chamela, Jalisco, Mexico. The Chamela-Cuixmala Biosphere Reserve is located on the Pacific coast (19º 30' N, 105º 03' W). The study site is between the San Nicolas River in the north and the Cuixmala River in the south, centred in the surroundings of the Chamela Biological Station (Fig. 1). With altitudes lower than 200 m, the climate has no marked seasonality with respect to temperature. Mean monthly maxima range from 28.8 to 32.2 ºC, and the minima from 15.9 to 22.6 ºC. Mean annual precipitation is 707 mm. The rainy season lasts four months on average, starting at the beginning of July and ending at the beginning of November (Bullock 1988).

Chamela belongs to the Jalisco Block (JB), which constitutes a tectono-stratigraphic assemblage from the Late Cretaceous to Early Tertiary (Paleocene), with volcanic and volcaniclastic deposits and marine sedimentary sequences intruded by granitoid plutons. The plutonic and volcanic rocks of the JB are part of the magmatic arc, which is found

southeastward along the terrain of the state of Guerrero. On the other hand, Chamela is aseismic and is located on the North American tectonic plate. It is characterized by an undulating landscape, the presence of mineral, soil with low permeability and organic matter.

Palo Verde, Guanacaste, Costa Rica. The Palo Verde Biological Station (Fig. 1) is located in the Palo Verde National Park (10º 20' N, 85º 18' W) on the Pacific slope, in the Province of Guanacaste and halfway up the basin of the Tempisque River at an altitude of
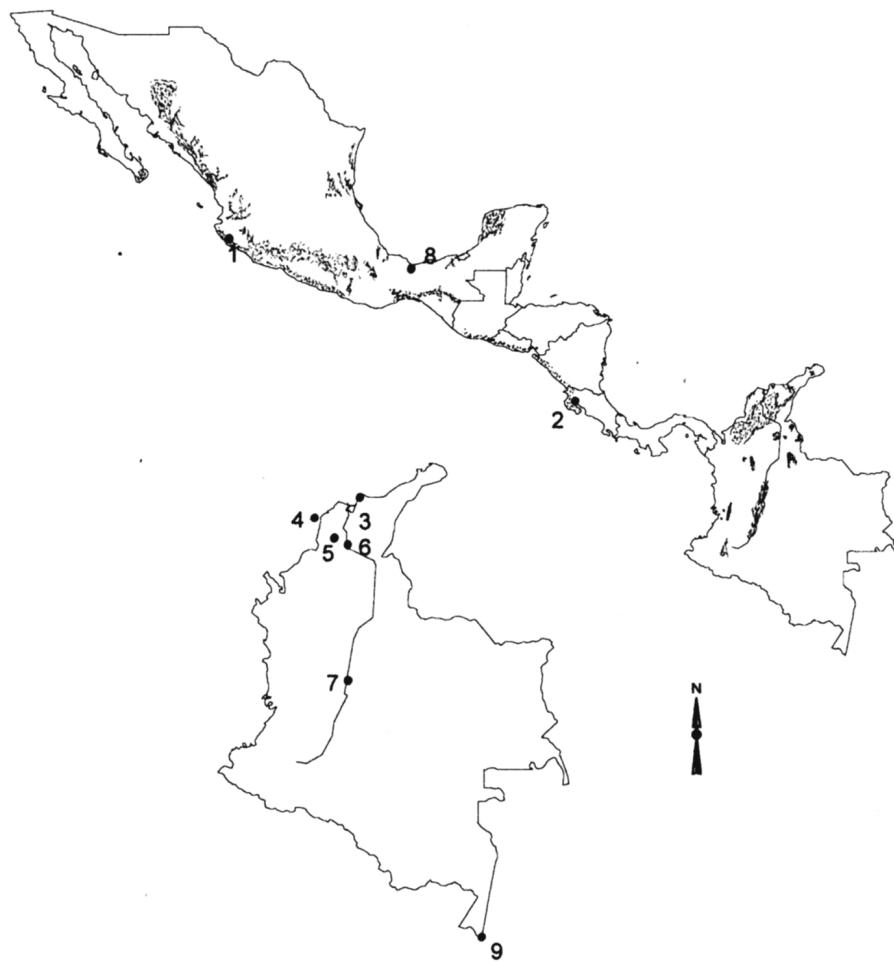
Figure 1
Study sites, DTF (1- 7): 1 = Chamela, 2 = Palo Verde, 3 = Neguanje, 4 = Tierra Bomba, 5 = Los Colorados, 6 = Zambrano, 7 = Norte del Tolima; TRF (8-9): 8 = Los Tuxtlas, 9 = Leticia (Amazonas). The dotted area corresponds to the distribution of DFT, based on Gómez (1982); IAvH (1997 b), CONABIO (1990) and Trejo & Dirzo (2002).

Table 1
Bibliography consulted for the selection of geomorphological characters.

Mexico	López-Ramos 1980, Bullock 1988, Bandy *et al*. 1999, Ferrari *et al.* 1999, Ferrari & Rosas-Elguera 1999, Rutz 2002, Campo-Alves 2003, Hernández-Quintero 2003, Sommer-Cervantes *et al.* 2003.
Costa Rica	Schmidt-Effing 1980, Rich & Rich 1983, Vásquez 1983, Alvarado *et al.* 1986, Chiesa *et al.* 1994, Henríquez *et al.* 1994, Meschede *et al*. 2000, Nelson & Nietzen 2000, Alfaro *et al.* 2001, Jaccard *et al*. 2001, Montero 2001, Cuevas *et al*. 2003.
Colombia	Taborda 1950, Rubio *et al*. 1977, Galvis *et al*. 1979, Aucott 1983, González *et al*. 1988, Malagón 1988, Sánchez *et al.* 1998, Sánchez-Valbuena 1992, París & Romero 1994, Giunta *et al*. 1996, Molina 1996, Herrera *et al*. 2001, Ramón *et al*. 2001, Caro & Spratt 2003.

Table 2
Geological-geomorphological characters and their states

1. Land profile. undulating (0), valley (1), flat (2)
2. Potassium. low (0), optimal (1)
3. Organic material in the soil. high (1), low (0)
4. Most abundant minerals in the sandy fraction of the soils. feldspar (0), quartz (1), olivine- pyroxene (2), amphiboles (3)
5. Tectonic plate. Caribe (0), North America (1), South America (2)
6. Seismicity. high (0), low-absent (1)
7. Faults. present (0), absent (1)
8. Geological era. Mesozoic (0), Tertiary (1), Quaternary (2)
9. Geological period. Middle Jurassic– Late Cretaceous (0), Eogene [Oligocene, Eocene, Paleocene] (1), Neogene [Pliocene, Miocene] (2), Pleistocene, Holocene (3)
10. Magnetism. low (0), high (1)
11. Type of rock. sedimentary (0), igneous (1), metamorphic (2)
12. Nearby volcanic range. present (0), absent (1)
13. Soil permeability. high to moderate (0), low (1)
14. Origin of rock. marine (0), continental (1)
15. Evolution of the soil profile. zoned (highly evolved) (0), not zoned (young or slightly developed) (1)
16. Origin of the plate. Paleozoic (0), Mesozoic (1)
17. Metals. Ag, Pt, Au, Fe. absent (0), presente (1)
18. Bouguer's anomalies (gravimetric anomalies). positive (0), negative (1)

10 to 50 m. Mean annual temperature ranges from 24.0 to 27.8 ºC and mean annual precipitation is 1750 mm (Quigley & Platt 2003), with a 6.5 month long dry season each year (SIEPAC 2003).

It is characterized by an undulating landscape, with slightly developed soils, and the most abundant minerals are olivine-pyroxene. The local fault is responsible for the seismicity. The Palo Verde region dates from the Paleocene to Early Eocene. This site is characterized by high magnetism, and is located on the Caribbean tectonic plate **Colombia, Caribbean Region**. The sites selected (Fig. 1) have been described by Mendoza (1999). Located between 50 and 300 m, their mean temperatures are greater than 24 ºC and they receive 700 to 2000 mm of precipitation per year. There are two marked dry seasons per year (IAvH 2000). This region is represented by four sites:

a) Zambrano: Forest Reserve, Monterrey. Located in the Departament of Bolivar, Zambrano Municipality (9º 37' 48" N, 74º 54' 44" W) at 155 m. Mean annual precipitation is 1048 mm.

b) Los Colorados. Located in the Departament of Bolivar, San Juan de Nepomuceno Municipality (9º 51' 33" N, 75º 06' 38"W), at 300 m. Mean annual precipitation is 1189 mm. This remnant of DTF belongs to the Los Colorados Flora and Fauna Sanctuary Conservation Unit.

c) Tierra Bomba Island. Located in the Department of Bolivar, Cartagena Municipality (10º 21' 36" N, 75º 34' 11" W), at 50 m. Mean annual precipitation is 789 mm.

d) Neguanje. Located in the Department of Magdalena, in the Santa Marta Municipality (11º 18'05" N, 74º 06' 11" W) at 300 m. Mean annual precipitation is 1420 mm. Neguanje belongs to the Tayrona National Park.

The Caribbean Region is located between the Perijá to the east and the Sierra Nevada. On the surface, fluvial and lacustrine sediments from the Quaternary predominate. It is characterized by a sequence of sandy, slime and clay, and feldspar is the most abundant mineral in the sandy fraction of the soil. It is aseismic and located on the Caribbean tectonic plate. In geological terms, Neguanje belongs to the geotectonic province of Santa Marta (land originating in the Mesozoic: Middle Jurassic to Late Cretaceous) and the other three sites belong to the province of the Caribbean Plain. Zambrano belongs to the San Jorge-Plato geostructure (the land dates from the Quaternary), Los Colorados to the San Jacinto Belt (the land dates from the Tertiary: Late Eocene) and Cartagena to the Sinú Belt (Tierra Bomba is from the Quaternary). The Sierra Nevada is associated with the Santa Marta fault and the Caribbean Plain is associated with the Romeral system fault in the west.

North Tolima. We selected the study area described by Escobar (1997). It is located on the east side bank of the Magdalena River (Fig. 1), 130 km from the city of Ibagué in the jurisdiction of the municipalities of Honda, Armero-Guayabal and Piedras, at (4º 15' - 5º 10' N, 74º 45' - 74º 50' W) at 250 m. Mean annual precipitation is 1387 mm and the mean annual temperature is 28 ºC, with two well defined dry periods, one from December to March and the other from June to August.

North Tolima forms part of the Upper Magdalena River Valley, an inter-Andina valley on the eastern slope of the Cordillera Central. It belongs to the Honda formation dating

from the Tertiary: Miocene. There are faults nearby and it is associated with the Plio-quaternary volcanic activity of the Cordillera Central, as reflected in its notable seismicity.

Los Tuxtlas, Veracruz, Mexico. The Los Tuxtlas Biological Station is located in the foothills of the San Martin Volcano, 19 km north of the city of Catemaco in the state of Veracruz (Fig. 1; 18º 34' - 18º 36' N, 95º 04'- 95º 09'W) at 150 to 530 m. Mean annual precipitation is 4560 mm and the mean annual temperature is 23.7 ºC (Morón 1979).

Los Tuxtlas Reserve belongs to the formation La Laja, which dated Oligocene and is located on the North American tectonic plate. It is characterized by an undulating landscape, igneous rocks of continental origin, nearby mountains, soils with high permeability and organic material, and high seismicity.

Leticia, Amazonas, Colombia. The Colombian Amazon has a humid tropical climate. The site is located at 4º 8' S, 70º 1' W, and 96 m (Fig. 1). Mean annual precipitation is 3500 mm, with the majority of the rain falling between April and June. Mean annual temperature is 26 ºC, with maximum temperatures in October and November 35 ºC. It is cooler in July with minima from 20 to 25 ºC (Galvis *et al*. 1979).

It is characterized by an undulating landscape, with highly evolved soils, a limited presence of minerals and low levels of natural fertility. Quartz dominated more than 90% of the sandy fraction and potassium was scarce. This geomorph developed over sedimentary rocks with a thick grain. The Quaternary deposits are comprised of sand, possibly of eolic origin, with recent terraces and alluvial deposits. This is an aseismic region located on the South American plate.

Ingroup and Outgroup

Our decision to use a real outgroup is based on the fact that the rain forest provides ecological characteristics that contrast with those of dry forest and take into account the previous hypotheses about its probable origin in neotropical forest. Also, rain forest is supposed to be older than dry forest (see Sarmiento 1975, Platt *et al.* 1981, Gentry 1982, Hooghiemstra & Van der Hammen 2001, Richardson *et al.* 2001, Hooghiemstra *et al*. 2002, Graham 2003). The use of an outgroup provides both a geographical context and vegetation formations that contrast with the characteristics of the areas where the Scarabaeinae we are studying are currently found.

Geomorphological cladogram

Historical and geomorphological relationships were analyzed following Craw (1988). The seven dry forests make up the ingroup, however our analysis differs because for the outgroup we have used real sites of tropical rain forest, instead of coding for the outgroup with zeros. The rain forests selected carrying out the analysis using this outgroup allows the cladogram to be polarized and hence produces the more parsimonious solution than one that uses zeros.

In order to select characters and assign character states for each of the sites, more than fifty references were consulted. The list of the main studies consulted is presented by country in Table 1.

The geologic-geomorphological characters provide evidence from different sources of characters: geomorphostructural, geophysical and edaphic. The geomorphostructural

characteristics of the terrain are defined by its geological and morphostructural history (origin and evolution) and by the lithological composition of the materials. Geophysical characters include the geotectonic, magnetic and gravimetric anomalies of the physiographical regions. On the other hand, the origin of the soil is influenced by the relative material, relief, climate and the organisms that are present.

Eighteen characters and their states were selected (Tables 2, 3). Ambiguous characters were discarded as were those for which there is insufficient information for more than two sites. All the characters were given equal weight, with three ordered characters: 8, 9 and 16. These characters were taken as unordered because they are related to chronological sequences of events associated to the scale of geological time.

Cladogram of the areas of affinity for the Canthonini

The relationships of DTF were analyzed using Parsimony Analysis of Endemicity (PAE), where the taxa are analogous to the sites and the characters to the species. In contrast to the methodology proposed by Rosen (1988) where the cladogram is rooted in a hypothetical ancestral area coded in zeros, here we use an external group, the outgroup, of real sites. The ingroup and outgroup are the same as mentioned for the previous analysis.

We chose PAE because it allows for the use of an outgroup in the analysis, the polarization of the cladogram, the addition of taxonomic hierarchies and it has a small data matrix.

A cladogram of the areas was generated using lists of the species (Table 4) present in each forest, indicating presence (1) or absence (0) according to the matrix (Table 5). Given that 24 of the 28 species belong to the genus *Canthon,* the subgenera of this taxon were included. The PAUP 4.0b10 (Swofford 2002) program with Acctran optimization and exhaustive search was used. The results were analyzed based on the majority consensus tree as it offered the greatest resolution.

Table 3
Matrix with character states for the cladogram of geomorphological areas.

	123456789012345678
Leticia (C)	000121123001010000
Neguanje (C)	210301000120110100
Zambrano (C)	210001123101110101
Los Colorados (C)	210001011101100101
T. Bomba (C)	210001123101000100
N. Tolima (C)	110020012100100010
Chamela (M)	010011011010111010
Los Tuxtlas (M)	001210111010011000
P. Ve rde (CR)	011200011110101100

Table 4

List of Canthonini species from the study forests. Numbers are those used in the matrix of Table 5. The subgenera of the genus *Canthon* are *Glaphyrocanthon* (*Gl*.), *Canthon* (*C*.), *Goniocanthon* (*G*.).

List of Canthonini species from the study forests
1 *Canthon (C.) aequinoctialis* Harold
2 *C. (Gl.) acutus* Harold
3 *C. (Gl.) corporali* Balthasar
4 *C. (C.) cyanellus cyanellus* LeConte
5 *C. (C.) cyanellus sallei* Harold
6 *C. (C.) deyrollei* Harold
7 *C. (Gl.) euryscelis* Bates
8 *C. (Gl.) femoralis* (Chevrolat)
9 *C. (G.) fulgidus* Redtenbacher
10 *C. (C.) humectus riverai* Halffter & Halffter
11 *C. (C.) indigaceus indigaceus* LeConte
12 *C. (C.) indigaceus chiapas* Robinson
13 *C. (C.) indigaceus chevrolati* Harold
14 *C. (C.) juvencus* Harold
15 *C. (C.) lituratus* (Germar)
16 *C. (Gl.) luteicollis* Erichson
17 *C. (Gl.) meridionalis* (Martínez, Halffter & Halffter)
18 *C. (C.) morsei* Howden
19 *C. (C.) mutabilis* Harold
20 *C. (Gl.) pacificus* Rivera & Halffter
21 *C. (Gl.) semiopacus* Harold
22 *C. septemmaculatus* (Latreille)
23 *C. (Gl.) subhyalinus* Harold
24 *C. (Gl.) vazquezae* (Martínez, Halffter & Halffter)
25 *Cryptocanthon peckorum* Howden
26 *Pseudocanthon perplexus* (LeConte)
27 *Agamopus lampros* Bates
28 *Malagoniella as*tyanax (Harold)

Table 5

Data matrix for the cladogram of the Canthonini areas

	1234567890123456789 0123456789012
Chamela (M)	0011000001100000000 1000001101001
Los Tuxtlas (M)	0001001100010000010 0001101001001
P. Verde (CR)	0000111000010001100 000001 111001
N. Tolima (C)	1100100000000110011 0001000011001
Zambrano (C)	0000100000000110000 0010000011010
Los Colorados (C)	1000100000000100000 0001000101001
T. Bomba (C)	0000100000000110000 0000000001000
Neguanje (C)	0000100000000110000 0000000001000
Leticia (C)	1000000010000001000 0100010001101

Canthonini Species

All the genera of Canthonini present in the forests studied are included in the analysis, with the exception of *Deltochilum* for which there is insufficient taxonomic and biogeographical information.

In order to compile the lists for Palo Verde and the Mexican site, in addition to a review of the publications mentioned below, the following data bases were used: INBio (Costa Rica) and SNIB-CONABIO (Mexico). The following publications were consulted: Chamela - Morón *et al*. (1988), Andresen (2005); Palo Verde - Kohlmann & Wilkinson (2003); North Tolima - Escobar (1997), Bustos-Gómez & Lopera-Toro (2003); Caribbean Region of Colombia - Escobar (1998, 2000a); species lists for these Colombian sites were also provided by F. Escobar; Leticia – list compiled by Bruce Gill, 12, I, 1997 with material collected by Howden & Nealis (1975), Escobar (2000a), Medina *et al*. (2001); Los Tuxtlas - Morón (1979), Halffter *et al*. (1992), Favila & Díaz (1997), Deloya & Morón (1998), Díaz (1998, 2003).

Canthon deyrollei was described by Harold in 1868, with the type locality unknown. It has been included for Colombia, without any other data in numerous publications (Vulcano & Pereira 1964, Howden & Young 1981, Solis & Kohlmann 2002). In the publications that we consulted for Colombia this species is either not recorded or is not assigned a locality. Hence, the record for Colombia was not included.

Canthon cyanellus and *C. indigaceus* are included in the analysis with their respective subspecies according to Halffter (1961).

Geographical distribution of Canthonini

There are many studies that include the geographical distribution of Canthonini in Mexico. Some of those that we consulted for this study are: Halffter 1961, 1964, 1976; Martínez *et al*.1964; Halffter & Matthews 1966; Barrera 1969; Martínez & Halffter 1972; Morón & Terrón 1984; Morón *et al*. 1985, 1986; Deloya *et al*. 1987; Delgado 1989; Kohlmann & Halffter 1990; Palacios-Ríos *et al*. 1990; Arellano 1992, 2002; Deloya 1992; Capistrán 1992; Estrada *et al*. 1993; Deloya & Morón 1994; García-Real 1995; Halffter *et al*. 1995. The most recent and relevant publications on *Canthon* in Mexico are Rivera-Cervantes & Halffter (1999) and Halffter (1961, 2003). Solis & Kohlmann (2002) review *Canthon* for Costa Rica, as do Howden & Young (1981) for Panama. In Colombia there are several local revisions (Amézquita *et al*.1999, Escobar 2000b, Escobar & Chacón de Ulloa 2000, Neita *et al*. 2003, Pulido *et al*. 2003). The catalogue prepared by Medina *et al*. (2001) list the species for Colombia. Information about the geographic distribution of Canthonini in America is given in Bates (1886-1890), Blackwelder (1944), Vulcano & Pereira (1964), Halffter & Martínez (1966, 1977), as well as in the previously cited articles.

RESULTS

Geomorphological cladogram

The 50% majority consensus tree of four equally parsimonious trees is shown in Figure 2. The cladogram has 43 steps, a consistency index (CI) of 0.60 and a retention index of 0.56. The Colombia and Palo Verde (Costa Rica) sites are sister groups and

these two, in turn are sister group to Chamela (Mexico). Los Tuxtlas (Mexico) represents the first clade branching out, being the sister group to the other sites included in the analysis.
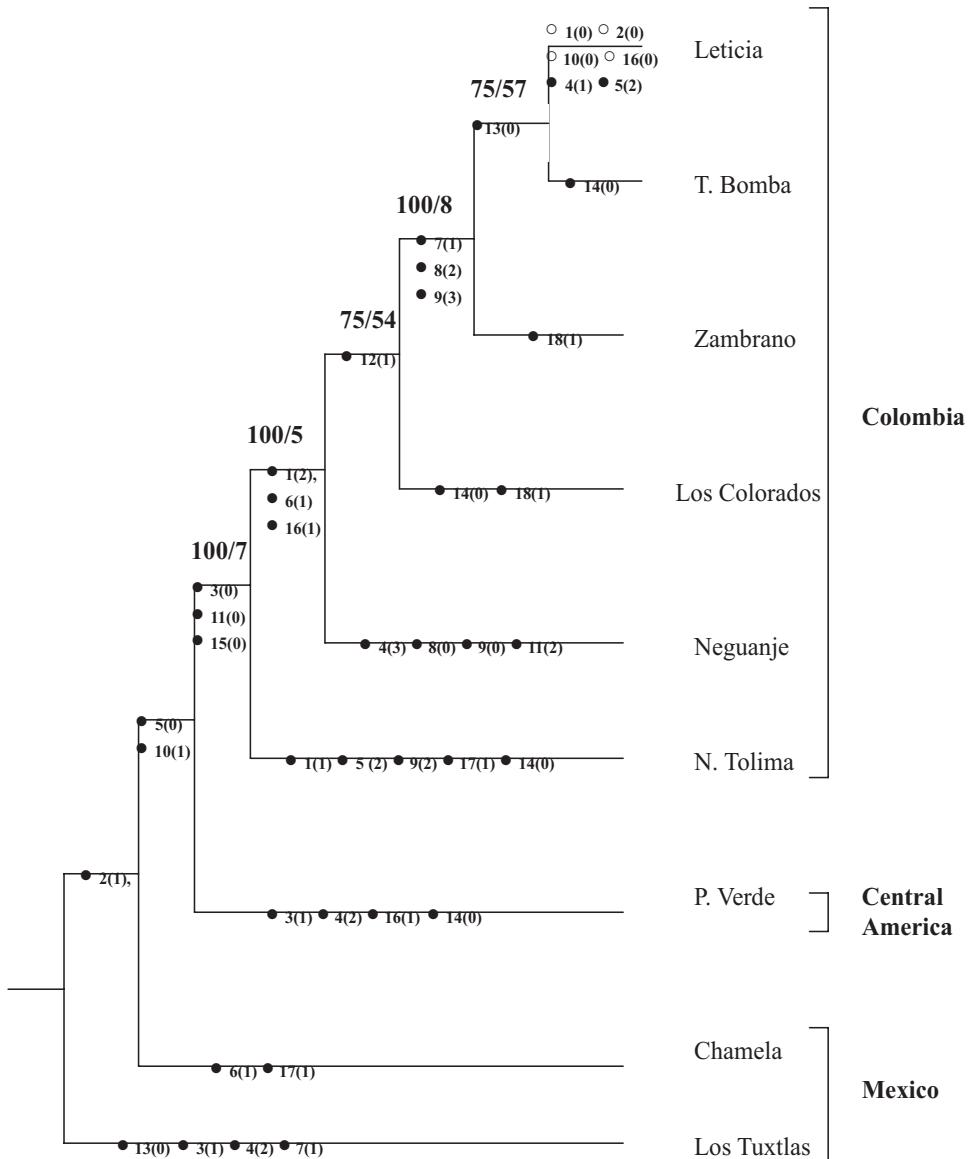
Figure 2

Cladogram of geological areas. The numbers above the nodes indicate 50% majority consensus tree frequency / Jackknife frequency with 20% deletion, 500 replicas. In each clade the appearance of derived = • and reversed =∘ characters is indicated.

There are two well supported clades, the first includes Leticia, Tierra Bomba and Zambrano which have both the era and geological period in common: Quaternary: Pleistocene, Holocene. They are also free of tectonic faults. The second well supported clade grouped all the DTF of Colombia and Leticia. All of the sites in Colombia (except Neguanje) have sedimentary rock, though it originates from different processes. In Leticia, the rock results from dendritic accumulations, terraces and alluvial deposits from the margins of the Amazon River. At Tierra Bomba, it originates in marine deposits. In Zambrano, it results from the fluvial-deltaic action of the Magdalena River, at Los Colorados it comes from rocks corresponding to carbonate facies and in the Upper Magdalena River Valley, it is comprised of carbonacious and clay sediments that are both sandy and conglomerate. The soils of the sites are highly developed and have low concentrations of organic material.

Palo Verde and the majority of the sites in Colombia (except Leticia) are characterized by high magnetism and are located on the Caribbean tectonic plate (except Leticia and N. Tolima). Chamela is a sister group to Palo Verde and Colombia, where the soils have optimum concentrations of potassium (except Leticia).

On the other hand the forests studied in the Caribbean Region (except Neguanje) and Leticia (the Amazon) are on sites of very recent geological origin (Quaternary) compared to the DTF of North Tolima, Costa Rica (Palo Verde) and Mexico (Los Tuxtlas and Chamela) which are of Tertiary origin.

The assemblage of the Caribbean Region, Colombia
The areas where Los Colorados and Neguanje are found, are part of a mosaic of blocks that later came together to form the Caribbean Region. Los Colorados belongs to the San Jacinto Fold Belt which is the result of the interaction between the oceanic crust of the southwestern Caribbean and the continental crust of northern South America. Forces of tension and compression alternated along the platform's margin, especially during the pre-Andina period of orogeny (Middle Eocene) which lifted, folded and shaped this belt. The geomorphological features of the Santa Marta Massif (from which the Neguanje is derived) are the result of its location during the Mesozoic-Tertiary at the intersection of faults on the northeastern corner of South America (González *et al*. 1988). According to Ujueta (2003) this Massif should be considered a northern extension of the Cordillera Central and its relief is a result of mostly vertical tectonic movement accompanied by moderate horizontal movement.

The tectonic history of San Jacinto, the location of the Sierra Nevada of Santa Marta and the sedimentation of the Plato and San Jorge basins, is correlated in space and time from the Late Miocene to the Pliocene (Caro & Spratt 2003). The assemblage and the sedimentation of the Caribbean Region of Colombia ended in the Quaternary. It is likely that the climatic and ecological changes were shared by all the sites of the Caribbean Coast of Colombia and so reflect in one way or another the affinities of the biota present in the DTF. The Caribbean Region, together with the north of Venezuela makes up the phytogeographic region of Northern South America (Gentry 1995).

Geomorphological relationships of the study sites and their relationship to the origin of DTF

Three events have exerted a great effect on the evolution of Neotropical flora: the rise of the Andes, the exchange of biota with North America after the formation of the Central American Isthmus and the climatic fluctuations of the Pleistocene (Guariguata & Katan 2002). This, in addition to the culmination of the majority of orogenic processes that occurred on the continental land of Mexico toward the end of the Pliocene (see Challenger 1998) and the sedimentation of some parts of the mid- and lower Balsas River basin in the Pleistocene. The convergence of

the DTF studied can be attributed to the climatic and ecological events of recent geological time, probably since the Pleistocene. This confirms the observations of Gentry (1982) who suggests that the high number of species in the dry tropical area of Mexico is probably the result of an active evolutionary diversification in response to the increase in dry climate regimes during the Pliocene and the Pleistocene. This is in accordance with the higher rate of speciation of the genus *Bursera* (toward the Pliocene) and its concentration in areas of intermediate and low altitudes of the Pacific Slope of Mexico, and in particular the Balsas River Basin (see Becerra 2005, Rzedowski *et al*. 2005).

One can think about a general process of south-north expansion since, as Rzedowski (1978) has said, the dry tropical forests of Mexico are characterized by a strong predominance of neotropical elements, and the scarcity or absence of holarctic elements. Although dry forests have their origin in the Pleistocene, it is likely that their current, dry conditions were set during the Middle Holocene in the Caribbean Region of Colombia, as well as on the Pacific coast of Mexico and Costa Rica. During the Middle Holocene, about 5000 to 7000 years B.P. (Steig 1999), the dominant climate system was ITCZ (Intertropical Convergence Zone), given that the ENSO (El Niño-Southern Oscillation) was absent or weak (Fontugne *et al*. 1999, Cole 2001, Tudhope *et al*. 2001, Riedinger *et al.* 2002). Haugh *et al*. (2001) propose that the driest climatic phase of the Holocene results from the change in the ITCZ to its current position.

Cladogram of the areas of affinity of Canthonini
The cladogram of the areas of affinity of the Canthonini, with 28 taxa and three subgenera of *Canthon* (Fig. 3) is the result of the majority consensus of three trees, with 40 steps, and CI of 0.77 and an RI of 0.64. The cladogram groups the Colombian DTF as follows: the first group is comprised of the forests of Tierra Bomba, Zambrano and Neguanje (Caribbean Region); the second is North Tolima alone, and the third group is comprised of Los Colorados, also of the Caribbean Region. In the first group the subgenus *Glaphyrocanthon* is not represented by a single species; in the other two groups this subgenus is represented by *Canthon (Gl.) subhyalinus*.

The Canthonini of the dry tropical forest of Chamela are more closely related to those of the forests of Colombia. Those of Palo Verde show an affinity to both those of Chamela and those of Colombia. The canthonines of the two tropical rain forests are totally different from each other and do not share any species.

There are three species that characterize the relationships between the dry forests of Colombia: *Canthon juvencus*, *C. cyanellus sallei* and *C. lituratus* (except in Los Colorados). The Amazon (Leticia) only shares *C. aequinoctialis* with the dry forests of North Tolima and Los Colorados Caribbean Region, Colombia).

Chamela has the most exclusive species (*Canthon corporali, C. humectus* and *C. pacificus*), and is followed by Palo Verde (Costa Rica): *Canthon deyrollei* and *C. meridionalis*, and North Tolima (Colombia) with *C. acutus*.

Eighty-six percent of the species included in the analysis belong to the genus *Canthon*. To explain these results and explore why such species are found in the forests studied, their distribution patterns are analyzed below (see Table 4 and Appendix 1).

Analysis of the distribution of Canthonini in the dry forests studied
The cladogram of the species of *Canthon* for North America (including Mexico) proposed by Kohlmann & Halffter (1990) shows the spread of this genus from South America in two big expansion events: the first towards the Miocene and the second towards the Plio-Pleistocene

and continuing to the Recent (see also Halffter 1964, 1976). The phyletic lines that correspond to the first expansion were not influenced by the events that affected the integration and distribution of the dry forests which came afterwards. Their presence in these forests (Chamela) is a result of later colonization. In contrast, the species of the second expansion exhibit a correspondence to the historical and biogeographical conditions that influenced the distribution of DTF: orography that was broadly similar to the current situation, the reestablishment of the connection and exchange of biota between South and North America, and an expansion of the dry conditions in the Holocene.
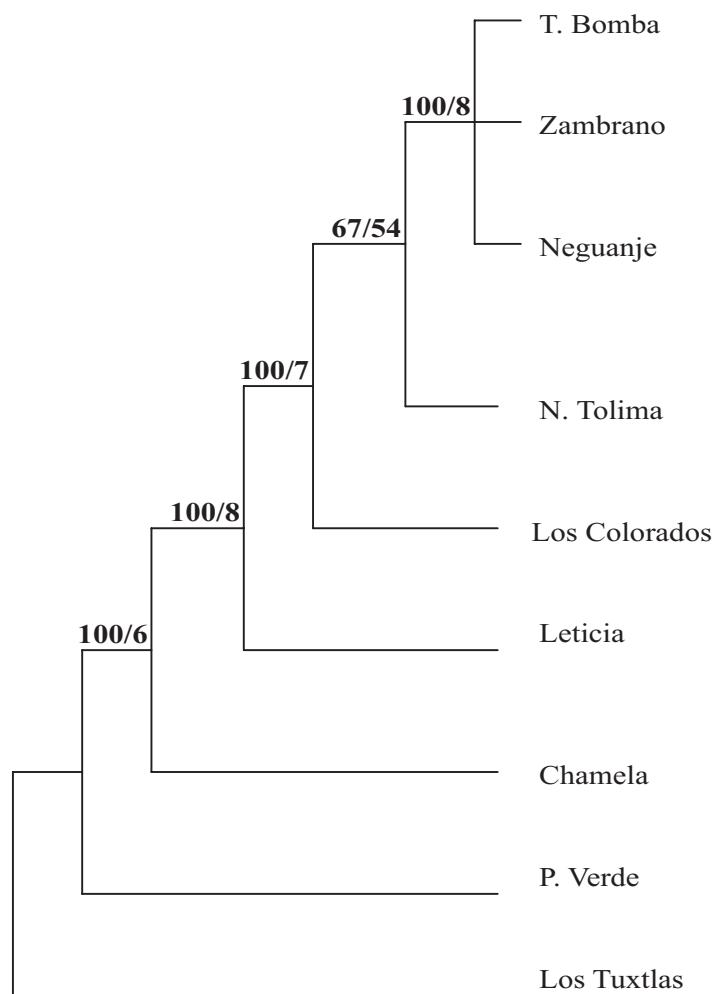
Figure 3
Cladogram of the areas of affinity of Canthonini. The numbers above the nodes indicate 50% majority consensus tree frequency / Jackknife frequency with 20% deletion, 500 replicas.

In order to explain the presence of Canthonini species in the enclaves of DTF we have studied both the distribution patterns proposed by Halffter (see Halffter 1964, 1976; Kohlmann & Halffter 1990) and the phyletic lines proposed for taxa of the genus *Canthon* according to the taxonomic affinities recognized by Halffter & Martínez (1977), and propose a pattern of speciation *in situ*.

Pattern 1

This pattern is observed for species belonging to the phyletic lines that expanded through Mexico, most likely before the Miocene (the High Plains Distribution Pattern of Halffter). These were the earliest species of Neotropical affinity to penetrate the Mexican Transition Zone (MTZ) (Halffter 1976, 1978). *Canthon (C.) humectus* belongs to this pattern, and represents a phyletically isolated line within the subgenus *Canthon* according to Halffter & Martínez (1977). Of the eight subspecies (Halffter & Halffter 2003) distributed throughout the High Plains of Mexico, Oaxaca, Chiapas and Guatemala, only *C. humectus riverai* Halffter y Halffter is found in Chamela, a new record not indicated by Andresen (2005); perhaps because it is outside of the area she studied. This species occurs at the lowest altitude for both the species and Canthonini found on the High Plains. It was previously collected in the lower part of the Manantlán Mountain Range (Jalisco) in DTF at altitudes from 700 to 1000 m. Its presence in Chamela can be considered a result of secondary expansion. In a study of the entire Scarabaeoidea superfamily in Chamela, Morón *et al*. (1988) found some species with the ancient MTZ dispersal patterns, though the majority have the Neotropical Pattern that developed from the Pliocene onwards (see below).

Pattern 2

These species participated in the expansion that probably began in the Pliocene with the reestablishment of the Panamanian connection, and have different degrees of northwards expansion in North and Central America, to the United States of America (and thus together result in the Typical Neotropical Distribution Pattern of Halffter). The affinities of these species with the South American fauna are much better defined than is the case for Pattern 1 (see affinities under each species). The penetration of these species into the MTZ (Pliocene onwards) could have occurred in distinct stages, depending on the species' antiquity. The most ancient species have undergone processes of subspeciation in the MTZ. We will examine the distribution of these species, from the oldest (and with the widest distribution) to the most recent.

a) Species with a wide distribution that reaches the United States of America.
Canthon (Canthon) indigaceus LeConte ranges from Panama to Texas and Arizona in the United States. In Mexico it is found in tropical landscapes on the Gulf slope, the Pacific slope and the Yucatan Peninsula. It is comprised of three subspecies that are found under different ecological conditions: *Canthon i. chiapas* in TRF; *C. i. chevrolati* in places with greater insolation, with less or no woody vegetation; and *C. i. indigaceus* in DTF or more xerophyllous vegetation. In Chamela we found *C. i. indigaceus*; in Guanacaste, *C. i. chevrolati*; and in the TRF of Los Tuxtlas, *C. i. chiapas*. Overall, *C. i. indigaceus* is a good example of a species exhibiting the Typical Neotropical Pattern with a wide distribution in the MTZ. As in the previous case (*Canthon humectus*), this species constitutes a phyletic line within the subgenus *Canthon* (Halffter & Martínez 1977) that has only one species.

Canthon (C.) cyanellus LeConte has a similar geographic history and distribution, although the latter is broader. It is found from Peru and Brazil to the southern United States and under a wide variety of ecological conditions though it is usually associated with tropical forests or

treed sites along an altitudinal range from sea level to 2600 m. This species is found at all the DTF sites we studied and in Los Tuxtlas, but not in Leticia.

In Mexico it is found all along the Pacific coast, from Chiapas to Jalisco and on the Atlantic slope it is found on the Yucatan Peninsula and along the Gulf Coast of Mexico up to Tamaulipas and Nuevo León. In the interior of Mexico it is found in the states of Puebla, Morelos, Hidalgo and San Luis Potosí. In Central America, it is found on both the Pacific and the Atlantic slopes; in northern Panama it is found near the Caribbean Sea (Bocas del Toro) and to the south on the border with Colombia in the Darien region on the Pacific coast. In Colombia, according to our findings this species is found throughout the Caribbean Region and the high valley of the Magdalena River, as well as in the Department of Meta (Amézquita *et al*. 1999, Medina *et al*. 2001). In Venezuela this species occurs in Táriba, San Cristóbal, as well as in Arima, Trinidad and in Uaupés, Brazil (the Amazon) according to the records of Solís & Kohlmann (2002). *Canthon cyanellus* belongs to a phyletic line (the bispinus line) with many species in South America (Halffter & Martínez 1977).

Malagoniella (Malagoniella) astyanax (Harold). The genus *Malagoniella* is distributed throughout the Neotropical region, except in Chile and the Antilles. It is richest in species in Argentina, Uruguay, Paraguay and southern Brasil (Halffter & Martínez 1966). The subgenus *Malagoniella* has a similar distribution. It includes the only taxon found in the north, *M. (M.) astyanax yucateca* (Harold), that is found in Central America, Neotropical areas of Mexico and at a point on the border of the United States of America. The other subspecies that make up *M. astyanax* are South American. Citations for Colombia possibly refer to *M. (M.) astyanax columbica* (Harold), a subspecies for which the distribution is limited to Colombia (Halffter & Martínez 1966), where it is found in the DTF of Zambrano and North Tolima, as well as in the Departments of Chocó and Magdalena (Medina *et al*. 2001). This species appears to have a preference for DTF and has not been recorded in Leticia (the Amazon).

Malagoniella (M.) astyanax yucateca (Harold) has a very wide distribution in Mexico and Central America, but has been found at isolated points that are often separated by great distances. In this case, it is difficult to attribute this to capture inefficiency (at least for many of the places where it has not been found), given that this is a large and very striking species. It has been collected in Brownsville, Texas, on the border with Mexico, and also at Tamazunchale (San Luis Potosí), Quintana Roo, Escárcega (Campeche), Puerto Ángel (Oaxaca), Cacahoatan, Tapachula and Rosario Izapa (Chiapas), Yucatan (Bates 1886-1890; Halffter & Martínez 1966; SNIB-CONABIO database)**,** Guatemala, in the west of Nicaragua and Costa Rica. The Chiapas and Central American sites are on the Pacific slope. In Costa Rica it is restricted to the Guanacaste region, to the northwest of the Pacific coast, over an altitudinal range of 10 to 400 m. In the present study, it is recorded for Palo Verde. Except for the capture in Brownsville (Texas), the rest were captured in tropical forest. *M. astyanax yucateca* appears to be most often associated with seasonal forests (i.e. those that have a dry season). It has not been found in TRF (Los Tuxtlas, Veracruz or Selva Lacandona, Chiapas) within its distribution perimeter.

The distribution of *M. astyanax* appears to reflect an ancient expansion from South America, one that is currently quite fragmented.

Pseudocanthon perplexus (LeConte). The genus *Pseudocanthon* Bates is comprised of eight species, and two of these are found in Mexico. Of the Mexican species, one is found in

the Antilles where there are also five endemic species. The other species is South American. *Pseudocanthon perplexus* is found in Mexico in both TRF and DTF. It is captured sporadically in sites that are distant from each other. Its distribution extends from the United States of America down to South America. It was found in Chamela and Palo Verde of the DTF we studied.

In Mexico it is distributed along the coast of the Gulf of Mexico up to the eastern United States, and on the Pacific coast to Sonora. In Costa Rica, it has been recorded in Guanacaste Province and in Alajuela on the Cordillera Central, over an altitudinal range of 10 to 540 m (INBio database). In Panama, it has been found in Balboa in the Canal Zone (Pacific coast).

b) Species with limited penetration into Mexico.

Canthon (C.) morsei Howden is distributed from Ecuador to the warm areas of Mexico, where it extends along the Pacific slope from Chiapas (Halffter *et al*. 1992) to Jalisco (García-Real 1995). Along the Atlantic slope it ranges northwards up to Tamaulipas. In Costa Rica it is found in the north on the Pacific coast (Solis & Kohlmann 2002). In Colombia, it is found in the Upper Magdalena River Valley (Tolima). This species is associated with DTF and TRF. In the DTF studied, it was recorded in Palo Verde and in Colombia only in North Tolima. In Mexico, it was not found in the DTF of Chamela, although it is has been recorded in deciduous and semideciduous tropical forests in the state of Jalisco relatively close to Chamela.

According to Halffter & Martínez (1977) *C. morsei* belongs to a phyletic line of the subgenus *Canthon* that includes other South American species.

Canthon (Glaphyrocanthon) subhyalinus Harold is distributed from Bolivia to Mexico and is associated with TRF, especially those sites with monkeys (Halffter 1991, Estrada *et al*, 1993, Rivera-Cervantes & Halffter, 1999). This species was not found in the DTF of Chamela or Costa Rica. In Colombia it is associated with DTF in Tolima and in Los Colorados (Bolívar); other records for Colombia include the Departments of Antioquia and Cundinamarca (Medina *et al*. 2001). In Panama, Howden & Young (1981) have recorded it for Darien, Santa Fe, and on the Pacific coast and in the Caribbean on Barro Colorado and in the Canal Zone. In Costa Rica it is found in the foothills of premontane wet forest. In Mexico it is only found in the south in the states of Chiapas, Quintana Roo and Veracruz. *Canthon subhyalinus* is a beetle associated with TRF (Rivera-Cervantes & Halffter 1999), and so it is probable that the neighbouring vegetation between TRF and DTF facilitates the dispersal of this species toward DTF. This explains the presence of *C. subhyalinus* in Los Colorados, where the DTF includes a patch of TRF, a lone remnant in the Caribbean Region of Colombia (Gentry 1995). It is also found in the DTF of North Tolima, which is between two mountain ranges and in the foothills of the mountain where wet montane forest predominates.

The northern distribution limit for *C. subhyalinus* coincides with that of the howler monkey, *Alouatta palliata*. It is probable that the dispersal of these species coincide from South America up to Los Tuxtlas. This is supported by field observations of the arboreal behavior of these beetles and their attraction to the dung of these monkeys (Howden & Young 1981, Halffter 1991, Estrada *et al*. 1993, Rivera-Cervantes & Halffter 1999). There is additional support in the origin of these monkeys, Late Miocene to the Pliocene, and their dispersal during the Pleistocene (Cortés-Ortiz *et al*. 2003), as well as the biogeographic pattern proposed in this study for *C. subhyalinus*.

Canthon (Gl.) euryscelis Bates belongs to the same group of species of the subgenus *Glaphyrocanthon* as *C.* (*Gl*.) *subhyalinus* (see Rivera-Cervantes & Halffter 1999). It is

distributed in TRF from Mexico to Panama. In the DTF we studied, it was collected at Palo Verde (Guanacaste). Solis & Kohlmann (2002) indicate that it has a broad tolerance of climate, and is found from sites with marked seasonality (altitude < 800 m in the Province of Guanacaste) to very humid ones. In Mexico it has been recorded in the TRF of Los Tuxtlas.

Agamopus lampros Bates belongs to a genus (currently under revision by Fernando Vaz de Mello) with four South American species, of which *A. lampros* extends to Central America and the tropical areas of Mexico. We recorded this species in the DTF of Chamela, Palo Verde (Guanacaste) and Los Colorados (Colombia).

c) The species mentioned below belong to South American phyletic lines whose northern geographic distribution only extends to Central America.
Canthon (Canthon) mutabilis Harold, within the subgenus *Canthon,* belongs to the bispinus line that, as mentioned in the section on *C. cyanellus,* is comprised of many South American species. Its distribution extends from Argentina to Costa Rica. It was found in Palo Verde (Guanacaste) and in North Tolima (Colombia). Solis & Kohlmann (2002) indicate that in Costa Rica it is found from sites that are very humid to those with marked seasonality and a dry season as long as six months. In Colombia, Medina *et al*. (2001) have recorded it for the Departments of Bolívar and Meta, associated with dry conditions. *Canthon juvencus*, *C. mutabilis* and *C. meridionalis* are abundant in the driest forests of some of the smallest islands in Lake Gatun and Gamboa (Caribbean region) near the continent (Gill 1991).

Canthon (C.) lituratus (Germar) is also widely dispersed from Argentina to Costa Rica. It belongs to a phyletic line within the subgenus *Canthon* that includes another South American species (Halffter & Martínez 1977). In Colombia it is found in Tolima and in the Caribbean Region in all the DTF studied, except for Los Colorados. In Colombia, Medina *et al*. (2001) have recorded it for the Departament of Valle. In Costa Rica it is only found to the southwest of the Pacific coast, in the savannahs bordering the Térraba River (Solis & Kohlmann 2002). Its distribution extends southwards from the Pacific, and it has also been recorded for the provinces of Chiriqui and Cocle in Panama at altitudes above 800 m (Howden & Young 1981).

Canthon (C.) juvencus Harold is found from Brazil to Costa Rica. In Colombia it is found in the DTF of the Caribbean Region and in the Upper Magdalena River Valley (Tolima) as well as in other Departments in Colombia: Guainia, Guaviare, and Meta (Amézquita *et al*. 1999, Medina *et al*. 2001, Escobar 2000b). In Costa Rica it is restricted to the southern Pacific in TRF located below 500 m (Solis & Kohlmann 2002). It is found in Panama in the pronvinces of Panama, Colon and the Canal Zone (Howden & Young 1981).

Canthon septemmaculatus (Latreille) has a broad distribution range from Argentina to Costa Rica. In the DTF studied, it was only recorded in Zambrano Caribbean Region, Colombia. Medina *et al*. (2001) have recorded it for the Colombian Departments of Bolívar, Chocó, Meta, Caquetá and Nariño. In Panama it has been recorded in the provinces of Los Santos, Coclé, Panamá and the Canal Zone. In Costa Rica it is only found to the southwest of the Pacific coast, in the savannas surrounding the Térraba River (Solis & Kohlmann 2002).

Canthon (C.) aequinoctialis Harold occurs from Brazil to Belize. According to Halffter & Martínez (1977) it belongs to a South American phyletic line of the genus *Canthon*. In Colombia it is

found in both the DTF of the Upper Magdalena River Valley (Tolima), in Los Colorados (Caribbean Region) and in the TRF of Leticia (the Amazon). It has also been found in the Departments of Antioquia, Caquetá, Choco, Guainia, Guaviare, Meta, Nariño, Valle, and Cauca (Escobar 2000 a, Medina *et al*. 2001, Neita *et al*. 2003, Pulido *et al*. 2003). In Panama it is found to the north, on the Pacific coast and in the Canal Zone on the Caribbean. In Costa Rica it is spread out along the Caribbean and to the north of the country, but it was not recorded in Palo Verde (Guanacaste). On the Pacific coast, it has been cited for two sectors: to the south on the Osa Peninsula and in the basin of the River Tárcoles, with a marked preference for TRF (Solis & Kohlmann 2002).

Pattern 3
These taxa likely reflect the processes of speciation *in situ* in the DTF of Mexico, Costa Rica and Colombia.

Glaphyrocanthon, a subgenus of *Canthon* with many South American species, has two phyletic lines in Mexico with a clear origin in the north of South America. We have already referred to one of these lines, that of *C. (Gl.) subhyalinus*. The second line is comprised of an isolated species with South American affinities. In addition there is the viridis group with strong speciation in Mexico and which clearly belongs to the subgenus *Glaphyrocanthon* although it has no evident relationship to South American species.

The viridis group is comprised of 15 species, of which only *C. (Gl.) meridionalis* Martínez, Halffter y Halffter has a distribution that expands towards Central America, opposite to the dominant direction for the distribution of the Canthonini studied. Several of the species of this group are associated with TRF, many others are found in DTF.

Canthon (Glaphyrocanthon) pacificus Rivera y Halffter and *C. (Gl.) corporali* Balthasar belong to this group and both form part of a set of species that are distributed in Mexico along the Pacific slope, from the state of Nayarit to the state of Oaxaca. *Canthon (Gl.) corporali* is widely distributed in association with DTF, including the Balsas River Basin and the coast of the Pacific on both sides of its outlet. *Canthon (Gl.) pacificus* is found in dry deciduous and semideciduous forests of the Pacific coast, from the state of Jalisco to the state of Oaxaca.

From the same viridis group in Guanacaste the lone species *C. (Gl.) meridionalis* Martínez, Halffter y Halffter is found and extends to Central America: Guatemala, El Salvador, Nicaragua, and Costa Rica (Solis & Kohlmann 2002). In Costa Rica it has a wide distribution, on both the Pacific and the Atlantic sides (Solis & Kohlmann 2002).

Canthon (C.) deyrollei Harold has a geographic distribution from Guatemala to Costa Rica. It is the only species in its phyletic line (Halffter & Martínez 1977). In Costa Rica it is restricted to the area with the greatest climatic seasonality, i.e. land below 600 m in the province of Guanacaste, in the northwest of Costa Rica (Solis & Kohlmann 2002).

Canthon (Gl.) acutus Harold was collected in North Tolima. It has also been found in other Departments in Colombia: Bolívar, Guainia and Meta at elevations of 300 m (Medina *et al*. 2001).

DISCUSSION

1) The geological (Fig. 2) and Canthonini species composition (Fig. 3) cladograms only coincide in their general features. The dry tropical forests from Mexico to Colombia arose during a relatively recent geological stage. Hence, historical geological events

prior to the Pliocene do not appear to have affected the distribution of this vegetation type. Its distribution is determined by a combination of temperature and rainfall conditions, particularly by a prolonged and marked dry season (see Rzedowski 1978).

2) The flora of dry tropical forests is almost exclusively comprised of species with Neotropical affinities (Rzedowski 1978). The Canthonini fauna has the same affinities. As shown by Trejo (2005), there is a high degree of plant species exchange between different dry tropical forest sites. It is not surprising that the same phenomenon occurs in the Canthonini.

The cladograms of the dry tropical forests and the Canthonini exhibit the same affinities found by Gentry (1995) for flora; i.e. a strong similarity between the dry forests of northern Colombia and Venezuela with that of Chamela, with 15 shared genera, while Chamela and Guanacaste (Costa Rica) only share six genera.

3) The Canthonini species found in the dry tropical forests studied show a clear gradient of affinity associated with the different degrees of expansion of the Canthonini from South America. In spite of the great distance and the ecological barriers that exist between Colombia and Chamela, the affinities are marked and appear to indicate a certain degree of continuity among the dry forests studied.

There is little doubt that the expansion of the distribution area of South American Canthonini, and that of many other Scarabaeinae with the same biogeographical history was greatly facilitated by the presence of mammalian megafauna that has since disappeared (see Janzen & Martin 1982). Nevertheless, there are differences among the enclaves of dry tropical forest. In Chamela, the only pre-Pliocene expansion species was collected (*Canthon humectus*), along with several species of ancient expansion within the Neotropical Pattern, and several species whose distribution in Mexico is more recent, including two belonging to a group (*Canthon* (*Glaphyrocanthon*) viridis group) which speciated in Mexico. Palo Verde has a mix of Plio-Pleistocene and recent expansion species. In Colombia, species with a South American distribution dominate, although it shares species with Palo Verde and Chamela.

The biogeographical hypothesis proposed in the Introduction about the origin of Canthonini and their northwards expansion at different times and with different degrees of penetration is supported. The relationships between distinct phyletic lines and even species, with South American fauna clearly demonstrate these biogeographical phenomena.

4) Several of the species found in Colombia, but not in Palo Verde or Chamela, have the northern limit of their distribution in the Térraba River basin in the extreme south of Costa Rica on the Pacific coast. This is the case for *C. lituratus*, *C. juvencus*, and *C. septemmaculatus* (see Solis & Kohlmann 2002). As these species do not reach Palo Verde the differences of this site with those of Colombia are accentuated. This northern limit in the distribution of South American species to the extreme south of Costa Rica is interesting. The lowlands of Nicaragua to the north of Lake Nicaragua were proposed by Halffter (1976) as the southern limit of the Mexican Transition Zone. The present study shows the South American affinity of the Canthonini of Costa Rica for dry tropical forest

(they share 40% of the species with the DTF of North Tolima), and this seems to apply in general to those species found in other types of vegetation (see Solis & Kohlmann 2002).

5) A good number of the species found in the sites we studied are characteristic of dry tropical forest, and even exclusive to this vegetation type. However, some species are shared with tropical rain forest. The proportion of shared species is much lower in Chamela, moderate in Palo Verde and greatest in the sites of Colombia. The latter is also reflected in the greater affinity of the Canthonini of Colombian DTF with those of Leticia (TRF), than with those of the DTF of Chamela (Fig. 3). Palo Verde shares 30% of its species with Los Tuxtlas, a forest where the DTF and the TRF species of Mesoamerica meet.

6) As regards *in situ* speciation, the most notable example is that of the viridis group, which has no direct relationship with the South American fauna of *Canthon* (*Glaphyrocanthon*). This group underwent much diversification in Mexico that appears to be recent and influenced by the process of drying out during the Holocene (many of its species are adapted to dry forest).

7) The enclaves of dry tropical forest in Colombia, in both the Caribbean Region and the Upper Magdalena Valley, are close to tropical rain forest. In the first case, Neguanje is part of the Province of the Sierra Nevada of Santa Marta where the vegetation change with increasing altitude and in Los Colorados there is still a remanent of rain forest. The Upper Magdalena River Valley is surrounded by rain forest on the skirts of the Cordillera Central and the Cordillera Oriental, and to the north by the Middle Magdalena Valley. This allows them to share species with adjacent ecosystems.

8) The Canthonini fauna of the tropical rain forests (Los Tuxtlas and Leticia) that were used as the outgroup, is very different between these two rain forests and also different from the fauna of the dry tropical forests. Considering all Scarabaeoidea, the similarity in species between Chamela and Los Tuxtlas is only 13 (Sørensen's QS index), while between Chamela and other dry tropical forest in Mexico the value is 41 (Morón *et al.* 1988).

9) The quality of the species list is the main limitation of the biogeographical analysis presented here. We have gathered all of the published information as well as that recorded in the databases of CONABIO and INBIO. Even so, these collections cannot be considered exhaustive, especially for Colombia.

10) The predominance of roller species (Canthonini) in dry tropical forest is well defined. On average 33.45% of the Scarabaeinae species found are Canthonini, a value that rises to 35.45% if we exclude Neguanje as the least representative site. In contrast, in the tropical rain forests studied, on average only 28% are rollers. The affinity of the rollers for sunny conditions is even greater in sites that are drier and have very open vegetation.

11) There have been several studies of the changes in the abundance of Scarabaeinae species from the dry season to the rainy season in dry tropical forest: Chamela (Andresen 2005), North Tolima (Escobar 1997), Guanacaste, Costa Rica (Janzen 1983) have produced similar results and emphasize the severity of the dry season. Soil humidity and ambient temperature control the activity and life cycle of Scarabaeinae (Halffter 1991, Martínez & Montes de Oca 1994, Bustos-Gómez & Lopera-Toro 2003, Andresen 2005). On the other

hand, the Scarabaeinae of dry tropical forests show a marked tendency for a generalist diet (copro-necrophagous). In Chamela 70% of Scarabaeinae (Andresen 2005) and in the north of Tolima 71% (Bustos-Gómez & Lopera-Toro 2003) have this type of diet.

Closing Remarks

The biogeographical analysis of areas of dry tropical forest in Mesoamerica and Colombia has provided and integrated geological, geomorphological, climatic and ecological elements that have brought us closer to understanding the origin and relationships of Neotropical dry forests.

The use of an outgroup polarized the cladograms, adding a new dimension to the study by establishing an axis for comparison that stood out in all analyses. The analises carried out, along with previous knowledge of the group allowed for an explanation of the spatio-temporal dynamics exhibited by the Canthonini in dry tropical forests.

Dry tropical forest represents a setting where the processes of vicariance and dispersal occur. This study reveals Canthonini's routes of dispersal via the dry forests while the speciation processes of some *Canthon*, appearing to be synchronous with the establishment of the dry forests of Mesoamerica and Colombia, also indicate the affinities of Canthonini to dry tropical forest, very similar to that of the flora of said ecosystem.

Biogeographical and ecological elements were brought together and these allowed us to explain both their presence in and the preference of some Canthonini for dry forest, and/or their exclusive distribution in some dry forests of Colombia and their absence from those of Mesoamerica, as was the case for *C. (Gl.) subhyalinus*, so clearly demonstrated by the PAE.

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APPENDIX 1
Scarabaeinae (Canthonini and other tribes) of the forests studied

MEXICO, CHAMELA

Agamopus lampros Bates
Canthon corporali Balthasar
Canthon pacificus Rivera & Halffter
Canthon cyanellus cyanellus LeConte
Canthon humectus riverai Halffter & Halffter
Canthon indigaceus LeConte
Pseudocanthon perplexus (LeConte)
Deltochilum timidum Howden
Deltochilum gibbosum (Fabricius)
Phanaeus demon Laporte
Phanaeus furiosus Bates
Coprophanaeus pluto Harold
Digitonthophagus gazella (Fabricius)
Onthophagus landolti Harold
Onthophagus igualensis Bates
Onthophagus hoepfneri Harold
Canthidium sp.
Dichotomius colonicus (Say)
Dichotomius amplicollis (Harold)
Ateuchus rodriguezi (Borre)
Uroxys sp.
Copris lugubris Boheman

PALO VERDE, COSTA RICA

Agamopus lampros Bates
Canthon cyanellus sallei Harold
Canthon deyrollei Harold
Canthon euryscelis Bates
Canthon indigaceus chevrolati Harold
Canthon meridionalis (Martinez, Halffter & Halffter)
Canthon morsei Howden
Canthon mutabilis Harold
Pseudocanthon perplexus (LeConte)
Deltochilum lobipes Bates
Malagoniella astyanax (Harold)
Phanaeus wagneri Harold
Phanaeus demon Laporte
Phanaeus eximius Bates
Coprophanaeus telamon (Erichson)
Coprophanaeus pluto (Harold)
Onthophagus acuminatus Harold

Onthophagus championi Bates
Onthophagus landolti Harold
Onthophagus hoepfneri Harold
Onthophagus marginicollis Harold
Onthophagus batesi Howden & Cartwright
Canthidium laetum Harold
Canthidium guanacaste Howden & Gill
Dichotomius yucatanus (Bates)
Dichotomius centralis (Harold)
Dichotomius annae Kohlmann & Solis
Ateuchus rodriguezi (Borre)
Copris lugubris Boheman

COLOMBIA, CARIBE REGION

Zambrano
Canthon cyanellus sallei Harold
Canthon juvencus Harold
Canthon lituratus (Germar)
Canthon septemmacutatus (Latreille)
Malagoniella astyanax (Harold)
Coprophanaeus jasius (Olivier)
Canthidium sp.
Dichotomius belus (Harold)
Onthophagus marginicollis Harold
Onthophagus lebasi Boucomont
Uroxys sp.
Eurysternus impressicollis Laporte

Los Colorados
Agamopus lampros Bates
Canthon aequinoctalis Harold
Canthon cyanellus sallei Harold
Canthon juvencus Harold
Canthon subhyallinus Harold
Coprophanaeus jasius (Olivier)
Diabroctis cadmus Harold
Phanaeus hermes Harold
Canthidium sp.
Dichotomius belus (Harold)
Onthophagus marginicollis Harold
Onthophagus lebasi Boucomont
Onthophagus sp.
Uroxys sp.

Tierra Bomba
Canthon cyanellus sallei Harold
Canthon juvencus Harold

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Canthon lituratus (Germar)
Diabroctis cadmus Harold
Canthidium sp.
Dichotomius belus (Harold)
Onthophagus marginicollis Harold
Onthophagus lebasi Boucomont
Onthophagus landolti Harold
Uroxys sp.
Eurysternus impressicollis Laporte

Neguanje
Canthon cyanellus sallei Harold
Canthon juvencus Harold
Canthon lituratus (Germar)
Phanaeus prasinus Harold
Canthidium sp.
Dichotomius belus (Harold)
Dichotomius sp.
Dichotomius sp.
Onthophagus marginicollis Harold
Onthophagus lebasi Boucomont
Onthophagus landolti Harold
Eurysternus impressicollis Laporte
Eurysternus caribaeus (Herbst)

COLOMBIA, NORTH TOLIMA

Canthon acutus Harold
Canthon aequinoctialis Harold
Canthon cyanellus sallei Harold
Canthon juvencus Harold
Canthon lituratus (Germar)
Canthon morsei Howden
Canthon mutabilis Harold
Canthon subhyalinus Harold
Malagoniella astyanax (Harold)
Phanaeus hermes Harold
Dichotomius belus (Harold)
Dichotomius sp. 1
Dichotomius sp. 2
Onthophagus landolti (Harold)
Onthophagus lebasi (Boucomont)
Onthophagus marginicollis (Harold)
Onthophagus rubrescens (Blanchard)
Canthidium sp.
Ateuchus sp.
Uroxys sp.
Canthidium sp.
Eurysternus plebejus (Harold)

MEXICO, LOS TUXTLAS (for rainforest, M. Favila pers. com.)

Canthon euryscelis Bates
Canthon femoralis (Chevrolat)
Canthon morsei Howden
Canthon vazquezae (Martinez, Halffter & Halffter)
Canthon subhyalinus Harold
Canthon edmondsi Rivera & Halffter
Deltochilum scabriusculum Bates
Deltochilum pseudoparile Paulian
Delthochilum gibbosum sublaeve Bates
Phanaeus endymion Harold
Sulcophanaeus chryseicollis (Harold)
Onthophagus nasicornis Harold
Onthophagus rhinolophus Harold
Canthidium aff. ardens Bates
Canthidium centrale Boucomont
Canthidium aff. perceptibile Howden & Young
Scatimus ovatus Harold
Uroxys boneti Pereira & Halffter
Uroxys bidentis Howden & Young
Uroxys transversifrons Howden & Gill
Ontherus mexicanus Harold
Bdelyropsis newtoni Howden
Dichotomius satanas (Harold)
Copris laeviceps Harold
Eurysternus angustulus (Harold)
Eurysternus caribaeus (Herbst)
Eurysternus velutinus Bates

COLOMBIA, LETICIA

Canthon aequinoctialis Harold
Canthon fulgidus Redtenbacher
Canthon luteicollis Erichson
Canthon semiopacus Harold
Cryptocanthon peckrorum Howden
Canthonella n. sp.
Scybalocanthon sp.
Deltochilum amazonicum Bates
Deltochilum carinatum Westwood
Deltochilum sp. 1
Deltochilum sp. 2
Deltochilum sp. 3
Coprophanaeus telamon (Erichson)
Coprophanaeus n. sp.
Oxysternon conspicillatum (Weber)

Oxysternon silenus Laporte
Phanaeus bispinus Bates
Phanaeus cambeforti Arnaud
Phanaeus chalcomelas (Perty)
Phanaeus meleagris Blanchard
Onthophagus haematopus Harold
Onthophagus sp. 1
Onthophagus sp. 2
Onthophagus sp. 3
Ontherus pubens Génier
Ontherus diabolicus Génier
Uroxys sp. 1
Uroxys sp. 2
Dichotomius boreus (Oliver)
Dichotomius mamillatus (Felsche)
Dichotomius ohausi (Luederwalt)
Dichotomius podalirius (Felsche)
Dichotomius sp. 1
Dichotomius sp. 2
Dichotomius sp. 3
Dichotomius sp. 4
Canthidium bicolor Bouc.
Canthidium gerstaeckeri Harold
Canthidium sp. 1
Canthidium sp. 2
Canthidium sp. 3
Canthidium sp. 4
Canthidium sp. 5
Bdelyrus sp.
Ateuchus murrayi (Harold)
Ateuchus sp. 1
Ateuchus sp. 2
Eurysternus caribaeus Herbst
Eurysternus cayennensis Laporte
Eurysternus confusus Jessop
Eurysternus foedus Guérin
Eurysternus hirtellus Dalman
Eurysternus inflexus (Germar)
Eurysternus velutinus Bates