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BIOGEOGRAPHICAL ANALYSIS OF SCARABAEINAE AND GEOTRUPINAE ALONG A TRANSECT IN CENTRAL MEXICO (Coleoptera, Scarabaeoidea)

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INTRODUCTION

Transects that cover a broad range of altitudes, climates and vegetation types over a large area such as the Mexican Transition Zone (MTZ), provide a good tool for the study of the distribution of any group or groups of biota and the causes that might have determined their distribution. Transects do not provide equally useful information in any geographic area. In a homogeneous region, from a historical biogeographical point of view, transects will mainly reflect the influence of climate conditions on the distribution of living things. However, what we find in the MTZ is not what we would expect if distribution were determined solely by climatic conditions. As proposed by Halffter (1964, 1976, 1987, 2003) and applied by many authors (see, for example, chapters in the books by Llorente-Bousquets et al., 1996, 2000, 2004; Llorente-Bousquets & Morrone 2002; and Morrone & Llorente-Bousquets 2006) the situation in the MTZ is much more complex than would be expected at a simple limit between the Nearctic and Neotropical regions. There is a true Transition Zone which runs from the SW of the United States of America down to Lake Nicaragua. Having made the same observation for plants, Rzedowski (1993) proposed the concept of Mega-Mexico which covers the same territory and complex biogeographical composition as Halffter's Mexican Transition Zone. In addition, there is an altitu-

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dinal transition because in all of the Mexican mountain ranges the upper altitudes (generally above 2400 m a.s.l.) are inhabited by organisms of Nearctic affinity, while the coastal plains (generally below 1200 m a.s.l.) are inhabited by fauna with Neotropical affinities. When humidity is high enough, there is a transition strip between two altitudinal limits and it is rich in endemic species.

The Mexican Plateau does not follow this pattern since the fauna of ancient groups - such as the majority of insects - have South American origins that are particular to them and have evolved in situ. These, in part, expand to the SW and S of the United States of America.

From the mid-Cenozoic and under geological scenarios that have changed relatively little (if, for the moment, we leave aside the gradual configuration of the great transverse mountain range - the Mexican Volcanic Belt – since the mid-Cenozoic), taxa of northern affinities (Nearctic) have expanded their distribution southwards, mainly following the mountain ranges with a general N-S orientation. In the opposite direction, taxa that are Gondwanian in origin (Neotropical) have expanded northwards using mainly, but not exclusively, the coastal plains of both littoral zones. These dispersal phenomena, along with their concomitant vicariance and strong development of endemic forms (especially on the Mexican Plateau), are much more evident in ancient groups of organisms; that is, in those whose presence in the MTZ goes back at least as far as the mid-Cenozoic. In groups with more modern distributions (for example, the majority of mammals and birds), the separation between the fauna of Nearctic and that of Neotropical origin is clearer and the transition character of the MTZ less marked.

For biogeographic analysis the advantage of an altitudinal transect such as the one we study here is that it allows us to determine the "dependence" of Nearctic taxa on mountains as dispersal routes and that of Neotropical taxa on coastal plains, as well as their levels of contact. It also allows us to see how current geographic and climate conditions influence distributions that might be considered historical. The only predecessors of this study, carried out on the scale of a true transect rather than a study of altitudinal distribution along a mountain or ravine, are those by Halffter et al. (1995) done on a W-E transect running from the Mexican Plateau to the coast of the Gulf of Mexico in the region of the Cofre de Perote, state of Veracruz, and the study by García-Real (1995) which analyzes a gradient, also with a W-E orientation, from the Manantlán Sierra (mountain range) in the Mexican Pacific littoral zone to the coastal plain in the state of Jalisco. In our study we cover a larger transect that has a general S-NNE orientation, from the Pachuca Sierra in the state of Hidalgo, central Mexico, to the coastal plains known as Las Huastecas (fig 1). Our transect is characterized by changes in vegetation type, as might be expected from the differences in altitude: 2840 m between the sites at the extremes we sampled (2960 and 120 m a.s.l.). It also has an interesting characteristic in that the middle of it crosses an arid zone that includes one of the most southern penetrations of the fauna of ancient South American origin that is evolving in the driest part of the Mexican Plateau.

The main purpose of the study is to establish the altitudinal distribution of the different historical-biogeographical elements that make up the MTZ fauna. Accordingly, the transect covers landscapes where species or groups of species that follow all of the distribution patterns

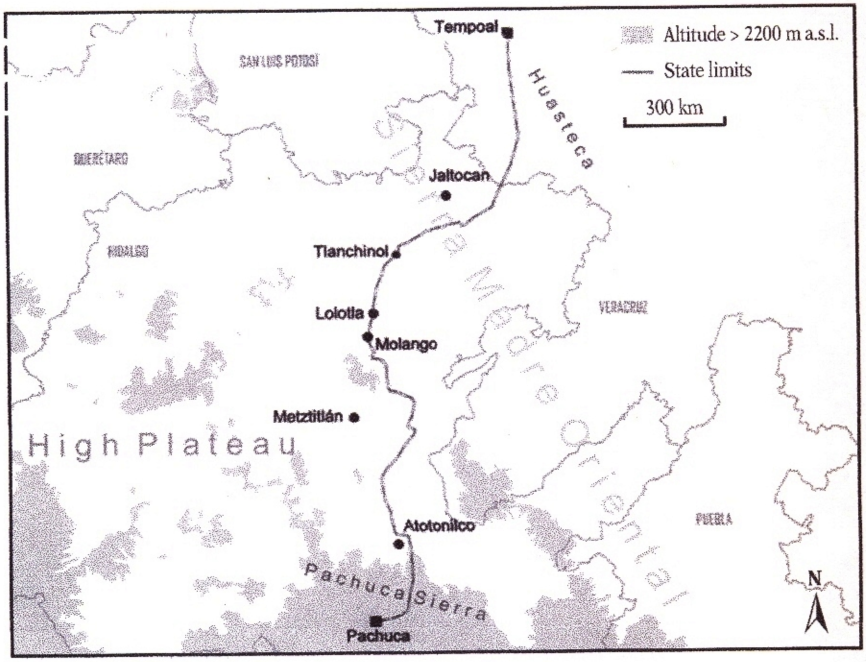

Fig. 1 – Map of the Hidalgo transect, Mexico. Prepared by Matthias Rös.

established by Halffter (1964, 1976, 1987, 2003) for this fauna dominate successively or are the only component. So, from south to north the transect includes landscapes with taxa of Nearctic affinity, two different landscapes, one temperate and the other arid with the taxa of the High Plateau, a fourth landscape corresponding to the transition strip with Neotropical taxa, and finally, several types of vegetation that make up a landscape completely dominated by Neotropical taxa.

For our study we have chosen two groups from the Scarabaeoidea superfamily: subfamily Geotrupinae (Geotrupidae) and subfamily Scarabaeinae (Scarabaeidae). These were chosen for several reasons: the ease with which it is possible to carry out systematic and highly significant captures for both groups, our familiarity with the groups and ability to identify all species without error, and because both groups have been used in previous biogeographic analyses. Owing to the latter there is a wealth of bibliography on the topic and this makes it possible to establish distributions outside of the Hidalgo transect.

The information used (presence-absence in a given place) is based on our own capture data, the databases of CONABIO for georeferenced captures where vegetation type was identified, and from the literature. The two latter sources have been particularly useful for establishing the distribution of the fauna outside of our transect and for addressing the relationship with general distribution patterns for each of the species recorded in the transect.

Our aim is to:

- demonstrate that the presence of different species of Geotrupinae and Scarabaeinae at different altitudes along the transect is determined by historical biogeographical reasons, since these beetles are distributed and occur altitudinally according to their distribution patterns in the MTZ (see Discussion). We expect that the species gradient will show a gradient in the distribution patterns; the latter studied more to date as horizontal spatial projections than as altitudinal distributions;
- understand to what extent the current vegetation type and land use, including those directly associated with human activity, have influenced the current distribution of Geotrupinae and Scarabaeinae along the gradient;
- describe the relationship within the gradient and in a more general way for the MTZ between landscape units (see definition in

Transcript Description) and the distribution patterns of the entomofauna. To this end we did various analyses (see Discussion). The first was based on landscape units and we analyzed the species of Geotrupinae and Scarabaeinae found in them, indicating the distribution pattern of each. With this analysis we intend to show how and to what degree the different distribution patterns contribute to the fauna of each landscape unit. The second was a parsimony analysis of endemicity among landscapes, using the species found in each landscape. In the third and final analysis (see Conclusions) we inverted the first analysis and used distribution pattern as the unit of study (instead of the landscape), and examined their presence in the transect overall;

- demonstrate the usefulness of an analytical tool such as distribution patterns for a descriptive analysis that seeks to establish hypotheses with strong historical and biogeographical content for a large, complex area.

Transect description

As a fundamental geographic and ecological unit within which to measure the presence of beetles in the transect, we selected the landscape. Of the different definitions of landscape in the literature, that which totally coincides with our use of the term is that of Bertrand (1970), which states that a landscape "is a portion of space characterized by a dynamic, and therefore unstable, combination of differentiated geographic elements - physical, biological and anthropic - that, being dialectically related among themselves, make of the landscape an indivisible whole that evolves as a unit, both under the effects among the elements that it is comprised of and the effect of the particular dynamics of each element". Methodology based on landscape units is integrative. It provides a spatial or geographic dimension to elements that observed from another perspective would be difficult to address simultaneously.

Our transect (fig. 1) is oriented in a S-NE direction from the Pachuca Sierra (2960 m a.s.l.), located a few kilometres from the city of the same name, to the town of Tempoal (120 m a.s.l.). Its entire length is approximately 150 km, all falling within the state of Hidalgo in central Mexico. The transect follows the line of federal highway 105 that runs from Pachuca to Tuxpan. In order to select suitable collecting sites that were accessible and had original vegetation as intact as possible, the transect was extended 20 km to either side of the highway, resulting in a 40 km wide strip between the Pachuca Sierra and Tempoal. As expected, considering the altitudinal differences (more than 2800 m), the transect crosses several different landscapes, each with one or two types of vegetation. From north to south, below we give a diagnosis of each of the landscapes. Detailed information about the vegetation types can be found in Rzedowski (1983).

The Pachuca Sierra. This mountain range extends NE up as far as the Mexican Basin at the southern part of the Mexican Plateau (fig. 2). Its orientation is approximately SE-NW. It forms part of the Mexican Volcanic Belt although between this huge range and the Pachuca range there is approximately 70 km of High Plateau, and both its northern and southern extremes are very close to the Sierra Madre Oriental (the Zacualtipán Sierra in the north). The main types of vegetation are *Abies* forests at the highest reaches and pine and pine-

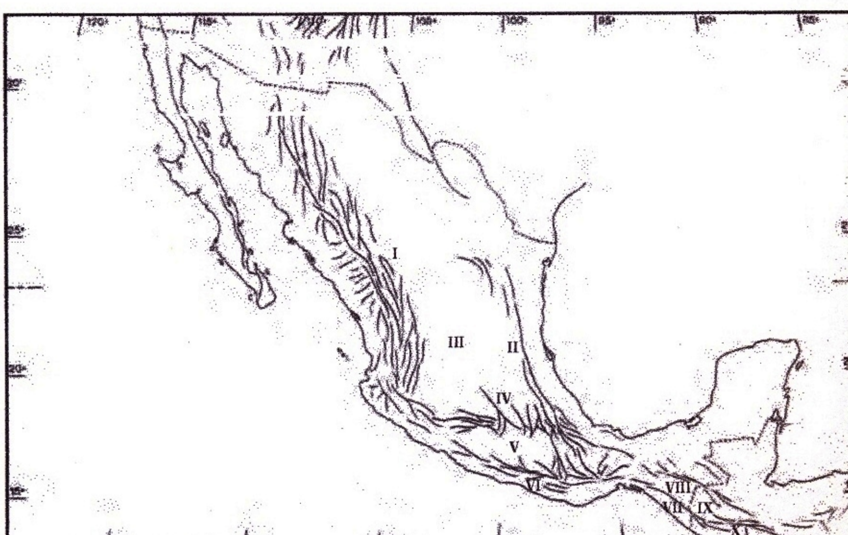

Fig. 2 – Main physiographic regions of Mexico and northern Central America. I. Sierra Madre Occidental, II. Sierra Madre Oriental, III. Mexican Plateau, IV. Mexican Volcanic Belt, V. Balsas River Basin, VI. Sierra Madre del Sur, VII. Chiapas Sierra Madre, VIII. Central Massif of Chiapas, IX. Guatemala Plateau, X. Central American Nucleus. From Zunino & Halffter, 1988.

oak forests at intermediate and low altitudes. The dominant stratum of the pine-oak forests has species of *Pinus* and *Quercus* trees, 12-18 m high. Trees are spaced out but there are no large canopy gaps. Rainfall is 800 to 1200 mm per year; mean annual maximum temperature is 26 to 28°C; mean annual minimum temperature is -2°C.

THE MEXICAN PLATEAU. This plateau (fig. 2), located in the centre and north of the country, covers approximately one quarter of Mexico. It is surrounded by a large U that, from west to east, is comprised of the Sierra Madre Occidental, the Mexican Volcanic Belt (its southern limit) and the Sierra Madre Oriental mountain ranges. To the south, its mean altitude is over 2000 m a.s.l.

The part of the High Plateau that crosses the transect before arriving at the Metztitlán Canyon (which is also on the High Plateau, although it is a landscape in its own right) is drier than its southern extreme which is the Valley of Mexico. The vegetation is pine-oak and oak forest on the hillsides and mountain slopes; pasture and xerophilous scrub on the flat part that has been greatly transformed by human activities.

The oak forests are generally dense and comprised of different species of *Quercus* with hard, flat, coriaceous leaves and fissured bark. Epiphytes such as bromeliads, orchids and some cacti are common.

The xerophilous scrub is described in the Metztitlán Canyon section. The presence of pastures in this part of the High Plateau is the result of a disturbance process caused by the removal of the forest over a long period of time. The strata are well defined: the tree layer is dominated by *Acacia schaffneri* which reaches a maximum height of 2.5 m, and has a typically umbrella shaped canopy. The herbaceous layer, very diverse, appears mainly during the rainy season. Rainfall is 400 to 600 mm per year. Mean maximum temperature is 28 to 30°C; mean minimum temperature is -4°C.

THE METZTITLÁN CANYON. The canyon crosses the transect in a general NW-SE direction. It was formed by the Metztitlán River which empties into the lagoon of the same name at its north-western end. There the canyon opens up to the Mexican Plateau which is drier than that presented in the Mexican Plateau section.

To the north, the canyon is limited by the Zacualtipán Sierra (see fig. 1) which casts a marked orographic shadow over the canyon, diverting the rain-laden winds from the north that bring humidity from the Gulf (NE-SW). This, together with the broad connection in the NW with the dry region of the Mexican Plateau creates arid conditions that favour the penetration of biotic elements from the dry Plateau. Throughout most of the canyon, mean annual precipitation is approximately 500 mm, reaching 600 and 800 mm at higher altitudes. Mean annual temperatures vary from 18 to 22°C. Mean annual maximum temperatures vary between 34 and 36°C; mean minimum temperature is 0°C.

The highest part of the canyon has pine forest, but most of its area (especially the steep sides) is covered with submontane scrub, xerophilous scrub and crassicaulous scrub. Submontane scrub occurs between 1800 and 1600 m a.s.l. on hills with gentle slopes and an east-southeast exposure. The shrub layer predominates in this community, representing 80 to 90% of the cover. Individual plants are as tall as two metres, with the exception of some *Yucca* individuals which are much taller and occur sporadically in the vegetation.

Within the xerophilous scrub are a group of communities dominated by bushes that grow on the arid and semiarid parts of the Metztitlán Canyon. The species of this scrub are rarely taller than four metres. Their stems ramify from the base or very close to the soil and exhibit different adaptations (spines, small leaves) that allow them to survive in environments where water is scarce. Crassicaulous scrub includes communities from arid and subarid climates in which the most notable plants are the large cacti (including columnar species) that often play the role of physiognomic dominants on the landscape. Mixed with these species are shrubby and herbaceous plants, all xerophilous and often spiny.

The Metztitlán Canyon (under protection as a Biosphere Reserve) is the most characteristic element on our transect and distinguishes the transect from any other that could be set up towards the east, from central Mexico to the Gulf of Mexico coastal plain. There is ample information, with a rich bibliography on the Metztitlán Canyon in the National Commission of Protected Areas (2003).

THE ZACUALTIPÁN SIERRA. This mountain range branches off from the Sierra Madre Oriental (fig. 2) and penetrates the Plateau in a north-western direction. Beetles were collected on the eastern slope that receives the rain-laden winds from the Gulf of Mexico and is much more humid.

Vegetation types include mixed pine-oak forest at high altitudes, and cloud forest at intermediate altitudes, along with semideciduous tropical forest at some lower altitude locations. Within the mountainous zones, cloud forest occupies sites that are wetter than those where *Quercus* and *Pinus* occur, and that are also cooler than the sites where tropical forest is found. This therefore is a discontinuous altitudinal transition band that occurs on the slopes of Mexican mountains that receive sufficient rain, between a lower limit of 1000 m a.s.l. and an upper limit of 1500 m a.s.l. In the transect, this type of forest occurs in the areas that receive more rainfall owing to the combined action of the rain-laden winds and the "nortes", i.e. seasonal masses of cold air from the north that cause rainfall in the autumn and winter months.

As indicated by Rzedowski (1983) the flora of cloud forest has interesting geographical links. On one hand, there is a significant number of species that also occurs in the United States of America and in Canada, or there is a closely related species in that region to the north. Most of these are trees. However, the southern taxa that is comprised of genera and species common to the Andean region of South America is quantitatively more important. It is also interesting that it is in this type of vegetation where relationships with Asian flora are evident. Physiognomically the forest is dense, generally 15 to 35 m high, although tree size can vary over a wider range and some are as tall as 60 m. In our transect, cloud forest represents a strip where climate and landscape change; i.e. between the arid Mexican Plateau the warmer and more humid Tropics. There is also a biogeographical transition as mentioned for plants, and as will be discussed, for the beetles. Annual rainfall is 500 to 2000 mm; mean annual maximum temperatures are 32 to 34°C; mean annual minimum temperature is -4°C.

THE SLOPE TOWARDS THE GULF-LAS HUASTECAS REGION. From the Zacualtipán Sierra to the Gulf of Mexico the landscape slopes down to the sea and as altitude decreases tropical conditions become more prevalent. At the top of the slope (above 1100 m a.s.l.) there are remnants of cloud forest, especially in the wetter ravines. This forest is replaced by semideciduous or deciduous tropical forest at an intermediate altitude (between 1100 and 1500 m a.s.l.). Lower down where there is less rain this forest is replaced by low deciduous forest. The bottom of the slope (and the transect) has been greatly modified for raising cattle and forests have been replaced by pastures.

The plant communities of tropical deciduous forest are characterized by a marked seasonality: for a period of 6 to 7 months all or the majority of the trees are leafless. Although the trees in this type of forest are tall (8 to 12 m on average), it is possible to distinguish between a medium and a low deciduous forest, the latter being notably shorter. The trees of deciduous forest are characterized by their low branching; their canopies are as wide as or wider than their height, which affects the amount of shade they provide (and the beetles) when they are in leaf.

Climate, and particularly the temperature, on the slope varies with altitude. At the top, annual rainfall ranges from 2000 to 2500 mm; mean annual maximum temperatures are 30 to 32°C; mean annual minimum temperature is 2°C. Lower down on the slope annual rainfall is 1500 to 2000 mm; mean annual maximum temperatures are 38 to 40°C; mean annual minimum temperature is 6°C.

Sampling methods

Field data were obtained using pitfall traps baited with horse and sheep dung, and with ethylene glycol as a preservative at high and intermediate altitudes. In deciduous forest human excrement and fish were used separately as attractants. Flight interception traps were also used. These consist of a transparent plastic sheet hung vertically in the vegetation. Flying organisms collide with the sheet and fall into collection containers with ethylene glycol (Márquez Luna 2005).

Complementary data were obtained by the direct observation of excrement, cadavers, etc. to ensure more a complete representation of the beetle fauna in the inventories. Each sampling or collecting point was georeferenced using a GPS, noting the altitude and vegetation type. The material collected has been deposited in the collections of the INECOL (Instituto de Ecología, A.C.) and the CCUAEH of the Autonomous University of the State of Hidalgo (Universidad Autónoma del Estado de Hidalgo) in Mexico, and in the CEUA of Alicante University (Universidad de Alicante), Spain.

The Parsimony Analysis of Endemicity (PAE) was applied based on Escalante & Morrone (2003) using the landscapes as the areas of endemism, and the presence (1) or absence (0) of species as shown in Table 1. The programs Nona version 2.0 (Goloboff 1993) and Winclada version 0.9.99 (Nixon 2000) were used to obtain and edit, respectively, the cladograms as was the Bootstrap statistical test.

Results: beetles in the landscape units along the transect

Tab. 1 lists all the species of Scarabaeinae and Geotrupinae collected along the transect. The landscape where they were collected and the sites are indicated. The type of habitat in which each species was found and the altitudinal limits within which it was collected are also reported. Previous studies of the region such as those by Morón & Terrón (1984) and Morón (1994), and particularly that of Delgado & Márquez (2006) on the Scarabaeoidea of the state of Hidalgo were very useful in the preparation of this table.

Discussion: biogeographical and macroecological analysis

Since our biogeographical analysis is based on the distribution patterns proposed by Halffter (1964, 1976, 1987, 2003; see discussion and synthesis in Morrone & Márquez 2008) for the insects of the MTZ, we feel it would be interesting to relate how these patterns were established. A distribution pattern is a reference that is established based on the additive and average distribution areas of a set of species for which the biogeographic origin is assumed to coincide approximately. The concept of distribution pattern (originally called dispersal pattern) was introduced by Halffter (1974, 1975, 1976) and defined as the current distribution of a group of organisms that has originated or has come together as said group in a specific area, coexisted for a long time and has a common biogeographical history. These patterns are a synthesis and reference model with which to compare the current distribution of a suprageneric group, that of a genus or of a species (see analysis in Lobo 2007). It is necessary to understand that it is implicit in Halffter's concept that in its features the pattern corresponds to a dispersal that occurred at a specific geological time, also within a particular geographic and ecological scenario. This is why in the MTZ we speak of ancient patterns (lower and middle Cenozoic) and recent patterns (Pliocene to present).

Tab. 1 – Especies de Geotrupini y Scarabaeinae colectadas o registradas para el transecto: 1datos de colectas propias de los autores, 2dato tomado de Trotta-Moreu et al. (2008); 3datos tomados de Delgado y Márquez (2006); 4especies que además están en los Bancos de Datos de CONABIO o citadas en la literatura del área del transecto (e.g. Morón y Terrón 1984; Morón 1994). Las dos especies introducidas no están numeradas.

	Especie	Sierra de Pachuca	Altiplano	Meztitlán	Zacualtipán	Huasteca	Tipo de hábitat en el transecto	Altitud en el transecto según colectas (m s.n.m.)
	Geotrupini							
1	*Ceratotrupes bolivari* Halffter y Martínez	[1]Omitlán					Bosque de pino, encino, pino-encino, pastizal alpino	2407 a 2960
2	*Onthotrupes herbeus* (Jekel)	[2]Seis millas al NE de Pachuca						
3	*Onthotrupes sallei* (Jekel)	[1]Omitlán, [1]Carretera hacia El Chico					Bosque de pino-encino, bosque de encino, pastizal	2386 a 2579
	Scarabaeinae							
4	*Ateuchus illaesum* (Harold)				[3]Tianguistengo, [1]Chilijapa, [3]Atezca, [3]Molango, [3]Otongo	[1]Tamala	Bosque mesófilo, bosque tropical subcaducifolio	567 a 1323
5	*Canthidium* sp.					Acatepec	Bosque tropical caducifolio	315
6	*Canthon (Glaphyrocanthon) circulatus* Harold[4]				[3]Otongo	[1]Atlapexco, [1]Acatepec	Bosque tropical caducifolio y subcaducifolio	315 a 1080
7	*Canthon (Glaphyrocanthon) viridis* Palisot de Beauvois			[1]Santa Mónica			Matorral submontano	1830
8	*Canthon cyanellus cyanellus* LeConte					[1]Tamala, [1]Acatepec, [3]Huejutla	Bosque tropical caducifolio	315 a 567
9	*Canthon humectus hidalgoensis* Bates			[1]Santa Mónica, [3]Barranca de Metztitlán	[3]Zacualtipán		Matorral crasicaule y matorral submontano, pastizales	1810 a 1836
10	*Canthon humectus humectus* (Say)		[1]Sto. Domingo, [3]Atotonilco el Grande, [3]San Miguel Regla	[1,3]Santa Mónica, [3]Vaquerías, [3]Barranca de Metztitlán	[3]Molango		Pastizal, bosque de encino, esporàdicamente en matorral submontano	1830 a 2288

continued

	Especie	Sierra de Pachuca	Altiplano	Meztitlán	Zacualtipán	Huasteca	Tipo de hábitat en el transecto	Altitud en el transecto según colectas (m s.n.m.)
11	*Canthon imitador* Brown		[3]Atotonilco el Grande	[1]Santa Mónica, [3]Vaquerias,[3]Barranca de Metztitlán, [3]Mezquititlán	[3]Zacualtipán [1]Eloxochitlán, [1]Molango		Matorral crassicaule, matorral submontano, pastizales, bosque mesófilo	1700 a 1836
12	*Canthon indigaceus chevrolati* Harold					[1]Atlapexco	Bosque tropical caducifolio, pastizal	120
13	*Canthon indigaceus chiapas* Robinson[4]				[3]Tlanchinol, [3]Otongo		Bosque mesófilo y bosque tropical caducifolio	1080 a 1500
	Canthon grupo *morsei*					Acatepec	Bosque tropical caducifolio	315
14	*Copris armatus* Harold	[1,3]El Chico, [3]Real del Monte	[3]Huasca, [3]Pachuca				Bosque de abeto, pino y pino-encino	2288-2960 (la captura de esta especie a 1836 m s.n.m. puede considerarse como excepcional)
15	*Copris incertus* (Say)				[1]Sta. Mónica, [1]Zacualtipán,[3]Otongo, [1]Lontla,[1]Chilijapa, [1,3]Tlanchinol,[3]Molango, [3]Acuatitlán,[3]Ixtlahuaco, [3]Atezca y [3]Lolotla	[1]Atlapexco, [1]Acatepec	Bosque mesófilo, bosque mixto, bosque tropical caducifolio	168 a 1938
16	*Copris laeviceps* Harold				[3]Otongo	[1]Acatepec	Bosque tropical caducifolio y subcaducifolio	315 a 1080
17	*Coprophanaeus gilli* Arnaud				[3]Molango,[1,3]Tlanchinol, [3]Otongo	[1]Acatepec	Bosque mesófilo y bosque tropical caducifolio y subcaducifolio	315 a 1450
18	*Coprophanaeus telamon corythus* (Harold)[4]				[3]Otongo		Bosque tropical subcaducifolio	1080
19	*Deltochilum gibbosum sublaeve* Bates[4]				[3]Otongo	[1]Acatepec	Bosque tropical caducifolio y subcaducifolio	315 a 1080
20	*Deltochilum lobipes* Bates					[1]Acatepec	Bosque tropical caducifolio	315
21	*Deltochilum mexicanum* Burmeister				[1]Sto. Domingo,[1]La Mojonera,[3]Zacualtipán, [1,3]Tlanchinol,[3]Atezca, [3]Otongo		Bosque mixto, bosque mesófilo, bosque tropical subcaducifolio	1120 a 1886

continued

	Especie	Sierra de Pachuca	Altiplano	Meztitlán	Zacualtipán	Huasteca	Tipo de hábitat en el transecto	Altitud en el transecto según colectas (m s.n.m.)
22	*Deltochilum scabriusculum* Bates				[3]Otongo	[1]Acatepec	Bosque tropical caducifolio y subcaducifolio	315 a 1080
23	*Dichotomius amplicollis* (Harold)				[3]Otongo	[1]Acatepec	Bosque tropical caducifolio y subcaducifolio	315 a 1080
24	*Dichotomius colonicus* (Say)			[1]Santa Mónica	[3]Atezca, [3]Molango, [3]Otongo	[1]Acatepec	Matorral submontano, pastizales, encinar, bosque mesófilo, bosque tropical caducifolio y subcaducifolio	315 a 1836
25	*Dichotomius satanas* Harold				[1]Sto. Domingo, [1]Zacualtipán, [1,3]Tlanchinol, [3]Atezca, [3]Lolotla, [3]Ixtlahuaco, [3]Xochicoatán, [3]Otongo		Bosque mixto, bosque mesófilo, bosque de encino, bosque tropical subcaducifolio	1300 a 1883
	Digitonthophagus gazella (Fabricius)			[1]Santa Mónica		[1]Atlapexco	Matorrales crasicaule y submontano, bosque tropical caducifolio	168 a 1830
	Euoniticellus intermedius Reiche			[1]Santa Mónica	[3]Tlanchinol		Matorral submontano y bosque mesófilo	1435-1830
26	*Eurysternus magnus* Laporte				[1,3]Tlanchinol, [3]Molango-Atezca, [3]Otongo		Bosque mesófilo y bosque tropical subcaducifolio	1435 a 1450
27	*Eurysternus mexicanus* Harold				[1]Tlanchinol, [3]Atezca, [3]Otongo	[1]Tamala, [1]Acatepec	Bosque mesófilo, pastizal, bosque tropical caducifolio y subcaducifolio	567 a 1450
28	*Ontherus mexicanus* Harold				[1]La Mojonera, [1,3]Zacualtipán, [1]Chilijapa, [3]Acuatitlán, [3]Atezca, [3]Lolotla, [3]Molango, [3]Tlanchinol, [1]Tepehuacán		Bosque de encino, bosque mesófilo, bosque mixto, bosque tropical caducifolio	1147 a 1900
	Onthophagus alluvius H.& C.			[1]Santa Mónica			Matorral submontano	1830
	Onthophagus aureofuscus Bates	[1]Matías Rodríguez (Singuilucan)					Bosque de pino-encino	2740

continued

	Especie	Sierra de Pachuca	Altiplano	Meztitlán	Zacualtipán	Huasteca	Tipo de hábitat en el transecto	Altitud en el transecto según colectas (m s.n.m.)
29	*Onthophagus batesi* Howden y Cartwright[4]				[3]Atezca,[3]Otongo		Bosque tropical caducifolio y subcaducifolio	168 a 1340
30	*Onthophagus* sp. nov.[1]				[1]Tlanchinol, [1]Tepehuacán		Bosque mesófilo, bosque tropical caducifolio	1120 a 1450
31	*Onthophagus chevrolati chevrolati* Harold	[1]Rancho Santa Elena,[1]Omitlán de Juárez,[3]El Chico, [3]Real del Monte	[3]Atotonilco,[3]Huasca		[3]Zacualtipán		Bosque de pino-encino, pastizal alpino, bosque de abetos	2386 a 2900
32	*Onthophagus corrosus* Bates					[1]Tamala	Bosque tropical subcaducifolio	567
33	*Onthophagus cyanellus* Bates[4]				[3]Tianguistengo, [3]Zacualtipán,[3]Atezca, [3]Acuatitlán, [3]Molocotlán, [3]Tlanchinol, [3]Xochicoatlán, [3]Otongo		Bosque mesófilo, bosque de encino, bosque tropical subcaducifolio	650 a 1500
	Onthophagus fuscus Zunino & Halffter	[1]El Chico					Bosque de oyamel	2950
	Onthophagus gibsoni Hown. & Gén.			[1]Santa Mónica			Matorral submontano	1830
34	*Onthophagus hidalgus* Zunino y Halffter		[3]Huasca		Tepehuacan		Bosque de pino-encino, bosque tropical subcaducifolio	1174-2400
35	*Onthophagus igualensis* Bates[4]			[1]Santa Mónica Metztitlán			Matorral crassicaule y submontano	1452 a 1830
36	*Onthophagus incensus* Say				[1]Sto. Domingo, [1,3]Zacualtipán, [3]Tianguistengo, [1]Chilijapa, [1,3]Tlanchinol, [3]Atezca, [3]Molango, [3]Xochicoatlán, [3]Otongo	[1]Tamala, [1]Acatepec	Bosque mesófilo, bosque mixto, bosque mesófilo, bosque de encino, bosque tropical caducifolio y subcaducifolio	315 a 1883
	Onthophagus knulli H. & C.			[1]Santa Mónica			Matorral submontano	1830
37	*Onthophagus landolti* Harold[4]			[1]Santa Mónica Metztitlán			Matorral crassicaule y submontano	1452 a 1830

continued

	Especie	Sierra de Pachuca	Altiplano	Meztitlán	Zacualtipán	Huasteca	Tipo de hábitat en el transecto	Altitud en el transecto según colectas (m s.n.m.)
38	*Onthophagus landolti texanus* Howden y Cartwright					[1]Atlapexco	Bosque tropical caducifolio, pastizal	120 a 168
39	*Onthophagus lecontei* Harold		[1]Mineral de la Reforma, [1]Huasca, [3]Pachuca, [3]Real del Monte	[1]Santa Mónica	[3]Zacualtipán		Matorral xerófilo, submontano y crasicaule, bosque de pino-encino, bosque de encino	1810 a 2400
40	*Onthophagus longimanus* Bates					[1]Acatepec	Bosque tropical caducifolio	315
41	*Onthophagus mexicanus* Bates	[1]El chico	[1]Mineral de la Reforma, [1]Huasca	[1]Santa Mónica	[3]Zacualtipán		Matorral submontano, pastizal, bosque de encino; bosque de oyamel	1830 a 2950
42	*Onthophagus durangoensis* Balthasar				[3]Molango, [3]Otongo		Bosque mesófilo, bosque tropical subcaducifolio	650 a 1080
43	*Onthophagus nasicornis* Harold[4]				[3]Atezca, [3]Otongo	[1]Tamala	Bosque mesófilo y bosque tropical subcaducifolio	567 a 650
44	*Onthophagus rostratus* Har.				[1]Chilijapa		Bosque mesófilo	1323
	Onthophagus subtropicus Howd. & Cartwr.			[1]Santa Mónica			Matorral submontano	1830
				[1]Santa Mónica			Matorral submontano	1830
45	*Phanaeus adonis* Harold[4]		[3]Atotonilco,[3]Huasca	[1]Santa Mónica			Matorral crasicaule y matorral submontano, pastizales	1810 a 1836
46	*Phanaeus amethystinus* Harold[4]				[1]La Mojonera, [3]Zacualtipán, [1]Tlanchinol, [4]Molango		Bosque mesófilo	1300
47	*Phanaeus genieri* Arnaud[4]				[3]Atezca, [3]Tlanchinol, [3]Otongo		Bosque mesófilo y bosque tropical subcaducifolio	650-1435
48	*Phanaeus palliatus* Sturm		[1]Sto. Domingo, [1]Acatlán				Bosque de encino, bosque de pino-encino, pastizal	2240 a 2579
49	*Phanaeus quadridens* Say		[3]Huasca,[3]Pachuca, [3]San Miguel Regla				Pastizal, bosque de encino	1830 a 2400
50	*Phanaeus sallei* Harold[4]				[3]Atezca, [3]Otongo		Bosque tropical subcaducifolio	650 a 1080
51	*Uroxys deavilai* Delgado y Kohlmann					[1]Acatepec	Bosque tropical caducifolio	315

The process of constructing a distribution pattern is equivalent to the move from individual to the generalized tracks of León Croizat; though for the distribution patterns there is a previous phylogenetic hypothesis. Croizat's individual tracks refer to supposedly monophyletic groups and, a fortiori, also to standard tracks.

The advantages of using distribution patterns in a region like the MTZ are evident. They allow us to posit general biogeographical hypotheses for a defined space and compare what happens in that space with the distribution in larger geographic areas, such as the MTZ. In addition, it is also possible to contrast the patterns with the distribution of a broad scale of ecological and climate conditions, and even with natural resource use by humans and this gives a macroecological perspective.

All the distribution patterns defined by Halffter for the MTZ occur in our transect, and for the distribution pattern of the Plateau the biota from both temperate and arid conditions are included. The study transect provides an excellent representation of the very diverse biota (with their different biogeographical origins, and times of geological penetration) that characterize the MTZ.

For the analysis of the relationship between landscape units and beetles we use the units (from S to NE) described in previous sections, including a discussion of the more or less close association between the distribution of the beetles and the dominant vegetation types.

Pachuca Sierra. All of the taxa found in this landscape unit have northern affinities, with none of Neotropical origin. This confirms, once again, the northern biogeographical origin of the insects that live over 2400 m a.s.l. in the mountains of the MTZ. However, these taxa with northern affinities have two distribution patterns that differ in time since their penetration into the MTZ. The more recent one, in geological terms, is the Nearctic Pattern exhibited by the Geotrupinae. Following this we describe the other distribution pattern, the Paleoamerican, exhibited by species that penetrated the MTZ much earlier.

The Geotrupinae are restricted to the mountains of the MTZ, between 3200 and 2000 m a.s.l., with the exception of the occasional species that occurs a little lower down. The genus *Onthotrupes* is endemic to Mexico, except for one species found as far as Guatemala and El Salvador. Its distribution is limited to the Mexican Volcanic Belt and the Sierra Madre del Sur. The *Onthotrupes* found along the transect belong to a group of species distributed in the Mexican Volcanic Belt and the adjacent part of the Sierra Madre Oriental (Trotta-Moreu 2008).

The genus *Ceratotrupes* is also endemic to Mexico. Of its three species, two have a wide distribution with that of *C. bolivari* being the broadest of all the Geotrupinae. It extends from the north of the Sierra Madre Occidental (Chihuahua, Sonora and Durango) through the entire Mexican Volcanic Belt to its limit in Veracruz, and is also found in some sites in the Sierra Madre del Sur (Guerrero, Oaxaca) (fig. 3). Within their distribution the three species of Geotrupinae prefer pine forests at lower altitudes and are most frequent in the mountain pastures at the highest part of their range.

The Scarabaeinae found in the Pachuca Sierra have a different distribution pattern that originated in the north, but penetrated the MTZ much, much earlier. This pattern includes genera that clearly originate in the Old World, penetrated the MTZ (and the Americas in general) a long time ago and have lines of species that are totally limited to the mountains (Paleoamerican Mountain Pattern). There are also lines that have invaded the Plateau (Paleoamerican Mexican Plateau

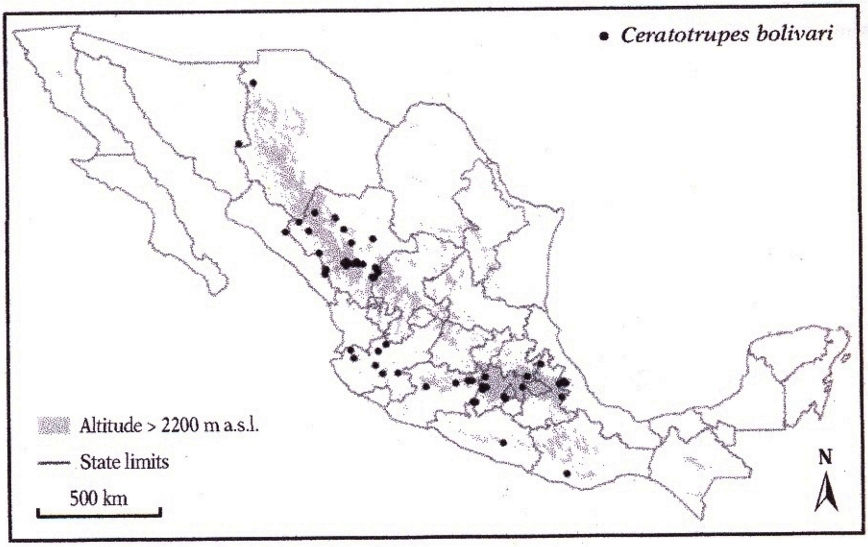

Fig. 3 – Distribution map for *Ceratotrupes bolivari*, an example of the Nearctic Distribution Pattern. Prepared with data from CONABIO and Trotta-Moreu *et al.*, 2008. Map prepared by Matthias Rös.

Pattern), or the tropical lowlands (Paleoamerican Tropical Pattern); in all cases with strong in situ differentiation and speciation. The Paleoamerican genera exhibit broad ecological diversification, both in the Americas and in the Old World. In the Americas and outside the Americas there is a marked contrast between the Paleoamerican taxa and those that follow the Nearctic Pattern. Outside the Americas the Nearctic genera are associated with cold or temperate-cold climates.

Of the three Paleoamerican taxa currently in the Pachuca Sierra, *Copris armatus* belongs to the armatus complex (see Matthews 1961) comprised of a set of species exclusive to the mountains of Mexico and Central America. Concretely, *C. armatus* is the species with the highest distribution (1830 to 3000 m a.s.l.). It is found in the Mexican Volcanic Belt and the surroundings of the Sierra Madre Occidental and Sierra Oriental mountain ranges.

The distribution of *Onthophagus chevrolati chevrolati* is very similar (fig. 4). The genus *Onthophagus* has numerous species in the MTZ. They belong to the chevrolati group, and within this group belong to the subgroup that is also called *chevrolati*, for which all species exhibit the Paleoamerican Mountain Pattern.

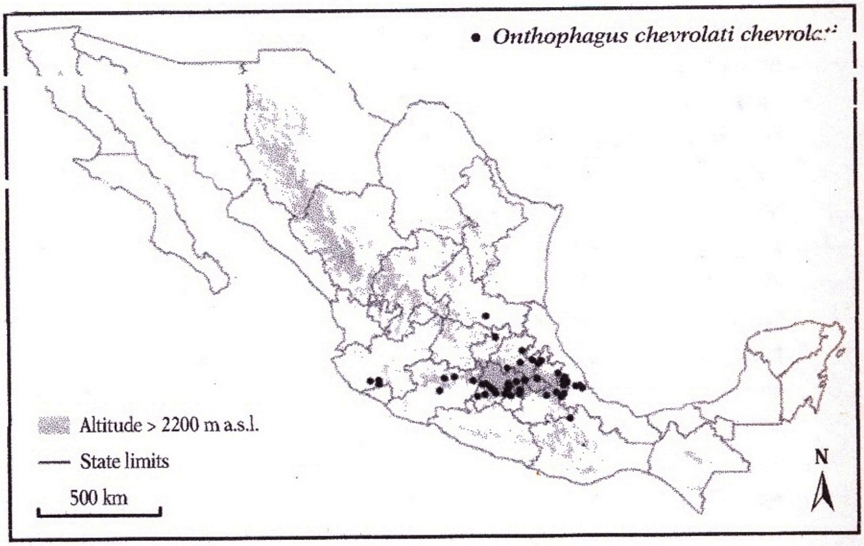

Fig. 4 – Distribution map for *Onthophagus chevrolati chevrolati*, an example of the Paleoamerican Mountain Pattern. Prepared with data from CONABIO and Zunino & Halffter, 1988. Map prepared by Matthias Rös.

The genus *Onthophagus*, as such, illustrates the Paleoamerican Pattern very well. It is a genus that clearly originated in the Old World where the greatest variety and number of phyletic lines are found, as are the most primitive forms and the greatest taxonomic and morphological richness and diversity (see the comprehensive discussion in Zunino & Halffter 1988). The subgenus *Onthophagus* to which all the American species belong, appears to have originated in the east of the Palaearctic region or in the Chinese Transition Zone (Zunino & Halffter 1988).

There is morphological evidence that strongly supports the supposition that the *chevrolati* and *mexicanus* groups - and it is the latter to which we are referring when we speak of the Mexican Plateau landscape - have a common origin in the same ancestral Asian trunk (see Zunino & Halffter 1988). However, just as there are morphological affinities between the two groups, different biogeographical tendencies are also evident. The *mexicanus* group has, in the United States, primarily species from the eastern U.S.A., and in the MTZ it has Plateau species (plus two from Guatemala). In the United States the *chevrolati* group has few species, mostly from the SW. The most noteworthy aspect of its geographic distribution is its success in the mountains of the MTZ and to the south of the Mexican Volcanic Belt.

In the *chevrolati* group, the *chevrolati* complex of species extends from Arizona (the Chihuahua Sierra), along the Sierra Madre Occidental and the Mexican Volcanic Belt (fig. 2). Along this volcanic belt the taxon with the widest distribution is *Onthophagus chevrolati chevrolati* (fig. 4), found from 2400 to 3800 m a.s.l. This is also the species of Scarabaeinae found at the highest altitude in the MTZ. In the western part of its distribution (Michoacán) it can be found at 2000 m a.s.l., and in the eastern extreme (Puebla and particularly Veracruz) as low as 1600 m a.s.l. In addition to inhabiting the Mexican Volcanic Belt, it is found in some of the mountains south of the Plateau and near the large mountain ranges (Mexican Volcanic Belt and the Sierra Madre Oriental). These mountain ranges are found in the states of Guanajuato, Querétaro, Hidalgo and San Luis Potosí. It is also found in the north of the Puebla-Oaxaca Mountain System, where these mountains make contact with the Mexican Volcanic Belt.

The current shape of the geographic dispersal of *Onthophagus chevrolati chevrolati* is aggressive and probably recent, given the young geological age of several of the mountains where it occurs. The wide altitudinal range over which it is distributed it can be found in different types of temperate-cold forests, as well as in high mountain grasslands. The same occurs with *Copris armatus* which is more common in grasslands. This tendency toward more sunny conditions is also found in Europe for species of both genera in temperate and temperate-cold landscapes.

In the same *chevrolati* group, in the Pachuca Sierra there are two other taxa: *Onthophagus fuscus parafuscus* cited as *O. fuscus orientalis* by Zunino & Halffter (1988) for the Sierra Madre Oriental and *Onthophagus aureofuscus* cited for the Puebla-Oaxaca Mountain System and a limited area in the Sierra Madre Occidental (Zunino & Halffter 1988). Its capture in the Pachuca Sierra broadens its distribution to north of the Mexican Volcanic Belt, partly filling the separation between the two disconnected areas mentioned previously.

There is a fourth species of *Onthophagus*, *O. mexicanus*, which though characteristic of the Mexican Plateau, ascends the mountains (mentioned with the beetles of Mexican Plateau).

In summary, the Pachuca Sierra landscape unit has an extremely coherent biogeographical composition comprised of taxa with the Nearctic and Paleoamerican Mountain Patterns. With a slight change in the species composition (but not in the genera or phyletic lines) it has the beetles that we would find in any of the high regions of the Mexican Volcanic Belt. Recent panbiogeographical analyses (Morrone & Márquez 2000; Morrone & Márquez 2003; Abramovich et al. 2004; Morrone 2005 and bibliography cited therein) confirm the existence of generalized tracks of northern affinity that cover the Sierra Madre Occidental, the Sierra Madre Oriental and the Sierra Madre del Sur, as well as the Mexican Volcanic Belt. From an ecological perspective, there are no forest or grassland specialists. The same species are found in both vegetation types, although as mentioned, there are more individuals in the grasslands: a result of the known heliophile tendency of Scarabaeinae in temperate and temperate-cold climates (e.g. *Copris lunaris* (L.) in Europe).

THE MEXICAN PLATEAU. In very few places in the world is it possible to find such a marked contrast over such a short distance as that which occurs between the Pachuca Sierra (or any other mountain range of the Mexican Volcanic Belt) and the Mexican Plateau. Where they meet there is a difference of only a few dozen metres in altitude and the same is true of the horizontal distance as they are separated by only a few hundred metres; yet the contrast is stark. There is a physiognomic contrast: mountains covered with coniferous forest juxtaposed with a treeless Plateau (with the exception of some hills with *Quercus*), but the greatest differences are in their geological and biogeographical history.

At the elevation that begins in the Miocene and the formation of the southern limit (Mexican Volcanic Belt) from the Miocene to the Pleistocene, with points that are even active today, the Mexican Plateau is isolated and becomes an area of important diversification and speciation for the oldest lineages of insects and plants; both those of South American origin (the *Canthon* and *Phanaeus* lines for example), and those originating in the north (the *Onthophagus* lines, for example). This is a very important phenomenon that marks the biogeographic affinities of an area that covers more than two thirds of the MTZ.

On the Plateau there are no Nearctic lineages and the Paleoamerican Mountain lineages are marginal (*Copris armatus, O. c. chevrolati* and *O. hidalgus*). In their place, there are lineages of clear Neotropical provenance (different species, but the same genera as in South America), though evolved in and characteristic of the Plateau. These lineages belong to the Mexican Plateau Distribution Pattern, and dominate the composition of the fauna in many insect groups, including the Scarabaeinae. Additionally, for these beetles, there are some groups of *Onthophagus* that belong to the Paleoamerican Distribution Pattern on the Plateau.

The fauna characteristics of the Plateau are determined by:

- the absolute dominance of Neotropical genera with their own phyletic lineages exclusive to the Plateau;
- the presence of lines of *Onthophagus* with species that evolved on the Plateau (Paleoamerican Plateau Pattern), and are different from those that are found in the mountains (Paleoamerican Mountain Pattern);
- The phenomenon of vertical Plateau-to-Mountain colonization is limited (one of the few examples is that of *Phanaeus palliatus* which we explore below). The distributions of the taxa originating in the north and characteristic of the mountains have resulted from processes of horizontal dispersal, following the large mountain ranges of the MTZ, and taking advantage of the coldest periods (see Lobo & Halffter 2000).

There is, in the Scarabaeinae a type of trophic resource exploitation: roller species that are not found in the mountains. Making a ball of dung and rolling it is a way of relocating the dung that is usually associated with more open, sunny conditions. The rollers are represented by two species on the temperate Plateau, though there are five species (42% of the total number of native species) in the arid region of the Plateau (the Metztitlán Canyon).

The group of eight subspecies that make up *Canthon humectus* (Say) is distributed in and very characteristic of the Mexico, Oaxaca and Chiapas-Guatemala Plateaus (Halffter & Halffter 2003). These are the most abundant Scarabaeinae in sunny conditions (pastures, xerophilous scrub, etc.) and are very common on these Plateaus. Their abundance may have risen with the increase in domestic mammals introduced by the Europeans (see discussion in the Metztitlán Canyon section). The *C. humectus* group is an excellent example of the Plateau Distribution Pattern because, even though the genus *Canthon* of Neotropical origin is widely distributed in the Americas, *C. humectus* belongs to a phyletic line with only this one species. It is exclusive to the Plateaus mentioned with a limited expansion to southern Texas (Halffter & Martínez 1977; Halffter & Halffter 2003).

There are two subspecies on the transect: *C. (C.) humectus humectus* on the temperate Plateau and *C. (C.) humectus hidalgoensis* on the arid Plateau (Metztitlán Canyon). The distribution of the first subspecies (fig. 5) covers all of the south, temperate region of the Mexican Plateau, from Michoacán to Veracruz, and the temperate region of Chihuahua. It is very abundant in pastures.

The other subspecies, *C. humectus hidalgoensis*, is found on the arid Plateau (Metztitlán Canyon). Its distribution (fig. 5) extends from the south of the Plateau to the north and northeast: Guanajuato, Querétaro and Hidalgo as far as Durango and Chihuahua, down in the east to Tamaulipas, Brownsville (Texas) and Nuevo León (Halffter 1961). It is found at a lower altitude and in drier conditions than *C. humectus humectus* is, in pastures and xerophilous scrub. The distributions of the two subspecies come into contact right at the high points of the Metztitlán Canyon.

We mentioned *Canthon imitator,* which enters the edges of the temperate Plateau, when we spoke of the Metztitlán Canyon. *Phanaeus quadridens* has a biogeographic history and a distribution very similar to those of *C. humectus humectus*. It belongs to a Neotropical genus that is widely distributed in the Americas. This species belongs to a group within the subgenus *Phanaeus* (the *quadridens* group) along with *Ph. palliatus* and *Ph. damodes* (see Edmonds 1994). It is a large tunnelling Scarabaeinae and is most abundant in pastures and other open vegetation formations on the Plateau.

Phanaeus palliatus is, of all the species with the Plateau Distribution Pattern, that which goes to the highest altitudes in the mountains. It is found between 1800 and 2800 m a.s.l. in the Mexican Volcanic Belt, Puebla and Hidalgo as far as Jalisco, and in the south of the Sierra Madre Occidental (Durango). It is often found along the edges of pine or pine-oak forests (Edmonds 1994).

A third species of *Phanaeus*, *Ph. adonis*, is characteristic of the dry Plateau (Metztitlán Canyon), with a limited penetration into the temperate Plateau.

For the genus *Onthophagus* on the Plateau, there are four species. *O. chevrolati chevrolati*, presented above, is characteristic of the mountains and extends down to the Plateau. *Onthophagus hidalgus* is found at the highest points on the Plateau landscape in the sur-

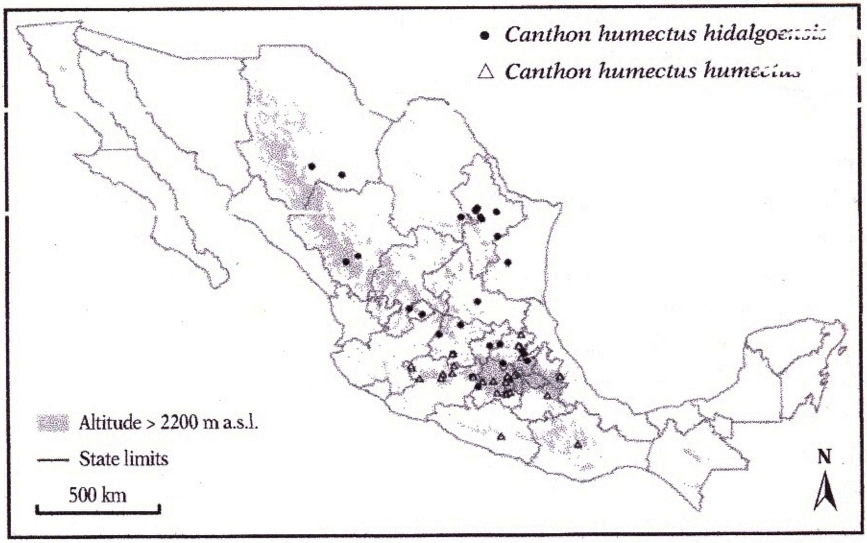

Fig. 5 – Distribution map for *Canthon humectus humectus* (which circles) and *C. h. hidalgoensis* (black circles), examples of the Plateau Distribution Pattern. Prepared with data from CONABIO and Halffter, 1962, and later publicacions. Map prepared by Matthias Rös.

roundings of the Pachuca Sierra. This species belongs to the chevrolati complex and is very closely related to *O. chevrolati*. It is distributed along the Sierra Madre Oriental, from its point of contact with the Mexican Volcanic Belt (in the states of Puebla and Hidalgo), to its northern limit up at Monterrey (Nuevo León). Though the majority of the known sites are in the mountains, some places - especially in the south of its distribution - penetrate the Plateau in a limited manner (Zunino & Halffter 1988). Also found on the Plateau, *Onthophagus lecontei* belongs to the *landolti* group which has the highest species diversity in North America. *O. lecontei* has a very broad distribution on the Plateau, from the south up to Durango, San Luis Potosí and Nuevo León, and it is also found in Oaxaca. It represents a Paleoamerican Distribution on the Plateau, although in the transect it was found as high as 2400 m a.s.l., as occurs with *O. mexicanus*. From the *mexicanus* group there is *O. mexicanus*. This species has a wide distribution in the south and east of the Plateau, Oaxaca and the foothills of the Mexican Volcanic Belt (a distribution typical of the Paleoamerican Plateau Pattern).

From the other Palaearctic group, as a penetration from the Pachuca Sierra, we have *Copris armatus*. This species, which we mentioned for the previous landscape, can exceptionally be found as low as 1836 m a.s.l., although its general lower altitude limit is 2300 m a.s.l. and it is common at higher altitudes (see comments in the section on the Pachuca Sierra).

As a group the beetles of the temperate Plateau are very coherent in their ecological demands: heliophile conditions provided by the pastures and open types of vegetation. The only species associated with forests, *P. palliatus*, is preferentially found at the forest edges.

In terms of its phylogenetic-biogeographic-historical composition, the Plateau is an excellent example of the complexity of the MTZ. Although Neotropical taxa dominate, there is a Paleoamerican component represented by genera of northern origin: *Onthophagus* and *Copris*. Common to all the species characteristic of this landscape is that they have evolved on and are a distinguishing characteristic of the Plateau.

THE METZTITLÁN CANYON. Metztitlán is a penetration of the arid Plateau into the transect. In the SE part (which is included in the transect), there is a relatively narrow canyon that at its highest has conditions similar to those of the temperate Plateau, and on its slopes and at the bottom is much more arid. To the NW the canyon broadens until it opens onto the central-eastern part of the Mexican Plateau, the arid characteristics of which are marked.

This canyon is comprised of a rich representation of the Scarabaeinae of the arid Plateau, plus some penetrations from the tropical lowlands. For reasons we will discuss further on, this canyon has one of the richest Scarabaeinae fauna on the transect: we have mentioned the five roller species, all belonging to the genus *Canthon*, and to these we must add three tunneler species, including two introduced in the Americas.

We have mentioned the two subspecies of *Canthon humectus*. One (*C. h. humectus*) is shared with the temperate Plateau and the other (*C. h. hidalgoensis*) is characteristic of the dry Plateau. Additionally, there are three other species from this genus. All three, though characteristic of the arid Plateau, have a broad distribution to the north that reaches Texas and even further into the United States. All are found (as is *C. h. hidalgoensis*) at altitudes lower than that of *C. h. humectus*.

Canthon imitator is found in the United States in the states of Texas, Oklahoma, Arizona, Colorado and Florida, and as far north as Michigan. In Mexico it is found in the north-eastern states: Tamaulipas, Nuevo León and San Luis Potosí, reaching Hidalgo in the centre of the country, i.e. the southern limit of its distribution (Halffter 1961). Although like the species typical of the Plateau (the group of subspecies of *C. humectus*) it has a Neotropical affiliation, it belongs to the *pilularius* group which diversifies in the United States. As occurs for *Canthon (Boreocanthon) puncticollis* which we address below, it forms part of the group of species that, though of Neotropical phyletic origin, have evolved in the United States where some of them penetrate the Mexican Plateau where it is driest. Because of its biogeographical-historical origins, this distribution is equivalent the typical Plateau Distribution Pattern, but is associated with more arid conditions. In the Metztitlán Canyon, *C. imitator* is found in pastures, in the different types of xerophilous scrub and even in pine forest in the highest parts of canyon.

We include *Canthon (Boreocanthon) puncticollis* in this discussion even though it has not been strictly collected in the transect, but rather in the same canyon, a little to the NW. Its biogeographical history is very similar to that of *C. imitator*, although *C. puncticollis* has a greater affinity for arid conditions, being one of the very few Scarabaeinae found in the deserts in northern Mexico (Lobo 1996). The state of Hidalgo appears to be the southern limit of its distribution.

From the subgenus *Glaphyrocanthon*, *Canthon (Gl.) viridis* belongs to a group (*viridis*) with numerous and diversified species in Mexico (see Rivera-Cervantes & Halffter 1999). *Canthon (Gl.) viridis* is the only species of its group that has a distribution in the north, and up into the United States. In Mexico, it is only known for the northeast: Nuevo León and Tamaulipas. Its presence in Hidalgo represents a very important increase in its distribution area.

Although the distribution of *C. viridis* appears similar to those of *C. imitator* and *C. puncticollis* owing to their extensive presence in the United States, from a phylogenetic perspective, disregarding for the moment the Neotropical affinities (all belong to the typically Neotropical genus *Canthon*), their histories are quite different. *C. imitator* and *C. puncticollis* belong to groups of species that have evolved in the United States with a certain degree of penetration into Mexico (greater in the subgenus *Boreocanthon* to which *C. puncticollis* belongs). In contrast, *Canthon viridis* belongs to a group of species that is very characteristic of Mexico (abundant in tropical conditions), with *C. viridis* the only species that extends to the north.

The two species of *Phanaeus* on the temperate Plateau are replaced in the canyon by *P. adonis*. This species belongs to the *triangularis* group (see Edmonds 1994), which also includes *P. triangularis*, a species found in the southeast of the United States: from Kansas to Louisiana-Texas, up to the border with the Carolinas. Once again in the Metztitlán Canyon we find a species belonging to a group with a Neotropical affiliation, but that has evolved in the United States. The distribution of *P. adonis* extends from the Texas coastal plain (Cameron Co.) to the open forests of the Sierra Madre Oriental of Nuevo León to Hidalgo between 350 and 2100 m a.s.l. (D. Edmonds pers. com.).

The Paleoamerican genus *Onthophagus* is well represented in the Metztitlán Canyon. In addition to *O. lecontei* which is also found on the Mexican Plateau, from the same group of species (*landolti* group) there are *O. landolti* and *O. igualensis*, two new records for the state of Hidalgo. According to the information in the CONABIO databases, the distribution of *O. landolti* is discontinuous: in central Veracruz it is found between 200 and 1200 m a.s.l., and in western Mexico (Jalisco-Colima) it is found on the Pacific slope between 700 and 900 m a.s.l. According to the same source, *O. igualensis* is found on the Pacific slope (Jalisco) between 700 and 1000 m a.s.l. in the Balsas River Basin and surrounding areas (the states of Puebla, Morelos, Guerrero and Oaxaca) between 1100 and 1700 m a.s.l., and in the Central Depression of Chiapas. Both species inhabit a wide variety of habitats, but are partial to those with some degree of xerophilous conditions such as those of deciduous forest. They can clearly be considered within the Tropical Paleoamerican Pattern. Their presence in the Metztitlán Canyon is, without a doubt, favoured by its arid conditions.

Onthophagus mexicanus, from the *mexicanus* group, is also found here (see the section on the Mexican Plateau).

In addition to the *Onthophagus* species mentioned, there are five additional species in the Metztitlán Canyon, all with phylogenetic affinities that have yet to be properly established: *Onthophagus alluvius, O. gibsoni, O. knulli, O. subtropicus* and *O.* n. sp. 2. The richness of *Onthophagus* in the canyon is exceptional, with nine species.

The species that penetrate the Metztitlán Canyon from the tropical lowlands, form a third set of species. *Dichotomius colonicus* belongs to a Neotropical genus. It is widely distributed throughout the tropical lowlands, particularly those sites with no arboreal cover. It belongs to the Typical Neotropical Pattern and its presence in the Metztitlán Canyon can be considered a penetration via vertical colonization. With the same method of penetration, two species introduced in the United States arrive in the Metztitlán Canyon: *Euoniticellus intermedius* and *Digitonthophagus gazella* (for their expansion in Mexico see Montes de Oca & Halffter 1998). Both species adapt well to arid conditions (Lobo 1996) and have a tremendous capacity for dispersal and colonization.

The species found in the Metztitlán Canyon (with the exception of the odd species with a broad ecological tolerance) are adapted to arid conditions with intense insolation at the least. It is quite possible that this ecological trait has contributed to the richness of a fauna with diverse origins. This is exceptional in the MTZ where the dry areas have fauna poor in Scarabaeini, see for example, the arid part of the Tehuacán Valley, or the desert zones of the northern Mexican Plateau.

The Scarabaeinae fauna of the Metztitlán Canyon is unexpectedly rich in individuals, even considering that 94% of them are *C. h. hidalgoensis* (Verdú et al. 2007). On the other hand, this abundance is constant even in those locations where livestock of European origin is pastured (goats, cattle, horses, donkeys) (Verdú et al. 2007).

To understand the current richness of the Scarabaeinae, we must note that only two species of large herbivorous mammals are currently common on the Plateau (the mule deer *Odocolileus hemionus* and the white-tailed deer *O. virginianus*), along with the herbivorous mammals introduced from Europe that are present in rustic livestock grazing conditions. In contrast, during the Pleistocene and in some cases until well into the Recent, there were 61 species of large mammals, among them gigantic animals such as the mammoth (*Mammuthus* spp.) and the American mastodon (*Mammuth americanum*). Of the Mexican paleomastofauna (much of it associated with the Mexican Plateau), one order, six families, 29 genera and 77 species went extinct between the end of the Pleistocene and the Recent (Arroyo-Cabrales et al., in press). The majority of these species were large herbivores (64.1% of the total) and they lived on the Plateau. Their extinction must have created crisis conditions for the Scarabaeinae, although we must keep in mind that this extinction was gradual and some species, such as the pronghorn, persisted in the south-central Plateau until historic times (there are descriptions of very successful hunts even in the 17th C). The introduction of herbivorous mammals by the Spanish and their rapid expansion and even their return to the wild filled this semi-vacuum of food availability. However, even today, the pellets and dung piles of the herbivorous mammals are in many places underused. This, and the ease with which the introduced species in the United States have expanded are evidence that the Scarabaeinae communities are far from saturated.

ZACUALTIPÁN SIERRA. For the first time along the trajectory we find a tropical Scarabaeinae fauna comprised of two genera (*Onthophagus* and *Copris*) that are Paleoamerican in their lines of tropical distribution (Tropical Paleoamerican Pattern) and an abundant set of species belonging to genera with South American affinities. The tropical character of this mountain range does not include the few species that expand from the Mexican Plateau to Zacualtipán, belonging to both *Canthon*, and *Onthophagus*.

The Zacualtipán Sierra is the landscape on the transect with the most species: a total of 34. This exceptional richness is fostered by the humid tropical conditions that prevail in the part of the mountains exposed to the trade winds (where we did most of our collecting), and by the marked relief that has created a variety of habitats. The Zacualtipán Sierra is covered with cloud forest that at lower altitudes is replaced by deciduous and semi-deciduous tropical forest. Human activities have opened many gaps in the forest, primarily for cattle pastures. In the Zacualtipán Sierra, we observe for the first time on the transect genera abundant in South American species and of a strictly Neotropical character, such as *Coprophanaeus*, *Deltochilum* and *Eurysternus*.

The species richness of Scarabaeinae in the Zacualtipán Sierra (34 species) reaches the level of other landscapes in the MTZ that are dominated by tropical forests that are fragmented to some degree: 49 species in the Montes Azules Biosphere Reserve, located in the Lacandona rainforest in the state of Chiapas (tropical evergreen forest) which is the highest number for any landscape in the MTZ (Navarrete & Halffter 2008); 44 species in the landscape with very fragmented tropical evergreen forest in Los Tuxtlas, Veracruz (Favila 2005); and 33 species en the Laucha, Guatemala, a landscape with fragmented evergreen forest (Avendaño-Mendoza et al. 2005). In deciduous and semideciduous tropical forests the number of species is lower. In the only landscape with cloud forest where beetles have been systematically collected (in the surroundings of Xalapa, Veracruz), there are 18 species (Halffter et al. 2007).

The tropical nature of the Zacualtipán Sierra is confirmed by the number of species (13) that share a lower altitudinal level: the slope down to the Gulf–Las Huastecas. In the latter landscape, the lower rainfall and gentler topography result in only 21 species, more than half of which are shared with the Zacualtipán Sierra. An ecological characteristic of the Scarabaeinae in the Zacualtipán Sierra (another confirmation of the importance of the Neotropical influence) is that for the first time along the trajectory of the transect we find necrophagous or copronecrophagous species (predominantly necrophagous). This feeding habit is characteristic of many of the species from the Neotropical region.

For the biogeographical analysis we first have the species that belong to genera of northern origin. Then, there are species that belong to genera of Neotropical origin, and they can be separated into three sets of species: the first is comprised of the Mexican Plateau species that extend to Zacualtipán, the second has species strictly associated with cloud forest and the band of altitudes where it occurs (Mountain Mesoamerican Pattern), and the third is comprised of the tropical species that have a wide distribution in Mexico.

Species of genera with northern affinities and that are distributed in the mountains or on the Mexican Plateau. Four species of *Onthophagus* arrive in the Zacualtipán Sierra and have the characteristics mentioned in the subtitle: *O. chevrolati chevrolati* is a species typical of the Mountain Paleoamerican Pattern. *O. lecontei*, *O. mexicanus* and *O. hidalgus* are three species with the Plateau Paleoamerican Pattern that also reside high in the mountains (see respective sections).

Species belonging to genera with northern affinities and a tropical distribution (Tropical Paleoamerican Pattern). *Copris incertus* and *C. laeviceps* belong to the only tropical branch of the genus *Copris* in the Americas, a branch that in addition to these two species includes *Copris lugubris* which inhabits lower altitudes (Matthews, 1961). *Copris incertus* has a fairly broad altitudinal distribution, reaching 2000 m a.s.l. It is mainly found in forests, but also in pastures near forests. *Copris laeviceps* is found at lower altitudes and of the three species in this line, is the one that is most strictly associated with tropical forests, including tropical evergreen forest at the lowest altitudes of its distribution.

The genus *Onthophagus* is amply represented in this landscape. In addition to the four species mentioned that come from higher altitudes, there are another seven species. This total of eleven species makes the Zacualtipán Sierra the richest landscape in *Onthophagus* in the transect. Of the seven species of *Onthophagus* that have a tropical distribution, *O. cyanellus* and *O. incensus* are very abundant in the cloud forest and its gaps, though they are also widely distributed at lower altitudes. *O. batesi*, *O. nasicornis*, *O. rostratus* and *O. mextesus* [currently *O. durangoensis* Balthasar (Pulido & Zunino 2007)] all have a broad tropical distribution. The five species belong to the Typical Neotropical Pattern. The distribution of *Onthophagus* n. sp.1 appears to be limited to cloud forest, and therefore falls into the Mountain Mesoamerican Pattern.

Species belonging to genera with Neotropical affinities, characteristic of the Mexican Plateau. Three species of *Canthon* characteristic of the Plateau arrive at the Zacualtipán Sierra: *C. humectus humectus* from the temperate Plateau, *C. humectus hidalgoensis* and *C. imitator* from the arid Plateau (see respective sections). Since the distribution of these three *Canthon* extends quite far north of Zacualtipán, their presence in the mountains depends on the presence of suitable ecological conditions: temperate pastures or open, sunny areas at a certain altitude for *C. h. humectus*; open, drier areas for the other two species. As mentioned for some species of *Onthophagus* and now for the *Canthon* species, in the Zacualtipán Sierra, the presence of species with vertical expansions to their distribution is very important. Among them, we include those that come down from the Plateau, mentioned above, and those that come up from the tropical lowlands (such as *Copris*, several species of *Onthophagus* and others from genera with Neotropical affinities). The horizontal distribution is represented by species exclusive to cloud forest, the same ones that we find in different fragments of this type of forest in Mexico, particularly on the Gulf slope (Mountain Mesoamerican Pattern).

Species characteristic of cloud forest (Mountain Mesoamerican Pattern). These species can have northern or Neotropical affinities. Their main characteristic is their association with cloud forest and the altitudes and environmental conditions where they are found. We have mentioned that *Onthophagus* n. sp. has these characteristics. Of the genera with a Neotropical affiliation, the following species have the traits mentioned: *Eurysternus magnus* belongs to a genus that is widely represented in South America and the tropical lowlands of the MTZ. In our transect it is limited to cloud forest and semideciduous forest in the Zacualtipán Sierra. Outside of the transect it is found in other places with cloud forest (or neighbouring gaps) in the states of Veracruz and Chiapas. *Deltochilum mexicanum* also belongs to a genus that is widely distributed throughout South America and the tropical part of the MTZ (fig. 6). In the Zacualtipán Sierra this species is found between 1120 and 1886 m a.s.l., in cloud forest and semideciduous forest. Outside of the transect it has a broad distribution over a similar altitudinal range (1100 to 2500 m a.s.l.), although in a protected ravine, with forest, it can be found as low as 900 m a.s.l. *Phanaeus amethystinus* also belongs to a genus with Neotropical affinities and numerous phyletic lines in the Americas. In the Zacualtipán Sierra it is found between 1300 and 2060 m a.s.l., preferentially in pastures near forest. Outside of the transect its distribution covers Veracruz and Chiapas, between 1300 and 2700 m a.s.l., in cloud forest, other forests and gaps near forests.

As seen from the above, in spite of the high number of species found in the Zacualtipán Sierra landscape, there are very few species that are exclusive to its most characteristic habitats. The vast majority of the Scarabaeinae collected on this landscape have arrived by upwards vertical colonization from the tropical lowlands or downwards from the Plateau and the Sierra Madre Oriental. Vertical colonization processes dominate in the Zacualtipán Sierra.

Species of Neotropical genera with a broad distribution in the tropics (Typical Neotropical Pattern). Two species with a very broad altitudinal distribution - *Ontherus mexicanus* and *Dichotomius colonicus* - are found in the Zacualtipán Sierra; the first associated with cloud forest and other types of forest, and *D. colonicus* occasionally in forest but mainly in open places.

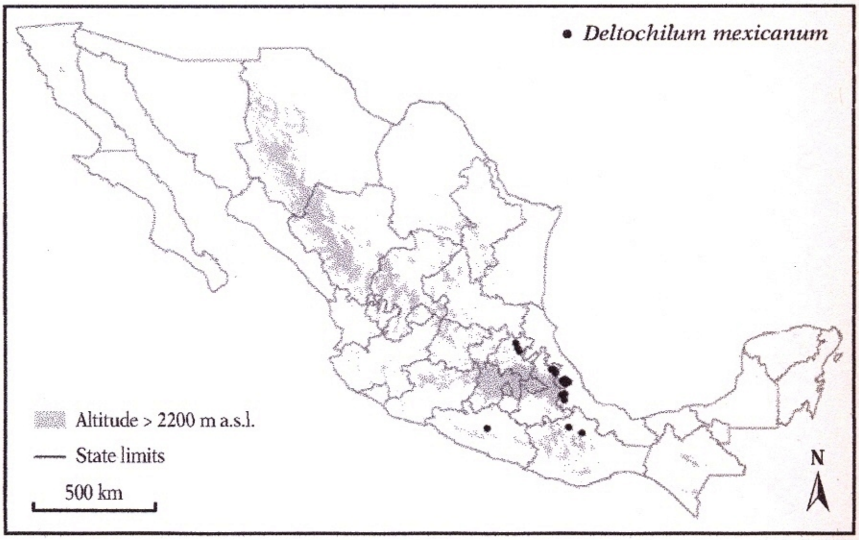

Fig. 6 – Distribution map for *Deltochilum mexicanum*, an example of the Mesoamerican Mountain Pattern. Prepared with data from CONABIO and the literature. Map prepared by Matthias Rös.

As mentioned, the list of species belonging to Neotropical genera that are characteristic of the lowlands that move up to the Zacualtipán Sierra is long. These species (unless otherwise indicated) are found in cloud forest or semideciduous forest. Outside of the transect they are characteristic of the tropical forests of the MTZ. These species are: *Dichotomius satanas* (very characteristic of cloud forest, although it is also found at lower altitudes, always in tropical forest), *D. amplicollis*, *Ateuchus illaesum*, *Phanaeus genieri*, *Ph. sallei*, *Coprophanaeus telamon corythus* (fig. 7), *C. gilli* and *Eurysternus mexicanus*. The species introduced in America (*Euoniticellus intermedius*) prefers sunny sites. The roller species are well represented. In addition to those that Zacualtipán shares with the Plateau, or that belong to the Mountain Mesoamerican Pattern (vide supra), the following are shared with the tropical lowlands: *Canthon* (*Glaphyrocanthon*) *circulatus*, *Canthon indigaceus chiapas*, *Deltochilum scabrisculum* and *D. gibbosum sublaeve*.

THE SLOPE DOWN TO THE GULF-LAS HUASTECAS. As mentioned, this landscape has many species in common with Zacualtipán (70%).

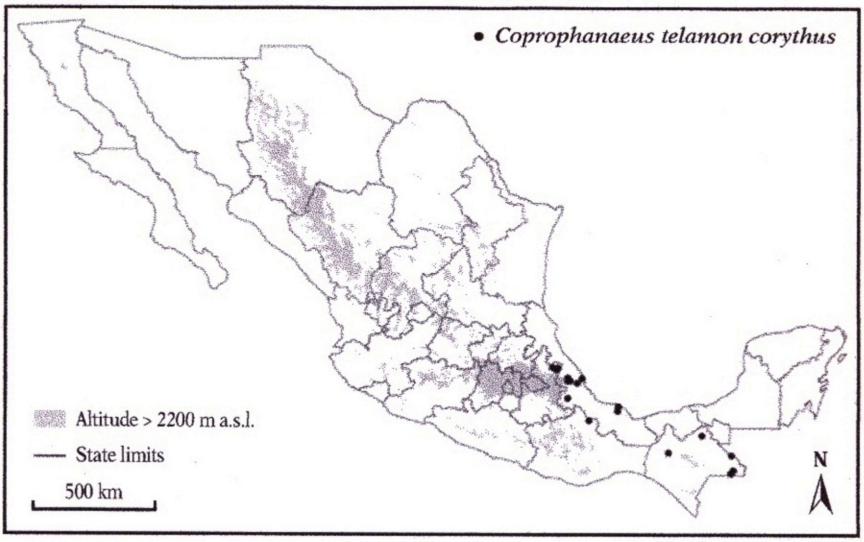

Fig. 7 – Distribution map for *Coprophanaeus telamon corythus*, an example of the Typical Neotropical Pattern. Prepared with data from CONABIO and the literature. Map prepared by Matthias Rös.

However, it does have some species that characterize it: those collected in the lowest areas. The gradual slope results in the deciduous forests of intermediate altitudes, including some remnants of cloud forest, descending through protected ravines that are more humid. Of the landscapes on the transect, Zacualtipán and the slope down to the Gulf-Las Huastecas are the most similar. Their biogeographical history is very similar. The only difference is the presence of Mountain Mesoamerican Pattern species in the cloud forest of Zacualtipán. The differences are ecological: the slope is increasingly dry and hot. And at its lowest, in La Huasteca, much of the forest has been cleared to make way for cattle pastures.

The slope down to the Gulf-Las Huastecas is only inhabited by tropical species. Of these, *Onthophagus* and *Copris* belong to the Tropical Paleoamerican Pattern. The rest are South American genera with a Typical Neotropical Distribution Pattern. The following 13 species are shared with Zacualtipán: *Ateuchus illaesum*, *Canthon* (*Glaphyrocanthon*) *circulatus*, *Copris incertus*, *C. laeviceps*, *Coprophanaeus gilli*, *Deltochilum gibbosum sublaeve*, *D. scabriusculum*, *Dichotomius amplicollis*, *D. colonicus*, *Eurysternus mexicanus*, *Onthophagus incen-*

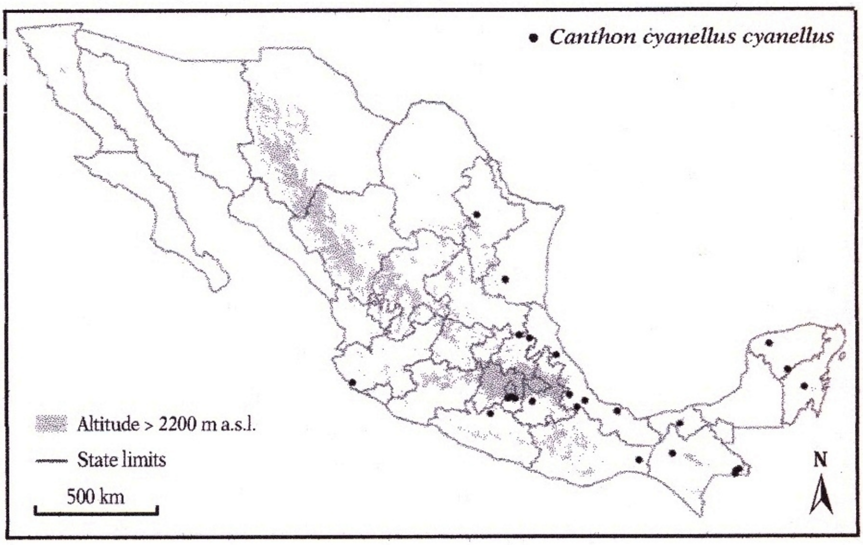

Fig. 8 – Distribution map for *Canthon cyanellus cyanellus*, an example of the Typical Neotropical Pattern. Prepared with data from CONABIO, Halffter, 1962 and later publications. Map prepared by Matthias Rös.

sus, O. batesi and *O. nasicornis*. The following nine species are only found in the lowest landscape. In contrast to the previous group, some of these species can be found in sunny habitats or on the edges of deciduous forest: *Canthon cyanellus cyanellus* (fig. 8), *C. indigaceus chevrolati*, *C. morsei* group, *Deltochilum lobipes*, *Digitonthophagus gazella* (a species introduced in the Americas), *Onthophagus corrosus*, *O. landolti texanus*, *O. longimanus* and *Uroxys deavilai*.

Parsimony analysis of endemicity

The parsimony analysis of endemicity (PAE) returned two equally parsimonious cladograms (L = 69, IC = 85, IR = 62). The strict consensus tree (fig. 9; L = 73, IC = 80, IR = 68) shows that each landscape has its own or endemic species. The Pachuca Sierra has five species, the Mexican Plateau has two and Metztitlán nine. Zacualtipán (including all of the sites with cloud forest and tropical forest over 1000 m a.s.l.) has the highest number of endemic species with 13 and la Huasteca (below 700 m a.s.l.) has eight endemic species. Only Zacualtipán and la Huasteca are historically related because they share the distributions of 12 species. These two landscapes could be a generalized track. The Pachuca Sierra, the Mexican Plateau and Metztitlán do not share species that would suggest any historical relationship between them, or indicate that they make up a generalized track.

The relationship between the Zacualtipán and La Huasteca landscapes was supported (95% probability; Bootstrap analysis, fig. 9). Similar results were obtained for several species from eight families of Coleoptera (Márquez & Morrone 2004) and the analysis of 690 species of Staphylinidae (Márquez & Asiain 2006). For these, the biogeographic province Sierra Madre Oriental has been considered as split into two areas of endemism, a northern one that includes part of the states of Coahuila, Nuevo León and the north of San Luis Potosí, and a southern section that includes parts of the states of Guanajuato, southern San Luis Potosí, Querétaro, Hidalgo, Puebla and Veracruz. Our landscape Zacualtipán is located in the southern portion of the Sierra Madre Oriental delimited in those studies, while La Huasteca is a landscape that has been considered part of the Gulf of Mexico province. So, the results obtained for Geotrupinae and Scarabaeinae are congruent with those of previous studies.

On the other hand, the results of the PAE do not reflect any his-

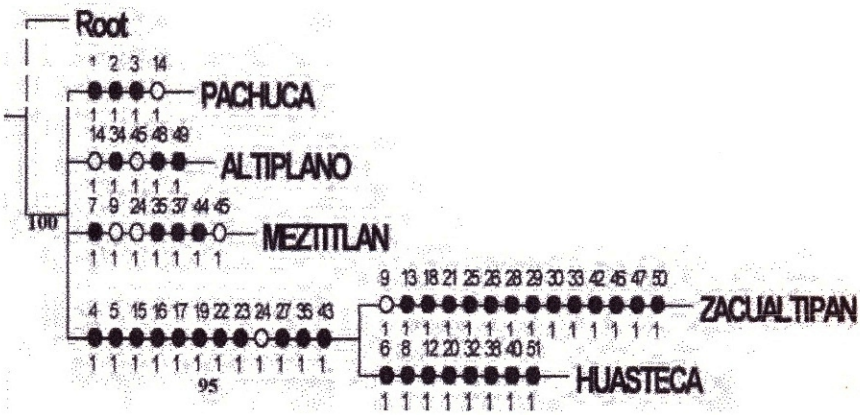

Fig. 9 – Cladograma de consenso estricto resultante del análisis PAE. Los círculos negros corresponden a especies registradas exclusivamente del paisaje o de un único nodo (endémicas) y los círculos blancos corresponden a especies registradas en dos o mas paisajes. Los números corresponden con el número de cada especie del cuadro 1. Los valores debajo de cada nodo son los porcentajes resultantes de la prueba Jacknife.

torical relationship between the other three landscapes, though there is strong support for them each having at least two of their own species, making them each an area with different endemisms. The lack of a relationship between these landscapes could indicate that in this transect the beetle fauna has been subjected to different biogeographical histories, highlighted by an impressive mix of Neotropical taxa (Zacualtipán and Huasteca) with northern taxa (Pachuca Sierra, the Mexican Plateau and Metztitlán), making the transect in particular and the state in general highly diverse (Delgado & Márquez 2006). The separation of the Mexican Plateau from both Metztitlán and the Pachuca Sierra is interesting because they are three different, unrelated landscapes. The Mexican Plateau is located between the Pachuca Sierra and Metztitlán, which would lead us to expect that it would share some species with one or both of its neighbouring landscapes.

Comparison with other transects

Cofre de Perote - The Coast of Veracruz. The taxonomic composition and even the biogeographic analysis of the Scarabaeinae and Geotrupinae on the transect between the Cofre de Perote Mountain and the Veracruz Coast (central Veracruz) has been addressed by several authors, though not necessarily covering the same altitudinal ranges and, in the case of Trotta et al. 2007, only for Geotrupinae: Arellano 1992, Martín-Piera & Lobo 1993, Halffter et al. 1995, Arellano & Halffter 2003, Trotta et al. 2007. For the purposes of comparison with our Hidalgo transect, we use and summarize information from the five studies cited, indicating the particular source of information where appropriate.

Arellano & Halffter (2003) set up and described in detail three landscape units on this transect: the Tropical Landscape at 0 to 1000 m a.s.l., comprised of coastal plains originally covered with intermediate and low altitude deciduous forest that exhibits intense transformation for agricultural and livestock use. The Transition Landscape from 1000 to los 2000 m a.s.l., with valleys and hills with steeper slopes at its upper limit; cloud forest, oak forest and pine-oak forest. It is also characterized by a broad region of coffee plantations that encompass the remnant fragments of cloud forest, and pastures for dairy farming. The Mountain Landscape located above 2000 m a.s.l. (with the captures of Trotta et al. (2007) specimens were collected as high as 3200 m a.s.l.). This landscape is characterized by pine forest, fir forest, mountain pastures and clearings used for a variety of agricultural activities, along with grasslands. In this landscape, Arellano & Halffter (2003) include species from the eastern edge of the Mexican Plateau, collected in the foothills, that we treat separately in the analysis.

This transect is completely comparable with that of Hidalgo, with some exceptions. There is nothing similar to the arid Mexican Plateau (Metztitlán Canyon). The mountain captures are very important, in the first place because of the sheer area of the mountains around the Cofre de Perote Mountain (an intrusion of the Mexican Volcanic Belt within the Sierra Madre Oriental) and also because of the greater capture effort made by Trotta et al. (2007).

Arellano & Halffter (2003), on studying the α and β diversity within the three landscapes, mention important differences between sites in the Tropical Landscape. In the deciduous forest the number of species per capture site ranged from 8 to 15, and in the pastures from 9 to 14. The total number of species for this landscape is 28, including one introduced species (*Digitonthophagus gazella*). All the evidence indicates that this high degree of complementarity between sites, found also in other tropical forests (Navarrete & Halffter 2008;

Escobar et al. 2008; Quintero & Halffter in press), occurs in the lower part of the Hidalgo transect (on the slope down to the Gulf-Las Huastecas), although this has not been studied specifically.

Between the Tropical landscape of the Veracruz transect and the slope down to the Gulf-Las Huastecas, the taxonomic and biogeographic composition is very similar; with the same species in several instances.

For the Tropical Paleoamerican Pattern there are three species of *Onthophagus* and one of *Copris*, plus one species (*Sisyphus mexicanus* Harold) belonging to a genus that was not captured in the Hidalgo transect, although given its geographic distribution it could well appear there. The other species belong to the Typical Neotropical Patterns, with the same separation between species that prefer sites with deciduous forest and those that prefer sunny sites.

The Transition Landscape of the Cofre de Perote transect has 25 species of Scarabaeinae (including an introduced one, *Euoniticellus intermedius*) and a Geotrupinae (*Onthotrupes nebularum*) that is found in the highest parts of this landscape.

The number of species is lower than that recorded for Zacualtipán, but the latter is genuinely exceptional and, its fauna also includes some species from the Mexican Plateau while in the Transition Landscape of the Cofre de Perote these are limited to *Canthon humectus*. We found the same genera and the same biogeographic composition: *Onthophagus* and *Copris* with the Tropical Paleoamerican Pattern, some species with the Mountain Mesoamerican Pattern (almost all of these shared with Zacualtipán) and the rest (the majority) of the species belonging to the Typical Neotropical Pattern and, as for Zacualtipán, partially shared with the lower landscape.

The lack of roller species in the Transition Landscape of the Cofre transect is striking. In the cloud forests and coffee plantations there are abundant *Deltochilum mexicanum*, but in the numerous pastures there is not a single species, in spite of the abundance of dung (we have previously mentioned that *Canthon humectus* is only found in the highest parts of the landscape and as an extension from the Mexican Plateau where it is abundant). In Zacualtipán the situation is very different. There are three species of rollers that arrive from the Mexican Plateau and all together eight species belonging to *Canthon* and *Deltochilum*. Why are there no rollers in the Transition Landscape of the Cofre de Perote transect? This is a question for which we do not yet have a result that can be generalized. Even so, for the Cofre de Perote altitudinal transect it has been observed that roller beetles belonging to the genus *Canthon* need a minimum temperature of 22.3 to 26°C in order to be active (specifically, to fly). Taking into account that the mean temperature of cloud forests is around 18°C, with minima around 14.9°C and maxima of 20.4°C, this is why colonization of the Transition Landscape on the Cofre transect would be very difficult or impossible for tropical *Canthon* species (Verdú et al. 2007). It does not appear that there is a historical biogeographic reason since the genera *Canthon* and *Deltochilum* are found in landscapes that are at higher and lower altitudes than the Transition Landscape, and are actually quite abundant below it. It is worth mentioning that in the three transects that we compare, the two already addressed and the Manantlán transect (vide infra) the really important differences are found in the cloud forest and the Transition Landscape, and these differences primarily affect the genera of Neotropical Origin. Is it possible that the colonization by these genera of cloud forests and their landscapes has been different depending on the geographic location? This is a topic that is ripe for study and requires a comparative analysis that includes more sites with cloud forest.

The genus *Onthophagus* is rich in species, both in Zacualtipán (11 species), and in the Transition Landscape of the Cofre de Perote transect. In both transects this landscape level is where the greatest number of *Onthophagus* species are found.

In the Cofre de Perote transect, collections were only made on the edge of the Mexican Plateau: two species of *Onthophagus*, *Canthon humectus sayi* Robinson (a subspecies very closely related to *Canthon humectus humectus*), and two species from the lower level and which barely penetrate the Plateau: *Ontherus mexicanus* and *Phanaeus amethystinus*. The taxonomic and biogeographic composition is the same as that of the Temperate Plateau in the Hidalgo Transect.

In the Mountain Landscape, as in the Pachuca Sierra, there are the same species in forests and in the high altitude meadows. The Mountain Paleoamerican Pattern is well represented: five species of *Onthophagus* and one of *Copris*. The main difference is in the number of Geotrupinae species (six). These include *Ceratotrupes bolivari* Halffter & Martínez. In the genus *Onthotrupes* (see comments in the section on the Pachuca Sierra) there are three species: *O. herbeus*, shared with the Pachuca Sierra; *O. nebularum* Howden, characteristic of the mountains of the east of central Mexico; and *O. sobrinus* Jekel. The most abundant species of Geotrupinae is *Halffterius rufoclavatus* (Jekel). *Megatrupes fisheri* (Howden) is also present.

There are several explanations for this richness of Geotrupinae species (exceptional for the mountains of Mexico): the large area occupied by the mountain and the variety of habitats in the Cofre de Perote region, but above all there is a biogeographical reason. The Cofre is the point of contact between the Mexican Volcanic Belt and the Sierra Madre Oriental, and this favours the overlap of species belonging to the Nearctic Pattern that are characteristic of one mountain range or the other.

THE MANANTLÁN TRANSECT: JALISCO - COLIMA. The comparison of an altitudinal transect on the Pacific coast at the western end of the Mexican Volcanic Belt puts the capacity for generalization and the usefulness of the Distribution Patterns of the Mexican Transition Zone to the test. We expect to find the same distribution patterns as those of the Hidalgo and Cofre de Perote Transects, with the same altitudinal and macroecological distribution. We also expect to find the same genera with minimal differences, although a good percentage of the species would be different.

We base our comments on the transect sampled by García Real (1995) in the Manantlán Sierra. For the Mountain Transition landscapes in particular we have also used information from Zunino & Halffter (1997) and Rivera-Cervantes & García-Real (1998). The final result is therefore new, although much is owed to García-Real (1995).

The Manantlán Sierra forms part of the Sierra Madre del Sur where it meets the Mexican Volcanic Belt. Its topography is rugged and it covers a broad altitudinal range from 400 to 2860 m a.s.l. From lower altitudes upwards, the dominant vegetation types are: deciduous and semideciduous forest between 400 and 1200 m a.s.l.; where there is enough humidity, there is cloud forest between 700 and 2400 m a.s.l.; in drier locations there are oak forest and pine-oak forest up to locations above 1500 m a.s.l.; pine forest is mainly found between 1800 and 2400 m a.s.l.; and fir forest at the highest altitudes. Overall, the altitudinal succession of the vegetation is similar to that of the other transects studied, with one exception: there is no definite Plateau.

Taking into account the altitude and vegetation types of the sites collected by García-Real (1995), we divide the transect into three landscapes: Tropical Landscape up to 1000 m a.s.l., dominated by tropical deciduous forest; Transition Landscape between 1900 and 2300 m a.s.l., with cloud forest and pine forest; Mountain Landscape over 2300 m a.s.l., with pine and fir forests.

In the Tropical Landscape we found 22 species belonging to genera that follow the Typical Neotropical Pattern, plus eight species of *Onthophagus* (six shared with the Hidalgo Transect), and the one introduced in the Americas, *Digitonthophagus gazella*.

The tropical landscapes of the three transects are the most similar of all the landscape types. This is evidence of Neotropical fauna of relatively recent expansion (middle Pliocene onwards) which, with few differences, has expanded northwards following the coastal plains of both shores (Typical Neotropical Pattern). As we have mentioned, this fauna is different from that with the ancient Neotropical origin and that is characteristic of the Mexican Plateau. In the tropical landscapes these species with the Typical Neotropical Pattern join the species of *Onthophagus* and in two of the transects they join *Copris,* which makes an important contribution of northern affinities (Tropical Paleoamerican Pattern) to tropical landscapes.

For Manantlán, in the high part of the Tropical Landscape (between 830 and 1100 m a.s.l., deciduous forest) we find *Canthon humectus riverai* Halffter & Halffter, a subspecies that belongs to a species that is very characteristic of the Plateau: *C. humectus*. In western Mexico (Jalisco), taking advantage of the gradual slope from the Plateau, two subspecies of *C. humectus* pass it towards lower lands: *C. h. riverai* which according to different observations reaches altitudes even lower than those mentioned, always on the Pacific slope in Jalisco, and *C. h. assimilis* Robinson which also passes the Plateau and moves to lower altitudes (see Halffter & Halffter 2003).

In the Transition Landscape (represented by a single collection site at 1900 m a.s.l.) a species that is very characteristic of the Mountain Mesoamerican Pattern (Paleoamerican component) was found, *Liatongus rhinocerulus* (Bates), along with a species of *Onthophagus* with the Mountain Paleoamerican Pattern (*Onthophagus chevrolati chevrolati*) and two species with the Nearctic Pattern: the Geotrupinae *Ceratotrupes fronticornis* and *Megatrupes fisheri*. There is only one species with Neotropical affinities (*Canthidium* sp.).

Of all the transition landscapes in the three transects this is, by far, the poorest in species. *Onthophagus* and the two Geotrupinae are shared with the mountain landscape, where they are more typical. Most remarkable is that there is a single Scarabaeinae of Neotropical affinity, something without parallel in the other transition landscapes studied. We cannot discount the possibility that the data available for the Manantlán Transition Landscape are insufficient. What is evident is that together, these landscapes have a fauna with marked northern affinities.

We have mentioned that the greatest differences are found between the three transects in the transition landscape (leaving aside the penetration of the arid Plateau into the Hidalgo Transect) and that they are determined by the very different contribution of the genera of Neotropical origin. Whereas in the tropical landscape this fauna is a dominant component and is also similar in the three transects, at the Transition level there are large differences for which we have not found a conclusive explanation: the lack of roller species in the open sites in the Veracruz Transect, and the oddness of finding a single species of Neotropical affinity (*Canthidium* sp.) in Manantlán. It is evident that colonization by the Neotropical taxa of the transition landscape (and of the cloud forest and its gaps) has been unequal, and difficult for the Neotropical genera, with the easily noted exception of what happens in Zacualtipán.

The Mountain Landscape in Manantlán, the upper reaches of which have been better collected (there is only information for three sites between 2100 and 2300 m a.s.l.), include four species of *Onthophagus* (one shared with the Transition Landscape: *O. chevrolati chevrolati*) and *Copris armatus*, all belonging to the Mountain Paleoamerican Pattern. Additionally, there are the two species of Geotrupinae mentioned for the Transition Landscape. Together, and as occurs in the mountain landscapes of the other transects, this fauna is northern in affinity, lacking any Neotropical taxa.

Conclusions: the effects of the Mexican transition zone distribution patterns on the biogeographical formation of the Hidalgo transect

On examining the species found in each landscape, or in the endemism analysis, the biogeographic heterogeneity of the Hidalgo Transect stands out. This was expected since this transect is a slice of a representative portion of the MTZ. Any slice that is large enough and covers the large differences in altitude will exhibit the double composition that characterizes the MTZ: taxa of northern affinity and those of South American affinity.

Our transect is particularly illustrative because it shows this double origin in all its complexity. Not only are the affinities (origins) different, but in each case it is also possible to distinguish between genera (or lines of species) of early penetration into the MTZ that have speciated there profusely, and the more recent arrivals.

For the lineages of northern affinity, this distinction is very clear: the genera of ancient penetration, *Onthophagus* and *Copris*, are represented by different species in all the landscapes. The northern affinities of both genera and their origin in the Old World are supported by all the authors who have addressed the issue. In spite of the large number of species belonging to the northern genera that inhabit the MTZ, these correspond to a few phyletic lines in comparison to those that are found in the Old World. Their diversification in the MTZ can be explained by their early penetration, certainly in the Lower or Middle Cenozoic, and a later diversification owing to macroecological conditions. It is important to remember that communication between what is today the MTZ and the North American Block did not suffer any important interruptions during the entire Cenozoic, as far as the Isthmus of Tehuantepec. The Transition Zone has the role of a North American peninsula. The barriers and their concomitant isolating and vicariance effects started in the mid-Cenozoic *within* the area of the MTZ, with mountain building such as the Mexican Volcanic Belt and important changes in climate. These are the changes that result in the lineages of ancient northern origin dividing into subpatterns that differ according to their ecological affinities. With *Copris* there are only two phyletic groups represented in the Transect. The *armatus* group which is widely distributed in the mountains (Mountain Paleoamerican Pattern) and the *incertus* group with a tropical distribution (Tropical Paleoamerican Pattern). For *Onthophagus*, possibly having penetrated the MTZ much earlier and above all with a notable capacity for speciation and adaptation to the broadest of ecological conditions, there is yet another pattern: the Plateau Paleoamerican Pattern, which is comprised of species characteristic of the Mexican Plateau.

The northern lineages of recent penetration - in our transect the

Geotrupinae - arrived at the MTZ when the mountains and climates were similar to their conditions at present. This is a fauna of temperate-cold climates. Its distribution in the MTZ follows the mountain ranges. Discontinuities in these mountains (often relatively recent) have favoured the coexistence of widely distributed species (such as the *Ceratotrupes*) with others of much more limited distribution (such as the *Onthotrupes* and *Halffterius*).

Although the connection with the south has up to the Middle Pliocene been more difficult and had long interruptions, it is also possible to identify an ancient component and a modern one among the lineages of Neotropical affinity. The ancient component is comprised of a few lines that arrived at the Plateau before its isolation by the gradual rising of the Mexican Volcanic Belt, a phenomenon that began in the Miocene. These lines were isolated on the Plateau, where they underwent notable differentiation and speciation (Plateau Distribution Pattern) that has, in spite of their isolation, and taking advantage of the slopes of the Plateau, a secondary expansion toward the periphery, especially in the west (Jalisco) and north (Nuevo León - Texas). With the same origin and timeframe, we have the lines that evolved in the north of the Plateau and its prolongation into the United States. These lines are adapted to more arid conditions, and have in several instances their southern distribution limit in the state of Hidalgo, in our transect in the Metztitlán Canyon. The analysis of endemisms reflects the differences between the two Plateau faunas: that of the Temperate Plateau and the fauna of the Metztitlán Canyon.

With the consolidation of the Panamanian Bridge (Middle Pliocene), the expansion of the Neotropical fauna northwards became much more fluid and intense; massive even in the tropical lowlands. A migration began in the Scarabaeinae that may still be underway. This broad expansion of beetles with clear South American affinities (in many cases even at the species level) is what makes up the Typical Neotropical Pattern that dominates the Zacualtipán and Gulf-Las Huastecas Slope landscapes.

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SUMMARY

Scarabaeinae and Geotrupinae (Coleoptera, Scarabaeoidea) species composition is analyzed along a 150 km long altitudinal transect that runs S-NE in the Mexican Transition Zone. The transect is located in the state of Hidalgo in central-eastern Mexico.

The spatial unit of analysis is the landscape. The transect crosses five different landscapes.

As terms of reference for studying the geographic distribution of the species, the entomofauna distribution patterns for the Mexican Transition Zone were used. The transect includes all the patterns established by Halffter for this zone.

Only genera with northern origins were found in landscape of the Pachuca Sierra (mountain range). The two landscapes of the High Plateau (temperate and arid) have one genus with a northern origin (*Onthophagus*), along with species belonging to genera with Neotropical origins that evolved on the High Plateau. For the landscapes of the Zacualtipán Sierra and the slope down to the Gulf–Las Huastecas region genera of Neotropical affinity dominate, and there are also some species with a tropical distribution and of northern-Old World origin.

The relationship between the mountains and the phyletic lineages or genera of northern origin and of recent entry into the Mexican Transition Zone is confirmed, as is that between the tropical lowlands and the Neotropical lines or genera, also recent arrivals. Taxa that arrived a long time ago, of either origin, do not exhibit this geographic-ecological dependence.

The Hidalgo Transect is compared with two other, similar transects sampled in the Mexican Transition Zone: the Cofre de Perote–Gulf Coast transect (Veracruz) and that of Manantlán (Jalisco). In the mountain landscapes, High Plateau and Tropical Lowlands, there were no important differences in the species composition of the groups studied. In contrast, in the Transition landscape (Zacualtipán in the Hidalgo Transect) there were very notable differences. In the Cofre de Perote transect, an important functional group is missing from the treeless habitats: the roller Scarabaeinae. For the same landscape, in Manantlán, lineages with Neotropical affinities are represented by a single species which completely dominates the beetles of northern affinities. This contrasts markedly with the Hidalgo and Cofre de Perote transects where, in the Transition landscape, Neotropical taxa are well represented. It appears that, unlike the tropical lowlands where (geologically recent) penetration of Neotropical taxa is massive in all three transects, in the transition landscapes (originally covered by cloud forest) the penetration of Neotropical taxa is highly variable, and depends on the mountain range in which they are found.

In the Conclusions section, we analyze how the beetle fauna with different distribution patterns have contributed to the composition of the fauna of the Hidalgo Transect and in general that of the Mexican Transition Zone, resulting in a mixture (genera with northern-Old World affinity, and genera with Neotropical affinities) that give the Mexican Transition Zone its unique character.

REFERENCES

Abrahamovich, A., N.B. Díaz & J.J. Morrone. 2004. Distributional patterns of the Neotropical and Andean species of the genus *Bombus* (Hymenoptera: Apidae). Acta Zoológica Mexicana (n.s.), 20: 99-117.

Arellano, L. 1992. Distribución y abundancia de Scarabaeidae y Silphidae (Insecta Coleoptera) en un transecto altitudinal en el Estado de Veracruz. Thesis. Facultad de Ciencias, UNAM, México. 139 pp.

Arellano, L. & G. Halffter. 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. Acta Zoológica Mexicana (n.s.), 90: 27-76.

Arroyo-Cabrales, J. (in press). La diversidad de México en el pasado. In: J. Sarukhan (ed.) Dos Estudio País. CONABIO, México.

Avendaño-Mendoza, C., A. Morón-Ríos, B.E. Cano & J. León-Cortés. 2005. Dung beetle community (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical landscape at the Laucha Region, Guatemala. Biodiversity Conservation, 14: 801-822.

Bertrand, G. 1970. Ecologie de l'espace géographique. Recherches pour une science du paysage. Societé de Biogeographie, 406: 195-205.

Comisión Nacional de Áreas Naturales Protegidas, 2003. Programa de Manejo Reserva de la Biosfera Barranca de Metztitlán. CONANP, SEMARNAT, México. 202 pp.

Delgado, L. & J. Márquez. 2006. Estado del conocimiento y conservación de los Coleópteros Scarabaeoidea (Insecta) del Estado de Hidalgo, México. Acta Zoológica Mexicana (n.s.), 22 (2): 57-108.

Edmonds, W.D. 1994. A revision of *Phanaeus* MacLeay, a New World genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Contributions in Science, 443: 1-105.

Escalante, T. & J.J. Morrone. 2003. ¿Para qué sirve el análisis de parsimonia de endemismos?, pp. 167-172. In: J.J. Morrone & J. Llorente (eds.). Una perspectiva latinoamericana de la biogeografía. Las Prensas de Ciencias, UNAM, México, D.F.

Escobar, F., G. Halffter, A. Solís, V. Halffter & D. Navarrete. 2008. Temporal shifts in dung beetle community structure within a protected area of tropical wet forest: a 35 year study and its implications for long-term conservation. Journal of Applied Ecology, 45: 1584-1592.

Favila, M.E. 2005. Diversidad alpha y beta de los escarabajos del estiércol (Scarabaeinae) en Los Tuxtlas, México, pp 209-212. In: G. Halffter, J. Soberón, P. Koleff & A. Melic (eds.). Sobre Diversidad Biológica: el significado de las diversidades alfa, beta y gamma. Monografías 3er. Milenio - M3M, vol. 4, Sociedad Entomológica Aragonesa, Zaragoza, España.

García-Real, E. 1995. Abundancia, distribución y estructura de la comunidad de escarabajos coprofágos y necrófagos (Coleoptera: Scarabaeidae), en un gradiente altitudinal de la Sierra de Manantlán, Jalisco-Colima, México. MSc. Thesis. Colegio de Postgraduados, Montecillo, México. 129 pp.

Goloboff, P.A. Nona versión 2.0. Published by the autor, Tucumán.

Halffter, G. 1961. Monografía de las especies norteamericanas del género *Canthon* Hoffsg. Ciencia (Mex.), 20 (9-12): 225-320.

Halffter, G. 1964. La entomofauna americana, ideas acerca de su origen y distribución. Folia Entomológica Mexicana, 6: 1-108.

Halffter, G. 1974. Elements anciens de l'Entomofaune Neotropicale: ses implications biogéographiques. Quaestiones Entomologicae, 10: 223-262.

Halffter, G. 1975. Elements anciens de l'Entomofaune Neotropicale: ses implications biogéographiques. Memoires du Muséum National d'Histoire Naturelle, Paris. N.S. Série A, Zoologie, 88: 114-145.

Halffter, G. 1976. Distribución de los insectos en la Zona de Transición Mexicana:

Relaciones con la entomofauna de Norteamérica. Folia Entomológica Mexicana, 35: 1-64.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review, Entomology, 32: 95-114.

Halffter, G. 2003. Biogeografía de la entomofauna de montaña de México y América Central, pp. 87-97. In: Morrone, J.J. & J. Llorente-Bousquets (eds.). Una perspectiva latinoamericana de la biogeografía. Las Prensas de Ciencias, UNAM, México.

Halffter, G., M.E. Favila & L. Arellano. 1995. Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican Transition Zone and its biogeographical implications. Elytron, 9: 151-185.

Halffter, G. & A. Martínez. 1977. Monografía de los Canthonina americanos, Parte IV. (Coleoptera, Scarabaeidae). Folia Entomológica Mexicana, 38: 29-107.

Halffter, G., E. Pineda, L. Arellano & F. Escobar. 2007. Instability of copronecrofagous beetle assemblages (Coleoptera: Scarabaeinae) in a mountainous tropical landscape of Mexico. Environmental Entomology, 36 (6): 1397-1407.

Halffter, V. & G. Halffter. 2003. Nuevas subespecies de *Canthon humectus* (Say) (Coleoptera: Scarabaeidae: Scarabaeinae). Folia Entomológica Mexicana, 42 (3): 329-340.

Llorente-Bousquets, J., A.N. García-Aldrete & E. González Soriano (eds.) 1996. Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una síntesis de su conocimiento, Vol. I. Universidad Nacional Autónoma de México, México. 660 pp.

Llorente-Bousquets, J., E. González-Soriano & N. Papavero (eds.). 2000. Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una síntesis de su conocimiento, Vol. II. Universidad Nacional Autónoma de México, México. 676 pp.

Llorente-Bousquets, J. & J.J. Morrone (eds.). 2002. Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una síntesis de su conocimiento, Vol. III. Universidad Nacional de México, México. 690 pp.

Llorente-Bousquets, J., J.J. Morrone, O. Yañez & I. Vargas (eds.). 2004. Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una síntesis de su conocimiento, Vol. IV. Las Prensas de Ciencias, UNAM, México. 790 pp.

Lobo, J.M. 1996. Diversity, biogeographical considerations and spatial structure of a recently invaded dung beetle (Coleoptera: Scarabaeoidea) community in the Chihuahuan desert. Global Ecology and Biogeography Letters, 5.

Lobo, J.M. 2007. Los "Patrones de Dispersión" de la fauna ibérica de Scarabaeinae (Coleoptera), pp. 159-177. In: M. Zunino & A. Melic (eds.). Escarabajos, Diversidad y Conservación Biológica. Ensayos en Homenaje a Gonzalo Halffter. Monografías 3er Milenio, M3M, Vol. 7. Sociedad Entomológica Aragonesa, Zaragoza, España.

Lobo, J.M. & G. Halffter. 2000. Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagus beetles (Coleoptera: Scarabaeoidea): a comparative study. Annals of the Entomological Society of America, 93 (1): 115-126.

Marquez, J. & J. Asiain. 2006. Patrones de distribución de la familia Staphylinidae (Coleoptera), pp. 157-236. In: J.J. Morrone & J. Llorente-Bousquets (eds.). Componentes bióticos principales de la entomofauna mexicana. Las Prensas de Ciencias, UNAM, México, D.F.

Márquez, J. & J.J. Morrone. 2004. Relaciones biogeográficas basadas en la distribución de Coleoptera (Insecta), pp. 375-392. In: I. Luna, D. Espinosa & J.J. Morrone (eds.). Biodiversidad de la Sierra Madre Oriental. Las Prensas de Ciencias. Facultad de Ciencias, UNAM, México, D.F.

Martín-Piera, F. & J.M. Lobo. 1993. Altitudinal distribution patterns of copro-necrophage Scarabaeoidea (Coleoptera) in Veracruz, Mexico. Coleopterists Bulletin, 47 (4): 321-334.

Matthews, E.G. 1961. A revision of the genus *Copris* Müller of the Western Hemisphere (Coleop. Scarab.). Entomologica Americana, n.s., 41: 1-137.

Montes de Oca, E. & G. Halffter. 1998. Invasion of Mexico by *Euoniticellus intermedius* (Reiche): Reflections of the expansion of introduced dung beetle species (Coleoptera: Scarabaeinae). Studies on Neotropical Fauna and Environment, 33: 37-45.

Morón, M.A. 1994. Fauna de Coleoptera Lamellicornia en las montañas del Noreste de Hidalgo, México. Acta Zoológica Mexicana (n.s.), 63: 7-59.

Morón, M.A. & R.A. Terrón. 1984. Distribución altitudinal y estacional de los insectos necrófilos en la Sierra Norte de Hidalgo, México. Acta Zoológica Mexicana (n.s.), 3: 1-47.

Morrone, J.J. 2005. Hacia una síntesis biogeográfica de México. Revista Mexicana de Biodiversidad, 76 (2): 207-252.

Morrone, J.J. & J. Llorente-Bousquest (eds.) 2006. Componentes bióticos principales de la entomofauna mexicana, 2 volumes. Las Prensas de Ciencias, UNAM, México.

Morrone, J.J. & J. Márquez. 2000. Halffter's Mexican Transition Zone, beetle generalised tracks and geographical homology. Journal of Biogeography, 28: 635-650.

Morrone, J.J. & J. Márquez. 2003. Aproximación a un Atlas Biogeográfico mexicano: componentes bióticos principales y provincias biogeográficas, pp. 217-220. In: J.J. Morrone & J. Llorente (eds.). Una perspectiva latinoamericana de la biogeografía. Las Prensas de Ciencias. Facultad de Ciencias, UNAM, México.

Morrone, J.J. & J. Márquez. 2008. Biodiversity of Mexican terrestrial arthropods (Arachnida and Hexapoda): A biogeografical puzzle. Acta Zoológica Mexicana (n.s.), 24(1): 15-41.

Navarrete, D., & G. Halffter. 2008. Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. Biodiversity and Conservation, 17: 2869-2898.

Nixon, K. 2000. WinClada version 0.9.99. Published by the autor, Ithaca, Nueva York.

Rivera-Cervantes, L.E. & E. García-Real. 1998. Análisis preliminar sobre la composición de los escarabajos necrófilos (Coleoptera: Silphidae y Scarabaeidae) presentes en dos bosques de pino (uno dañado por fuego) en la Estación Científica Las Joyas, Sierra de Manantlán, Jalisco, México. Dugesiana, 5 (1): 11-22.

Rivera-Cervantes, L.E. & G. Halffter. 1999. Monografía de las especies mexicanas de *Canthon* del subgénero *Glaphyrocanthon* (Coleoptera: Scarabaeidae: Scarabaeinae). Acta Zoológica Mexicana (n.s.), 77: 23-150.

Rzedowski, J. 1983. Vegetación de México (segunda reimpresión). Editorial Limusa, México, 432 pp.

Rzedowski, J. 1993. Diversity and origins of the Phanerogamic Flora of Mexico, pp. 129-144. In: T.P. Ramamoorthy, R. Bye, A. Lot & J. Fa (eds.). Biological Diversity of Mexico: origins and distribution. Oxford University Press, Nueva York.

Trotta-Moreu, N., J.M. Lobo & F.J. Cabrero-Sañudo. 2008. Distribución conocida y potencial de Geotrupinae (Coleoptera: Scarabaeoidea) en México. Acta Zoológica Mexicana (n.s.), 24 (2): 39-65.

Trotta-Moreu, N. E. Montes de Oca & I. Martínez. 2007. Ecological and representative characteristics of *Geotrupes (Halffterius) rufoclavatus* Jekel, 1865 (Coleoptera: Geotrupidae: Geotrupinae) on the Cofre de Perote Volcano (Veracruz, Mexico). Coleopterists Bulletin, 61 (3): 435-446.

Verdú, J.R., C.E. Moreno, G. Sánchez-Rojas, C. Numa, E. Galante & G. Halffter. 2007.

Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. Biological Conservation, 140: 308-317.
ZUNINO, M. & G. HALFFTER. 1988. Análisis Taxonómico, Ecológico y Biogeográfico de un grupo americano de *Onthophagus* (Coleoptera: Scarabaeidae). Monografía IX, Museo Regionale di Science Naturali, Torino, 211 pp.
ZUNINO, M. & G. HALFFTER. 1997. Sobre *Onthophagus* Latreille, 1802 americanos (Coleoptera: Scarabaeidae: Scarabaeinae). Elytron, 11: 157-178.