

ALTITUDINAL DISTRIBUTION PATTERNS OF COPRO-NECROPHAGE SCARABAEOIDEA (COLEOPTERA) IN VERACRUZ, MÉXICO¹

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ABSTRACT

Patterns of altitudinal distribution of copro-necrophage scarabaeoid communities on a subtropical mountain of the Mexican Transition Zone (Volcanic Transverse Belt, Veracruz) are compared with those of a Mediterranean cordillera (Central Iberian System). The influence of vegetation on community structure was also checked. It was found that the number of species decreases and the copro-necrophage scarabaeoid community structure undergoes modification as altitude increases. Although the number of species was small, altitudinal segregation in the Mexican Transition Zone is like that in the Central Iberian System (Aphodiidae and Geotrupidae at higher altitudes, Scarabaeidae at lower ones). Anthropogenic fragmentation and transformation of primary forests in subtropical areas (mountain mesophilous and conifer forest) result in a qualitative and quantitative change in the structure of communities. This phenomenon is attenuated in mountain forests by the impoverishment of fauna due to the increase in altitude.

Coprophage Scarabaeoidea families in the Central Mountain System of the Iberian Peninsula are segregated according to altitude, largely due to historical causes. The distribution with elevational gradient of these taxa is effectively a present-day ecological response to the environmental conditions that reigned in their hypothetical ancestral areas (Martín-Piera *et al.* 1993).

Distribution related to altitude of insects in tropical areas has also been investigated (Janzen *et al.* 1976 and Wolda 1987), but there are few data for the tropical copro-necrophage Scarabaeoidea that bear causal explanations like those proposed by Martín-Piera *et al.* (1993) for the Iberian Peninsula.

The Dispersal-Pattern concept of Halffter (1976) has gained acceptance among descriptive Scarabaeoidea biogeographers. This concept is based on Reig's (1962, 1968) concept of Coenochron: "an animal or plant group or community, whatever its origin, which enters into a given area between definite limits of geological time." In its original version, the dispersal pattern corresponded to the present-day distribution of a coenochron (Halffter 1972). Both concepts are used to deal with dispersion that took place during a certain geologic period, with its own particular ecological and geographical setting (see also Halffter 1962, 1964, 1972, 1976, 1978, 1987).

The environmental and biological diversity that co-occurs with the elevational gradient in the Mexican subtropical zone (Rzedowski 1981) enables

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² The order of appearance of the author's names was established at random.

organisms belonging to different dispersal patterns to coexist within this geographic area. The superposition of fauna representative of different dispersal patterns in the Mesoamerican area (Halffter 1976) has been the essential feature of the Mexican Transition Zone concept. This concept has also been applied to the Chinese Transition Zone and the Euro-Mediterranean area (Zunino 1984, 1985). As the transition zones are areas that contain a mixture of species representative of different dispersal patterns, one would expect that variation in fauna as a function of altitude is a reflection of regional changes in fauna due to historical causes. To a certain extent, the cordilleras are regional transition zones within geographic transition zones. Thus mountain chains in transition zones have come to be seen as natural "laboratories," ideal for testing the causal explanation proposed by Martín-Piera *et al.* (1993).

Taking these ideas as working hypotheses, altitudinal distribution patterns of copro-necrophage Scarabaeoidea in a cordillera of the Mexican Transition Zone (Veracruz) were studied to establish a comparison with altitudinal distributions observed in the Central Iberian System.

The influence of vegetation on the structure of copro-necrophage scarabaeid communities was also analysed. The aim was to determine if the differences found by authors in tropical areas (Howden and Nealis 1975; Peck and Forsyth 1982; Klein 1989) hold in subtropical areas (mesophilous mountain forest) and in mountainous areas (coniferous forest of *Pinus* and *Abies*).

METHODS

Six sampling stations at altitudes from 1,500 to 4,000 m were chosen on the eastern slopes of the Transverse Volcanic Belt in the state of Veracruz, México. The sampling stations were: Banderilla, 1,500 m altitude (U.T.M. Coordinates: 14QQS1566); Acajete, 2,000 m (U.T.M.: 14QQS0766); Sierra del Agua 2,500 m (U.T.M.: 14QPS9167); Los Pescados 3,000 m (U.T.M.: 14QPS9463); El Conejo, 3,500 m (U.T.M.: 14QPS9358), and El Cofre de Perote, 4,000 m (U.T.M.: 14QPS9456). As a check on the reliability of the sampling, the first three stations were chosen to coincide with the last three of a prior transect (Arellano 1992), which had its highest station on Sierra del Agua (2,500 m).

Four pitfall traps (sampling units) of proven efficiency (Lobo *et al.* 1988; Veiga *et al.* 1989) were placed at each of the stations. Two of the traps were in forest habitat and two in open areas (at lower elevations, in livestock pastures named "potreros"; at higher elevations, in alpine meadows named "zacatonales"). Taking into account the copro-necrophage habits of the tropical fauna of Scarabaeoidea (Hanski 1989), one trap of each pair was baited with 200 gr of fresh cow dung and the other with 100 gr of squid. The forest habitat of the stations at 1,500 m and 2,000 m consisted of groves of mesophilous mountain forest ("acahuales"); that of the remaining stations, coniferous forests of *Pinus* and *Abies*.

The transect was made up of a total of 24 pitfall traps (sampling units), located in pairs, in 12 habitats (samples) placed in 6 sampling stations. The traps were left in the field from July 9 to 12, 1991. The timing of this study took into account the data from other studies (Morón and Terrón, 1984) and the recommendations of the research staff of the Instituto de Ecología of Xalapa.

To determine the influence of vegetation on the structure communities, complementary sampling was done from July 17 to 19, but only in the Banderilla (1,500 m) and los Pescados (3,000 m) stations. At both stations, 4 groups

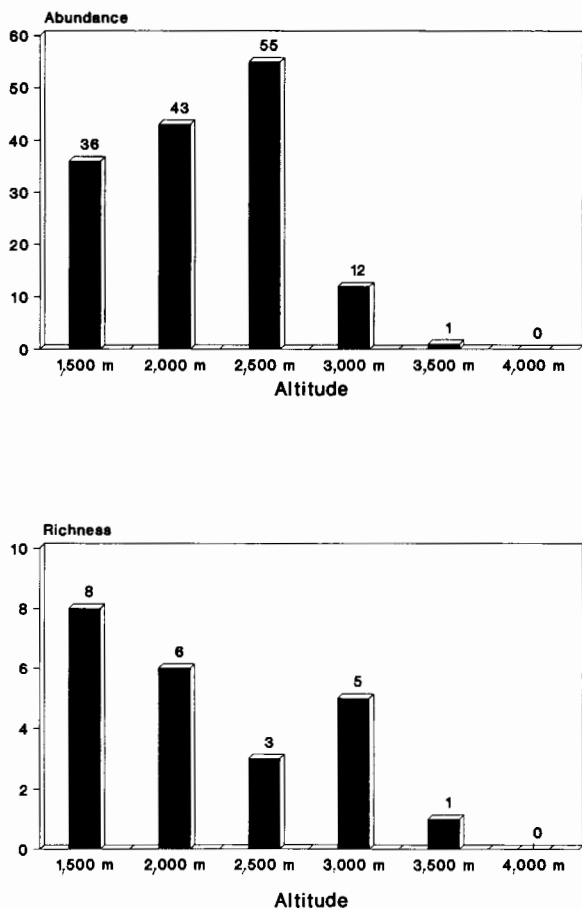


Fig. 2. Altitudinal variation in the richness and abundance of copro-necrophage Scaraboidea in the "Banderilla"- "Cofre de Perote" transect, Veracruz, México.

of 3 traps were set; two groups were placed in forest (3 traps baited with fresh cow dung and 3 with squid), and 2 in pastures, similarly baited. Unfortunately, the squid was stolen, probably by small vertebrates, from eleven of the twelve traps; so from this second sample period only the traps baited with cow dung (three in forest and three in open areas) provided samples used in the study.

RESULTS

Specimens (147) of 18 species were collected from the altitude transect (Fig. 1). In general terms, the number of species caught (richness), and the total abundance (number of specimens), was notably lower at stations of greater elevation (Fig. 2). However, total abundance was greater in Sierra del Agua (2,500 m), due to the dominance of *Onthophagus aureofuscus* Bates. No species

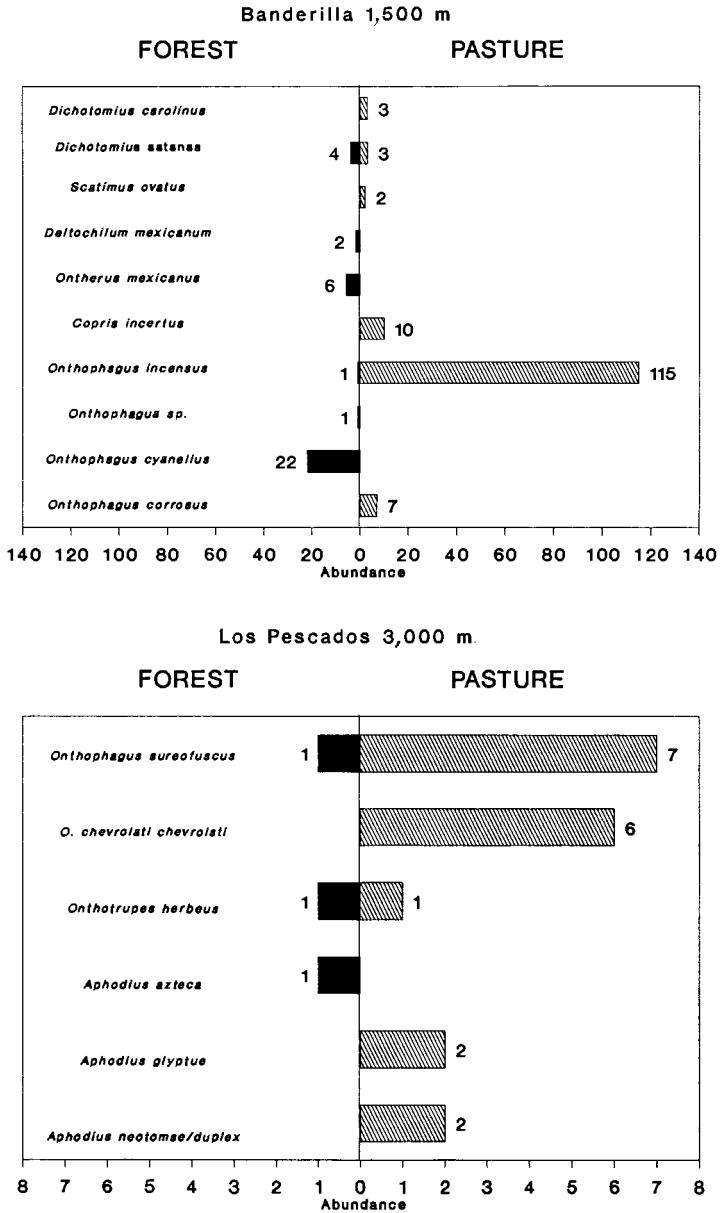


Fig. 3. Relative abundance and richness of copro-necrophage Scarabaeoidea in "Banderilla," (mesophilous mountain forest ["acahuales"]) and livestock pastures ["potreros"] and "Los Pescados" (coniferous forest and alpine meadows ["zacatonales"]), Veracruz, México.

of Scarabaeoidea was captured in Cofre de Perote (4,000 m), and only one species of *Aphodius* was captured in the second-highest station, El Conejo (3,500 m).

These results improve the sampling of Arellano (1992; unpublished data) carried out in the same region, where 480 feces samples were examined by hand, and 1,140 pitfall traps of two models were used. So, Arellano's study amounts to 1,620 sampling units (SU). Since we only use 24 SUs (see Methods), one notes a major difference in the average of specimens/SU: 0.75 (1,222 spcm./1,620 SU, Arellano), as opposed to 6.12 (147 spcm/24 SU; current study). From the common stations (Banderilla and Acajete), the richness obtained in both samplings turned out to be very similar: there were 11 species from Banderilla, 6 species from Acajete (Arellano); 8 and 6 in the present study. Likewise, the average of species/SU is very different for both studies: 11 spp./372 SU = 0.03 at Banderilla, and 6/372 = 0.01 at Acajete (Arellano); 8/4 = 2 at Banderilla and 6/4 = 1.5 at Acajete (current study).

The taxonomic composition of the communities varied with elevation. All of the species captured at the lowest altitude station belong to the family Scarabaeidae (Fig. 1). Two species of Aphodiidae and four species of Scarabaeidae were collected at 2,000 m; the latter family dominated numerically. Only one species of Geotrupidae and two species of Scarabaeidae were caught at 2,500 m, and the latter was again numerically dominant. However, three species of Aphodiidae, one species of Scarabaeidae and one species of Geotrupidae were captured at the 3,000 m station. The only specimen captured at 3,500 m was an aphodiid. Species belonging to the Neotropical genera of the tribes Dichotomiini (*Dichotomius*) and Canthonini (*Ontherus*, *Scatimus* and *Deltochilum*), and the only representative of the tribe Coprini (*Copris*) disappeared at elevations greater than 2,000 m, and were replaced by Paleo-American elements of the tribe Onthophagini (*Onthophagus*). Some species of *Onthophagus* belonging to the *O. chevrolati* group occurred with the Aphodiidae and Geotrupidae, above 2,500 m.

The complementary sample, taken only from Banderilla (1,500 m) and Los Pescados (3,000 m) consisted of a total of 149 specimens and revealed the presence of one more species of *Onthophagus*, in Banderilla probably one of Boucomont's (1932) "group III." Taking into consideration the set of captures made at these two stations (197 specimens = 149 from the complementary sample + 48 from altitude sample [see Fig. 1]), Fig. 3 shows the distribution of the number of specimens from each species according to biomes. Of the species that appear in the mesophilous mountain forest (1,500 m), four were not captured in the contiguous pasture (*Deltochilum mexicanus* Burmeister, *Ontherus mexicanus* Harold, *Onthophagus* sp. and *O. cyanellus* Bates), one appears both inside and outside the forest (*Dichotomius satanas* [Harold]), another four were only collected in pasture (*D. carolinus* L., *Scatimus ovatus* Harold, *Copris incertus* Say and *O. corrosus* Bates) and only one appeared in numbers in pasture (*O. incensus* Say). The value of the dissimilarity percentage (Beals 1984) between the inventories obtained in both biomes is 0.95, very close to the maximum dissimilarity value (1.0). A total of six species was captured at the 3,000 m station, but in this case, only one specimen of *Aphodius* appeared exclusively in coniferous forest (Fig. 3). Nevertheless, three species (*Onthophagus chevrolati chevrolati* Harold, *Aphodius glyptus* and *A. neotomae* Fall and Cockerell or *A. duplex* Bates) were captured in an adjacent pasture and not within the forest. In this case the dissimilarity percentage (0.81) is smaller.

DISCUSSION

COMPARISON WITH OTHER REGIONS. The scarcity of beetles in the samples is striking, considering the diversity of habitats examined (Fig. 1) and compared with the 4,831 specimens of 57 species captured with 30 traps, in a similar sampling study carried out in the Iberian Peninsula (Martín-Piera *et al.* 1993). Thus, a richness numerically lower than three times and an abundance 33 times less was obtained in the present study. An average of 345 specimens and 15 species was taken from each pair of identical traps set at each sampling point in that European area; 12.2 specimens and 3 species in the current study. However, these results are not anomalous when compared with other sampling made by Arellano (1992 and unpublished data) who collected 1,222 specimens of 19 species with 1,620 pitfall sampling units, in the same region.

Other studies carried out in Mexico also showed this paucity of beetles. Morón and Terrón (1984) found 9 species of Scarabaeoidea at two sites at 650 m and 1,550 m in the Sierra Norte de Hidalgo (Sierra Madre Oriental) and Morón and Zaragoza (1976) found 13 species in a site in the state of Mexico. In the rain forests of Mexico, Halffter (1991) and Halffter *et al.* (1992) found a number of species which ranged from 29 in Palenque (Chiapas) to 18 in Laguna Verde (Veracruz). Likewise, in studies that have been carried out in other tropical areas, between 27 and 53 species appeared in samples collected from a number of traps which ranged from 453 to 10,911 (Hanski 1989). Therefore, as opposed to what one might expect from other comparisons of tropical communities with temperate ones (MacArthur 1969), the number of species of Scarabaeoidea is not much greater in the tropical and subtropical regions.

By comparison, going from northern to southern Europe there is a considerable increase in richness (Hanski 1986; Lobo 1992). This might be taken to indicate that communities established in sub-tropical Mesoamerican areas are less saturated with species at present than are the communities of the warm-temperate regions of the Old World. Thus it would seem less likely that the structuring force operating on such communities should be competition. Invasion and colonization by species from neighbouring geographical regions would thus have been facilitated. Even so, it has generally been argued that competition is intense between the tropical copro-necrophage scarabaeoid communities (Hanski 1989; Hanski and Cambefort 1991). Therefore it is fitting to ask what caused the scarcity of these beetles in the sampled communities of the Transverse Volcanic Belt.

Studies done in Mexico corroborate the difference in fauna between the biomes of the forests and open areas (Kohlmann and Sánchez-Colón 1984; Kohlmann 1991). We found that the beetles that inhabit the mesophilous mountain forest are different from those found in nearby pastures (Fig. 3), although the captures made in the coniferous forest at greater altitudes do not support a similar segregation of habitat. Mesoamerican tropical forest shelters a scarabaeoid fauna highly adapted to this medium (Halffter and Matthews 1966). Fragmentation and/or transformation of this forest has abruptly reduced the richness of its fauna (Peck and Forsyth 1982; Klein 1989). The modification of the tropical forest in Colombia has similarly reduced the number of species from 60 to 6 (Howden and Nealis 1975).

Extinction of the megafauna during the quaternary (Janzen 1983; Patterson and Pascual 1968), eruptions of the Transverse Volcanic Belt during the Pleistocene and lack of connection between this mountain chain and the western

Sierra Madre (Halffter 1987) may have been other factors which brought about the paucity of fauna so notable today.

ALTITUDE, RICHNESS AND ABUNDANCE. As one ascends the mountain, the richness in fauna decreases and the composition of the communities changes (Figs. 1, 2). Eight and six species were collected in the sample sites located in the mesophilous mountain forest (at 1,500 and 2,000 m, respectively); 3, 5 and 1 species were caught at 2,500–3,500 m in those located in the coniferous forest, while no species was captured in the pastures at higher elevations. Decrease in richness coupled with increase in altitude has been noted frequently (Wolda 1987). Only three species of Scarabaeoidea were captured in the Sierra Norte de Hidalgo at an elevation of 1,550 m. Morón and Terrón (1984) and Arellano (1992) captured only 2 species (1 Scarabaeidae and 1 Geotrupidae) at 2,500 m during one year of sampling in the Sierra del Agua. Luis-Martínez and Llorente-Bousquets (1990) comment on the same tendency in the Papilionoidea of the Cañada de los Dínamos (Valley of Mexico). The richness of this superfamily fell from 47 to 11 species as altitude increased by only 500 m. The critical horizon for the Papilionidae, Nymphalidae and Lycaenidae, the three best represented families, was at an elevation of 2,800 m. Finally, between 5 and 10 species of Scarabaeoidea per site appear in southeast Asia at elevations between 1,000 and 1,700 m, and no scarabaeoids were captured at altitudes greater than 2,000 m (Hanski 1983; Hanski and Krikken 1991).

While the number of species captured during a year-long sampling program in the Central Iberian System also decreased as the altitude increased, the decline was not so pronounced as in the alpine pastures (44 species at 1,000 m; 32 at 1,500 m and 23 at 2,000 m; Lobo unpublished; see also Lobo 1992).

As Janzen (1967) has pointed out, mountains form an environmental barrier which is much more impassable for tropical species than for species from temperate ecosystems, adapted as they are to seasonal fluctuations. The higher elevations in the mountain ranges in the south of Mesoamerica are also poor in species, due to the absence of Nearctic species and to the colonizing difficulties encountered by the Neotropical fauna from lower altitudes (Halffter 1987). The heightened effect of the tropical mountain barrier and the lack of connection between the Transverse Volcanic Belt and the Mexican longitudinal mountain systems (which acted as corridors for fauna during the Pleistocene) are probably the two most important factors leading to the scarcity of orophilous fauna in the areas examined in this study.

ALTITUDE AND TAXONOMIC COMPOSITION AND DISPERSAL PATTERNS. The specimens taken at the sampling stations located within the Mesophilous mountain forest were mostly Scarabaeidae belonging to typical Neotropical genera. Of the more than 270 species of *Dichotomius*, *Scatimus*, *Ontherus* and *Deltochilum*, only 4 are present in the Nearctic Region (Cambefort 1991). The mesophilous mountain forest, intermediate between coniferous and tropical forest, is characterized by its lack of autochthonous Scarabaeoidea fauna, having been populated by invading species from neighboring beetle communities (Kohlmann 1991). The penetration of these Neotropical species into Mesoamerica began after the last geographical contact between North and South America in the middle of the Pliocene (Halffter 1987).

As altitude increases, species of *Onthophagus* and *Copris* become better represented. These two are genuine representatives of the Paleo-American dispersal pattern (Halffter 1962, 1964, 1972, 1976, 1978, 1987). Although these genera are practically cosmopolitan, with more than 50% of their species in

the Afrotropical region, they are poorly represented in South America. It is thought that they colonized and diversified in South America during the Cretaceous-Eocene period. At present the majority of the Mesoamerican species are concentrated in mountainous zones and in high plateaus.

This change in fauna with altitude, described by Halffter (1976, 1987), is completed, according to that author, by the presence of elements of Nearctic origin in the zones of higher altitude. According to Halffter the Nearctic dispersal pattern would be composed of species of recent penetration (Plio-Pleistocene) into the Mexican Transition Zone which do not belong to the family Scarabaeidae. Within the Scarabaeoidea, the most notable example is the family Geotrupidae. In the present study only one geotrupid (*Onthotrupes herbeus* (Jeckel)) was captured, while Arellano (1992) captured two more species, *Onthotrupes nebularum* (Howden) and *Ceratotrupes bolivari* Halffter and Martínez at a site located between Acajete and Sierra del Agua (Cruz Blanca: 2,340 m). These three species belong to the exclusively American tribe Ceratotruperini (Zunino 1984), with its clearly discontinuous present-day area of distribution to the north and south of the Río Bravo. For Zunino (1984), the Geotrupinae could be found in North America since the end of the Cretaceous, and the Ceratotruperini go back to the Tertiary period. Zunino believes that present American Ceratotruperini come from a western lineage of the ancestral eurafrican Geotrupinae. If so, it is doubtful that the dispersal pattern of the American Geotrupinae is a typically Nearctic one, although the Pleistocene glaciations must have influenced the present-day distribution. Halffter (1964, 1976, 1987) himself distinguished an older Nearctic line within this dispersal pattern that is distributed at lower altitudes in the Mexican mountains and that is faunistically related to North America's Eastern zone. Ceratotruperini disappear in western North America. Phylogenetic and distributional data suggest the antiquity of the American Ceratotruperini.

The aforementioned species of Geotrupidae, together with two species of *Onthophagus* from the *O. chevrolati* group, appeared in stations at 2,500 m and 3,000 m. The genus *Onthophagus* has been considered Paleo-American. The slight taxonomic difference of the orophilous species of the *O. chevrolati* group may be the result of recent allopatric speciation, as a consequence of post-Pleistocene isolation after geographic expansion during the Quaternary (Zunino and Halffter 1988).

The remainder of the captured species are Aphodiidae of the large, cosmopolitan genus *Aphodius*. Taxonomy of the Mesoamerican species of this genus is not well known. Therefore, a certain degree of uncertainty in our findings could be expected. To overcome as far as possible this problem identifications were checked by a specialist in taxonomy of the genus *Aphodius* (G. Dellacasa).

Aphodius, the dominant genus in the northernmost coprophage communities (Hanski 1986), is scarcely represented in the tropics, and can be considered an essentially Holarctic group. Nevertheless, North America has its own aphodiine fauna that is taxonomically and ecologically differentiated from east to west (Gordon 1983). There are also subfamilies of Aphodiidae with a good number of endemic genera in the Neotropical region (Dellacasa 1987). These factors seem to corroborate the antiquity of the family on the American continent.

The aphodiine subgenera *Chilothorax*, *Gonaphodielus*, *Amidorus* and *Agri-linus* colonize the mountains of Veracruz. Members of the first two subgenera appear at 2,000 m, the other two only between 3,000 and 3,500 m. *Amidorus* and *Agri-linus* have a quasi-cosmopolitan distribution, with representatives in

the Palearctic and Nearctic regions, Meso- and Central America and the Afrotropical Region (South Africa and Zaire). *Agrilinus* is even present in the Oriental Region (Malayan archipelago). This distribution resembles that of the genera *Onthophagus* and *Copris* and defines the Paleo-American pattern (Halffter 1976). The taxonomic diversity of *Onthophagus* and *Copris* however, is not comparable with that of the former *Amidorus* and *Agrilinus* whose Holarctic fraction exceeds 85% (87.3% in *Amidorus* and 92.5% in *Agrilinus*). Since adequate phylogenetic reconstructions are lacking, it seems appropriate to speak of lines of holarctic distribution and recent Nearctic dispersion. We shall return to this point.

With regard to the two subgenera that appear in the transition zone between the mesophilous mountain and coniferous forest, we must clearly distinguish *Gonaphodiellus* from *Chilothorax*. The latter is the most speciose of the 134 genera of Aphodiini (Dellacasa, 1987), with a geographic range wider than those of *Agrilinus* and *Amidorus*. The genus is represented in Palearctic and Nearctic regions, Meso- and Central America, Macaronesia (Canary Islands), Sub-Saharan Africa (Niger and Senegal) and Australia.

Once again, the percentages of taxonomic distribution swing strongly in favour of the Holarctic fraction (70.2%), so that one is inclined to consider the idea of a line of holarctic distribution and recent Nearctic dispersion in this case. The same cannot be said for the subgenus *Gonaphodiellus* with its nine Neotropical species, two Mexican species and one South African species. Considered together, the data suggest a Neotropical origin for this subgenus.

Therefore, while the abundance of *Gonaphodiellus* corroborates Kohlmann's (1991) explanation of the absence of autochthonous Scarabaeoidea in the mesophilous mountain forest, the presence of *Agrilinus*, *Chilothorax* and *Amidorus* suggest Holarctic relationships for the most recent Nearctic groups.

THE NEARCTIC DISPERSAL PATTERN: A REDEFINITION. To return to our argument, the original formulation of the Nearctic dispersal pattern (Halffter, 1976)—eleven years later named the Nearctic Distribution Pattern (Halffter 1987)—refers to Holarctic and/or Nearctic groups of recent (Plio-Pleistocene) penetration into the Mexican Transition Zone. Within this Nearctic pattern Halffter distinguished lines related faunistically with eastern North America and Holarctic lines, though did not provide examples for Scarabaeoidea. Although we accept Halffter's distinction, we feel that the content of the Nearctic dispersal pattern is still heterogeneous, hence it should be clearly stated with examples. In spite of Palestini and Zunino's (1988: 14) arguments, we believe that there should be at least three Scarabaeoidea coenochrons within what has come to be called the Nearctic dispersal or distribution pattern: Paleo-Nearctic, Neo-Nearctic and Holarctic. The ecological and phylogenetic information content of the first two qualify them as authentic Taxonomic Pulses in the sense of Erwin (1985); not so the Holarctic one.

We define these three new dispersal patterns as follows:

Paleo-Nearctic Pattern: The Paleo-Nearctic pattern is represented by species belonging to Western euramerican lineages of ancient (Cretaceous-Paleocene) origin, and Cenozoic autochthonous American radiation, e.g., Ceratotruperini (Zunino 1984).

Neo-Nearctic Pattern: The Neo-Nearctic pattern is represented by species or group of species of Paleo-American ancestors, phylogenetically related with extra-American groups, but of more recent differentiation (Pre-Miocene), e.g., *Onthophagus* of the *chevrolati* group (Zunino 1988, Zunino and Halffter 1988).

Holarctic Pattern: To the Holarctic pattern belong species of recent (Plio-

Pleistocene) Nearctic dispersion, taxonomically related to palearctic groups (Halfiter 1987). Only some, if any, groups of *Aphodius* (e.g., *Agrilinus*, *Chilothorax* and *Amidorus*) can be included.

The present shape of all their distribution areas was probably very strongly influenced, on a regional scale, by the Pleistocene glaciations and/or the most remote paleogeographic events (orogenic processes, marine transgressions/regressions, vulcanism).

CONCLUSIONS

1. There is a striking faunistic paucity in the scarabaeoid copro-necrophagous communities of the Veracruz mountains. The elevational gradient also corresponds with a modification in the composition of these communities. Richness decreases with altitude much more in tropical and subtropical areas than in temperate ones.

The general tendency toward the impoverishment of fauna in the higher elevations of subtropical mountains is exacerbated in the Transverse Volcanic Belt by the overall scarcity of fauna in this mountain chain.

2. Even though the paucity of fauna is extreme, the data of this study in the Mexican Transition Zone corroborate the pattern of segregation with elevational gradient described by Martín-Piera *et al.* (1992) in the Iberian Peninsula: Aphodiidae and Geotrupidae in the heights, and Scarabaeidae at lower altitudes. The existence of such segregation implies that variations in the geographic range of the species (mainly as a consequence of Pleistocene glaciations) have played an important role in structuring the communities of Transition Zones. In some cases the species that inhabit the highest altitudes would have invaded the Mexican Transition Zone recently from the Nearctic region (*Aphodius* of the subgenera *Chilothorax*, *Amidorus* and *Agrilinus*), even though these recent Nearctic lines seem to have a Palearctic origin. Others are older American elements (*Onthotrupes*, *Onthophagus* and *Aphodius* of the subgenus *Gonaphodielus*) whose areas would have recently expanded and contracted with the climatic variations of the Pleistocene, starting from small autochthonous populations that invaded through the Mexican mountain chains until they were left isolated in the Transverse Volcanic Belt by the last withdrawal of the Quaternary ice sheets. Whatever the case, one is dealing with modifications of geographic range, rather than new speciation (Coope 1979), although genetic drift in these isolated orophilous populations may have been a frequently occurring and relatively recent phenomenon (Kavanaugh 1979, Halfiter 1987).

The fact that this taxonomic segregation with altitude also occurs with latitude and time on various scales (Martín-Piera *et al.* 1993), supports the idea that the present altitudinal range of these taxa might be the consequence of environmental conditions that reigned in their hypothetic ancestral areas.

3. Indications are that, as in tropical areas (Howden and Nealis 1975; Peck and Forsyth 1982; Klein 1989), antropoc fragmentation and transformation of primary forest in subtropical areas (mesophilous mountain and coniferous forest) causes a qualitative and quantitative change in the structure of scarabaeoid copro-necrophagous communities. Forest species do not colonize pastures, nor do pasture species enter forest, except in the case of more ecologically flexible species such as *Dichotomius satanas* and *Onthophagus aureofuscus*. This tendency is masked in the mountain forests where the increase in altitude diminishes the richness of the fauna.

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LITERATURE CITED

- ARELLANO, L. 1992. Distribución y abundancia de Scarabaeinae y Silphidae (Insecta, Coleoptera) en un transecto altitudinal en el estado de Veracruz. Tesis de Licenciatura. U.A.M. Facultad de Ciencias Departamento de Biología, Mexico, D.F. 139 pp (Inédita).
- BEALS, E. W. 1984. Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. *Advan. Ecol. Res.* 14:1-55.
- BOUCOMONT, A. 1932. Synopsis des *Onthophagus* de Amérique du Sud (Col., Scarab.). *Ann. Soc. Entomol. Fr.* 101:293-332.
- CAMBEFORT, Y. 1991. Biogeography and evolution [pp. 51-67]. *In: Dung beetle ecology*. Hanski, I., and Y. Cambefort (editors). Princeton University Press, Princeton, NJ. 481 pp.
- COOPE, G. R. 1979. Late Cenozoic fossil Coleoptera: Evolution, biogeography and ecology. *Ann. Rev. Ecol. Syst.* 10:247-267.
- DELLACASA, M. 1987. Contribution to a world-wide catalogue of Aegialidae, Aphodiidae, Aulonocnemidae, Termitotrogidae (Coleoptera, Scarabaeoidea). *Mem. Soc. Entomol. Ital.* 66:3-455.
- ERWIN, T. L. 1985. The taxon pulse: A general pattern of lineage radiation and extinction among carabid beetles [pp. 437-472]. *In: Taxonomy, phylogeny and zoogeography of beetles and ants*. Ball, G. E. (editor). Junk Publishers. 514 pp.
- GORDON, R. D. 1983. Studies on the genus *Aphodius* of the USA and Canada (Coleoptera, Scarabaeidae). 7. Food and habitat distribution, key to eastern species. *Proc. Entomol. Soc. Wash.* 85:633-652.
- HALFFTER, G. 1962. Explicación preliminar de la distribución geográfica de los Scarabaeidae mexicanos. *Acta Zool. Mex.* 5:1-17.
- . 1964. La entomofauna americana. Ideas acerca de su origen y distribución. *Folia Entomol. Mex.* 6:1-104.
- . 1972. Elements anciens de l'entomofaune Neotropicale: Ses implications Intercontinentales au Cours du Mesozoïque. 17th Congr. Int. Zool., Monte-Carlo 1:1-40.
- . 1976. Distribución de los insectos en la zona de transición mexicana. Relaciones con la entomofauna de norteamérica. *Folia Entomol. Mex.* 35:1-64.
- . 1978. Un nuevo patrón de dispersión en la Zona de Transición Mexicana: El Mesoamericano de montaña. *Folia Entomol. Mex.* 39-40:219-226.
- . 1987. Biogeography of the montane entomofauna of Mexico and Central America. *Ann. Rev. Entomol.* 32:95-114.
- . 1991. Historical and ecological factors determining the geographical distribution of beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomol. Mex.* 82:195-238.
- , M. E. FAVILA, AND V. HALFFTER. 1992. A comparative study of the structure of the scarab guild in mexican tropical rain forests and derived ecosystems. *Folia Entomol. Mex.* 84:131-156.
- HALFFTER, G., AND E. G. MATTHEWS. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomol. Mex.* 12-14: 1-312.
- HANSKI, I. 1983. Distributional ecology and abundance of dung and carrion-feeding

- beetles (Scarabaeidae) in tropical rain forests in Sarawak, Borneo. *Acta Zool. Fenn.* 167:1-45.
- . 1986. Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. *Acta Oecol. Oecol. Gener.* 9(2):171-187.
- . 1989. Dung Beetles [pp. 449-511]. *In: Tropical rain forest ecosystems.* Lieth, H., and M. J. A. Werger (editors). Elsevier Science Publishers, B. V., Amsterdam.
- , AND Y. CAMBEFORT. 1991. Resource partitioning [pp. 330-349]. *In: Dung beetle ecology.* I. Hanski and Y. Cambefort (editors). Princeton University Press, Princeton, New Jersey. 481 pp.
- , AND J. KRICKEN. 1991. Dung beetles in tropical forests in south-east Asia [pp. 179-197]. *In: Dung beetle ecology.* Hanski, I., and Y. Cambefort (editors). Princeton University Press, Princeton, NJ. 481 pp.
- HOWDEN, H. F., AND V. G. NEALIS. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica* 7:77-83.
- JANZEN, D. H. 1967. Why mountain passes are higher in the tropics?. *Am. Nat.* 101: 233-249.
- . 1983. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican Deciduous forest and adjacent horse pasture. *Oikos* 41: 274-283.
- , M. ATAROFF, M. FARINAS, S. REYES, N. RINCON, A. SOLER, P. SORIANO, AND M. VERA. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8:193-203.
- KAVANAUGH, D. H. 1979. Rates of taxonomically significant differentiation in relation to geographical isolation and habitat: examples from a study of the Nearctic *Nebria* fauna [pp. 35-37]. *In: Carabid beetles: Their evolution, natural history, and classification.* Erwin, T. L., G. E. Ball and D. R. Whitehead (editors). Junk, The Hague. 635 pp.
- KLEIN, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* 70(6):1715-1725.
- KOHLMANN, B. 1991. Dung beetles in subtropical North America [pp. 116-132]. *In: Dung beetle ecology.* Hanski, I., and Y. Cambefort (editors). Princeton University Press, Princeton, NJ. 481 pp.
- , AND S. SÁNCHEZ-COLON. 1984. Structure of a Scarabaeinae community: A numerical-behavioural study (Coleoptera, Scarabaeidae). *Acta Zool. Mex.* 2:1-27.
- LOBO, J. M. 1992. Biogeografía de los Scarabaeoidea coprófagos del Macizo Central de Gredos (Sistema Central Ibérico). *Ecología Mediterránea* 18:69-80.
- , F. MARTÍN-PIERA, AND C. M. VEIGA. 1988. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). I: Características determinantes de su capacidad de captura. *Rev. Ecol. Biol. Sol* 25(1):77-100.
- LUIS-MARTÍNEZ, A., AND J. LLORENTE-BOUSQUETS. 1990. Mariposas en el Valle de Mexico: Introducción e historia I. Distribución local y estacional de los Papilionoidea de la Cañada de los Dinamos, Magdalena Contreras, D. F. Mexico. *Folia Entomol. Mex.* 78:95-198.
- MACARTHUR, R. H. 1969. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* 1:19-30.
- MARTÍN-PIERA, F., C. M. VEIGA, AND J. M. LOBO. 1992. Ecology and biogeography of dung-beetle communities (Coleoptera, Scarabaeoidea) in an iberian mountain range. *J. Biogeogr.* 19:677-691.
- MORÓN, M. A., AND R. A. TERRÓN. 1984. Distribución altitudinal y estacional de los insectos necrófilos en la Sierra Norte de Hidalgo, México. *Acta Zool. Mex. (N.S.)* 3:1-47.
- , AND S. C. ZARAGOZA. 1976. Coleópteros Melolonthidae y Scarabaeidae de Villa de Allende, estado de México. *Ann. Inst. Biol. Univ. Aun. México* 47(2):83-118.
- PALESTRINI, C., AND M. ZUNINO. 1988. L'analisi dell'entomofauna nella Zone di Transizione: Prospettive e problemi. *BIOGEOGRAPHIA. Lav. della Soc. ital. Biog: Il Concepto di Soglia Biogeografica.* N.S. 12(1986):11-25.

- PATTERSON, B., AND R. PASCUAL. 1968. Evolution of mammals on southern continents. V. The fossil mammal fauna of South America. *Q. Rev. Biol.* 43:409-451.
- PECK, S. B., AND A. FORSYTH. 1982. Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). *Can. J. Zool.* 60:1624-1634.
- REIG, O. 1962. Las integraciones cenogenéticas en el desarrollo de la fauna de vertebrados tetrápodos de América del Sur. *Ameghiniana* 2(8):131-140.
- . 1968. Peuplement en vertébrés tétrapodes de l'Amérique du Sud [pp. 215-260]. *In: Biologie de l'Amérique Australe* 4. Delamere Deboutille, C., and E. Rapoport (editors). C. N.R.S., Paris.
- RZEDOWSKI, J. 1981. Vegetación de Mexico. Limusa (editores) México. 432 pp.
- VEIGA, C. M., J. M. LOBO, AND F. MARTÍN-PIERA. 1989. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). II: Análisis de efectividad. *Rev. Ecol. Biol. Sol.* 26(1):91-109.
- WOLDA, H. 1987. Altitude, habitat and tropical insect diversity. *Biol. J. Linn. Soc.* 30: 313-323.
- ZUNINO, M. 1984. Sistematica generica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupidae), filogenesi della sottofamiglia e considerazioni biogeografiche. *Boll. Mus. Reg. Sci. Nat. Torino* 2:9-162.
- . 1985. Gli Scarabaeoidea coprofagi dell'area Euromediterranea: relazioni filetiche e biogeografiche. *Atti. XIV Congr. naz. Ital. Entomol., Palermo, Erice, Bagheria.* 321-325 pp.
- , AND G. HALFFTER. 1988. Análisis taxonómico, ecológico y biogeográfico de un grupo americano de *Onthophagus* (Coleoptera: Scarabaeidae). *Monogr. Mus. Reg. Sci. Nat. Torino, Monogr.* 9. 211 pp.

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