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Halffter, Gonzalo

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Historical and ecological factors determining the geographical distribution of beetles⁽¹⁾ (Coleoptera: Scarabaeidae: Scarabaeinae)

GONZALO HALFFTER

Instituto de Ecología Apartado Postal 63 - Xalapa, Veracruz 91000, Mexico

SUMMARY

In an attempt to answer the question, «Does community biogeography exist other than at the descriptive level?», the relation of the Scarabs (Coleoptera: Scarabaeidae: Scarabaeinae) with the tropical forests of the Americas, Africa and Southeast Asia is analyzed. More than a synthesis of what is known of the Scarabaeinae guild in the tropical forests of the three continents, it is a journey into the structure as well as the similarities and differences of the guild on each continent. In addition, as far as current information allows, these are compared with the guild in the savannas.

For several aspects (for example, species richness of the guild in the American tropical forests) answers (e.g. necrophagy) and possible hypotheses are proposed. Gaps in the available information are identified. A review of the growing bibliography on the theme is included, as well as unpublished data.

INTRODUCTION

If we wish to investigate the biogeography of communities, the first thing we must ask is: What is a community? When I was studying, forty years ago, the answer was very clear. Frederic E. Clements and V.E. Shelford's ideas, so brightly and elegantly synthesized by Eugene P. Odum, defined the community as a unit, an evolving continuity in space as well as in time. The community was seen as a kind of superorganism. To base biogeographical investigation on this concept was a very logical and advantageous thing to do.

However, progress in mathematics was, and still is, a problem for biologists, especially for ecologists. In the 1950's ecology was shocked by the development of information theory. The perception of the similarity between Shannon's diversity equation and Boltzmann's equation for entropy provided the temptation to analyze the diversity of a community as a thermodynamic phenomenon. In the early 70's the community-superorganism concept was

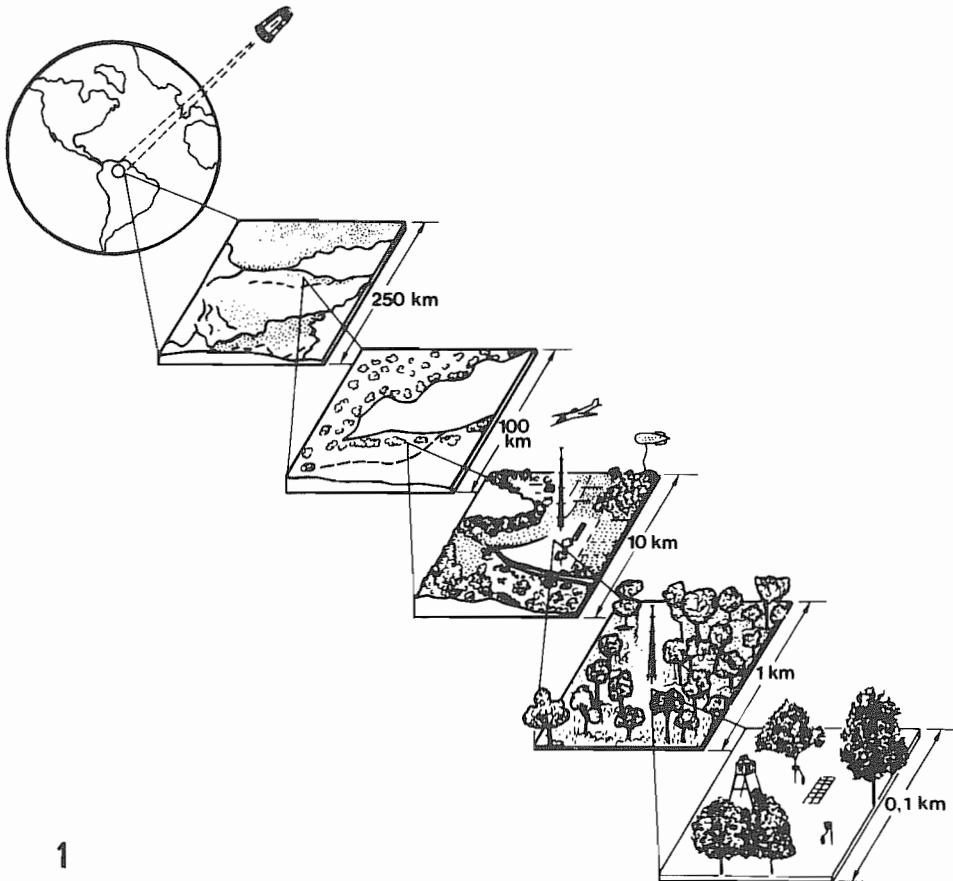
⁽¹⁾ This paper was presented at the XXVIII Congress of the Società Italiana di Biogeografia as the introductory conference to the theme «Community Biogeography», Turin, September, 1990. The work forms part of the project «Animal Ecology and Behaviour» of the Instituto de Ecología, México and was supported by the project «Ecology of the nesting behaviour of dung-rolling beetles (Coleoptera: Scarabaeinae) from tropical forests» No. D112-903528, CONACyT, Mexico, and by the project «Animal ecology in the State of Veracruz», No. DGICSA-902467, Secretaría de Educación Pública, México.

abandoned. At that time, a strong school in the area of demography arose with authors such as Robert MacArthur and John L. Harper. MacArthur revived selection as the mechanism responsible for community structure and function. Current evolutionary ecology focussed its attention on individuals. Under this new approach the community is only seen as an ecological system of more than one species. For several authors, everything except the individual is perceived as environment including, of course, all other biota. Under these circumstances, where is the sense in developing biogeography (or, much less, historical biogeography) of the community, that is, of something which is a random result modified by environmental parameters? If the community is a simple association and has no past, neither in historical-biological time nor in geological time, its composition and spatial distribution is the result of the interplay between the elements of the physical environment and the ecological requirements of each organism. Aside from the descriptive aspect, there is no place for a biogeography of communities. Contemporary ecology does not take historical processes into account as a source of information. Instead, it attempts to be an experimental science, and thus out of space and historical time. Added to conceptual changes are human differences. Ecologists do not easily accept the language of biogeographers, nor are biogeographers familiar with the contributions and methods of ecologists. Knowing that I am stepping onto difficult territory, I will try to act as an ecotone animal, moving between two worlds and using the beetles of the Scarabaeinae subfamily, which have been studied during the last 25 years, as the medium for this discourse.

1. DIFFERENCES IN APPROACH

One's point of observation can change the entire scenario, including the components of the problem one wishes to analyze, by altering the limit of resolution. Figure 1 shows how observation distance modifies not only the scale of the problem, but also its content. The first three scenarios belong to classical biogeography, the last two to ecology and the fourth represents an intermediate position. The more general scenarios are not necessarily a simple accumulation of the particular ones, nor are the latter only a breakdown of the more general ones. Each level has its own characteristics, objectives and research methodology.

Historical and statistical biogeography always portray the Earth as the setting for events, even when the distribution being analyzed is limited to a mountain. In fact, this setting has no limits other than those of the planet and it is within this framework that each taxon or group of taxa establishes its particular distribution in accordance with its evolutionary history and the evolution of the framework within which it exists, (i.e. the Earth). When we analyze a community we limit ourselves to either one or several defined geographical areas characterized by certain climatic parameters. The criteria determining our approach has undergone a genuine «zoom» effect. When we



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Fig. 1 - The observation distance changes the scale and content of the study area (see text). Redrawn from the U.S. National Research Council (1986) and from di Castri and Hadley (1988).

analyze a guild we limit ourselves even more, since we do not analyze the entire community, but rather, what happens at a specific site. Currently, spatial macrodistribution and evolutionary time are losing importance with respect to methodology. From this point of view, the structure being studied only exists for a given moment and the elements which intervened in its configuration are the one which are should investigate.

The community⁽²⁾ is formed by an assemblage of guilds which interact under certain conditions of widely ranging environmental parameters. The transition from one community to another, or in other words, the establishment of the limits of a community, occurs when there is a change in some of the determinant parameters. From this point of view, community biogeography can go no further than the descriptive phase. Although there is some truth to this, the combining of studies on structure and function of a community with the historical-evolutionary studies of biogeography (with its in-

clination to global explanations) can both pose problems and offer unexpected solutions.

2. THE BEETLE GUILD

In this paper, when we speak of beetles, we refer to Scarabaeinae, a monophyletic group of some 6,000 species which represent approximately 200 genera. The dung of herbivorous mammals is the main food of the subfamily. Many morphological, ethological and ecological features are associated with the peculiarities of this food type (see Halffter and Edmonds, 1982). In several papers (see particularly Halffter, 1959; Halffter and Matthews, 1966; Halffter and Edmonds, 1982) it has been stated that the principal event which allowed the Scarabaeinae to appear and flourish as a monophyletic group was the transition from saprophagy (general and primitive in the great Scarabaeoides group) to the exploitation of dung of the great vertebrates. No other animal group takes advantage of this resource in such a diverse manner, nor with such complex and efficient ethological responses as do the Scarabaeinae.

To understand the Scarabaeinae as animals, and to understand the way in which they integrate into guilds, there are three primary considerations: those related to food habits, mentioned previously, their association with the soil and the K strategy which is common to the subfamily. The dung and the beetles both occupy the soil. As imagos, the beetles spend a great portion of their time within the soil. Their pre-imago life, from egg to pupa (see Figure 2) is spent beneath the surface of the soil. Their nesting is associated with the soil and the protection which it affords them. It is not unusual that most of the characteristic behavioural features of the Scarabaeinae, i.e. the relocation of food for the adult and for nidification, are closely related to life within the soil.

The relocation of food from its original site to a protected one is effected by one of two processes: vertical or horizontal relocation (Figures 3 and 4). Vertical relocation consists of packing a portion of food into a previously excavated burrow. Horizontal relocation requires that the beetle form a ball from the food source, roll it a certain distance and then bury it. Dung relocation by Scarabaeinae is perhaps the most complex of all relocation strategies found in insects, with the exception of the Hymenoptera. It is so important that many of the most striking morphological structures and behavioural displays of these beetles are closely related to relocation mechanisms (Halffter and Edmonds, 1982; Edmonds, 1983).

The last fundamental feature, the K strategy, is common to the group and is the result of a series of phenomena. These include an exceptional reduction in fecundity, complex and efficient processes of nesting, an association between these processes and co-operation between the sexes and the evolution of this co-operation to the status of true subsocial behaviour which is only reached by some species (from an analysis of the interaction among ec-

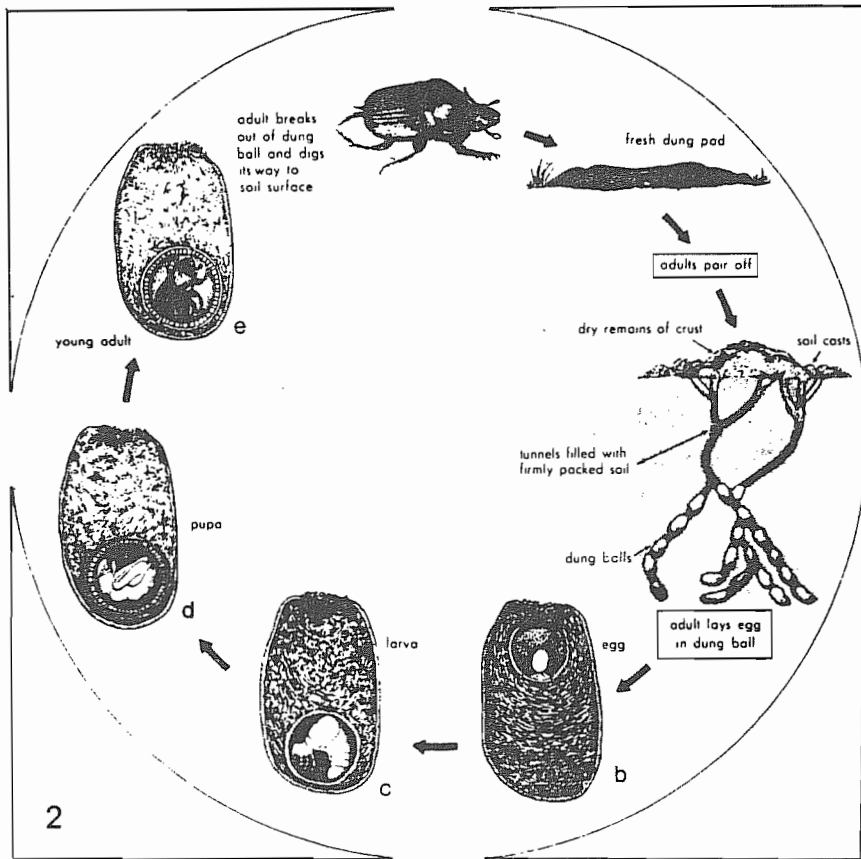


Fig. 2 - The life cycle of a Scarabaeinae: *Digitonthophagus gazella* (F.). (From Bornemissza, 1976).

ological pressures and behaviour, see Halffter and Edmonds, 1982; Halffter, 1991).

The Scarabaeinae subfamily is cosmopolitan. This subfamily is found in warm-temperate ecosystems, however its diversity in these environments runs a distant second to that of the intertropical area. To give an idea of this difference, we would like to point out that a single site of a South American tropical forest contains more than 50 species, while all of Europe and the Mediterranean area contain less than 90 species, of which some 60 species belong to only one genus (*Onthophagus*). As we move northwards from the tropics the number of species diminishes markedly until the Scarabaeinae are completely replaced by other coprophagous coleopterous of the same family, the Aphodiinae and the Geotrupini (Geotrupinae). The same reduction in the number of species occurs when ascending the mountains of the intertropical area.

Almost all species of the Scarabaeinae family are restricted to areas where

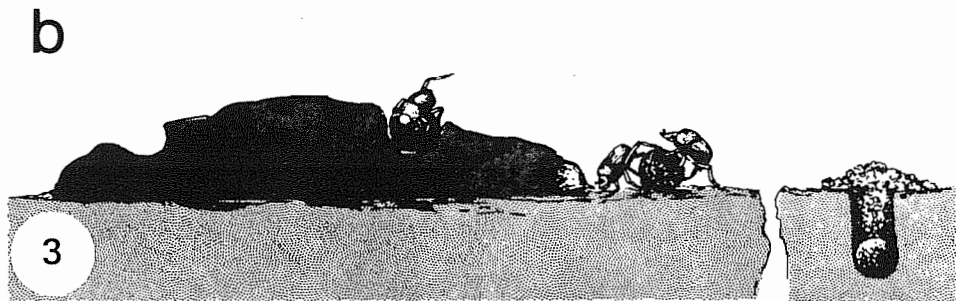
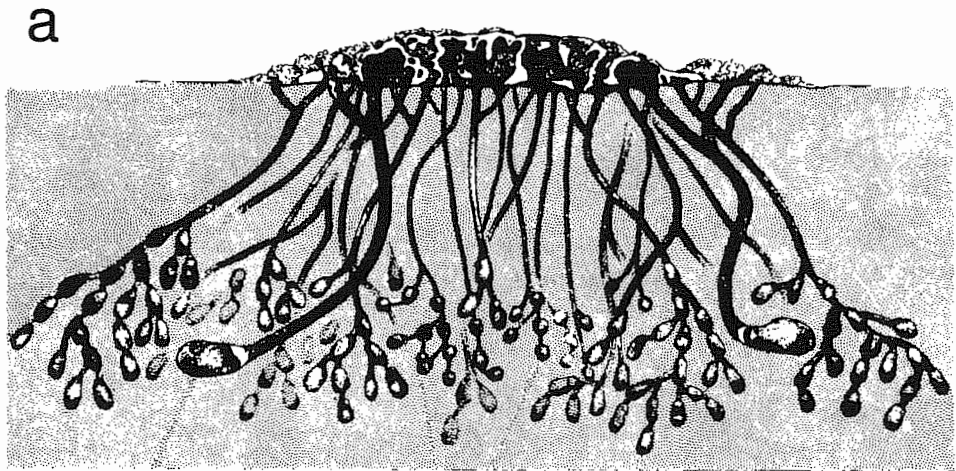


Fig. 3 - Relocation in Scarabaeinae: a) vertical relocation, b) horizontal relocation (From Bornemissza, 1976).

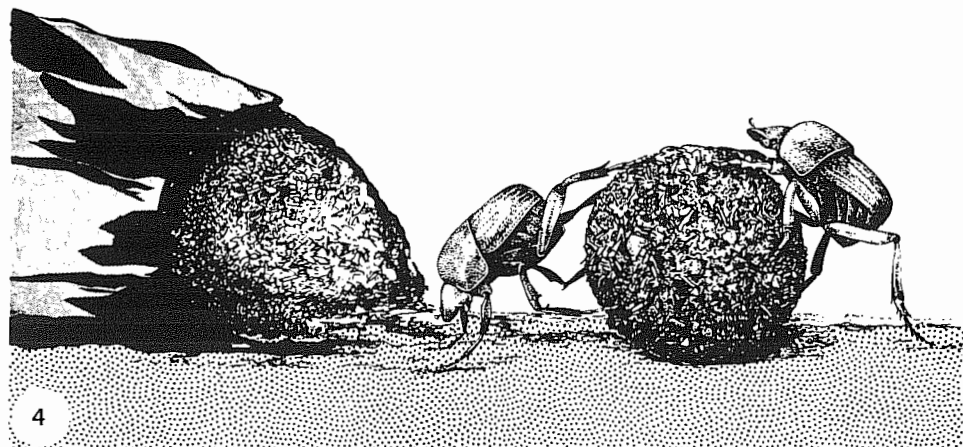


Fig. 4 - A pair of rolling beetles (*Sisyphus spinipes*) beginning the process of horizontal relocation. (From Halffter and Edmonds, 1982).

precipitation exceeds 250 mm per year, with an average annual temperature above 15 °C. Several authors (see references in Halffter and Edmonds, 1982) point out that within these limits vegetation cover is the factor which has the greatest effect on their distribution. In tropical regions it is quite common to find distinct differences in the species composition of the guild of the forests and that of the guild found in clear cuts. The Scarabaeinae are very stenotopic in relation to the vegetation which, to them, represents a set of factors including variation in atmospheric temperature and humidity, soil surface temperature, as well as the degree of direct solar incidence. Outside of the tropics, for example in the Mediterranean, vegetation cover does not seem to be as important a determinant of guild composition, although it is still an important factor in Scarabaeinae distribution (Lumaret, 1978, 1979^{ab} and ^b, and 1983; Lumaret and Kirk, 1987).

Shallow soils contain reduced Scarabaeinae fauna. This has been observed in tropical forests in soils which have developed on a very superficial substratum, as in Sarawak (Hanski, 1989: 490-491) and in Mexico in the northern part of the Yucatán Peninsula (Morón *et al.*, 1986; Halffter, unpublished information). The lack of soil seems to affect nesting in several Scarabaeinae species.

In almost all tropical and warm-temperate communities, the Scarabaeinae constitute a very well-defined guild and an important one with respect to the structure and functioning of the community (see Table II). The high definition of this guild results from the taxonomic affinities of its components (a consequence of its clear monophyletic origin), such as a food resource which is explicitly defined in time and space. To the preceding considerations we have to add that many of the species, because they are strikingly stenotopic, are particularly associated with a specific community and therefore contribute to specializing the guild in different communities. As we move northwards it becomes increasingly difficult to consider the Scarabaeinae as a compact guild. In non-tropical environments the paucity of species which preceeds their complete absence, and the fact that they are not the principal coleopterous in the dung, relegates them to a secondary role in the areas in which they are found.

The guild is organized around three fundamental dimensions of the niche: time, space and food. Since the activities of different species (in particular their frequency peaks) are not synchronous throughout the year (Morón and Terrón, 1984; Morón *et al.*, 1985; Walter, 1978), guild organization differs in time. However, the most clear division of time occurs during the day. Not only is there little overlap between species which are active during the day and those during the night, but careful study can determine the exact hours of activity. On Barro Colorado Island, Panama, *Canthon angustatus*, a specialist of howler monkey (*Alouatta*) dung, is primarily active from 0600h to 1000h and from 1500h to 1800h. These are the periods of defecation of the monkey, which is the most important producer of dung on the island (Howden and Young, 1981).

In relation to space, we have pointed out that each community has a guild which shares very few species with neighbouring guilds, particularly under tropical conditions. Space plays a very important role within the guild. The relocation, either horizontal or vertical, of dung is a way of obtaining space and also of dividing it, i.e. of separating the space which corresponds to each species. With vertical relocation in particular, space is transformed from two dimensions into three dimensions.

Compared to time and space, food seems to play a secondary role in the separation of species of the guild. The greater part of the species components of the guild are food generalists or euryphages. The presence of food specialists (stenophages) helps to reduce competition and increases the diversity of the guild. Specialization with respect to food however, plays a smaller role than the different relocation mechanisms or the separation in time on the whole.

Competition is the element which determines the distribution of species along the three niche dimensions. It is not common to find species with very similar behaviour patterns coexisting. On the contrary, the coexistence of species which differ somewhat in behaviour (e.g. differences in depth of food relocation), or the coexistence of euryphagous and stenophagous species, may result in superimposition of species belonging to the same genus within a guild. Predation and mortality caused by parasites and illnesses seem to play a much less important role than beetle-beetle competition.

Their phylogenetic antiquity and the high number of genera with a more or less wide Gondwanian distribution, makes these beetles an interesting group for purposes of historic biogeographical studies. Also, thanks to articles written during recent years, the Scarabaeinae are becoming a useful tool for community interpretation. The capture technique by means of food pit-falls has greatly contributed to the extant body of information on beetles, making them ideal for research in ecology. These traps are easy to place and provide systematic results and hence a very good representation of the fauna at a given location. This capture system provides data which makes the interpretation of the separation of species in the three dimensions of the ecological niche and the quantitative treatment of results possible. Ecological studies in recent years provide exceptional information on the guild of beetles however, at the same time these studies evoke interesting questions which in some cases can be answered from a biogeographical perspective.

3. HOW DOES THE GUILD BEHAVE IN MAJOR TROPICAL ECOSYSTEMS?

Until a few years ago, no information which might establish the biome-guild relationship in different biogeographic tropical regions existed. Today, we can begin to understand this relationship by considering two distinct sources which are not often seen as compatible: historical-evolutionary ideas and current data from the ecological analysis of the guild in some locations.

Within the historical-evolutionary hypothesis: 1) The Scarabaeinae should

be more diverse in the African savannas, where a larger number of great mammals occur (Table 1) and where similar conditions to those which gave rise to the expansion of the subfamily exist (particularly those that give relocation its ecological significance). 2) There should be fewer species in tropical forests than in grasslands since the former have smaller populations of large mammals and therefore, less dung. 3) Tropical forest species should have derived morphological and ethological characteristics. 4) On the other hand, given taxonomical and historical-evolutionary affinities, the similarity between the guilds in the tropical forest of Africa and Southeast Asia should be greater than the similarity between that of either of these two regions and the guild in the tropical forest of the Americas.

These hypotheses, logical results of the biogeographical-evolutionary knowledge, have only been validated in part. The African savannas are certainly the ecosystems which are richest in Scarabaeinae (Table II), however in the Americas the tropical forests contain many more species than do the herbaceous formations. The guild is unexpectedly rich in all tropical forests but the derived feature is more common to the Americas and Borneo, and moreso for ecological aspects than morphological ones. With respect to the fourth assumption, there is no relationship between the taxonomic-biogeographical affinity and the structural affinity in the comparison of the Americas, Africa and Borneo.

A study by Cambefort, 1985 (1986), carried out in the Ivory Coast, West Africa, illustrates what happens with hypotheses 1 and 2. The Comoé savanna, which is still inhabited by native large mammals, has a very rich group of 187 Scarabaeinae species. However, while the number of species is very high in the tropical rain forests of Tai (also in the Ivory Coast), their diversity is less than half (78) that of the Comoé savanna. In spite of the fact that large mammals still inhabit Tai, not only is the number of species less, but so is the number of individuals and the amount of biomass. The latter is ten times less than that found in the savanna. Cambefort pints out that dung is attacked vigorously under favourable conditions in the savanna, while in Tai dung is used to a lesser extent by the beetles. This supports hypotheses 1 and 2.

Table 1 - Species of mammals, excluding bats

Tropical rain forest:	
Barro Colorado, Panama	51
Kartabo, Guiana	61
Bukit Langan, Malaysia	> 50
Makokou, Gabon	89
Gogol, Papua New Guinea	27
Analamazoatra, Madagascar	20
Savanna Mosaic:	
Lamto, Ivory Coast	96
Serengeti savanna, Tanzania	105

Adapted from Bourlière, 1983.

Table 2 - Species diversity of Scarabaeinae in different communities

Tropical rain forest:			
<i>Africa</i>		<i>Africa</i>	
Tai, Ivory Coast (1)	69	Kenia, only elephant dung (11)	100
Plateau Bateke, Zaire (2)	29 (15)	Ivory Coast (12)	124
		Plateau Bateke, Zaire (13)	83 (27)
<i>Southeast Asia</i>			
Sarawak (3)	55		
<i>America</i>		<i>America</i>	
Palenque, Mexico (4)	31	Palenque, clear-cut areas (14)	6
Boca del Chajul, Mexico (5)	29		
Los Tuxtlas, Mexico (6)	28		
Barro Colorado, Panama (7)	40	<i>Other Communities</i>	
Colombia (8)	53	Pine-oak forest with clear-cut	
Colombian Amazonia (9)	60	areas, Villa de Allende, Mexico (15)	9
Central Amazonia (Manaus) (10)	55	Navacerrada prairies, España (16)	14

Numbers of Scarabaeinae species in distinct well-collected sites. (1) Cambefort (1983) analyzed four tropical forest sites in the Ivory Coast and found that the number of species varied between 31 and 69. Tai is the site richest in Scarabaeinae. At the other sites the total number of species includes an important component of savanna elements. In his captures, Cambefort did not use carrion therefore a very small number of strictly necrophagous beetles must be added to the numbers which he cites above. In another paper the same author [Cambefort, 1985 (1986)] reports 78 species for Tai. (2) Gallery and secondary forests. Species which are shared with the savanna are indicated in parentheses. Data used is from Walter, 1977. (3) Captures corresponding to three distinct types of lowland tropical forest in Gunung Mulu National Park. Data used is from Hanski, 1983. (4) Chiapas, México. Collections made by G. and V. Halffter and Imelda Martínez May 21-24, 1965 (unpublished data). (5) Chiapas, México. Data used is from Morón, Villalobos and Deloya, 1985. (6) Includes the 27 species reported by Morón (1979) in addition to *Cryptocanthos* sp. (G. Halffter unpublished). (7) From Young, 1978. (8) Data used is from Howden and Nealis, 1975. The authors sampled in three sites and cite 47 to 53 species. (9) From Howden and Nealis, 1975. (10) From Klein, 1989. (11) From Kingston, 1977. (12) Cambefort (1983), without using carrion bait, collected from 77 to 124 species in four savanna sites in the Ivory Coast. (13) The number of species shared with the tropical forest in the same area are shown in parentheses. From Walter, 1977. (14) Cleared land 500 m from the edge of the tropical forest. Same site as in note 4. (15) Pineoak forest with wide clear cut areas, located in a mountainous zone (2,400-3,000 m.a.s.l.) in the south of the Mexican High Plateau (Transverse Volcanic System). After Morón and Zaragoza, 1976. (16) Open area with no trees or shrubs. After Lobo, Martín-Piera and Veiga, 1988.

In spite of the relatively greater species richness of the neotropical forests (compared with that of the American savannas or temperate ecosystems), Cambefort's data indicates that it is in Africa where the tropical forests and particularly the savannas have richer beetle fauna (This of course, depends on the area being inhabited by large vertebrates). What is new is that the beetles of the tropical forests of the Americas are better adapted to overcome the limitation imposed by the lack (or drastic reduction) of mammalian megafauna. The evolutionary-ecological reasons for this will be discussed next.

4. WHY DO THE TROPICAL FORESTS OF THE AMERICAS HAVE SUCH RICH SCARABAEINAE FAUNA?

The territory occupied by the tropical forests of the Neotropics represents an area which is not equalled in any other region of the world. In the ne-

otropics the savannas are comparatively smaller than, and do not currently have the large mammalian fauna richness of, the African savannas. Information accumulated in recent years allows us to assume that, in spite of the variations (and contractions) of the area occupied by the tropical forests, the evolutionary continuity of this kind of community was not interrupted in South America. A greater number of «tropical forest refugia» have been found in the interpluvials of the Pleistocene in South America than in Africa (Haffer, 1969; Laurent, 1973; Vanzolini, 1973).

Tropical South America is the centre of evolution and diversification of a good number of Scarabaeinae phyletic lines (Halffter, 1974). The current area and the evolutionary continuity of the community as well as its association with major Scarabaeinae phylogenetic processes are three good explanation for the richness of the Scarabaeinae in the tropical forests of the Americas. However, they are not sufficient to explain the success of the guild in environments which seem unfavourable for Scarabaeinae. This success can be explained by a series of ecological arguments.

Before dealing with these ecological arguments, I would like to remind the reader of the relative paucity of species of the guild in the tropical grasslands of the Americas. In the first place, it must be pointed out that this lack of Scarabaeinae species richness corresponds to Mesoamerica (tropical Mexico and Central America as far as Costa Rica). We do not have quantitative data for the savannas of tropical South America. The small amount of scattered information seems to indicate that the fauna associated with herbaceous formations is less diverse than that associated with the forests. That is, we do know that the Scarabaeinae are not as varied nor do they have as a high a degree of endemism as in temperate arid grasslands of South America (Martínez, 1959).

It is debatable as to whether the savannas of Mesoamerica are original and stable formations or whether they are a result of local edaphic circumstances, spontaneous fires, human activity or some combination of these factors. It is evident that in modern times, until the last 50 years, Mesoamerican savannas had not been a dominant formation. Herbaceous and open formations have existed for a much longer time in tropical South America (Sarmiento and Monasterio, 1975). Xerica and open ecosystems occupied greater areas at the end of the Pleistocene (and probably during many other periods of the Cenozoic) than that currently occupied by tropical forest in the middle of Amazonia.

5. WHAT ARE THE ECOLOGICAL AND EVOLUTIONARY-ECOLOGICAL ARGUMENTS?

The extinction of mammalian megafauna (animals whose adult weight exceeds 40 kg) at the beginning of the Recent was an historical event of enormous ecological consequence with respect to the richness and ecological performance of present Mexican and Central American Scarabaeinae fauna and

many other plants and animals. Paul S. Martin has thoroughly studied this phenomenon (Martin and Klein, 1989; Martin, 1989). Janzen and Martin (1982) point out that «The number of species of large Central American Pleistocene herbivores in Neogene deposits of the last 10 million years exceeds the number present in the past 10,000 years. Tapir, deer, peccaries, monkeys and capybara occur as Pleistocene fossils, but the remains of gomphotheres (mastodon-like proboscidiens), ground sloths, glyptodonts, extinct equids, *Mixotoxodon*, *Toxodon*, and other extinct large herbivorous animals are more common. If Neotropical ecologists and evolutionary biologists wish to determine who eats fruit, who carries sticky seeds, and who browses, grazes, tramples and voids that segment of the habitat that would have been within reach of a variety of megafaunal trunks, snouts, tongues and teeth, the missing megafauna must be considered».

As for the question, «Why are there so many Scarabaeinae in the tropics of the Americas?», a very important part of the answer may lie in the existence of this mammalian megafauna. It seems natural to associate the diversity of large mammals with the richness of Scarabaeinae which benefitted from the dung produced by the former, in the same way that we associate the great diversity and number of Cenozoic mammals on the South American continent with the abundance of Scarabaeinae fossil remains. Taking this into account the richness attained by the guild of beetle species (as well as the abundance of individuals), in spite of the recent extinction of the megafauna in the tropical forests of the Americas, remains unexplained. The expansion of the tropical forest is a relatively new phenomenon, which contributes to making the richness of the Scarabaeinae guild in these ecosystems even more remarkable. Savannas, shrubland and seasonal deciduous forests dominated these areas during the Late Pliocene and Early Pleistocene. This is shown by the kind of mammals that used the Central American land bridge during this time. It was not until the Late Pleistocene that the bridge became a tropical forest corridor. The savanna, at least in the north and central parts of the Central American bridge, appeared again during the glaciations. Much of the fauna of the savanna, including *Bison* and *Mammuthus*, reached as far south as Nicaragua (see Webb, 1985).

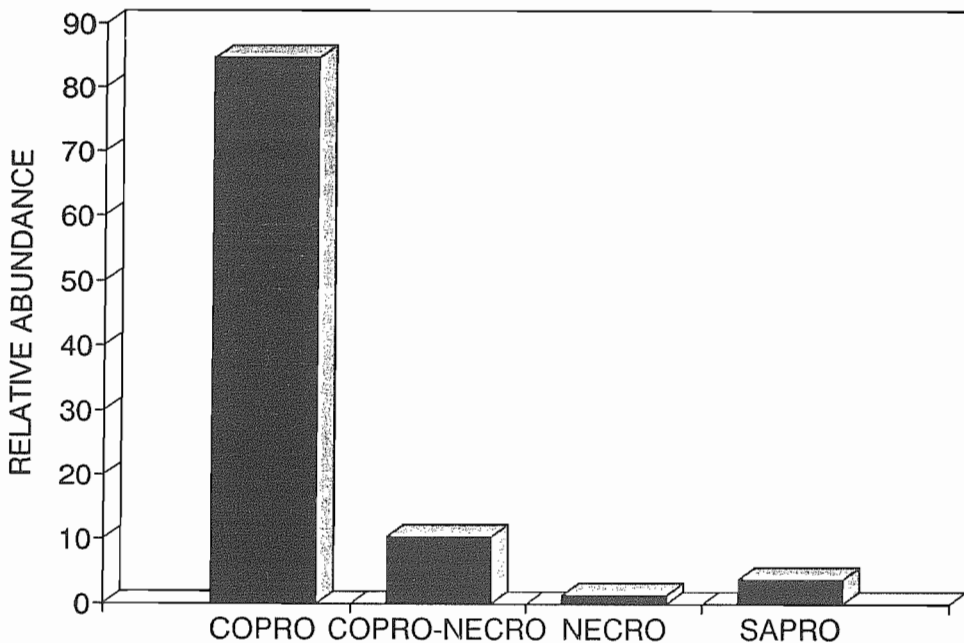
As do the plants of the region (see Raven and Axelrod, 1974), the beetles of the Mesoamerican tropical forests have a predominant South American origin. Few of the species of Septentrional origin are adapted to tropical forests (see Halffter, 1974 and 1976). The extinction of mammalian megafauna, the predominance of tropical rain forests and the expansion of the beetle fauna associated with these tropical forest are all recent evolutionary phenomena in Central America and the south of Mexico. Therefore, the features adopted by the guild in these tropical forests are recent phenomena.

Halffter and Matthews (1966) were the first to suggest an ecological explanation for the richness of Scarabaeinae species in the tropical forests of the Americas, i.e. the transformation of many coprophagous to copro-necrophagous or strictly necrophagous species. Hanski (1983, 1989) shared Halff-

ter and Matthews' ideas and extended this explanation to Borneo. Like Halffter and Matthews, he used the African tropical forest, where Scarabaeinae are very abundant but rarely necrophagous, as the basis for comparison (Table III).

Many studies indicate that changes in behaviour are rapid and usually precede morphological or anatomical changes (see Wcislo, 1989, for a discussion on behaviour related to environment and evolutionary change; Mayr, 1988, synthesizes this idea when he states that «...almost invariably, a change in behaviour is the crucial factor initiating evolutionary innovation»). The adoption of necrophagous, copro-necrophagous and saprophagous habits by many species of Scarabaeinae would represent the great change in behaviour which could explain beetle guild richness in the tropical forests of Borneo and the Americas. The change from a coprophagous habit to a necrophagous (or saprophagous) habit implies changes which are less drastic than one might expect. Adults are microphagous. Micro-organisms and juices are filtered through the setae of their membranous mouth parts. In the larvae, food is fermented by micro-organisms. The transition from dung to carrion as a food takes place without any morphologic or ethological modification (see Halffter and Matthews, 1966; Halffter and Edmonds, 1982). Nevertheless, necrophagy is almost completely limited to the tropics, particularly to tropical forests of the Americas and Southeast Asia.

Tab. 3 - Tai tropical forest (Ivory Coast, Africa). Distribution of Scarabaeinae species by diet type. Prepared from Cambefort's, 1985 (1986) data.



It is not possible to avoid the association between the phyletic diversity of beetles and the past richness of mammalian megafauna in the tropics of the Americas⁽⁴⁾. However, to understand the present richness of the group in tropical forests, in addition to considering the arguments presented in Chapter 4, and perhaps as the main argument, we have to emphasize the tendency towards necrophagy and saprophagy (consumption of rotten fruit). It is quite tempting to associate the extinction of a significant part of the mammalian megafauna with the trophic-ecological turn of the Scarabaeinae towards the benefit of consuming carrion and succulent fallen fruit. This partial change of feeding habit was much more important in the forests where competition from carrion-feeding birds is less. It is also in the tropical forests of the Americas where most of the cases of fruit saprophagy occur.

If we accept the former hypothesis of the development of necrophagy (and secondary saprophagy) of scarabs of the tropical forests of the Americas (and similarly, of Borneo), we do not necessarily have to consider necrophagy as a new phenomenon. What is new is its importance. This idea is supported by the abundance of generalist species (copro-necrophages and copro-saprophages), which are great in number compared to the few strictly necrophagous or saprophagous specialist (see Table IV). It also agrees with the fact that the great majority of cases of necrophagy occur in the neotropics and, according to I. Hanski's studies, in the tropical forests of Southeast Asia. In Africa, which is the only great continental area that did not suffer a massive extinction of large mammals at the end of the Pleistocene or beginning of the Recent, Scarabaeinae are almost exclusively coprophagous.

We have to point out that there is a lack of information about the guild in the South American and Southeast Asian savannas. Almost all of the quantitative information of tropical America and Asia comes from tropical evergreen forests such as the Colombian Amazon (Howden and Nealis, 1975), Barro Colorado Island, Panama (Young, 1978), Ecuador (Peck and Forsyth, 1982), Mexico (Morón and Terrón, 1984; Morón *et al.*, 1985), Manaus, Brazil (Klein, 1989), Sarawak (Hanski, 1983) and my partly published information on the tropical evergreen forests of Palenque (Chiapas), Nayarit, Los Tuxtlas (Veracruz) and several sites in French Guyana. The first quantitative information from savannas or areas with pastures in Mesoamerica is included in Table IV and Figures 5 through 7.

6. OTHER ECOLOGICAL ARGUMENTS

There are other ecological arguments which help to understand the guild diversity in tropical forests, which do not seem to be very favourable communities at first glance owing to the fact that tropical forest do not, with the exception of bats, have the richest mammal community. Firstly, the tropical forest is very heterogeneous. In whichever biogeographical region it occurs it is the most heterogeneous known community, and the tropical forests of the Americas are the richest in species. The base of this very heterogeneity are

Table 4 - Distribution of Scarabaeinae species by activity period and trophic preferences in four ecological conditions in the tropics of Mexico. After Halffter, Favila and Halffter, 1991

COPROPHAGOUS + GENERALISTS						
	Nocturnal			Diurnal		
Palenque	H'	J	R	H'	J	R
Rain forest	1.91	0.64	19	0.84	0.52	5
Forest edge	1.12	0.81	4	1.09	1.0	3
Grassland	—	—	1	0.48	0.43	3
L. Verde	1.41	0.78	6	1.81	0.78	10
NECROPHAGOUS						
	Nocturnal			Diurnal		
Palenque	H'	J	R	H'	J	R
Rain forest	0.76	0.42	6	0.41	0.60	2
Forest edge	1.03	0.94	3	0.56	0.81	2
Grassland	—	—	—	—	—	—
L. Verde	0.89	0.81	3	0.70	0.36	7
COPROPHAGOUS AND NECROPHAGOUS						
	Nocturnal			Diurnal		
Palenque	H'	J	R	H'	J	R
Rain Forest	2.08	0.69	20	1.82	0.79	10
L. Verde	1.59	0.76	8	1.79	0.77	10
COPROPHAGOUS + GENERALISTS			NECROPHAGOUS			
	Nocturnal			Diurnal		
Palenque	H'	J	R	H'	J	R
Rain Forest	2.44	0.74	26	0.96	0.69	4
L. Verde	2.23	0.82	15	0.93	0.84	3

H' Shannon-Wiener information index.

J Equitability ($H'/H' \text{ max}$)

R Richness

the incredible richness of the flora and the most complex vertical stratification known. These make the tropical forest the richest community with respect to ecological niches. Only in the tropical evergreen forests are soil-dwelling animals such as the Scarabaeinae, associated with the upper levels of the tree foliage. In the tropical forests beetles exhibit vertical activity which is different from the commonly observed low flight. The species which are associated with monkey droppings fly and are more common in the tree foliage at heights above 10 meters^(?).

RANK ABUNDANCE PLOTS PALENQUE

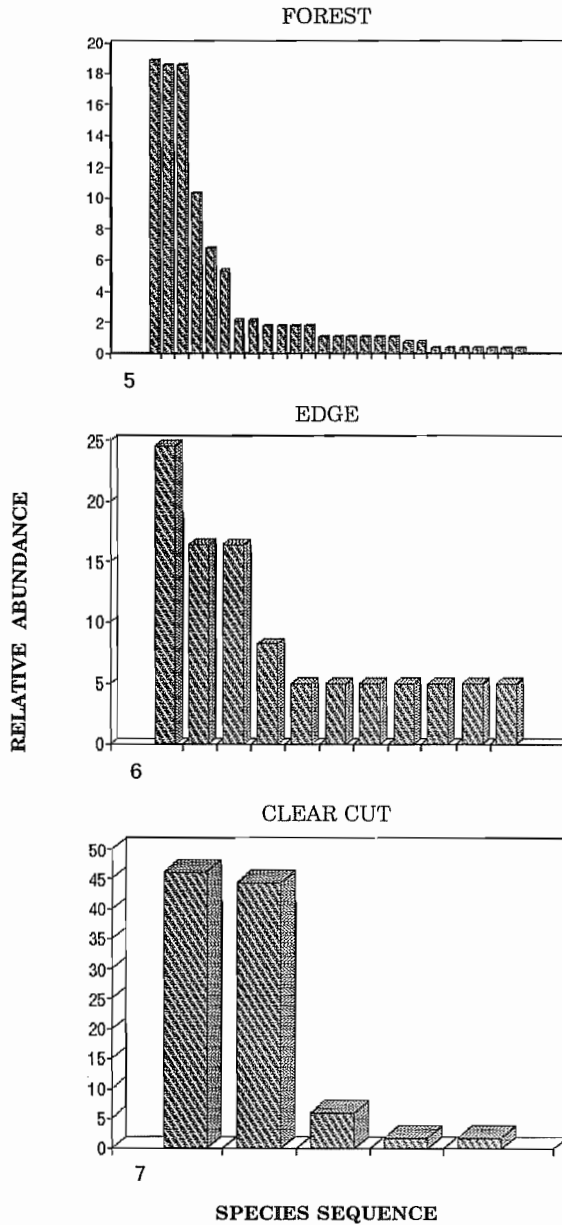


Fig. 5 to 7 - Scarabaeinae: The relationship between species-importance in three distinct ecological conditions in Palenque, Chiapas, Mexico. The **upper part** of the columns corresponds to captures made within the tropical forest, the **middle part** of the columns corresponds to those made at the edge of the tropical forest and the **lower part** to those made in a recent clear cut (After Halffter, Favila and Halffter, 1991).

A new strategy of food detection by beetles has been observed in tropical forests: that of perching on leaves and waiting for the odour to appear (Howden and Nealis, 1978; Howden and Young, 1981; Peck and Forsyth, 1982; Cambefort, 1984; Hanski, 1989).

In the tropical forests there also exists the possibility of a greater horizontal heterogeneity. Many years of capture data leads us to suspect that within the limits of a given tropical forest some beetle species have a patchy distribution. We do not refer here to the aggregated or contagious distribution which is characteristic of Scarabaeinae (associated with the discontinuous distribution of food sources) but rather to patches of hundreds or thousands of meters within an apparently uniform community⁽⁶⁾. The former does not mean that outside of the patch the species are not captured, however capture frequency is much lower. This horizontal heterogeneity seems to be related to the patchy distribution of other biota which are associated with beetles (for example, monkeys). It also appears to be related to guild arrangement. More studies are necessary, but it is possible that this patchiness is a manifestation of beta diversity within the guild.

Trophic generalists dominate in the tropical forests of Southeast Asia and the Americas, although a certain number of strictly coprophagous or necrophagous species are found⁽⁷⁾ (see also Table IV and Hanski, 1989). The former gives feeding an opportunistic strategy and allows the maintenance of a guild rich in species and in individuals. Since dung is an unpredictable and discontinuous resource as well as being highly ephemeral, particularly in the forest there is a competitive advantage to opportunistic feeding on carrion and decomposing fruit for trophic-generalist. Specialization in food detection such as flying towards it or perching, and particularly in relocation mechanisms, compensate for the possible disadvantages (aggregation and competition) of being a generalist. The presence of trophic specialists enriches the guild without increasing competition. These specialists are exclusively necrophagous or coprophagous or are species which only use specific kinds of dung (in extreme cases species are associated exclusively with snail dung - Halffter and Matthews, 1966, or sloth dung⁽⁷⁾, also see Hanski, 1989).

Optimal foraging theory states that specialization appears when the chosen food is sufficiently abundant. It seems reasonable to assume that the limited availability of a particular type of dung, together with intense competition, might make the generalist feeding strategy an advantageous one in tropical forests. Thus, for many species (though not all) competition does not increase specialization, but rather has the opposite effect, and favours trophic generalism. In support of this we note that many more coprophagous than copro-necrophagous (generalist) beetles are found in the African tropical evergreen forests, which are inhabited by a greater number of large mammals.

The higher frequency of opportunist-generalists in the tropical forests of the Americas and Southeast Asia contradicts the rather general idea that the fauna of tropical forests is primarily comprised of specialists.

Another important characteristic of the guild in tropical forests is the

distribution of the total number of individuals among a few species which are very abundant and of a limited number of individuals among many species (see Figures 4 to 8). In Los Tuxtlas, Veracruz, Mexico, collections of monkey and coatimundi droppings allowed the capture of 21 species of beetles. Eighty-one percent of the individuals captured belonged to 5 species and 62% of the individuals to 3 species (Estrada, Halffter and Coates-Estrada, 1991). The species-abundance curve differs from that which is common to simpler ecosystems, with fewer marginal niches, less varied trophic resources and perhaps less stable distribution as well as larger environmental oscillations. The available information, although sparse, clearly indicates that in these simpler ecosystems (i.e. grasslands - Figures 6 and 7) or temperate ecosystems (Hanski and Koskela, 1979) not only is the number of species lower, but there also tends to be more even distribution of individuals among species.

Where available food and number of individuals of beetles in tropical forest have been estimated (e.g. Estrada, Halffter and Coates-Estrada, 1991) the relationship between these factors corresponds to a saturated and stable guild, at least for abundant species (see also Hanski, 1989: 497). Many casual comments in the literature on the species abundance and the speed with which beetles locate droppings in tropical forests, as well as my own years of capture experience in the tropical forests of the Americas, support the former conclusion. However, to a certain extent these observations contradict Cambefort's, 1985 (1986) findings in a tropical forest in Tai where droppings are not completely exploited. Although more information is needed, this could be another difference between the guild in Africa and the guild in the Americas.

Differences in activity time contributes an increase in the number of niches in tropical forests. These types of communities have more nocturnal Scarabaeinae species (Table IV) however the separation of activity in time is more complex than a simple diurnal-nocturnal division. In the case of food, there are beetles which are active for long stretches of time and others which are active for much shorter periods of time.

In contrast, seasonal variation is not as great. These differences are never as marked as those found in temperate or tropical ecosystems with pronounced seasonality. Although there is a decrease in the number of individuals and the frequency with which the species are found during the dry season, the absence of significant seasonal variation results in almost continuous reproduction.

Density-independent factors (rhythm of excrement desiccation, climatic fluctuation, concentrated food deposition) are more important outside of the tropical forests than within them. In tropical forests, density-dependent factors (such as competition for food and nesting sites) are more important. This information all seems to confirm Hanski's statement (1989:508) that «...dung and carrion insects in tropical forests exemplify equilibrium assemblages of species, strongly affected by interspecific competition. Temperate

assemblages of species associated with dung and carrion represent communities which are less stable, characterized by great short-term and long-term fluctuations in abundance». Future studies on beetle population dynamics will confirm or refute this.

In the last four decades Mexico and Central America have suffered, and are still suffering, the rapid and extensive destruction of their humid tropical forests. Immediately after deforestation, or after a precarious agricultural stage, the clear cuts are sowed with grass and are devoted to cattle raising. In spite of the increased abundance of food associated with the cattle, very few species adapt to the new conditions and few species are associated with the cleared land (see Figures 6 and 7). This results in a fauna which is poor in Scarabaeinae species. As expected, induced pastures allow the spatial expansion of ubiquitous and tolerant species in relation to the environment (climatic factors, vegetation type), but the latter are more restricted in relation to food. There are coprophagous species which benefit from cattle dung, such as *Dichotomius carolinus* (L.) or the African species *Digitonthophagus gazella*. The latter was introduced to Texas in 1979 and is currently distributed further south than the Mexico-Guatemala border, having expanded southwards along the slope of the Gulf of Mexico as well as the Pacific slope.

Pastures which have a richer Scarabaeinae guild are found in such places as Laguna Verde, Veracruz, Mexico, where patches or remnants of tropical forest remain and some of the more tolerant Scarabaeinae forest guild species have persisted (Figure 8).

7. WHY IS THE SCARABAEINAE GUILD STRUCTURE OF THE TROPICAL FORESTS OF THE AMERICAS SIMILAR TO THAT OF SOUTHEAST ASIAN TROPICAL FOREST, WHILE THAT OF AFRICAN TROPICAL FORESTS IS DIFFERENT?

In the Americas and Borneo the similarities lie in the guild structure, including size, form and behavioural displays of member species. The taxonomic composition however, is very different as would be expected in regions with different biogeographic histories. In African forests the conditions which make necrophagy so important in the Americas and Borneo are not present. In Africa the number of large mammals is far greater. The biomass of arboreal primates is also greater⁸. In addition, other necrophagous insects, such as flies of the family Calliphoridae (Hanski, 1983) are present and more abundant than in the Americas and Borneo. In the Americas, and perhaps other tropical regions, ants compete strongly with Scarabaeinae for carrion (see Cornaby, 1974). Quantitative analysis which would allow the determination of the importance of Scarabaeinae in relation to other necrophagous insects in different regions is lacking.

To explain the structural similarity of the guild found in the forests of the Americas and in Borneo it appears that ecological convergence, most likely recent, is more important than taxonomic differences. Taxonomically, Africa

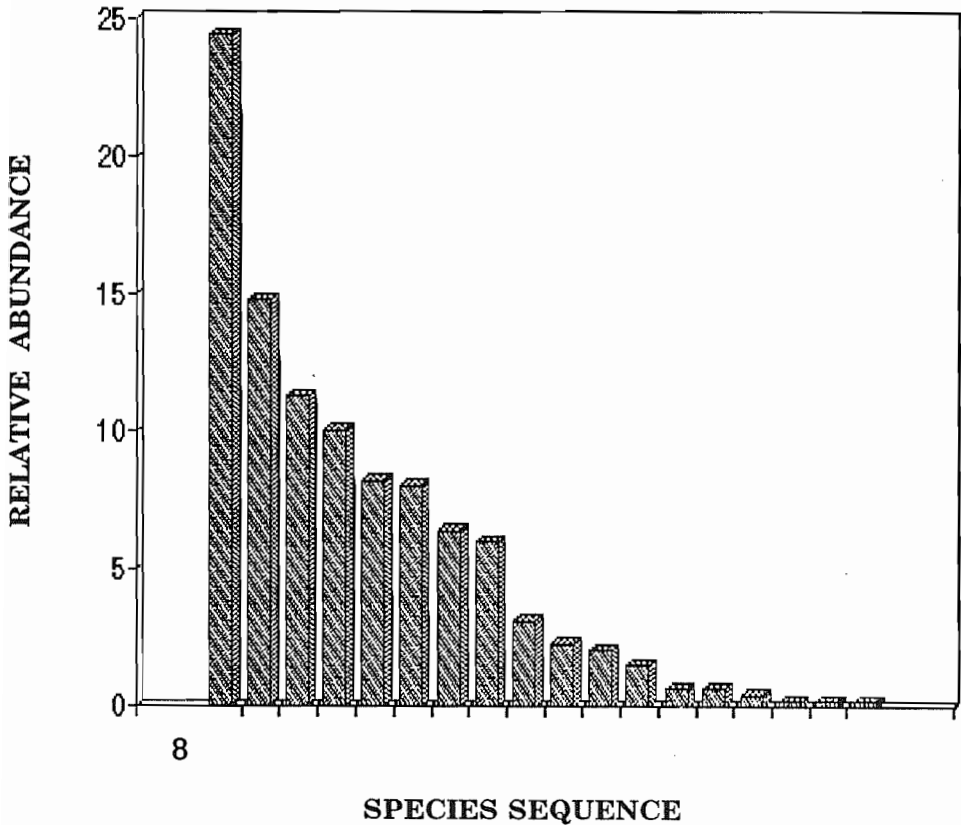


Fig. 8 - Scarabaeinae: The relationship between species-importance in a mosaic of vegetation types at Laguna Verde, Veracruz, Mexico (After Halffter, Favila and Halffter, 1991).

and Borneo have more affinities, primarily because of the spread of the dominant genera (such as *Onthophagus*, *Copris*, *Gymnopleurus*, *Sisyphus* etc.) across the great land masses of the Northern Hemisphere. We have seen that what is different is the ecological structure, illustrated both in the Americas and in Borneo by necrophagy and the predominance of trophic generalist species. At least in the Americas (and perhaps in Borneo), the beetle species are very stenotopic with respect to environmental conditions (see additional information of Africa in notes 7 and 9).

Why is the guild more diverse in one region than in another? According to Pianka (1974) there are several reasons for this: 1) a greater availability of sources; 2) narrower ecological niches for species; 3) superimposition of niches and 4) community saturation, i.e. fewer empty niches. If we apply this reasoning to the Americas (and the information currently available allows us to consider Borneo in some respects), resource availability has to be correlated with the transition of many species to necrophagy (exclusive or partial), and to a lesser degree, to saprophagy. Having experienced a very recent

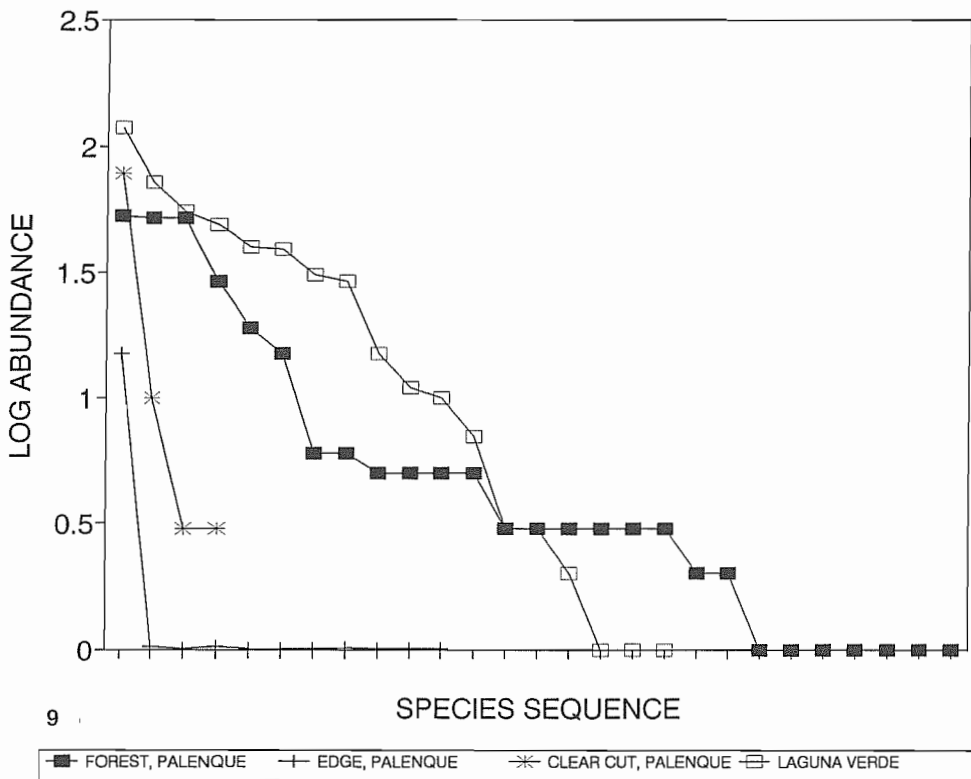


Fig. 9 - Comparison of Scarabaeinae species-importance curves for Palenque, Chiapas (tropical forest, tropical forest edge and clear cut) and Laguna Verde, Veracruz (After Halffter, Favila and Halffter, 1991).

expansion, the Mexican and Central American pastures, would not be expected to have such a high rate of trophic transformation. This would explain the lower number of species found in these environments, while the savannas of the Pleistocene must have had a rich beetle fauna associated with the extinct mammalian megafauna. In summary, the greater resource availability in the tropical forests of the Americas and Southeast Asia is a result of the exploitation of trophic resources such as carrion and fruit which are not exploited by Scarabaeinae in other ecosystems. Niche specialization in forests appears as differences in vertical and horizontal distribution as well as different daily activity patterns. In addition, the coexistence of generalist and stenotrophic species may also be considered as a type of specialization. Overlap is evident and occurs mostly in the food dimension, although it can also be observed in time and space. In assemblages, few species with wide niches coexist with many species with narrow niches as seen in the species abundance curves. With respect to environmental saturation, the few studies and observation which have been done on beetles in the tropical forests of the

Americas indicate saturated communities. The same is not found in the African forests. In spite of a greater availability of mammal dung droppings, and perhaps because of this availability, the beetles do not exploit carrion and decomposed fruit intensely. Thus in Africa, neither the trophic niche diversity nor the same degree of overlap between generalist and specialist species exists as is found in the Americas. Furthermore, according to Cambefort's observations even the dung resource is not completely exploited in Africa. It seems evident that, in spite of the species richness found in the African forest, the degree of «saturation» is less than in the savannas of the same continent.

8. COMMUNITY BIOGEOGRAPHY

Let us return to the original question. Does community biogeography exist beyond the descriptive level? The analysis of the relationship between the Scarabaeinae and tropical forests shows that community biogeography based primarily on historical-evolutionary arguments is not possible. This biogeography is possible when it deals with taxa with distinct hierarchies, but in the case of communities the current ecological conditions dominate. Nevertheless, many questions remain unanswered if we do not link ecological explanations to a historical perspective. The biological diversity of a given site is a result of the niche separation process, but it is also a result of the evolutionary history of the site. The existence of empty or partially occupied niches (e.g. Mexican and Central American savannas) as well as great changes in the behaviour of species (e.g. necrophagy) are all historical-evolutionary phenomena. It is not possible to continue with the idea of a community-superorganism as a unit which is well-defined in time and space, nor is it possible to consider the community simply as a random result of variations in environmental parameters. To develop a new perspective of the community, biogeographical analysis, at a level beyond that of description, makes sense even though neither the methods nor the objectives can be the same as those used when dealing with well-defined taxa. The comparative analysis of the guilds in different geographic situations would allow an exploration of the relative importance of ecological and historical-evolutionary elements.

9. ON REFLECTION

1. The tropical forests of the Americas and Borneo are rich, both in Scarabaeinae species and individuals and this richness is greater than might be expected. This results primarily from the high frequency of necrophagy and, to a lesser extent, saprophagy as food strategy which complements the exploitation of dung (Chapter 5).

2. The dominance of trophic generalist in the tropical forests of the Americas and Borneo allows for opportunistic feeding strategies and hence the maintenance of a guild which is rich in both species and individuals, in

spite of the lesser supply of dung. The disadvantages of the trophic generalism are compensated for by the diversification of food location and relocation mechanisms (Chapter 6).

3. Necrophagy and saprophagy are derived feeding habits which have allowed the Scarabaeinae to flourish in the tropical forests of the Americas and Borneo. The high frequency of these habits is recent, as is shown by the low percentage of specialists (Chapter 6).

4. The ecological structure of the guild is similar in the Americas and Borneo in spite of phylogenetic differences. However, ecological structure is different between Africa and Borneo, independent of similarities in taxonomic composition (Chapter 6).

5. In the tropical forests of the Americas and Borneo trophic generalists (copro-necrophages, copro-saprophages) are dominant. In Africa exclusively coprophagous species dominate (Chapter 7, note 7).

6. In the tropical forests of the Americas the frequency distribution indicates that there are few species which are very abundant and many more which have low numbers of individuals. In European temperate ecosystems distribution is more even (this may also occur in the tropical grasslands of the Americas, but information is limited) (Chapter 6).

7. New tactics for detection and exploitation of dung appear in tropical forests; i.e. perching and the exploitation of the vertical dimension (tree foliage). Both appear to be tactics suited to taking advantage of small or fragmented excrement on branches and leaves. Activity in the foliage at 10 meters or more above the ground is linked to the exclusive exploitation of arboreal mammal dung, principally that of monkeys (Chapter 6, note 5).

8. The species richness of the Scarabaeinae of the Americas can be associated with the rich mammal megafauna that went extinct at the end of the Pleistocene and during the Recent. The present richness in the tropical forests of the Americas is more a result of survival and expansion than of the emergence of new taxa (Chapter 5, note 4).

9. The ecosystem where the greatest number of species and individuals of Scarabaeinae is found is the African savanna. The previous statement supports the historic-evolutionary hypothesis (i.e. that the guild evolved in relation to the dung of large mammals; a mammalian megafauna that has not suffered great extinction in the Pleistocene-Recent), as well as the ecological hypotheses (greater number of large mammals) (Chapter 3, note 7).

10. The tropical grasslands of the Americas have notably fewer Scarabaeinae species than the tropical forests. This phenomenon is most notable in Mexico, where modern expansion of grasslands is a recent phenomenon. Studies of grasslands and open formations of South America are lacking, but doubtless these do not have a fauna equivalent to that of the African Savannas (Chapter 4).

11. The extinction of the large mammals in the Pleistocene and Recent in the Americas has had a greater effect on the Scarabaeinae guilds of grasslands than on the guilds of the tropical forests. This could be a result of a

greater success in the exploitation of carrion as a resource in tropical forests, but also results from the expansion of tropical forests in Central America and Mexico (where the difference in the richness of Scarabaeinae between the two ecosystems is most noticeable) during the Late Pleistocene and Recent (Chapters 5 & 7).

12. Scarabaeinae of the tropical rain forest and the tropical evergreen forest in Mexico show a noteworthy taxonomic similarity to the Scarabaeinae found in similar ecosystems of Central America and northern South America. This can be clearly associated with the recent expansion of the tropical forest towards the north.

13. In this article I propose more questions than answers. Many themes are touched on lightly but no solutions are proposed. Great possibilities exist in the comparative study of the guild in distinct ecosystems and in different geographical regions. Answers are important not only for knowledge of the guild itself, but also for the analysis of the historic and ecological facts which determine the distribution of living beings.

ACKNOWLEDGEMENTS

My awareness of the necessity for addressing the relationship between the Scarabaeinae and the biogeography resulted from the invitation by Professor Mario Zunino (University of Turin) to give a conference at the XXVIII Congresso della Società Italiana di Biogeografia. I am truly grateful to Professor Zunino for this challenge. The data on Palenque and Laguna Verde form part of a project currently being carried out by Mario Enrique Favila, Violeta Halffter and myself; I am grateful to my colleagues for the use these data. Jaime Alfredo Anguiano Solis of the Institute of Ecology prepared the graphs and diagrams for me. Dr. W. David Edmonds (California State University, Pomona, California) read an early version of the text and made valuable observations. I especially wish to thank Bianca Delfosse for her careful translation of the original Spanish text into English.

NOTES

(¹) *Ecosystem* is the *community* plus its abiotic components. Both terms are part of the same idea. The organisms live in interacting assemblages, with certain characteristics and with their own structural, functional and energetic processes. The idea that each one of these assemblages is a *system* implies that the organisms and the environment form, under certain conditions, an interacting unit that has distinct features which separate them from other equivalent units.

Golley (1983) indicates that the term ecosystem was coined by Tansley (1935), broadened by Evans (1956) and brought into general use thanks to Odum (1953). There is no doubt that for this reason, as for his treatment of other concepts in ecology, E.P. Odum's excellent and widely-read book is a landmark.

The term ecosystem, as well as that of community, is used with extraordinary laxity with respect to geographical scale.

(²) I use the term *tropical forest* as the generic name of the humid tropical forests. The term tropical forest applies to a large variety of communities, which may differ greatly in their floristic and faunal composition, but have physiognomic and structural similarities which are determined primarily by climatic conditions. The fact that ecological factors impose similarities and that historical-biogeographic factors impose differences is the core of the main question which this article addresses about the limits of the biogeography of communities.

(⁴) To give an idea of what tropical America has lost, Janzen and Martin (1982) indicate, «The present-day analogy is a tropical, forested African habitat stripped of its elephants, rhinoceroses, zebras, lands, bush pigs and other large herbivores and left alone for 10,000 years».

(⁵) Only in tropical forests do the Scarabaeinae leave the ground for significant periods of time. In any ecosystem, almost all species of Scarabaeinae seek new food sources while in flight. This is done at relatively low altitudes and during short periods of time relative to the time spent handling food on or under the ground. Only some species of tropical forests spend most of their time at heights greater than 10 meters, generally engaged in feeding. It is also possible that, in some cases, nesting is carried out above the ground.

We have pointed out that vertical relocation of food changes the beetle habitat to a three dimensional one. The conquest of greater heights in the forest further augments this space.

A first step in exploiting the foliage of forest trees is the incorporation of perching into feeding behaviour. While perched, the beetle may wait for and detect food without moving in a universe where food is ephemeral, not very abundant, and not always found on the ground. Perching can occur at different heights, and the height selected does not appear to be random. Random perching occurs in species which are almost all small in size and which inhabit tropical forests. As for other behavioural displays of beetle species of tropical forests, the first observations of this were made by F. Ohaus (1990, 1909). New data and a new discussion are presented in Halffter and Matthews (1966:89). In recent years abundant information has been published (Howden and Nealis, 1978; Young, 1978; Howden and Young, 1981; Peck and Forsyth 1982; Cambefort, 1982; Hanski, 1989).

There are few direct observations of the activities of the beetles during the time spent at these heights. Captures made by pitfall traps indicate the abundance of the beetles high in the tree foliage as well as their absence at low heights or ground level. There is a near-complete absence of information about whether the beetles are flying constantly, are perched on leaves and branches, or are eating and managing the excrement which they may find up in the foliage. This same lack of information occurs for the association between beetles and monkeys or sloths. A few species of beetles have been found in the fur of dead animals which have fallen from the trees. We have no direct observation of how they live on the animals.

The first report of a beetle species found at a height above 10 meters was made by Halffter and Matthews (1967:48) who reported a *Canthon* (*Glaphyrocanthon*) sp. in Palenque, Mexico. This beetle has since been identified as *Canthon* (*Gl.*) *subbyalinus* Harold and was captured during systematic sampling carried out by Gonzalo Halffter, Violeta Halffter and Imelda Martínez in what was then the tropical forest surrounding the Palenque Ruins, Chiapas, Mexico. This information was included in my doctoral dissertation (Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, March 1966) and was not published with the exception of the reference quoted at the beginning of the paragraph. Owing to their interesting nature, a synthesis of these notes is presented here.

In 1965 the tropical rain forest surrounded Palenque and extended from there as tropical rain or evergreen forest in every direction except towards the coastal plain which was already deforested. During five days (May 21-25) an intense collection of beetles was carried out around the archaeological area of Palenque, by placing pitfall traps with different bait throughout the forest, in the ecotones and in the clear cuts. The result of trapping was the capture of slightly more than 4000 beetles. More than 100 traps had been placed on the ground however only one *C. (Gl.) subbyalinus* was caught in a pitfall with human excrement. In contrast, pitfalls with human excrement which had been placed at a height of 15 m captured a mean of 22 individuals. *Ateles* and *Alouatta* monkeys were still common to the area at the time of the study and the presence of these animals in the trapping area was personally verified. For above-ground trapping, in addition to pitfalls with droppings, other pitfalls were baited with carrion. It was not possible to determine if any necrophagous or necro-coprophagous Scarabaeinae were attracted to the latter because when the traps were collected, all of them had been invaded by ants. After *C. (Gl.) subbyalinus* individuals were captured, they were maintained in terrariums and provided with human excrement. In this way a series of observations on their behaviour could be made. Construction of the ball. - Resting on the small mass of dung and supported on three pairs of legs, the beetle shapes and separates the initial mass with the clypeus. The anterior legs are occasionally used to facilitate this action. Then the anterior legs are used to add excrement to the mass while it is pushed backwards. The hind legs and occasionally the median legs stay in contact with the ball. This behaviour, although not uncommon to other species of the genus *Canthon*, explains how this species can form the ball when the dung is dispersed on a branch. When the ball has been separated the beetle passes over it several times, smoothing out any protruding portion with its anterior tibiae. The final touches are carried out by deliberate, repeated flattening movements of the anterior tibiae as well as the meso- and metathoracic tarsi. Meanwhile, with the anterior legs, small additional amounts of dung are incorporated. All these movements give the beetle the appearance of «dancing» on the ball. The separation procedure lasts from 10 to 15 minutes. During the following 10 minutes the beetle repeatedly passes over the ball before beginning to roll it.

Rolling. - The beetle carries this behaviour out from the «pushing position». The beetle rests on the

ground on its clypeus and anterior legs while it fastens its hind legs and, to a lesser degree the median legs to the ball. Rolled balls were often found on the small branches and leaves of the terrarium substratum. This leads us to believe that the beetles may leave many balls in the «high gardens» of tropical forests.

Pheromone Emission. - Beetles were observed in the position recognize as that assumed for pheromone emission (Bellés and Favila, 1983). That is, the beetle was lying against the dung mass, head downwards, supported by the anterior and median legs and with the hind legs stretched out. The hind legs were moved and rubbed along the body.

Flight. - Observed flight was slow, and specifically directed towards the dung, i.e. not zigzagging. This activity occurs during the day, and coincides with the periods of defecation of the howler monkey. These beetles have the ability to climb small branches and leaves. This activity is also observed in the tropical forests of French Guyana in closely related species (G. Halffter).

In Gabon (Africa) Walter (1983) collected 4 species in pitfalls located above 10 meters: *Ontobpagus laeiceps* d'Orbigny, *O. possoi* Walter, *O. abenomicans* d'Orbigny and *Sisyphus arboreus* Walter. A fifth species (*Ontobpagus rupassa* Walter) was collected at a height of five meters. Of the four species captured at 10 meters, all but *O. abenomicans* were also captured at 21 m. Walter associates *Ontobpagus laeiceps* and *O. possoi* as well as *Sisyphus* with the foliage of the tropical forest. A representative number of both sexes of these three species was captured between five and 21 meters. The greatest number of *O. possoi* were captured at 21 m, while the greatest number of *Ontobpagus laeiceps* and *Sisyphus arboreus* at 10 meters. These species were almost completely absent at ground level. It is not known where these species nest, i.e. whether nesting takes place in the debris that accumulates on epiphytes or whether the beetles let themselves fall to the ground in order to nest. Walter observed *Sisyphus* preparing and rolling balls on the tree traps.

Howden and Young (1981) report two «rolling» beetle species above 20 m in Panama [*Canthon* (*Glaphyrocanthon*) *angustatus* Harold and *C. (Gl.) subhyalinus* Harold]. Both species prepare the ball using monkey dropping left on the branches. Fastened to the ball, the beetle drops to the ground. Once on the ground the feeding or nesting behaviour follows the pattern commonly observed in rolling species. As are some other closely related species of the subgenus *Glaphyrocanthon*, *C. angustatus* and *C. subhyalinus* appear to be specifically associated with monkey droppings. They are found on the ground, but in lesser numbers than in the tree foliage. The exploitation of the tree foliage seems to be part of the food search strategy of these species. Falling to the ground with the ball is an effective form of maintaining contact.

C. angustatus is a specialist on howler monkey (*Alouatta palliata*) droppings which is the most abundant, available and predictable excrement where there has been no recent disturbance on Barro Colorado Island, Panama. Under these conditions it is the dominant species in the guild. According to Orrey P. Young (*in litt.* 3/17/1976; Howden and Young, 1981) *C. angustatus* begins foraging perched on the surface of a leaf with its antennae extended. It can detect the presence of fresh howler monkey dung up at a distance of at least 100 m. «Usually when a howler monkey defecates the fecal material hits many leaves and branches on the way down and in some cases will not even reach the ground. *Canthon angustatus* and the smaller, much less abundant *Canthon subhyalinus* are the only species that go up in seeking the fecal deposits».

Another *Canthon* (*Glaphyrocanthon*) of the Americas, *C. (GL.) femoralis femoralis* is associated with monkeys and the tree foliage. This subspecies has a wide dispersion in Mexican tropical forests and closely related taxa have a distribution which stretches towards the northwestern tropical forests of South America (Martínez and Halffter, 1972). *C. (GL.) femoralis femoralis* is commonly collected in pitfall traps containing human excrement placed on the ground in sites where monkeys are no longer found in tropical forests. Recent observations show, however, that they are abundant in the foliage in the few places where monkeys are still present. This species was one of the first beetles I observed perching on leaves (Halffter and Matthews, 1966: 89, and several later observations). Over several days Gonzalo and Violeta Halffter, together with a group of students, placed pitfall traps in the Estación de Biología Tropical (Tropical Biology Station) «Los Tuxtlas» of the Universidad Nacional Autónoma de México in August, 1987. Located in the state of Veracruz, on the coast of the Gulf of Mexico, the «Los Tuxtlas» Station is one of the few remaining areas with tropical rain forest and monkeys. Human excrement pitfalls placed on the ground captured a reduced number of *femoralis* individuals (mean: 3/pitfall). In contrast, pitfall traps with the same bait and at the same site, but at a height of 20 meters captured more than 25 individuals each. The number of individuals flying around the pitfall traps in the foliage was remarkable. At the same station, Estrada, Halffter and Coates-Estrada (1991) did sampling on the ground using the droppings of the howler monkey (*Alouatta palliata*) and the carnivorous *Nasua narica*. Fifty seven percent of the total number of beetles captured on the *Alouatta* dung were *C. (GL.) femoralis femoralis*. Ninety six percent of *C. (GL.) femoralis femoralis* individuals were captured on the monkey droppings.

Hanski (1989) points out that in Sulawesi a species of the genus *Ontobpagus* was captured only in the tree foliage.

To date all species collected in the tree foliage are small in size. These species represent a limited sample of a much more complex universe since only in very few studies have pitfall traps been placed in tropical forest canopies because of the difficulty of doing so.

The fact that a part of the adult life takes place on the ground explains why individuals are captured, although with much less frequency, in pitfall traps located on the ground. Neither the possibility that a certain number of balls (along with the beetle) remain in the above-ground «gardens», nor the possibility that nesting takes place up in the foliage can be excluded. In the case of the African genus *Sisyphus* there exists the precedent that three other species of the genus, which are associated with the ground, leave their nest-balls stuck to vegetation with dung (Paschalidis, 1974).

How do digging *Onthophagus* which are associated with the tree foliage nest? Walter (1983) suggests that species of this genus may lose the habit of packing one or several brood masses and use dung that remains in the tree foliage to nest. In Brazil the genus *Bdelyrus* (possibly a digger beetle, owing to its taxonomic affinity) has been collected several times at the base of bromelias and epiphytes several meters above the ground (Pereira, Vulcano and Martínez, 1960; see discussion in Halffter and Matthews, 1966: 35-36). This would represent another case of separation from the ground in which nesting may occur in the tree foliage although to date this has not been verified.

In addition to the species captured in pitfall traps placed in the tree foliage, some species have been collected from the hair of fallen arboreal mammals (see review in Halffter and Matthews, 1966: 43-45). *C. (Gl.) subhyalinus* has been captured from monkeys in Brazil. *C. (Gl.) quadriguttatus* (Olivier), closely related to the latter species, has been captured under the same conditions. Phoresis (Halffter, 1959; Halffter and Matthews, 1966) is even more noticeable in beetle species associated with sloths (*Bradypus*). Halffter and Matthews (1966) mention three species collected on the fur of sloths: *Uroxys gorgon* Arrow (Colombia), *Uroxys* sp. (Bolivia) and *Trichillum bradyorum* Boucomont (Costa Rica). In addition to *Uroxys gorgon* (Colombia and Panama) and *Pedarium bradyorum* (previously cited as *Trichillum* in Costa Rica) Ratcliffe (1980), Young (1981) and Howden and Young (1981) add *Uroxys metagorgon* (Howden and Young, Panama), *U. besti* Ratcliffe (Manaus) and *Trichillum adisi* (Ratcliffe) to the list of beetles which are associated with sloths.

«The role played by scarabs living on sloths remains an enigma for the most part. It is generally suspected that these beetles are phoretic coprophages dwelling on the sloth until such time as it defecates. The scarabs can then abandon their host and feed on the freshly deposited dung. *Trichillum adisi* was seen to do this, and larvae and pupae were recovered from the small dung pellets of the both... To my knowledge, however, no other scarab has been reported actually breeding in sloth dung» (Ratcliffe, 1980). Sloths descend from trees to defecate at intervals of approximately one week and the dung is buried in a superficial hole (Ratcliffe, 1980). The pellets are dry, very hard and odourless to human beings (Young, 1981). Sloth pellets are definitely not attractive to Scarabaeinae and Diptera fauna in general (Ratcliffe, 1980; Young, 1981). *Uroxys besti* has been seen fragmenting and burying small portions of sloth dung in the laboratory. Nevertheless, with the exception of *Trichillum adisi*, it is not known how the species of associated scarabs reproduce, although it is very likely that they follow a similar procedure to that of *T. adisi*.

Ratcliffe (1980) poses a series of questions on the relations between the scarabs and this totally arboreal mammal (*Bradypus*), to which we do not have a documented answer. I consider one of these questions particularly interesting: What are the activities of those scarabs that reside on a sloth host which is feeding in the foliage of a *varzea* (seasonally flooded) forest during high water? The sloths continue to descend at weekly intervals during the high water, but defecate into the water where the scarabs cannot follow. If the dung pellets of the sloth are a food resource and an oviposition site for these beetles, then the scarabs are up a tree (as it were) for two to five months out of the year while the forest is flooded. What are the beetles feeding on? Where do the larvae develop? Do the adults leave the sloths and, if so, where do they go?

(6) In areas where I have collected repeatedly over the last 40 years, some species (e.g. *Canthon cyanellus cyanellus*, *Canthon femoralis femoralis*, *Canthon euryscelis* and others in Los Tuxtlas, Veracruz, Mexico) appear in one site, but not in another which is only located a few thousand meters away. In general, the difference is not one of presence or absence, but rather, frequency. I have no information of an equivalent phenomenon in tropical herbaceous formations or in warm-temperature ecosystem. This heterogeneity is not explainable as a result of differences in the accumulation of food, height, temperature or macro-differences in precipitation. It has to be attributed to structural differences in the tropical forest and/or to competition within the guild.

(7) Compare the data from the Americas and Borneo included in the text with the following numbers for tropical Africa: 187 species of beetles in savannas and 78 in tropical forests in communities where mammalian megafauna still exist in the Ivory Coast [Cambeport, 1985 (1986)]. The distribution by food is also different in Africa. In the tropical forest of Tai, Ivory Coast, [Cambeport, 1985 (1986)] 66 species (84.6% of the total) are coprophages. Of these, 26 species (33.3% of the total) were not found anywhere except in the droppings of two very big mammals: elephants and buffaloes. The other coprophagous

species were also found in droppings of small hippopotamus, antelopes, primates, etc. A small number of species, (8, representing 10.3% of the total) were attracted by carrion, but only one species (1.3% of the total) is strictly necrophagous. Finally, 3 species (3.8% of the total) of the genus *Paraphytus* live in old decaying logs (probably primitive saprophagy). This trophic distribution supports the idea of a complete dominance of coprophagy in Africa (which is even probably greater in the savannas), with a large percentage of stenotrophic species.

The relation between Scarabaeinae and ecosystem in Africa is shown by Walter's (1989) data for the Bateke Plateau in Zaire. Only 6.5% of the species are found both in the savanna and the tropical forest, while 72% are typical of the savannas and 21.5% are found in tropical forests. A certain number of species of the savanna have ranges that occasionally extend into the tropical forest or vice versa. In Africa the distribution of species between ecosystem differs from the proportions found in the Americas. Once more, this indicates the existence of a much greater number of species in African savannas and relatively less specialization in the African tropical forest fauna in comparison to the Americas.

⁽⁸⁾ Although more information is needed, comparisons such as Bourliere's (1983:84) indicate that the biomass of arboreal primates is much greater in Africa or Sri Lanka, than in the tropical forests of Barro Colorado Island, Panama. Although sloths are important members of the arboreal fauna in the tropical forests of the Americas, their dung does not play a role in the Scarabaeinae guild. Sloth dung, which has a very peculiar consistency and is buried in the soil by the animal, is only exploited by a few, specialized Scarabaeinae (see note 5).

⁽⁹⁾ Cambefort (1984) presents a comparison of four tropical forest locations in the Ivory Coast which include evergreen, semi-deciduous and tropical forests extending from the equator northwards. The number of Scarabaeinae species of tropical forests decreases from 78 to 25 and then to 5 as we move northwards. The number of savanna species which inhabit the forests increases from 0 to 10 and then to 38 moving towards the north. This marked increase in overlap exists in all types of vegetation of savanna-tropical forest associations in tropical Africa. This gradation does not occur in the Americas however, there is a clear loss of tropical forest species in both natural and induced herbaceous ecosystems (see Halffter and Matthews, 1966; Howden and Nealis, 1975; Klein, 1989; Halffter, Favila and Halffter, 1991).

With respect and admiration, I dedicate this article to two great entomologists, Roy A. Crowson and Renaud Paulian.

LITERATURE CITED

- BELLES X., FAVILA M.E., 1983 - Protection chimique du nid chez *Canthon cyanellus cyanellus* (Coleoptera, Scarabaeinae). *Bull. Soc. ent. Fr.* **88**: 603-607.
- BORNEMISSZA G.F., 1976 - The Australian dung beetle project 1965-1975. *Australian meat Research Committee Review.* **30**: 1-32.
- BOURLIERE F., 1983 - Animal species diversity in tropical forests. In F.B. Golley (ed.) *Tropical Rain Forest Ecosystems: Structure and Function*. Elsevier Publ. pp. 77-91.
- CAMBEFORT Y., 1982 - Les coléoptères Scarabaeidae s. str. de Lamto (Côte d'Ivoire): structure des peuplements et rôle dans l'écosystème. *Annls. Soc. ent. Fr.* **18**(4): 333-359.
- CAMBEFORT Y., 1983 - Etude écologique des coléoptères Scarabaeidae de Côte d'Ivoire. Ph. D. Thesis. Université Pierre et Marie Curie, Paris. 294 pp.
- CAMBEFORT Y., 1984 - Etude écologique des coléoptères Scarabaeidae de Côte d'Ivoire. *Trav. Cherch. Lamto.* **3**: 1-294.
- CAMBEFORT Y., 1985 (1986) - Les coléoptères Scarabaeidae du Parc National de Taï (Côte d'Ivoire). *Revue fr. Ent. (N.S.)*. **7**(5): 337-342.
- CAMBEFORT Y., 1986 - Rôle des coléoptères Scarabaeidae dans l'enfouissement des excréments en savane guinéenne de Côte-d'Ivoire. *Acta Oecol., Oecol. Gen.* **7**(1): 17-25.
- CORNABY B.W., 1974 - Carrion reduction by animals in contrasting tropical habitats. *Biotropica* **6**(1): 51-53.
- DI CASTRI F., HADLEY M., 1988 - Enhancing the credibility of Ecology: interacting along and across hierarchical scales. *Geo-Journal.* **17**(1): 5-35.
- EDMONDS W.D., 1983 - Intervention des facteurs écologiques dans l'évolution de la nidification chez les Scarabaeinae (Col., Scarabaeidae). *Bull. Soc. ent. Fr.* **88**(7-8): 470-481.
- ESTRADA A., HALFFTER G., COATES-ESTRADA R., 1991 - Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico. (Submitted to publication).
- GOLLEY F.B., 1983 - Introduction (pp. 1-8). In F.B. Golley (ed.) *Tropical Rain Forest Ecosystems*. 381 pp. Ecosystems of the World, 14A. Elsevier Publ.

- HAFFER J., 1969 - Speciation in Amazonian forest birds. *Science*. **165**: 131-137.
- HALFFTER G., 1959 - Etología y paleontología de Scarabaeinae. *Ciencia (Méx)*. **19** (8-10): 165-178.
- HALFFTER G., 1974 - Eléments anciens de l'Entomofaune Neotropical: ses implications biogéographiques. *Quest. Ent.* **10**: 223-262.
- HALFFTER G., 1976 - Distribución de los insectos en la Zona de Transición Mexicana. Relaciones con la entomofauna de Norteamérica. *Folia Entomol. Mex.* **35**: 64 pp.
- HALFFTER G., 1992 - Feeding, bisexual cooperation and subsocial behavior in three groups of Coleoptera. In M. Zunino, X. Bellés and M. Blas (eds.) *Advances in Coleopterology*: 281-296. A.E.C., Barcelona.
- HALFFTER G., EDMONDS W.D., 1982 - The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutionary Approach. *Publs. Instituto de Ecología, Mexico, D.F.* **10**: 176 pp.
- HALFFTER G., FAVILA M.E., HALFFTER V., 1991 - Comparative studies on the structure of scarab guilds in Tropical rain forest. (Submitted to publication).
- HALFFTER G., MATTHEWS E.G., 1966 - The Natural History of Dung Beetles of the Subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomol. Mex.* **12-14**: 1-312.
- HALFFTER G., MATTHEWS E.G., 1967 - Los Scarabaeinae en la selva tropical americana. *Folia Entomol. Mex.* **15-16**: 47-48.
- 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.
- HANSKI I., 1989 - Dung Beetles. In *Tropical Rain Forest Ecosystems*. H. Lieth and M.J.A. Werger (eds.) Elsevier Science Publs. B.V., Amsterdam. pp. 489-511.
- HANSKI I., KOSKELA H., 1977 - Niche relations among dung-inhabiting beetles. *Oecologia (Berl.)*. **28**: 203-231.
- HANSKI I., KOSKELA H., 1979 - Resource partitioning in six guilds of dung-inhabiting beetles (Coleoptera). *Ann. Ent. Fenn.* **45**: 1-12.
- HOWDEN H.F., 1973 - A revision of the New World genus *Cryptocanthos* Balthasar (Coleoptera: Scarabaeidae). *Canadian Jour. Zool.* **51**(1): 39-48.
- HOWDEN H.F., NEALIS V.G., 1975 - Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica*. **7**: 7-83.
- HOWDEN H.F., NEALIS V.G., 1978 - Observations on height of perching in some tropical dung beetles (Scarabaeidae). *Biotropica*. **10**: 43-46.
- HOWDEN H.F., YOUNG O.P., 1981 - Panamian Scarabaeinae: Taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). *Contr. Amer. Entomol. Inst.* **18**: 1-204.
- JANZEN D.H., MARTIN P.S., 1982 - Neotropical anachronisms: the fruits the gomphotheres ate. *Science*. **215**: 19-27.
- KINGSTON T.J., 1977 - Natural Manuring by Elephants in Tsavo National Park, Kenya. D. Phil. Thesis, Univ. of Oxford, England.
- KLEIN B.C., 1989 - Effects on forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology*. **70** (6): 1715-1725.
- LAURENT R.F., 1973 - A parallel survey of equatorial amphibians and reptiles in Africa and South America. In B.J. Meggers et al. (eds.). *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, Smithsonian Press, Washington. pp. 259-266.
- LUMARET J.-P., 1978 - Biogéographie et écologie des scarabéides coprophages du Sud de la France. Ph. D. Thesis. Université du Languedoc. 254 pp.
- LUMARET J.-P., 1979a - Biogéographie et écologie des scarabéides coprophages du Sud de la France. I. Méthodologie et modèles de repartition. *Vie Milieu*. **28-29** (1): 1-34.
- LUMARET J.-P., 1979b - Biogéographie et écologie des scarabéides coprophages du Sud de la France II. - Analyse synécologique des répartitions. *Vie Milieu*. **28-29** (2): 179-201.
- LUMARET J.-P., 1983 - Structure des peuplements de coprophages scarabéides en région méditerranéenne française: relations entre les conditions écologiques et quelques paramètres biologiques des espèces. *Bull. Soc. ent. Fr.* **88** (7-8): 481-495.
- LUMARET J.-P., KIRK A., 1987 - Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeinae). *Acta Zool. Mex. (ns)*. **24**: 1-55.
- LOBO J.M., MARTIN-PIERA F., VEIGA C.M., 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.
- MARTIN P.S., 1989 - Prehistoric Overkill: The Global Model. pp. 354-403. In: Martin, P.S. and R.G. Klein (eds.) *Quaternary Extinctions. A Prehistoric Revolution*. The University of Arizona Press. Tucson, Arizona.
- MARTIN P.S., KLEIN R.G., 1989 - Quaternary Extinctions. A Prehistoric Revolution. The University of Arizona Press. Tucson, Arizona. Second printing. 892 pp.
- MARTINEZ A., 1959 - Catálogo de los Scarabaeinae Argentinos (Coleoptera). *Revista del Museo Argentino de Ciencias Naturales «Bernardino Rivadavia» Ciencias Zoológicas*. **5** (1): 126 pp.

- MARTINEZ A., HALFFTER G., 1972 - New taxa of American Canthonina (Coleoptera, Scarabaeinae). *Ent. Arb. Mus. Frey.* **23**: 33-66.
- MAYR E., 1988 - Toward a New Philosophy of Biology: Observations of an Evolutionist. Harvard Univ. Press, Cambridge.
- MORON M.A., 1979 - Fauna de coleópteros lamelicornios de la Estación de Biología Tropical «Los Tuxtles», Veracruz, UNAM, México. *An. Inst. Biol. UNAM, México.* **50**, ser. Zoología. **1**: 375-454.
- MORON M.A., CAMAL J.F., CANUL O., 1986 - Análisis de la entomofauna necrófila del área norte de la reserva de la biosfera Sian Ka'an, Quintana Roo, Méico. *Folia Entomol. Mex.* **69**: 83-98.
- MORON M.A., TERRON R.A., 1984 - Distribución altitudinal y estacional de los insectos necrófilos en la Sierra Norte de Hidalgo, México. *Acta Zool. Mex. (ns)*. **3**: 47 pp.
- MORON M.A., VILLALOBOS F.J., DELOYA C., 1985 - Fauna de coleópteros lamericornios de Boca de Chajul, Chiapas, México. *Folia Entomol. Mex.* **66**: 57-118.
- MORON M.A., ZARAGOZA S., 1976 - Coleópteros Melolonthidae y Scarabaeidae de Villa de Allende, Estado de México. *An. Inst. Biol. UNAM, México.* **47**, Ser. Zoología. **2**: 83-118.
- ODUM E.P., 1959 - Fundamentals of Ecology. 2d ed. W.B. Saunders Company. 546 pp.
- ODUM E.P., 1971 - Fundamentals of Ecology. 3 ed. W.D. Saunders Company. 574 pp.
- OHAUS F., 1900 - Bericht über eine entomologische Reise nach Central- Brasilien. *Stettiner Ent. Z.* **60**: 164-191, 193-274.
- OHAUS F., 1909 - Bericht über eine entomologische Studienreise in Sudamerika. *Stettiner Ent. Z.* **70**: 3-319.
- PASCHALIDIS K.M., 1974 - The genus *Sisyphus* Latr. (Coleoptera: Scarabaeidae) in Southern Africa. M.S. Thesis. Rhodes University, Grahamstown, South Africa.
- PECK S.B., FORSYTH A., 1982 - Composition, structure and comparative behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera, Scarabaeidae). *Can. J. Zool.* **60**: 1624-1634.
- PEREIRA F.S., VULCANO M.A., MARTINEZ A., 1960 - O genero *Bdelyrus* Harold, 1869. *Actas y Trabajos del Primer Congreso Sudamericano de Zoología* (La Plata 12-24 octubre 1959) Sección IV-Entomología. Tomo III: 155-164.
- PIANKA E.R., 1974 - Evolutionary Ecology. Harper and Row, New York, N.Y. 356 pp.
- RATCLIFFE B.C., 1980 - New species of Coprini (Coleoptera: Scarabaeidae: Scarabaeinae) taken from the pelage of three toed sloths (*Bradypus tridactylus* L.) (Edentata: Bradypodidae) in Central Amazonia with a brief commentary on scarab-sloth relationships. *Coleopt. Bull.* **34**: 337-350.
- RAVEN P.H., AXELROD D.I., 1974 - Angiosperm biogeography and past continental movements. *Ann. Mo. Bot. Gard.* **61**: 539-673.
- SARMIENTO G., MONASTERIO M., 1975 - A critical consideration of the environmental conditions associated with the occurrence of savanna ecosystems in tropical America. In F.B. Golley and E. Medina (eds.) *Tropical Ecological Systems*. Springer-Verlag, New York. 398 pp.
- U.S. NATIONAL RESEARCH COUNCIL, 1986 - Global change in the geosphere - biosphere. Initial priorities for an IGBP. National Academy Press.
- VANZOLINI P.E., 1973 - Paleoclimate, relief, and species multiplication in equatorial forests. In B.J. Meggers et al. (eds.) *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Press, Washington, pp. 255-258.
- YOUNG O.P., 1978 - Resource partitioning in a Neotropical scarab guild. Ph. D. Thesis, Univ. of Maryland, College Park, Md., 227 pp.
- YOUNG O.P., 1981 - The attraction of neotropical Scarabaeinae (Coleoptera, Scarabaeidae) to reptile and amphibian fecal material. *Coleopt. Bull.* **35**: 345-348.
- WALTER PH., 1977 - Repartition des Scarabaeidae coprophages dans les diverses formations vegetales du Plateau Bateke (Zaire). *Geo-Eco-Trop.* **4**: 259-275.
- WALTER PH., 1978 - Recherches écologiques sur les scarabéides coprophages d'une savanne du Zaïre. Ph. D. Thesis. Université des Sciences et Techniques du Languedoc. 353 pp.
- WALTER PH., 1980 - Comportement de recherche et d'exploitation d'une masse stercorale chez quelques coprophages afrotropicaux (Coleopt. Scarabaeidae). *Ann. Soc. Entomol. Fr. (N.S.)*. **16**: 307-323.
- WALTER PH., 1983 - Contribution a la connaissance des scarabéides coprophages du Gabon. (Col.) **2**. Présence de populations dans la canopée de la forêt gabonaise. *Bull. Soc. ent. France.* **88**: 514-521.
- WALTER PH., 1989 - Structure fonctionnelle d'un peuplement Afrotropical de scarabéides coprophages: un exemple des avantages et limites de l'utilisation du concept de gilde. *Bull. Soc. zool. Fr.* **114** (1): 135-140.
- WCISLO W.T., 1989 - Behavioral environments and evolutionary change. *Ann. Rev. Ecol. Syst.* **20**: 137-169.
- WEBB S.D., 1985 - Late Cenozoic Mammal Dispersal between the Americas. In F.G. Stehli y S.D. Webb (eds.). *The Great American Biotic Interchange*. Plenum Press, New York. 532 pp.