THE DISTRIBUTION OF LAND MOLLUSCS IN THE MADEIRAN ARCHIPELAGO

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With 6 figures and 10 tables

ABSTRACT

A survey of land molluscs has been made on Madeira. The species present in each sample are recorded and the sites from which they come are identified by six figure grid references. Cluster analysis has been applied to the results. The fauna appears to fall into three groups corresponding to geographical regions: 1) the Ponta de São Lourenço, 2) the south coast between Caniçal and Ponta do Pargo and 3) the mountain and north coast region. A transect study at Garajau shows localization of some species within the study area. The results are discussed in relation to the origin of the fauna of the archipelago.

INTRODUCTION

The Madeiran archipelago consists of three groups of islands: Madeira itself, Porto Santo and the two offshore islands Ilheu de Cima and Ilheu de Baixo together with a few isolated rocks, and the three Desertas (fig. 1). All are composed of basalt and lava flows with soils derived by weathering, and in one or two places strands of shell sand. Madeira is about 55 km long by 23 km wide, and rises to 1860 m. Owing to the high elevation of the central part, which leads to high cloud cover and temperature inversions, there are marked climatic changes over short distances. The island can be divided into three regions. Along the south coast there is a strip rising to about 800 m that is warm and fairly cloud-free. It has a low annual rainfall but is intensively cultivated with the aid of irrigation by water collected in the interior. The temperature is very stable. At Funchal it ranges from mean monthly values of around 17° C in winter to 21° C in summer. Inland, the temperature is lower. There is frequent snow in winter and persistent heavy rain may fall at other times of the year. Even dry days are often humid and overcast except on the peaks which stand out above the clouds. The eastern tip of the island is formed by the Ponta de São Lourenço. This is the driest and most sunny part, and forms a bare uncultivated strip

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a few km long rising in places to about 100 m. It possesses an extreme form of the south coast environment untempered by the cooling effect of the high mountain block that lies behind most of the rest of the southern coastline. The Desertas look like a southern extension of the São Lourenço peninsula and have a similar climate. All are arid with sparse vegetation. The highest point, on Deserta Grande, is no more than 440 m. Porto Santo, the second largest of the islands, rises in two groups of hills separated by a saddle to a maximum altitude of 517 m.

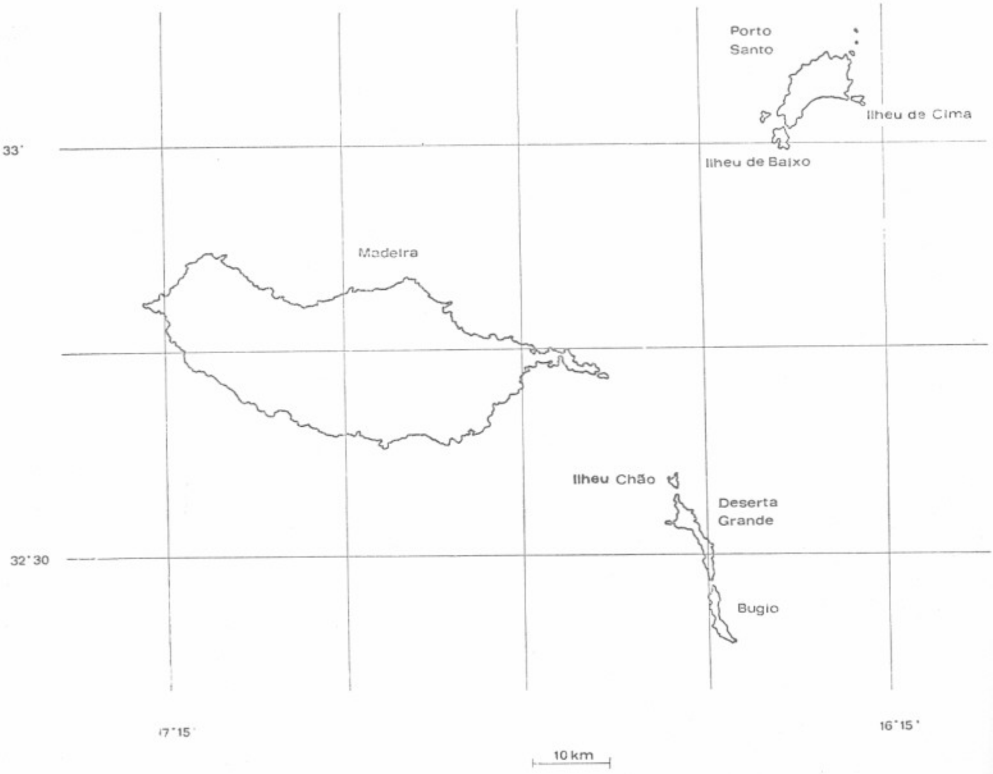

Fig. 1. — Map of the Madeiran archipelago showing the location of the islands discussed. The Salvage group (not figured) is more than 200 km to the south.

The high land has nothing like the moderating affect on climate produced by the great mass of Madeira. Porto Santo and its two outliers are warmer and more sunny than the greater part of Madeira, the weather conditions usually being more similar to those of the Desertas and the Ponta de São Lourenço. These islands and climates support an extremely diverse land mollusc fauna.

The ground work for the study of the land molluscs was laid in the nineteenth century. The results are found in the publications of Albers (1854), Lowe (1854), Paiva (1867), and collected together in Wollaston's *Testacea Atlantica* (1878). Somewhat later, the picture was extended by, among others, Noronha (1923), Cockerell (1922 a, b) and H. Watson (1923). A good review is provided by Mandahl-Barth (1943). It soon became apparent that the islands bear a very diverse mollusc fauna, most of it consisting of endemic species with comparatively distant affinities to the Palaearctic and N. African fauna, and that the few sand deposits on the islands contained related but distinct fossil species. Much interest was expressed in the origin and relationships of the fauna by Wollaston, R. B. Watson, (1876, 1889) and others. Wollaston was particularly conscious of the need to identify species precisely, having discussed their possible mutability with Darwin, Huxley, Hooker and Lyell (Wilson, 1971).

Cockerell (1922 b) pointed out that some of the living and fossil endemic species closely resemble fossils from the Eocene of France and Miocene of Germany, and suggested that the fauna has developed in isolation since the Miocene. More recent evidence indicates a shorter period of isolation. There is a fossiliferous reef deposit at about 300 to 360 m above sea level (Krejci-Graf, 1964, Watkins, Richardson and Mason, 1966). This is Miocene in age. Most of the island lies above it, and is therefore presumably the result of later volcanic activity. The part between 360 m and sea level must also have been exposed by uplifting at a period later than the Miocene although the rock may be older. Rock analyses by Watkins and Abdel-Monem (1971) provide ages of 3 million years or less. There is therefore no geological evidence that a separate fauna can have persisted here from the Miocene. Two carbon-14 datings on shells in «subfossil» deposits provide an age of about 1900 years for marine molluscs (*Patella* spp. and *Pecten* sp.) near Funchal, and about 5000 years for the land snail *Caseolus bowdichianus* (Férussac) in the famous calcareous deposit at Piedade on the Ponta de São Lourenço (Krejci-Graf, 1964). Madeira and Porto Santo are separated by a deep trench, and it is unlikely that they were ever connected.

There has been speculation about the time of arrival of the species common to the Palaearctic region. Watson (1876, 1889) suggests that *Testacella haliotidea, Helix aspersa* and *Discus rotundantus* (Müller) are very recent introductions as a result of human activity, and that the same may apply to *Rumina decollata, Cochlicella ventricosa, Testacella maugei,* and most of the other slugs. The evidence is slight, resting on their association with human habitation and absence from the subfossil deposits. *Helix aspersa* is now to be found in banana plantations, where it congregates on the stems of the banana plants in the folds of the emerging leaves (M. da Câmara, personal communication). An obvious recent human introduction to the islands was the specimen of *Cepaea nemoralis* (Linn.) found in 1920-21 by Vahl in Porto Santo (Mandahl-Barth, 1943). The species is not known to be established there: this was probably a single individual carried in agricultural produce or garden plants. The same explanation may well account for several of the species recorded by Jaekel (1970) but not otherwise known from Madeira. These comprise *Euconulus fulvus* (Müller), *Zonitoides nitidus* (Müller), *Vallonia costata* (Müller) and *Helicella conspurcata* (Draparnaud). Earlier, Wollaston drew attention to the occasional specimen of *Subulina striatella,* an African species similar to *Cochlicella ventricosa*. There is no reason to believe that it has ever become established. *Cochlicella ventricosa* and *Theba pisana* are both locally abundant species: the latter appears to have been present before the arrival of man.

There followed the publication of Nobre's monograph (1931), which reviewed the knowledge of the fauna and established a systematic key to the species, and the extensive anatomical work of Mandahl-Barth (1937, 1943). The latter author examined a large number of the species at one time referred to the genus *Helix* and put the classification on a modern morphological basis, using characters of the radula and reproductive system.

Although further work may lead to minor changes in classification, and probably to the reduction of some taxa long thought of as separate species to subspecific status, we now have a detailed picture of the composition of the faunas of the various islands. The question of how and why so many endemic species have evolved in this small land area has, however, received little attention since it was first noticed in the 19th century. To throw light on the problem it is necessary to know facts about the general ecology and distribution of the species — whether they are geographically separated within islands, whether there is niche specialization or evidence of competitive interaction, and so on. Precise locations are frequently given by the early authors for the individuals they describe, but evidence of the ranges is very limited, the majority or localities being in the vicinity of Funchal. In this paper we have begun to put the distributions of the Madeiran snails on a more quantitative basis than has formerly been attempted. The work was done in the months of July, August and September, 1970, not the best time of year for mollusc collecting, and it forms no more than a starting point. All records are given exact locations, however, and a reference collection of the shells as identified has been deposited in the Museu Municipal, together with a detailed list of the collecting sites. Future workers on the islands will therefore be able to confirm or amend our identifications and

	Species	Site — West from Câmara de Lobos														Site — East of Câmara										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Testacella maugei Férussac																									
2	Testacella haliotidea Draparnaud								1																	
3	Insulivitrina ruivensis (Gould)												1													
4	Insulivitrina marcida (Gould)																									
5	Insulivitrina nitida (Gould)																									
6	Vitrea crystallina (Mueller)		1																							
7	Oxychilus cellarius (Mueller)												1		1					1		1	1			
8	Vitrea scintilla (Lowe)	1		1			1	1		1						1	1			1		1				
9	Janulus bifrons (Lowe)														1								1			
10	Janulus stephanophora (Lowe)								1	1												1			1	
11	Punctum pusillum (Lowe)				1																					
12	Heterostoma paupercula (Lowe)						1																			
13	Geomitra tiarella (Webb & Berthelot)																									
14	Caseolus compactus (Lowe)																									
15	Caseolus leptostictus (Lowe)																									
16	Ochthephila maderensis (Wood)																					1			1	
17	Ochthephila compar (Lowe)	1	1		1		1	1							1	1						1				
18	Actinella arcta (Lowe)								1	1												1		1		
19	Actinella nitidiuscula (Lowe)		1				1	1	1	1										1					1	1
20	Discula tabellata (Lowe)	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1		1	1		1			1	1
21	Discula polymorpha (Lowe)																								1	
22	Cochlicella ventricosa (Draparnaud)																					1			1	
23	Caracollina lenticula (Férussac)															1					1					
24	Leptaxis erubescens (Lowe)						1									1				1						
25	Leptaxis undata (Lowe)																									
26	Theba pisana (Mueller)	1										1	1	1		1	1	1			1	1	1		1	1
27	Helix aspersa Linn.																									
28	Vallonia pulchella (Mueller)													1		1	1	1			1					
29	Rumina decollata (Linn.)						1					1	1		1	1				1						
30	Ferussacia t. tornatellina (Lowe)													1		1						1				
31	Ferussacia tornatellina melampoides (Lowe)								1													1			1	
32	Ferussacia terebella (Lowe)																									
33	Cochlicopa lubrica (Mueller)																									
34	Cecilioides acicula (Mueller)						1									1				1						
35	Lauria millegrana (Lowe)																			1						
36	Pupa umbilicata Draparnaud									1																
37	Clausilia deltostoma Lowe	1					1			1					1	1	1			1	1		1			
38	Clausilia exigua (Lowe)	1								1		1														
39	Craspedopoma lucidum (Lowe)									1																
40	Craspedopoma monizianum (Lowe)							1																		

Site No.	Earth sample taken	Grid reference	Approximate location
1		011601	Ponta do Pargo
2		017575	Rª das Galinhas
3		035563	W. of Calheta
4	*	058541	Arco da Calheta
5	*	066539	Madalena do Mar
6		076527	Ponta do Sol
7		086527	Rª de Caixa
8		093522	Rª Brava
9		100530	Rª Brava
10		122514	Cabo Girão
11		118512	Cabo Girão
12		130522	Estreito de Câmara de Lobos
13		136516	Quinta do Leo
14		144506	Câmara de Lobos.

Site No.	Earth sample taken
15	*
16	
17	
18	
19	*
20	
21	*
22	*
23	
24	
25	
26	
27	
28	*
29	*
30	*
31	
32	
33	
34	
35	
36	

Table 1

de Lobos to Caniçal

Site — Ponta de São Lourenço

Site — North and Central

26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
			1																			1										
			1																													
																														1		
		1	1		1	1		1																1			1					
	1	1		1	1	1			1		1				1													1			1	1
																											1					
	1												1																			
												1	1	1	1	1			1	1	1		1									
													1																			
											1		1			1	1	1	1	1												
	1			1					1					1																		
	1			1	1	1	1																									
		1																														
	1						1		1	1									1													
1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1				1
1	1	1		1	1		1	1		1	1	1		1	1	1	1	1	1	1	1											
									1				1	1	1																	
									1			1	1	1	1																	
			1																1													
1	1	1		1	1	1	1	1	1		1												1	1		1						
													1	1	1	1			1													
				1					1																							
	1												1						1													
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																				1												
																											1					
		1																														
				1	1	1		1			1		1		1					1							1					
	1			1							1													1								
																													1			

Grid reference	Approximate location
151502	Praia Formosa
149517	Pº dos Romeiros
148523	Rº do Vasco Gil
147530	Rº do Vasco Gil
155502	Clubo Naval, Funchal
161515	S. António
186507	S. Gonçalo
184515	S. Gonçalo
198519	Pº de Água
195503	Garajau
194505	Garajau
194506	Garajau
194505	Garajau
201514	Caniço
180525	Pº do Infante
202512	Caniço
209522	Gaula
213513	Gaula
216517	Porto Novo
219526	Gaula
233539	Água de Pena
237551	Machico

Site No.	Earth sample taken	Grid reference	Approximate location
37		242559	Caniçal
38		249558	Pedra do Pássaro
39		257561	Prainha, Piedade
40		258561	Prainha, Piedade
41		257561	Prainha, Piedade
42		258561	Prainha, Piedade
43		264562	Pº das Pedras Brancas
44		268564	Porto da Abra
45		274558	Ilheu do Desembarcadouro
46	*	285555	Ilheu de Fora
47	*	284554	Ilheu de Fora

Site No.	Earth sample taken	Grid reference	Approxima
48		035614	Achadas d:
49		048626	Porto Mon'
50		113555	Serra de Á
51		103597	S. Vicente
52		171605	S. Jorge
53		192587	Faial
54	*	188576	Faial — Rº
55		182568	Faial — Rº
56		173560	Rº Frio
57		172538	Vista Navi
58	*	151561	Pico do A

records. It is hoped that in due course a detailed survey will in this way be built up.

Material, methods and data.

A) *General survey*.

Collections of molluscs were made in many parts of the island. The main objective of our work at the time was collecting lizards, which necessitated setting traps for a period of between ½hr and lhr at each site. Much of this time was spent searching for snails, so that although the duration of sampling was not carefully controlled, each site represents a roughly similar collecting effort. Areas where few species were found have a relatively sparse or secretive fauna. Although we attempted to collect all species present at a site the smaller ones are almost certainly under-represented. In some localities earth and detritus samples were taken, and these were carefully searched in the laboratory by sieving and handsorting. The results are shown in table 1, with the sites including earth samples indicated. Most of the molluscs found were inactive and taken from beneath stones. In the more arid southerly and easterly parts of the island the snails were in a state of partial or complete aestivation. For this reason, too, the more secretive species will be under-represented.

The location of sample sites may present difficulties if local place names are relied upon. This is especially true when the language of the country is foreign to the collector or reader, so that the conventions in naming are not understood. We have experienced difficulty when attempting to establish the exact provenance of specimens of Madeiran snails in museum collections, and have therefore used a grid reference system of location. The advantages appear sufficient to urge its adoption in future work on the Madeiran fauna.

The grid provides a 6-figure reference by which any location may be specified to within a square of 200 m edge or 4 ha. It is rectangular and arranged parallel to the lines of latitude and was set up originally using the 1 in 50,000 scale map published by the Instituto Geográphico e Cadastral in 1958. The point 000600 coincides with the westernmost tip of the Ponta do Pargo, and 150500 is almost exactly coincident with the most southerly tip of Ponta da Cruz (see fig. 2). The grid references for all samples are recorded in table 1. We have summarized the distributions recorded in Nobre (1913) in table 2. Where the locality appears uncertain or ambiguous a record has been excluded; and we have provided grid references indicating approximately where we consider the sites to be.

In addition to the general collecting, four other series of samples were examined. The most complete of these was a transect on the Ponta do Garajau from the tip of the headland running inland towards the

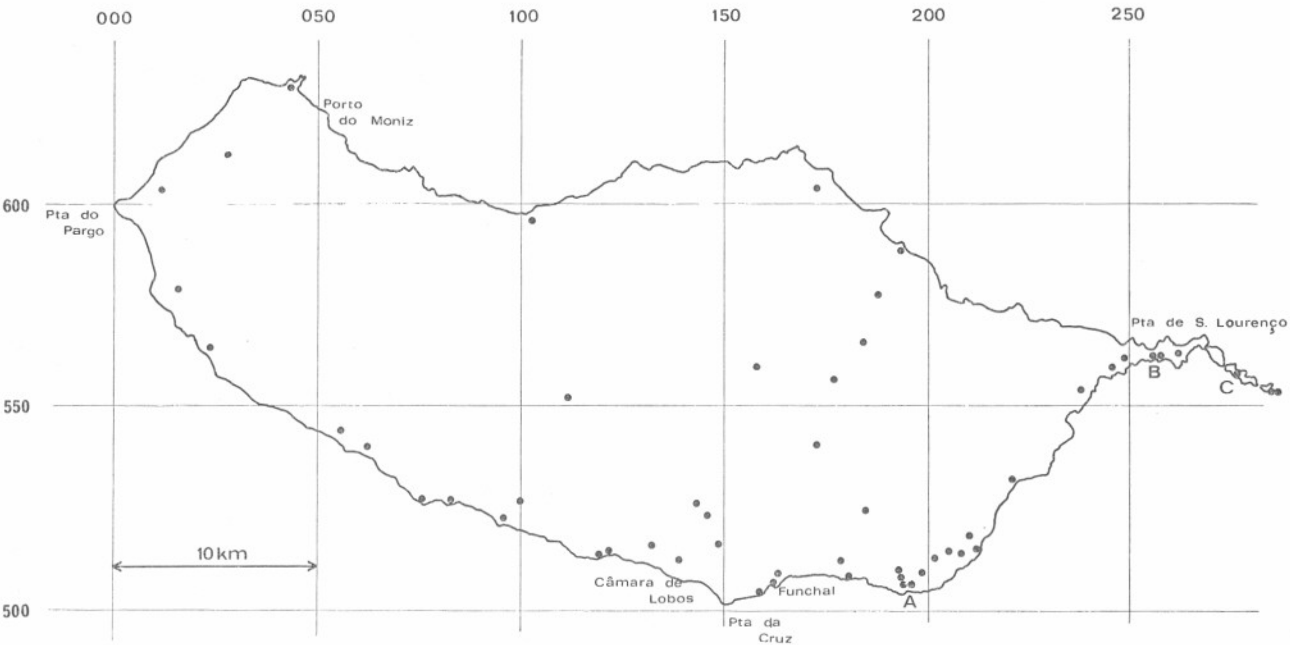

Fig. 2. — Map of Madeira showing main grid coordinates, collecting sites and transects. A — Garajau, B — Piedade, C — Ilheu do Desembarcadouro.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
I. ruivensis																																		1					1	1	
I. nitida																															1			1							
V. crystallina												1		1	1																		1					1			1
O. cellaria			1									1		1											1	1	1	1										1			
J. bifrons																				1																1					
J. stephanophora															1					1	1																	1			
P. pusillum									1								1																								
H. paupercula																									1				1	1											
C. compactus																											1		1												
C. leptostictus																				1	1			1																	
O. maderensis		1							1								1		1				1																		
O. compar						1	1	1	1										1				1																		
A. arcta	1	1		1											1	1				1	1					1														1	
A. nitidiuscula		1				1																														1					
D. tabellata						1	1													1																					
D. polymorpha	1																		1	1		1	1		1	1	1	1	1							1					
C. ventricosa							1		1			1		1	1														1												
C. lenticula									1			1		1									1			1															
L. erubescens		1						1						1		1	1	1									1	1	1	1	1		1								1
L. undata			1									1								1			1			1	1														
T. pisana															1					1							1	1	1												
H. aspersa												1		1			1																								
V. pulchella						1	1		1					1	1				1				1			1												1			
R. decollata										1	1		1	1	1										1		1														
C. deltostoma			1					1	1					1					1				1															1			
C. exigua		1			1									1	1					1			1										1	1				1			
C. lucidum								1						1	1		1															1	1				1	1	1		
C. monizianum																				1	1				1																

Site No.	Approximate GR.	Location
1	000600	Ponta do Pargo
2	010575	Fajã da Ovelha
3	015575	Rª de S. João
4	040545	Calheta
5	090525	Rª Brava
6	115510	Cabo Girão
7	135505	Câmara de Lobos
8	140520	Socorridos
9	145500	Praia Formosa
10	150500	Gorgulho
11	150505	S. Martinho
12	155515	S. Antonio
13	160505	Pontinha
14	165510	Funchal
15	170510	Sta. Luzia
16	170515	Rª J. Gomes
17	170520	Monte
18	170515	Bom Sucesso
19	180510	S. Gonçalo
20	190500	Garajau
21	195510	Caniço
22	200505	Ponta do Oliveira
23	210515	Porto Novo
24	210520	Gaula
25	220530	Sta Cruz
26	230545	Machico
27	245555	Caniçal
28	255560	Piedade
29	250560	Pª São Lourenço
30	040625	Porto Moniz
31	070605	Seixal
32	090595	Rª do Inferno
33	100595	S. Vicente
34	165605	S. Jorge
35	190580	Rª do Faial
36	200575	Porto da Cruz
37	060570	Rabaçal
38	140530	Piornais
39	175555	Rº Frio
40	175540	Poiso
41	210550	Santo da Serra

Table 2: — Distribution records from Nobre (1931) for species recorded in Table 1.

Pico do Infante, and stopping at a height of about 550 m. The literature suggests that this region has supported the most diverse mollusc fauna on the island. The calcareous sandy area around the hermitage of Nossa Senhora da Piedade was also examined by transect sampling from the summit of the hill down towards sea level. The other sites were on the Desembarcadouro at the east of the São Lourenço peninsula between Ponta do Furado and the Ilheu de Fora, and on the Desertas.

B) *Garajau transect.*

Samples were collected at regular intervals of 20 paces (approximately 12 m) along a line running from the statue on the point inland in the direction of the Pico do Infante. Each sample was taken from a quadrat of area 4 sq. ft. (0. 36 sq m) during a search lasting 10 minutes.

The vegetation changed from bare earth with stones, tussocks of low plants including grasses and prickly pear *(Opuntia* sp.*)* to cultivated land with fields that contained root crops or were fallow at the time. The fields were separated by dry-stone walls and interspersed with houses and occasional fig trees. As the ground rose the area of cultivation and human habitation gave way to coniferous plantation. A summary of the profile examined is given in figure 3. Snails were found from the most seaward end of the transect as far as the beginning of the woodland, throughout the whole of which all signs of molluscs were absent· This confirms our findings in coniferous plantations in other parts of the island. The numbers of individuals of each species found in each quadrat are recorded in table 3, which therefore differs from the tables above in showing density as well as presence or absence of species.

C) *Piedade transect*

This and the ensuing two sets of samples were less precisely measured but were undertaken to see whether any changes in density or replacement of species etc. were detectable over short distances. The results are sketchy but are recorded for the sake of completeness. Samples were taken at intervals of about 10 paces (6 m) along a line from the hermitage at the top of the hill downwards in a south-westerly direction towards the Prainha. As before an area of 0. 36 sq m was searched for 10 minutes at each stopping point. The transect was covered with a fairly uniform carpet of short grass and herbage some 5 cm high, lying over shell sand. In places the sandy substrate was exposed; and at the bottom there were also boulders of lava and calcareous breccia. The snails were mostly aestivating closely packed beneath these stones. Their increased density towards the seaward end (table 4) is due to the presence of boulders there. A few metres inland from the transect we also found the Black Widow spider *Latrodectus* sp.

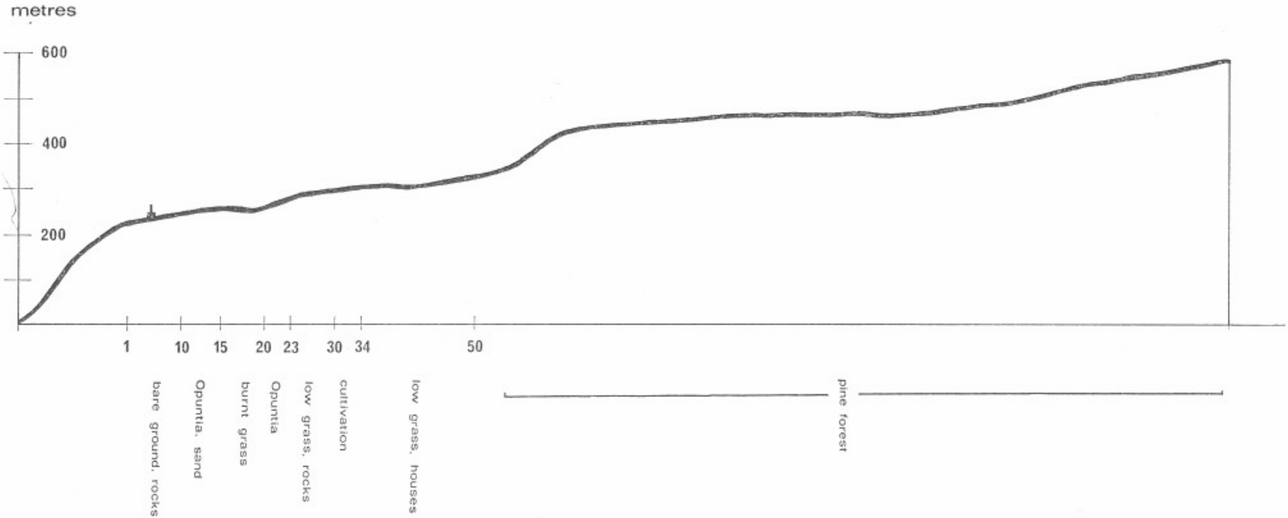

Fig. 3. — Profile of the Garajau transect, with position of quadrats and general vegetation type.

	Species	Quadrats																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	V. crystallina																1									
2	O. cellarius																									
3	J. bifrons				1	1	2	7	5					1	1						1	3			8	
4	C. compactus		3	1	1	3	1			3																
5	C. leptostictus	4	2	2	4		2	2			1					1			2	1		1		4		
6	A. arcta					6	5	6		1	1	1		1	6	1	4	5	2		16	1	4	5	8	1
7	A. nitidiuscula	4	2	19	5	21	4	16	4	14	4	7	1	4	8		14	15	12	4	4	7	3	10	4	3
8	D. tabellata	2				2	2																2	2		
9	D. polymorpha							2		4		1			1		2	2	1				1	6	10	5
10	L. undata							3				1			10		5	1			2	1	6		3	6
11	F. folliculus																								1	
12	F. tornatellina	1	2					1	4		1				1							2	1		5	
13	P. umbilicata																									
14	C. deltostoma											3											1	1	4	

	Species	Quadrats																								1 -	24 -
		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	23	49
1	V. crystallina																									1	1
2	O. cellarius				4	5	1																			0	10
3	J. bifrons																				1			1		22	10
4	C. compactus																									12	0
5	C. leptostictus																									26	0
6	A. arcta		1	8		4	7	2	2									2		1	11		1			65	48
7	A. nitidiuscula		6	4	1	2	3	6	21	4	20	4	3	4		3	1	11	6	12	3	1	2	3		182	127
8	D. tabellata																									10	0
9	D. polymorpha	1	5	2	4			4	7			1					1	2	4		12	2				20	60
10	L. undata				2		1		1	1									1		3		1		3	29	21
11	F. folliculus																									0	1
12	F. tornatellina																									13	5
13	P. umbilicata							1																		0	1
14	C. deltostoma																									5	4

Table 3: — Numbers of individuals found in quadrats on the Garajau transect. Quadrat numbers run from 1, at seaward end to 49 inland. For details see text and profile, fig. 2. The two right hand columns show totals for the first 23 and the subsequent 26 quadrats.

Species	Quadrats																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
H. paupercula	21	23	15	54	1	7	11	16							2	4	1		
C. compactus	2	3	2	3	1	2	1	1	3				1		2	4			2
A. nitidiuscula	3	2	5	6		4			2				5	9	2	5	1		1
D. tabellata											3			4					
D. polymorpha	12	3	5	75	4	4	12	3	9			2	6		3	4			
C. ventricosa	1	53	4																
T. pisana	15	20	16	11	6	1									1	3	2	7	2
F. tornetellina			10				1												
C. deltostoma		1	1										1						

Table 4: — Number of individuals of different species found on the Piedade transect. The quadrat numbers run from 1, near the Prainha, to 19 on the level ground at the top of the hill.

D) *Desembarcadouro*

Five separate collections were made along the length of the island. The sites are not known exactly but the collections were made at more or less equidistant intervals. In table 1 these records are lumped and represented as sample 45. There was, however, some variability in species

Species	Sites 1	2	3	4	5
H. paupercula	1	1			1
C. compactus	1	1	1	1	1
A. nitidiuscula	1	1	1	1	1
D. polymorpha	1	1	1	1	1
L. erubescens		1			
T. pisana	1				

Table 5: — Species present on the Penultimate islan. Sites are numbered from west to east.

composition between localities, so that presence or absence is recorded separately for each site in table 5. The site numbers run eastwards, starting with No. 1 collected just above the landing place at the western end. The general impression while collecting suggested that there is a decrease in density of all species from west to east, and confirmed the evidence of the table that *T. pisana* is restricted to the western end.

E) *Desertas*

Samples were taken on all three islands. They consisted of one general collection from the plateau of Ilheu Chão, one from the southern end of Bugio above the landing stage to the north of the lighthouse, and several from Deserta Grande. The series on the main island started on the grassy north-facing valley above the Ponta da Castanheira and continued southward over the saddle into the main vegetated valley as far as the ruined building at its southern end. The first four sites (numbers 1 to 4) are in the north-facing valley, No. 4 being just north of the saddle near what appears to be a former artificial dewpond. This is the southern end of the area where we found the large endemic lycosid spider *Lycosa ingens,* although Bristowe (1963) found it as far south as the ruined house. The next eight samples (numbers 5 to 12) were spaced out more or less equidistantly between the saddle and the house.

For the rest of its length the island is extremely eroded, and in places very precipitous. Vegetation is extremely sparse: limited to lichens, mosses and the occasional low shrub. During our brief visits to this part no snails were found until we reached the area known as the «threshing floor». This is a little to the south of the steps cut in the west-facing cliff that lead down to the southern landing point, or doca. It consists of the remains of dry-stone walled enclosures and a shallow stone-paved depression that could have been at one time a threshing floor or, perhaps more probably, another dew pond. A sample (No. 13) was taken from beneath these stones, and the final sample was collected at the most southerly point of the island where the cliff falls to the channel separating Deserta Grande from Bugio. The results are shown in table 6.

RESULTS AND DISCUSSION

a) General consideration of the fauna of the archipelago.

The Madeiran islands are characterised by a large number and wide variety of molluscan species. There is a high frequency of endemic species. The first question to consider is whether isolation of the islands from the mainland and from each other is of particular importance in leading to variety, or whether isolation is also accompanied by a high degree of niche diversity.

MacArthur and Wilson (1967) have surveyed the evidence on the relation between area of islands and the number of species they support. For isolated islands they show that the regression of logarithm of number of species on logarithm of area usually has a slope between 0.25 and 0.35 in a wide range of animal groups. The coefficient defining the position of the regression line in relation to the y-axis (log species) varies between groups and would rise for colonised islands with many niches and fall for those with few niches. When islands in a group are closely adjacent to each other the slope of the regression line is much flatter (0. 12 to 0. 17), the smaller islands receiving constant recruitment from the larger ones and so maintaining a wide variety of species. Peake (1969) gives data for land molluscs in the Solomon Islands. There is a relatively steep slope of about 0. 35. The value of the intercept coefficient is about -0. 24. In the Indian Ocean, the islands may be grouped into two categories so far as average numbers of mollusc species are concerned. On high volcanic islands faunas are relatively rich with a high value for the constant (about 0.70) while on low coral islands there is a poorer fauna of species with greater powers of dispersal (indicated by a constant of about 0.25). The slope of log number on log area is the same in each case (Peake 1971).

Comparison of this kind does not provide a clear indication of whether or not the Madeiran fauna falls within the generally established range. Politically, the archipelago consists of seven islands all within

Species	Chão	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Bugio
H. paupercula	1	1	1					1		1						
C. leptostictus			1													1
C. micromphalus	1											1			1	
A. nitidiuscula	1	1	1	1	1	1			1	1						1
D. polymorpha	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1
A. laciniosa	1															
L. leonina										1						
L. erubescens	1		1	1	1	1	1			1						
L. vulcania	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1
C. deltostoma		1	1	1	1			1		1		1	1	1	1	1
A. arcta																1
L. millegrana															1	
F. tornetellina				1												

Table 6: — Samples from the Desertas. The numbered sites are on Deserta Grande — see text for location

Species first referred to in this table are *Caseolus micromphalus* (Lowe), *Actinella laciniosa* (Lowe), *Leptaxis leonina* (Lowe) and *Leptaxis vulcania* (Lowe)

30 km of each other (some only separated by a matter of metres), together with the Salvage group. These are more than 200 km. from the rest and nearer to the Canary Islands than to Madeira. They are therefore very isolated from the rest, and leave, if they are excluded from the comparison, a relatively homogeneous group. Wollaston records the number of species present on the different islands (table 7). Excluding

Island	No. of Species	Area (km^2)
Madeira	96	740
Chão	9	0.3
Deserta Grande	23	10.4
Bugio	27	3.3
Porto Santo	57	39
Cima	17	0.3
Baixo	14	1.5
Selvagem Grande	1	2.3

Table 7: — Number of species recorded by Wollaston (1878) and approximate land area for the islands of the Madeiran archipelago

the Salvage Islands the species/area regression has a value of 0. 270 agreeing very well with estimates obtained by other authors for different fauna elements and archipelagos· The constant coefficient is 1. 19. The Salvages possess only one species *(Theba pisana),* and if they are included the slope is steepened to 0. 328.

Perhaps the conclusion to be drawn from the slope of 0. 27 or greater is that a very short distance by sea forms an efficient barrier to terrestrial molluscs, that the populations are therefore as isolated as they would be on islands separated by much greater geographical distances, and that the variation in diversity of fauna with land area bears the relation shown by other animal groups on isolated islands. The high frequency of endemic species is consistent with this view of the efficiency of sea as a barrier to colonization by land molluscs.

It is of interest to consider whether the variation in species composition from one island to another fits any particular pattern. Some numerical taxonomic methods of assessing affinity will be discussed as methods of comparison. The raw material is the data on presence or absence on each island of each of the 150 species involved, as given by Wollaston.

All the methods considered belong to types described by Sokal and Sneath (1963) for data that may be recorded as present or absent. The data are arranged in a table with columns representing islands or sites (in numerical taxonomy, groups of organisms) and the rows representing species (or in numerical taxonomy, characters). Every entry in the table is zero or 1, representing absence or presence. For N sites there are ½ N (N-1) comparisons between pairs to be made, and for the purpose of comparison the data are arranged according to the following table.

	+	a	b
Site 1	—	c	d
		—	+

Site 2

Each letter represents the number of species in the category. Thus, b is the number of species common to both sites, c is the number included in the study that are absent from both sites, and so on. Four indices of similarity have been considered, which provide the results shown in tables 8 to 10.

a) Jaccard Index (Sokal and Sneath). This is simply the number of species common to both islands of a pair divided by the total number of species present on the two, or b/(a+b+d). The results are given in table 8, right, and may be clustered to produce the diagram of relationship shown in fig. 4. Madeira stands out as different from both the Desertan and Porto Santan groups, Deserta Grande and Bugio are

Madeira	Chão	D. G.	Bugio	Porto Santo	Cima	Baixo	
	0.06	0.13	0.19	0.12	0.03	0.03	Madeira
0.65		0.39	0.24	0.08	0.13	0.15	Chão
0.56	1.00		0.52	0.13	0.08	0.09	Deserta Grande
0.69	0.72	0.60		0.18	0.07	0.08	Bugio
0.20	0.52	0.31	0.39		0.28	0.22	Porto Santo
0.15	0.25	0.11	0.12	0.92		0.48	Cima
0.19	0.23	0.14	0.15	0.91	0.58		Baixo .

Table 8: — Jaccard Index (upper right) and Maximum Similarity (lower left) for comparison of species composition between islands.

more similar than either is to Chão. Cima and Baixo are more alike than either is to Porto Santo. This index excludes category c, a

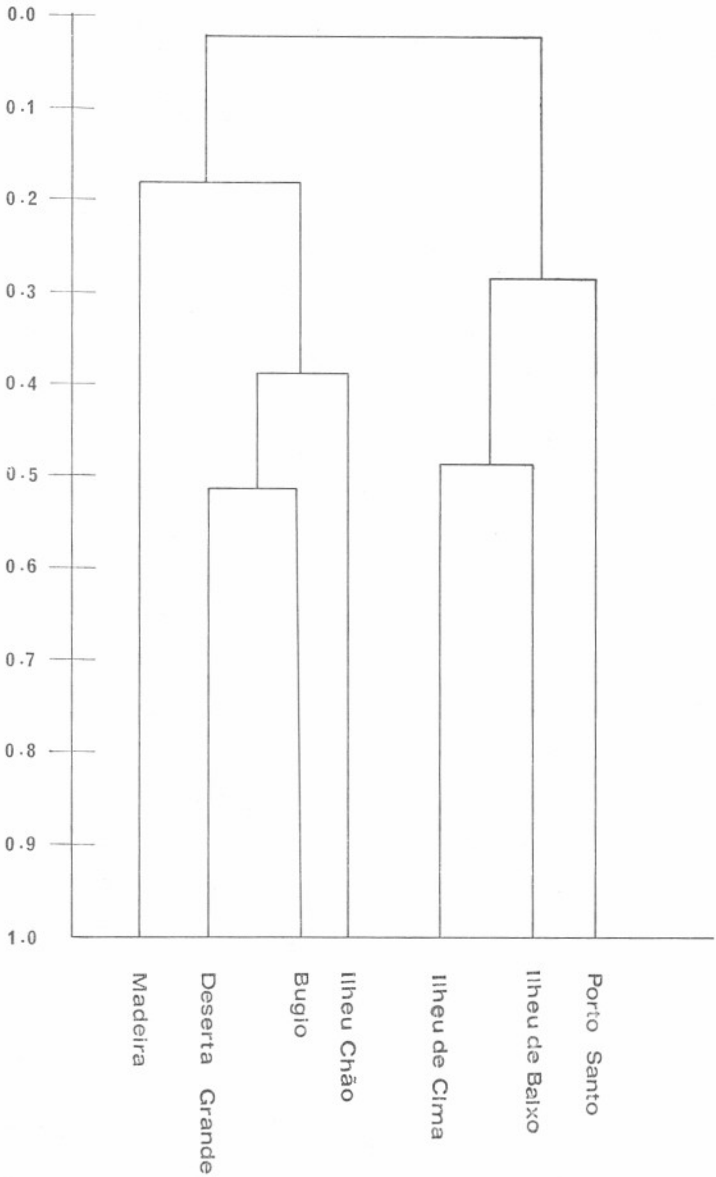

Fig. 4. — Cluster diagram for similarity of mollusc faunas of islands, based on Jaccard index. Linkages represent distances between groups.

procedure that is reasonable if species present on neither island are irrelevant to the comparison: and it is also highly sensitive to difference in number of species per island. When comparing Madeira and Chão, for example, the highest value the index could attain occurs when all 9 species on Ilheu Chão are also among the 96 species on Madeira. The maximum is therefore 0. 09. In the comparison between Deserta Grande and Bugio, on the other hand, the maximum value is 0. 85. The Jaccard Index, may, therefore, vary greatly even when one island of the pair has no species exclusively its own. The variation can be overcome by calculating the next index.

b) Maximum Similarity. This is b (b+d) / (a+b+d) (a b) or b (a+b) / (a+b+d) (b+d), whichever is the larger. The effect of difference in number of species is now removed and the index measures degree of similarity in the species that are present (table 8, left). It will, however, be affected markedly if the taxonomist has made some populations specifically rather than sub-specifically distinct from others merely because they are allopatric. Wollaston gives three species of *Leptaxis*. These are *L. undata* on Madeira, *L. vulcania* on Ilheu Chão and Deserta Grande and *L. leonina* on Bugio and the southern tip of Deserta Grande. They are grouped together as subspecies by Mandahl-Barth (1943), a procedure that will alter the relative position of Ilheu Chão to quite a large extent. Before considering the most suitable indices, two others will be presented.

c) Simple Matching Index (Sokal and Sneath). This is (b+c) / (a+b+c+d). Here the negative class is included, and difference in number of species between islands is accordingly taken into account to

Chão	D. G.	Bugio	Porto Santo	Cima	Baixo	
0.38	0.39	0.45	0.19	0.29	0.31	Madeira
	0.91	0.85	0.63	0.87	0.89	Chão
		0.89	0.59	0.77	0.79	Deserta Grande
			0.61	0.75	0.77	Bugio
				0.72	0.70	Porto Santo
					0.93	Cima

Table 9: — Simple matching index for comparison between islands

an extent intermediate between the two preceding indices. There are 150 recent terrestrial species in all on the archipelago. If all species on the less populated island were present on the more populated one, the simple Matching Index would register 63/150 = 0.42 for the comparison between Madeira and Ilheu Chão, but 146/150 = 0. 97

for the comparison between Deserta Grande and Bugio. The results are shown in table 9.

d) Disequilibrium Coefficient, D'. This is the determinant bc — ad adjusted by multiplying by the marginal totals so that it varies between — 1 and + 1. The method of adjustment is described by Lewontin (1964) and by Turner (1968). D' is similar to several indices given by Sokal and Sneath, but has been used in studies of genetic linkage disequilibrium. The value calculated has the additional feature compared with previous indices that positive values signify association, negative value disassociation, and values about zero random association of species. Given that the fraction of the total number of species on Madeira is 96/150 and the fraction on Ilheu Chão is 9/150 the expected number of overlapping species on the assumption of random distribution is 9 x 96/150, or 6.

Madeira	Chão	D. G.	Bugio	Porto Santo	Cima	Baixo	
	0.00	- 0.05	0.03	- 0.61	- 0.72	- 0.67	Madeira
0.00		0.35	0.21	0.03	0.12	0.16	Chão
.01	46.16		0.56	0.01	0.02	0.04	Deserta Grande
0.97	19.07	53.15		0.06	- 0.02	0.02	Bugio
49.03	0.59	0.00	0.96		0.19	0.15	Porto Santo
15.68	2.58	0.00	0.00	23.01		0.55	Cima
10.19	3.85	0.08	0.00	17.24	49.09		Baixo

Table 10: — Disequilibrium Coefficient D' (upper right) and corrected χ^2 value (lower left) for comparison between islands. χ^2 has one degree of freedom).

Tendencies to association or disassociation may be tested by calculating χ^2 values for the pairs. The observed figures for D' and for χ^2 are given in table 10, right and left respectively. A three-dimensional clustering diagram based on D' is shown in figure 5. All connecting links are associated with highly significant χ^2 values, except for the link from Madeira to the Desertas, for which D' is about zero.

At least three hypotheses may be proposed to account for the distribution of species.

i) The islands may all have similar habitats available, but as a result of isolation the faunas have diverged so that different species occupy similar niches on different islands.

ii) Little divergence has occurred and the ecologies of the islands are similar, except that small islands carry only a fraction of the niches available on the larger ones. Limited sets of species are therefore present on each island, the variety determined availability of niches.

iii) The ecologies of the islands are sufficiently different as to elicit adaptive variation in the molluscs to exploit the available niches.

So far as general habitat types are concerned, the three Desertas, Ilheu de Cima and Ilheu de Baixo are all relatively dry and stony with thin soil and vegetation cover. Porto Santo is a considerably larger island

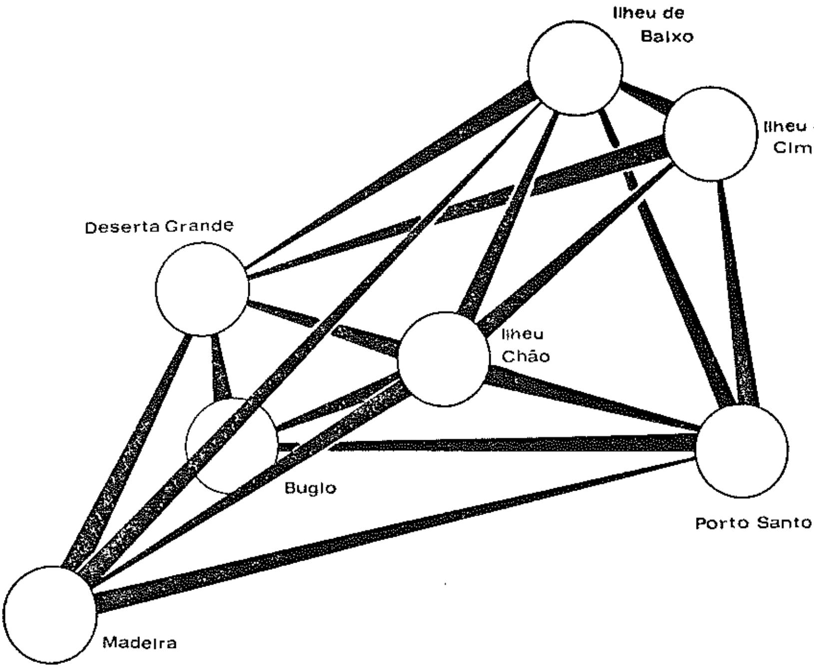

Fig. 5. — Three-dimensional diagram of faunal similarity based on D' index. The distances are 1 — D'. Two main groupings are seen, but the two sets of satellite islands are closer to each other than are the main islands Madeira and Porto Santo.

with mountains rising to 517 m, and also an extensive sandy beach backed by lowlying terrain. Madeira is much the largest island. The eastern tip, the Ponta de São Lourenço, somewhat resembles the Desertas with in places a similar short vegetation including *Suaeda* and *Mesembryanthemum*. A south-eastern stretch of coastline from Caniçal to Funchal is relatively dry and lowlying and approaches the Ponta in character, although the vegetation is very disturbed by cultivation, while the mass of land to the north and west rises to 1860 m, is frequently cloud-covered and has a much more temperate and moist climate than any other part of the archipelago.

The three suggestions for the origin of the faunal diversity are not, of course, always mutually exclusive. If we are to make any decision as to which may have a dominant effect on the basis of the numerical classification, it is clear that the four methods a to d are not all equally useful and that some may be positively misleading. The most critical index is probably D'. If hypothesis (i) predominates D' should usually be negative and should have an increasingly negative value with increasing geographic isolation. If hypothesis (ii) is important most of the linkages should lie about D' = O, while on hypothesis (iii) the classification should separate islands into habitat groups — possibly the four entities Madeira, Porto Santo, Deserta Grande / Bugio and Ilheu de Cima / Ilheu Chão / Ilheu de Baixo. It does not appear possible to make distinct predictions on each of the three hypotheses using any of the other indices. The Jaccard Index may, in addition, give a false impression of the relations by giving undue weight to the differences in area. For these reasons we prefer D'.

Inspection of the D' matrix and diagram shows that we can at least rule out hypothesis (ii). There are two major groupings — the Porto Santo complex and Madeira with the Desertas. The range of overlap of habitat types is great, and many of the species exclusive to one group have very similar representatives in the other group. This is true of species in the genera *Ferussacia, Pupa* and *Leptaxis* and of a number of the helicids. The difference can be put down to divergence in similar habitats and niches as a result of isolation. In Madeira one group of species tends to be restricted to the higher ground (see below). This includes *Craspedopoma, Vitrina* and *Testacella* and is associated with the cool humid habitats restricted to that area. The smaller islands show relationships to their adjacent large island of a degree more or less to be expected on the basis of a random sampling of species and niches from the large neighbour, but it is noticeable that the satellites of the two groups converge on one another. This is partly because of the similar size of their faunas, but also indicates a proportionately large overlap of species. In Ilheu Chão, Ilheu de Cima and Ilheu de Baixo a substantial fraction of the faunas is formed by the three universal species, *Discula polymorpha, Heterostoma paupercula* and *Clausilia deltostoma*. The first two are limited to the south coast of Madeira. *H. paupercula* has a narrow range on the Ponta de São Lourenço and an apparently isolated colony at Porto Moniz. Thus, owing to their small sizes and relatively low altitudes the smaller islands tend to have a common and limited selection from the total range of niches.

Finally it may be noted that the numerical taxonomist would probably say that these methods have very limited validity when so few characters (or mollusc species) are considered in some of the comparisons. The small sample size is inherent in the situation, however, and does not make the problem of the origin of the faunal diversity less interesting. Any discussion of this problem requires judgment of the faunal similarities of the islands. The application of the numerical indices forces the investigator to make decisions as to what criteria are important in assessing distinctness; and in this case it provides an index D', that appears to be a useful measure of overall similarity or difference.

b) Madeira and Desertas

GENERAL SURVEY

Grouping procedures were attempted using the larger species in the 58 general collections made in Madeira, and the 16 from the Desertas. The method can give only a rough indication of similarities owing to the small number of species per sample. By removing from consideration samples with less than five species we took out all those collected in the mountains or on the north coast of Madeira except for one at Faial. These areas have on average a less varied mollusc fauna than the south coast and eastern peninsula. Clustering on the basis of maximum similarity was chosen since it is least affected by variation in species number in the samples. It separates the fauna of the Ponta de São Lourenço from that of the rest of the south coast, within which there are minor variations, and groups the eastern Ponta with the Desertas (fig. 6). Since there is at least one geographical separation involved on the mainland, the data in table 1 were arranged in four groups, representing from left to right the collections from 1) Ponta do Pargo to Câmara de Lobos, 2) Câmara de Lobos to west of the tunnel between Machico and Caniçal, 3) from east of the tunnel to the Ilheu de Fora, and 4) the north coast and central mountain samples.

There are some ubiquitous species, such as *O. cellaria,* present about equally in all areas, but others with distinctly limited distributions. *L. undata* occurs everywhere but most commonly in the central part of the south coast. *D. polymorpha* is present only on the south coast from east of Funchal to the most easterly tip of the island. *C. compactus* and *H. paupercula* are species of the Ponta de São Lourenço (with the exception of the one record of *H. paupercula* from Porto Moniz). *Cochlicella ventricosa* is also a species of the drier south-east. It is interesting to note that in western Europe it tends to be restricted to more humid habitats, while open, dry and coastal regions are occupied by the very similar species *C. acuta* (G. Lewis, personal communication). In Madeira it is the only species of the genus, and appears to have taken over the habitat of *C. acuta.*

In two cases it is possible tentatively to identify pairs of species that occupy similar niches and replace each other from east to west. *Caracollina lenticula* is an eastern species, absent from the north coast

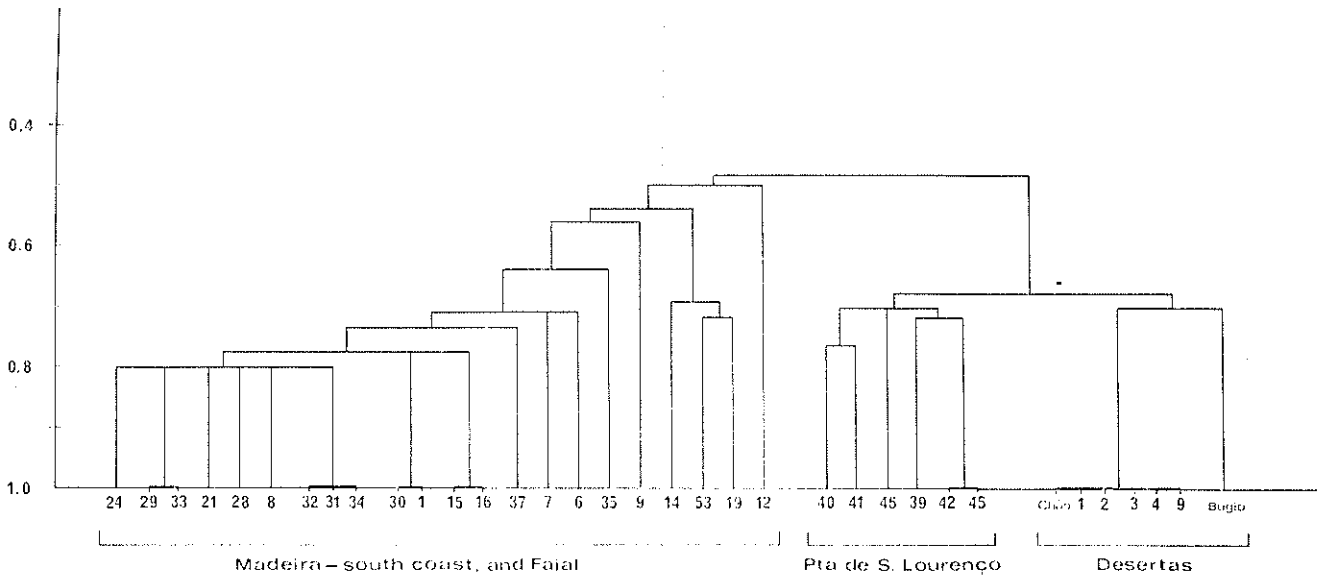

Fig. 6. — Cluster diagram for Madeiran and Desertan samples based on maximum similarity index. Linkages represent minimum distances between groups. Sample numbers for Madeira in table 1; for Deserta Grande in table 6.

and thinly represented in the south as one moves towards Ponta do Pargo. Its place appears to be taken by *Ochthephila maderensis,* a quite distinct species but one of similar size and habit. Both are moderately depressed, about 7 mm in breadth and found in the interstices of soil and rubble or at ground level among living or dead foliage. Similarly, *A. arcta* is restricted to sites west of Machico, while *H. paupercula* occurs on the eastern peninsula. These species are smaller than the two preceding ones (about 4 mm) and were often found tightly attached in the pits and depressions on the underside of boulders. The shells of both western species are banded beneath and have brown markings dorsally, while the eastern ones are bandless and unpigmented.

These impressions, based on very limited evidence, are confirmed by the records in table 2, taken from Nobre's monograph. The distinctions are reinforced by the distributions of some of the rarer species. Thus, most of the slugs including *Testacella,* and species in the genera *Vitrina* and *Craspedopoma* are restricted to the more humid northern regions, where they replace the abundant «*Helicella*-like» species of the south.

A few slugs were collected that are not included in table 1. These were kindly identified for us by Mr. A. E. Ellis, and include *Limax flavus* from a house in Funchal and young individuals from a roadside near Funchal that are probably *Limax maximus.* To the north of the island on the Encumeada — S. Vicente road we obtained *Arion intermedius.* This species is not recorded by Nobre. According to Quick (1960) it is present in the Azores, as well as Portugal, but he does not mention Madeira. At Ribeiro Frio we found young specimens of an *Arion* species and *Agriolimax caruanae.* Neither this species nor *A. laevis* are recorded by Nobre, the only species in the genus that he gives being *A. agrestis. A. caruanae* has, however, been found in the Azores and the Canary Islands. Among a number of slugs sent to us from Madeira by G. E. Maul were *Milax gagates* (18 specimens) and *Arion lusitanicus* (4 specimens). The former species has been recorded previously from Madeira and the Azores, but *A. lusitanicus* appears to be a new record for the island. Both the species of *Testacella* recorded in table 1 were collected as dead shells only.

GARAJAU TRANSECT

The altitudinal transect at Garajau indicates that there is some ecological limitation of the species in this area. The greatest overall density was found at the southern end (roughly quadrats 1 to 23). The numbers then decline as far as quadrat 49, at the edge of the woodland, where the molluscs die out. The upper half of the area includes houses and cultivated fields while the lower part is not at the moment so disturbed. Much the most common species is *A. nitidiuscula,* comprising 46 per cent of the total, followed in order of abundance by *A. arcta,* *D. polymorpha, L. undata* and *J. bifrons,* which together make up a further 41 per cent of the total. *A. nitidiuscula* is most dense in the southern segment with 182 individuals found up to and including quadrat 23, and 127 above it. The same distribution is seen in *A. arcta,* with 65 and 48 individuals respectively in the two halves of the transect. The reverse order is found in *D. polymorpha,* represented by 20 individuals in the lower half and 60 in the upper half. The difference in distribution of *arcta* and *nitidiuscula* is measured by a χ^2 value of 0.02 (P = 0.89). When these two species are grouped, comparison with *D. polymorpha* provides $\chi^2_{(1)} = 29.0$, which is highly significant. *D. polymorpha* is therefore more closely associated with, and perhaps more tolerant of, the human habitation and cultivation in the area, than are the other two species.

L. undata appears to be generally distributed with no peaks of density, while *J. bifrons* is most common in the first nine quadrats, lying in the bare rock and sparse grass of the southern end. Among the uncommon species, *C. compactus, C. leptostictus* and *D. tabellata* are entirely confined to the lower half. *O. cellaria* only occured beneath fig trees in the cultivated area on the higher ground to the north.

If the limited survey carried out truly reflects the pattern in the area, then there may be quite marked localisation of species in particular vegetation types or other elements of the habitat along the southern coastal strip. The most obvious associated factor is the degree of human cultivation and land use: where the land is undisturbed there is a greater diversity and higher density of molluscs than where it is in use. The exception to this generalization is *D. polymorpha,* which is most common in the inhabited area. Presence or absence of *Opuntia* on the cultivated part has had no discernable effect.

PIEDADE TRANSECT

The transect consisted of a string of quadrats running from fairly level ground at the base of the hill (quadrats 1 to 6), up the steep hillside (quadrats 7 to 15) to level ground at the top (quadrats 16 to 19). The most notable feature is the dependence of many molluscs on large stones beneath which they congregate, at least in the summer season. The stones are present on the level areas. Of the common species *T. pisana* and *H. paupercula* are almost entirely confined to them. *D. polymorpha, A. nitidiuscula* and *C. compactus,* on the other hand, are more widespread, being present in some numbers also among the short grass of the steep intermediate area. *Cochlicella ventricosa* is entirely limited to the bottom of the transect.

SUMMARY AND CONCLUSIONS

Three regions are recognisable on Madeira: 1) a low dry and sunny area on the eastern peninsula with its own distinct fauna that has affinities with the Desertas, 2) a similar but less extreme region along the south coast, within which there are clines of abundance from east to west in several species, and 3) the high temperate and cloudy region to the north. Since rock and soils are very similar in composition throughout the island, the most important features determining these faunal regions are probably climate and vegetation. The isolated position of the islands in the Atlantic is responsible for the high frequency of endemic species. The sea appears to form a very effective barrier to molluscs, so that there are numerous instances of evolutionary divergence between similar species on different islands of the archipelago. Coupled with these factors, the ecological diversity of Madeira has promoted the development of the three distinctive faunas occupying very restricted territories. The Garajau and Piedade transects provide at least an indication of niche specialization between species within small areas. It will be interesting to know whether these ecotopes can be confirmed in greater detail and the niches defined more exactly after more extensive surveys. The rate at which the south coast is being transformed into a tourist centre suggests that little time is left to study the varied endemic fauna of the area in a relatively undisturbed state. The preferred habitats of the snails and of the tourists closely coincide.

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