

**ANTS ON THE TEPUIES OF THE GUIANA SHIELD:
A ZOOGEOGRAPHIC STUDY**

**HORMIGAS DE LOS TEPUIES DEL MACIZO GUAYANES:
UN ESTUDIO ZOOGEOGRAFICO**

Klaus Jaffe*, John Lattke** and Roger Perez-Hernández***

**Departamento de Biología de Organismos, Universidad Simon Bolivar, Apartado Postal 89.000,
Caracas 1080-A, Venezuela.*

***Fundación Terramar, Apartado 89.000 Caracas 1080-A,
Venezuela.*

****Instituto de Zoología Tropical, Universidad Central de Venezuela, Apartado Postal 47058,
Caracas 1041-A, Venezuela*

SUMMARY

A survey of ant fauna on the summits (> 1,500 m) of 9 Tepuies revealed the presence of 28 species from 16 genera. All the genera were of groups widespread in the Neotropics and the species were either conspecific with, or closely related to, others found in the surrounding lowlands. The evidence points toward recent colonization of Tepuies and possibly recent speciation by endemic ants, a few thousand years ago.

Key Words: Formicidae, Tepuies, ecological history, Hylea, island biogeography, ants, speciation.

RESUMEN

Un muestreo de la fauna de hormigas en la parte más elevada (> 1.500 m) de 9 Tepuies, indicó la presencia de 28 especies pertenecientes a 16 géneros. Todos los géneros encontrados representan grupos ampliamente distribuidos en el Neotrópico y las especies fueron coespecíficas o estrechamente relacionadas con otras que se encuentran en las regiones circundantes de menor altitud. La evidencia tiende a indicar la existencia tanto de una colonización reciente de los Tepuies como de una posible especiación por las hormigas endémicas, hace unos miles de años atrás.

Palabras Claves: Formicidae, Tepuies, historia ecológica, Hylea, biogeografía de islas, hormigas, especiación.

INTRODUCTION

The biogeography of the ancient Guiana Shield and its Tepuy summits is controversial. A number of theories have been erected based upon the distribution of different types of organisms (Hoogmoed 1979). The existence of relicts before topographical and ecological isolation set in has been one theory put forth to explain the endemicities of plant species and genera of the region (Maguire 1971). More recently, as the extent of climatic changes during the last glaciation were recognized, the relict hypothesis fell into disfavor and the refuge theory took its place. During the Wisconsinian Glaciation the general climate was much drier than it is now, except for certain areas where more humid conditions reigned, enabling the existence of biota that elsewhere did not survive the adverse climate (Brown 1977, Haffer 1979). In a way this was simply a modification of the relict explanation, postulating the existence of seminal ancestral forms in climatically benign refuge areas.

Recently Schubert (1987), based upon paleoecological studies (Schubert and Fritz 1985), has seriously questioned the existence of Pleistocene biological refuges. Soil from the top of one Tepuy has been dated as being only about 8,000 years old (Schubert and Fritz 1985), implying that the presence of summit flora and fauna is a relatively recent phenomenon. A more quantitative survey of plants in summits and lowland showed that the endemicity on tepuies is lower than formerly claimed, as for example among ferns and phanerogams, only 10 to 15 % can be considered endemic to summits (Steyermark 1982). A survey (Jaffe et al. 1989) of the ant fauna of three neighboring tepuy summits also lead the authors to suspect recent colonization by ants. In this study we extend the survey on ant fauna to nine tepuies spread over all the Guayana highshield.

METHODS

Ants collected during different expeditions from 1983 to 1989 on Venezuelan Tepuy summits 1,500 m or more in altitude were examined and identified.

All collections were carried out by the authors, with some additional material provided by third persons, and were based on at least 20 person/hours of collecting time at each site, excepting Yuruani where we collected for only one hour. Studies of collecting efficiency in savannas indicate that 8-10 hours of collecting time sufficed for capturing over 75% of the ant species present and giving reliable information on species frequency (Romero and Jaffe 1989). Collection effort was focused on ground foraging species and consisted of hand collection, use of pitfall traps, baits, overturning logs and stones. We sampled the few trees presents for arboreal ants.

Ants from the surrounding lowland forests were sampled, at the following sites: Kukanan river valley; the vicinity of San Ignacio de Yuruani; Isla Raton in Cañon del Diablo next to Auyan Tepui, Canaima; forests along Akanan and Aparaman rivers, forests near Culebra in the vicinity of Marawaka Tepuy. Collecting methods were as described above, including the sifting of leaf litter and subsequent processing through Winkler sacks. Winkler sacks were not used on the summits due to difficulties in processing the water saturated histosols characteristic of tepuies. The collecting times in the lowland areas represent at least 30 man/hours per site, but the arboreal fauna was only occasionally sampled.

Identification of ant was performed down to the genus level for all samples, to the species level in some cases, and to morphospecies in those genera where recent revisions are lacking. Thus, morphospecies are clearly distinct among them if they are indicated with different numbers, but we do not know if some or all of them occur elsewhere. Comparisons were made with the samples from each summit and with ants from the surrounding lowlands, in order to detect the presence of any summit species in the lowlands.

Multivariate analysis (parametric and non parametric) was carried out using the PC statistical package SYSTAT for determining the relations between species number, summit area and altitude of all the Tepuies. Here we present only the data from the parametric analysis as they were very similar to those obtained using non-parametric methods.

The Tepuies considered (Fig. 1) can be divided into different systems of neighboring tops: I-

Roraima, Kukenan, and Yuruani; II- Aparaman tepuies group; III- Auyan; IV- Chimanta tepuies group; V- Huachamakari, Marawaka Norte and Marawaka Sur. The summits have inclement weather conditions and in the case of higher tops, such as Kukenan, the average yearly temperature is 8°C with

3,700 mm of annual precipitation (Vareschi 1980). Vegetation is found only in sheltered sites where gusts and rain do not eliminate the meager amounts of acidic soil that accumulates. Plant communities are mostly composed of herbaceous and low shrubby vegetation with occasional thickets of stunted forests.

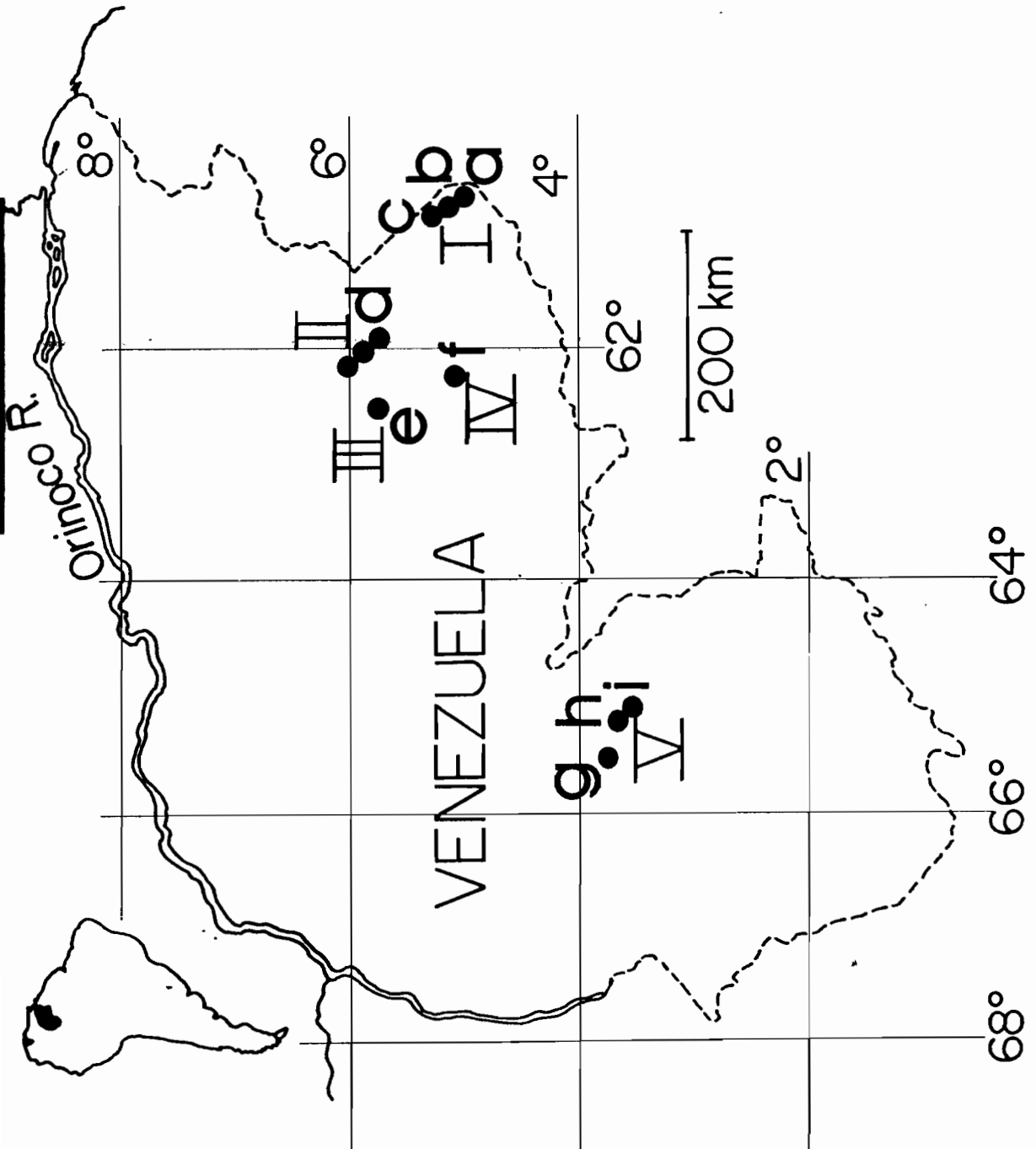


Fig. 1: Southern Venezuela showing location of Tepuy sampled. Meaning of the letters as in Table I.

The summits of each Tepuy are relatively flat and thus, the altitudes given represent a close approximation to the altitude of most areas on the summit (in a range of ± 200 m), except for Marawaka, which has a more irregular topography on its summit.

RESULTS

A total of 28 species from 16 genera were

collected from 9 summits. All of the genera found are widely distributed in the neotropics, most are present in New World temperate zones and many can also be found in other parts of the world. Only *Myrmelachista* and *Megalomyrmex* are restricted to the Neotropics. The number of ant species and genera in the lowlands greatly surpass the number found on the summits and only those related to the Tepuy fauna are considered in Table 1.

Multiple linear regression analysis showed that

Table 1. Ant species found on tepuy summits of Roraima (a), Kukenan (b), Yuruani (c), Aparaman (d), Auyan (e), Chimanta (f), Huachamakari (g), Marawaka Norte (h), Marawaka Sur (i) and lowlands (j). The lowland column represents a composite of the lowland sites; x represent the same species shared with the summit and "●" represent ants of the same genus as those found on the summit.

ANT SPECIES	COLLECTING LOCALITIES									
	a	b	c	d	e	f	g	h	i	j
PONERINAE										
<i>Hypoconerops sp 1</i>							x			●
<i>Hypoconerops sp 2</i>					x	x				●
<i>Anochetus inermis complex</i>					x					x
<i>Gnamptogenys gracilis</i>					x					x
MYRMICINAE										
<i>Solenopsis (Diplorhoptrum) sp 1</i>	x	x	x							●
<i>Solenopsis (Diplorhoptrum) sp 2</i>							x	x		●
<i>Solenopsis (Diplorhoptrum) sp 3</i>					x	x				●
<i>Solenopsis (Diplorhoptrum) sp 4</i>				x						●
<i>Megalomyrmex modestus</i>					x	x				●
<i>Pheidole sp 1</i>								x		●
<i>Pheidole sp 2</i>								x		x
<i>Procryptocerus sp 1</i>					x					●
<i>Acromyrmex sp 1 x x x</i>										●
<i>Cyphomyrmex sp (rimosus group)</i>					x					x
<i>Crematogaster sp 1</i>					x					●
FORMICINAE										
<i>Camponotus crassus</i>					x	x	x	x		x
<i>Camponotus (Tanaemyrmex) sp 1</i>					x					x
<i>Camponotus (Tanaemyrmex) sp 2</i>						x				●
<i>Camponotus sexguttatus</i>				x	x	x				x
<i>Paratrechina sp 1</i>								x	x	x
<i>Paratrechina sp 2</i>						x				●
<i>Myrmelachista sp 1</i>				x						●
<i>Myrmelachista sp 2</i>						x				●
<i>Brachymyrmex sp 1</i>					x	x				●
<i>Brachymyrmex sp 2</i>					x					●
PSEUDOMYRICINAE										
<i>Pseudomyrmex sp (simplex group)</i>					x					x
DOLICHODERINAE										
<i>Iridomyrmex sp 1</i>								x	x	●
<i>Iridomyrmex sp 2</i>							x			●

species richness correlates significantly with both, altitude and summit area (Table 2); the correlations maintain their significance even if Auyantepuy, with the largest summit area and the largest species number, is excluded from the analysis (not shown).

An inverse relationship between altitude and species richness was evident (Table 2). It is especially noticeable that the higher summits with little vegetation and large rocky areas, such as Roraima, Kukenan and Yuruani have only one species. The Marawaka summits, of comparable altitude but with more vegetation, are not so depauperate and 2-4 ant species could be found.

A positive relationship between summit area and species richness was also evident. The summits with the greatest number of species were also the largest, i.e. Chimanta and Auyan Tepuy.

The most common species, *Camponotus crassus*, is widespread throughout the neotropics (Kempf 1972) and can be found in a variety of habitats. The same is true for *Camponotus sexguttatus*, another species collected at relatively widely separated sites. *C. sexguttatus* populations found on two summits differed slightly in coloration from each other and

from samples taken elsewhere in the region. Most other ant species were only found on the summits and nowhere else, though species with a similar habitus were always collected in samples from the surrounding forests. The species of *Solenopsis (Diplorhoptrum)* apparently belong to the same species complex, all being morphologically very similar, but with consistent interpopulation differences. These species, when present, were found to be common on the summits. Leaf litter samples from lower forests near Kukenan and Auyan Tepuy failed to reveal the presence of the summit species of *S. (Diplorhoptrum)*, though other species of the same group were captured. The *Megalomyrmex* species on Aparaman and Auyan Tepuy are closely related, differing in size and coloration. Other ant species were shared by mountain tops only in the case of neighboring summits: Roraima, Kukenan and Yuruani; Huachamakari and Marawaka Norte respectively shared the same *S. (Diplorhoptrum)* species. A similar situation was also observed for *Paratrechina* 1, found on both Marawaka summits, and *Iridomyrmex* 1, shared by all summits of tepuy system V. The *Procrptocerus* and *Myrmelachista*

Table 2. Multivariate analysis of species richness vs altitude and summit area of the tepuy. Model: Species richness = constant + Altitude + Summit Area.

Tepuy	species (N)	Altitude	Area (km ²)
g. Huachamakari	5	1700	40
e. Auyan	14	1750	750
d. Aparaman	5	1800	30
f. Chimanta	10	2000	300
c. Yuruani	1	2300	5
i. Marawaka Sur	2	2500	140
h. Marawaka Norte	4	2500	130
b. Kukenan	1	2700	30
a. Roraima	1	2700	40

Multiple R = 0.971

Variable	Coefficient	Std. error	Std. coef.	t	p(2 tail)
Constant	10.968	2.572	0.000	4.26	0.005
Area	0.013	0.002	0.731	6.74	0.001
Altitude	-0.004	0.001	-0.397	-3.66	0.011

species could be present in lowland areas but they are mostly arboreal and this habitat was only occasionally sampled in the lowlands.

DISCUSSION

Despite our scant knowledge of the Guiana Shield ant fauna, the data show recognizable trends. The inverse relationship between altitude and number of ant species in the tropics has already been observed and discussed (Brown 1973), who showed that the maximum ant species number was found at an altitude of 800 m. In the case of Tepuies, this situation can be attributed to the environmental extremes of the higher tops which conceivably makes successful occupation difficult for most potential colonizers. Collection of other insects also show the same trend and insect diversity in general is much lower on Tepuies than in the surrounding forest.

A direct relationship between area and diversity is confluent with island biogeography theories (McArthur and Wilson 1967), although in the case of Tepuies, part of the fauna is derived from the surrounding lowland forest rather than some distant montane source. The larger summits offer a greater diversity of habitats and this should translate into more opportunities for colonization. The greater number of species on Chimanta and Auyan Tepui can be explained by their moderately harsh climate conditions (less altitude), if compared with Kukenan for example, in addition to their larger summit areas.

The higher number of species observed on Marawaka than on Kukenan, despite similar altitudes, could be attributed to topographical differences. The less abrupt slopes of the summit of Marawaka could make the habitable area of this Tepuy larger than that represented by the summit area and altitude, explaining the difference observed in species number.

The presence of the same ant species on neighboring summits (e.g. Kukenan, Yuruani and Roraima; Auyan and Chimanta; Marawaka Norte and Marawaka Sur) hints to colonization from other tops. The winds could favor the spread of winged sexual forms of an established species from one summit to another, as at least the most common

species on the summits have winged sexual forms which are very light and easily carried by the wind.

None of the species collected on the summits could be considered radically different from the lowland ant fauna, as all the genera found on the summits were present in the surrounding lowlands, nor relicts representing mostly extinct ant lineages were found. The *Solenopsis (Diplorhoptum)* species are interesting due to their evident closeness, and widespread distribution in cool climates in other latitudes and in other high altitude areas (the Andes for example). The four species could be derived from a single ancestral species, as they are very closely related (morphologically very similar) and in fact could even be considered as subspecies. The present isolation of these species could be recent, if we accept the existence of epochs when the climate allowed for a widespread distribution of the ancestral species. The patchy distribution found at present is coincident with the vicariant biogeography (Croizat 1976) assuming that the ancestral population was splitted and isolated in distinct sub-populations due to climatic changes. That is, we may assume that the ancestral species had a wide distribution in the Guayana highland shield and that due to paleoclimatic changes, the habitat of the species was splitted and reduced to the Tepuy summits. From there on, populations became isolated and started differentiating.

Schubert (1987) proposes a model of general aridity and savanna habitats for this region during the cooler glacial period, having dated the last dry period on the Tepuies about 8,000 years from present. Although Schubert and Huber (1990) point to the existence of alluvial fans, tentatively dated as Pleistocene in age, suggesting some precipitation and the presence of waterways and thus, providing humid habitats. If the phenomenon occurring after that described by Schubert (i.e. an increase in general humidity) was the one responsible for the fragmentation and isolation of the populations of *Solenopsis (Diplorhoptum)*, their speciation on the Tepuies may have started to occur about 8,000 years ago.

Our findings are apparently partially contradictory to those of Cook (1974), who studied the avifauna of the Tepuies. Cook found, as we did, a negative

correlation between species number and altitude but did not find any correlation between species number and summit area. We believe that if Cook's data are re-analyzed, eliminating migrant bird species and applying a multivariate analysis to the data correlating simultaneously altitude and area, as we did here, this contradiction may disappear.

In conclusion, we may use different hypothesis to explain our results:

1. The actual distribution of ants on Tepuy summits can be explained qualitatively and quantitatively considering the Tepuies as biogeographical islands. We clearly demonstrated that the summit areas, isolated from the surrounding lowlands due to their distinct climate (altitude), represent a limitation to species numbers, thus, controlling colonization of ants.
2. The distribution of the four species of *Solenopsis* (*Diplorhoptrum*) can be explained by a putative climatic vicariant phenomena.
3. The theory of the paradigm of the vicariant biogeography (Rosen 1985) requires the existence of a relationship between the phylogeny of the species and their biogeographic distribution. Except for the *Solenopsis* species, the cladogram of Formicidae (Baroni-Urbani 1989, Jaffe 1984) do not match any area cladogram of the Tepuies. This suggest a rather recent and aleatory colonization of these mountain tops by ants, supporting the conclusions of Jaffe, et. al. (1989).

Thus, our results can be explained by two different theories, traditionally considered to be contradictory. The panbiogeographic method (Croizat 1976) may explain the distribution of the *Solenopsis* species, whereas the theory of island biogeography (MacArthur and Wilson 1967) explains the dependence on area and altitude of the ant species diversity of the Tepuies. This duality may be explained by assuming different ages and ways of colonization by different lineages of ants.

ACKNOWLEDGEMENTS

Acknowledgements to Dr. O. Huber for sending us ants collected from Chimanta Tepuy and to

Aimara Dominquez for preparing ant specimens. We thank Dr. P. Ward for fruitful criticisms on earlier versions of this manuscript.

REFERENCES

- Baroni-Urbani, C. 1989. Phylogeny and behavioural evolution in ants with a discussion of the role of behaviour in evolutionary processes. *Ethology Ecology and Evolution* 1: 137-168.
- Brown, K. 1977. Geographical patterns of evolution in neotropical forest Lepidoptera, p 118-160. *In: Descimon H (ed) Biogeographie et Evolution en Amerique Tropicale*. Publication de Laboratoire de Zoology, Ecole Science Naturele.
- Brown, W. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas, p. 161-186. *In: Meggers, B. J., Ayensu, E. S. and Duckworth, W. D. (eds.), Tropical Forest Ecosystems in Africa and South America, a Review*. Smithsonian, Washington.
- Cook, R.E. 1974. Origin of the highland avifauna of southern Venezuela. *Systematic Zoology* 23: 257-264.
- Croizat, L. 1976. Biogeografía analítica y sintética (panbiogeografía) de las Americas. *Boletín de la Academia de Ciencias Físicas, Matemáticas y Naturales (Venezuela)*, XV and XVI.
- Haffer, J. 1979. Quaternary biogeography of tropical lowland South America. *In Duellman W E (ed) The South American Herpetofauna: Its Origin, Evolution and Dispersal: Museum of Natural History, University of Kansas Monographs* 7: 107-139.
- Hoogmoed, M. 1979. The herpetofauna of the Guianan Region. *In Duellman W E (ed) op. cit.* 7: 241-268.
- Jaffe, K. 1984. Negentropy and the evolution of chemical recruitment in ants. *Journal of Theoretical Biology* 106: 587-604.
- Jaffe, K., H. Romero and J. Lattke. 1989. Mirmecofauna de los Tepuyes Marahuaka y Huachamakare. *Acta Terramaris* 1: 33-37
- Kempf, W. 1972. Catalogo abreviado das formigas da regio Neotropical. *Studia Entomologica* 15: 3-344.
- MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. *Monographs in Population Biology*, Princeton University Press.
- Maguire, B. 1971. On the flora of the Guayana Highland, p. 63-78. *In: Stern, W. L. (ed.) Adaptive Aspects of Insular Evolution*. Washington University Press.
- Romero, H. and K. Jaffe. 1989. A comparison of methods for

ANTS OF THE TEPUIS

- sampling ants in savannahs. *Biotropica* 21, 234-237.
- Rosen, D.E. 1985. Geological hierarchies and biogeographic congruence in the Caribbean. *Annales of the Missouri Botanical Garden*, 72: 630-659.
- Schubert, C. 1987. Climatic changes during the last glacial maximum in northern South America and the Caribbean: a review. *Interciencia* 13:128-137.
- Schubert, C. and P. Fritz. 1985. Radiocarbon ages of peat, Guayana Highlands (Venezuela). *Naturwissenschaften* 72:427-429
- Schubert, C. and O. Huber. 1990. The Gran sabana: Panorama of a Region. Cuadernos Lagoven, Caracas.
- Steyermark, J. 1982. Relationships of some Venezuelan forest refuges with lowland tropical floras. p. 182-220. *In*: Prance, G. T. (ed.), *Biological Diversification in the Tropics*, Columbia University Press.
- Vareschi, V. 1980. *Vegetationsoekologie der Tropen*. Ulmer Verlag, Stuttgart.