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Land snails on Porto Santo: adaptive and non-adaptive radiation

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CONTENTS

SUMMARY

A survey has been made of the land snail fauna of Porto Santo, Madeiran archipelago. Porto Santo is an isolated island about 12 km long by 5 km wide. The fauna is exceptionally species-rich and characterisied by radiations of species in several families, especially the Helicidae. Sixty-five samples from the mainland and five offshore islets yielded 56 species, 84 % of them endemic, with a mean of 11.5 species per site, and marked regional differentiation in faunal composition. A given site produces on average only approximately one fifth of the number of species possible, equivalent to a value for Whittaker's index of diversity of 4.5.

Patterns of localization occur on the peaks to the east and west of the island, with numerous cases of replacement by congeneric and morphologically similar species. Local areas have assemblages of species differing in shell size and shape, which probably exploit different niches, the pattern in one area paralleling that in others. The low-lying sandy areas which separate these areas are now unfavourable to many endemic species; those which do occur in them tend to have island-wide distributions. Morphological variation in such species appears to have ecological rather than geographical correlates. We conclude that adaptive responses have occurred, but that much of the species richness can be interpreted as non-adaptive, that is, due to allopatric divergence in isolation by species which retain similar niches. Even on so small a land mass the topography is such that for many land molluscs it represents a cluster of refuges intermittantly connected through impermanent and often unfavourable sandy environments, on each of which evolution proceeds independently. Differences in distribution patterns between families probably arise because they evolved at different times in the island's history. These results are compared with those from snail faunas in other parts of the world, some of which are similar to them.

1. INTRODUCTION

The land snail fauna of the Madeiran islands is related to the European fauna and represents an endemic evolutionary radiation occurring before and during the Pleistocene. Up to 20 distinct colonizations could be involved (Cameron & Cook 1992). Compared with continental faunas the archipelago is rich in species but poor in families and genera. Some 250 species have been recognized, 70 % of which are endemic and some now extinct (Waldén 1983). Evolution is in part the result of species proliferation within different islands of the group, whereas in other cases it has probably followed transport between them (Waldén 1984; Cameron & Cook 1989; Cook *et al*. 1990). The balance of genera (and the number of species in each) differs between island groups.

Porto Santo is the oldest and, per unit area, the most species-rich island of the group, having more species of the numerically dominant Helicidae than Madeira, which is about 18-fold larger (Cameron & Cook 1992). The difference is the more striking, given the lower altitude and much more limited range of habitats available on the smaller island. Porto Santo has long been known for the extreme localization of some of its species (e.g. Wollaston 1878; Cockerell 1922). It is of interest to know whether distribution patterns reflect clear ecological differences (adaptive radiation) or represent geographical differentiation in essentially similar ecological conditions (defined by Gittenberger (1991) as non-adaptive radiation). Cases of the latter, especially when accompanied by evidence of environmental discontinuities, can give important clues to the processes of speciation (Cook *et al.* 1990; Cameron 1992).

As part of our study of the evolution of the snail fauna of the Madeiran islands, a visit was made to Porto Santo in August/September 1993 to examine these problems and to collect material for genetic analysis. Fossil samples were also collected by G. A. Goodfriend for dating and to relate past distributions to current ones. These will also be compared with the fossil sequence on Madeira (Cook *et al.* 1993; Goodfriend *et al.* 1994, 1995).

2. THE ISLAND AND ITS HABITATS

Porto Santo is a small island, about 12 km long and 5 km broad (figure 1), with a number of offshore islets. Unlike Madeira, from which it is separated by a deep marine trench, it is surrounded by a platform of shallow water; clearly it has been much larger du sea level depressions in the Pleistocene, and at s time would have been united with the offshore islet consists of two areas of high ground separated b central sandy plain on which a large air strip and main town are now situated. In the west, the isol Pico da Ana Ferreira rises to 283 m. Separated fro by a valley, a low ridge of hills to northwest (of wl the highest point, the Espigão, is 270 m) bounds west side of the island. The islet of Ferro is situa close offshore to west, and south of it the islet of Ba In the east the highest point on Porto Santo is the I do Facho, rising as a cone to 517 m. To its west is Pico do Castello (437 m) and to the northeast I Juliana (440 m). Further northeast is Pico Bra (450 m), currently being eroded by wave action o north side into vertiginous sea cliffs, from which can look down to the islets of Cenouras and F Proceeding south along the east coast is Pico Concelho (324 m), and continuing to the south co the Pico do Macarico (285 m) and Pico de B (206 m) face the islet of Cima. These features shown in figure 1.

No native forest remains on the island; there recent plantations on the peaks of Ana Ferre Castello, Facho and Branco. On the hills and r

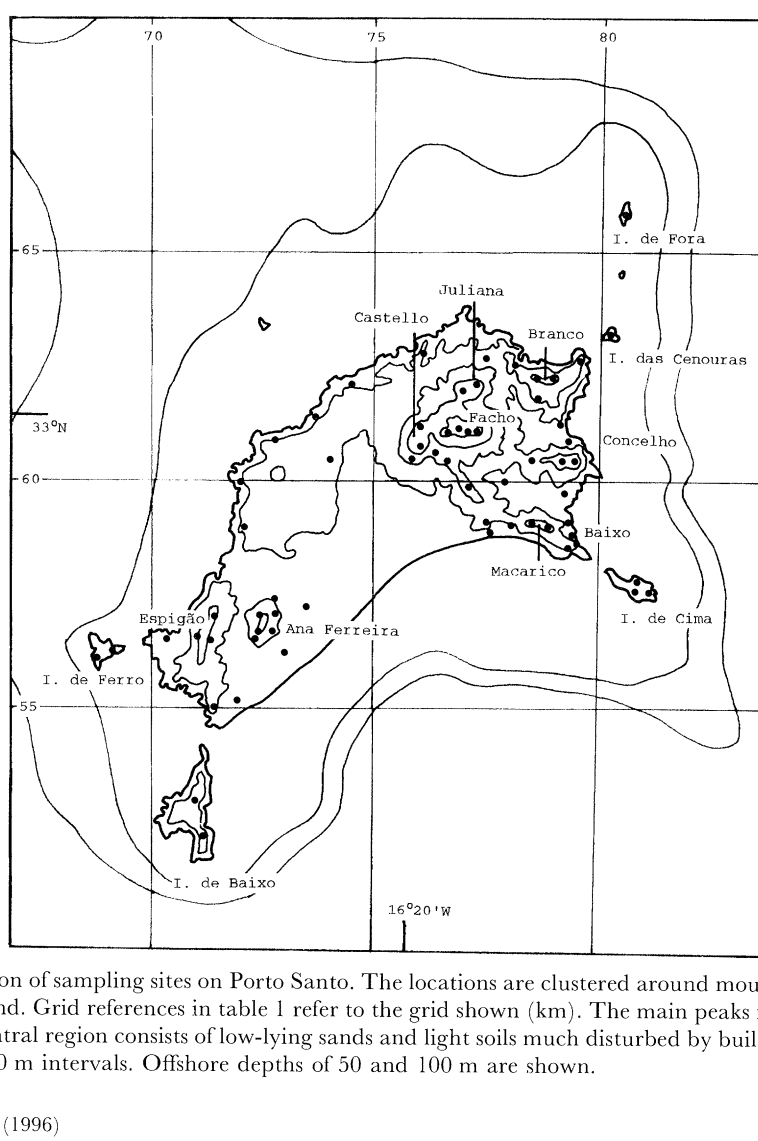

Figure 1. Distribution of sampling sites on Porto Santo. The locations are clustered around mountains situated at the two ends of the island. Grid references in table 1 refer to the grid shown (km). The main peaks referred to in the text are named. The central region consists of low-lying sands and light soils much disturbed by building and agriculture. Contours are at 100 m intervals. Offshore depths of 50 and 100 m are shown.

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some coastal cliffs, the predominant habitat is one of open, rocky ground, often with crags or scree. Vegetation is usually sparse and heavily grazed, with occasional stands of native shrubs. In lower and flatter areas the volcanic substrate is overlain by thick sandy deposits. Generally these areas have been subject to greater physical disturbance, with mobile sand often present. Vegetation is either very sparse or forms a continuous grazed turf with few exposed rocks.

Many of the gentler slopes are terraced, and were used for cultivation in the past. Some slopes are made up of massive deposits of hill-wash, and sand has sometimes blown up 150 m or more above sea level. The tops of the three larger islets (Ilhéu de Ferro, Ilhéu de Baixo and Ilhéu de Cima) are relatively flat, with accumulations of sand which has solidified into calcrenite. Vegetation is extremely sparse, as also on the Ilhéu das Cenouras and Ilhéu de Fora.

Annual rainfall is low (ca. 400 mm at sea level), falling mostly in winter. The highest hills are frequently mist-covered, and undoubtedly have more rainfall and lower evaporation.

3. MATERIALS AND METHODS

Samples of molluscs were collected at 65 localities, which include the mountain ranges to west and east of the island, the plain between and the five offshore islets named above. At each site a search was made by two collectors for roughly half an hour, particular attention being paid to places which are likely to be refuges for snails, such as the undersurface of boulders, cracks in rocks and the base of shrubs and grasses. Notes on the habitat type and ecology were made. Soil and litter were also collected for future sieving. The samples were brought back to the laboratory for identification, and some material stored at -80 °C for genetic study. Vertical slab polyacrylamide electrophoresis has been used to characterize genetic variation in some of the endemic helicids.

The samples have been numbered consecutively from west to east (table 1). Samples 1 and 2 are from the I. de Ferro, 3 and 4 from the I. de Baixo, both at the west end of the mainland. The rest come from the mainland except for the last five. Samples 61–63 are from I. de Cima, 64 is from the I. das Cenouras and the final sample comes from the most isolated rocky islet, the I. de Fora. Table 1 also gives a grid reference for the site (which may be related to figure 1), the log book number of the sample, scores of a number of environmental variables and the number of endemic and non-endemic species found.

In the environmental variable section of table 1, six features are distinguished. For each of them an initial letter represents a more disadvantageous state than a dash, so that the number of initial letters (from 0 to 6) is a rough score of the disadvantageousness of a site. For example, sample 6 is judged to be satisfactory as a habitat for snails, having no negative features. On the other hand, near it sample 8 scores five negative features, being sandy, having neither rock for refuges nor native vegetation, and being terraced and turf-covered. In this case, the differences are reflected in the number of species present and in the ratio of endemics to non-endemics. Identifications were made by R.A.D.C. with reference, where problems arose, to the collections at the Natural History Museum, London, and the National Museum of Wales. The species present at each site are shown in Appendix 1. Although an indication of abundance is available from the number of shells of each species collected, the value of this is reduced by the high incidence of dead individuals in some species, but not others, at some sites, and only presence/absence is indicated.

Most of the species listed were described in the nineteenth century, and are detailed in Wollaston (1878). Although these descriptions are based entirely on shell morphology, we are confident that almost without exception we are dealing with genuine biological species. Wollaston's species, both here and in Madeira, have stood up to subsequent re-examination remarkably well (Waldén 1983). He had a tendency to lump, rather than to split. Although we do not have detailed morphological information on many species, we have observed many cases of sympatry or parapatry in which two similar species are clearly distinct, with no intermediates and no cases of apparent hybridization or clinal change between typical members of different species.

4. RESULTS

The survey produced a list of 56 species, of which 47 are endemic to the archipelago (Appendix 1). Of these, 51 species (42 endemic) were found on Porto Santo itself. For the islets, the equivalent figures are, I. de Ferro: 15 (13), I. de Baixo: 15 (13), I. de Cima 15 (13), I. das Cenouras: 9 (7) and I. de Fora: 9 (8). The endemic species belong to 5 families, of which the Helicidae is by far the best represented (32 species).

The mean number of species per site is 11.5 ± 0.39, with a range from 5–20. Inspection of the data suggests that there is both ecological and geographical differentiation in the site diversities and in the distribution of individual species. Mainly western and eastern groups, comprising 30 of 56 species, have been separated in table 2 from those with more general distributions.

(*a*) *Site diversities*

Examination of the association of species richness with position and the ecologically disadvantageous factors listed in table 1 demonstrates some significant effects (table 3). At the western end of the island (samples 5–25 inclusive) the mean number of endemic species in predominantly sandy sites is 5.7, compared with 10.3 for volcanic sites. For the eastern end (samples 26 to 60) the equivalent figures are 7.7 and 12.3. The presence of sand clearly has a depressing effect on endemic species, although among non-endemics there are more species in sandy than volcanic sites (means of 2.2 compared with 1.0).

Disadvantageous factors, usually associated with disturbance, also depress the diversity of endemic

Table 1. *Samples of snails collected on Porto Santo and the adjoining islets, showing location, details of habitat type and number of species for each sample*

(First column: samples numbered consecutively arranged roughly from west to east. Second column: grid references of samples, taken from the 1:50000 map of Porto Santo published by the Instituto Geográphico e Cadastral, Lisbon, 1970. Third column: field book number indicating date and sample number for that date, the six columns therein (labelled 1–6) provide information on disadvantageous features of a site. The letters have the following meanings: S – presence of sand; N – no boulders, screes or cliffs (or C – sea-cliff only with few refuges); A – absence of native shrubs and Euphorbias; T – terraced land or recently cultivated if flat; D – disturbance by quarrying, forestry, rubbish etc; M – meadow with predominant turf cover. The two final columns are TE – number of endemics, TN – number of non-endemics in sample.)

number	grid ref.	field no.	1	2	3	4	5	6	TE	TN
1	691561	30.8.1	S	—	—	—	—	—	11	2
2	688559	30.8.2	S	—	—	—	—	—	12	1
3	711521	28.8.1	S	—	—	—	—	—	13	1
4	709530	28.8.2	S	N	A	—	—	—	9	2
5	705565	27.8.1	S	—	—	—	—	—	10	2
6	714550	18.8.1	—	—	—	—	—	—	12	2
7	711559	18.8.2	—	—	A	T	—	M	9	2
8	718550	3.9.6	S	N	A	T	—	M	3	3
9	711565	18.8.4	—	—	—	T	D	—	10	1
10	714564	18.8.3	—	N	A	—	—	M	9	0
11	715568	18.8.5	—	N	—	—	—	M	7	0
12	725564	16.8.1	—	—	—	—	—	—	13	1
13	725566	16.8.2	—	—	—	—	—	—	13	0
14	726567	24.8.3	—	—	—	—	—	—	10	0
15	725569	16.8.3	—	—	—	—	—	M	10	0
16	727569	16.8.4	—	—	—	—	—	M	10	0
17	727572	24.8.2	—	—	—	T	—	M	10	1
18	730562	24.8.4	S	N	A	T	—	M	4	4
19	725573	24.8.1	S	N	A	T	—	M	3	2
20	720590	19.8.1	S	C	—	—	—	—	7	2
21	722598	19.8.2	S	C	—	—	—	—	7	1
22	728608	19.8.3	S	C	—	T	—	—	8	1
23	738612	29.8.1	S	C	—	T	D	—	6	4
24	740603	3.9.5	S	N	—	T	D	M	4	3
25	744619	3.9.4	S	N	—	—	D	—	5	2
26	760626	3.9.1	—	—	—	—	—	—	7	1
27	758603	23.8.3	—	—	—	T	—	—	14	3
28	760605	23.8.2	—	—	—	—	—	—	12	0
29	760610	23.8.1	—	—	—	T	D	—	9	1
30	761605	21.8.2	—	—	A	T	D	M	10	4
31	764603	21.8.1	—	—	—	—	—	—	13	1
32	771597	21.8.3	—	—	—	—	—	—	14	0
33	775591	21.8.4	—	—	—	—	D	—	11	1
34	775589	2.9.1	—	—	A	T	—	M	8	2
35	779591	21.8.5	—	—	A	T	—	M	9	2
36	779600	3.9.3	—	N	A	T	—	M	16	1
37	768610	20.8.4	—	—	—	—	—	—	15	2
38	769610	20.8.3	—	—	—	—	—	—	11	3
39	770610	20.8.2	—	—	—	—	—	—	11	1
40	772609	20.8.1	—	—	—	—	—	—	14	3
41	770619	29.8.2	—	—	—	—	—	—	11	0
42	772618	29.8.3	—	—	—	—	—	—	15	0
43	775625	3.9.2	—	—	—	—	—	—	14	0
44	780624	26.8.4	—	—	A	—	—	—	10	0
45	783616	31.8.4	—	—	A	—	—	—	16	1
46	784621	31.8.1	—	N	A	T	—	—	10	1
47	788619	31.8.2	—	—	—	—	—	—	13	0
48	795624	31.8.3	—	—	—	—	—	—	16	0
49	791611	2.9.6	—	—	—	T	—	—	7	1
50	794608	2.9.5	—	—	A	—	—	—	15	1
51	793604	26.8.3	—	—	—	—	—	—	15	1
52	790603	26.8.2	—	—	—	—	—	—	19	1
53	783604	26.8.1	—	—	A	—	—	—	11	1
54	791597	2.9.2	S	—	A	T	—	—	7	2
55	793592	2.9.3	S	—	—	—	—	—	8	3
56	795587	2.9.4	S	N	A	—	D	—	6	1
57	794586	17.8.1	S	—	—	—	—	—	10	1

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Table 1 (*cont.*)

number	grid ref.	field no.	1	2	3	4	5	6	TE	TN
58	792586	22.8.3	S	—	—	—	—	—	15	1
59	789589	22.8.2	—	—	—	—	—	—	13	1
60	785590	22.8.1	—	—	—	—	—	—	13	1
61	804578	25.8.2	S	N	—	—	—	—	6	1
62	806577	25.8.3	—	—	—	—	—	—	12	1
63	809577	25.8.1	—	—	—	—	—	—	12	2
64	801630	1.9.2	—	—	—	—	—	—	7	2
65	806656	1.9.1	—	—	—	—	—	—	8	1

species, but have the opposite effect on non-endemics. With respect to non-endemics the effect is due to the distribution of the sand-loving species *Theba pisana* and *Cochlicella acuta*; other rarer species such as *Vitrea contracta*, *Testacella maugei* and *Balea perversa* have restricted montane distributions, probably indicative of native status. The predominance of sand is the most important single factor affecting species diversity: because it occurs at low altitudes, high sites tend to be richer than low ones.

Amongst endemic species, the larger and higher area of hills in the east is consistently richer than that in the west. Amongst offshore islets, the three larger ones have richer faunas than might be expected from their predominantly sandy soils, but they also have more loose rock and less disturbance of other types than similar sites on Porto Santo.

Even when the most disturbed sites are excluded, the mean number of endemic species per site is considerably less than the total number recorded, indicating a considerable degree of geographical differentiation in an apparently ecologically uniform environment. A simple estimate of this is given by Whittaker's index of diversity $I = S/\alpha$, where S = total species recorded, and α = mean number per site (Cody 1986; Cameron 1992, 1995). Overall, this has a value of 4.5. Removing the 9 most disturbed sites (sandy, and with at least three disadvantageous factors) reduces it slightly to 4.2. Put another way, any one site is likely to yield only a quarter of the fauna known to occur in similar habitats within the island and islets.

(*b*) *Patterns of species distribution*

Such heterogeneity between sites could be brought about in a variety of ways, including inadequate sampling efficiency or a shifting pattern of local extinctions and colonizations. In fact, there is good evidence for the existence of geographical patterns which would not arise from either of these causes.

The tendency to localized distributions can be seen when the data are clustered. There are two main ways of making such groupings, depending on whether or not species are included which are absent in the pair of sites being compared but present in some others of the series. If these paired absences are not included, a similarity measurement such as the Jaccard Index (which leaves them out) is likely to measure both coincidence of species and difference in number of species present i.e. both taxonomic and ecological similarity. There may be good reasons for doing this, so long as we can be reasonably sure that the sample includes all the species present. If some are missing by chance, the difference between pairs of sites is accidentally inflated. This is not true of measures based on the determinant of the presence/absence contingency table, which are distributed about zero if the taxonomic similarity is what would be expected from chance sampling of all the species available. Such a measure is appropriate here, and the index used is the determinant divided by a form of its standard error; the rationale is given by Cook *et al.* (1990). The pairwise similarities obtained have been clustered using the UPGMA method on SPSS to provide figure 2.

Given that the average number of species per site is no more than 11.5, the tendency to group geographically is striking. Starting at the top of the figure there is a group of 15 sites (as displayed, they run from sample 31 to sample 45), which come from the eastern mountains. The seven sites below them (33–35) are from the south of this area, centred on Pico do Macarico. Then there is a sequence mostly from the west of the island (samples 15–53). These come from the Pico de Ana Ferreira (the first six), from the Espigão hills across the valley to the northwest (the next three) and two sites from the east are then appended. Five sites (37–29 on the diagram) form a well defined group from the Pico do Facho. From here the groupings become less well defined and the sites include the more disturbed and sandy low-lying areas. A grouping starting at sample 4 and ending at sample 49 contains the islands of Ferro, Baixo and Cima plus a sandy site from the east coast.

To provide an averaged pattern based in part on frequency of occurrence, the samples were grouped serially into 13 sets of 5 and the frequency of each species within each set was scored from 0 to 5. Because the samples are arranged geographically this arrangement more or less distinguishes different regions of the islands. From west to east the categories are: (i) western islands; (ii) the Espigão hills; (iii) west Ana Ferreira; (iv) east Ana Ferreira; (v) the Fonte da Areia region of the north coast; (vi) Pico do Castello; (vii) high land around the Rocha de Nossa Senhora south of Pico do Castello; (viii) Pico do Facho; (ix) Pico Juliana; (x) Pico Branco; (xi) Pico do Concelho; (xii) Pico do Macarico; and (xiii) the eastern islands. The similarities between groups were then estimated using

Table 2. *Species restricted to west or east of Porto Santo and those distributed widely*

(Endemics and non-endemics are separated. Species endemic to the Madeiras but found on other islands are indicated by ~. Names in parentheses are of species represented only once in the samples.)

west	throughout	east
endemics		
Pupillidae		
Leiostyla corneocostata		
L. relevata		
L. ferraria		
	L. monticola	
	L. calathiscus	
Vitrinidae		
	Eucobresia media	
Ferrusaciidae		
	Cecilioides eulima	
	Amphorella melampoides	
		A. triticea
	A. oryza	
		A. tuberculata
A. cimensis		
	A. gracilis	
	Cylichnidia ovuliformis	
Clausiliidae		
	Boettgeria lowei	
Helicidae		
	~ *Heterostoma paupercula*	
	Geomitra coronata	
	Spirorbula obtecta	
	S. depauperata	
	~ *Caseolus compactus*	
		C. consors
	C. commixtus	
C. abjectus		
		(*C. subcalliferus*)
		(*C. calculus*)
	C. hartungi	
	C. punctulatus	
		Actinella effugiens
		Lemniscia michaudi
		Discula bicarinata
		D. echinulata
D. leacockiana		
		D. oxytropis
		D. turricula
		D. cheiranticola
	D. calcigena	
		D. pulvinata
D. attrita		
		D. albersi
		D. rotula
(*D. tectiformis*)		
	Pseudocampylaea portosanctana	
		~ *Leptaxis erubescens*
		L. wollastoni
	L. nivosa	
		Lampadia webbiana
Helix subplicata		
non-endemics		
Zonitidae		
		Vitrea contracta
Ferussaciidae		
	Oxychilus alliarius	
	(*Cecilioides acicula*)	
Subulinidae		
	Rumina decollata	
Clausiliidae		
		Balea perversa
Testacellida		
		Testacella maugei
Helicidae		
	Cochlicella acuta	
	Caracollina lenticula	
	Theba pisana	

Table 3. *Mean number of species per site for endemic and non-endemic species on Porto Santo mainland in relation to geography and habitat condition*

(No geographical differentiation is seen in non-endemics. s.e. = standard error, n = sample size. Disadvantageous indicators are those scored in table 1.)

	substrate		number of disadvantage indicators		
	sandy	volcanic	0	1–2	3 or more
endemic species					
west mean	5.7	10.3	11.3	8.6	4.2
s.e.	0.73	0.54	0.61	0.44	0.48
n	10	11	6	9	6
east mean	7.7	12.3	13.4	10.7	8.7
s.e.	0.85	0.52	0.60	0.84	0.87
n	4	31	18	12	5
non-endemic species					
mean	2.2	1.0	0.8	1.3	2.5
s.e.	0.28	0.15	0.19	0.19	0.36
n	14	42	24	21	11

Nei's Distance index and clustered by the UPGMA method. The result is shown in figure 3. Groups covering the Pico de Ana Ferreira (samples 11–20) are the most distinct. At the other end of the island, the mountainous eastern region of Pico Juliana and Pico Branco forms a cluster, slightly different from the southeastern area of Pico do Concelho and Pico do Macarico (samples 51–60). The highest point of the island, Pico do Facho (samples 36–40) is somewhat distinct, whereas the islets to the west and east and the central and western lower lands form another cluster.

The pattern is to some extent the result of distribution of non-endemics. Thus the Pico do Facho includes in its complement (and has at least since the 19th century) both *Balea perversa* and *Testacella maugei*, European species, and *Leptaxis erubescens*, a species present on Madeira and the Desertas but with a very restricted distribution on Porto Santo. The low lying areas of the mainland and the islets are home to the anthropophilic non-endemics *Rumina decollata*, *Cochlicella acuta* and *Theba pisana*.

The clear distinctions between areas, however, are a consequence of the very restricted distributions of some endemics, which appear to have originated in, and not to have dispersed from, small parts of the island. Inspection of individual species distributions shows that many patterns, which are not always coincident, contribute to the whole. Some suites of closely related species, very similar in size and shape, show near perfect patterns of allopatric or parapatric replacement.

We collected 12 species in the genus *Discula*. Five belong to the subgenus *Discula*, five to *Hystricella*, one to *Callina* and one (*D. tectiformis*, which was rare) to *Mandahlia*. Species in the first of these are *D. cheiranticola*, *D. calcigena*, *D. pulvinata*, *D. attrita* and *D. albersi*, measuring 8–10 mm in diameter, keeled and relatively disc-shaped and with lightly ridged or finely tuberculate sculpture. The subgenus *Hystricella* consists of *D. bicarinata*, *D. echinulata*, *D. leacockiana*, *D. oxytropis* and *D. turricula*. These are smaller, 5–6 mm in

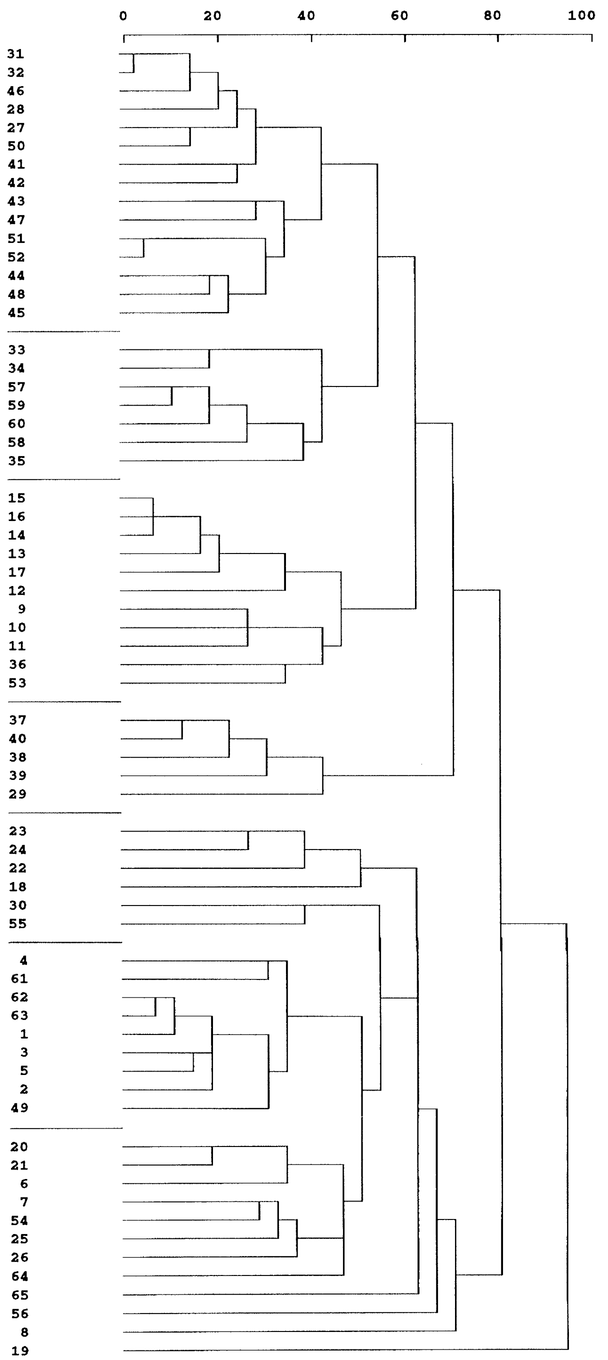

Figure 2. Cluster diagram for faunal similarity of the 65 samples, based on the determinant of the presence/absence contingency table. The scale is proportion of the least recorded similarity.

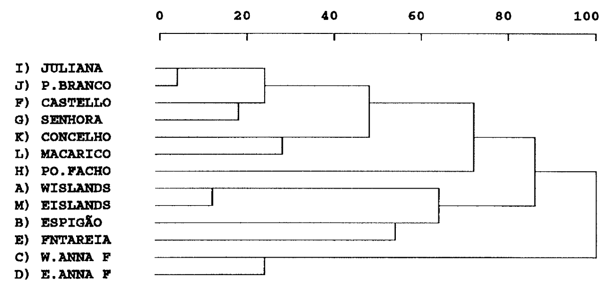

Figure 3. Cluster diagram showing the faunal relations based on frequency of presence within groups of five sites, based on Nei's distance statistic.

diameter, higher spired and tending to have strongly tuberculate sculpture. There is also a tendency to have two keels or ridges round the shell, well developed in *D. bicarinata* and *D. turricula*. The aperture is downturned and reflected outward to allow close adherence to rock surfaces, whereas the type subgenus does not have this characteristic. The two groups are adapted to different niches.

Within subgenera, the species tend to be allopatric but pairs from different subgenera overlap. *D. attrita* (*Discula*) and *D. leacockiana* (*Hystricella*), are almost restricted to the Pico de Ana Ferreira. *D. echinulata* and *D. bicarinata* (both *Hystricella*) have allopatric distributions in the high land to the east, the first on Pico Branco alone and the second more widespread. In some of the lower-lying parts, *D. bicarinata* coexists with *D. calcigena* (*Discula*), as does *D. turricula* on the I. de Cima. *D. calcigena* is widespread in lower-lying areas of the island and on the I. de Ferro, I. de Baixo and I. de Fora as well as I. de Cima. Like *D. polymorpha* on Madeira and the Desertas but unlike most Porto Santan endemics, it appears to tolerate somewhat sandy conditions. In a restricted sandy part of the north side of Porto Santo, however, it is replaced by *D.* (*Discula*) *pulvinata*, which is similar in appearance but considerably higher-spired. There are thus some species with restricted ranges which are probably replacement pairs, others which coexist, and a range from very localized to broad distribution. These patterns are illustrated in table 4 and figure 4.

Sometimes, as with the smaller *Caseolus* species (figure 5), the pattern is less clear because two or more species coexist, but analysis of coincidence indicates that there are fewer sites with no or one species or three or more than expected ($\chi^2 = 27.6$, 2 d.f., $P < 0.001$), and most have restricted and coherent ranges. In two other cases, overlap is more complete; *Amphorella* species appear to be distributed at random with respect to each other ($\chi^2 = 3.7$, 3 d.f., n.s.) but show considerable differences in size. The two *Spirorbula* species also overlap considerably. They differ in appearance and show some ecological segregation, *S. obtecta* being the only endemic species really to flourish on disturbed sandy substrates.

There are also a number of species which have restricted and coherent distributions, but lack equivalents elsewhere (e.g. *Lampadia webbiana*). Such species are more frequent in the east, and contribute to the higher diversity levels there than in the west.

A further group of species are either widely distributed (e.g. *Leptaxis nivosa*, *Boettgeria lowei*), or have disjunct distributions at both ends of the island (e.g. *Pseudocampylaea portosanctana*). *L. nivosa* has a distinct colour form on I. de Ferro. Fossil material indicates that some of the disjunct distributions and those of some other rare and restricted species are relicts; they were once more widely distributed.

(*c*) *Variation in shell morphology within species*

Morphological variation was examined in two common endemic taxa, *Boettgeria lowei* and *Heterostoma* *paupercula*. Results are presented elsewhere (Cameron *et al.* 1995) but some details are worth noting here in connection with the taxonomic and ecological variation between sites.

The genus *Boettgeria* is represented on Porto Santo by the single species *B. lowei* (Groh & Hemmen 1984). It is found characteristically on rocks, where is was most frequently collected from resting sites in cracks in basaltic outcrops which were beginning to decompose. It is widespread and not restricted to particular parts of the island or vegetation types. Shell height (mm) and the number of ribs present on the body whorl were measured in 33 samples from widely dispersed sites. The altitude of each sample locality was scored. There is no clear differentiation between individuals from different parts of the island but variation appears to be associated with altitude, higher sites producing smaller individuals with higher rib counts, although these two variables are not strongly associated.

Heterostoma paupercula, one of the most common endemics on Porto Santo, the Desertas and parts of Madeira, is present in 62 of the 65 samples. This species varies in shell morphology and genitalia, to such an extent that it has been interpreted as being up to three species (see Waldén 1983). We concluded that the pattern indicates the existence of a single variable species (Lace 1992; Cook & Lace 1993), and to confirm or modify this view, shells were scored for size, pigmentation and presence or absence of a peristomal tooth (Cameron *et al.* 1995). No clear geographical pattern is seen: size, tooth frequency and frequency of pigmented shell sometimes change over short distances but appear to vary independently of each other. Animals from sandy localities are, however, more likely to be large and pale-shelled than those from rocky, mountain sites. In both examples there is therefore an indication of ecotypic variation.

(*d*) *Enzyme variation between species*

As a start to assessing the genetic affinities of the endemic helicids, eight enzyme systems have been studied using vertical slab polyacrylamide gel electrophoresis (Pharmacia GE2/4LS). Homogenates were crushed in 30% sucrose with mercaptoethanol for partial denaturization. Bromophenol blue was added as a standard. The enzymes examined were Aspartate Amino Transferase (AAT), Acid Phosphatase (ACP), Alkaline Phosphatase (AKP), Esterase (EST), α-Glycerophosphate Dehydrogenase (GDP), Malate Dehydrogenase (MDH), Malic Enzyme (MOD), and Phosphogluconate Dehydrogenase (PGD). All the protocols followed were from Pasteur *et al.* (1988). Samples consisting of digestive gland and columellar muscle were compared with foot muscle for band resolution. Foot muscle shows fewer bands and less intense banding, so that runs have been carried out either on whole animals, when the species is small, or digestive gland and columellar muscle for larger species. A sample consisted of ten individuals per gel.

Thirteen species in the family Helicidae were examined; they are *Heterostoma paupercula*, *Geomitra coronata*, *Caseolus commixtus*, *C. abjectus*, *C. calculus*, *C. punctulatus*, *Discula bicarinata*, *D. calcigena*, *D. rotula*, *D. polymorpha*, *Pseudocampylaea portosanctana*, *Leptaxis nivosa* and *L. undata*. Of these, *Discula polymorpha* and *Leptaxis undata* come from Madeira, the rest are from Porto Santo. *Boettgeria lowei* (Clausiliidae) was included in the comparison, as a species distant from the helicids.

Mobility of all the bands detected was recorded. It was often impossible to interpret the resulting patterns as genetic loci, so that similarity in electromorphs has of necessity been used for comparison between species. When band mobility is recorded to the nearest percentage, the helicids show as much differentiation between each other as they do from *Boettgeria*. At the other extreme, if the bands were to be grouped into two or three broad categories, all species would show a high degree of similarity. Grouping has therefore been optimized by providing the greatest separation of *Boettgeria* from the majority of the species. With the data here, this turns out to require a grouping of around 10%. The resulting patterns have been clustered as before, using Nei's index and the UPGMA

Table 4. *Distribution pattern in species of the genus* Discula

(Six locations have been distinguished, they are: 1 Western islands and lowlands; 2 Pico de Ana Ferreira; 3 the peaks of Juliana, Facho and Castello; 4 the peaks of Concelho, Macarico and Baixo; 5 Pico Branco; and 6 the I. de Cima. Within subgenera the species are ecological equivalents and tend to be allopatric, pairs for different subgenera coexist. *D. calcigena* has a broad and disjunct distribution at lower altitudes. *D. rotula* has a broad distribution in the east at higher altitudes.)

location	*1*	*2*	*3*	*4*	*5*	*6*
subgenus *Hystricella*						
36 *D. bicarinata*	—	—	■	■	—	—
37 *D. echinulata*	—	—	—	—	■	—
38 *D. leacockiana*	—	■	—	—	—	—
39 *D. oxytropis*	—	—	—	■	—	—
40 *D. turricula*	—	—	—	—	—	■
subgenus *Discula*						
41 *D. cheiranticola*	—	—	■	■	—	—
42 *D. calcigena*	■	—	—	■	—	■
44 *D. attrita*	—	■	—	—	—	—
45 *D. albersi*	—	—	—	■	—	—
subgenus *Callina*						
46 *D. rotula*	—	—	■	■	■	—

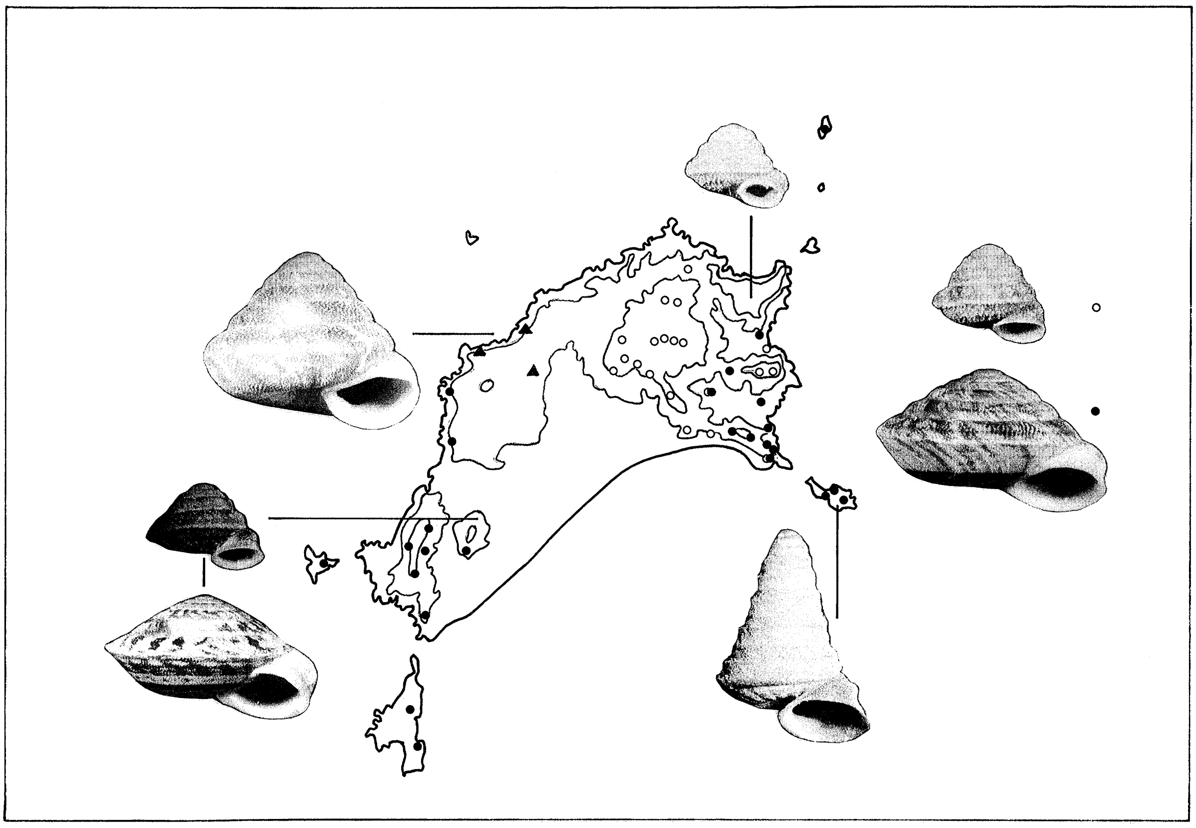

Figure 4. Distribution on Porto Santo of seven species of *Discula* belonging to the subgenera *Discula* and *Hystricella*. Clockwise from bottom left, *D.* (*Discula*) *attrita* and *D.* (*Hystricella*) *leacockiana*, both limited to Pico de Ana Ferreira; *D.* (*Discula*) *pulvinata* (triangles), limited to sandy north west; *D.* (*Hystricella*) *echinulata*, limited to Pico Branco; *D.* (*Hystricella*) *bicarinata* (open circles) and *D.* (*Discula*) *calcigena* (closed circles), both with more widespread distributions, the first on the eastern higher land and the second in a range of locations and habitats, including offshore islets; *D.* (*Hystricella*) *turricula*, limited to Ilhéu de Cima. *D. calcigena* on I. de Fora has been distinguished as subspecies *gomesiana* and on I. de Baixo as subspecies *papilio*. All species to the same scale; *D. calcigena* is 10.0 mm in breadth.

clustering procedure (figure 6). *Heterostoma paupercula* and the genus *Leptaxis* separate well from other helicids, and to a lesser extent the two species in the genera *Geomitra* and *Pseudocampylaea*, which associate with each other. Further systems will need to be examined to differentiate the other species, but this examination starts to indicate the degree of distinctness to be expected.

The study of *Heterostoma paupercula* by Lace (1992), based on allele frequencies at three polymorphic loci (LAP, GPI, GOT), indicated high levels of inbreeding, with $F_{IS} = 0.245$, and high differentiation between islands in the archipelago, measured by $F_{GT} = 0.267$ (Cook & Lace 1993). As Porto Santan species appear to have low mobility and small ranges, inbreeding could be a general phenomenon. In a sample of seven populations of *Leptaxis nivosa* the eight enzyme systems examined here have been resolved into 12 loci. Mean polymorphism is 0.180 ± 0.087, whereas mean heterozygosity is estimated as 0.044 ± 0.025. The mean number of alleles per locus was 1.56. Brown & Richardson (1988), reviewing the information then available for terrestrial molluscs, found mean heterozygosities of zero for selfers, 0.047 for facultative selfers and 0.089 for outcrossers. The level of variability in *L. nivosa* is low compared with some other molluscan studies, although characteristic of cross-fertilizing or partially selfing species (see also Nevo *et al.* 1988). Gene flow is likely to be very low in these animals, as indicated also by ecological studies, such as that of Schilthusen and Lombaerts (1994) for *Albinaria corrugata* in similar habitats in Crete, or Baur's (1988) study of *Chondrina clienta*.

5. DISCUSSION

Porto Santo is the oldest island of the Madeiran archipelago, dating back to at least 12 Ma BP. It has not suffered the repeated massive volcanic events which punctuated the history of Madeira (outlined in Cook *et al.* 1990), and presents an aspect of groups of volcanic cones topped with rocky outcrops, falling steeply in slopes covered by thin soil to a sandy plain. It is separated from Madeira, some 40 km away, by deep ocean floor. Extreme lows of sea level 18000 and 120000 years BP exposed a much larger land area, surviving now as a shallow coastal shelf (figure 1), joined the islets to the mainland and provided the source of the very extensive sand deposits which now occur. Porto Santo was not itself subject to repeated vulcanism, but volcanic activity on Madeira was so

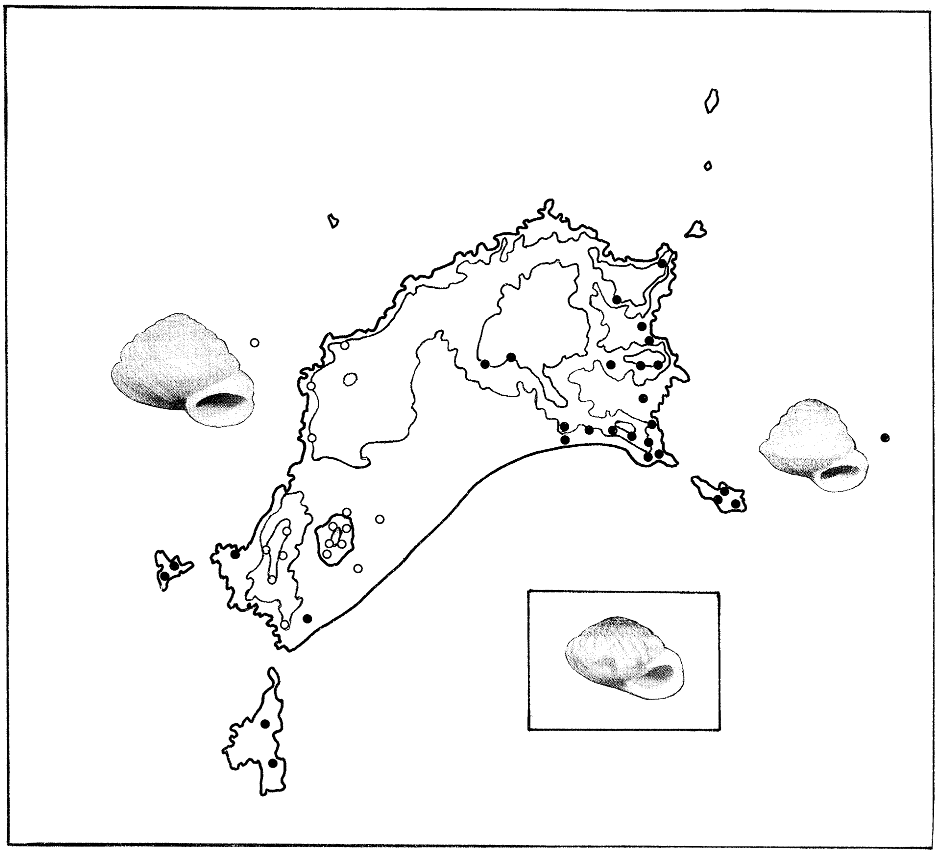

Figure 5. Distribution on Porto Santo of three species of *Caseolus*. *C. abjectus* (open circles) is a western species on Pico de Ana Ferreira and neighbouring high and low areas. *C. commixtus* (closed circles) is mostly eastern and on the islets. *C. compactus* (inset) is widespread and overlaps the other two. The distributions do not map on to those of Figure 4. Breadth of *C. compactus* is 5.3 mm.

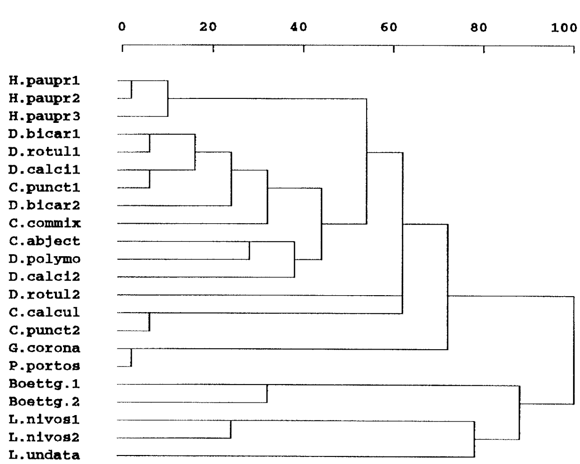

Figure 6. Species clustering in Helicidae, based on band mobility for 8 enzyme systems. Band grouping has been chosen so as to achieve good separation of the Clausiliid *Boettgeria lowei* from the majority of helicids. *Heterostoma* (**H. paupr**) and *Leptaxis* (**L.....**) separate from the rest of the Helicidae. In the helicids, *Geomitra coronata* (**G. corona**) and *Pseudocampylaea portosanctana* (**P. portos**) may be somewhat distinct from the rest in the genera *Discula* and *Caseolus*. *L. undata* and *Discula polymorpha* are Madeiran species, the rest were collected on Porto Santo.

massive that it could have caused serious damage to Porto Santo as a terrestrial environment, through tidal wave action and deposition of ash. Several phases of high sea level would have reduced the connection between the eastern and western parts of the island (sea level changes are summarized by Goodfriend *et al.* 1995). Intensive cultivation began with human settlement in 1420 (see Goodfriend *et al.* 1994). The indigenous flora, including *Dracaena* forest, was almost extinguished and cultivation, terracing and grazing of animals extended to the highest parts of the mountains. As part of an erosion control and climate amelioration programme, extensive tree planting has now begun; much of this consists of pines but a variety of others trees have been planted, including a few dragon trees.

Given the ecological changes wrought by colonization it may be wondered that so many endemic species have survived. We have shown that on Madeira several endemics declined and became extinct after human occupation, but others appear to have flourished and may have extended their range (Goodfriend *et al.* 1994). The comparative robustness of the molluscan fauna of the archipelago is assisted by the fact that the snails tend to be associated with the ground layer and the rocky outcrops, rather than with the higher standing parts of the indigenous vegetation (the fauna of the laurisilva on Madeira is an exception, but stretches of those woodlands are intact). The most abundant non-endemic on Porto Santo is *Theba pisana*, a species which thrives in Mediterranean climates and sandy conditions and aestivates exposed on shrubs and the dead flower heads of herbs etc. None of the living endemic helicids have this behaviour pattern, and they usually aestivate on the undersurface of loose rocks or in cracks in bedrock.

The low-lying parts of the island suffered a number of natural and human-induced cycles of instability, and have probably almost always provided poor habitats for endemic species. Where endemic species such as *Boettgeria lowei* and *Heterostoma paupercula* are capable of surviving in this environment, and are widespread, they do not show geographical variation in morphology, which correlates instead with environmental features. Overall however, conditions may never have been stable for long enough to allow this process to produce sand specialists among the endemic fauna. The introduced species which tolerate sandy conditions have exploited empty niches, a classical pattern by which species richness increases on islands.

The Whittaker's *I* value of 4.5 is considerably higher than that recorded for temperate forests in northern Europe and North America, where all species are Holocene immigrants, but lower than that for camaenid snails in northwest Australia. In the Australian case, cyclical fluctuation in rainfall regimes has led to contractions and expansions of suitable environmental 'islands' over 5–6 Ma. The result has been a massive radiation of allopatric species of Camaenidae, occupying similar niches in each island (Solem 1988; Cameron 1992, 1995). Smaller non-camaenids have higher levels of passive dispersal, have been less drastically restricted by arid periods and have larger geographical ranges. Gittenberger (1991) referred to patterns of the Camaenid type as non-adaptive radiations, in which microgeographically replacing forms do not differ in their key adaptations. He was discussing the clausiliid genus *Albinaria* on eastern Mediterranean islands. The pattern on Porto Santo parallels that found in some faunas of the eastern Mediterranean region (Mylonas 1984; Schilthuisen 1994; R. A. D. Cameron, M. Mylonas & K. Vardinoyannis, unpublished data), and the two have probably experienced a similar sequence of varied environmental fluctuations.

Intra-island speciation in snails is common on volcanic oceanic islands (Solem 1990); it may be frequently non-adaptive in part, and driven by volcanic disturbances and sharp topographical barriers. Porto Santo is atypical, having been volcanically inactive for at least 10 Ma, and having, in general, low and eroded relief. The very high level of diversity on such a small and barren island appears to be the result of a very particular combination of relief, substrates and environmental changes. Even Madeira, only 40 km away but with a more varied volcanic history, does not show the same degree of geographical differentiation independent of habitat.

The molluscan fauna of the Madeiran islands has been comparatively well known since the nineteenth century, when it was the subject of exceptionally careful taxonomic and distributional studies (for background, see Cook 1995). We now need to set up models which are testable and capable of rejection, to establish what the patterns tell us about species formation. Simply dividing the number of species in the Madeiras by the available time and the number of probable founder colonizations gives a speciation rate of one per 300000 years (Cook 1995), which is not especially fast. The families involved probably arrived at different times, however, and their radiations occurred under different sets of conditions. That could be the clue to why different families have their present-day distributions, which tend not to map on to each other.

The general model which emerges for Porto Santo is of a small land mass which, to the snails inhabiting it, is even smaller than it appears to us, being a cluster of inhabitable patches represented by the existing hills. The effectiveness of the sandy barriers between them has varied with time. The refuges themselves differ in size and height, and thus in the protection they afford against natural fluctuations in climate or sand-blow. This is probably why the hill-top refuges of the west are depauperate relative to the larger and more interconnected hills of the east.

In the east of the island, there are three faunal groupings, that of the highest hill, Pico do Facho, that of the other northerly hills, and that of the southeastern and lower Pico do Concelho and Pico do Macarico. Many species are common to all three, none are found in the first and last alone, but eight helicids are missing from Pico do Facho and present elsewhere whereas only one is present on all northern hills but not in the southeast. Comparable figures for all other families are 2 and 7, a significantly different distribution (Fisher's exact test, $P = 0.015$). The high hills of the north have a better present representation of non-helicids. Compared with them, helicids have done less well on the high and rather bleak summit of Pico do Facho and better on the lower hills of the southeast.

Allopatric speciation results from accidental geographic separation, followed by genetic divergence. Divergence could be the result of selection by the environment, if new territory is colonized, or consequent upon competition if a new set of competing species is encountered, or again it could simply be stochastic and non-adaptive. Speciation events such as those in small and large *Discula*, appear non-adaptive. They probably constitute the majority of cases, and are a result of the topography. Others, like those involving *Amphorella* or *Spirorbula*, resulted in ecological differentiation and subsequent coexistence. We can speculate that the latter events took place earlier than the former because greater changes have occurred. Differences in distributions between *Discus* and *Caseolus* in the Helicidae, and between helicids and non-helicids in the eastern mountains, also suggest radiations occurring at different periods. A two-pronged approach is required to substantiate these hypotheses. On the one hand, it is necessary to study the ecology of several sets of species, sympatric and allopatric, and measure their degree of overlap. On the other, the genetic similarities and dates of divergence of these sets must be established. Molecular studies are essential for this purpose.

Even on the evidence now available, however, the diversity of snails on Porto Santo appears to owe much to 'non-adaptive' radiation in Gittenberger's (1991) sense. It makes a similar substantial contribution to

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regional diversity in other snail faunas in areas with fluctuating environments and stable, but periodically isolated, refuges (Cameron 1992, R. A. D. Cameron, unpublished data). The scale of such radiations will vary both with the mobility of the organisms and with the distribution of refugia, and will be most evident in groups with narrow and demanding habitat requirements. Such radiations probably make an important contribution to regional diversity in many other groups of animals and plants.

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APPENDIX

Distribution of species between samples in survey of Porto Santo and offshore islets. Samples are numbered from 1 to 65. Location of samples is shown in figure 1 and further details are in table 1. Authorities for names are given by Waldén (1983)

species	1	2	3	4	5	6	7	8	9	10
1 *Leiostyla corneocostata*	—	—	—	—	—	■	—	—	—	—
2 *Leiostyla relevata*	—	—	■	—	—	—	—	—	—	—
3 *Leiostyla ferraria*	—	—	—	—	—	—	—	—	—	—
4 *Leiostyla monticola*	—	—	—	—	—	—	—	—	—	—
5 *Leiostyla calathiscus*	—	—	—	—	—	—	—	—	—	—
6 *Vitrea contracta*	—	—	—	—	—	—	—	—	—	—
7 *Eucobresia media*	—	—	—	—	—	—	—	—	■	—
8 *Oxychilus alliarius*[a]	—	—	—	—	—	—	—	—	—	—
9 *Cecilioides acicula*[a]	—	—	—	—	—	—	—	—	—	—
10 *Cecilioides eulima*	—	—	—	—	—	■	—	—	—	—
11 *Amphorella melampoides*	■	■	■	—	■	■	—	■	—	—
12 *Amphorella triticea*	—	—	—	—	—	—	—	—	—	—
13 *Amphorella oryza*	—	■	—	—	—	—	■	—	■	■
14 *Amphorella tuberculata*	—	—	—	—	—	—	—	—	—	—
15 *Amphorella cimensis*	—	—	—	—	—	■	—	—	—	—
16 *Amphorella gracilis*	—	—	—	—	—	—	—	—	■	■
17 *Cylichnidia ovuliformis*	—	—	—	—	—	—	—	—	—	—
18 *Rumina decollata*[a]	—	—	—	—	■	—	—	■	—	—
19 *Boettgeria lowei*	■	■	■	—	■	■	—	—	■	—
20 *Balea perversa*[a]	—	—	—	—	—	—	—	—	—	—
21 *Testacella maugei*	—	—	—	—	—	—	—	—	—	—
22 *Heterostoma paupercula*	■	■	■	■	■	■	■	■	■■	■
23 *Geomitra coronata*	—	—	—	—	—	—	—	—	—	—
24 *Spirorbula obtecta*	■	■	■	■	■	■	■	—	—	—
25 *Spirorbula depauperata*	■	■	—	—	—	—	■	—	—	—
26 *Caseolus compactus*	—	■	■	■	—	—	—	—	■	■
27 *Caseolus consors*	—	—	—	—	—	—	—	—	—	—
28 *Caseolus commixtus*	■	■	■	■	■	—	—	■	—	—
29 *Caseolus abjectus*	—	—	—	—	—	■	■	—	■	■
30 *Caseolus subcalliferus*	—	—	—	—	—	—	—	—	—	—
31 *Caseolus calculus*	—	—	—	—	—	—	—	—	—	—
32 *Caseolus hartungi*	■	■	■	■	■	■	■	—	—	—
33 *Caseolus punctulatus*	■	■	■	■	■	■	■	—	■	■
34 *Actinella effugiens*	—	—	—	—	—	—	—	—	—	—
35 *Lemniscia michaudi*	—	—	—	—	—	—	—	—	—	—
36 *Discula bicarinata*	—	—	—	—	—	—	—	—	—	—
37 *Discula echinulata*	—	—	—	—	—	—	—	—	—	—
38 *Discula leacockiana*	—	—	—	—	—	—	—	—	—	—
39 *Discula oxytropis*	—	—	—	—	—	—	—	—	—	—
40 *Discula turricula*	—	—	—	—	—	—	—	—	—	—
41 *Discula cheiranticola*	—	—	—	—	—	—	—	—	—	—
42 *Discula calcigena*	■	—	■	■	■	■	■	—	■	■
43 *Discula pulvinata*	—	—	—	—	—	—	—	—	—	—
44 *Discula attrita*	—	—	—	—	—	—	—	—	—	■
45 *Discula albersi*	—	—	—	—	—	—	—	—	—	—
46 *Discula rotula*	—	—	—	—	—	—	—	—	—	—
47 *Discula tectiformis*	—	—	—	—	—	■	—	—	—	—
48 *Ps. portosanctana*	■	■	■	■	■	—	—	—	—	—
49 *Cochlicella acuta*[a]	■	—	—	■	—	—	—	■	—	—
50 *Caracollina lenticula*[a]	—	—	—	—	—	■	■	—	—	—
51 *Leptaxis erubescens*	—	—	—	—	—	—	—	—	—	—
52 *Leptaxis wollastoni*	—	—	—	—	—	—	—	—	—	—
53 *Leptaxis nivosa*	■	■	■	—	■	—	■	—	■	■
54 *Theba pisana*[a]	■	■	■	■	■	■	■	■	■	—
55 *Lampadia webbiana*	—	—	—	—	—	—	—	—	—	—
56 *Helix subplicata*	—	—	■	■	—	—	—	—	—	—
species per sample	13	13	14	11	12	14	11	6	11	9
endemics	11	12	13	9	10	12	9	3	10	9
non-endemics	2	1	1	2	2	2	2	3	1	0

sample	11	12	13	14	15	16	17	18	19	20
1 *Leiostyla corneocostata*	—	—	—	—	—	—	—	—	—	—
2 *Leiostyla relevata*	—	—	—	—	—	—	—	—	—	—
3 *Leiostyla ferraria*	—	—	■	■	■	■	■	—	—	—
4 *Leiostyla monticola*	—	■	—	—	—	—	—	—	—	—
5 *Leiostyla calathiscus*	—	—	■	—	—	—	—	—	—	—
6 *Vitrea contracta*	—	—	—	—	—	—	—	—	—	—
7 *Eucobresia media*	—	■	—	—	—	—	—	—	—	—
8 *Oxychilus alliarius*[a]	—	—	—	—	—	—	—	—	—	—
9 *Cecilioides acicula*[a]	—	—	—	—	—	—	—	—	—	—
10 *Cecilioides eulima*	—	—	—	—	—	—	—	—	—	—
11 *Amphorella melampoides*	—	—	—	—	—	—	—	—	—	—
12 *Amphorella triticea*	—	—	—	—	—	—	—	—	—	—
13 *Amphorella oryza*	■	■	■	■	■	■	■	—	—	■
14 *Amphorella tuberculata*	—	—	—	—	—	—	—	—	—	—
15 *Amphorella cimensis*	—	—	—	—	—	—	—	—	—	—
16 *Amphorella gracilis*	—	■	■	■	■	■	—	—	■	—
17 *Cylichnidia ovuliformis*	—	■	■	—	—	—	—	—	—	—
18 *Rumina decollata*[a]	—	—	—	—	—	—	—	■	—	—
19 *Boettgeria lowei*	—	■	■	■	■	■	■	—	—	■
20 *Balea perversa*[a]	—	—	—	—	—	—	—	—	—	—
21 *Testacella maugei*[a]	—	—	—	—	—	—	—	—	—	—
22 *Heterostoma paupercula*	■	■	■	■	■	■	■	■	—	■
23 *Geomitra coronata*	—	■	—	—	—	—	—	—	—	—
24 *Spirorbula obtecta*	—	—	—	—	—	—	—	■	■	—
25 *Spirorbula depauperata*	—	—	■	—	—	—	■	—	—	—
26 *Caseolus compactus*	■	—	■	■	■	■	■	■	—	—
27 *Caseolus consors*	—	—	—	—	—	—	—	—	—	—
28 *Caseolus commixtus*	—	—	—	—	—	—	—	—	—	—
29 *Caseolus abjectus*	■	■	■	■	■	■	■	■	■	■
30 *Caseolus subcalliferus*	—	—	—	—	—	—	—	—	—	—
31 *Caseolus calculus*	—	—	—	—	—	—	—	—	—	—
32 *Caseolus hartungi*	—	—	—	—	—	—	—	—	—	■
33 *Caseolus punctulatus*	■	—	—	—	—	—	—	—	—	■
34 *Actinella effugiens*	—	—	—	—	—	—	—	—	—	—
35 *Lemniscia michaudi*	—	—	—	—	—	—	—	—	—	—
36 *Discula bicarinata*	—	—	—	—	—	—	—	—	—	—
37 *Discula echinulata*	—	—	—	—	—	—	—	—	—	—
38 *Discula leacockiana*	—	■	■	■	■	■	■	—	—	—
39 *Discula oxytropis*	—	—	—	—	—	—	—	—	—	—
40 *Discula turricula*	—	—	—	—	—	—	—	—	—	—
41 *Discula cheiranticola*	—	—	—	—	—	—	—	—	—	—
42 *Discula calcigena*	■	■	—	—	—	—	—	—	—	■
43 *Discula pulvinata*	—	—	—	—	—	—	—	—	—	—
44 *Discula attrita*	—	■	■	■	■	■	■	—	—	—
45 *Discula albersi*	—	—	—	—	—	—	—	—	—	—
46 *Discula rotula*	—	—	—	—	—	—	—	—	—	—
47 *Discula tectiformis*	—	—	—	—	—	—	—	—	—	—
48 *Ps. portosanctana*	—	—	—	—	—	—	—	—	—	—
49 *Cochlicella acuta*[a]	—	—	—	—	—	—	—	■	■	—
50 *Caracollina lenticula*[a]	—	—	—	—	—	—	—	■	—	■
51 *Leptaxis erubescens*	—	—	—	—	—	—	—	—	—	—
52 *Leptaxis wollastoni*	—	—	—	—	—	—	—	—	—	—
53 *Leptaxis nivosa*	■	■	■	■	■	■	■	—	—	—
54 *Theba pisana*[a]	—	■	—	—	—	—	■	■	■	■
55 *Lampadia webbiana*	—	—	—	—	—	—	—	—	—	—
56 *Helix subplicata*	—	—	—	—	—	—	—	—	—	—
species per sample	7	14	13	10	10	10	11	8	5	9
endemics	7	13	13	10	10	10	10	4	3	7
non-endemics	0	1	0	0	0	0	1	4	2	2

sample	21	22	23	24	25	26	27	28	29	30
1 *Leiostyla corneocostata*	—	—	—	—	—	—	—	—	—	—
2 *Leiostyla relevata*	—	—	—	—	—	—	—	—	—	—
3 *Leiostyla ferraria*	—	—	—	—	—	—	—	—	—	—
4 *Leiostyla monticola*	—	—	—	—	—	—	—	■	—	—
5 *Leiostyla calathiscus*	—	—	—	—	—	—	—	—	■	—
6 *Vitrea contracta*[a]	—	—	—	—	—	—	—	—	—	■
7 *Eucobresia media*	—	—	—	—	—	—	■	—	—	—
8 *Oxychilus alliarius*[a]	—	—	—	—	—	—	—	—	■	—
9 *Cecilioides acicula*[a]	—	—	—	—	—	—	—	—	—	—
10 *Cecilioides eulima*	—	—	—	—	—	—	—	—	—	—
11 *Amphorella melampoides*	—	—	—	—	—	—	—	—	—	—
12 *Amphorella triticea*	—	—	—	—	—	—	—	—	■	—
13 *Amphorella oryza*	■	—	—	—	—	■	■	■	—	—
14 *Amphorella tuberculata*	—	—	—	—	—	—	—	—	■	—
15 *Amphorella cimensis*	—	—	—	—	—	—	—	—	—	—
16 *Amphorella gracilis*	—	—	—	—	—	—	■	■	—	—
17 *Cylichnidia ovuliformis*	—	—	—	—	—	—	—	—	—	—
18 *Rumina decollata*[a]	—	—	■	—	—	—	—	—	—	■
19 *Boettgeria lowei*	■	■	—	—	—	—	■	■	■	■
20 *Balea perversa*[a]	—	—	—	—	—	—	—	—	—	—
21 *Testacella maugei*[a]	—	—	—	—	—	—	■	—	—	—
22 *Heterostoma paupercula*	■	■	■	■	■	■	■	■	■	■
23 *Geomitra coronata*	—	—	—	—	—	—	—	—	—	—
24 *Spirorbula obtecta*	—	—	—	—	■	■	■	—	—	■
25 *Spirorbula depauperata*	—	—	—	—	—	—	■	■	■	—
26 *Caseolus compactus*	—	■	■	■	—	—	■	■	■	■
27 *Caseolus consors*	—	—	—	—	—	—	■	—	■	—
28 *Caseolus commixtus*	—	—	—	—	—	—	■	—	—	■
29 *Caseolus abjectus*	■	■	—	—	—	—	—	—	—	—
30 *Caseolus subcalliferus*	—	—	—	—	—	—	—	—	—	—
31 *Caseolus calculus*	—	—	—	—	—	—	—	—	—	—
32 *Caseolus hartungi*	■	■	■	—	■	■	—	—	—	—
33 *Caseolus punctulatus*	■	■	■	■	■	■	■	■	—	■
34 *Actinella effugiens*	—	—	—	—	—	—	—	—	—	—
35 *Lemniscia michaudi*	—	—	—	—	—	—	—	■	—	—
36 *Discula bicarinata*	—	—	—	—	—	—	■	■	■	■
37 *Discula echinulata*	—	—	—	—	—	—	—	—	—	—
38 *Discula leacockiana*	—	—	—	—	—	—	—	—	—	—
39 *Discula oxytropis*	—	—	—	—	—	—	—	—	—	—
40 *Discula turricula*	—	—	—	—	—	—	—	—	—	—
41 *Discula cheiranticola*	—	—	—	—	—	■	—	—	—	■
42 *Discula calcigena*	■	—	—	—	—	—	—	—	—	—
43 *Discula pulvinata*	—	■	■	■	—	—	—	—	—	—
44 *Discula attrita*	—	—	—	—	—	—	—	—	—	—
45 *Discula albersi*	—	—	—	—	—	—	—	—	—	—
46 *Discula rotula*	—	—	—	—	—	—	■	■	—	■
47 *Discula tectiformis*	—	—	—	—	—	—	—	—	—	—
48 *Ps. portosanctana*	—	—	—	—	—	—	—	—	—	—
49 *Cochlicella acuta*[a]	—	—	■	■	—	—	—	—	—	—
50 *Caracollina lenticula*[a]	—	—	■	■	■	—	■	—	—	■
51 *Leptaxis erubescens*	—	—	—	—	—	—	—	—	—	—
52 *Leptaxis wollastoni*	—	—	—	—	—	—	—	—	—	—
53 *Leptaxis nivosa*	—	■	■	—	■	■	■	■	—	■
54 *Theba pisana*[a]	■	■	■	■	■	■	■	—	—	■
55 *Lampadia webbiana*	—	—	—	—	—	—	—	—	—	—
56 *Helix subplicata*	—	—	—	—	—	—	—	—	—	—
species per sample	8	9	10	7	7	8	17	12	10	14
endemics	7	8	6	4	5	7	14	12	9	10
non-endemics	1	1	4	3	2	1	3	0	1	4

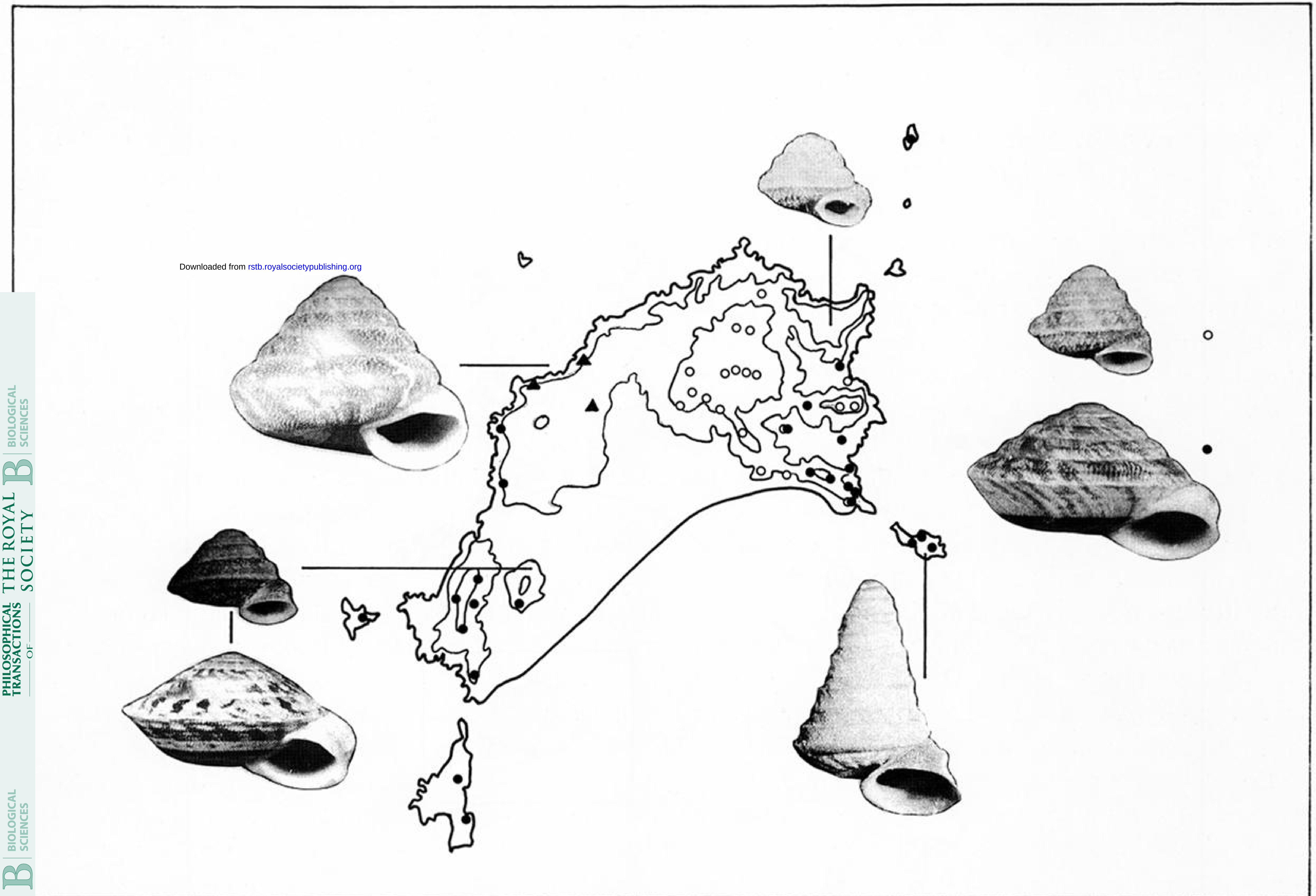
sample	31	32	33	34	35	36	37	38	39	40
1 *Leiostyla corneocostata*	—	—	—	—	—	—	—	—	—	—
2 *Leiostyla relevata*	—	—	—	—	—	—	—	—	—	—
3 *Leiostyla ferraria*	—	—	—	—	—	—	—	—	—	—
4 *Leiostyla monticola*	—	■	■	■	—	—	■	—	—	—
5 *Leiostyla calathiscus*	—	—	—	—	—	—	■	—	—	■
6 *Vitrea contracta*[a]	—	—	—	—	—	—	■	■	■	■
7 *Eucobresia media*	■	■	—	—	—	—	—	—	—	—
8 *Oxychilus alliarius*[a]	—	—	—	—	—	—	—	—	—	—
9 *Cecilioides acicula*[a]	—	—	—	—	—	—	—	■	—	—
10 *Cecilioides eulima*	—	—	—	—	—	—	—	—	—	—
11 *Amphorella melampoides*	—	—	—	—	—	—	—	—	—	—
12 *Amphorella triticea*	■	■	■	—	—	—	■	■	■	■
13 *Amphorella oryza*	■	■	■	■	■	■	—	■	—	—
14 *Amphorella tuberculata*	—	—	—	—	—	—	■	■	■	■
15 *Amphorella cimensis*	—	—	—	—	—	—	—	—	—	—
16 *Amphorella gracilis*	■	■	■	—	■	■	—	—	—	■
17 *Cylichnidia ovuliformis*	—	—	—	—	—	—	■	■	—	■
18 *Rumina decollata*[a]	—	—	—	■	—	—	—	—	—	—
19 *Boettgeria lowei*	■	■	■	■	—	■	■	■	■	■
20 *Balea perversa*[a]	—	—	—	—	—	—	■	—	—	■
21 *Testacella maugei*[a]	—	—	—	—	—	—	—	■	—	■
22 *Heterostoma paupercula*	■	■	■	■	■	■	■	■	—	■
23 *Geomitra coronata*	—	—	—	—	—	—	—	—	—	—
24 *Spirorbula obtecta*	—	—	—	—	—	—	—	—	—	■
25 *Spirorbula depauperata*	■	■	■	■	■	—	—	—	■	—
26 *Caseolus compactus*	■	■	—	—	—	■	■	■	■	■
27 *Caseolus consors*	—	—	■	■	—	■	■	■	■	■
28 *Caseolus commixtus*	—	—	■	■	■	—	—	—	—	—
29 *Caseolus abjectus*	—	—	—	—	—	—	—	—	—	—
30 *Caseolus subcalliferus*	—	—	—	—	—	—	—	—	—	—
31 *Caseolus calculus*	—	—	—	—	—	—	—	—	—	—
32 *Caseolus hartungi*	—	—	—	—	—	—	—	—	—	—
33 *Caseolus punctulatus*	■	■	—	—	—	—	■	■	■	■
34 *Actinella effugiens*	—	—	—	—	—	—	—	—	—	—
35 *Lemniscia michaudi*	—	—	—	—	—	—	■	—	—	■
36 *Discula bicarinata*	■	■	■	—	■	■	■	■	■	■
37 *Discula echinulata*	—	—	—	—	—	—	—	—	—	—
38 *Discula leacockiana*	—	—	—	—	—	—	—	—	—	—
39 *Discula oxytropis*	—	—	—	—	■	—	—	—	—	—
40 *Discula turricula*	—	—	—	—	—	—	—	—	—	—
41 *Discula cheiranticola*	—	—	—	—	—	—	—	—	—	—
42 *Discula calcigena*	—	—	—	—	—	■	—	—	—	—
43 *Discula pulvinata*	—	—	—	—	—	—	—	—	—	—
44 *Discula attrita*	—	—	—	—	—	—	—	—	—	—
45 *Discula albersi*	■	■	—	—	■	—	—	—	—	—
46 *Discula rotula*	■	■	—	—	—	—	■	—	■	—
47 *Discula tectiformis*	—	—	—	—	—	—	—	—	—	—
48 *Ps. portosanctana*	—	—	—	—	—	■	—	—	—	—
49 *Cochlicella acuta*[a]	—	—	—	—	—	—	—	—	—	—
50 *Caracollina lenticula*[a]	—	—	—	—	■	—	—	—	—	—
51 *Leptaxis erubescens*	—	—	—	—	—	—	■	—	■	—
52 *Leptaxis wollastoni*	—	—	—	—	—	—	—	—	—	—
53 *Leptaxis nivosa*	■	■	■	■	■	■	■	■	■	■
54 *Theba pisana*[a]	■	—	■	■	■	■	—	—	—	—
55 *Lampadia webbiana*	—	—	—	—	—	—	—	—	—	—
56 *Helix subplicata*	—	—	—	—	—	—	—	—	—	—
species per sample	14	14	12	10	11	11	17	14	12	17
endemics	13	14	11	8	9	10	15	11	11	14
non-endemics	1	0	1	2	2	1	2	3	1	3

sample	41	42	43	44	45	46	47	48	49	50
1 *Leiostyla corneocostata*	—	—	—	—	—	—	—	—	—	—
2 *Leiostyla relevata*	—	—	—	—	—	—	—	—	—	—
3 *Leiostyla ferraria*	—	—	—	—	—	—	—	—	—	—
4 *Leiostyla monticola*	—	—	—	—	—	—	—	—	—	■
5 *Leiostyla calathiscus*	—	—	—	—	—	—	—	■	—	—
6 *Vitrea contracta*[a]	—	—	—	—	—	—	—	—	—	—
7 *Eucobresia media*	—	■	■	—	■	■	—	—	—	■
8 *Oxychilus alliarius*[a]	—	—	—	—	—	—	—	—	—	—
9 *Cecilioides acicula*[a]	—	—	—	—	—	—	—	—	—	—
10 *Cecilioides eulima*	—	—	—	—	—	—	—	—	—	—
11 *Amphorella melampoides*	—	—	—	—	—	—	—	—	■	—
12 *Amphorella triticea*	■	■	—	■	■	—	■	■	—	—
13 *Amphorella oryza*	■	■	■	—	■	■	—	■	—	■
14 *Amphorella tuberculata*	—	—	■	—	—	—	■	—	—	—
15 *Amphorella cimensis*	—	—	—	—	—	—	—	—	—	—
16 *Amphorella gracilis*	■	■	—	—	■	■	■	—	—	■
17 *Cylichnidia ovuliformis*	—	—	—	—	—	—	—	—	—	—
18 *Rumina decollata*[a]	—	—	—	—	—	—	—	—	—	—
19 *Boettgeria lowei*	■	■	■	■	■	■	■	■	—	■■
20 *Balea perversa*[a]	—	—	—	—	—	—	—	—	—	—
21 *Testacella maugei*[a]	—	—	—	—	—	—	—	—	—	—
22 *Heterostoma paupercula*	■	■	■	■	■	■	■	■	■■	■
23 *Geomitra coronata*	—	—	—	—	—	—	—	—	—	—
24 *Spirorbula obtecta*	—	■	—	—	—	—	—	■	■	—
25 *Spirorbula depauperata*	■	■	■	■	■	■	■	■	—	■
26 *Caseolus compactus*	■	■	■	■	■	■	■	■	—	■
27 *Caseolus consors*	■	—	—	—	—	—	■	—	—	■
28 *Caseolus commixtus*	—	—	—	■	■	—	—	■	■	■
29 *Caseolus abjectus*	—	—	—	—	—	—	—	—	—	—
30 *Caseolus subcalliferus*	—	—	—	—	—	—	—	■	—	—
31 *Caseolus calculus*	—	—	—	—	—	—	—	—	—	—
32 *Caseolus hartungi*	—	■	■	■	■	—	—	■	■	■
33 *Caseolus punctulatus*	■	■	■	■	■	■	■	■	■	■
34 *Actinella effugiens*	—	■	—	—	—	—	—	—	—	■
35 *Lemniscia michaudi*	■	■	■	—	—	—	■	—	—	—
36 *Discula bicarinata*	■	■	—	—	—	—	—	—	—	■
37 *Discula echinulata*	—	—	■	■	■	—	■	■	—	—
38 *Discula leacockiana*	—	—	—	—	—	—	—	—	—	—
39 *Discula oxytropis*	—	—	—	—	—	—	—	—	—	—
40 *Discula turricula*	—	—	—	—	—	—	—	—	—	—
41 *Discula cheiranticola*	—	—	■	—	—	—	—	■	—	—
42 *Discula calcigena*	—	—	—	—	—	—	—	—	■	—
43 *Discula pulvinata*	—	—	—	—	—	—	—	—	—	—
44 *Discula attrita*	—	—	—	—	—	—	—	—	—	—
45 *Discula albersi*	—	—	—	—	—	—	—	—	—	—
46 *Discula rotula*	—	■	■	■	■	■	■	■	—	■
47 *Discula tectiformis*	—	—	—	—	—	—	—	—	—	—
48 *Ps. portosanctana*	—	—	—	—	■	—	—	—	—	—
49 *Cochlicella acuta*[a]	—	—	—	—	—	—	—	—	—	—
50 *Caracollina lenticula*[a]	—	—	—	—	■	—	—	—	—	—
51 *Leptaxis erubescens*	—	—	—	—	—	—	—	—	—	—
52 *Leptaxis wollastoni*	—	—	—	—	—	—	—	—	—	—
53 *Leptaxis nivosa*	—	—	■	—	■	■	■	■	—	—
54 *Theba pisana*[a]	—	—	—	—	—	■	—	—	■	■
55 *Lampadia webbiana*	—	—	—	—	■	—	—	—	—	—
56 *Helix subplicata*	—	—	—	—	—	—	—	—	—	—
species per sample	11	15	14	10	17	11	13	16	8	16
endemics	11	15	14	10	16	10	13	16	7	15
non-endemics	0	0	0	0	1	1	0	0	1	1

sample	51	52	53	54	55	56	57	58	59	60
1 *Leiostyla corneocostata*	—	—	—	—	—	—	—	—	—	—
2 *Leiostyla relevata*	—	—	—	—	—	—	—	—	—	—
3 *Leiostyla ferraria*	—	—	—	—	—	—	—	—	—	—
4 *Leiostyla monticola*	—	—	—	—	—	—	—	—	—	—
5 *Leiostyla calathiscus*	—	—	—	—	—	—	—	—	—	—
6 *Vitrea contracta*[a]	—	—	—	—	—	—	—	—	—	—
7 *Eucobresia media*	—	—	—	—	—	■	■	—	■	—
8 *Oxychilus alliarius*[a]	—	—	—	—	—	—	—	—	—	—
9 *Cecilioides acicula*[a]	—	—	—	—	—	—	—	—	—	—
10 *Cecilioides eulima*	—	—	—	—	—	—	—	—	—	—
11 *Amphorella melampoides*	—	—	—	—	—	—	—	—	—	—
12 *Amphorella triticea*	■	■	—	—	—	—	—	■	■	—
13 *Amphorella oryza*	■	■	■	■	■	—	■	■	■	▪▪
14 *Amphorella tuberculata*	—	—	—	—	—	—	—	—	—	—
15 *Amphorella cimensis*	—	—	—	—	—	—	—	—	—	—
16 *Amphorella gracilis*	—	■	—	—	—	—	—	■	—	—
17 *Cylichnidia ovuliformis*	—	■	—	—	—	—	—	■	—	—
18 *Rumina decollata*[a]	—	—	—	—	■	—	—	—	—	—
19 *Boettgeria lowei*	■	■	■	—	■	—	■	■	■	■
20 *Balea perversa*[a]	—	—	—	—	—	—	—	—	—	—
21 *Testacella maugei*[a]	—	—	—	—	—	—	—	—	—	—
22 *Heterostoma paupercula*	■	■	■	■	■	—	■	■	■	■
23 *Geomitra coronata*	—	—	—	—	—	—	—	■	—	—
24 *Spirorbula obtecta*	■	■	—	■	■	—	—	—	—	—
25 *Spirorbula depauperata*	■	■	—	—	■	—	■	■	■	■
26 *Caseolus compactus*	—	■	■	—	—	—	—	—	—	—
27 *Caseolus consors*	■	■	—	—	—	—	—	—	—	—
28 *Caseolus commixtus*	■	■	■	■	■	■	■	■	■	■
29 *Caseolus abjectus*	—	—	—	—	—	—	—	—	—	—
30 *Caseolus subcalliferus*	—	—	—	—	—	—	—	—	—	—
31 *Caseolus calculus*	—	—	—	—	—	—	—	—	—	—
32 *Caseolus hartungi*	—	—	—	■	—	—	—	—	—	—
33 *Caseolus punctulatus*	■	■	■	—	■	■	■	■	■	■
34 *Actinella effugiens*	—	■	—	—	—	—	—	—	■	—
35 *Lemniscia michaudi*	—	■	—	—	—	—	—	—	—	—
36 *Discula bicarinata*	—	—	—	—	—	—	—	■	—	—
37 *Discula echinulata*	■	■	—	—	—	—	—	—	—	—
38 *Discula leacockiana*	—	—	—	—	—	—	—	—	—	—
39 *Discula oxytropis*	■	—	—	—	—	■	■	■	■	■
40 *Discula turricula*	—	—	—	—	—	—	—	—	—	—
41 *Discula cheiranticola*	■	■	—	—	—	—	—	—	—	■
42 *Discula calcigena*	—	—	■	■	■	■	■	■	■	■
43 *Discula pulvinata*	—	—	—	—	—	—	—	—	—	—
44 *Discula attrita*	—	—	—	—	—	—	—	—	—	—
45 *Discula albersi*	—	—	■	—	—	—	—	—	■	■
46 *Discula rotula*	■	■	■	—	—	—	—	—	—	—
47 *Discula tectiformis*	—	—	—	—	—	—	—	—	—	—
48 *Ps. portosanctana*	—	—	■	—	—	—	—	—	—	■
49 *Cochlicella acuta*[a]	—	—	—	—	—	—	—	—	—	—
50 *Caracollina lenticula*[a]	—	—	—	■	■	—	—	—	—	—
51 *Leptaxis erubescens*	—	—	—	—	—	—	—	—	—	—
52 *Leptaxis wollastoni*	—	—	—	—	—	—	—	—	—	—
53 *Leptaxis nivosa*	■	■	■	■	—	■	■	■	■	▪▪
54 *Theba pisana*[a]	■	■	■	■	■	■	■	■	■	■
55 *Lampadia webbiana*	■	■	—	—	—	—	—	■	—	■
56 *Helix subplicata*	—	—	—	—	—	—	—	—	—	—
species per sample	16	20	12	9	11	7	11	16	14	14
endemics	15	19	11	7	8	6	10	15	13	13
non-endemics	1	1	1	2	3	1	1	1	1	1

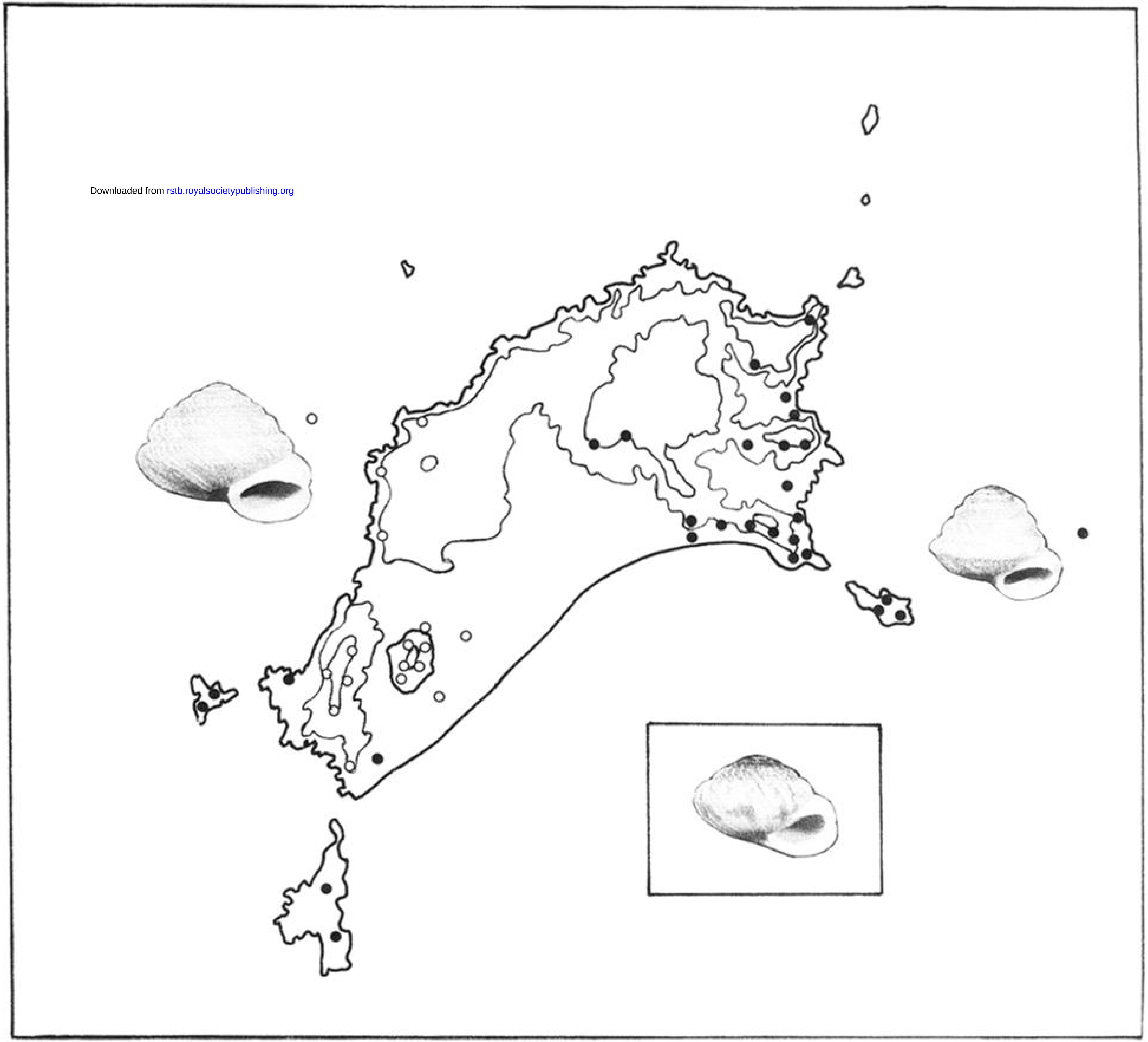
sample	61	62	63	64	65	records
1 *Leiostyla corneocostata*	—	—	—	—	—	1
2 *Leiostyla relevata*	—	—	—	—	—	1
3 *Leiostyla ferraria*	—	—	—	—	—	5
4 *Leiostyla monticola*	—	—	—	—	—	7
5 *Leiostyla calathiscus*	—	—	—	—	—	5
6 *Vitrea contracta*[a]	—	—	—	—	—	5
7 *Eucobresia media*	—	—	—	—	—	13
8 *Oxychilus alliarius*[a]	—	—	—	—	—	1
9 *Cecilioides acicula*[a]	—	—	—	■	—	2
10 *Cecilioides eulima*	—	—	—	■	—	2
11 *Amphorella melampoides*	—	■	■	—	■	10
12 *Amphorella triticea*	—	—	—	—	—	18
13 *Amphorella oryza*	—	—	—	■	—	40
14 *Amphorella tuberculata*	—	—	—	—	—	7
15 *Amphorella cimensis*	—	—	—	—	—	1
16 *Amphorella gracilis*	—	—	—	—	—	24
17 *Cylichnidia ovuliformis*	—	—	—	—	—	7
18 *Rumina decollata*[a]	—	—	—	—	—	7
19 *Boettgeria lowei*	—	■	■	—	—	47
20 *Balea perversa*[a]	—	—	—	—	—	2
21 *Testacella maugei*[a]	—	—	—	—	—	3
22 *Heterostoma paupercula*	■	■	■	■	■	62
23 *Geomitra coronata*	—	—	—	—	—	2
24 *Spirorbula obtecta*	—	—	—	—	—	21
25 *Spirorbula depauperata*	—	■	■	—	■	33
26 *Caseolus compactus*	—	—	—	—	■	38
27 *Caseolus consors*	—	—	—	—	—	14
28 *Caseolus commixtus*	■	■	■	—	—	29
29 *Caseolus abjectus*	—	—	—	—	—	16
30 *Caseolus subcalliferus*	—	—	—	—	—	1
31 *Caseolus calculus*	—	—	■	—	—	1
32 *Caseolus hartungi*	■	■	■	■	—	25
33 *Caseolus punctulatus*	■	■	■	■	■	50
34 *Actinella effugiens*	—	■	—	—	■	6
35 *Lemniscia michaudi*	—	—	—	—	—	8
36 *Discula bicarinata*	—	—	—	—	—	17
37 *Discula echinulata*	—	—	—	—	—	7
38 *Discula leacockiana*	—	—	—	—	—	6
39 *Discula oxytropis*	—	—	—	—	—	7
40 *Discula turricula*	—	■	■	—	—	2
41 *Discula cheiranticola*	—	—	—	—	—	7
42 *Discula calcigena*	■	■	■	—	■	26
43 *Discula pulvinata*	—	—	—	—	—	3
44 *Discula attrita*	—	—	—	—	—	7
45 *Discula albersi*	—	—	—	—	—	6
46 *Discula rotula*	—	—	—	—	—	18
47 *Discula tectiformis*	—	—	—	—	—	1
48 *Ps. portosanctana*	■	■	■	■	—	13
49 *Cochlicella acuta*[a]	—	—	■	—	—	8
50 *Caracollina lenticula*[a]	—	—	—	—	—	13
51 *Leptaxis erubescens*	—	—	—	—	—	2
52 *Leptaxis wollastoni*	—	—	—	—	■	1
53 *Leptaxis nivosa*	—	■	■	■	—	48
54 *Theba pisana*[a]	■	■	■	■	■	45
55 *Lampadia webbiana*	—	—	—	—	—	5
56 *Helix subplicata*	—	—	—	—	—	2
species per sample	7	13	14	9	9	758
endemics	6	12	12	7	8	
non-endemics	1	1	2	2	1	

[a] Non-endemic species.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

'igure 4. Distribution on Porto Santo of seven species of *Discula* belonging to the subgenera *Discula* and *Hystricella*. 'lockwise from bottom left, *D*. (*Discula*) *attrita* and *D*. (*Hystricella*) *leacockiana*, both limited to Pico de Ana Ferreira;). (*Discula*) *pulvinata* (triangles), limited to sandy north west; *D*. (*Hystricella*) *echinulata*, limited to Pico Branco; *D*. *Hystricella*) *bicarinata* (open circles) and *D*. (*Discula*) *calcigena* (closed circles), both with more widespread listributions, the first on the eastern higher land and the second in a range of locations and habitats, including ›ffshore islets; *D*. (*Hystricella*) *turricula*, limited to Ilhéu de Cima. *D. calcigena* on I. de Fora has been distinguished as ubspecies *gomesiana* and on I. de Baixo as subspecies *papilio*. All species to the same scale; *D. calcigena* is 10.0 mm in ›readth.



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gure 5. Distribution on Porto Santo of three species of *Caseolus*. *C. abjectus* (open circles) is a western species on Pico Ana Ferreira and neighbouring high and low areas. *C. commixtus* (closed circles) is mostly eastern and on the islets. *compactus* (inset) is widespread and overlaps the other two. The distributions do not map on to those of Figure 4. eadth of *C. compactus* is 5.3 mm.