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BIOGEOGRAPHY OF THE AZOREAN COLEOPTERA

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With 1 map, 25 figures and 6 tables

ABSTRACT. After 140 years of study, the Azorean beetle fauna is, in some islands, still poorly known, with 51 families, 305 genera, and 524 species present in the whole archipelago (61 of which - 11.6% - seem to be endemic). The intention of this account was to investigate which factors could best predict the number of species from each Azorean island. The correlations between the known distribution of the Azorean Coleoptera per island (total species, autochthonous species, total of endemics, exclusive endemics), and the area, distance from mainland, altitude and geological age were computed. We found that there were good correlations between the species diversity and the geological age of the islands, most remarkable being the value of $r=0.83$ ($p<0.005$) for the exclusive endemics. Considering only the autochthonous species we will find an interesting Mediterranean-Macaronesian component, with the endemics reaching 29%. This Mediterranean-Macaronesian component reaches 31.4% of the autochthonous species; moreover, there is a close taxonomic relation between many Azorean neo-endemics and related Madeiran and Canarian species. These two facts can signify a colonization with Macaronesian origin by "stepping stones". Apparently the poverty of the Azorean Coleoptera is somewhat illusory, because the differences in diversity between the Azores and other Macaronesian archipelagoes may be explained, in a probable order of importance by: isolation, geological youth, lack of strong diversity in some ecological parameters and an unsuitably humid climate. The disastrous action of the Pleistocene glaciations, though difficult to prove, could be alternative or complementary to the other factors.

RESUMO. Após 140 anos de estudo, a fauna de Coleópteros de algumas das ilhas dos Açores é ainda muito mal conhecida, estando inventariadas para este arquipélago 51 famílias, 305 géneros, e 524 espécies, das quais 61 são endémicas (11.6%). Com o objectivo de investigar quais os melhores factores predictivos do número de espécies de cada ilha, fomos estudar a correlação entre a distribuição conhecida dos Coleópteros por ilha (espécies totais, espécies autóctones, espécies endémicas totais e espécies endémicas exclusivas), com a área, distância ao continente, altitude máxima e idade geológica das ilhas. A análise das correlações idade-diversidade

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obtidas para os Coleópteros dos Açores, não parece deixar dúvidas sobre a importância da idade geológica na diversificação da fauna destas ilhas, sendo notável a correlação obtida entre o número de espécies endémicas exclusivas de cada ilha e a idade geológica ($r= 0.83$; $p<0,005$). Se tivermos em conta apenas as espécies autóctones, encontramos uma componente Mediterrânica-Macaronésica muito interessante, com uma percentagem de endemismos de 29%. Essa componente Mediterrânica associada à percentagem de espécies Macaronésicas perfaz cerca de 31.4% das espécies autóctones. Por outro lado, há uma relação taxonómica próxima de muitos neo-endemismos dos Açores com espécies da Madeira e Canárias. Estes dois factos dão sentido a uma colonização proveniente de um "Rosário de ilhas" Macaronésico (*stepping stones theory*). Os factores que parecem melhor explicar as dissimilaridades entre essa fauna e a dos arquipélagos Macaronésicos vizinhos, são por ordem de importância: Isolamento, idade geológica recente, baixa diversidade de alguns parametros ecológicos, clima muito húmido. A acção nefasta das glaciações Pleistocénicas, embora difícil de provar, é uma alternativa atraente e complementar das apresentadas.

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1. INTRODUCTION

It is well known that Charles Darwin was an enthusiastic collector of beetles. Nevertheless, and in spite of being in the Azores during the expedition of the *Beagle* (Terceira, September 1836) (KEYNES, 1988), no collections were made; and in spite of discussing some mechanisms of dispersal quoting Madeira, no significant comments were made concerning the insects of the Azores.

In fact, at first sight the plants and animals of the Azores are small cause for excitement; but as we will see in this study, even the most sceptical observer could be surprised, given a more attentive perusal of the evidence. Concerning the arthropods, this apparent dullness is, in part, responsible for the ignorance concerning the faunistic composition of many groups of insects from this archipelago. CROTCH (1867), commenting on this subject, emphasizes both the labour of the English entomologist T. V. WOLLASTON (who for several years intensively prospected the archipelagoes of Madeira, the Canaries and Cape Verde, but not the Azores!), and also the almost complete indifference manifested by naturalists and entomologists in general, regarding the Azores.

On the other hand, the isolation of these islands in the Atlantic ocean (distances from the mainland are 1600 km from Lisbon and 1900 km from Newfoundland), their youth (8 m.y., the oldest) and their climate (extremely humid), could be factors that explain the apparent poverty of their insect fauna (we will return to this subject later).

What is most enticing for the researcher is that these islands, because of their isolation and youth, are an excellent model system of nine islands of different geological ages [between 0.037 and 8.12 m.y. (ABDEL-MONEM *et al.*, 1975)] in an insular evolutionary process.

Our purpose is to discover and trace the data and observations on the natural history of the Azorean beetles. When necessary or possible some comparative analysis are made with the other Macaronesian archipelagoes. The present known facts prove that the coleopterous fauna of the Cape Verde Islands has nothing in common with the fauna of the Canaries and Madeira (GEISTHARDT, 1982). In fact, as a consequence of his meridional geographical localization it has been established that Cape Verde has a flora (NICOLÁS *et al.*, 1989) and fauna (BAEZ, 1982a and b; ORÓMÍ, 1982) very dissimilar from the other three northern archipelagoes.

The latest checklist of beetles (Coleoptera) from the Azores (BORGES, 1990), is recent. This catalogue brings up to date the lists of MÉQUIGNON (1946) and SERRANO (1982) (see also Table 1 from BORGES, *op. cit.*), including modern taxonomical aspects and systematic reordination of families, genera and species, probably more in tune with current phylogenetical knowledge concerning the order Coleoptera.

Unfortunately, there are no such lists available for the archipelagoes of Madeira and the Canaries, making impossible the realization of any biogeographical analysis at the Macaronesian level. GEISTHARDT (1988), however, recently published a current list of Cape Verde beetles.

Schouw, a Danish phytogeographer, was one of the earliest to realize the similarities between these different groups of islands, and also the northwestern coast of Africa, in his biogeographical region *Sempervivorum* (ISRAELSON, pers. comm.). SUNDING (1979) accepts this idea, giving the name of "Macaronesian Enclave" to this area on the mainland, comprising southern Morocco and Spanish West Africa.

Philip Barker Webb, an English botanist, coined the name MACARONESIA ("lucky islands"), which did not include the African part (see WEBB & BERTHELOT, 1836-50). To start with, Macaronesia was probably intended to be the same as Canaries; however, the famous German phytogeographer ENGLER (1879) (*in* SUNDING, 1979) included all four archipelagoes in this entity, thereby giving a decisive impetus towards the acceptance of the name by botanists and zoologists.

However, many zoologists are more hesitant and often try to evade the term by using "Atlantic Islands" and not Macaronesia. During this work we will use the term Macaronesia (*sensu* WEBB & BERTHELOT, 1836-50), because it is at the moment the one with most generalized acceptance. When we mention the archipelago of Madeira we include in it the Desertas, Porto Santo and Selvagens.

In this contribution to the biogeography of Azorean beetles we will use as a framework "A checklist of the Coleoptera from the Azores" by BORGES (1990).

2. THE AZORES

2.1. GEOGRAPHY AND GEOPHYSICS

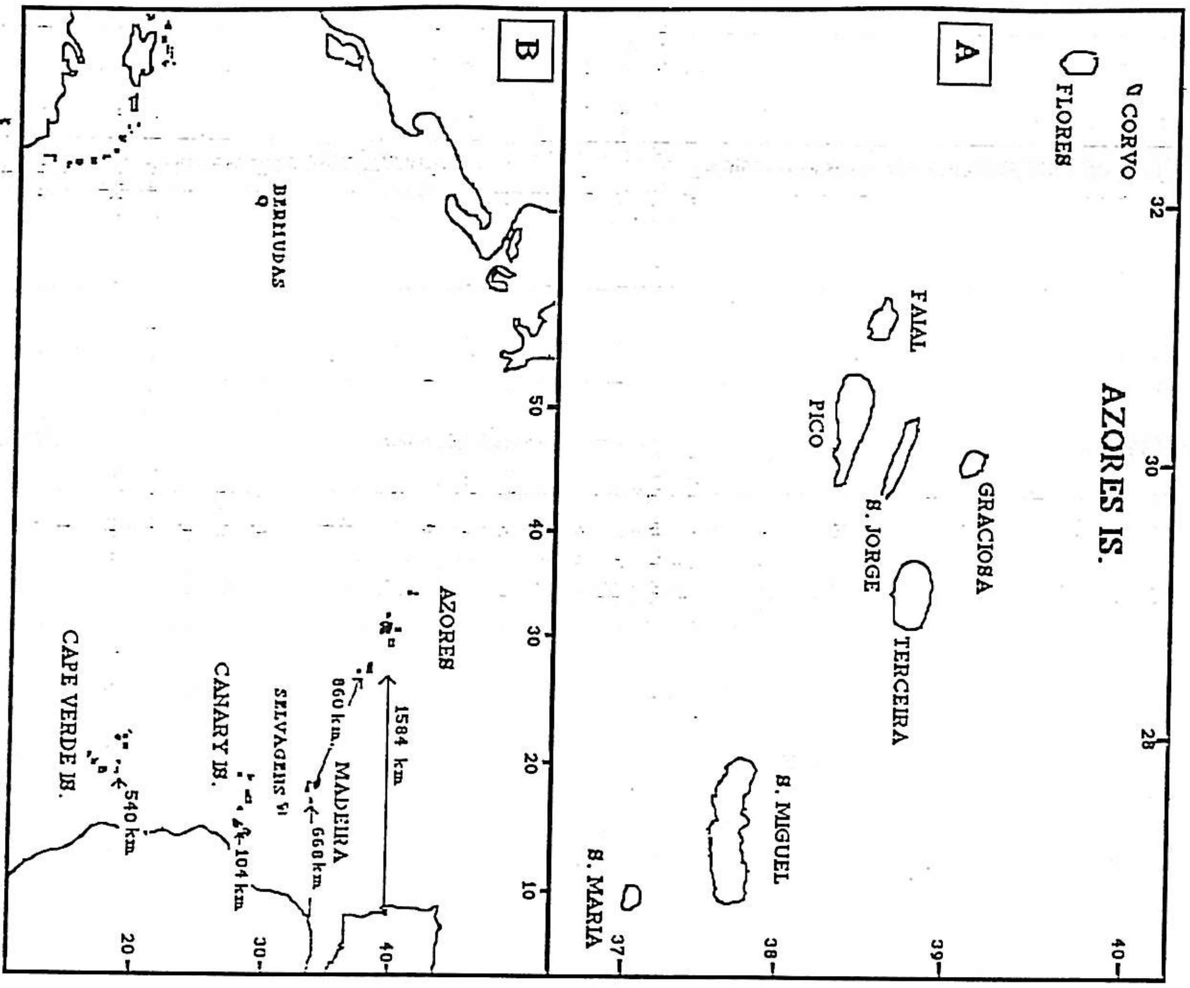
The Azorean archipelago is located in the North Atlantic, at the triple junction of the Eurasian, African and North American plates. The distance between the Azores and the mainland is about 1390 Km, calculated from Cabo da Roca (the most westerly point of the European continent). It is formed by nine volcanic islands, aligned on a WNW-ESE trend, which are distributed into three groups: the occidental group of Corvo and Flores; the central group of Faial, Pico, Graciosa, São Jorge and Terceira; and the oriental group of São Miguel and Santa Maria (Map I - A).

The largest island is S. Miguel (757 km^2), and the smallest is Corvo (17 km^2). S. Maria is the most southerly island (37° N, 25° W), and Flores is the most westerly one (31° W). The most northerly one is Corvo (39,7° N) (see Table 1 and Map I - A).

The distance between Corvo and Santa Maria, the islands farthest apart, is about 615 km. Corvo lies approximately at the same distance from the Iberian Peninsula and from Newfoundland. All the information concerning the longitude (long.), latitude (lat.), area, maximum altitude, distances from the mainland and geological age of each island are given in Table 1. In this table the same type of information is also given for the archipelagoes of Madeira, Canaries and Cape Verde (see also Map I - B).

Discovered by the Portuguese navigators in 1432, the Azores seem already to have been vaguely known, being indicated on older maps. Flores and Corvo were the last to be discovered, in 1452.

The present Azorean landscape is strongly modified by the presence of Man and only in small areas (DIAS, 1988) where the soil or climate was too rough, have primitive conditions remained unchanged. Nowadays over 260,000 people live in these islands (DREPA, 1988).



Map I.- A: The Azores Islands; B: Atlantic islands with the Macaronesian Archipelagoes and Cape Verde Islands (Modified from WUNDERLICH, 1991).

ISLANDS	Long.(W)	Lat.(N)	Dist. from the nearest mainland (km)	Area (km^2)	Altitude (m)	Geological Age (m.y.)		
AZORES						A	B	C
CORVO	30.8	39.7	2148	17	718	?	?	?
FLORES	30.9	39.4	2152	142	915	0.010	0.62(2.9)	1.8
FAIAL	28.5	38.5	1908	172	1043	2.6	0.73	0.73
PICO	28.2	38.5	1860	433	2351	1.1	0.037	0.037
GRACIOSA	27.8	39.1	1844	62	402	0.62	0.62	2.5
S. JORGE	27.9	38.7	1832	246	1053	2	0.55	0.55
TERCEIRA	27.2	38.7	1764	402	1023	2	0.30	2
S. MIGUEL	25.5	37.7	1584	757	1103	4	4.01	4.01
S. MARIA	25.1	36.9	1588	97	587	8	8.12	8.12
Western Group	30.8-30.9	39.4-39.7	2148	159	915	0.010	0.60(2.9)	1.8
Central Group	27.2-28.5	38.7-39.1	1764	1315	2351	0.62-2.6	0.037-0.73	0.037-2.5
Eastern Group	25.1-25.5	36.9-37.7	1584	854	1103	4.0-8.0	4.01-8.12	4.01-8.12
TOTAL	25.1-30.9	36.9-39.7	1584	2328	2351	0.010-8.0	0.037-8.12	0.037-8.12
MADEIRA	16.3-16.9	32.7-33	668	814	1860	60-70		
CANARIES	13.6-17.9	27.6-29	104	7542	3717	35-40		
CAPE VERDE	22.8-25.2	14.8-17	540	4033	2829	>100		

Table 1.- Comparison of some physical features of the Azorean islands with those of the archipelagoes of Madeira, the Canaries and Cape Verde. A- FORJAZ (pers. comm.); B- ABDEL-MONEM *et. al.* (1975); FERAUD *et. al.* (1980); C- QUEIROZ (1990). m.y. - Million years.

Erosion effects are very important in these islands. Stormy waves, thrown up by strong Atlantic winds, mold the shape of the coastal cliffs, that on S. Jorge reaches 100 m in height. Torrential water courses cleave deep mountain streams on the surface, as on Flores, S. Jorge and S. Miguel. The relief is pronounced, with a few planaltic regions on the islands of Pico, Graciosa, Terceira, S. Miguel and S. Maria. Pico is the highest island of the archipelago (2531 m), Graciosa being the one of lowest altitude (402 m) (Table1).

2.1.1. AGE AND ORIGIN OF THE ISLANDS

All the islands have a volcanic origin, and there are many examples of historical volcanic eruptions (*vide* WESTON, 1964). The geological age of the nine islands is very dissimilar. Because their formation took a long period of time, these islands present both recent volcanic morphology (e.g. Pico) or more eroded, ancient formations (*e.g.* Flores and S. Maria). There are several studies concerning the geological dating of the Azorean islands, but unfortunately there is no agreement concerning the age of some islands.

Three alternatives are proposed: one following FORJAZ (pers. comm.) (Table 1; column A), another with the results obtained by ABDEL-MONEM *et al.* (1975) and FERAUD *et al.* (1980) (Table 1; column B) with the K/Ar method; finally one following QUEIROZ (1990) (Table 1; column C). This last author follows, in part, ABDEL-MONEM *et al.* (*op. cit.*) and FERAUD *et al.* (*op. cit.*) but also other recent studies (e.g. FORJAZ, 1986b; WHITE *et al.*, 1976; AZEVEDO *et al.* , 1986, all *in* QUEIROZ, 1990).

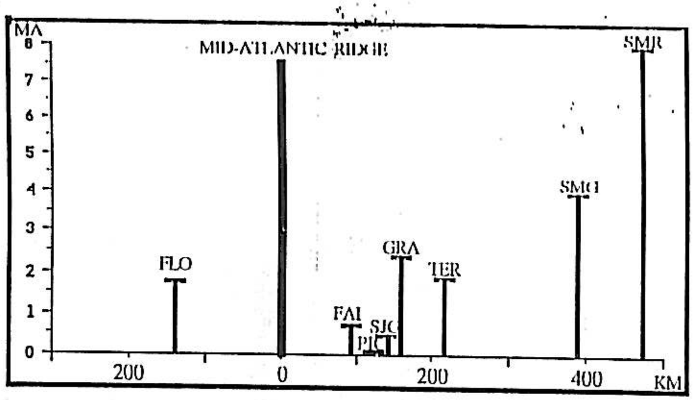


Figure 1.- Relation between the age of each of the Azorean islands and the Middle Atlantic Ridge. The geological ages are those proposed by QUEIROZ (1990)

In Fig. 1 is presented the data of QUEIROZ (1990) in a graphical way. The age of the differerent islands of the archipelago is not positively correlated with their distance from the Middle Atlantic Ridge (FERAUD *et al.*, 1980). The same could be inferred from the ages proposed by FORJAZ (pers. comm.) or ABDEL-MONEM *et al.* (1975) / FERAUD *et al.* (1980).

As we can see from Table 1, different ages have been proposed for some islands, but nevertheless the oriental group is the oldest one, with 8.12.million years (S. Maria) (ABDEL-MONEM *et al.* ,1975), coming from the middle of the Miocene. SERUGHETTI & ROCHE (1968) (*in* RYALL *et al.*, 1983) propose about 2.9 m.y. of age for Flores (Table 1; column B), but AZEVEDO *et al.* (1986) (*in* QUEIROZ, 1990) estimate the age of this island as 1.8 m.y.. The central group is the youngest one.

It should also be pointed out that the geological datings of the Azorean islands are far from being considered totally correct, mainly because the geological samples dated were probably not taken from the older stratigraphic layers (NUNES, pers. comm.).

There is some evidence of underwater mountains in this archipelago. To the west of Flores there is an old, now submerged island (RYALL *et al.*, 1983). Near S. Maria, to the east of the island, there is the Formigas complex of about 4,65 m.y. (ABDEL-MONEM *et al.* ,1975). In the Azorean sea there are some well known fishing-banks like the Princesa Alice (-44 m), Banco dos Açores (-18 m) and Banco D. João de Castro (-14 m). In the latter a small island was formed in 1720, disappearing a little later (ROUCH, 1966-67).

There are also some other underwater mountains interspersed between Madeira and the Portuguese coast (EVERS *et al.*, 1970), which are well known fishing banks [Goringe (-49 m), Gettysburg (-23 m), Ormonde (-35 m), Ampere (-40 m), Seine (-59 m) and Josephine (-150 m)] (BAEZ & PINTO, 1983).

Some biogeographers (HEER, 1856; JEANNEL, 1946; PEYERIMHOFF, 1946; UYTTENBOOGAART, 1946; MATEU, 1961; VANDEL, 1961) have supported the theory that sometime in the past (late Tertiary) "land bridges" occurred between the Macaronesian archipelagoes (*e.g.* Madeira, Canaries and Cape Verde) and the mainland. The acceptance of the Plate Tectonic mechanisms and the confirmed volcanic origin of the Azores, made it a totally oceanic archipelago (*sensu* WOLLASTON, 1854).

In spite of the three groups of Azorean islands being separated from each other by channels 1000 to 2000 m deep, the channel between Faial and Pico has zones of less than 100 m deep [*e.g.* -20 m e -50 m (BERTHOIS, 1953)].

The eastern part of all Azorean islands are, geologically, the oldest ones. This is connected with the seismo-volcanic mechanisms of this archipelago (FORJAZ, pers. comm.), which is important because the occurrence and distribution of the Azorean autochthonous beetles are to some extent related to it (see below).

2.2. CLIMATE

Located at a mean latitude of 38° 30′ and surrounded by the Atlantic Ocean, the Azores enjoy the benefits of a mild and agreeable climate.

The influence of the warm Gulf Stream is important, allowing temperatures at sea level to be quite similar in the southeastern and in the northwestern islands. The same can be said of the humidity (AGOSTINHO, 1966).

Low thermal amplitude and high precipitation and humidity are properties of this archipelago, with its strong oceanic climate.

The mean temperature values of each month change regularly during the year, with a maximum in August and a minimum in February, the seasons beginning in the Azores one month later than on the mainland (AGOSTINHO, *op. cit.*). The mean annual temperature is 17.5° C.

The air spatial distribution of the temperature in a region is mainly affected by physiographical factors, like altitude and orientation, the nature of the soil and its covering, and the proximity of the sea. Most of the available data concerned with the Azorean climate are from a restricted low altitude band, the climate of high altitudes being still unrecorded (DIAS, 1989). Considering the fact that most of the autochthonous vegetation areas of the archipelago are situated in high altitudes, we can easily understand the importance of knowing the climate of these elevated areas.

The local macroclimate is strongly affected by the so-called "Azorean Anticyclone", always present in the eastern part of the North Atlantic. When centralized to the southwest of the archipelago, it is responsible for the distribution of the warm, wet trade winds (SW, NW), which make the climate temperate (BETTENCOURT, 1979).

At high altitudes, the ecological action of the trade winds over vegetation is extremely important (DIAS, 1989). The rain precipitation seems to be directly dependent on the air circulation caused by these trade winds, making the rainiest islands the occidental ones (Flores and Corvo) and the driest one S. Maria (AGOSTINHO, 1941) (*in* DIAS, *op. cit.*).

The insolation percentage in the Azores is very low, being in February about 30% and in August about 45%. Therefore, nebulosity does not suffer a great seasonal oscillation, but remains stable throughout the year. This fact is very important, making it possible for each island to define at high altitudes a "cloud-zone forest" (SJÖGREN, 1990), where a fog interception phenomenon occurs. The resulting horizontal rain has great ecological importance and is a consequence of the Föehn effect (DIAS, 1989). In these cloud-zones, the rainfall (vertical and horizontal) is high, leaving the air saturated with moisture and the soil waterlogged. In these conditions anoxia phenomena occur in the soil. The significant increase in rainfall as well as the dominance of the *Sphagnum* species in high altitudes, decreases the pH values (DIAS, *op. cit.*) with an ecological diversity decrease (see below).

2.2.1. PAST CLIMATIC CHANGES

The Pleistocene climatic changes could have had some influence in the Azores. Thus, as we have already seen, the channel between Faial and Pico has zones of less than 100 m depth, and it is therefore possible that at the height of the glaciation about 18,000 years ago, the lowering of the sea level could have permitted a terrestrial passage between these islands (EASON & ASHMOLE, 1992) [Estimates of the glacial sea level range from less than 80 to over 130 m below the present level (BLOOM, 1971)].

It seems probable, simply by virtue of the fact that the Azores are the most northern archipelago of Macaronesia, that it should have suffered most from the influence of the glaciations (ISRAELSON, 1990).

It is the position of the polar front that is crucial to the argument. Thus, at the height of the glaciation about 18,000 years ago, it lay approximately along latitude 42° N, and remained close to that position until about 14,000 years ago. The circulation pattern then underwent a dramatic change (COOPE, 1986). In the eastern North Atlantic the polar front moved very rapidly northwards, so that by about 13,000 years ago it was situated to the north of the islands and the summer surface temperatures rose about 7° C (RUDDIMAN *et al.*, 1977) (*in* COOPE, *op. cit.*). This general pattern of retreat was interrupted by a brief return to glacial conditions between 11,000 and 10,000 years ago, when the polar front moved southwards to latitude 50° N (RUDDIMAN & MCINTYRE, 1981). The postglacial climatic amelioration must have been extremely rapid; by 9,000 years ago the polar front had returned to the conditions of about 13,000 years ago, with a warm climate.

We should point out that seven complete climatic cycles have occurred in the past 600,000 years, within which at least 11 separate major southward advances of polar water have taken place (RUDDIMAN & MCINTYRE, 1976).

2.3. VEGETATION

Following the list of HANSEN (1988), we find about 1,011 species in the Azorean vascular flora, but only 1/3 of those are autochthonous to the archipelago (at about 300 species).

We think the best way to relate the vegetation and the diversity of the Azorean Coleoptera will be to follow a typological and uniform classification for the present-day vegetation of this archipelago. Several classification models have been proposed for the current Azorean vegetation in recent decades (TUTIN & WARBURG,1953; DANSEREAU, 1970; SJÖGREN, 1973; LÜPNITZ, 1975), all of them based on altitudinal zonation. However, for most of the Azorean islands the altitudinal zonation has a poor explanatory value (DIAS, pers. comm.).

DIAS (1991) presents a botanical model less detailed but of great practical use. Moreover, the Azorean Vegetation Maps follow the DIAS (*op. cit.*) classification, because of which we also follow it. The Vegetation Zones considered are:

Climax pattern of autochthonous forest - dominated by Azorean or Macaronesian endemic arboreous species. The five subunities considered by the author will not be followed by us, because they are excessively refined for our proposal;

Seral spontaneous vegetation - zones where the plant communities are in a dynamic natural process of succession towards a potential climax local vegetation. Dominated by the endemic species;

Coast vegetation - where the plant communities are restricted to the coast border. It includes the cliffs, the lava flows and the rare sand dunes and sand plains;

Marshy, Lakes and Wet peatland vegetation mires - of very common occurrence in the Azores, these zones include important plant communities, *e.g.*: in the Lakes [*Littorella uniflora* (L.) Ascherschon - *Eleocharis* sp.); -Wet peatland vegetation mires (*Sphagnum palustre* L. - *Eleocharis multicaulis* (Sm) Desv.].

Woodlands - mainly eucalyptus forests (*Eucalyptus globulus* Labill.), cryptomeria forests [*Cryptomeria japonica* (L. fil.) D. Don.], pine forests and mixed woodland;

Pasture - this is at present the dominant vegetation zone in the Azores. In high altitudes there is a special type of pasture, "The Semi-natural pasture" (SJÖGREN, 1973);

Permanent Agriculture - mainly fruit trees;

Multiple Agriculture - several types of agricultural developments, *e.g.*: familiar developments, greenhouses, crops, etc..

3. THE AZOREAN COLEOPTERA

3.1. INTRODUCTION

Until now most of the works dealing with Azorean Coleoptera were of the faunistic type. Most of them are mainly devoted either to the description of new species or to indicating discoveries that are new to the whole archipelago or to a particular island.

Other, complementary types of approaches have also been made. The family Carabidae was submitted to an elaborate revision by LINDROTH (1960), in a work which also offers some reflections on overseas dispersal.

Similar types of Biogeographic approaches have also been made by other authors, and we can cite the following contributions: MÉQUIGNON (1935, 1946); UYTTENBOOGAART (1946); SERRANO (1982); SOUSA (1985); BORGES (1990) and ISRAELSON (1990).

It also should be pointed out that there is a total lack of any kind of ecological work about Azorean Coleoptera. Some such study, dealing with the Arthropoda of the Azorean natural zones, is rather urgently needed, because the autochthonous habitats have been destroyed and altered by the introduction of invader species.

A vast and unexplored field of study dealing with the ecology and evolution of Azorean insects is open to future research. Nevertheless, some preliminary studies have already begun for the genera *Trechus* (Carabidae) and *Tarphius* (Colydiidae) [*vide* BORGES & OROMÍ (1991) and BORGES (1991a), respectively].

3.2. DIVERSITY

3.2.1. THE LIST OF SPECIES

As PECK & PECK (1990) have pointed out, the strength or weakness of a biogeographical analysis lies in the quality of the systematics upon which it is based. In this work we will follow the most recent checklist of Azorean Coleoptera from BORGES (1990). However, for the analysis that we intend to do, new types of information will be extracted.

The species are classified in several categories of colonization (see Table 2), as introduced, native, or endemic, following the nomenclature of PECK & PECK (*op. cit.*). For the determination of the introduced species we follow the works of CROTCH (1867), MÉQUIGNON (1946), LINDROTH (1960) and GUIMARÃES & BEIJA (1974).

FAMILIES	GENERA		SPECIES				E.M.N.C.
	TOTAL	ENDEMICS	TOTAL	INTROD.	NATIVES	ENDEMICS(%)	
CARABIDAE	32	1	47	22	10	15(31.9)	18
DYTISCIDAE	5	-	9	-	7	2(22.2)	9
GYRINIDAE	1	-	1	-	1	-	1
HYDRAENIDAE	1	-	1	-	-	1(100)	1
HYDROPHILIDAE	6	-	14	12	2	-	2
PTILIIDAE	5	-	10	5	5	-	5
SILPHIDAE	1	-	1	1	-	-	-
SCYDMAENIDAE	3	-	4	1	2	1(25.0)	3
STAPHYLINIDAE	58	-	121	73	39	9(7.4)	47
PSELAPHIDAE	2	-	2	-	2	-	2
HISTERIDAE	5	-	12	12	-	-	-
SCARABAEIDAE	9	-	13	9	4	-	4
DRYOPIDAE	1	-	2	-	2	-	2
ELATERIDAE	6	1	8	4	1	3(37.5)	3
THROSCIDAE	1	-	2	1	1	-	1
BUPRESTIDAE	2	-	3	2	1	-	1
DERMESTIDAE	3	-	7	7	-	-	-
LYCTIDAE	1	-	1	1	-	-	-
BOSTRICHIDAE	2	-	2	1	1	-	1
ANOBIIDAE	7	-	10	5	5	-	5
PTINIDAE	3	-	6	3	2	1(16.7)	3
TROGOSITIDAE	1	-	2	2	-	-	-
CLERIDAE	2	-	4	4	-	-	-
MELYRIDAE	3	-	4	-	4	-	4
NITIDULIDAE	10	-	23	18	5	-	5
SPHINDIDAE	1	-	1	1	-	-	-
MONOTOMIDAE	1	-	5	5	-	-	-
CUCUJIDAE	9	-	15	10	4	1(6.7)	5
CRYPTOPHAGIDAE	3	-	9	9	-	-	-
EROTYLIDAE	1	-	1	1	-	-	-
PHALACRIDAE	3	-	5	2	3	-	3
CERYLONIDAE	2	-	2	-	2	-	2
ENDOMYCHIDAE	1	-	1	1	-	-	-
COCCINELLIDAE	12	-	22	14	8	-	8
CORYLOPHIDAE	5	-	6	3	3	-	3
MEROPHYSIDAE	2		3	1	-	2(66.6)	2
LATRIDIIDAE	7	-	12	8	3	1(8.3)	4
CISIDAE	1	-	1	-	-	1(100)	1
COLYDIIDAE	2	-	9	-	1	8(88.9)	2
MYCETOPHAGIDAE	3	-	4	2	2	-	2
OEDEMERIDAE	1	-	1	1	-	-	-
ANTHICIDAE	4	-	5	4	1	-	1
TENEBRIONIDAE	12	-	18	12	5	1(5.6)	6
ANASPIDAE	1	-	1	-	1	-	1
CERAMBYCIDAE	10	1	11	5	4	2(20.0)	6
CHRYSOMELIDAE	10	-	17	13	1	3(17.6)	4
BRUCHIDAE	4	-	7	6	1	-	1
APIONIDAE	2	-	2	2	-	-	-
RHYNCHOPHORIDAE	3	-	4	4	-	-	-
CURCULIONIDAE	27	2	42	20	13	9(21.4)	22
SCOLYTIDAE	9	-	11	7	3	1(9.1)	4
TOTAL=	306	5	524	314(59.9)	149(28.5)	61(11.6)	194

Table 2.-Number of beetle genera and species from the Azores per family. E.M.N.C.= Estimate of the minimal number of colonists.

Native species occur naturally in the Azores and are also known in other archipelagoes and on the continental mainland. Endemic species are those that occur only in the Azores. When we need to refer together to native and endemic species we will use the word "autochthonous".

In this work, we present another checklist (see Table 4), which deals solely with the Azorean endemic species of Coleoptera. Endemics are divided into neo-endemics (N) and paleo-endemics (P) (*sensu* LINDROTH, 1960).

As in PECK & PECK (1990) we analyse the island beetle fauna on the basis of their feeding guild or trophic function in the island´s ecosystem. Like earlier authors, we use the system of BECKER (1975) but with some adaptations (see STORK, 1987): Predators (p); Saprophagous (s), Fungivores (f) and Herbivores (h).

All of the trophic data are based on information drawn from MÉQUIGNON (1946) and GRASSÉ (1965), being generalizations from continental faunas.

3.2.2. PRELIMINARY CONSIDERATIONS

The Azorean beetle fauna is now known to consist of 524 species and subspecies, in 306 genera, in 51 families (Table 2). This makes beetles the most diverse of all the orders of insects (BORGES, 1990). The Dipterous insects with 415 species (SOUSA, 1985) are the second most diverse order.

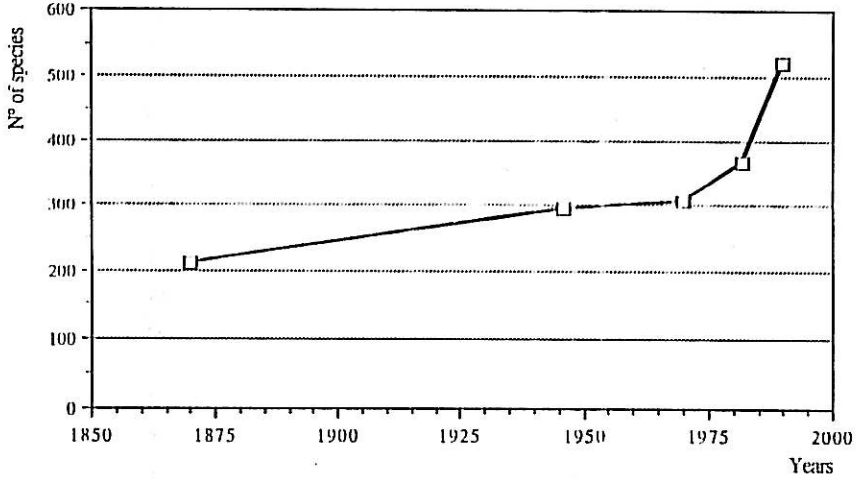


Figure 2.- Rate of increase in the total number of reported beetle species from the Azores (see Table I in BORGES, 1990).

During the past decade there has been a great increase in the number of new species of Coleoptera recorded in the Azores (Fig. 2). Recently, two more species of *Tarphius* (Colydiidae) (BORGES, 1991a), as well as a new genus, a new species and a new subspecies of ground-beetle (Carabidae) were described, from this archipelago (see BORGES & SERRANO, in print.).

The probable causes for this increase are:

- the utilization of more efficient techniques of capture, with the use of several types of traps (*e.g.* pitfalls, colour traps) and baits (*e.g.* rotten fruit, vinegar, Turquin, etc.) (see BORGES, 1990, 1991a, in prep.; BORGES & DIAS, in prep.);
- the organization of several specialized expeditions, which explored habitats hitherto neglected (*e.g.* lava tube caves, lava flows, MSS, etc.) (see BORGES & OROMÍ, 1991 and in print; OROMÍ & BORGES, 1991; BORGES, in print);
- the fact that some *taxa* of problematic determination have finally been submitted to a more precise study (*e.g.* Staphylinidae) (*vide* ISRAELSON, 1984, 1985a, 1990; GILLERFORS, 1986b, 1988; BORGES, 1990).

The most diverse families are Staphylinidae (58 genera, 121 species), Carabidae (32 genera, 47 species), Curculionidae (27 genera, 42 species), Nitidulidae (10 genera, 23 species) and Coccinellidae (12 genera, 22 species) (BORGES, 1990). Dealing only with the autochthonous species the values are: Staphylinidae (34 genera, 48 species), Carabidae (15 genera, 25 species), Curculionidae (16 genera, 22 species), Colydiidae (2 genera, 9 species) and Dytiscidae (5 genera, 9 species).

The number of known species for each island is now: 21 species from Corvo, 182 from Flores, 212 from Faial, 155 from Pico, 101 from Graciosa, 121 from S. Jorge, 245 from Terceira, 336 from S. Miguel and 251 from S. Maria (up-dated from BORGES, 1990).

From Fig. 3 (see also Table 3), we can get an idea of the distribution of the species island by island, most notable being the fact that those islands with most species are also the best explored (*i.e.* Terceira, S. Miguel and S. Maria).

The percentage of autochthonous species is more or less similar on every island (see Table 3), being smallest on Graciosa (only 28%) and greatest on Corvo and Faial (43%). On the other islands of the archipelago, this percentage oscillates between 32 and 41%. There is no significant variation between the groups of islands, the percentage being 37% in the central group, 39% in the occidental group and 40% in the oriental group.

ISLANDS	Total n° spp(*)		Intr. n° spp. (%)	Autocht. n°spp. (%)(+)	Endemics (Exclusive)		% of Endemism(*)		% of Exclusive End.		% End.(+)
AZORES	A	B	B	B	A	B	A	B	A	B	B
CORVO	19	21	12 (57)	9 (43)	4(-)	3(-)	21.1	14.2	-	-	33.3
FLORES	97	182	110 (60)	72 (40)	11(4)	17(4)	11.3	9.3	36.4	23.5	23.6
FAIAL	164	212	136 (64)	76 (36)	11(1)	12(2)	6.7	5.6	9.1	16.6	15.8
PICO	41	155	89 (57)	66 (43)	5(2)	20(5)	13.2	12.9	40.0	25.0	30.3
GRACIOSA	23	101	73 (72)	28 (28)	2(-)	4(-)	8.7	4.0	-	-	14.2
S. JORGE	71	121	77 (64)	44 (36)	8(1)	8(1)	11.3	6.6	12.5	12.5	18.2
TERCEIRA	102	245	167 (68)	78 (32)	9(1)	14(3)	8.9	5.7	11.1	21.4	17.9
S. MIGUEL	255	336	201 (60)	135 (40)	21(13)	28(12)	8.3	8.3	61.9	42.9	20.7
S. MARIA	79	251	149 (59)	102 (41)	6(2)	23(12)	7.6	9.2	33.3	52.2	22.5
Western Group	99	184	112 (61)	72 (39)	11(4)	17(4)	11.1	9.2	36.4	23.5	23.6
Central Group	219	356	226 (63)	130 (37)	15(5)	33(11)	6.8	9.3	33.3	33.3	25.4
Eastern Group	277	418	249 (60)	169 (40)	23(15)	46(24)	8.3	11.0	65.2	52.1	27.2
TOTAL	367	524	314 (60)	210 (40)	36	61	9.8	11.6	-	-	29.0
MADEIRA(1)	-	±1000	-	-	-	±390	-	39	-	-	-
CANARIES(2)	-	±1700	-	-	-	±935	-	55	-	-	-
C. VERDE(3)	-	470	-	-	-	146	-	31	-	-	-

Table 3.- Comparison of the beetle fauna of different Macaronesian islands and Cape Verde. A= SERRANO (1982); B= modified from BORGES (1990); (1) and (2) ISRAELSON (pers. comm.); (3) GEISTHARDT (1988).

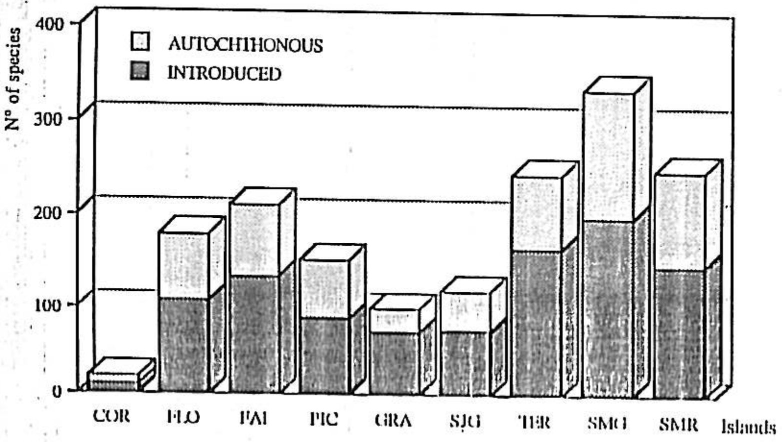


Figure 3.- Distribution of the autochthonous and introduced species of beetle by the nine Azorean islands.

3.2.3. NUMBER OF SPECIES, AREA, DISTANCE FROM THE MAINLAND, ALTITUDE AND GEOLOGICAL AGE IN THE AZORES

With the recent publication of a checklist of Coleoptera from the Azores (BORGES, 1990), it is now possible to seek for the most salient factors for predicting the number of species on each island.

ISRAELSON (1984) emphasizes the fact that the different Azorean islands are not equally well explored. In this case, it will be the total number of days or weeks of collecting effort of expeditions contributing coleopterological data to the Azores, that will explain the diversity differences between the islands. Unfortunately we know only the periods of permanency of each expedition in the archipelago (see in this respect BORGES, 1991b), and there are no available data for the permanency on each island. Consequently we shall not investigate the correlation between days or weeks of collecting effort with the diversity, but we will use the area, distances from the mainland, altitude and geological age, in order to know what is the best predictor for species number.

According to the Equilibrium Theory of Island Biogeography from MACARTHUR & WILSON (1967), the number of species living on an island is a balance between immigration and extinction. The immigration rate is more influenced by distance from the source area, and the extinction rate by the island's size. MACARTHUR & WILSON (*op. cit.*) also predict that a dynamic equilibrium, characterized by constancy of species number and species turnover, will be reached. Validating one of the predictions does not in itself validate the other one, and it is possible that a dynamic equilibrium is present while still remaining true that other factors than area or isolation determine species number (WERFF, 1983); for instance, altitude (OROMÍ, 1982) and geological age (WILCOX, 1978).

As CONNOR & MCCOY (1979) pointed out, a fundamental question is whether regression or correlation should be used in species-area analysis. The authors conclude that if one is interested only in the degree of relation between species number and area, correlation is the appropriate method. Keeping in mind (a) the small number of islands and (b) the range of areas, distances from the mainland, altitudes, and geological ages involved (extending over only two or three orders of magnitude), the best model for the beetles is that using the untransformed variables (WILLIAMS, 1982). In the linear model the number of species is controlled by passive samples from the "pool" of species and does not imply a balance between immigration and extinction.

However, the correlation results obtained by us should be viewed with caution, because according to SIMBERLOFF (1970), about 90% of the studied fauna should be known, and we cannot guarantee that. In reality, there has been an enormous increase in the number of known beetles in the Azores during the past decade (see Fig. 2). Comparing the list of SERRANO (1982) and that of BORGES (1990) there has been an increase of: 10% in Corvo, 88% in Flores, 30% in Faial, 273% in Pico, 334% in Graciosa, 72% in S. Jorge, 139% in Terceira, 32% in S. Miguel and 214% in S. Maria (see Fig. 4).

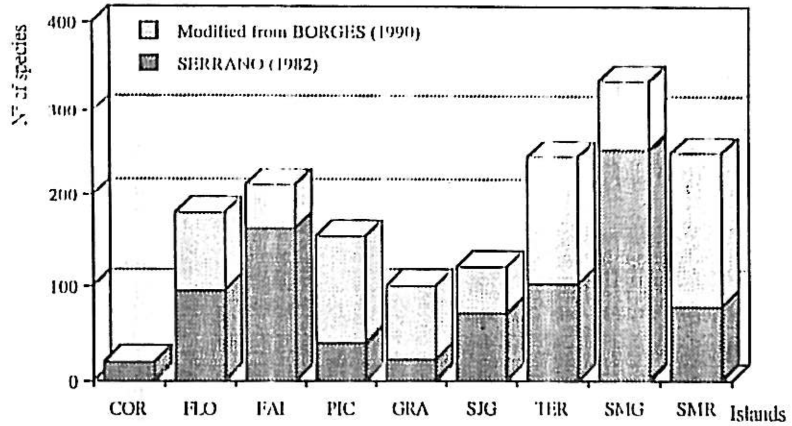


Figure 4.- Increase in the number of beetles known to occur in the nine Azorean islands between 1982 and 1990.

The following analysis will deal with four groups of beetle species:

Total species - the total number of species on each island (total number of the introduced, native and endemic ones);

Autochthonous species - the total number of the native and endemic species;

Total endemic species - the total number of endemic species on each island;

Exclusive endemic species - endemic species exclusive to each island.

3.2.3.1. AREA

As has been noted by several authors, the surface-areas of the islands are expected to show some relation to their diversity. Larger islands receive a larger sample of colonizing organisms than a small island. Because larger samples might contain more species, larger islands will have more species than small ones (CONNOR & McCOY, 1979).

Secondly, large islands tend to have a greater variety of habitats than small ones. The larger the number of habitats, the larger the number of species that can be established on an island (LACK, 1973).

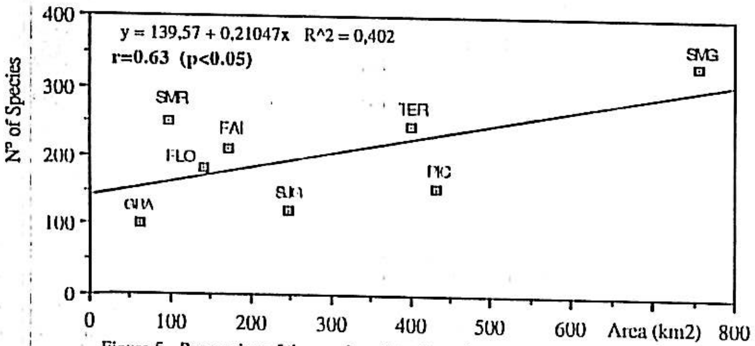


Figure 5.- Regression of the number of total species against the areas. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

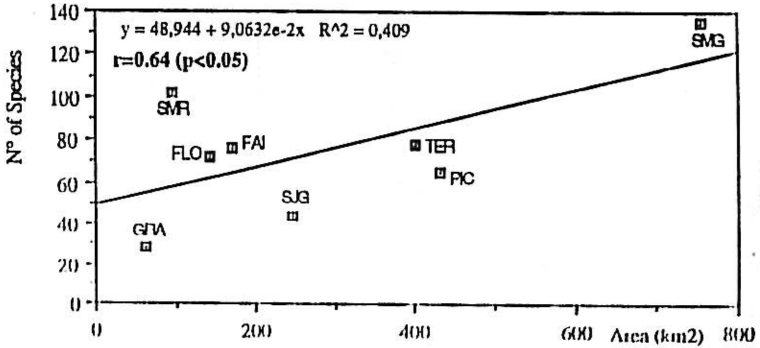


Figure 6.- Regression of the number of autochthonous species against the areas. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

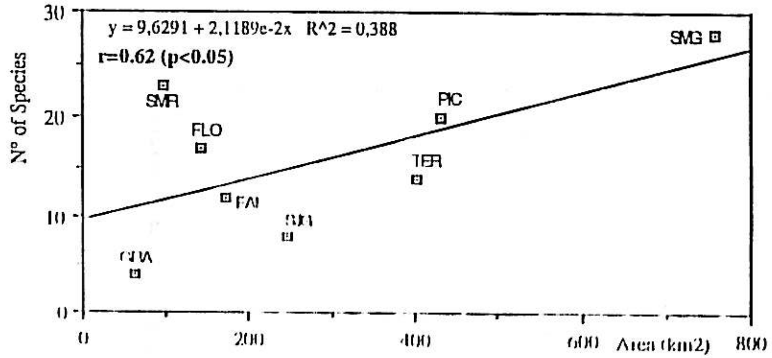


Figure 7.- Regression of the number of total endemic species against the areas. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

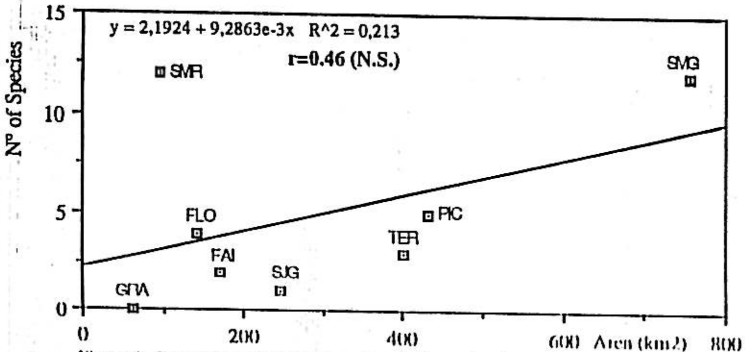


Figure 8.- Regression of the number of exclusive endemic species against the areas. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

In our case, it was shown that the species-area relation complies with the classic prevision of MACARTHUR and WILSON (Figs. 5, 6 and 7).

There is a correlation between the surface-area and the diversity of the islands. However, the correlation value (r) decreases with the smallness of the species group, being statistically not significant with the exclusive endemic beetle species (Fig. 8). Because of that, the **r** values obtained for the total and autochthonous species (with highest values in the best studied islands) are very probably a consequence not of an area effect but of a collecting effort effect (see Figs. 5 and 6). [Furthermore, SJÖGREN (1990) and VIEIRA & PINTUREAU (1991) support the view that there are no apparent positive correlations between area with vascular plants or with Lepidoptera fauna diversity, in the Azores].

Recently, BALLETTO *et al.* (1990), plotting the log of surface-areas on Madeira and the Azorean islands against that of species numbers of Coleoptera, Mollusca and birds, found statistically significant correlations in all cases. However, in the case of beetles the authors could only use data available before 1987 using the total number of species; since then other work has been done (see BORGES, 1990). Moreover, PECK (1991) working data on tropical oceanic islands showed a significant relationship between number of beetle species and island area.

3.2.3.2. DISTANCE FROM THE MAINLAND

As shown by the Equilibrium Theory of Island Biogeography (MACARTHUR & WILSON, 1967), the immigration rate is most heavily influenced by the distance from the source area, and therefore the distances of individual islands from the mainland are expected to present some relation to their diversity. Islands farther from their source area have both a lower number of potential colonizing species and a less frequent arrival of new species.

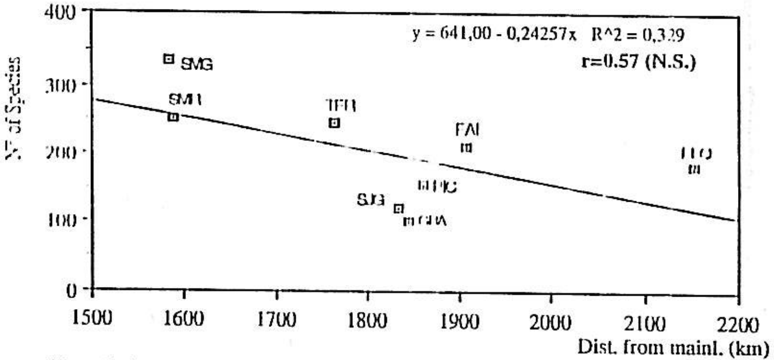


Figure 9.- Regression of the number of total species against the distances from the mainland. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

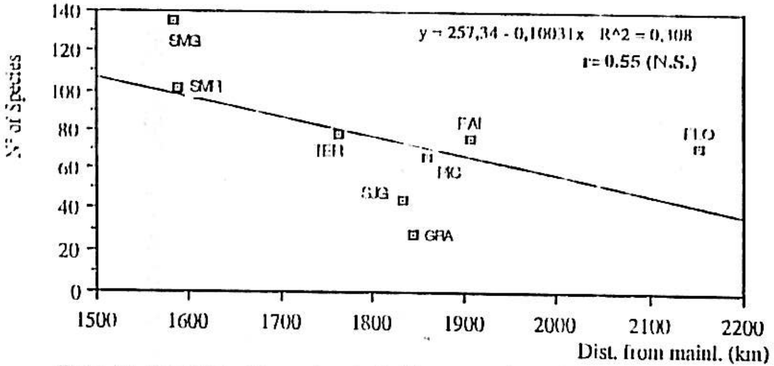


Figure 10.- Regression of the number of autochthonous species against the distances from the mainland. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

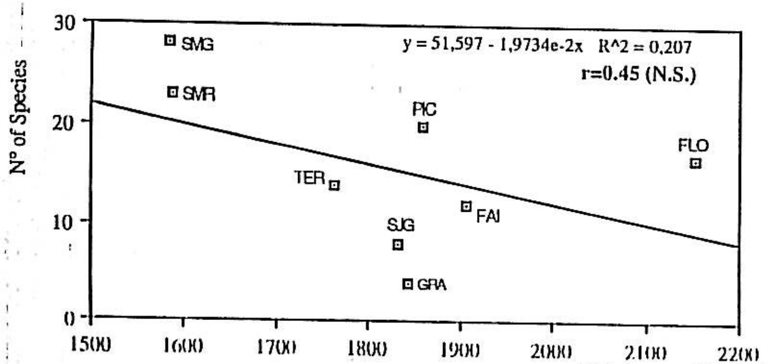


Figure 11.- Regression of the number of total endemic species against the distances from the mainland. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira. SMG= S. Miguel; SMR= S. Maria.

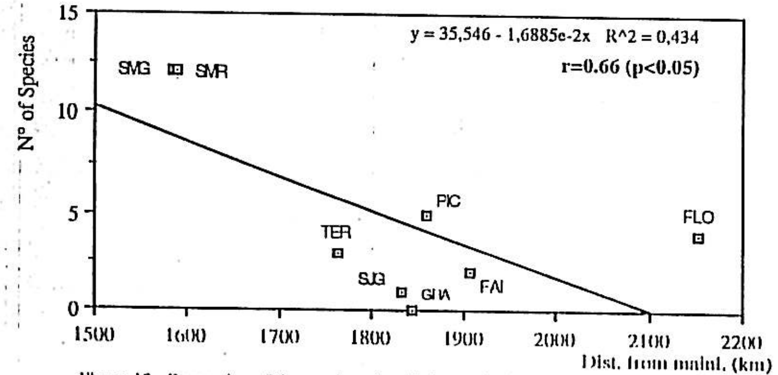


Figure 12.- Regression of the number of exclusive endemic species against the distances from the mainland. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

LINDROTH (1960) affirmed that the geographical isolation of the Azores is a clear obstacle to presumptive immigrants. We found that only the regression of exclusive endemic species against distances of individual islands from the mainland do actually provide a statistically significant correlation (r=0.66; P<0.05) (see Fig. 12)

However, it is not possible to prove if the correlation obtained with the exclusive endemic species has a biological meaning, or if it is a consequence of the islands located nearest the mainland being simultaneously the best studied ones (*i.e.* S.Maria, S. Miguel and Terceira).

3.2.3.3. ALTITUDE

BAEZ (1982b) obtained a significant positive correlation between the altitude of the several Canarian islands and the number of species of Muscoidea; and the same correlation holds for the Chrysomelidae Alticinae from that archipelago (BIONDI, 1987).

There is also a statistical significant correlation between the diversity of the Azorean vascular plants and the altitude of the several islands (SJÖGREN, 1990). For this author, the different altitudes in the Azores form a higher diversity of climatic conditions and consequently of biotopes.

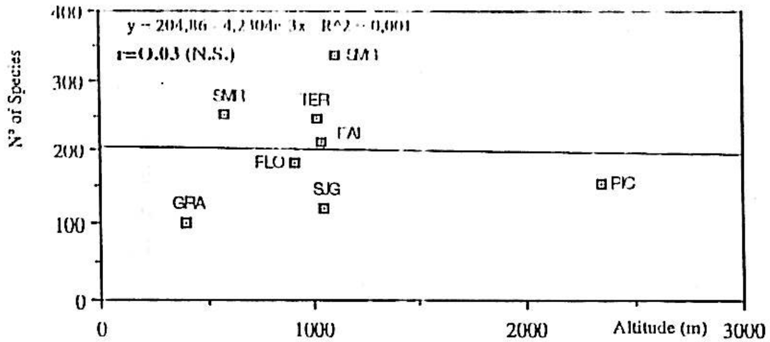


Figure 13.- Regression of the number of total species against the altitude. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

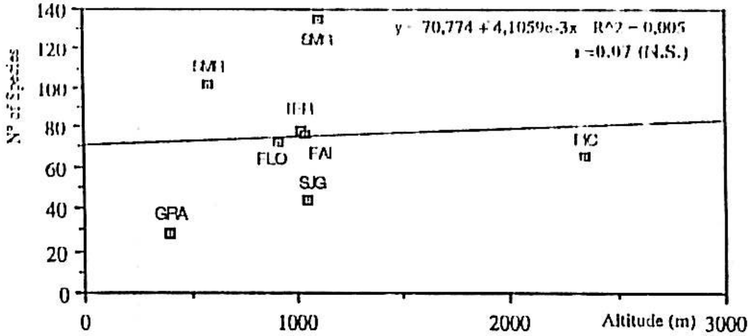


Figure 14.-Regression of the number of autochthonous species against the altitude. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

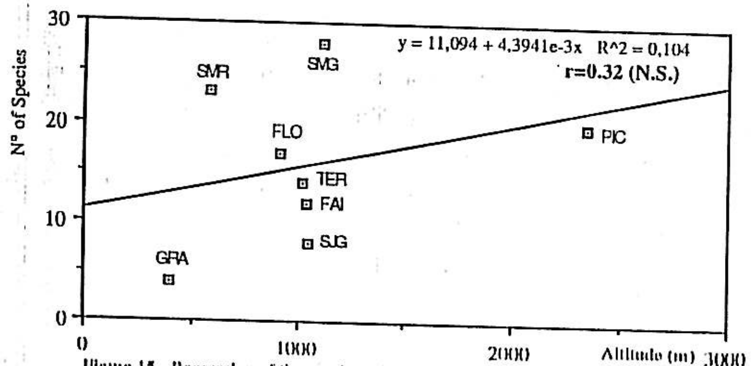


Figure 15.- Regression of the number of total endemic species against the altitude. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

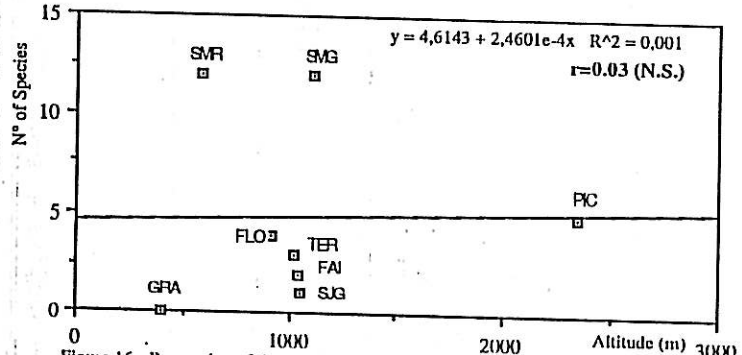


Figure 16.- Regression of the number of exclusive endemic species against the altitude. FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

There is a weak correlation between altitude and the total endemic species (r=0.32), but only 10% of the variation is explained (r^2= 0.10), being statistically not significant (Fig. 15).

As previously pointed out by OROMÍ (1982), who worked on a family of beetles (Tenebrionidae), there is no correlation of fauna with altitude in the Azores (see also Figs. 13, 14 and 16), but it is possible to find such types of correlation in the other Macaronesian archipelagoes. A possible reason for this could be the fact that in the Canary Islands, for instance, high islands have four zones, a sub-alpine zone, pine forest, laurel forest and a xerophytic zone, all simply related to the effect of the trade winds, the number of vascular plant species being strongly related to elevation, though there is still an area effect as well (BRAMWELL & BRAMWELL, 1974). In the Azores such types of differentiation are not possible (DIAS, pers. comm.).

3.2.3.4. GEOLOGICAL AGE

Evolutive radiation occurs on continents as well as on islands, and the amount of adaptive radiation must depend upon the age of an island´s fauna as well as upon the mode of origin (DARLINGTON, 1938).

WILCOX (1978) found that species diversity and age are significantly correlated for lizards on Post-Pleistocene Land-Bridge Islands. However, FAETH & CONNOR (1979) found some errors in the ages estimated by WILCOX (*op. cit.*), and proposed an alternative explanation for his results.

For oceanic and volcanic islands, like the Azores, geological age - though often neglected - could be a good biogeographical predictor. For instance, MACHADO (1976) contends that the isolation by lava flows of the populations in the Canaries, could promote speciation.

During this work (2.1.1.; see also Table 1) we offer three different proposals for geological dating from the nine Azorean islands. For the following regressions we will use the datings of ABDEL-MONEM *et al.* (1975) and FERAUD *et al.* (1980) (column B from Table 1), because they are currently the most generally accepted ones. Later, we will investigate which of the proposals is the best predictor for the current distribution of the Coleoptera from the Azores (see Table 6).

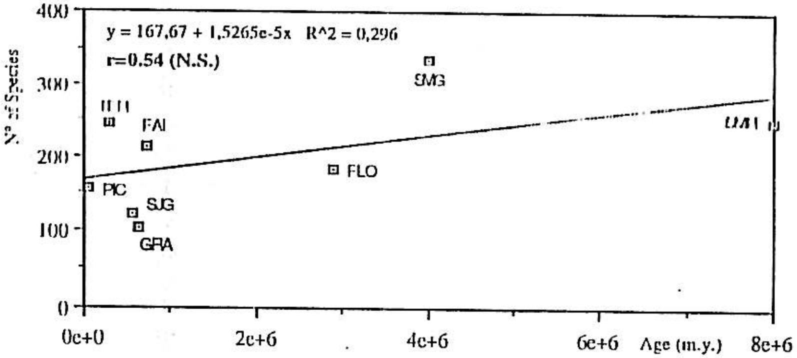


Figure 17.- Regression of the number of total species against the geological age (sensu ABDEL-MONEM et al., 1975 and FERAUD et al., 1980).
FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

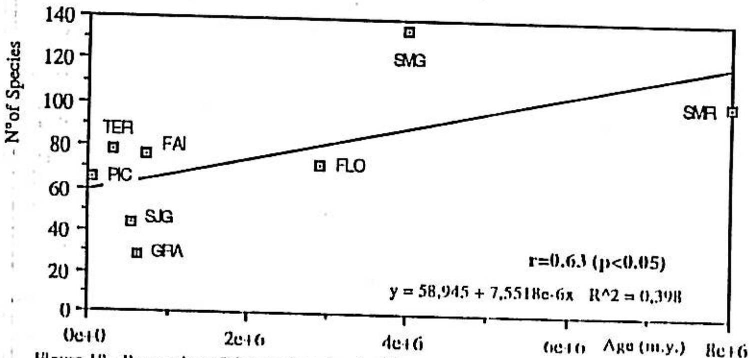


Figure 18.- Regression of the number of autochthonous species against the geological age (sensu ABDEL-MONEM et al., 1975 and FERAUD et al., 1980).
FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

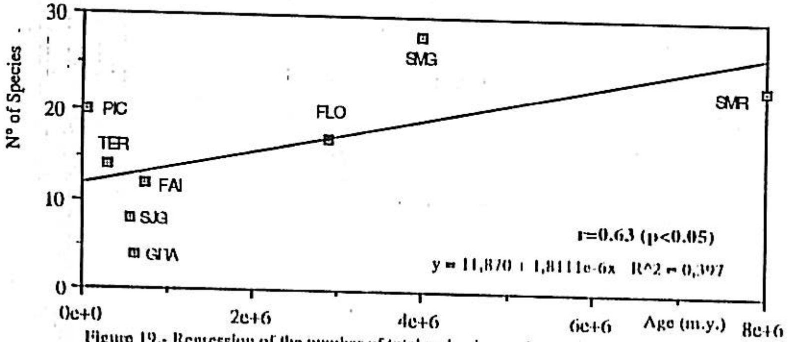


Figure 19.- Regression of the number of total endemic species against geological age. (sensu ABDEL-MONEM et al., 1975 and FERAUD et al., 1980).
FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

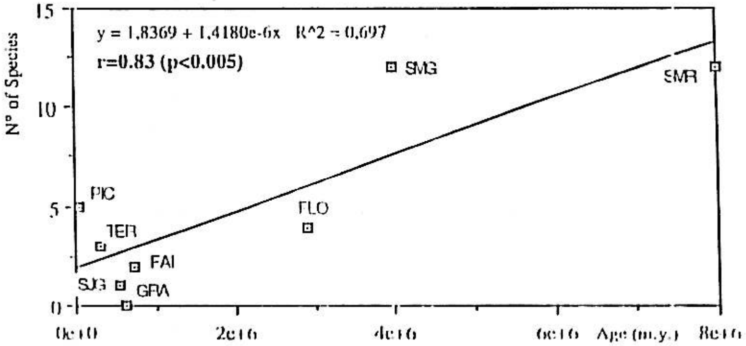


Figure 20. Regression of the number of exclusive endemic species against the geological age (sensu ABDEL-MONEM et al., 1975 and FERAUD et al., 1980).
FLO= Flores; FAI= Faial; PIC= Pico; GRA= Graciosa; SJG= S. Jorge; TER= Terceira; SMG= S. Miguel; SMR= S. Maria.

From an analysis of the correlation coefficients that have been calculated for the relationship between surface-area, distance from mainland, altitude, or geological age on the one hand, and the beetle species number for the Azores on the other, it has been found that the geological age is the best predictor for the total endemic species and for the exclusive endemic species (see Figs. 19 and 20).

Most notable is the correlation value obtained between the geological age and the exclusive endemic species (r= 0.83) (p< 0.005) (Fig. 20) (see below).

3.2.4. ENDEMISM

Oceanic islands tend to present high rates of endemism, in particular at the genus or species level (CARLQUIST, 1974). During the 1980s the number of known endemic beetle species from the Azores underwent a great increase (Fig. 21), with 27 new *taxa* described.

About 11.6% of Azorean beetles are endemic, a total of 61 species (Tabs 2, 3 and 4). A total of 5 endemic genera occur, with one species each (Table 4) [another new genus was recently described (see BORGES & SERRANO, in print.)].

Only 4 families have endemic genera (Table 2). The genera *Pseudanchomenus* TARNIER, 1860 [and also *Cedrorum* n. gen. (BORGES & SERRANO, *op. cit.*)] (Carabidae), *Alestrus* MÉQUIGNON, 1942 (Elateridae) and *Crotchiella* ISRAELSON, 1985 (Cerambycidae) probably represent ancient colonizations, being true relicts and authentic paleo-endemics. The

PB	T.C.	DISTR.	LIST OF SPECIES	COR	FLO	FAI	PIC	GRA	SJG	TER	SMG	SMR
			CARABIDAE									
	p	P	*Ocydromus derelictus* ALLUAUD, 1926		+							
+	p	N	*Ocydromus schmidti azoricus* LINDROTH, 1960		+	+	+				+	
+	p	N	*Thalassophilus azoricus* OROMÍ & BORGES, 1991								+	
	p	N	*Trechus torretassoi* JEANNEL, 1937								+	
+	p	N	*Trechus picoensis* MACHADO, 1988				+					
+	p	N	*Trechus terceiranus* MACHADO, 1988							+		
+	p	N	*Trechus montanheirorum* OROMÍ & BORGES, 1991				+					
+	p	N	*Trechus jorgensis* OROMÍ & BORGES, 1991						+			
+	p	N	*Calathus lundbladi* COLAS, 1938								+	
+	p	N	*Calathus vicenteorum* SCHATZMAYR, 1937									+
	p	N	*Calathus extensicollis* PUTZEYS, 1863				+					
+	p	N	*Calathus carvalhoi* SERRANO & BORGES, 1986							+		
+	p	N	*Olisthopus inclavatus* ISRAELSON, 1983									+
+	p	P	*Pseudanchomenus aptinoides* TARNIER, 1860				+				+	
	p	N	*Bradycellus chavesi* ALLUAUD, 1918								+	
			DYTISCIDAE									
+	p	N	*Hydroporus guernei* RÉGIMBART, 1891	+	+	+	+		+	+	+	+
+	p	N	*Agabus godmani* CROTCH, 1867		+	+	+	+	+	+	+	
			HYDRAENIDAE									
	h	N	*Ochthebius frey* D'ORCHYMONT, 1940		+	+						+
			SCYDMAENIDAE									
	p	N	*Euconnus azoricus* FRANZ, 1969							+		
			STAPHYLINIDAE									
+	p	N	*Phloeonomus azoricus* FAUVEL, 1900		+		+			+	+	
	p	N	*Xantholinus longiventris miguelensis* (MÉQUIGNON, 1942)								+	
	p	N	*Aleochara freyi* BERNHAUER, 1940-49				+					
	p	N	*Geostiba melanocephala* (CROTCH, 1867)								+	
	p	N	*Atheta (Nothotecta) caprariensis* ISRAELSON, 1985								+	
	p	N	*Atheta (Nothotecta)* dryochares ISRAELSON, 1985								+	
	p	N	*Atheta (Hummleriella) azorica* BERNHAUER, 1936 ? ?									
	p	P	*Atheta (Geostibops) aptera* ISRAELSON, 1985		+							
	p	N	*Phytosus schatzmayeri* BERNHAUER, 1941								+	
			ELATERIDAE									
+	s	N	*Heteroderes azoricus* TARNIER, 1860	+	+	+	+	+	+	+	+	+
+	s	N	*Heteroderes melliculus moreleti* TARNIER, 1860			+		+	+	+		+

Table 4.- Checklist of the Azorean endemic beetle species (adapted from BORGES, 1990). PB= In the author's collection; T.C.=Trophic category: p-predators, s-saprophagous, f-fungivores, h-herbivores; P=Paleo-endemic, N=Neo-endemic.

PB	T.C.	DISTR.	LIST OF SPECIES	COR	FLO	FAI	PIC	GRA	SJG	TER	SMG	SMR
			ELATERIDAE									
+	h	P	*Alestrus dolosus* (CROTCH, 1867)		+					+	+	
			PTINIDAE									
+	s	N	*Sphaericus velhocabrali* ISRAELSON, 1984									+
			CUCUJIDAE									
	p	P	*Leptophloeus azoricus* RATTI, 1972									+
			MEROPHYSIDAE									
	s	N	*Holoparamecus azoricus* MÉQUIGNON, 1942								+	
	s	N	*Gietella faialensis* MENIER & CONSTANTIN, 1988			+						
			LATRIDIIDAE									
+	s	N	*Metophthalmus occidentalis* ISRAELSON, 1984			+						+
			CISIDAE									
+	f	N	*Atlantocis gillerforsi* ISRAELSON, 1985		+		+				+	+
			COLYDIIDAE									
+	p	N	*Tarphius wollastoni* CROTCH, 1867		+	+						
+	p	N	*Tarphius rufonodulosus* ISRAELSON, 1984									+
+	p	N	*Tarphius depressus* GILLERFORS, 1985									+
+	p	N	*Tarphius tornvalli* GILLERFORS, 1985				+				+	
+	p	N	*Tarphius azoricus* GILLERFORS, 1986		+		+			+	+	
	p	N	*Tarphius acuminatus* GILLERFORS, 1986				+					
+	p	N	*Tarphius pomboi* BORGES, 1991									+
+	p	N	*Tarphius serranoi* BORGES, 1991									+
			TENEBRIONIDAE									
	s	N	*Helops azoricus* CROTCH, 1867								+	
			CERAMBYCIDAE									
	h	N	[illegible] REITTER, 1894								+	
	h	P	*Crotchiella brachyptera* ISRAELSON, 1985				+				+	+
			CHRYSOMELIDAE									
	h	N	*Mniophilosoma obscurum* GILLERFORS, 1986		+							
	h	N	*Psylliodes vehemens azorica* JACOBSON, 1922			+						
+	h	N	*Longitarsus azoricus* ISRAELSON, 1990							+		+
			CURCULIONIDAE									
+	h	N	*Otiorhynchus trophonius azoricus* UYTTENBOOGAART,1940			+	+		+	+	+	+
+	h	N	*Laparocerus azoricus* DROUET, 1859	+	+	+	+	+	+	+	+	
	h	N	*[illegible] lepidopterus* UYTTENBOOGAART, 1940 ??						+			+
	h	P	*Neocnemis occidentalis* CROTCH, 1867									+

Tab. 4.- (Contin.).

PB	T.C.	DISTR.	LIST OF SPECIES	COR	FLO	FAI	PIC	GRA	SJG	TER	SMG	SMR
			CURCULIONIDAE									
	h	P	*Hypera multifida* ISRAELSON, 1984									+
	h	P	*Pseudechinosoma nodosum* HUSTACHE, 1936		+		+				+	+
	h	P	*Acalles droueti* CROTCH, 1867		+							
+	h	N	*Acalles subcarinatus* ISRAELSON, 1984		+		+			+	+	+
+	h	N	*Caulotrupis parvus* ISRAELSON, 1985									+
			SCOLYTIDAE									
	h	N	*Phloeosinus gillerforsi* BRIGHT, 1987				+				+	
32			Number of species= 61	3	17	12	20	4	8	14	28	23

Tab. 4.- (Contin.).

genera *Pseudechinosoma* HUSTACHE, 1936 and *Neocnemis* CROTCH, 1867 (Curculionidae) have known related *taxa* and are probably neo-endemics.

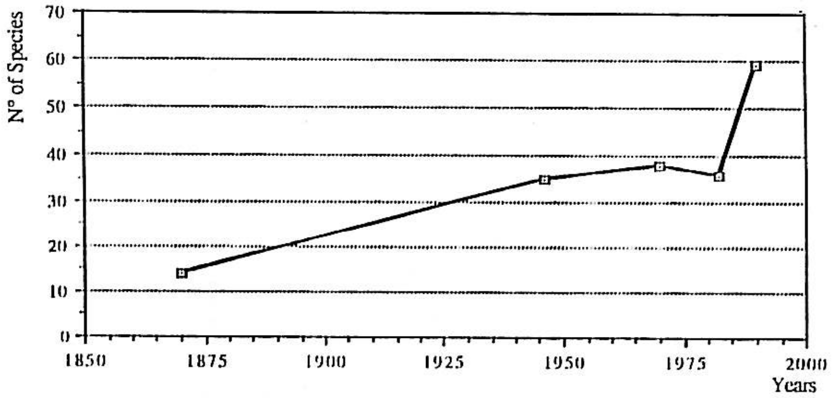


Figure 21.- Rate of increase in the total number of recorded endemic beetle species from the Azores (see Table I in BORGES, 1990).

Two of the four first genera have American affinities: *Pseudanchomenus* has characteristics similar to some North-American *taxa* (LINDROTH, 1960); *Crotchiella* belongs to the *Achrysonini*, a Cerambycinae tribe well diversified in the Neotropical Region, but with scattered representatives in North America and in the tropics and subtropics of the Old World (ISRAELSON, 1985b).

Relict species are one of the most remarkable characteristics of insular faunas (CARLQUIST, 1965). In the Azores there are some examples, represented by some of the following paleo-endemic species (*sensu* LINDROTH, *op. cit.*): *Ocydromus derelictus* ALLUAUD, 1926, *Pseudanchomenus aptinoides* TARNIER, 1860, *Cedrorum azoricus* n. gen. n.sp. (BORGES & SERRANO, in print.), *Atheta* (*Geostibops*) *aptera* ISRAELSON, 1985, *Alestrus dolosus* (CROTCH, 1867), *Leptophloeus azoricus* RATTI, 1972, *Crotchiella brachyptera* ISRAELSON, 1985, *Neocnemis occidentalis* CROTCH, 1867, *Hypera multifida* ISRAELSON, 1984, *Pseudechinosoma nodosum* HUSTACHE, 1936, *Acalles droueti* CROTCH, 1867, and perhaps even more (see Table 4).

Also remarkable is the presence of three paleo-endemics exclusive to Flores (*Ocydromus derelictus*, *Atheta aptera* and *Acalles droueti*) and three species exclusive to S. Maria (*Leptophloeus azoricus*, *Neocnemis occidentalis* and *Hypera multifida*).

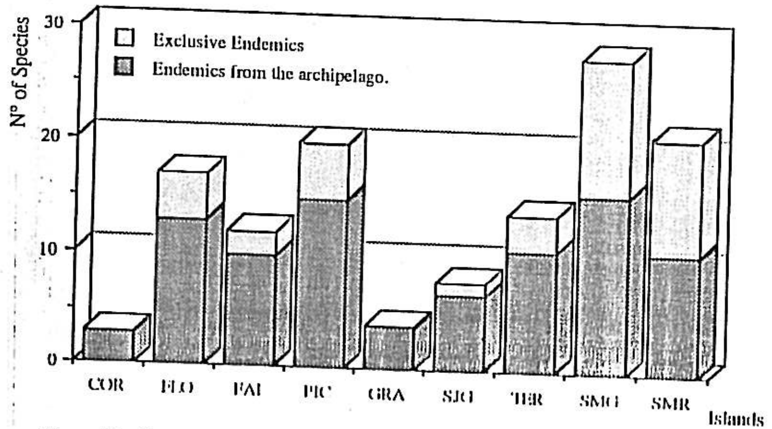


Figure 22.- Number of the endemic beetles known to occur in the nine Azorean Islands.

Flores and S. Maria have a high relative number of total and exclusive endemics, being both geologically ancient islands. Consequently the results obtained in 3.2.3.4., suggesting a good correlation value between geological age and exclusive endemic species (r= 0.83) (p< 0.005) (Fig. 20), are here confirmed and strengthened. The analysis of Fig. 23 is still more illustrative for our purposes, since, with the exception of Pico (a geologically young island), it is the geologically oldest islands which have the highest rates of endemism (*i.e.* Flores, S. Miguel and S. Maria).

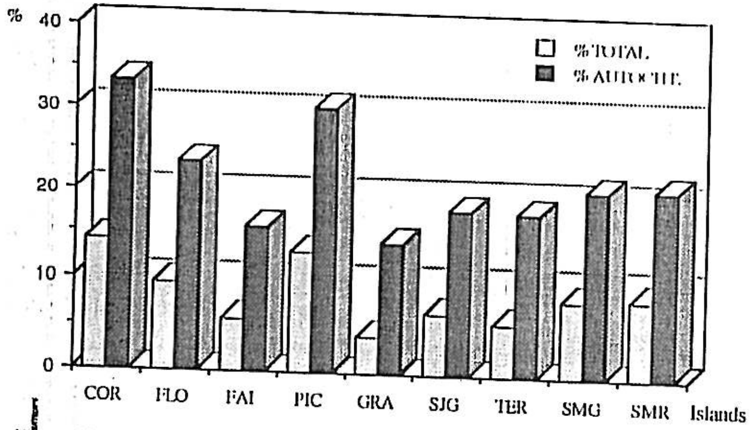


Figure 23.- Percentage of the endemic beetles known to occur in the nine Azorean islands.

Oceanic islands, such as Hawaii and Galapagos, are famous for having allowed the evolutionary development of spectacular "swarms" of endemic species from one or a few ancestral stocks (PECK & PECK, 1990). In the Azores there are three known examples of such a phenomenon in the genera *Trechus* (Carabidae), *Calathus* (Carabidae) and *Tarphius* (Colydiidae). In each of them it seems confirmed that an ancestral species has given rise to the currently occurring group of species.

Most of the endemic species are allopatrically distributed in the Azores, with the exception of the *Tarphius* species (ISRAELSON, 1990; BORGES, 1991a) and of the paleo-endemic ground-beetle species *Pseudanchomenus aptinoides* TARNIER (found on Pico and S. Miguel) (BORGES, 1990). The ground-beetle *Cedrorum azoricus* n. gen. n. sp. has a new subspecies (*caveirensis* n. ssp.) occurring on Pico, being the nominate subspecies found on Terceira and S. Maria (BORGES & SERRANO, in print.). In the genus *Tarphius* (Table 4), it is possible to find three species that occur on more than one island, and on Flores, Pico, S. Miguel and S. Maria there are sympatric species (BORGES, 1991a) (*cf.* 4.4.).

4. COLONIZATION AND EVOLUTION OF THE AZOREAN COLEOPTERA

4.1. COLONIZATION MECHANISMES

Entomologists like JEANNEL (1946), PEYERIMHOFF (1946), UYTTENBOOGAART (1946), MATEU (1961), VANDEL (1961) and others, were defenders of the continental origin of the archipelagoes of Madeira, the Canaries and Cape Verde, or, at least, proposed the ancient occurrence of one or more "land bridges" between these islands and the mainland.

HEER (1856) similarly defended the occurrence of a submarine plate -the Atlantis- connecting Europe, America and the oceanic islands (including the Azores). The hypothesis of the Atlantis, an old continent some tens of millions of years old (different from the Plato´s Atlantis), of pre-historic age, was defended subsequently only by JEANNEL (*op. cit.*), with now obsolete arguments.

Nowadays, knowledge about Plate Tectonics refutes this possibility. It is proved that the direction in which the ocean floor was expanding was precisely the opposite direction, that is, Europe retreating from Africa and the Americas, with the Atlantic archipelagoes being of volcanic origin. Besides, FRUCTUOSO (1591) and WALLACE (1872) had previously defended an oceanic origin for the Azores, the islands being colonized by means of "long-distance dispersal" (CARLQUIST, 1966; GRESSITT, 1974).

SIMBERLOFF (1981) reminded us that a good colonizer needs, first of all, the capacity to reach an oceanic island. ZIMMERMAN (1948) (*in* PECK & PECK, 1990) recognizes four principal mechanisms by which fauna can arrive at an oceanic island:

(1) - on the surface of the ocean by rafting on flotsam, by floating, or by swimming;
(2) - through the air by active flight, or by means of passive transport by air currents;
(3) - by being carried in or on another organism;
(4) - by being carried intentionally or unintentionally by man.

(1) (2) - In spite of the existence of some dispersal records involving rafting or floating for some archipelagoes, there are no such direct observations for the Azorean sea. ASHMOLE & ASHMOLE (1988) studied the insect dispersal on the large oceanic island of Tenerife (Canaries), concluding that the catches obtained in the neuston and kite nets indicated that many arthropods are blown out to sea from the island. Very probably the same is true for the mainland, and many insects can reach the islands over the surface of the ocean. The colonizing individuals may have been adults, or even eggs, larvae, or pupae in or on floating plant matter, including whole trees (PECK & PECK, 1990).

The pioneering experimental work of J. L. GRESSITT and his colleagues has demonstrated the abundance of insects carried in the air over the sea, at both low and high altitudes - the aerial plankton (see references in PECK & PECK, 1990).

The oceanic location of the Azores does not seem concordant with the arrival of plants and animals from Western Europe. The warm current of the Gulf Stream dominates the entire Azorean area throughout the year, with the occurrence of superficial currents with a North/South or North--west/South-east orientation. On the other hand, the prevailing winds in the Azores have a South--west orientation in winter, and a North-east orientation in summer (FERREIRA, 1955).

Consequently, all types of colonization by sea or air in this archipelago would seem to stand every chance of being of American origin. Nevertheless, we should remember that the North--Atlantic circulation underwent some periods of great change during the last Pleistocene glaciations (RUDDIMAN & MCINTYRE, 1981; COOPE, 1986), and also in all probability during the earlier ones. Although the direction of the prevailing winds and sea-currents favoured a western colonization, the fact is that the known beetle species in the Azores have a predominantly Palaearctic-Occidental origin (BORGES, 1990; see discussion above).

(3) - Although some beetle species that live in birds´ nests could be logical candidates for a type of colonization "on another organism", we can draw no conclusion here because there is no survey of bird-beetle or birds´ nest -beetle associations in the Azores.

(4) - Discovered by the Portuguese navigators in 1432, the Azores seem already to have been vaguely known, being indicated on older maps. For a great many years this archipelago provided ports of call for ships coming from the Americas. Some Neotropical beetle species known to occur in the Azores may have been introduced in this way (MÉQUIGNON, 1935). GUIMARÃES & BEIJA (1974) presented a list of beetles that infest stored products in this archipelago, all of them species highly synanthropic or anthropochoric. We calculate that of the species now present (524 species), as much as 314 species (59.9 %) (Table 2) have been probably unintentionally introduced, a lot of them recently. This gives us an indication of human influence on the current composition of the beetle fauna in the Azores (Fig. 3).

4.2. ZOOGEOGRAPHICAL ORIGIN OF THE COLONISTS

4.2.1. THE GENERA

It is of particular interest to investigate the zoogeographical origin of the genera with autochthonous species of Coleoptera in the Azores. The genera have been referred to the following categories (PEYERIMHOFF, 1946):

1.- HOLARCTIC: In this category occur genera with some endemics in the Azores; *e.g. Trechus*, *Calathus*, *Olisthopus*, *Bradycellus*, *Hydroporus*, *Agabus* and *Helops*. Others colonized these islands by natural means but have not speciated, namely the genera *Coelambus*, *Habrocerus*, *Scobicia*, *Nicobium*, *Lasioderma*, *Anaspis* and *Sitona*. All of them are well represented in the Mediterranean fauna .

2.- PALAEARCTIC: It should be pointed out that in the Azores there is a poverty of genera with a Euroasiatic distribution. Only the genera *Campalita*, *Blaps* and *Aromia*, the last with an endemic species, could be included in this category. *Campalita olivieri* is the only known example in the Azores of a primitive xerothermic feature, with some current representatives in desert areas.

3.- WESTERN PALAEARCTIC: In practice, this includes genera with a Mediterranean distribution. It is the case of *Aepus*, *Thalassophilus* (with a relict cavernicolous species in the Azores), *Tarphius* (eight endemic species in the archipelago), *Anommatus*, *Cathormiocerus* and *Caulotrupis* (each with one endemic species each), *Amaurorhinus* and *Liparthrum*.

4.- MACARONESIA: The genera *Prostheca*, *Hegeter*, *Gietella* and *Laparocerus* (the last two with each one endemic species) belong to this category.

4.2.2. THE SPECIES

With the purpose of investigating the origin of known beetle species in the Azores, we have classified the species into the several Biogeographical Regions, resulting in the graphics presented in Figs. 24 and 25.

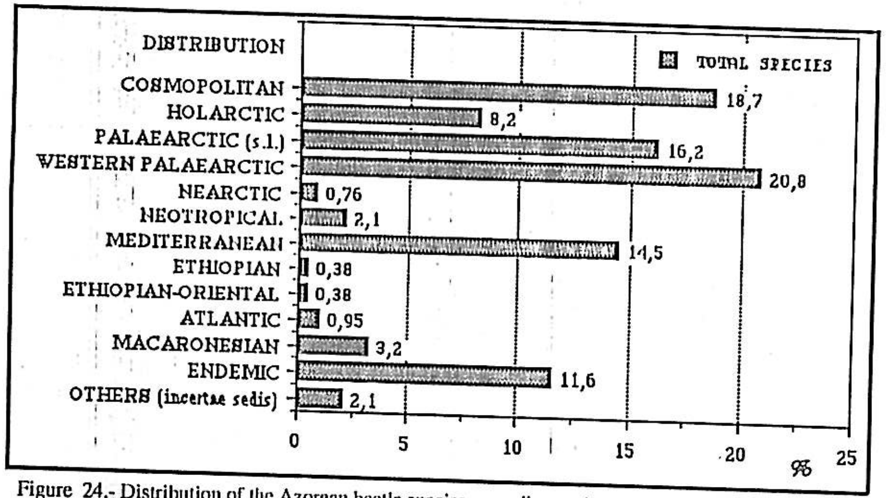


Figure 24.- Distribution of the Azorean beetle species according to the major Biogeographical areas (using the total number of species).

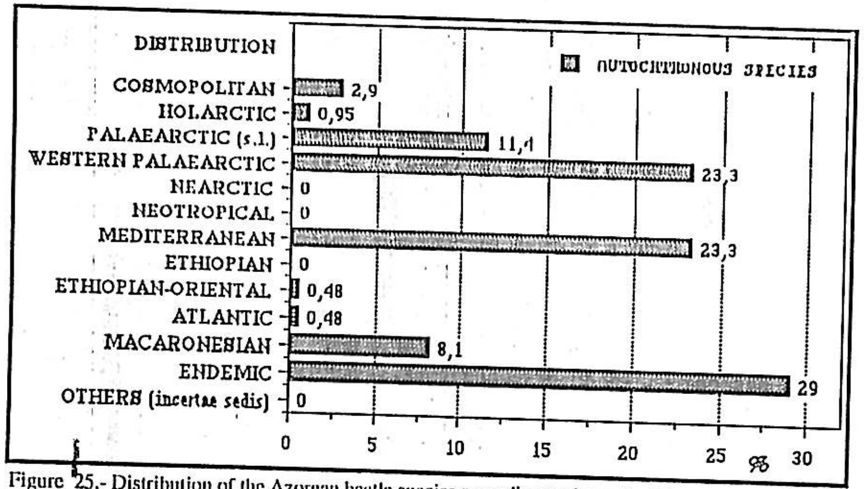


Figure 25.- Distribution of the Azorean beetle species according to the major Biogeographical areas (using the autochthonous species).

An analysis of Figs. 24 and 25 may lead to the following conclusions:

1. The low rate of endemism in the Azores, the smallest among the Macaronesian and Cape Verde Islands beetle faunas, is a relative concept, because, as we can see from Fig. 25, the endemic species (29%) supplant all other zoogeographical categories in the autochthonous species. Using the total number of species, it should be remembered that Cape Verde has 31% of endemism However, the Canaries with 55% and Madeira with 39% still show some disparity;

2. It should also be noted that the European affinity predominant when working with the total species (Fig. 24) is less important when working with the autochthonous species (Fig. 25), being replaced by a Mediterranean-Macaronesian affinity;

3. There is an important proportion of introduced species that, when out of the analysis (Fig. 25), renders less important the Cosmopolitan, Holarctic and Neotropical components of the Azorean beetle fauna;

4. Nevertheless, the Western-Palaearctic component is still very important in the beetle fauna of this archipelago (Figs. 24 and 25).

4.2.3. COMPARISON WITH THE OTHER MACARONESIAN ARCHIPELAGOES AND CAPE VERDE ISLANDS

Of the 524 species of beetle species now known to occur in the Azores, 197 have not been recorded in the other archipelagoes in Macaronesia and Cape Verde; 61 of them are Azorean endemics. The remaining 327 occur also in one or more of the other archipelagoes in Macaronesia and Cape Verde Islands: 64 on Madeira alone, 35 in the Canaries alone, 4 in the Cape Verde Islands alone, 162 on Madeira and the Canaries, 3 on Madeira and the Cape Verde Islands, 4 on the Canaries and the Cape Verde Islands and 55 on Madeira, the Canaries and the Cape Verde Islands (modified from BORGES, 1990).

If the same type of analysis is made for only the autochthonous species (210; see Tabs. 2 and 3) we get the following results: 94 have not been recorded in the other archipelagoes in Macaronesia, 61 of them being Azorean endemics; and of the remaining 129, 36 occur only on Madeira, 11 only in the Canaries, 1 only in the Cape Verde Islands, 57 on Madeira and the Canaries, 1 on Madeira and the Cape Verde Islands, 2 in the Canaries and the Cape Verde Islands and 8 on Madeira, the Canaries and the Cape Verde Islands.

These results show that, there is a great similarity between the Azorean and Madeiran beetle fauna and an almost total lack of relation to the Cape Verde beetles.

MADEIRA

The Madeiran fauna is essentially of Mediterranean type, with some African elements (UYTTENBOOGAART, 1946; MATEU, 1961). Recently ERBER & HINTERSEHER (1988) cited 26 new species for this archipelago, most of them with a European-Mediterranean distribution.

CANARIES

The Canaries have some beetle fauna with a strong Mediterranean component (North African and Southern Iberian), but they also have some recently immigrated African elements, mainly on the islands nearest to the African mainland, Fuerteventura and Lanzarote (MATEU, *op. cit.*; BAEZ & PINTO, 1983).

Other feature of this fauna is the high rate of endemism (UYTTENBOOGART, *op. cit.*) that in the beetles reaches about 55% (see Table 3) and equally remarkable being the high proportion of endemic genera (*e.g.* 19% in the Carabidae, MATEU, *op. cit.*) and the adaptive radiation that has occurred in some genera (see 4.4.).

CAPE VERDE

The Cape Verde Islands were colonized mainly by a fauna originating in tropical Africa, and also by a significant proportion of Mediterranean elements (UYTTENBOOGART, 1946; MATEU, 1968; SERRANO, 1982). Concerning the autochthonous beetle species, the rate of endemism is high but varies from group to group (MATEU, *op. cit.*).

Nevertheless, OROMÍ (1982) insists that the Azores and the Cape Verde Islands are marginal zones of the Macaronesia.

4.2.4. ON THE ORIGIN OF THE AZOREAN COLEOPTERA

It seems fairly evident that the location of an oceanic island and the direction of the prevailing winds and sea currents will determine the geographic origin of the arrivals.

Close analysis of the Azorean fauna reveals the presence of a remarkable European component. Although this archipelago is located between the Old and the New World, there is a considerable lack of autochthonous American elements. The unique American beetle species occurrences were, beyond dispute, introduced by man (MÉQUIGNON, 1935).

This Palaearctic component is obvious in Figs. 24 and 25, and is against the direction of the prevailing winds and sea currents. This is the North Atlantic biogeographical paradigm.

Considering that the autochthonous beetles of the Azorean archipelago came by natural means, that is by long distance dispersal, we offer the following hypothesis by way of explanation:

a) Large-scale changes in climatic conditions during the Pleistocene Age (COOPE, 1979, 1986), suggesting that the direction of the winds may have changed during these events (CRAFFORD *et al.*, 1986). From this, it will be seen that we are discussing the paleo-winds and paleo-currents of UYTTENBOOGAART (1946) (see also SOUSA, 1985). Thus, the Azorean autochthonous beetle species, remarkably, could be pre-Pleistocene relicts;

b) Nevertheless, the importance of winds originating in North Africa, called "LESTE", for the dispersal of insects to the Madeiran archipelago has been proved (CLASSEY, 1966). Besides, it is equally true that sometimes such winds reach the Azores, carrying several insects, as happened in the summer of 1987 with the arrival in the Azores of locusts from Africa. WALLACE (1872) also emphasizes the fact that the storms which occur throughout the year in the North Atlantic carry with them to the Azores several species of birds, and very probably insects too.

c) Our botanical knowledge of the Azores is more advanced than the entomological. DIAS (pers. comm.) points out the relevance of the Atlantic-Mediterranean Azorean flora, based on the presence of old *taxa* originating in Tethiano-Tertiary flora (DIAS, 1989). At the time of the formation of the first Azorean islands the Laurel Tertiary Vegetation was already completely extinct on the European mainland, and also on part of the American. As a consequence of this fact, the islands did not have access to species samples directly from the mainland, but from previously filtered samples (filtered by distance and by specific insular features) of the Canaries-Madeira-Josephine complex. Thus, DIAS (*op. cit.*) talks about a "Double Insularity" for the Azorean archipelago (see also BALLETTO *et al.*, 1990 and WUNDERLICH, 1991).

This third hypothesis seems to us extremely attractive, being, in some sense, reconcilable with the second one. On the other hand, observing Fig. 25, it is evident that the Mediterranean component of the Azorean autochthonous beetle species (a known common feature of Madeira and the Canaries) has been underestimated. In all probability this is because we work most frequently with the total number of species, with a high synanthropic palaearctic component (Fig. 24).

This Mediterranean component, combined with the Macaronesian component, reaches 31.4% of the autochthonous species; besides, there is a close relationship between the Azorean neo-endemics and some Madeiran and Canarian relatives. These two facts give plausibility to a colonization originating along a Macaronesian "Island Rosary" (DIAS, 1989) [the "stepping stones" of MACARTHUR & WILSON (1967)].

BALLETTO *et al.* (1990) go further, and state that some Macaronesian species may have migrated from the Azores to Madeira and the Canary Islands, and, moreover, that the genealogical relationships of the Madeiran fauna are roughly intermediate between those of the Azores and those of the Canary Islands, but rather closer to the former than to the latter. However, we do not agree with these authors when they conclude that the flightless or scarcely vagile terrestrial species cannot migrate from the Azores, because as ASHMOLE & ASHMOLE (1988) had recently demonstrated, a wide variety of endemic species from Tenerife, some flightless or scarcely vagile, do participate in aerial dispersal.

4.3. ESTABLISHMENT OF THE COLONISTS

TAKHTAJAN (1969) (*in* DIAS, 1989) stressed that "arriving there is only half of the problem"; that is, the dynamics of the establishment of colonist species is the other half of the problem, and is even less well understood. In fact, the number of *taxa* in one island is not only a consequence of their dispersal capacity but also of their ability to establish themselves (CARLQUIST, 1966 and 1974).

Several factors should occur simultaneously in order that the establishment of a species may became successfull, such as: the availability of a favourable habitat and the presence of the respective sexual partner (SIMBERLOFF, 1981). The relative absence of predators and parasites is another important condition. JOHNSON (1982) points out the importance of parthenogenesis in the insular faunas, in particular in the Ptiliidae. Such phenomena occur in the Azores, *e.g.* one species of the family Corylophidae [*Sericoderus lateralis* (GYLLENHAL)] (ISRAELSON, 1985a); probably also in some species of the Curculionidae (see BUCKLAND, 1988).

EHRLICH (1986) defines a successeful invader species as one with the following features: abundant in original range, polyphagous, short generation times, much genetic variability, resistancy to a wide variety of physical conditions, and one in which a fertilized female is able to colonize alone.

MACARTHUR & WILSON (1967) introduced into ecology the terms "r -selection" and "K-selection", originally for naming the reproductive strategies of natural populations; "r-selection" signified a highly selective capacity for increasing a population from a few individuals and "K-selection" was originally applied to a high competitive capacity in a population with a stable number of individuals. PIANKA (1970) enlarged the meaning of these terms, relating them to two different life strategies of natural populations. Therefore, the successeful invader species, defined by EHRLICH (1986), fits the selective strategy type *r* (for more information see PIANKA, 1970 and PARRY, 1981).

The lack of suitable plants will reduce to some extent the success of any establishment by a herbivorous species, while the survival chances of a polyphagous predator or of a saprophagous one will be high, because of their less pronounced specialization (BECKER, 1975). This seems to be particularly true on islands, where the occurrence of a specialized herbivore species is less representative than on the mainland, causing predators to be much more frequent on the islands. The results obtained for the Azores seem to support the theory of BECKER (*op. cit.*), since specialists like the herbivore and fungivore species represent only 30% of the endemics and 28% of the native species (Table 5). In this respect it is enlightening that the Curculionidae, many of them specialized herbivores, are represented in the Azores by relatively few species, whereas the Curculionidae is usually one of the most species rich beetle families.

The minimum number of ancestral natural colonizations of the islands is estimated as the minimum number of colonists necessary to give rise to monophyletic groups occurring on the islands, the sister-groups of which occur outside the archipelago (PECK & PECK, 1990).

Using only the endemic and native species (that is, the autochthonous) we can thus estimate about 194 colonizations for the 210 species from the archipelago (Table 3). Working only with the endemics, we obtain about 45 successfull colonizations for the 61 species known to occur. These results are a little surprising, since for an oceanic island we would not normally expect such a high number of colonist species in relation to the number of the autochthonous species. Over a period of 8 million years, it means an average rate of one successful colonization every 41,237 years.

In the Azores, the relative poverty of the insect herbivore species, when compared to the archipelagoes of Madeira and the Canaries, has been emphasized by several authors (*e.g.* MÉQUIGNON, 1946; SERRANO, 1982; QUARTAU, 1982a), it can be closely associated with the relative poverty of the natural flora in this archipelago (DIAS, 1989; BORGES & DIAS, in prep.).

CARLQUIST (1966) points out that the corollas of the flowers from the oceanic islands have generally simple configurations, enabling pollination to be done by a large set of pollinators. On the other hand, BORGES & DIAS (*op. cit.*), after some studies with colour traps, confirmed recently the primitive nature of the insect-plant relationship in the Climax pattern of autochthonous forest and High Altitude Natural Pasture communities in the Azores. In fact, these authors found a preferential attraction of the potential pollinators for white and yellow, the

FAMILIES	NATIVES	ENDEMICS
	p,s,f,h	p,s,f,h
CARABIDAE	10,0,0,0	15,0,0,0
DYTISCIDAE	7,0,0,0	2,0,0,0
GYRINIDAE	1,0,0,0	-
HYDRAENIDAE	-	0,0,0,1
HYDROPHILIDAE	0,2,0,0	-
PTILIIDAE	0,5,0,0	-
SILPHIDAE	-	-
SCYDMAENIDAE	2,0,0,0	1,0,0,0
STAPHYLINIDAE	38,1,0,0	9,0,0,0
PSELAPHIDAE	0,0,2,0	-
HISTERIDAE	-	-
SCARABAEIDAE	0,4,0,0	-
DRYOPIDAE	0,0,0,2	-
ELATERIDAE	0,0,0,1	0,2,0,1
THROSCIDAE	0,1,0,0	-
BUPRESTIDAE	0,0,0,1	-
DERMESTIDAE	-	-
LYCTIDAE	-	-
BOSTRICHIDAE	0,0,0,1	-
ANOBIIDAE	0,0,0,5	-
PTINIDAE	0,2,0,0	0,1,0,0
TROGOSITIDAE	-	-
CLERIDAE	-	-
MELYRIDAE	4,0,0,0	-
NITIDULIDAE	0,0,0,5	-
SPHINDIDAE	-	-
MONOTOMIDAE	-	-
CUCUJIDAE	3,1,0,0	1,0,0,0
CRYPTOPHAGIDAE	-	-
EROTYLIDAE	-	-
PHALACRIDAE	0,3,0,0	-
CERYLONIDAE	1,1,0,0	-
ENDOMYCHIDAE	-	-
COCCINELLIDAE	8,0,0,0	-
CORYLOPHIDAE	3,0,0,0	-
MEROPHYSIDAE	-	0,2,0,0
LATRIDIIDAE	0,3,0,0	0,1,0,0
CISIDAE	-	0,0,1,0
COLYDIIDAE	1,0,0,0	8,0,0,0
MYCETOPHAGIDAE	0,1,1,0	-
OEDEMERIDAE	-	-
ANTHICIDAE	1,0,0,0	-
TENEBRIONIDAE	0,5,0,0	0,1,0,0
ANASPIDAE	0,0,0,1	-
CERAMBYCIDAE	0,0,0,4	0,0,0,2
CHRYSOMELIDAE	0,0,0,1	0,0,0,3
BRUCHIDAE	0,0,0,1	-
APIONIDAE	-	-
RHYNCHOPHORIDAE	-	-
CURCULIONIDAE	0,0,0,13	0,0,0,9
SCOLYTIDAE	0,0,0,3	0,0,0,1
TOTAL=	79,29,3,38	36,7,1,17
%	53.0;19.5;2.0;25.5	59.0;11.5;1.6;27.9

Table 5.- Trophic categories of native and endemic Azorean beetle species; p= Predators; s= Saprophagous; f= Fungivores; h= Herbivores.

primitive colours of the corollas. Thus, we think that a phenomenon of "limited co-evolution" has occurred in the Azores, that restrained pollinators and more developed corollas have become successfully established because of the absence of synchronism in the arrival of each of these elements (see also BORGES & DIAS, in prep.).

Beetles (being primitive pollinators) are present in these two habitats (Climax pattern of autochthonous forest and High Altitude Natural Pasture), but not very well related to pollination; some well known anthophilous families like Elateridae, Scarabaeidae, Cleridae, Meloidae, Buprestidae, Melyridae and Oedemeridae are practically absent in these Azorean high altitude areas, being families that have few or no anthophilous representatives in this archipelago (see BORGES, 1990).

ERBER (1986) suggested as an important reason for the scarcity and limited distribution of the Madeiran Chrysomelidae, the dependence of these species on a particular type of food. The scarcity in the Azores of this usually diverse family could probably be put down to the same cause.

However, we should also not forget that the prevailing climatic conditions in the Azores (extremely oceanic and moist) could have prevented the successful establishment of many species.

4.4. EVOLUTION AFTER THE SPECIES ARRIVAL

Several evolutionary phenomena can be observed in the insular faunas. There is no doubt that brachyptery and aptery are very common insular adaptations in the insects (LINDROTH, 1960; QUARTAU, 1982b; SERRANO, 1983; BASILEWSKY, 1985).

Such phenomena can be found in many of the endemic Azorean beetles, and their occurrence could be interpreted in two ways: that these are species in which the ancestor colonist was already apterous; or that they are species that descended from a winged colonist, the wingless condition resulting from a secondary evolutionary insular process.

In the first category we could almost certainly include the *Tarphius* (Colydiidae), since its wings are known not to function in any known world species of the genus. The Carabidae (*e.g. Trechus* and *Calathus*) are probably good examples of the second category.

LINDROTH (*op. cit.*) found a negative correlation between the known distribution of the endemic Azorean ground-beetles and their lack of flying capacity; that is, the seven species of endemic Carabidae known to occur in the archipelago were all apterous or brachypterous and are restricted to one island. Nowadays, we know 14 endemic species of ground-beetles in the Azores (see Table 4), which with the exception of *Olisthopus inclavatus* ISRAELSON (endemic to S. Maria), are all more or less unable to fly.

However, BORGES (1990) recently cited the paleo-endemic species *Pseudanchomenus aptinoides* TARNIER on Pico, the species now being known to occur on two different islands (Pico and S. Miguel). Moreover, BORGES & SERRANO (in print) found *Cedrorum azoricus* n.gen. n.sp. on Pico (*caveirensis* n. ssp.), Terceira and S. Maria (nominate subspecies *azoricus*). This gives an important clue to the ancestry of these species, very probably both relict species and inhabitants of the old primitive Azorean Laurel forests.

We should also consider the opportunities for evolution and for adaptive radiation, possessed by endemics; such opportunities are dependent on two main factors (PECK & PECK, 1990): a low frequency of immigration, and ecological opportunity offered by ecological diversity. Therefore, we can explain the few examples of adaptive radiation in Azorean beetles (see also 4.3.) - probably only documented in two genera (*Trechus* and *Tarphius*) - by the scarcity of habitats in this archipelago, or, in other words (as pointed out by QUARTAU, 1982a), by the low ecological diversity of these islands.

Reverting to the argument of 4.3. (see also Table 2) on the number of ancestral colonizations, we estimate that in the Azores 1.4 new species arise per ancestral colonization. Comparing this result with that obtained by PECK & PECK (1990) for the Galapagos, we note a similarity in the speciation rate between the two archipelagoes, something remarkable, but probably a coincidence without deep biological meaning.

On Madeira and in the Canaries there are remarkable examples of insular evolution and adaptive radiation. Thus, in the Canary Islands the genus *Laparocerus* (Curculionidae) has more than 60 endemic species, the most impressive case of speciation in the Macaronesian islands (BAEZ, 1982a). Also in this archipelago occur other examples: *Attalus* (Malachiidae) with 43 species, *Cardiophorus* (Elateridae) with 26 species, *Hegeter* (Tenebrionidae) with 20 species, *Calathus* (Carabidae) with 22 species, *Tarphius* (Colydiidae) with 20 species, *Atheta* (Staphylinidae) with 15 species (BAEZ, *op. cit.*) and also *Trechus* (Carabidae) with 18 species (BORGES & OROMÍ, 1991). In the Madeiran archipelago there are also some examples: *Trechus* (Carabidae) with 22 species (BORGES & OROMÍ, *op. cit.*), *Calathus* (Carabidae) with 6 species (MATEU, 1970), *Tarphius* (Colydiidae) with 21 species (FRANZ, 1969), *Ochthebius* (Hydrophilidae) with 5 species, *Nesotes* (Tenebrionidae) with 14 species, *Laparocerus* (Curculionidae) with 22 species, *Caulotrupis* (Curculionidae) with 9 species, *Acalles* (Curculionidae) with 8 species (LUNDBLAD, 1958).

In Azorean beetles there are only three known examples of insular diversification, in the genera *Calathus* (Carabidae) with 4 species, *Trechus* (Carabidae) with 5 species and *Tarphius* (Colydiidae) with 8 species.

- The Azorean *Calathus* -

The genus *Calathus* has four species in the Azores, distributed on four different islands (see Table 4). Therefore, it is one of the few known examples in Azorean insects of speciation by geographical isolation on several islands.

LINDROTH (1960), in his revision of Azorean ground-beetles, considered that this was the most interesting genus of Carabid beetles. All four known species belong to the *melanocephalus - mollis* group, and unlike the true, and probably ancestral species, *C. mollis* MARSHAM (that has a West-European and Northern-African distribution) they are brachypterous.

SERRANO & BORGES (1986) stated that, according to aedeagus morphology, *C. carvalhoi* from Terceira is the species most closely related to *C. mollis*. On the other hand, *C. extensicollis* from Pico is the most distantly related, since the internal sac of the aedeagus has some particular features that isolate this species from the others (LINDROTH, 1960).

Recently, with the utilization of Pitfall traps (see also BORGES, in prep.), we collected the species from S. Miguel (*C. lundbladi*) and S. Maria (*C. vicenteorum*) in the Climax pattern of autochthonous forest, at high altitude. In spite of the use of a large number of traps (40 in S. Miguel and 120 in S. Maria) few specimens were collected, probably because the present resident populations of these two species are not very large.

- The Azorean *Trechus* -

After the several cave beetle collections that have been made during Biospeleological expeditions to the Azores - two directed by N.P. ASHMOLE (Edinburgh University) and P. OROMÍ (La Laguna University) and supported by the National Geographic Society, USA (July - August 1987 and 1989; the latter also with our participation); two expeditions of the Speleological group "Os Montanheiros" to the island of Pico in May 1989 and March 1990, also with our participation; and an expedition carried out by us in April 1990 to S. Miguel (*vide* OROMÍ & BORGES, 1991; BORGES & OROMÍ, 1991 and in print) - we can now say that the Azorean cave beetle fauna has finally become an object of study.

As a consequence of this the last catalogue of the Azorean Coleoptera made by BORGES (1990) refers to four more species of *Trechus* (Trechinae) and one of *Thalassophilus* (Trechodinae) (see Table 4). Nevertheless, the fauna from lava tubes occurring on some islands in the Azores remain inadequately explored, and it is therefore possible that more ground-beetles may be found in this habitat in the near future. The lack of records from the older islands (Corvo, Flores and S. Maria), where no true volcanic tubes can be found, leads us to the necessity of exploring the MSS ("Milieu Souterrain Superficiel") of this islands (see BORGES, in print).

The hypogean Azorean *Trechus* spp. have retained remnants of eyes, but show marked adaptations in other characters, such as depigmentation, elongated appendages, incipient physogastry, etc.; but *Thalassophilus azoricus* is even more troglomorphic, less pigmented and with no eyes at all (MACHADO, 1988; BORGES & OROMÍ, 1991).

BORGES & OROMÍ (*op. cit.*) have pointed out that the most interesting fact related to the Azorean *Trechus* spp. is the peculiar distribution of the two species from Pico, *T. picoensis* and *T. montanheirorum*.

These two species live in the same lava tube "Gruta dos Montanheiros" (Pico) (occurring in sympatry in the entrance to the cave), and show different degrees of troglomorphy (reduction of eyes and bodily pigmentation). Recently HOCH & HOWARTH (1989) presented a similar case in two new cave dwelling species of a new Australian cixiid genus (Homoptera : Fulgoroidea). *T. picoensis* is regarded as being troglobitic (obligatory cavernicole), and *T. montanheirorum* as being troglophilic (facultative cavernicole).

As OROMÍ & BORGES (1991) pointed out, some of the most obvious differences between the two species are those relating to adaptation to cave life (eye reduction, depigmentation) which are more marked in *T. picoensis*; some other differences like those of the male genitalia and chaetotaxy have probably evolved without relation to the hypogean environment.

It is considered likely that they represent a single invasion into the cave environment, being sister-species (BORGES & OROMÍ, 1991; see also HOCH & HOWARTH,1989).

Another remarkable fact related to the distribution of the Azorean *Trechus* spp. is connected with the known distribution of *T. terceiranus*. In fact, previously known from only two caves (Gruta do Coelho and Gruta dos Balcões) it is now reported from two more (Algar do Carvão and Gruta do Caldeira). Several specimens were also collected in the mesocavernous shallow stratum - MSS [the "Milieu Souterrain Superficiel" *sensu* JUBERTHIE (1983)]. This was the first reference to a troglobite in the Azorean MSS (BORGES & OROMÍ, *op. cit.*).

- The Azorean *Tarphius* -

As in the previous genus, only in recent times have most of the currently known *Tarphius* species from the Azores been discovered.

SERRANO (1982) in his checklist of Azorean beetles, referred to the presence of only one species, *T. wollastoni* (Faial and Flores). However, on several occasions had he expressed his surprise to the present writer that no more species occurred on the other islands (SERRANO, pers. comm.). Later, BORGES (1990) listed six species, the total number of known species of *Tarphius* now being eight (BORGES, 1991a).

The distribution of these eight species island by island calls for some comment. Thus, while of the forty or more species of *Tarphius* known from Madeira and the Canaries, only about 7% of the species occur simultaneously in more than one island (ISRAELSON, pers. comm.), in the Azores this is true for about 40% of the species (Table 4).

It is generally accepted that no adaptive radiation phenomenon occurs in the speciation events of the genera *Trechus* and *Calathus* in Azores, since the species of each of these genera have similar ecological needs (although in the case of *T. picoensis* and *T. montanheirorum* this might be arguable).

However, some casual observations made by the present writer (see also BORGES, 1991a) seem to suggest the occurrence of a phenomenon of adaptive radiation in the four *Tarphius* species known to occur on S. Maria, that in all probability have the same ancestor. The presence in the eight species of similar nodular and aedeagus patterns, seems to confirm this hypothesis (ISRAELSON, 1984, 1990; GILLERFORS, 1985, 1986a; BORGES, 1991a).

T. depressus and *T. rufonodulosus* were collected by us in general subcortical habitats, and less frequently in Pitfall traps. *T. pomboi* and *T. serranoi* were always collected in Pitfall traps. We may conclude, therefore, that the two latter species occupy a different habitat, living probably among litter and debris, while the two former species live under bark and decaying wood.

Also remarkable is the fact that *T. serranoi* was collected only in Climax pattern of autochthonous forest, though *T. pomboi* was collected also in a *Cryptomeria* sp. forest, showing a great ecological plasticity.

These four *Tarphius* species are endemic to one island (S. Maria), occurring only in one small natural high altitude Laurel forest, the Pico Alto. The geographical isolation or isolation caused by a plant adaptive sift are not applicable in this case, though we can think of several separate invasions of the common ancestor species. These species are very probably predators, and it is common to find *T. depressus* and *T. rufonodulosus* under the bark of the same trunk, side by side, all four species living in the same area.

ISRAELSON (pers. comm.), supports the view that some variants have probably appeared which are still unknown, *T. serranoi* being a hybrid of *T. pomboi* and *T. depressus*.

The fact that the descriptions by BORGES (1991a) of *T. pomboi* and *T. serranoi* are based on a type series made up almost entirely of females (only one male per species) leads us to the hypothesis that these species have some parthenogenetical methods of reproduction.

Following GILLERFORS (pers. comm.), the Azorean *Tarphius* spp. constitutes a complex of forms; some have reached the status of valid species but some are still undergoing development.

According to BORGES (*op. cit.*), there is a curious relationship between the nodular pattern and the known distribution of some *Tarphius* species in the Azores. Two species that occur on more than one island, *T. tornvalli* and *T. azoricus*, have the same nodular and aedeagus patterns and are probably sister species; *T. wollastoni* and *T. depressus* have nodular and aedeagus patterns in common: *T. depressus* lives on the oldest and most easterly island (S. Maria) and is probably the oldest species, while *T. wollastoni* lives on the western islands of Faial and Flores, being probably a younger species. According to GILLERFORS (1986a), support for this theory can be found in the size of elytral nodules, generally less well developed in *T. depressus* than in *T. wollastoni*.

Three species have the aedeagus pattern in common [*T. acuminatus* (Pico), *T. serranoi* and *T. rufonodulosus* (S. Maria)], and two of them have the same ecology, *T. acuminatus* (Pico) and *T. serranoi* (S. Maria), living among litter and debris (the same seems to apply to *T. pomboi*); the third species, *T. rufonodulosus* lives under bark and decaying wood and because of its poorly developed nodules is probably an older species (BORGES, 1991a).

Of course, at this stage we can only speculate, because almost nothing is known about the biology and ecology of this genus, making necessary the realization of some genetical and ecological studies to confirm or clarify the earlier statements. We should also not forget that there are no records of *Tarphius* for Corvo, Graciosa or S. Jorge.

4.4.1. DIVERSITY AND ENDEMISM *VS.* VEGETATION ZONES

Up to now there has not been any published work dealing with the insect-plant relationship in the major Vegetation categories from the Azores.

In all probability, many species occur in more than one vegetation type. Nevertheless, the analysis of the endemic species records for the several Azorean islands, added to our own experience, tempts us to conclude that most of the endemic *taxa* can be found in the Azorean primitive Laurel forests.

Thus, in the **Climax pattern of autochthonous forest** we can find the following species: *Ocydromus derelictus* ALLUAUD, *Trechus torretassoi* JEANNEL, *Calathus* spp., *Olisthopus inclavatus* ISRAELSON, *Pseudanchomenus aptinoides* TARNIER, *Cedrorum azoricus azoricus* BORGES & SERRANO, *Bradycellus chavesi* ALLUAUD, *Euconnus azoricus* FRANZ, *Phloeonomus azoricus* FAUVEL, *Geostiba melanocephala* (CROTCH), *Alestrus dolosus* (CROTCH), *Leptophloeus azoricus* RATTI, *Metophthalmus occidentalis* ISRAELSON, *Tarphius* spp., *Helops azoricus* CROTCH, *Aromia thea* REITTER, *Crotchiella brachyptera* ISRAELSON, *Laparocerus azoricus* DROUET, *Pseudechinosoma nodosum* HUSTACHE, *Acalles* spp., *Caulotrupis parvus* ISRAELSON and *Phloeosinus gillerforsi* BRIGHT.

Some of these species (*e.g. Olisthopus inclavatus*, *Euconnus azoricus*, *Phloeonomus azoricus*, *Leptophloeus azoricus*, *Metophthalmus occidentalis* , *Tarphius* spp., *Crotchiella brachyptera* , *Laparocerus azoricus*, *Pseudechinosoma nodosum* and probably still others) can also be found in other habitats (like **Woodlands**). The fact that **Climax pattern of autochthonous forest** from the Azores has been in great part destroyed by man may produce as a consequence an alternative adaptation of some generalist species to other habitats.

Species like *Calathus carvalhoi* SERRANO & BORGES, *Atheta caprariensis* ISRAELSON, *A. dryochares* ISRAELSON, *Sphaericus velhocabrali* ISRAELSON and *Atlantoscis gillerforsi* ISRAELSON, though we think they could live in **Climax pattern of autochthonous forest**, have only been found up to now in other habitats (*e.g. Eucalyptus* forests, *Cryptomeria* forests, Vine, etc.). The known population of *Tarphius azoricus* on Terceira has, up to now, been found by us only in *Pinus* forest (see also BORGES, 1991a).

The **Seral spontaneous vegetation**, by its features, can easily lodge most of the endemic species referred to above, at least in the older stages.

The **Coast Vegetation** is a badly studied zone, probably because of the difficulty of access to some of the high cliffs. However, some species are known to occur, like *Ochthebius frey* D`ORCHYMONT in small salt-water ponds in the basaltic rock and *Gietella faialensis* MENIER & CONSTANTIN in the recent lavas of the Capelinhos Volcano.

In **Marshes, Lakes and Wet peatland vegetation mires** occur species like *Ocydromus schmidti azoricus* LINDROTH (a species that was previously collected on the summit of Pico mountain; BORGES, 1990), *Cedrorum azoricus caveirensis* BORGES & SERRANO, *Trechus torretassoi* JEANNEL, *Hydroporus guernei* RÉGIMBART, *Agabus godmani* CROTCH, *Atheta aptera* ISRAELSON and *Mniophilosoma obscurum* GILLERFORS.

In **Woodlands** (***Eucalyptus*** **forests,** ***Cryptomeria*** **forests, pine forests and mixed woodland)** live, as already mentioned, many species natural to **Climax pattern of autochthonous forest**, that secondarily colonize this new habitat. In this category we may also include two species not cited before, *Heteroderes azoricus* TARNIER and *Otiorhynchus trophonius azoricus* UYTTENBOOGAART.

Occupying large areas of all the Azorean islands is **Pasture**. In this highly anthropomorphic habitat can be found species like *Heteroderes azoricus* TARNIER, *Heteroderes melliculus moreleti* TARNIER, *Psylliodes vehemens azorica* JACOBSON, *Longitarsus azoricus* ISRAELSON, *Otiorhynchus trophonius azoricus* UYTTENBOOGAART and *Hypera multifida* ISRAELSON.

Finally, in **Permanent Agriculture** occur species like *Sphaericus velhocabrali* ISRAELSON and *Crotchiella brachyptera* ISRAELSON, both in vines, and *Acalles subcarinatus* ISRAELSON, in fruit trees.

Unfortunately, it is only recently that beetle collectors have explored **Climax pattern of autochthonous forest** with any intensity, discovering many new species to science. On the other hand, the difficulties of access to these natural areas can function as a natural way of conserving its rich and unique beetle fauna.

5. DISCUSSION AND GENERAL CONCLUSIONS

Practically all entomologists that have worked on the arthropod fauna of the Azores cite its poverty, when compared to the other Macaronesian archipelagoesas, as the main feature of this archipelago. During the course of the present work we have already noted several aspects related to this phenomenon, concerning the beetle fauna. Now, we intend to summarize some of the statements presented earlier, and demystify the situation.

Recently, BORGES (1990) summarized the several possible explanations for the ultimate poverty of the Azorean beetle fauna:

1 - Unfavourable climate for many species. Constant high levels of humidity cause a general levelling of abiotic conditions, resulting in a pronounced poverty of biotopes (see LINDROTH, 1960);

2 - The occurrence in the Azores of large-scale volcanic activity, with many recent historical eruptions, may have as a consequence the destruction of local faunas (see also LINDROTH, *op. cit.* and SOUSA, 1985);

3 - The influence of human activity, with the loss of natural habitats and with the probable extinction of some native or endemic beetle species;

4 - Long distances from the nearest mainland - geographical isolation;

5 - The recent geological age of the Azores - 8 Million years. The Azores were probably the object of a secondary colonization, receiving their fauna not from the mainland but from the intermediate islands;

6 - Insufficient exploration may also be important: in the last seven years 28 species of Coleoptera from the Azores were described as new to science;

To these can also be added:

7 - The role of the Pleistocene Glaciations (see ISRAELSON, 1990; EASON & ASHMOLE, 1992).

Nevertheless, it seems that though it is true that comparing the amount of endemism of the Azorean beetles (11.6%) with those of Madeira (39%) and the Canary Islands (55%), we can truly consider the former to be low, it is also true that the percentage of 29% obtained when working only with the autochthonous species oblige us to reflect more carefully upon the figures.

We should also remember that the amount of endemism in Madeira and the Canaries would be superior if we were working also with the autochthonous species of these archipelagoes. Nevertheless, such differences will never be as marked as in the Azores example, since the number of introduced species (most of which are widely distributed) would be similar in the Azores, Madeira and the Canaries, the total number of known species in these last two archipelagoes being much higher. Thus, in absolute terms the value of 29% of endemism for the autochthonous beetle species from the Azores shows an unexpected relative "wealth".

Let us now analyse in some detail the reasons usually given for the poverty of the Azorean beetle fauna:

(1) - CLIMATE. The extremely oceanic climate of the Azores, with more or less constantly high levels of humidity throughout the year, is an important factor, mainly because of a general levelling of abiotic conditions provoked by high levels of waterlogged soil. In fact, S. Maria, being the driest island of the archipelago, has a wide variety of habitats, mainly the xerophytic ones, with the occurrence of some species well adapted to these biotopes, not easily found on the other islands.

On the other hand, if we relate the low thermic amplitude and high precipitation and humidity to the homogeneity of the (usually acid) Azorean soils, we have conditions conducive to a low level of ecological diversity (QUARTAU, 1982a).

(2) - VOLCANIC ACTIVITY. The volcanic phenomena of these islands are often used to explain the destruction of local faunas and the consequent extinction of many species. On the other hand, as pointed out by SOUSA (1985), the volcanic phenomena have encouraged the dispersal of some populations, which, colonizing other islands, led to the occurrence of speciation events with a resulting increase in diversity.

At the same time, the Hawaiian type lava flows prevalent in the Azores could isolate two or more populations (CARLQUIST, 1966; see also MACHADO, 1976), leading to speciation events. To support this idea, we have the hypogean fauna of the Azores, with several species recently described (see 3.1). BORGES & OROMÍ (1991) have affirmed that volcanic activity could have had an important role in the two speciation events that led to the formation of the species *Trechus picoensis* and *T. montanheirorum* from the Gruta dos Montanheiros (Pico). According to these authors, the two speciation processes probably occurred during a breakdown of ecological equilibrium related to volcanic events, with the destruction of the natural laurel forest and consequent potential isolation of cave and surface populations.

For instance, if in the Azores the cave colonization could not be explained by the Pleistocene-effect theory (BARR, 1985) [since this Atlantic archipelago remained out of the direct influence of the last glaciations (see COOPE, 1986)], we can perhaps apply a similar theory to explain the evolution of terrestrial troglobites in the Azores, replacing climate by volcanic activity. Another hypothesis is the adaptive-shift theory (HOWARTH, 1973), first applied to the Hawaiian Islands. This theory does not invoke isolation during climatic (or possible volcanic) changes, but instead proposes that the partly adapted ancestors shifted into newly developing niches (HOLSINGER, 1988).

Another interesting example studied is the occurrence of the endemic species *Gietella faialensis* MENIER & CONSTANTIN (Merophysidae) in the Capelinhos Volcano (a historical eruption from 1957-58 in Faial), that has its most closely related species, *Gietella fortunata* MENIER & CONSTANTIN living in the Canaries; the two species live in the same biotope, the recent lavas near the seashore (MENIER & CONSTANTIN, 1988, 1989). *Gietella* MENIER & CONSTANTIN being an endemic Macaronesian genus (with only these two species known), reinforcement is given to the hypothesis that lava flows (very common in some archipelagoes like the Azores, the Canaries, Galapagos, Hawaii, etc.), can not only cause the extinction of some local fauna, but can also isolate others, promoting phenomena of genetic drift and leading to the occurrence of speciation events (BORGES & OROMÍ, 1991; MACHADO, 1976).

Recently BORGES & OROMÍ (*op. cit.*) made the first record of a troglobite species, *Trechus terceiranus* (Terceira) to the MSS ("Milieu Souterrain Superficiel"). Since then, we have collected other species in this biotope (on Terceira and S. Maria), most of them not having been studied yet (see BORGES, in print). Nevertheless, the centipede, *Lithobius obscurus azoreae* EASON & ASHMOLE, was recently recorded for the MSS of Terceira by EASON & ASHMOLE (1992).

Thus, observing the diversity of the endemic cave fauna of the islands of Faial, Pico, S. Jorge, Terceira and S. Miguel (see OROMÍ *et al.*, 1990; BORGES & OROMÍ, 1991 and in print), we can say that the volcanic activity of these islands is probably an agent of diversification leading to the creation of new disposal biotopes (*e.g.* lava flows, lava tubes, MSS). Therefore, we are in partial disagreement with BALLETTO *et al.* (1990) when, to explain the poverty of the Azorean fauna, they point out the importance of the devastating action of frequent volcanic eruptions. Moreover, the example adduced by these authors betrays a lack of knowledge, because the "Capelinhos" eruption added new land to Faial and did not destroy a considerable part of the island, as they affirm.

(3) - HUMAN INTERFERENCE. The significance of human interference can be observed in three different ways: (a) destroying the Laurel Vegetation areas in the Azores probably leads to the extinction of some autochthonous beetle species; (b) replacing the autochthonous vegetation by industrial woodlands and pasture diversifies the number of available biotopes; (c) introducing new species mainly with a cosmopolitan feature enriches the total fauna, but could also lead to the extinction of some autochthonous beetle species by competition or other interactions.

It seems to us that the destruction of Laurel Vegetation areas in the Azores may have led to the extinction of autochthonous beetle species. However, the *Tarphius azoricus* population of Terceira has, up to now, been found by us only in a *Pinus* forest, in the geologically oldest part of the island (see also BORGES 1990 and 1991a). This fact seems to show that, in spite of the natural forest having been destroyed in this area, this species was capable of adapting to a new habitat. The conquest of these new biotopes by beetles endemic to the Azores was all the easier because, a lot of them being predators, they must have had a comparatively good chance of adapting themselves to somewhat altered conditions (ISRAELSON, 1990; see also BORGES, 1991a)

Nevertheless, LINDBERG (1965) (*in* GRESSITT, 1974) pointed out the fact that some of the beetle species described by T. V. WOLLASTON in the Macaronesian islands are nowadays extinct; BORGES & OROMÍ (1991) subsequently observed that it is not surprising that the troglobitic species of *Trechus* from the Azores are relicts, in spite of not being very old, because the epigean environment has been strongly modified by human alteration.

(4) - GEOGRAPHICAL ISOLATION. Without doubt the geographical isolation of the Azores is one of the most important factors in explaining its relative "poverty". These islands were probably subject to a colonization of Macaronesian origin by "stepping stones" (*e.g.* Madeira). We are talking here of a "Double Insularity" phenomenon (DIAS, 1989). On its own, this fact would explain the relative poverty, since the Azores have been subject to a double filtration in the acquisition of its fauna. The fact that a great part of the neo-endemics in the Azores have some sister groups of species on Madeira and in the Canaries could perhaps sustain the above hypothesis.

However, it should also not be forgotten that the Azores include a Boreal component in its endemic beetle fauna, something not found in the other Macaronesian archipelagoes. This fact enhances the probability of a colonization with its origin on the European mainland.

(5) - GEOLOGICAL AGE. The recent geological age of the Azores seems to be the most plausible explanation for the relative low amount of endemism of this archipelago.

As was shown by the biogeographical analysis made above (3.2.3.), the geological age of each Azorean island seems to be more important than the area and the distance from the nearest mainland, in the distribution of its endemic beetle species. The older islands (Flores, S. Miguel and S. Maria) have a higher number of total and exclusive endemic beetle species than the younger islands, even though Flores and S. Maria are islands with a smaller area.

Also revealing is the fact that Flores and S. Maria each has three exclusive paleo-endemics (see Table 4); thus geological age has great influence in the differential (inter-island) diversification of the Azorean beetle fauna.

Moreover, as pointed out by BORGES & OROMÍ (1991), there is a clear correlation between the degree of adaptation of cavernicolous beetle fauna from the Azores and the age of the islands. Thus, one of the oldest islands, S. Miguel, possesses the most highly evolved cavernicolous species, the *Thalassophilus azoricus*, while the hypogean and less evolved *Trechus* species are on the youngest, central, islands.

The island of Pico is the only one that presents a disharmony in the relation between its fauna and its geological age. In fact, in spite of being one of the youngest Azorean islands, it has a high percentage of total and exclusive endemics. This can be explained by the following facts:

- it is the second largest island and the island with highest altitude, thus increasing the chances of having a high level of biotopes diversity;
- having undergone recent volcanic activity, it has young lava tubes and lava flows, together with the presence of a well diversified cave fauna;

- the northeastern part of the island is the oldest part, it being there that most of the endemic beetle species, associated with the old Climax pattern of autochthonous forest, occur.

Nevertheless, we should not exclude the possibility of this island being older than we nowadays think (NUNES, pers. comm.). In fact, *P. aptinoides* TARNIER (found on Pico and S. Miguel) and *Cedrorum azoricus* n. sp. (found on Terceira, Pico and S. Maria) occur simultaneously on a old island (S. Miguel or S. Maria) and on a geologically young island(s) (Pico or / and Terceira). This leads us to the hypothesis that both are paleo-endemics (*sensu* LINDROTH, 1960), being relict species and inhabitants of the Climax pattern of autochthonous forest. The fact that *C. azoricus* n. sp. has a primitive female genitalia reinforces this hypothesis (BORGES & SERRANO, in print).

It will also be useful to investigate which set of geological ages attributed to the Azores (columns A, B and C, Table 1) is the most harmonious with our data concerning the distribution of beetle species island by island.

PROPOSALS	N°. Total of Spp.	Autochth. Spp.	Total End.	Excl. End.
A - FORJAZ (pers. comm.)	0.58; $r^2=0.34$ (n.s.)	0.61; $r^2=0.38$ (n.s.)	0.54; $r^2=0.29$ (n.s.)	**0.77; $r^2=0.60$ ($p<0.025$)**
B - ABDEL-MONEM *et al.* (1975) and FERAUD *et al.* (1980)	0.54; $r^2=0.30$ (n.s.)	**0.63; $r^2=0.40$ ($p<0.05$)**	**0.63; $r^2=0.40$ ($p<0.05$)**	**0.83; $r^2=0.70$ ($p<0.005$)**
C - QUEIROZ (1990)	0.51; $r^2=0.27$ (n.s.)	0.54; $r^2=0.29$ (n.s.)	0.49; $r^2=0.24$ (n.s.)	**0.76; $r^2=0.58$ ($p<0.025$)**

Table 6.- Correlations obtained between the number of species and the geological ages proposed for the Azorean islands. In bold the correlations statistically significant.

From Table 6 it can be affirmed that the set of geological ages proposed for the Azorean islands by ABDEL MONEM *et al.* (1975) and FERAUD *et al.* (1980) (column B, Table 1) is in the closest agreement with the known distribution of Azorean beetle species, since the obtained correlations are statistically significant for almost all the sets of species used. Remarkable, too, is the fact that the three sets of geological ages studied are equally well correlated with the exclusive endemic species of each island.

(6) -INADEQUATE COLLECTION. If we consider the fact that the genera *Trechus* and *Tarphius* have respectively 5 and 8 species currently known to occur in the Azores, when ten years ago only one species of each was known, the idea is reinforced that the Azorean beetle fauna is not so poor as thought by earlier authors.

Probably a close study of some habitats with an increasing field effort will provide some new records for this archipelago. Some islands remain badly studied, and because of that the number of endemic beetle species recorded will continue to increase, along, probably, with the percentage of endemism (see for instance BORGES & SERRANO, in print).

(7) - PLEISTOCENE GLACIATIONS. An alternative hypothesis to those cited above would be the disastrous action of the Pleistocene Glaciations (ISRAELSON, pers. comm.; EASON & ASHMOLE, 1992). As the northernmost archipelago of Macaronesia, the Azores may have suffered the disastrous influence of the last Quaternary glaciations (ISRAELSON, 1990), when the climate of the islands will have been dry and cold. Thus, a great part of the original Azorean fauna may have become extinct, only some species surviving - namely, the present-day paleo-endemisms of LINDROTH (1960). These species are related to no known present-day continental *taxa*, and are wingless. A large number of the other autochthonous beetle species in the Azores may have reached the islands after these glaciations, some of them being neo-endemisms ("weak -species", *sensu* ISRAELSON, *op. cit.*).

During the course of this work we have presented some data on paleo-climatology (2.2.1.) that could support this hypothesis. Nevertheless, it seems that about 18,000 years ago, the Arctic Polar Front, centred along latitude 42° N, marked the fundamental dividing line for all climatic regimens, the southern area being one of relative stability (MCINTYRE *et al.*, 1976).

COOPE (1986) also affirmed that the fauna and flora of the Azores (and of the other southern Macaronesian archipelagoes) have not been subjected to the repeated exterminations and recolonizations that were imposed upon those of more northerly Atlantic islands (*e.g.* the Shetlands, the Faeroes, Iceland and Greenland) by the comings and goings of the polar front. Probably only the investigation of the Quaternary fossils of the Azores will tell us more about this subject.

According to the Equilibrium Theory of Island Biogeography by MACARTHUR & WILSON (1967), the "poverty" of Azorean beetle fauna must be related to the respective areas of the islands, their ecological diversity and their degree of isolation. In this archipelago, however it is possible that many habitats (biotopes) are still free (or not studied by the entomologists), and that geological age (rather than area or geographical isolation) could be the best biogeographical factor to explain the diversity and distribution of beetle species throughout the nine Azorean islands.

LINDROTH (1960), using indices of the "catching area" and of the "catching angle" from Madeira and the Azores, tried to explain at species level, the differences between these two archipelagoes, reaching the conclusion that if their fauna were the result only of a colonization by long distance dispersal through the air, it might be expected that Madeira would have four times more species than the Azores. On the other hand, we should not exclude the hypothesis of some autochthonous beetle "specialists" have been exterminated because they were more sensitive to the disturbance of their habitat by man (or possibly by volcanic activity). BORGES & DIAS (in prep.) confirm the lack of specialized pollinators in the Azores, appearing only "generalist" species in the Climax pattern of autochthonous forest. In this case we could not hold human action responsible, because the study was performed in an undisturbed area of high altitude.

We may conclude that the poverty of the Azorean Coleoptera is somewhat illusory, because the differences in diversity between the Azores and other Macaronesian archipelagoes may be explained, in a probable order of importance by: **isolation, geological youth, lack of strong diversity in several ecological parameters** and **an unsuitable humid climate.** The disastrous action of the Pleistocene glaciations, in spite of being difficult to prove, could provide an alternative or complementary explanation to the others (see for instance EASON & ASHMOLE, 1992).

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7. SUMÁRIO

O arquipélago dos Açores está situado no meio do oceano Atlântico (dista cerca de 1600 km de Lisboa e 1900 km da Terra Nova), e desde à cerca de 8 milhões de anos que está disponível à colonização terrestre. Após 140 anos de estudo, a fauna de Coleópteros de algumas das ilhas é ainda muito mal conhecida, estando inventariadas para o arquipélago 51 famílias, 305 géneros, e 524 espécies, das quais 61 são endémicas (11.6%). Com o objectivo de investigar quais os melhores factores predictivos do número de espécies de cada ilha, fomos estudar a correlação entre a distribuição conhecida dos Coleópteros por ilha (espécies totais, espécies autóctones, espécies endémicas totais e espécies endémicas exclusivas), com a área, distância ao continente,

altitude máxima e idade geológica das ilhas. A análise das correlações idade-diversidade obtidas para os Coleópteros dos Açores, não parece deixar dúvidas sobre a importância da idade geológica na diversificação da fauna destas ilhas, sendo notável a correlação obtida entre o número de espécies endémicas exclusivas de cada ilha e a idade geológica ($r= 0.83$; $p<0,005$). Não existe correlação faunística com a altitude neste arquipélago ($r=0.32$, $p>0,2$; para as espécies endémicas totais). Há uma certa correlação diversidade-superfície das ilhas (*e.g.* $r=0.64$, $p<0,05$; para as espécies autóctones); no entanto, ela vai diminuindo à medida que se restringe o leque de espécies utilizado (há igualmente um decréscimo do coeficiente de correlação, r). Estes dados fazem-nos pensar que as correlações obtidas para as espécies totais e para as autóctones estarão falseadas pelo facto das ilhas maiores terem sido as melhor estudadas, logo possuindo mais espécies citadas. Quanto à relação diversidade-distância ao continente mais próximo, apenas se encontrou uma correlação estatisticamente significativa entre a distância ao continente e o número de espécies endémicas exclusivas ($r=0.66$; $P<0.05$). Apesar disso, não é possível afirmar que a correlação obtida tem significado biológico, já que, as ilhas localizadas mais perto do continente são simultâneamente as mais bem estudadas (e.g., S.Maria, S. Miguel e Terceira) As ilhas Flores e S. Maria são ilhas geologicamente antigas sendo simultâneamente das mais pequenas do arquipélago. Apesar da sua área possuem, no entanto, a maior quantidade de endemismos totais e exclusivos. É de realçar ainda a presença de três paleo-endemismos com distribuição restrita às Flores (*Ocydromus derelictus*, *Atheta aptera* e *Acalles droueti*) e outros três conhecidos unicamente de S. Maria (*Leptophloeus azoricus*, *Neocnemis occidentalis* e *Hypera multifida*). Assim fica confirmada a influência da idade geológica na distribuição dos Coleópteros dos Açores. Do ponto de vista zoogeográfico a coleopterofauna açoreana é constituida principalmente por espécies de vasta distribuição (cosmopolitas, holárcticas, paleárcticas) e parece que grande parte dos imigrantes iniciais terão tido uma origem Paleárctico-Ocidental. No entanto, se tivermos em conta apenas as espécies autóctones, encontramos uma componente Mediterrânica-Macaronésica muito interessante, com uma percentagem de endemismos de 29%. Essa componente Mediterrânica associada à percentagem de espécies Macaronésicas perfaz cerca de 31.4% das espécies autóctones. Por outro lado, há uma relação taxonómica próxima de muitos neo-endemismos dos Açores com espécies da Madeira e Canárias. Estes dois factos dão sentido a uma colonização proveniente de um "Rosário de ilhas" Macaronésico (*stepping stones theory*). As espécies nativas constituem 28.5% da fauna, 11.6% são endémicas para uma ou mais ilhas, e 59.9% foram introduzidas pelo Homem. Das 210 espécies autóctones (*i.e.*, espécies nativas e endémicas) estimou-se que foram necessárias 194 colonizações ancestrais com sucesso. Por outro lado, 45 colonizações

ancestrais com sucesso terão sido necessárias para originar as 61 espécies endémicas do arquipélago. Durante 8 milhões de anos terá havido uma taxa de uma colonização com sucesso por cada 41 237 anos, e ter-se-ão formado 1.4 espécies novas por colonização ancestral. Poucas famílias (4) possuem géneros endémicos (6), que devem representar colonizações antigas. A dispersão transoceânica pelo ar e a acção do Homem terão sido os agentes que mais contribuíram para a actual fauna de Coleópteros dos Açores. Neste arquipélago, espécies especialistas como os herbívoros e fungívoros representam apenas 30% dos endemismos e 28% das espécies nativas, o que estará relacionado com uma baixa diversidade ecológica que inclui uma baixa diversidade da vegetação. Ocorrem enxames de espécies em três géneros de espécies ápteras, *Trechus* e *Calathus* (Carabidae) e *Tarphius* (Colydiidae). O fenómeno de radiação adaptativa parece ocorrer apenas no género *Tarphius*. O género *Calathus* possui quatro espécies nos Açores, distribuídas por quatro ilhas, constituindo assim, um dos poucos exemplos conhecido neste arquipélago de especiação por isolamento. O aspecto mais interessante relacionado com a evolução dos *Trechus* dos Açores é a distribuição simpátrica das duas espécies da ilha do Pico, *T. picoensis* e *T. montanheirorum*. Estas duas espécies deverão ser espécies-irmãs sendo *taxa* monofiléticos, tendo-se dado duas invasões separadas (alocrónicas) da espécie ancestral, ocorrendo assim uma especiação alopátrica clássica e subsequente simpatria. Quanto ao género *Tarphius*, das oito espécies conhecidas, quatro são endémicas de uma ilha (S. Maria) ocorrendo todas numa pequena montanha. São sugeridas algumas possíveis explicações para tal distribuição, não sendo de desprezar fenómenos de radiação adaptativa e hibridação. Tenta-se igualmente estabelecer, uma tentativa de relação entre a distribuição dos Coleópteros endémicos e as grandes unidades de vegetação dos Açores. Finalmente, analisa-se detalhadamente as causas normalmente apontadas para a pobreza da fauna dos Açores: clima desfavorável, actividade vulcânica, acção humana, isolamento geográfico, idade geológica recente, exploração insuficiente e glaciações Pleistocénicas. Compara-se a diversidade específica e a percentagem de endemismos dos Açores com os arquipélagos da Madeira, Canárias e Cabo Verde, concluindo-se que essa pobreza é relativa. Os factores que parecem melhor explicar as dissimilaridades entre essa fauna e a dos arquipélagos Macaronésicos vizinhos, são por ordem de importância: isolamento, idade geológica recente, baixa diversidade de alguns parâmetros ecológicos, clima muito húmido. A acção nefasta das glaciações Pleistocénicas, embora difícil de provar, é uma alternativa atraente e complementar das apresentadas.

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