

## **SPATIAL DISTRIBUTION OF THREE GROUPS OF COLEOPTERA ALONG AN ALTITUDINAL TRANSECT IN THE MEXICAN TRANSITION ZONE AND ITS BIOGEOGRAPHICAL IMPLICATIONS**

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### **ABSTRACT**

**Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican Transition Zone and its biogeographical implications.**

Historical biogeography is based on hypotheses. The phenomena on which it is based, like all those that occur only once (historical phenomena), depend on a complex, global series of circumstances that cannot be repeated. Hypotheses can however, be subjected to various tests with the evidence provided by concrete data. These tests are even more valuable when the methods are different from those used to generate the hypotheses.

This article examines the patterns of distribution proposed by HALFFTER for the insects found in the Mexican Transition Zone, using the distribution of three groups of coprophagous and necrophagous beetles (Scarabaeinae and Geotrupinae: Scarabaeoidea and Silphidae) along an altitudinal transect. Strictly speaking, the transect extends from 450 to 2,600 masl; however, for the purpose of comparison with other capture records, in this study it has been extended from sea level to 4,282 masl. The transect is located in the center of the state of Veracruz, Mexico, reaching from the coast of the Gulf of Mexico up to the Cofre de Perote mountain. This is an area where notable species replacement occurs, and that has at least five distinct groups of fauna over a linear distance of 80 km.

The study demonstrates that the patterns of distribution correspond to well-defined altitudinal zoning, with an intermediate band where elements of tropical and northern affinity overlap, resulting in a true transition zone. The altitude at which this overlap occurs is, in part, controlled by vegetation type. In the original forests, the transition zone occurs where cloud forest is found; in the prairies it occurs at the next altitudinal level (1,770-2,600 masl).

The concept of distribution pattern is discussed and the division of the Paleoamerican pattern into four patterns proposed. Though today these are distributed differently, they share origin. The relationship of the taxa studied to vegetation type is analyzed, along with other ecological characteristics: species richness, trophic preferences, relocation of food, forage availability and daily activity cycles.

This study highlights the point that biogeographical analysis based on distribution patterns provides a useful approach to the study of altitudinal succession in a transition zone.

**Key words:** Coleoptera, Scarabaeinae, Silphidae, Geotrupinae, altitudinal distribution, Veracruz, biogeography.

## INTRODUCTION

In one of the classic books on biogeography, «*Zoogeography. The Geographical Distribution of Animals*», PHILIP J. DARLINGTON JR. (1957) analyzed the transition between Nearctic and Neotropical vertebrate fauna in Mexico and Central America. Of the different geographical transition areas in the world, the most rich and complex is the Mexican Transition Zone (MTZ), thus named by HALFFTER in 1964 (for analysis, see HALFFTER, 1964; 1976; 1987; ZUNINO & HALFFTER, 1988). Found between the Nearctic and Neotropical regions, the Mexican Transition Zone, more than any other, is characterized by the overlap of elements of different affinity and by intense *in situ* development of flora and fauna. In the MTZ, the dominance of overlap (i.e., the superimposition of elements with distinct biogeographic affinities) over the subtraction characteristic of other equivalent areas (e.g., the Saharan band between the Palearctic and Ethiopian regions), has several causes. The generally North-South orientation of the Mexican mountain ranges makes them an ideal path for the arrival of mountain elements from the North. The only great transverse mountain formation, the Transverse Volcanic System, is an area of intense speciation (with marked processes of *vicariance*), *in addition to a connection to the Occidental and Oriental Sierras* and those in the South of the country. The fact that a lot part of the MTZ occurs in tropical conditions creates, combined with the pronounced relief, orography, an exceptional mosaic of climates.

Furthermore, two large groups of rich biotic assemblages with very different evolutionary histories and phylogenetic affinities come into contact in the MTZ. These are the faunistic elements that comprise the Nearctic and Neotropical regions, and their plant equivalents.

As a result of these conditions, elements of Nearctic and Neotropical phylogenetic origin overlap in the MTZ. Their evolutionary ancestors came from the North or the South. In both cases there was a series of ancient migrations in addition to modern ones. Elements of ancient origin are characterized by a high differentiation *in situ*, resulting in a high degree of endemism.

To explain the broad characteristics of the geographic distribution of present day entomofauna in the MTZ, HALFFTER (1962, 1964, 1974, 1976, 1978, 1987) proposed a group of distribution patterns<sup>1</sup>, based as much on the origin and phylogenetics of the taxa as on the possible geological and climatic history of the region, and examined the influence of these factors on the present geographic distribution. Orography and current ecological characteristics were also cited as influential factors. A distribution pattern is a reference and comparison point for analyzing and dealing with the peculiarities of the distribution of each taxa (HALFFTER, 1976). The distribution pattern synthesizes the essential characteristics of the distribution of a group of organisms that originated in, or arrived at, a given area during a given geological period, and has been subjected to the same macroecological pressures for a prolonged period (HALFFTER, 1987). As such, phylogenetic affinities at the level of great lines, the effects of historical (i.e., geological and ecological) and current phenomena have a combined effect on the

<sup>1</sup> Although in some of his earlier work HALFFTER uses the term «dispersal pattern», this is not correct since the pattern is not determined exclusively by dispersal phenomena, but also by the evolution which has occurred in the zone and, therefore, by vicariance.

distribution patterns in the MTZ. That is to say, phylogenetics and vicariance are combined.

In the determination of distribution patterns, this study has sought to present hypotheses that include different factors of arguments: current distribution, phylogenetics, geological history. The establishment of a series of paradigms has been attempted, in order to deal with the distribution of different taxa, and so present general hypotheses for the biogeography of the Mexican Transition Zone.

The MTZ distribution patterns proposed by HALFFTER are:

**Paleoamerican Pattern<sup>2</sup>.** Comprised of frequently cosmopolitan genera, whose main center of evolution was the Old World, where they occur with greater taxonomic and ecological diversity, and where they predominate in warm and warm-temperate climates. They arrived in the Americas a long time ago, probably via the Bering Strait. Only very few of the original lines of each genus reached this continent. In spite of the great diversification of species in North America and in the MTZ, this is demonstrated by the degree of taxonomic affinity (coherence) among the present-day groups of species. Away from the American Continent, the closest phylogenetic relationships (although always distant) are with East Asian species.

The Paleoamerican ancestral lines extended through Mexico before the great changes in orography that occurred during and after the Miocene. This ancient penetration is evident from the presence of current Paleoamerican genera in spite of the barriers that current the High Plateau and mountain systems represent. Species have evolved *in situ* and have established their distribution areas under much more modern conditions, and therefore copy the formation of the recent distribution patterns (Nearctic and Neotropical) with respect to their limits, but not with respect to their phylogenetic affinities (See an analysis of this phenomenon in ZUNINO & HALFFTER, 1988). The Paleoamerican distribution pattern is, together with another very ancient pattern –that of the Plateau–, the one with the highest occurrence of speciation and the highest degree of endemism in the MTZ, since the genera (not the species) tend to be found under very different ecological conditions. There are also genera with very limited distributions, represented by relict species.

<sup>2</sup>In a recent article, THOMAS (1993) indicates that HALFFTER only considers a South American evolutionary origin for the Scarabaeinae of the MTZ (with the exception of those recently spread species of northern affinity: Nearctic Pattern). *This is not a precise interpretation of the information presented.* HALFFTER proposed the Paleoamerican Pattern in 1964 (p. 79-82). He developed on the original idea in 1976 (pp. 7-8, 17-28). The Mesoamerican Mountain Pattern was proposed by this author in 1978 and enlarged upon in 1987. In this last work he clearly indicates (p. 107) «The Meso-American montane pattern is represented by elements that evolved in the Central American Nucleos... The affinities are mainly of early South American origin, but this pattern also includes some elements from the region of Mexico north of the Isthmus of Tehuantepec». It is evident that the proportion of elements with South American and North American (Mexico, north of Tehuantepec) affinities will vary depending on the group of insects which is used for the analysis and on its ecological needs, as is correctly indicated by THOMAS (1993). However, it must be taken into account that this pattern was proposed as one of mixed affinities. We feel that this clarification eliminates any doubts about a process of one-way migration indicated by THOMAS (*loc. cit.*). It also makes clear that there is no incompatibility between the biogeographical hypotheses that HALFFTER has refined over the course of successive research and those which correspond to what THOMAS refers to as the «Faunistic School».

**Nearctic Pattern.** Genera with, on a global scale, holarctic or nearctic distribution and with relatively recent (Plio-Pleistocene) or recent penetration into the MTZ. In the MTZ they are restricted to the mountains of Mexico and northern Central America and are found in coniferous forests and on the High Plateau (above 1,700 masl). Ecologically, the elements of the nearctic pattern are adapted to a cool-temperate climate.

**Distribution Pattern on the Plateau.** Within the MTZ this pattern unites elements with a southern affinity and equivalent, with respect to their long history in the zone (but not their phylogenetic origin), so those elements that make up the Paleoamerican Pattern. This pattern includes South American genera which invaded Central America and Mexico a long time ago and are represented by very restricted lines which later diversified in the MTZ, with species endemic to the Mexican, Chiapas and Guatemalan Plateaus. These elements may penetrate fairly deeply into the United States, even forming groups of endemic species.

**Neotropical Pattern.** Followed by South American lines which have entered the MTZ in recent times (mid-Pliocene and later) across the tropical lowlands. The penetration of lines of neotropical origin into the North has occurred to varying degrees (low, moderate, high).

Those which achieved the lowest degree of penetration have recently spread. They have numerous species widely distributed throughout South America, but few species in the MTZ; and are limited to the forests of northern Central America, Chiapas and southern Mexico as far as the Tehuantepec Isthmus. Elements with a moderate degree of penetration include more ancient lines, with many South American species and few species in the MTZ, but with a wider distribution than those in the previous group since they have spread northwards along the coastal plains. Although they are common to forests, they are also found in other biomes. Finally, the group with the highest degree of penetration is formed by the oldest lines and comprises numerous species in the MTZ. These principally occupy the tropical region, the coastal plains in particular, but have also made their way to the interior of Mexico and the southeastern United States.

**Mesoamerican Mountain Pattern.** This group includes elements both with ancient North American affinities and with Mexican origins north of the Isthmus of Tehuantepec, which arrived at the Central American nucleus during the mid-Cenozoic, as well as lines with ancient South American affinities which evolved in the same area. The representatives of the Mesoamerican Mountain Pattern are strongly associated with mountain and cloud forests, occasionally penetrating oak-pine forests (see REYES-CASTILLO & HALFFTER, 1978; MORON, 1983, 1991).

The distribution patterns in the MTZ have been useful for research carried out on the latitudinal distribution of insects, taxonomic revisions and cladistic analyses (among others, see MORON & TERRON, 1984; LLORENTE-BOUSQUETS, 1983; QUINTERO & REYES-CASTILLO, 1983; ZUNINO, 1984; PALACIOS-VARGAS, 1988; ZUNINO & HALFFTER, 1988; KOHLMANN & HALFFTER, 1988, 1990; DELGADO, 1989; IBAÑEZ, 1989; LIEBHERR, 1991, 1994a; MORON 1991; CAPISTRAN, 1992; LLORENTE-BOUSQUETS & LUIS-MARTÍNEZ, 1993; THOMAS, 1993). Outside of the MTZ the Geographic Distribution Analysis method

proposed by HALFFTER has been used in the Chinese Transition Zone (ZUNINO, 1984), in the Euro-Mediterranean area (ZUNINO, 1985) and in the Central Iberian Mountain System of Spain (MARTIN-PIERA *et al.*, 1992). However, this type of analysis has been used infrequently to study the altitudinal zonation of insects in the MTZ (MAC VEAN & SCHUSTER 1981; LUIS-MARTÍNEZ & LLORENTE-BOUSQUETS, 1990; GARCIA-REAL, 1991; ARELLANO, 1992; VARGAS *et al.*, 1992; MARTIN-PIERA & LOBO, 1993; PONCE & LLORENTE, 1993). The Results and Discussion sections analyze recent comments on HALFFTER's patterns and present some modifications and clarifications which we feel are necessary.

In this article the biogeographical relationship between altitudinal and latitudinal distribution within the MTZ is examined using three groups of coprophagous and necrophagous Coleoptera: Scarabaeinae and Geotrupinae (Scarabaeoidea) and Silphidae, and asking the following questions:

1) In the MTZ flora and fauna of nearctic and neotropical origin (affinity) are segregated latitudinally. Elements of nearctic affinity dominate in the North and neotropical elements dominate in the South. Overlap of these two affinity groups occurs. Does the same phenomenon occur with respect to altitude? That is, when a mountain range offers favorable ecological conditions, is there a clear dominance of neotropical species in the lower tropical strip? Do elements of nearctic affinity dominate at higher altitudes? (In the Andes there are high mountain elements, which are clearly neotropical). Is there an intermediate strip where elements of different affinity overlap and a notable occurrence of endemism?

2) If altitude and its climatic derivatives, including vegetation type, are the group of current determining factors (i.e., in addition to historic elements) of distribution in mountains found in the MTZ, then what are the altitudinal limits for both the tropical and the nearctic species? What are the altitudinal limits of the overlap (or transition) zone for these two large complexes of fauna?

3) The activities of humankind have profoundly modified the vegetation of the MTZ. Deforestation and clearing pasture for cattle ranching have created heliophile habitats which are warmer and where the quantity of excrement available (mainly cow dung) is much greater than in the forests that have not been totally modified. This is not the only change. Coffee plantations are shady but have a reduced diversity of plants and animals, resulting in different effects on those Silphidae which make use of small carcasses and on the Scarabaeinae which are primarily coprophagous. How have these changes affected the distribution of the beetles studied? What is the biogeographical effect on the expansion of groups of fauna with nearctic and neotropical affinity?

## GEOGRAPHIC AREA, MATERIALS AND METHODS

The altitudinal gradient selected for this analysis is located in central Veracruz, Mexico (1938'-1901' lat. N, 9608'- 9712' long. W, Fig. 1), and includes eleven locations between 450 and 2,600 masl (Fig. 2). It forms part of the eastern slope of the Cofre de Perote mountain (Fig. 3), which dates back to the Pliocene, two or three million years BP (INEGI, 1988).

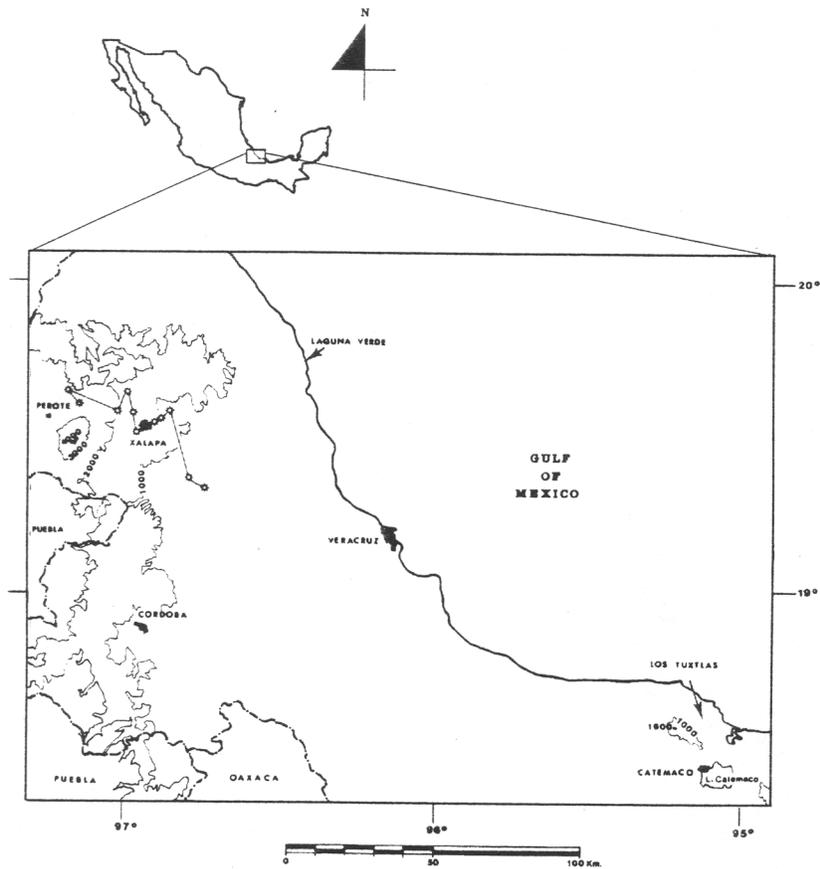


Fig. 1: Map of the central zone of the state of Veracruz, indicating the location of the study transect (line joining •) and the areas with which the transect was completed: Laguna Verde, Los Tuxtlas, Cofre de Perote.

In geological terms the study area is heterogeneous. The Transverse Volcanic System (general W-E orientation) extends down to the sea, is narrow and of volcanic origin. This divides the Sierra Madre Oriental which has a general N-S orientation, but turns W-E at its southern extreme. This range is composed of Jurassic, Cretaceous and Cenozoic sedimentary formations (see FERRUSQUIA-VILLA FRANCA, 1993). These have produced volcanic formations (andesites, basalt, riolite and ash deposits) occurring as overflows or breaches as well as exposed intrusive igneous rock from the Tertiary and sedimentary formations from the Mesozoic and the Quaternary (clay, sand, gravel and river alluvia; cretaceous limestone (GEISSERT & ROSSIGNOL, 1987; INEGI, 1988)).

There is a gradient of soils from the highest to lowest altitudes; andosols from 2,600 to 1,770 masl, andosol-lithosols and feozems between 1,530 and 1,100 masl, and feozems, luvisols and rendzinas from 900 to 450 masl (INEGI, 1988).

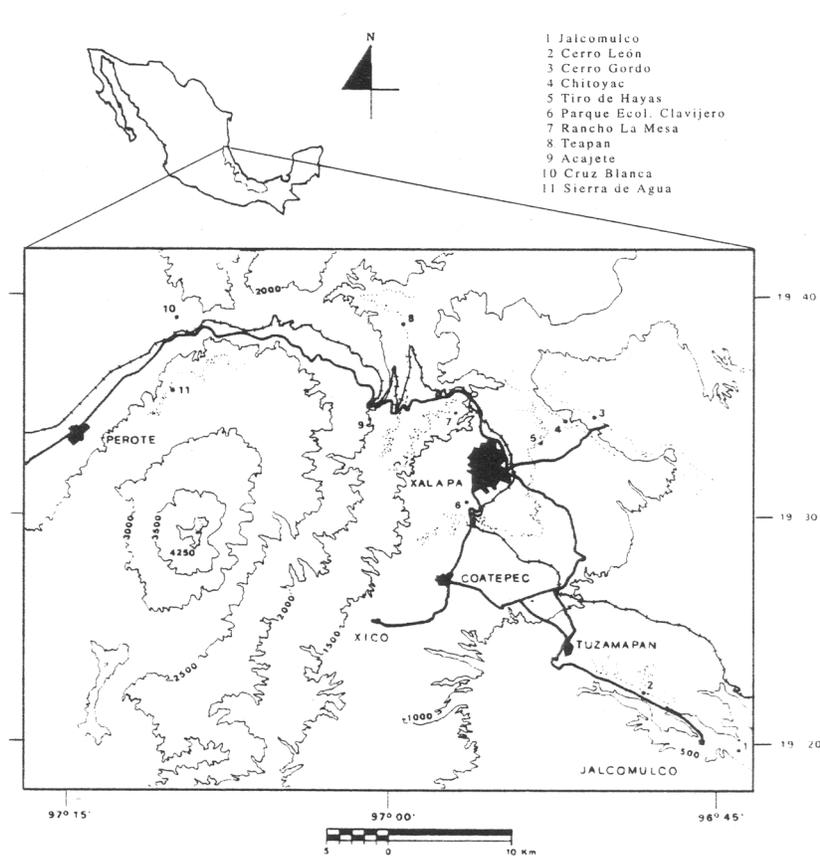


Fig. 2: Map indicating the exact position of capture sites on the altitudinal transect (see numbers).

In the high range (2,600 - 1,770 masl) there are pine forests, which descend into oak-pine forests and then into cloud forests (1,530 - 1,360 masl). These then disappear and medium altitude oak forest is found from 1,100 - 600 masl (not analyzed in this study). At lower altitudes this is replaced by low tropical deciduous forest (1,300 - 450 masl). This altitudinal vegetation transformation is related to the local climate regimen (SOTO & ANGULO, 1990). In the zones where pine forest is found there are four types of climate: C (fm) humid temperate with rain all year round, C (m) humid temperate with rain in summer, Cw2 subhumid temperate with rain in summer and CW1" dry subhumid temperate. Cloud forest occurs at the border of two climate types: C (fm)w"b(i)g, humid temperate with rain all year round and (A)C (fm) w"a(i)g, semiwarm humid, the warmest of the C temperate climates (ZOLA, 1987). Zones where low tropical deciduous forest is found are typified by Aw'(i)g, warm subhumid or intermediate climate.

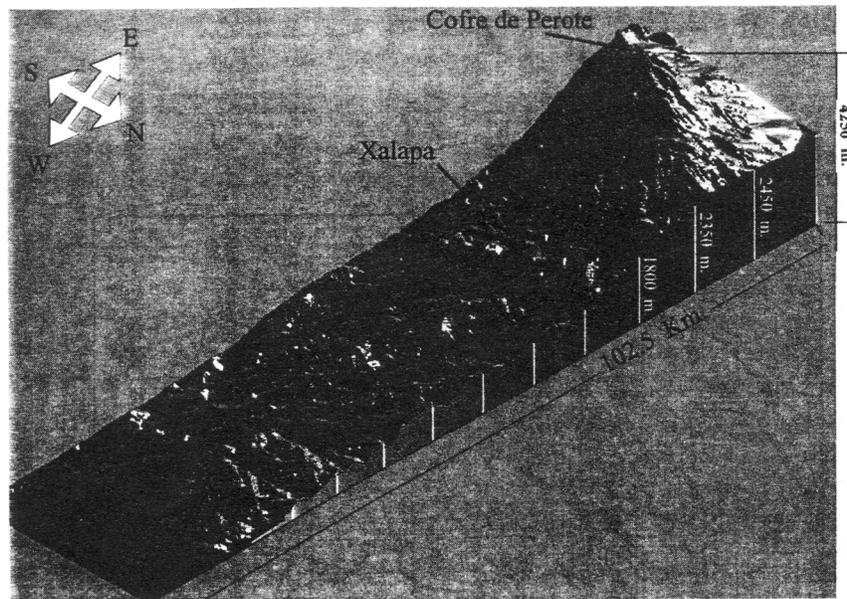


Fig. 3: Digital terrain model of the study transect with orientation map overlay. Note the deep gorges and ravines which allow tropical fauna to penetrate the mountains.

#### Synthesis of the Collection Sites

At each site (Fig. 2), collections were made separately within natural forests or in the least modified remnants and in the induced pastures. At medium altitudes collections were also made in coffee plantations. Jalcomulco (450 masl) and Cerro León (700 masl) have low tropical deciduous forest with trees up to 15 m in height. Most of the trees lose their leaves for periods as long as six months. The herbaceous stratum is abundant during the rainy season and sparse during the dry season. Soils are derived from calcareous (rendzinas and vertisols), blackish clays and are shallow with high overland flow, sloping land and rocky cliffs (GEISSERT & ROSSIGNOL, 1987). The climate is Aw 1'(i) g, warm-humid with rains in summer (GARCÍA, 1981).

Cerro Gordo (900 masl) and Chiltoyac (1,100 masl) have low deciduous forests. The dry season is longer than at the previously mentioned sites. The soils are formed by very recent basaltic lava (GEISSERT & ROSSIGNOL, *loc. cit.*), as well by shallow clay soils. The climate is Aw 1'(i)g, warm subhumid with rains in summer (GARCÍA, *loc cit.*).

Tiro de Hayas (1,300 masl) is located in the transition between tropical mountain forest and cloud forest. The remaining forests are located on very steep slopes. The soils are lithosols, with tepetate at some sites, volcanic ash or lapilli and cambisols. The climate is (A)C(fm)w"b(i)g, semiwarm humid (SOTO & ANGULO, 1990).

«Francisco Javier Clavijero» Ecological Park in Xalapa (1,360 masl) and Rancho La Mesa (1,530 masl). Cloud forest. The soils are typical andosols, dark brown, deep, slimy, very porous and associated with superficial lithosols and cambisols. The climate is C(fm)w''b(i)'g, humid temperate with rain all year round (SOTO & ANGULO, 1990).

Teapan (1,770 masl), Acajete (2,000 masl), Cruz Blanca (2,340 masl) and Sierra de Agua (2,600 masl) have different types of pine and oak-pine forests. The soils are derived from volcanic ash. The surface layer is dark humic andosols or light ochre andosols. These soils are spongy and loose. Climate varies with altitude. Between 1,700 and 2,000 masl climate is C(fm), humid temperate with rain all year round; at 2,340 masl climate is CW2, subhumid temperate with rains in summer; at 2,600 masl climate is CW1", subhumid temperate.

#### **Selection of study groups**

We use the subfamilies Scarabaeinae (Scarabaeidae) and Geotrupinae (Geotrupidae), as well as the family Silphidae, for the following reasons:

- 1) These groups have been used repeatedly in studies of biogeography and fauna. As such, good information on their distribution outside of the study transect is available.
- 2) It is possible to collect them systematically (using baited traps complemented by direct capture). Thus, with an adequate number of replicates, the majority of a species present at a given site can be captured.
- 3) There is reasonably good taxonomic information available for these groups, including the Mexican fauna.
- 4) The research team at the Instituto de Ecología has been working on the taxonomy, ecology and ethology of these insect groups for many years.

Aphodiinae<sup>3</sup> are not included in this study because they do not meet criteria 1, 3 or 4. It is especially difficult to identify Mexican fauna at the species level. In the European mountains the Aphodiinae are dominant among coprophagous beetles, in terms of both number of species and number of individuals (among recent articles, see, for example, LUMARET & STIERNET, 1989). This dominance is general as we move northwards in the Northern Hemisphere. (The nearctic and palearctic species are well-known). Under northern conditions the Aphodiinae would undoubtedly have been included.

#### **Capture Methods**

Each month from January to December of 1990 five traps baited with excrement (conventional coprotraps) and five baited with octopus (conventional necrotraps) were placed in each type of vegetation studied at each site. In order to capture the greatest number of species possible, direct captures of beetles on excrement were also done and a NTP-80 trap baited with octopus (MORON & TERRON, 1984) was placed in each forest to capture necrophagous species.

<sup>3</sup> In the absence of a definitive analysis for grouping at the level of family/subfamily within the Scarabaeoidea, we followed the most convincing and global system available to date, that of C. H. SCHOLTZ (1990). This author, mainly following ZUNINO (1984), with antecedents in CROWSON (1955), considers the group of Geotrupines as the family Geotrupidae. He also considers the Afodines as a the subfamily Aphodiinae within the family Scarabaeidae.

### Data Analysis

The questions we addressed have two fundamental components. The first is about the relationship of species distribution and ecological functions over the study transect. The second is about the relationship between species distribution and the theoretical patterns of biogeographical distribution they belong to. These two components were analyzed using the following procedure.

The analysis of the distribution of the beetles relative to the altitudinal gradient was obtained using a Two-Step classification, based on a matrix of data for total abundance (19 sites x 38 species from the baited trap sampling) using the MULTIVAR program (SANCHEZ-COLON & ORNELAS, 1989). The Two-Step method is one of inverse classification in which species are classified into groups with similar ecological tolerances (AUSTIN & BELBIN, 1982). This method of analyzing the ecological affinity of species has been used in floristic studies. Since it uses a data matrix of species by site, it should be applicable to our data.

In the Two-Step analysis the first step is the construction of an asymmetrical matrix of dissimilarities between species using the formula:

$$D_{ij} = \frac{\sum_{h=1}^n |X_{ih} - X_{jh}|}{\sum_{h=1}^n |X_{ih} + X_{jh}|}$$

where  $i$  and  $j$  are species,  $h$  is the collection site and  $X_{ih}$  is the value of species  $i$  in site  $h$ .

Since this index is sensitive to abundance effects, the quantitative data are normalized by species as follows (see AUSTIN & BELBIN, 1982):

$$X'_{ih} = \frac{X_{ih}}{\sum_{h=1}^n X_{ih}^2}$$

In the second step, a symmetrical matrix is obtained using the function:

$$T_{ij} = \sum_{k=1}^m |D_{ik} - D_{jk}|$$

where  $m$  is the total number of species, and  $D_{ik}$  is the dissimilarity value for species  $i$  in sample  $k$ .

Cluster analysis can be applied to the resulting matrix. Different clustering methods (UPGMA, WPGMA and Reciprocal Averages) were used in this study and obtained similar dendrograms. Only the dendrogram constructed with the UPGMA method applied to standardized data is presented here.

Next a distribution pattern was assigned to each species in the dendrogram, which allowed altitudinal range and vegetation type to be associated with distribution pattern.

For the purpose of biogeographical analysis, the Two-Step method has the limitation of assigning each species to a single group. Under natural conditions, it is not uncommon for the distribution of a given species to exceed that of the group to which it has been assigned. In this study this difficulty was overcome by including in «Results: Assigning distribution patterns to the CED species» a list of the other species which are found in the altitude and vegetation range concerned, after the analysis of the composition of each group.

## RESULTS

In the entire transect 3,878 beetles were captured in baited traps (see Table 1). The most abundant taxonomic group was the Scarabaeinae subfamily, for which 3,112 beetles belonging to 31 species were caught. For the Geotrupinae subfamily 37 beetles belonging to three species were caught. For the Silphidae family 729 beetles belonging to four species were caught.

The Scarabaeinae subfamily was the only one represented in the lowest part of the transect, and decreased in richness and abundance with altitude. The Silphidae family was captured from 1,100 masl. The greatest number of species was caught (4 of 4) between 1,770 and 2,000 masl, but the greatest number of individuals belonging to this family (465 of 729) was captured between 2,340 and 2,600 masl. Geotrupinae were only captured between 2,340 and 2,600 masl, although they are found at higher altitudes (see Discussion).

### Classification of species (CS)

The Two-Step classification resulted in six groups of species that could be associated with altitude and vegetation type (Fig. 4). The first two groups were exclusively Scarabaeinae. Group I contains forest species, while Group II contains pasture species. Species for both groups were caught between 450 and 1,000 masl, under warm subhumid climatic conditions.

Sixty-seven percent of the species in Group III were Scarabaeinae and the rest were Silphidae. These were found in cloud forests and coffee plantations. Group IV consisted of Scarabaeinae species from induced pastures close to cloud forest. Species from both of these groups were captured between 1,100 and 1,530 masl. It is between these altitudes that the mixture of fauna with tropical and nearctic affinities begins. This altitudinal stage corresponds to the transition between semiwarm humid and temperate humid climate.

Eighty-six percent of the species in Group V were Scarabaeinae and 14 % were Geotrupinae. This group included elements from induced pastures between 1,770 and 2,000 masl, which are infrequent in or absent from mountain forests.

Forty percent of the species in Group VI were Silphidae, 40 % were Geotrupinae and 20 % were Scarabaeinae. These were collected in pine forests (1,770-2,600 masl). The transition between temperate humid and temperate subhumid climate occurs above this altitudinal range.

### Assignment of Distribution Patterns to the species classifications.

#### *Group I*

Phylogenetically and biogeographically this group of tropical forest species contains of three types of elements (Table 2). First, there are those species that

VEGETATION	TDF		Coffee Pl.		CF		Pasture		Coffee Pl.		PF		Total
	(450-1100)		(1300-1530)		(1770-2600)								
<b>FAM. SCARABAEIDAE</b>													
<b>SUBFAM. SCARABAEINAE</b>													
<b>ONTHOPHAGINI TRIBE</b>													
1	<i>Onthophagus incensus</i> (Say), 1835.	1	3	-	69	408	1	-	-	-	169	651	
2	<i>Onthophagus chevrolati retusus</i> Harold, 1869.	-	-	-	-	-	-	-	2	279	281		
3	<i>Onthophagus cyanellus</i> Bates, 1887.	-	-	-	64	12	8	9	76	169			
4	<i>Onthophagus nasicornis</i> Harold, 1869.	-	-	-	2	-	13	-	-	15			
5	<i>Onthophagus aureofuscus</i> Bates, 1887.	-	-	-	-	-	-	12	-	12			
6	<i>Onthophagus mexexus</i> Howden, 1970.	-	-	-	-	3	-	4	23	30			
7	<i>Onthophagus landolti</i> Harold, 1880.	346	52	-	4	-	-	-	-	402			
8	<i>Onthophagus corrosus</i> Bates, 1887.	-	-	-	-	13	-	-	-	13			
9	<i>Onthophagus horpferi</i> Harold, 1869.	5	1	-	-	-	-	-	-	6			
10	<i>Digitonthophagus gazella</i> (Fabricius), 1787.	-	17	-	-	-	-	-	-	17			
<b>COPRINI TRIBE</b>													
<b>DICHOTOMIINA SUBTRIBE</b>													
11	<i>Dichotomius carolinus</i> (Say), 1835.	-	4	-	8	10	-	-	-	22			
12	<i>Dichotomius satanas</i> Harold, 1867.	-	-	1	38	-	20	-	-	59			
13	<i>Dichotomius centralis</i> Harold, 1869.	68	-	-	-	-	-	-	-	68			
14	<i>Scatimus ovatus</i> Harold, 1862.	-	-	-	5	23	-	-	-	28			
15	<i>Uroxys boneti</i> Pereira and Halffter, 1961.	56	-	-	-	-	-	-	-	56			
16	<i>Ontherus mexicanus</i> Harold, 1869.	-	-	-	-	-	-	-	45	45			
<b>PHANAEINA SUBTRIBE</b>													
17	<i>Phanaeus endymion</i> Harold, 1863.	29	-	2	9	-	-	-	-	40			
18	<i>Phanaeus tridens</i> Laporte, 1840.	-	1	-	-	-	-	-	-	1			
19	<i>Phanaeus umethystinus</i> Harold, 1863.	-	-	-	-	-	-	-	2	2			
20	<i>Coprophanaeus telamon corythus</i> Harold, 1863.	60	-	28	34	3	9	-	-	134			
<b>COPRINA SUBTRIBE</b>													
21	<i>Copris incertus</i> (Say), 1835.	-	-	-	48	168	-	-	49	265			
22	<i>Copris lugubris</i> Boheman, 1858.	-	36	-	-	-	-	-	-	36			
<b>EURYSTERNINI TRIBE</b>													
23	<i>Eurysternus magnus</i> Laporte, 1840.	-	-	-	2	-	-	-	-	2			
<b>SCARABAEINI TRIBE</b>													
<b>SISYPHINA SUBTRIBE</b>													
24	<i>Sisyphus mexicanus</i> Harold, 1863.	5	-	-	-	-	-	-	-	5			
<b>CANTHONINA SUBTRIBE</b>													
25	<i>Canthon humectus sayi</i> Robinson 1948.	-	-	-	-	-	-	-	36	36			
26	<i>Canthon indigaceus chevrolati</i> Harold, 1868.	5	21	-	-	-	-	-	-	26			
27	<i>Canthon cyanellus cyanellus</i> LeConte, 1869.	179	-	-	-	-	-	-	-	179			
28	<i>Canthon (Glaphyrocantion) viridis leechi</i> Martínez, Halffter and Halffter, 1964.	292	4	-	-	-	-	-	-	296			
29	<i>Deltochilum (Hsbomidium) gibbosum sublaeve</i> . Bates, 1887.	204	-	-	-	-	-	-	-	204			
30	<i>Deltochilum (Deltochilum) scabriusculum scabriusculum</i> Bates, 1887.	5	-	-	-	-	-	-	-	5			
31	<i>Deltochilum mexicanum</i> Burmeister, 1848.	-	-	-	7	-	-	-	-	7			
<b>TOTAL SCARABAEINAE</b>		<b>1255</b>	<b>139</b>	<b>31</b>	<b>290</b>	<b>640</b>	<b>51</b>	<b>27</b>	<b>679</b>	<b>3112</b>			
<b>FAM. GEOTRUPIDAE</b>													
<b>SUBFAM. GEOTRUPINAE</b>													
<b>CERATOTRUPINI TRIBE</b>													
32	<i>Ceratotrupes bolivari</i> Halffter y Martínez, 1962.	-	-	-	-	-	-	3	-	3			
33	<i>Onthotrupes nebularum</i> (Howden), 1964.	-	-	-	-	-	-	-	1	1			
34	<i>Onthotrupes herbeus</i> (Jeckel), 1865.	-	-	-	-	-	-	33	-	33			
<b>TOTAL GEOTRUPINAE</b>		<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>36</b>	<b>1</b>	<b>37</b>			
<b>FAM. SILPHIDAE</b>													
<b>SUBFAM. SILPHINAE</b>													
35	<i>Tanatophilus graniger</i> (Chevrolat), 1833.	-	-	-	-	-	-	52	4	56			
36	<i>Oxelytrum discicolle</i> (Brullé), 1840.	-	-	1	2	1	6	8	1	19			
<b>SUBFAM. NICROPHORINAE</b>													
37	<i>Nicrophorus mexicanus</i> Matthews, 1888.	-	-	-	-	-	-	503	12	515			
38	<i>Nicrophorus olidus</i> Matthews, 1888.	-	-	37	58	-	8	28	8	139			
<b>TOTAL SILPHIDAE</b>		<b>0</b>	<b>0</b>	<b>38</b>	<b>60</b>	<b>1</b>	<b>14</b>	<b>591</b>	<b>25</b>	<b>729</b>			
<b>TOTAL GENERAL</b>		<b>1255</b>	<b>139</b>	<b>69</b>	<b>350</b>	<b>641</b>	<b>65</b>	<b>654</b>	<b>705</b>	<b>3878</b>			

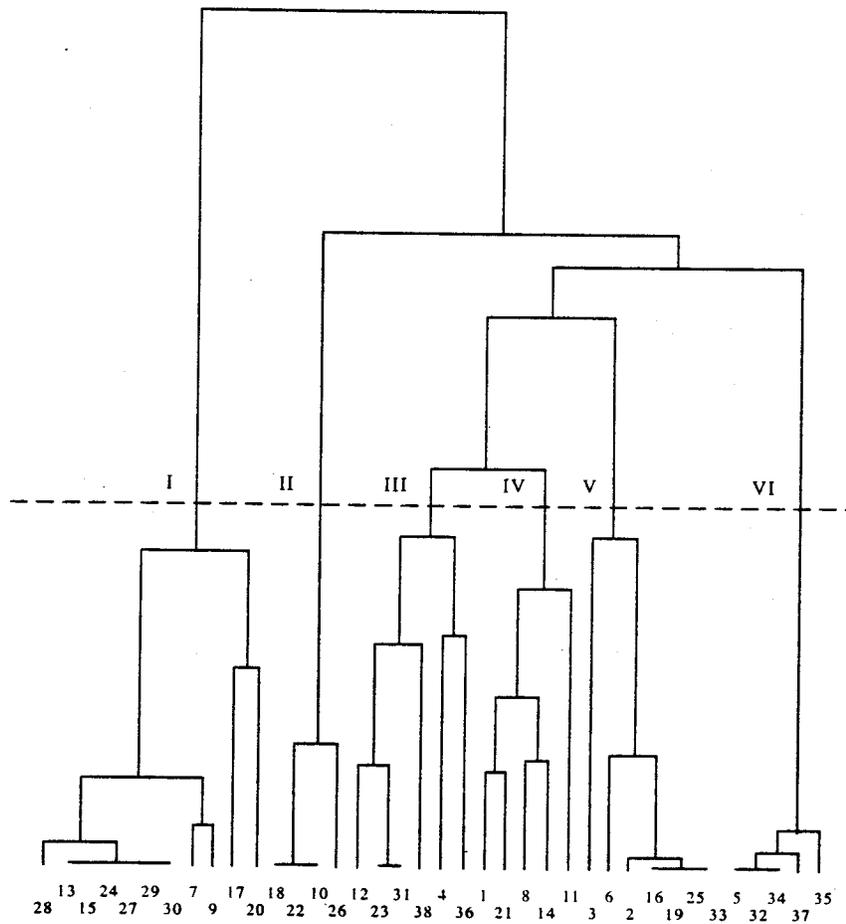


Fig. 4: Species classification using the «Two-Step» method. The number of each species is the same as in Tables 1 and 2.

Table 1: Altitudinal distribution of Scarabaeinae, Geotrupinae and Silphidae in different vegetation types: original and induced, in the central zone of the State of Veracruz. This table includes those species collected at the sample sites located on the transects and species classified according to the «Two-Step» method. Numbers correspond to the quantity of individuals captured. The number preceding each species is the same as in Figure 4 and Table 2. TDF: tropical deciduous forest CF: cloud forest PF: pine forest

correspond to the neotropical pattern of minimum penetration: *Uroxys boneti*, *Dichotomius centralis* and *Deltochilum (Deltochilum) scabriusculum scabriusculum*. Second, there are species representative of the neotropical distribution pattern with moderate penetration: *Phanaeus endymion*, *Coprophanæus telamon corythus*, *Deltochilum gibbosum*, *Canthon cyanellus cyanellus* and *Canthon (Glaphyrocantion) viridis leechi*. This second assemblage of species is not only found in tropical forest, but also in other types of vegetation such as cloud forest (except for species of the genus *Canthon*), pastures and coffee plantations. Third there are species of *Onthophagus* and *Sisyphus*. These genera correspond to the Paleoamerican pattern as defined by HALFFTER, and live under tropical or subtropical conditions: *Onthophagus landolti*<sup>4</sup>, *O. hoepfneri* and *Sisyphus mexicanus*.

*O. landolti* occurs from the United States to Colombia (HOWDEN & YOUNG, 1981). *O. hoepfneri* is found from Arizona to Nicaragua (ARNETT, 1983; MORON *et al.*, 1988); in Mexico it has been captured in relatively undisturbed deciduous tropical forests (DELOYA *et al.*, 1987; MORON *et al.*, 1988; DELOYA and CAPISTRAN, 1991). *Sisyphus mexicanus* has infrequent and isolated populations on the Gulf Coast (Tamaulipas, Veracruz), on the Yucatan Peninsula, and in the Mexican states of San Luis Potosí, Querétaro and Oaxaca, as well as in Costa Rica and Nicaragua (HOWDEN, 1965; HALFFTER, 1976; LOPEZ-GUERRERO, 1995).

The tropical forests in which Group I was collected are deciduous or semideciduous, and partially disturbed (see comparison with an evergreen tropical forest in the Discussion). This explains the capture of *Canthon (Gl.) viridis leechi*. This species is common to open tropical areas and is not normally found in undisturbed tropical forest. The same is true of two species which were not included in this group, but which were collected at the tropical forest sites: *O. incensus* (Group IV) and *Canthon indigaceus chevrolati* (Group II) (see Table 1).

#### Group II

Group II (Table 2), species from pastures on the lower part of the gradient, comprised *Copris lugubris*, which belongs to a Paleoamerican genus but is a species clearly adapted to the tropical conditions of the lowlands, *Phanaeus tridens* and *Canthon indigaceus chevrolati*, which follow the neotropical pattern of moderate penetration. These three species are well adapted to open tropical formations and are not found in forest except under disturbed conditions (see THOMAS, 1993). This has allowed them to successfully colonize anthropogenic ecosystems such as induced pastures. *Digitonthophagus gazella* was common in pastures (see Discussion, Tropical Paleoamerican Pattern).

In the capture sites of Group II, species were found which, owing to their relative abundance, were classified as Group I: *Onthophagus landolti*, *Onthophagus hoepfneri* and *Canthon (Gl.) viridis leechi*. The same occurred with *Onthophagus incensus* and *Dichotomius carolinus*, which were assigned to Group IV (see Table 1).

#### Groups III and IV

The species of Groups III and IV of the CS are found in the altitudinal band that was originally covered by cloud forest. This type of forest has a limited and

<sup>4</sup> There may be some ambiguity with respect to the separation of *Onthophagus landolti* and *O. schaefferi* HOWDEN & CARTWRIGHT (the latter has only been cited for Oklahoma and Texas).

GROUPS		HALFFTER'S DISTRIBUTION PATTERNS							
		NEOTROPICAL			MESO-AMERICAN	MEXICAN PLATEAU	PALEO-AMERICAN		NEARCTIC
SPECIES		MIN	MOD	MAX			RELICT	TROPICAL	MONTANE
I	15 <i>Uroxys boneti</i>			X					
	30 <i>Deltochilum scabriusculum</i>			X					
	13 <i>Dichotomius centralis</i>			X					
	27 <i>Canthon cyanellus</i>			X					
	29 <i>Deltochilum gibbosum</i>			X					
	17 <i>Phanaeus endymion</i>			X					
	28 <i>Canthon (Glyphyrocantion) viridis leechi</i>			X					
	20 <i>Coprophanaeus telamon</i>			X					
	7 <i>Onthophagus landolti</i>								X
	9 <i>Onthophagus hoepfneri</i>								X
24 <i>Sisyphus mexicanus</i>							X		
II	26 <i>Canthon indigaceus chevrolati</i>			X					
	18 <i>Phanaeus tridens</i>			X					
	22 <i>Copris lugubris</i>								X
	10 <i>Digitonthophagus gazella*</i>								
III	23 <i>Eurysternus magnus</i>			X					
	12 <i>Dichotomius satanas</i>			X					
	36 <i>Oxelytrum discicolle</i>			X					
	31 <i>Deltochilum mexicanum</i>				X				
	4 <i>Onthophagus nasicornis</i>							X	
	38 <i>Nicrophorus olidus</i>								X
IV	14 <i>Scatimus ovatus</i>			X					
	11 <i>Dichotomius carolinus</i>				X				
	21 <i>Copris incertus</i>								X
	1 <i>Onthophagus incensus</i>								X
	8 <i>Onthophagus corrosus</i>								X
V	16 <i>Ontherus mexicanus</i>				X				
	25 <i>Canthon humectus</i>					X			
	19 <i>Phanaeus amethystinus</i>				X				
	3 <i>Onthophagus cyanellus</i>				X				
	6 <i>Onthophagus mexitexu</i>				X				
	2 <i>Onthophagus chevrolati</i>								X
33 <i>Onthotrupes nebularam</i>								X	
VI	5 <i>Onthophagus aureofuscus</i>								X
	32 <i>Ceratotrupes bolivari</i>								X
	34 <i>Onthotrupes herbeus</i>								X
	37 <i>Nicrophorus mexicanus</i>								X
	35 <i>Tanatophilus graniger</i>								X

Table 2: Halffter's distribution patterns of Silphidae, Scarabaeinae and Geotrupinae species along the transect. Roman numerals correspond to the groups assigned by the «Two Step» classification and Arabic numbers correspond to the species listed in Table 1. Double lines between rows indicate altitudinal separation. A single line indicates, for each altitudinal level, a distinct vegetation type.

\*Introduced Indoafrikan species.

fragmented distribution in Mexico (see Application of Distribution Patterns to Altitudinal Analysis).

Of Group III, cloud forest and coffee plantations, *Eurysternus magnus*, *Dichotomius satanas* and *Oxelytrum discicolle* fall into the neotropical pattern with moderate penetration. *Onthophagus nasicornis* has a paleoamerican tropical distribution which reaches medium altitudes. *Deltochilum mexicanum* follows the Mesoamerican Mountain Pattern. *Nicrophorus olidus* (Silphidae) is the only species with a nearctic affinity.

The genus *Eurysternus* is widely distributed throughout South America and is found up into Mexico along the warm lowlands (HALFFTER & HALFFTER, 1977). *Eurysternus magnus* is found in tropical forests from Mexico to Central America (Costa Rica) (see JESSOP, 1985). The Dichotomiina are an essentially neotropical subtribe and are considered to be the ecological equivalent of the Coprina that are dominant in the Old World. *Dichotomius satanas* occurs in perennial tropical forests and cloud forests in the states of Hidalgo, Puebla, Veracruz, Oaxaca and Chiapas. It is also found in Central America, Colombia and Ecuador (MORON *et al.*, 1985). In spite of the fact that the American Silphids (*Necrodes*, *Tanatophilus*, *Nicrophorus*, among others) belong to nearctic lines, within this family there is a tropical genus, *Oxelytrum*, which probably originated in South America (PECK & ANDERSON, 1985). This genus has seven species which are exclusive to South America and one species which is very widely distributed, *Oxelytrum discicolle* which is found in southern Brazil and Paraguay (but not in the Amazon lowlands), in Argentina, Bolivia, Colombia, Peru, Venezuela, Central America, Mexico and the far south of Texas (PECK & ANDERSON, *op. cit.*) in tropical rainforest, cloud forest, dry scrub and other types of vegetation. *O. nasicornis* is a species which has been captured in Mexico in the states of Veracruz, Chiapas and Oaxaca, and in Costa Rica (BOUCOMONT, 1932; MORON, 1979; MORON & TERRON, 1984; MORON *et al.*, 1985). *Deltochilum mexicanum* is a species belonging to a neotropical genus and follows the Mesoamerican pattern. It is distributed through the warm and temperate zones of the Mexican states of Guerrero, Veracruz and Hidalgo in tropical montane forest (see MORON & TERRON, 1984). In our transect, it was found in cloud forest. *Nicrophorus olidus* is a species endemic to Mexico which belongs to a clearly holarctic genus. It is found in the Mexican states of Durango, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas and Veracruz, between altitudes of 300 masl and 3,000 masl (PECK & ANDERSON, 1985). *N. olidus* was only captured between 1,100 masl and 1,770 masl. At 1,770 masl, in pine forest, *N. olidus* and *N. mexicanus* were found together; however, above 2,000 masl only the latter was captured.

In addition to those species included in Group III, various species of very wide ecological distribution were found between 1,300 and 1,530 masl in cloud forest and coffee plantations, although they normally show a preference for open areas (see Table 1). These were *Onthophagus landolti* (Group I), *O. incensus*, *Copris incertus* and *Dichotomius carolinus* (Group IV) and *O. cyanellus* (Group V) as well as a species with a more restricted altitudinal distribution, *Scatimus ovatus* (Group IV). *Phanaeus endymion* and *Coprophanaeus telamon corythus* (Group I) were also found in these forests. These last two are typical tropical forest species but do range higher in altitude. Both were collected in cloud forest.

At cloud forest altitudes there is a true overlap of species with tropical (neotropical and paleoamerican) and nearctic distribution patterns. Considering the

species collected at these elevations, the tropical element is clearly dominant with 12 of the total 14 species collected.

Within group IV of the CS, three species (*Onthophagus incensus*, *O. corrosus* and *Copris incertus*) are Paleoamerican elements with tropical distributions. One species, *Dichotomius carolinus*, exhibits the Neotropical pattern with maximum penetration and *Scatimus ovatus* also exhibits the Neotropical pattern, but with moderate penetration (Table 2).

According to DELGADO (1989) *O. incensus* is found from Mexico to Costa Rica. In our gradient, this species was found as high as 2,000 masl, and was the species with the broadest altitudinal range in the transect (Table 1). *O. corrosus* is a rare Mexican species which has occasionally been found in the states of Guerrero, Oaxaca and Veracruz (150-1,300 masl) in areas characterized by humid climate (PEREIRA & HALFFTER, 1961). *Copris incertus* is distributed throughout Mexico, Costa Rica, Colombia and Ecuador (on the Pacific slopes of the Andes). In the South of its distribution range, it is found between 1,050 and 1,800 masl (MATTHEWS, 1961; HOWDEN & YOUNG, 1981). In Mexico, it is found between 150 and 1,360 masl (*loc. cit.*) in areas with tree cover, but not necessarily in forests. In a few places this species enters cloud forest. It is not found in the coastal lowlands of the Gulf of Mexico, where it is replaced by *Copris lugubris* (MATTHEWS, 1961). In our transect, we found *Copris incertus* between 1,360 and 1,770 masl, which widens the upper limit of the distribution range of this species. *Dichotomius carolinus* is very widely distributed in the MTZ and the United States (ARNETT, 1983). It is associated with human activities (cattle ranching) and is very abundant in disturbed tropical zones. In our transect it was caught in pastures at 450 to 1,520 masl. *Scatimus ovatus* exhibits the Neotropical pattern of distribution with moderate penetration (and perhaps should be included in the Mesoamerican Mountain pattern). It is distributed from Mexico to Colombia (HOWDEN & YOUNG, 1981). In Acahuzotla, Guerrero, this species was collected in oak-pine forests at medium altitudes or in open areas close to tropical forest (see DELGADO, 1989). In Manantlán, Jalisco, it has been caught in deciduous and semi-deciduous tropical forest between 700 and 1,000 masl (GARCIA REAL, 1991) and in Chiapas it has been found in oak-pine forests between 800 and 2,600 masl (THOMAS, 1993). In the transect this species was collected in pastures associated with cloud forest (1,360-1,530 masl).

In addition to the above-mentioned species, in pastures located at medium altitudes two species which are more abundant in forests (see Table 1) were captured: *Onthophagus cyanellus* (Group V) and *Coprophanæus telamon corythus* (Group I); as well as two other species (see Table 1); *O. mextexus* (Group V) and *Oxelytrum discicolle* (Group III).

#### Group V

This assemblage of species occurs in induced pastures located between 1,770 and 2,600 masl. It comprises two elements with South American affinities at the genus level. At the specific level, however, its distribution reflects the characteristics of the Mesoamerican Mountain pattern:

*Ontherus mexicanus* and *Phanaeus amethystinus*. There are also three species of *Onthophagus* which have two different distribution patterns: *O. mextexus* and *O. cyanellus* follow the Mesoamerican pattern with Paleoamerican affinities and *Onthophagus chevrolati retusus* follows the Paleoamerican Mountain Pattern (see

Discussion). This last pattern is also followed by the Geotrupine *Onthotrupes nebularum*<sup>3</sup>. *Canthon humectus sayi* corresponds to the Plateau Pattern.

*Ontherus mexicanus* was collected in pastures between 1,770 and 2,000 masl, although it has also been collected in cloud forest at 1,520 masl (MARTIN-PIERA & LOBO, 1993; THOMAS, 1993). The genus *Phanaeus* is neotropical in its phyletic affinities. There are two subgenera. The subgenus *Notiophanaeus* is principally South American with a limited expansion in the tropical forested areas of the MTZ. *Ph. endymion* belongs to this subgenus. The second subgenus, *Phanaeus* s. str., has its center of radiation in the MTZ with a notable spread into the United States. *Phanaeus amethystinus* and *Ph. tridens* belong to this subgenus. *Ph. amethystinus amethystinus* is found in mountains bordering on the East of the Central, Oaxacan and Chiapas Plateaus between 1,000 and 2,200 masl, most frequently above 1,500 masl (states of Tamaulipas, San Luis Potosí, Hidalgo, Veracruz, Oaxaca and Chiapas), according to EDMONDS, 1994.

*Onthophagus mextexus* is found in the United States (Texas), in some mountains of northeastern Mexico and in low abundance in Puebla (Teziutlan) and Veracruz (HOWDEN & CARTWRIGHT, 1963; HOWDEN, 1970). This species was collected in pastures between 1,550 and 2,000 masl. ZUNINO & HALFFTER (1988) mention that *Onthophagus cyanellus* is a species whose ancestral line reached the Central American nucleus and evolved there as a species at the same time as Mesoamerican elements with a South American origin. Later it spread to the North (the mountains of Oaxaca, the Sierra Madre Oriental to Tamaulipas) and southwards (Nicaragua, Costa Rica, Panama). In the study zone it was found in cloud forest, pine forests and their pastures between 1,300 and 2,000 masl. *O. chevrolati retusus* is a subspecies which is found in pine, oak-pine or oak forests. It sometimes is found in deforested areas and can reach the highest zones of the mountains to the East of the Transverse Volcanic System in Hidalgo, Querétaro and Veracruz. It is very abundant in the mountains and valleys of Oaxaca between 2,200 and 3,400 masl (ZUNINO & HALFFTER, 1988). In the transect, it was collected between 1,770 and 2,340 masl, with more captures in pastures. *Canthon humectus sayi*, of the Plateau Distribution Pattern, is distributed in temperate zones, but warmer ones than those occupied by *Canthon humectus humectus* (Say). *C. (c.) sayi* is found on the borders of the Sierra Madre Oriental (Veracruz) and the central valleys of Oaxaca, Puebla and Chiapas (HALFFTER, 1961). This species was captured in pastures close to pine forest between 1,770 and 2,340 masl. Of the subfamily Geotrupinae,

<sup>3</sup> In the work by HALFFTER on biogeography, the geotrupines are considered as the tribe Geotrupini, following the criteria set by HOWDEN (1955, 1964). MARIO ZUNINO (1984) not only did a taxonomic review of this entire group at the genus level, but also established phylogenetic-biogeographical affinities for the different genera. According to ZUNINO, the American geotrupines (with the subfamily level: Geotrupinae, within the family Geotrupidae) are included in the tribes Geotrupini (*sensu* ZUNINO) and Ceratotrupini. Although at present we feel that the Geotrupini of the MTZ should follow the Nearctic Pattern, the phylogenetic affinities as well as the distribution indicated by ZUNINO (*op. cit.*) for the Ceratotrupini, lead us to believe that, within the MTZ, this tribe belongs in the Paleoamerican Mountain pattern, with a great similarity to the distribution of the species of the genus *Copris* of the armatus line (see MATTHEWS, 1961; HALFFTER, 1976) and to those *Onthophagus* of the chevrolati group (see ZUNINO & HALFFTER, 1988). This was previously pointed out by MARTIN-PIERA & LOBO (1993). The Ceratotrupini are distributed in the E and SE of the Nearctic Region and in the MTZ. The genera which we cite in this study: *Ceratotrupes*, *Onthotrupes* and *Halffterius* are limited to the MTZ in their distribution.

the Ceratotruperini is made up of a series of genera from the E-SE of North America and of the MTZ (ZUNINO, 1984). The genus *Onthotrupes* is found between 2,200 and 3,200 masl, from the states of Durango and Hidalgo (Mexico) to the mountains of El Salvador and Guatemala, following the Sierra Madre Occidental, the Transverse Volcanic System, the southern Sierra Madre and the mountain ranges of northern Central America (HOWDEN, 1964). *Onthotrupes nebularum* is found in the Sierra Madre Oriental in the states of Oaxaca, Puebla and Veracruz between 1,400 and 3,000 masl. This species was only captured in Cruz Blanca, at 2,340 masl, in a pasture beside a pine forest.

In this altitudinal strip, with its characteristic vegetation type, in addition to the species of Group V the following were also collected (see Table 1): *Copris incertus* and *Onthophagus incensus* (Group IV), both Paleoamerican species with tropical distribution. *O. incensus* is associated with pastures and has the broadest altitudinal range within the transect. Four species of Silphidae were also captured: *Oxelytrum discicolle* (Group III), the nearctic species *Tanatophilus graniger* (Group VI), *Nicrophorus mexicanus* (Group VI) and *N. olidus* (Group III). In addition, once the classification of species (CS) had been completed, *Copris klugi klugi* Harold, 1869 was collected from grassland in Las Vigas (2,320 masl) and Cruz Blanca (2,340 masl). This species of *Copris* belongs (like all the MTZ species with the exception of the three tropical species *C. lugubris*, *C. incertus* and *C. laeviceps*) to the Paleoamerican Mountain pattern. Finding *C. klugi* was not a surprise, but rather an expected event.

The greatest overlap of distribution patterns occurs in the pastures of this altitudinal strip. Elements associated with high altitudes dominate, but perhaps as a result of deforestation which creates conditions that favor heliophiles, various mesoamerican, even tropical, elements move up the mountains. The result is a transition fauna which is endemic to the MTZ. Of a total of 14 species (including *Copris klugi*), six have northern affinities, one shows elements of neotropical affinity, but evolved on the Plateau, four are Mesoamerican and only three are tropically distributed. Of these three, two have Paleoamerican affinity. The other, *Oxelytrum discicolle*, which is widely distributed, is unique in following the Neotropical pattern.

#### Group VI

As we move into the pine forests, the Scarabaeinae fauna show what could be called the appearance of northern affinity (i.e., made up of species and even genera which are, for the most part, endemic), characteristic of the upper reaches of the Mexican mountains. Only Ceratotruperini, *Onthophagus* and Silphids are found. Group VI comprised *Ceratotruper bolivari*, *Onthotrupes herbeus*, *Onthophagus aureofuscus* and the Silphids: *Nicrophorus mexicanus* and *Tanatophilus graniger*.

The Paleoamerican Mountain elements include the genus *Ceratotruper* which are found in the coniferous forests (2,000-2,800 masl) of the Transverse Volcanic System, of the Sierra Madre Occidental and the Sierra Madre del Sur (HALFFTER & MARTINEZ, 1962). *Ceratotruper bolivari* is found in the states of Chihuahua, Sonora, Durango, Distrito Federal, Morelos, Querétaro and Veracruz (HALFFTER & MARTINEZ, 1962; HOWDEN, 1964). Specimens were only collected in pine forest at 2,340 masl. *Onthotrupes herbeus* is found in the states of Durango, Mexico, Morelos, Puebla and Veracruz. It was very abundant in pine forest at 2,600 masl. *Onthophagus aureofuscus* arose from the same trunk of *Onthophagus cyanellus*

(ZUNINO & HALFFTER, 1988) and has a vicariant distribution in Mexico: in the North, in the Sierra Madre Occidental (Durango), and much further to the South in the eastern part of the Transverse Volcanic System (where it was collected in pine forest at 2,600 masl) as well as in the Puebla-Oaxaca mountain range. For the Silphidae, *Nicrophorus mexicanus* extends its distribution southwards to El Salvador (PECK & ANDERSON, 1985). This species (nearctic pattern) was captured in the study transect between 1,770 and 2,600 masl, principally in pine forests (see Table 1). The genus *Tanatophilus* originated in the Old World (Eurasia) and has adapted to cold climates and high altitudes. *Tanatophilus graniger* is the only endemic species belonging to this genus in Mexico. It is found in the Distrito Federal and in the states of Nuevo León, Jalisco, Guerrero, Morelos, Puebla, Mexico, Hidalgo and Veracruz (PECK & ANDERSON, 1985). This species was collected in pastures between 1,770 and 2,000 masl and in pine forest at 2,600 masl.

In addition to the species which were included in Group VI, for this altitudinal range and in this type of vegetation the following were caught: *Onthophagus chevrolati retusus*, *O. cyanellus* and *O. mexitesus* (which were classified as Group V); *Oxelytrum discicolle* and *Nicrophorus olidus* (Group III).

## DISCUSSION

### Patterns of Insect Distribution in the MTZ

The section following this discussion (Application of the Distribution Patterns to Altitudinal Analysis) will seek to demonstrate that the distribution patterns proposed by HALFFTER are useful instruments for the analysis of altitudinal succession within the MTZ. In order to be used as instruments for biogeographical analysis, the patterns must display two key characteristics: 1) Include groups with similar evolutionary and biogeographical histories. 2) Represent similar macroecological conditions in their current distribution. The first is a historical-evolutionary requirement and the second is ecological. Both act upon a geographic matrix.

It is also important to remember the inherent characteristic of a pattern: *it is something that serves as a basis for comparison*. Patterns represent a synthesis, an abstraction of real distributions. In a way, a pattern is an average. If there was sufficient geopositioned capture data and reasonable information on phylogenetic and biogeographical affinities for the different groups of species, we would be able to synthesize the different types of distribution patterns using a series of aerographic analyses. Until these data are available, patterns must be proposed and tested with the available data (as we have done in this study).

Finally, it should be noted that the patterns proposed by HALFFTER were put forward for the analysis of a transition zone in which two flora and fauna of completely different origins not only come into contact, but also overlap as a result of a process that has lasted several million years and has occurred in a setting which, because of its orography and location within the tropics, is extremely complex.

Of the different patterns proposed by HALFFTER, the Paleoamerican meets the first of the two above mentioned requirements and concerns groups which originated in the Old World from which some phyletic lines penetrated America a long time ago. This pattern does not however meet the second requirement: that of a certain degree of unity in ecological conditions.

In America the lines which follow the Paleoamerican pattern are either the remnant of isolated penetrations, represented by species which are truly endemic or, on the contrary, are derived from lines which have been very successful and which have diversified in the MTZ under very different ecological conditions. These may have copies of genera with a northern affinity and more recent origin (those that belong to the Nearctic Pattern) in their distribution in the mountains; or in the tropics they may copy the distribution of groups with a clear South American affinity (those that belong to the Neotropical pattern), or they have formed a part of the assemblage that is highly characteristic of the MTZ and makes up the Mesoamerican pattern.

This ecological diversification can be considered a consequence of the antiquity of the Paleoamerican genera in the MTZ, and of its adaptive plasticity. Over time they have taken advantage of the different settings which the geography and ecology of the MTZ have offered. HALFFTER (1976) and ZUNINO & HALFFTER (1988) addressed this heterogeneity when they indicated the diversity of geographic and ecological conditions which the widely successful lines that make up the Paleoamerican pattern can follow.

In order to preserve the meaning originally proposed by HALFFTER (cited articles) as a distribution pattern, the Paleoamerican Pattern should be divided into the following patterns:

- The Paleoamerican Relict pattern
- The Paleoamerican Mountain pattern
- The Mesoamerican Mountain pattern (Paleoamerican elements)
- The Paleoamerican Tropical pattern

The origin of the genera or suprageneric groups in all cases is the same being in the Old World, as HALFFTER (1976) discusses in detail. The current geographical distribution is very different. In the case of the genera that have been successful in the Americas, a single genus might have lines which follow the terms of the four previously mentioned patterns, especially the latter three (for a very detailed analysis based on the *Onthophagus* of the chevrolati group, see ZUNINO & HALFFTER, 1988).

The Paleoamerican Relict Pattern includes species of genera which have a wide geographical and ecological distribution in the Old World and are represented by endemic species with a very restricted distribution in the MTZ. The aerography of this kind of species is very difficult to explain if one does not take extreme phenomena such as restriction and vicariance into account.

From the study transect, *Sisyphus mexicanus* falls into this Pattern as it has small, discontinuous populations (see Group I). The other species of *Sisyphus* which occurs in the Americas, is found in very restricted areas of the Sierra Madre Occidental (Durango and Sinaloa) and of the Transverse Volcanic System (HOWDEN, 1965; HALFFTER, 1976). This genus has many abundantly represented species widely distributed in the Old World.

The Paleoamerican Mountain Pattern includes those Paleoamerican lines which have colonized the Mexican mountain ranges and, to a lesser extent, those of Central America. These lines have undergone significant speciation, determined in the majority of cases by clear vicariance processes (see HALFFTER, 1987; ZUNINO & HALFFTER, 1988).

In our transect the Ceratotrumpini showed this type of distribution, as did *Onthophagus chevrolati retusus* and *Copris klugi klugi*. In addition, other species of *Onthophagus*, *O. hippopotamus* Harold, 1869 and *O. chevrolati chevrolati* Harold,

1869 (MARTIN-PIERA & LOBO, 1993; LOBO and HALFFTER, 1994), as well as a Ceratotruperini species *Halffterius rufoclavatus* (Jekel, 1865 (ARELLANO, unpublished data) occur in the same area, but at a higher altitude (2,900-3,100 masl) than that included in the transect.

Some species of Paleoamerican lineage very characteristic of the MTZ (see ZUNINO & HALFFTER, 1988) are included in the Mesoamerican Mountain Pattern. It must be remembered that this pattern can also include species with neotropical affinity (see HALFFTER, 1978). In the transect, *Onthophagus cyanellus* and *O. mextexus* belong to the Mesoamerican (of Paleoamerican origin) distribution.

The Paleoamerican Tropical Pattern includes distributions which follow the tropical conditions typical of the lowlands and moderate altitudes. These distributions may copy those that correspond to the Neotropical pattern in its geographic limits, while being completely different in terms of phylogeny and evolution. Species demonstrating the Paleoamerican Tropical Pattern belong to Old World genera that have been successful in the MTZ, where they have colonized the tropics with exclusive lines (precisely those that show the Paleoamerican Tropical Pattern). The presence of some of these species at moderate altitudes in the mountains can be considered as a colonization equivalent to that of some tropical species, favored by the same orographic and ecological factors: protected ravines, local humidity, little or no frost, etc., as is the case with *Onthophagus incensus*. On the transect various species of *Onthophagus* and *Copris* follow the Paleoamerican Tropical pattern.

*Digitonthophagus gazella* provides a model for how tropical Paleoamerican lines could have expanded. This Afro-Asiatic species was introduced to Texas in 1972 and, a few years later, to California. *D. gazella* has spread rapidly (see BARBERO & LOPEZ-GUERRERO, 1992; KOHLMANN, 1994). It currently occupies the coastal plains on the Gulf Slope, down to Chiapas and the Peten (Guatemala). It also occupies the coastal plains of the Pacific, and has moved inland to the Balsas Depression. This species has also reached the central-eastern zone of the Mexican Plateau and the tip of the Baja California Peninsula (something that is not seen in the tropical Paleoamerican lines). *D. gazella* inhabits open vegetation formations and, as such, its spread has been favored by the deforestation of the Mexican tropics resulting from the creation of induced pastures for cattle ranching. This species is a coprophage with a marked preference for cow dung.

In June of 1993 we were able to demonstrate that in Palenque, Chiapas, *D. gazella* which is numerous in sunny pastures with abundant cow dung does not enter the evergreen tropical forest. In our transect, this species was included in Group II. It was not collected in either deciduous or semi-deciduous forests, nor is it found above 1,000 masl.

#### **Application of Distribution Patterns to Altitudinal Analysis**

In answer to the first question asked (see Introduction), relief and overlap of fauna along the altitudinal gradient is similar to that proposed by HALFFTER for latitudinal gradients. According to HALFFTER (1976), as one moves to higher latitudes, tropical elements become more scarce as do nearctic or Paleoamerican mountain elements, as one moves to lower latitudes in the MTZ. There is a clear relationship between this finding and the altitudinal gradient: greater numbers of tropical species at lower altitudes and greater numbers of species of nearctic and Paleoamerican mountain affinity at higher altitudes.

This replacement also occurs in the families included in this study. Between sea level and 1,200-1,350 masl only Scarabaeinae were found. The Silphids appear at the previously mentioned altitudes, but are more abundant above 1,770 masl. The Ceratotruperini appear at 1,770 masl and dominate the highest segments of the transect.

At the species level, Group I comprises 75 % Neotropical Pattern species and 25 % Paleoamerican-tropical species (see Table 2). Group II, at the same altitudes (450 - 1,100 masl) but in pastures, is much less rich in species but has a similar biogeographical composition. Neotropical elements of minimum penetration (those most similar to Central and South American fauna) are only found in the forest (Group I).

If these data are compared with those presented by HALFFTER *et al.*, (1992) for two other areas in the state of Veracruz (see Fig. 1) located at a lower altitude of the transect, similar situations are found. These two areas are Laguna Verde, which could be considered an extension of the transect (40 masl) with a landscape that is a mosaic of patches of tropical forest dominated by induced pastures; and Los Tuxtlas (200 masl), the nearest site with evergreen tropical forest.

Of the three families studied, only Scarabaeinae were found at Laguna Verde and at Los Tuxtlas. This was the same as for the lower part of our transect [specimens of *Oxelytrum discicolle* were collected on the Santa Martha Volcano but at 850 masl (M.A. MORALES, com. pers.)]. At Laguna Verde there were 18 species in both pastures and patches of forest (5 species), compared to 17 species (see Table 1) for the transect, joining the forest fauna with that of the pastures (for Laguna Verde, in addition to HALFFTER *et al.*, 1992, see MONTES DE OCA & HALFFTER, 1995). Species composition is very similar, although some transect species are replaced by vicariants. For example, *Onthophagus incensus* is replaced in Laguna Verde by *O. batesi*, and there are two species of *Phanaeus* in Laguna Verde that are not found at the lowest altitudes of the transect. The most interesting point for our analysis is that the proportion between species of neotropical and Paleoamerican-tropical distribution is the same (3:1) in the two areas compared.

In Los Tuxtlas the Scarabaeinae fauna are much richer since there are 24 species in forest alone<sup>6</sup>. The proportion of neotropical to Paleoamerican tropical elements changes to 7:1, but, in addition, the percentage of neotropical species with minimum penetration increases considerably (66 % of the total). The neotropical character is much more marked (HALFFTER *et al.*, 1992).

The presence of species such as *Sulcophanaeus chryseicollis* Harold, 1863 in Los Tuxtlas and in Laguna Verde at altitudes of 650-680 m, but not in the corresponding area of the transect is interesting. There are other examples (*Dichotomius satanas*, *Phanaeus endymion*, *Onthophagus rhinolophus* Harold, 1869, *O. igualensis* Bates, 1887) which indicate that in central Veracruz the altitudinal distribution of several neotropical species is controlled by local orography and the influence of this factor on microclimate (see Fig. 3), which in turn determine the probability of finding rain forest within protected canyons at higher altitudes. In the study transect, the true overlap of fauna begins in the ecosystems located between 1,300 and 1,530 masl (Groups III and IV). Elements of different affinities overlap

<sup>6</sup> LOBO & MORON (1993) indicate 32 species for Los Tuxtlas, adding together those species found during two capture periods which are separated by a lapse of several years. This number includes the majority of forest species, but also some which are particular to pastures and to secondary formations that are close to the forest (at least 5).

at these altitudes (see Table 2). This altitudinal range was originally occupied by cloud forest. This type of forest still survives in patches, with varying degrees of disturbance, on steep slopes, in gullies and in other sites that are difficult to reach. RZEDOWSKI (1978) describes the altitudinal and climatic characteristics of this forest, as well as its distribution in Mexico. Biogeographically, it is a remarkable vegetation type since it has species –mostly trees– which also exist (or closely related species) in the eastern United States and Canada. These trees tend to be dominant and give the forest its typical physiognomy. Quantitatively the elements of meridional affinity are greater, with a good number of species in common with the Andes region of South America. In these plants, endemism at the genus level is scarce, although the number of species with a limited geographic distribution found in cloud forest is not insignificant (RZEDOWSKI, 1978).

LUNA *et al.* (1988) studied this type of forest in the area of Teocelo, Veracruz, which is both very close and similar to our transect. Specifically for this area of central Veracruz they found that the tropical element (not only neotropical) is the element best represented in all strata and quantitatively is the most important (79 %). Elements of holarctic origin are absent from the shrub flora, poorly represented in the herbaceous layer, and account for 20 % of the tree stratum. LUNA *et al.* (*op. cit.*) insist on the heterogeneity of the biogeographical affinities found in this forest.

With respect to the fauna, LLORENTE-BOUSQUETS & ESCALANTE-PLIEGO (1992) analyzed endemism in butterflies and birds in this type of forest. According to LUNA & LLORENTE-BOUSQUETS (1993) in Omiltemi, Guerrero State, Mexico, in the Southern Sierra Madre, the cloud forest has a greater number of vascular plants, fungi, butterflies and mammals than other montane forest. Only for birds, amphibians and reptiles is its species richness surpassed by the oak-pine forest.

THOMAS (1993:363) in a study of the fauna of the state of Chiapas indicates: «The cloud forest had far fewer species represented than the other forest types. However, the cloud forest had the highest proportion (30 %) of regional endemics». For his study THOMAS used all the Scarabaeidae considered to be one of three families of the Scarabaeoidea, (the others are Lucanidae and Passalidae). If the Melolonthidae (which were part of THOMAS's study) had been included in this study's analysis, the conclusions might have been similar (see MORON, 1983; 1991). In their study of Scolytidae and Platypodidae (Coleoptera) in cloud forest in the region of Xalapa, Veracruz (see Figs. 1 - 2), NOGUERA-MARTINEZ & ATKINSON (1990) indicated that more than 60 % of the genera found were predominantly neotropical, although they were not the same fauna as those inhabiting tropical lowlands. At the species level, cloud forest shares elements with forests of both higher and lower altitudes, but many of the species are restricted to this type of forest in Mexico and Central America.

In the altitudinal range that corresponds to cloud forest and derived ecosystems (see Groups III and IV in the Results section), 16 species we found. Two of these (*Nicrophorus olidus* and *Onthophagus cyanellus*) correspond to northern affinity patterns, five are exclusive to this altitudinal range and the others are tropical species that reach at this altitude. In spite of the well-defined characteristic of the transition level, the tropical characteristic dominates markedly.

At the next altitudinal level (1,770-2,600 masl) no species correspond to the Neotropical Pattern except *Oxelytrum discicolle*, which is a very widely distributed. There is an overlap of affinities in the pastures (Group V) which extends the area

of transition beginning at the lower altitude. Of the 14 species found in these pastures (Table 1 and *Copris klugi*), four correspond to the Mesoamerican Pattern, one to the Plateau, three to the Paleoamerican Mountain pattern and three the Nearctic Pattern. Only three are tropical in their distribution, including two species of the Paleoamerican Tropical pattern, and only one Neotropical (the aforementioned *O. discicolle*). The transitional character of the level is very marked, but unlike at the lower altitude there is a dominance of elements with a northern affinity (10), whereas there are only four with a South American affinity (and of these, only three at the genus level). The greater species richness of these pastures, in comparison to that of lower altitudes, stems from the appearance of nearctic elements, Mesoamerican elements (*Ontherus mexicanus* and *Phanaeus amethystinus*) as well as Plateau elements (*Canthon humectus sayi*) with South American affinity at the genus level.

At the same altitudinal range the oak-pine forests (Group VI) are inhabited by a fauna typical of the high mountains of Mexico: two nearctic species and three Paleoamerican Mountain species, in addition to five elements that were assigned to other groups (see Tables 1 - 2). Of these last elements, two (*Onthophagus cyanellus*, *O. mextexus*) correspond to the Mesoamerican Pattern with Paleoamerican affinities: *Onthophagus chevrolati reusus* to the Paleoamerican Mountain pattern; a fourth species (*Nicrophorus olidus*) is nearctic and was assigned to Group III; and the fifth is a widely distributed species (*Oxelytrum discicolle*). Northern elements dominate in the pine-oak forest. In the MTZ the distribution of these elements tends to follow that of mountain forests.

If we ascend higher than the upper limit of the study transect, between 2,500 and 3,000 masl we find *Onthophagus aureofuscus*, *O. chevrolati chevrolati* Harold, 1869 (MARTIN-PIERA & LOBO, 1993), *Megatrupes fisheri* Howden, 1967 and *Halffterius rufoclavatus* (LOPEZ-GUERRERO & L. ARELLANO, unpublished data), all four of which are species with the Paleoamerican Mountain distribution pattern. At these altitudes the Aphodiinae, specifically the genus *Aphodius*, become abundant. A third species of *Onthophagus*, (*O. hippopotamus*), is found at 2,900 to 3,100 masl in gopher burrows (Rodentia: Geomyidae) in addition to two other species of *Aphodius* (LOBO & HALFFTER, 1994).

For 3,000 masl, MARTIN-PIERA & LOBO (1993)<sup>7</sup> cite the first two species of *Onthophagus* mentioned in the previous paragraph, as well as *Onthotrupes herbeus* (which also correspond to the Paleoamerican Mountain distribution pattern), three species of *Aphodius*, and the silphid *Tanatophilus graniger* which is found between 2,400 and 3,500 masl. To this fauna we must also add the species found in gopher burrows. The same species of Scarabaeinae and Geotrupinae are found at these altitudes in both pastures and pine forests, although the number of individuals is lower within the forest. Different species of *Aphodius* are found in the pastures and in the forests.

MARTIN-PIERA & LOBO, (1993) point out an impoverishment of Scarabaeoidea fauna in the mountains of Mexico, specifically in the area of the study transect. They generalize this observation for tropical mountains, using comparisons with the situation in Spain. This point should be treated with caution. The articles by HANSKI (1983) and HANSKI & KRIKKEN (1991) cited by the authors in support of their generalization provide no real support of it. In 1983, HANSKI's

<sup>7</sup> For an analysis of the Nearctic Pattern see MARTIN-PIERA & LOBO, 1993. For information on Carabidae which follow this pattern see LIEBHERR, 1994 a and b.

work focussed on Mount Mulu (Sarawak, Borneo), the upper reaches of which has a low number of Scarabaeoidea species, a decrease he associated (as compared to lower altitudes) with the reduced size of the montane area (also see HANSKI, 1989). Mount Mulu is isolated in a world of tropical forest. In the same region, when the mountains form part of a range, the number of species is greater (see HANSKI, 1983; HANSKI & KRIKKEN, 1991).

In the tropics there appear to be two types of situation. When a mountain is recent and isolated from other mountains, at higher altitudes the Scarabaeoidea fauna can be reduced or non-existent. This is a phenomenon resulting from insularity. As such, HALFFTER & P. REYES-CASTILLO (unpublished data) found no copronecrophagous Scarabaeoidea in the high zones of the Talamanca Mountains (Costa Rica). This mountain range is young in geological terms (end of the Cenozoic) and is isolated. This is not the case for extensive, well-connected mountain ranges where a) the fauna come from temperate zones [for the Andes see the case of *Scybalophagus* (HALFFTER & MATTHEWS, 1966: 85-86; HALFFTER & MARTÍNEZ, 1968: 257-258)]; or b) the tropical fauna has had time to colonize higher up in the mountains [*Uroxys* in the Andes of Venezuela at 4,000 masl (HALFFTER, unpublished data); see several other examples in HALFFTER & MATTHEWS, 1966: 85-86].

In the MTZ in particular there is no vacuum of Scarabaeoidea fauna in the mountains. The Results section and Table 1 indicate that the numbers of species with a tropical affinity or distribution (Neotropical and Paleoamerican Tropical patterns) decrease above 1,750 masl and disappear higher up. However in the mountains of Mexico there is a replacement of fauna that is characteristic of the MTZ. Lines of northern affinity that follow the Paleoamerican Mountain and Nearctic Patterns appear. The Ceratotruperini, Nicrophorini, *Aphodius* and some Scarabaeinae of northern affinity are found on the same resources that the Scarabaeinae dominate at low and moderate altitudes. Although the number of species and individuals is generally lower in the mountains of Mexico than in the humid tropics, it is not possible to speak of a vacuum in the copronecrophagous Scarabaeoidea fauna. What is evident is that the very particular conditions characteristic of the Central Iberian Range (Cordillera Central Ibérica) (LOBO, 1992; MARTIN-PIERA *et al.*, 1992) or the French Alps (LUMARET & STIERNET, 1991) do not exist in the mountains of Mexico. In these Spain and France mountains, cattle and sheep use the pastures in the warmth of summer and this, combined with biogeographical and historical factors, allows beetle fauna normally associated with colder conditions to survive. Consequently Scarabaeoidea fauna flourish.

#### **Changes in distribution resulting from human activities**

In the study gradient, part of the forested area has been replaced by pastures and coffee plantations (the latter at cloud forest altitudes). On comparing the species collected in the forests and in areas of induced vegetation, notable differences were found.

From the biogeographical perspective (taking into account the number and types of distribution patterns) both tropical forest and tropical pasture had Neotropical and Paleoamerican tropical species; but neotropical elements with moderate and high penetration were found in greater numbers in pastures and open formations (Table 2).

At cloud forest altitudes, there were four different distribution patterns in the forest but only two in pastures at the same altitudes (Table 2). In contrast, in

cold-temperate pastures there was a greater number of patterns than in pine forest (Table 2).

In the altitudinal sequence of original forest, the greatest degree of overlap occurred in cloud forest. However, if we follow the pastures that have resulted from human activities, this area of overlap between elements of tropical affinity and those of northern affinity extends upwards to an altitude equivalent to that at which pine forest occurs. Hence, having followed the pastures, *Ontherus mexicanus* is found at altitudes of 2,000 masl.

Analysis shows that species richness was greater in tropical forest and cloud forest than in pastures and coffee plantations [at the same altitudes] (Fig. 5), while pine forest had fewer species than pasture [at the same altitude]. In original forests, species richness decreased at higher altitudes.

There are several parameters to consider from an ecological perspective: dominance and species shared between ecosystems occurring in the same altitudinal range, as well as resource partitioning in the different ecosystems.

The structure and composition of the beetle guild in forests was different from that of the pastures and coffee plantations. Of the Scarabaeoidea, *Deltochilum gibbosum sublaeve* and *Coprophanæus telamon corythus* (two necrophagous species) dominated (based on biomass) in low tropical forest while in pastures

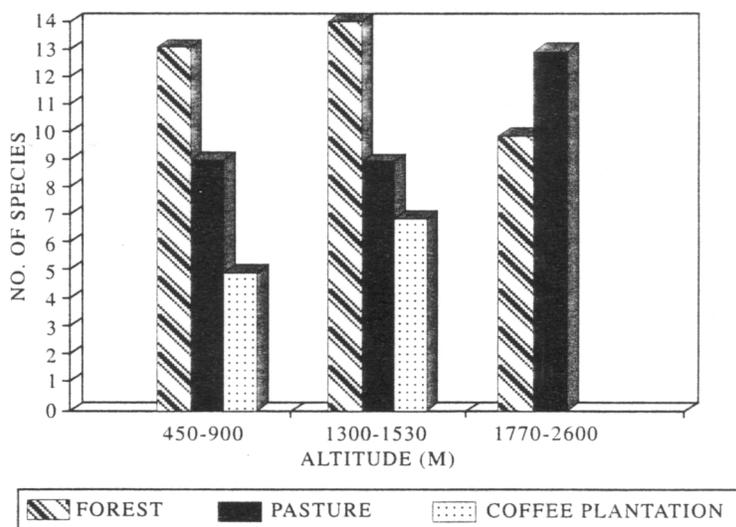


Fig. 5: Species richness (Scarabaeinae, Geotrupinae and Silphidae) in the different types of ecological formations of the three altitudinal segments of the transect.

neighbouring this forest, the dominant species were *Dichotomius carolinus* and *Copris lugubris* (two clearly coprophagous species). *C. t. corythus* dominated in coffee plantations at 1,110 masl. In cloud forest the dominant species were *C. t. corythus* and *Dichotomius satanas*, while in pastures bordering cloud forest the dominant species were *C. t. corythus* and *O. incensus*. In coffee plantations at medium altitudes the dominant species was *Dichotomius satanas*. In pine forest the dominant species was *Onthophagus mextexus*. However in neighbouring pastures *O. incensus* and *O. retusus* were dominant. For each altitudinal segment the dominant species in the forest were different from those dominant in the pasture. The exception is *Coprophanes telamon corythus* which was widely successful in both types of ecosystems up to moderate altitudes.

There were several species which were collected both in original and in induced vegetation (pastures and coffee plantations). In total (including Geotrupinae and Silphidae) between 450 and 900 masl 17 species were collected, 29.4 % of which were collected in both vegetation types. Between 1,300 and 1,530 masl, of a total of 16 species, 43.8 % were captured both in cloud forest and in pastures. From 1,770 to 2,600 masl, of a total of 16 species, 43.8 % were collected both in pine forest and in induced pasture.

Food use in Scarabaeoidea varied with vegetation type. In tropical forest and in cloud forest there were beetles that were generalists, coprophages and necrophages in similar proportions (Fig. 6). Pine forest had a greater proportion of coprophages than generalists, and only one necrophage. In tropical and high mountain pastures coprophages were more abundant than generalists, while in pastures close to cloud forest the opposite was true. Necrophages were not found in any pasture (Fig. 6). Burrower beetles were always more abundant than rollers in original forests and in tropical pastures. Nevertheless, rollers were very important in tropical forest. No rollers were found in pastures near to cloud forest or within pine forest. In the pastures of the highest altitudinal strip a few rollers were present (Fig. 6).

In the tropical forest, nocturnal beetles were more abundant than those active during the day, but the opposite was true in the pastures (Fig. 6). HALFFTER *et al.* (1992) found similar results. In both cloud forest and the accompanying pastures, nocturnal beetles dominated. There were no diurnal beetles in the pine forest, but in the neighbouring pastures there were.

To explain these differences in beetle fauna between undisturbed ecosystems and those which have been modified by humans, it is useful to recall what we expect in terms of the fauna-vegetation relationship for these three altitudinal segments, and the ways in which they have been altered.

In the low tropical zone, the dominant vegetation before human intervention was tropical forest (low and medium deciduous tropical forest) with a certain component of open formations. With the occurrence of deforestation for agricultural and ranching activities (the first dating back to early Prehispanic times) the possibilities for species adapted to open ecosystems (heliophiles) increased for a group of fauna that was already present. Furthermore, expansion in a generally North-South direction (and vice versa) for this type of species has been, and continues to be, very easy as there are no biogeographical barriers as long as they go no further than the altitudinal limits for this type of distribution. Clear evidence of this is provided by the current expansion of *Digitonthophagus gazella* (see Discussion: Distribution patterns of insects in the MTZ). In contrast, species which are strictly of the forest have been restricted by the drastic reduction in available habitat (see HALFFTER *et al.*, 1992 for an analysis of this phenomenon).

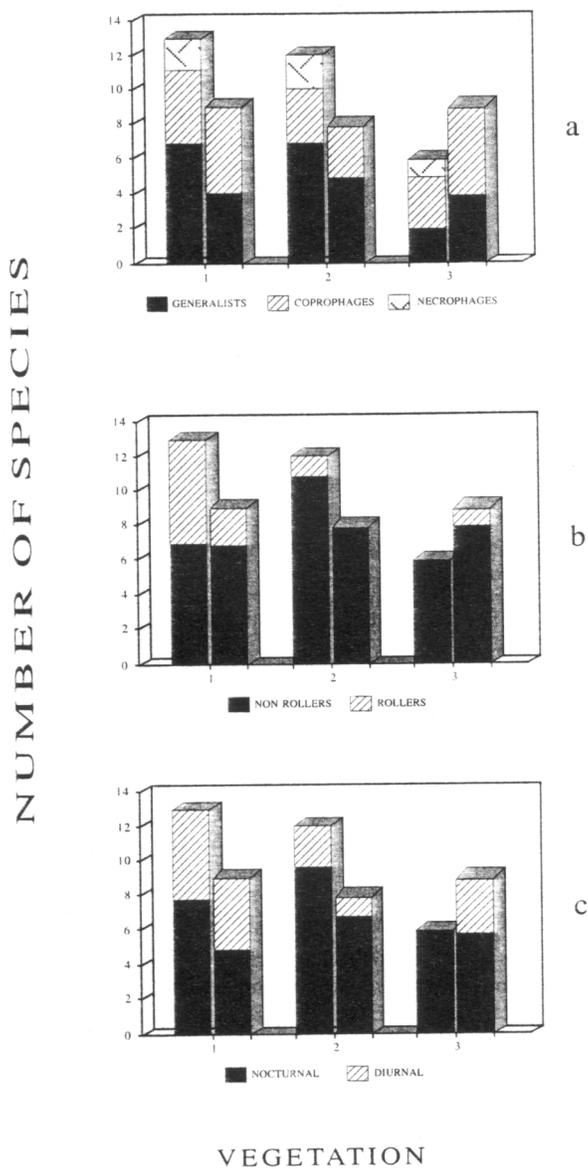


Fig. 6: Ecological organization of the Scarabaeoidea (Scarabaeinae and Geotrupinae) in the three altitudinal segments of the transect: 450 to 1100 masl; 1,300 to 1,530 masl; 1,770 to 2,600 masl. At each level the column on the left represents the forest ecosystem and that on the right, the pastures. Food preferences are indicated in «a». Food relocation methods is indicated in «b». Daily activity cycle is indicated in «c».

At medium altitudes the dominant vegetation was cloud forest and other similar forests (such as oak forest). Historically, these are areas that were occupied by Prehispanics, but never to the same extent as the lowlands of Veracruz. The transformation of the forest into cattle pastures and coffee plantations is a phenomenon that began in the XVIII century and became truly widespread in the XIX century (GONZALEZ DE COSSIO, 1957; PASQUEL, 1959; PRIETO, 1875; SCHIEDE, 1968; RODRIGUEZ, 1970; GARCIA, 1986). Currently, these activities are expanding and consequently the remaining forests are dwindling.

In this altitudinal strip there is no open ecosystem fauna that has evolved *in situ*. The altitudinal climatic zoning has been –in general terms– a barrier, and more so for tropical fauna from deforested areas moving upwards than for the descent of fauna adapted to high mountain pastures (Table 1). The pastures of the intermediate zone have been colonized by the most opportunistic elements from the cloud forest. Even so, there are notable absences, such as that of roller Scarabaeidae in pastures where dung is abundant.

The absence of coprophagous roller Scarabaeinae in the intermediate altitudinal zone is an interesting ecological and biogeographical phenomenon. At these altitudes the only roller captured in the transect was *Deltochilum mexicanum*, a species which is primarily necrophagous, exclusive to the forest and not abundant. Given the abundance of cow dung in this intermediate zone, an open formation roller coprophage is lacking (a *Canthon*). In comparison, the tropical lowlands had five species (of which *Canthon indigaceus chevrolati*, a coprophage common to open areas, is abundant). In the highest altitudinal strip there was a single species *Canthon humectus*, also a coprophage, which is abundant and common to open ecosystems.

In the highest segment of the transect, the presence of clearings and pastures with their own fauna is, as for the low tropical zone, an historical phenomenon (RAMIREZ, 1971; MELGAREJO, 1980; GEREZ, 1983). Deforestation, which has continued into the XX century and even more so in recent years, has created more possibilities of expansion for species adapted to heliophile conditions, such as a species of tropical phylogenetic origin (*Onterus*).

## CONCLUSIONS

The answer to the first of the three research questions posed in the Introduction is that the latitudinal distribution pattern of fauna typical of the MTZ is reproduced for altitude, and is better defined. For the groups and the transect studies, only species within the Neotropical or Paleoamerican Tropical patterns are found at lower altitudes. The altitude at which the overlap of different patterns is greatest is that originally occupied by cloud forest. At higher altitudes, although elements of northern affinity definitely dominate, there are some elements with an affinity (at the generic level) to Neotropical fauna.

The same phenomenon which is found at the level of pattern is found in the suprageneric taxa. Only the Scarabaeinae are found at the lowest level; at the intermediate level the Silphidae appear; and this latter family and the Geotrupinae dominate at the highest levels, with the appearance of coprophagous Aphodiinae, represented by *Aphodius*, a genus with clear northern affinities (For more on the presence of *Aphodius* at high mountain altitudes see LUMARET & STIERNET, 1991).

With respect to our second question, the altitudinal limits of the different patterns and of the species and suprageneric groups that fit them are detailed in the Results and Discussion sections. It is important to take phenomena such as anthropogenic vegetation change (see Discussion), mountain slope orientation and its climatic consequences into account. These may favor in one way or another the altitudinal displacement of the areas of distribution of species.

Although the altitudinal bands are fairly precise, they are not perfectly horizontal.

In response to our third question, the effects of human activities are evident. These create a certain vacuum in the pastures that were once cloud forest. Deforestation favors the upward expansion of species of tropical origin (heliophiles) (see Discussion).

Our general conclusion is that patterns of distribution are useful for the analysis of complexes of fauna in transition zones. The use of these patterns permits hypotheses based on the phylogenetics and distribution of species assemblages to be established. In turn, these hypotheses can be tested against actual capture and distribution data. Thus it is possible to arrive at conclusions and to have discussions (THOMAS, 1993; MARTIN-PIERA & LOBO, 1993) which eliminate the exclusively descriptive nature of analyses of fauna.

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