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Changes in the land snail fauna of eastern Madeira during the Quaternary

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CONTENTS

SUMMARY

Fossil land snails have been sampled from the aeolianite (indurated dune) deposits east of Caniçal, eastern Madeira. Eight sections, comprising a 40 m sequence, were studied. Dating of material was carried out using ^{14}C (conventional and accelerator mass spectroscopy), amino acid epimerization and U–Th techniques. The sequence is not continuous, but spans the period from middle Pleistocene (*ca.* 300 ka before present (BP)) to recent.

Quantitative samples of shells were taken from all the fossiliferous horizons. Forty-three species are recorded in 51 samples, with an average of 14.3 species per sample. Most of the species (29 in 43) occur throughout the sequence, showing that the fauna was established by the middle Pleistocene. Analysis of faunal similarity shows that although there is some mixing and redeposition, five groups of samples may be distinguished. These date from V and IV: latest Holocene (post colonization), III: middle Holocene (7000–3500 years BP), II: late Pleistocene (135–45 ka BP) and I: middle Pleistocene (*ca.* 300–135 ka BP).

Some European species (*Punctum pygmaeum*, *Plagyrona placida*) are present throughout the series, whereas others (*Theba pisana*, *Cochlicella barbara*) only appear in the most recent sediments. Some endemics are limited to part of the sequence. The earliest samples have good representation of grassland species. The composition then shifts towards woodland species and later returns to a grassland facies, probably as a result of disturbance by man. The faunal changes over the course of the Quaternary are quite substantial, being comparable to those seen in mainland faunas in the temperate zone, and indicate a major influence of climatic change.

Arrival of some species between 45 and 8 ka BP may be associated with lowered sea level and closer proximity of Madeira to the Deserta islands, but there is also evidence of species exchange between Madeira and the more distant island of Porto Santo, separated from it by a deep ocean floor. These findings provide information on the faunal exchanges and progressive evolution which have resulted in very high molluscan species diversity in the Madeiran archipelago.

1. INTRODUCTION

The Madeiran islands have a very rich land snail fauna. It is derived from the fauna present in Europe before the Pleistocene and includes an endemic evolutionary radiation which started before the Pleistocene. It was not directly affected by glaciation and developed independently of events in Europe and north Africa. The families present occur, living or fossil, in Europe. Up to 20 distinct colonizations could be

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involved (Cameron & Cook 1992). There is a range of sea mounts running northeast from the archipelago to the Iberian peninsula which could once have been islands, and if so, would have formed a route for colonization (Pastouret *et al.* 1980). Speciation took place on the islands, so that compared with continental faunas the archipelago is rich in species but poor in families and genera. Over 250 taxa have been recognized (Waldén 1983), 70% of which are endemic and some of which are now extinct. Examination of present-day distributions and affinities indicates that much allopatric speciation has taken place on different islands of the group (Cook *et al.* 1990; Waldén 1984). On the largest island of the group, Madeira itself, aeolian sands containing strata rich in fossil land snail shells occur in a small area on the São Lourenço peninsula at the eastern end of the island. The smaller island of Porto Santo has more extensive fossiliferous sand beds (Lietz & Schwartzbach 1971). The unique Madeiran deposit has been extensively destroyed to provide building material, and by 1991 some of the sections examined earlier by us had been removed. Exposures made by excavation have, however, allowed deposits of a wide range of ages to be sampled. In this paper, we examine the changes which have occurred from the middle Pleistocene to the present, in order to record the dynamics and timescale of evolution of a fauna exhibiting high species diversity. Specifically, we examine what effect relatively recent events (in the last several hundred thousand years) have had on this ancient island fauna, and we evaluate the relationship of faunal change (extinctions and introductions) to climatic change and human settlement.

2. LOCATION AND HISTORY

The Madeiran island group is located in the Atlantic ocean at 33°N, 900 km SW of Portugal and 800 km W of Morocco. It consists of the island of Madeira, which is 58 km at its largest dimension and rises to an altitude of 1820 m, and two other clusters of islands (figure 1). Porto Santo is 40 km NE, the ocean bed between the two dropping to 2600 m, so that connection between Porto Santo and Madeira can never have occurred. About 10 km SE of Madeira are the three Deserta islands, and these are linked to Madeira by a submarine ridge which falls to no more than 130 m along its crest. It is therefore possible that Madeira and the Desertas were connected as a result of sea level fall during a glacial phase, or at least that the gap between them was very narrow. Recent estimates indicate a sea level drop of 120 m radiocarbon dated at 17 ka BP (Fairbanks 1989). Porto Santo projects from a much larger shelf 200 m in depth or shallower, from which a number of other islets also emerge. It was probably at one time a much larger island, and the deposits on it containing fossil snails may have accumulated from sand blown from extensive beaches which existed at times of lower sea level. The shelf around Madeira is narrower, the coastline rises more steeply, often in cliffs, and the sand bed on the low-lying eastern Ponta de São Lourenço is the only fossiliferous deposit present.

Madeira appears to have been created by four main phases of volcanic activity. The first dates from between 20 and 12 Ma and the fourth from 0.75 Ma. (Zbyszewski 1972; Mitchell–Thomé 1985; outlined by Cook *et al.* 1990). The eastern peninsula is formed of

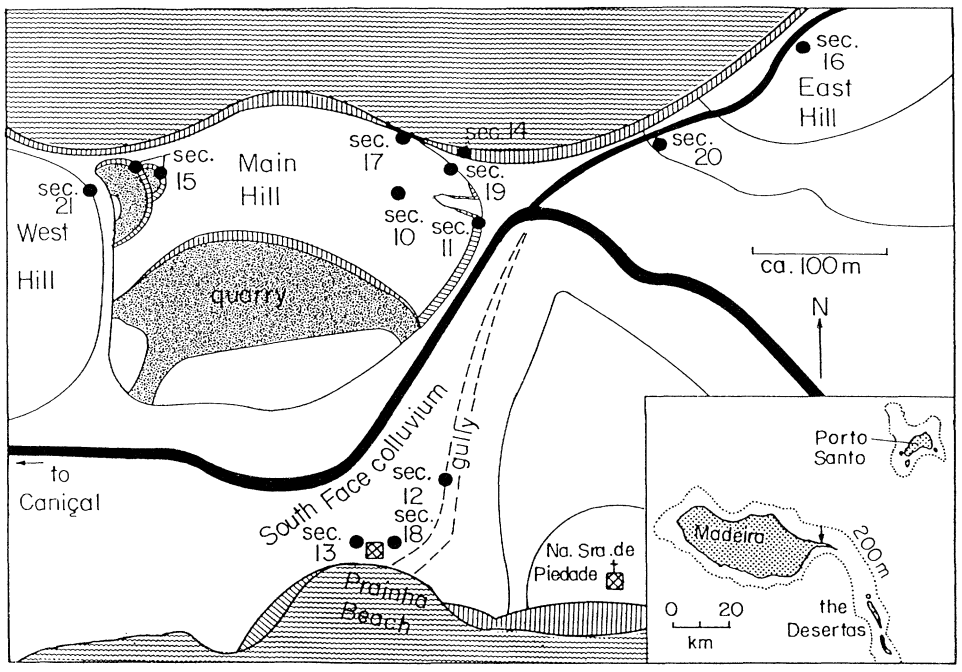

Figure 1. Map of the segment of the São Lourenço peninsula covered with aeolianite deposits, showing the general topography and the locations of the sections studied. Insert: Madeira and the neighbouring islands of the Desertas and Porto Santo. Arrow points to the location of the aeolianite deposits.

rocks between 0.74 and 4 Ma in age. Along the south coast of the island, including the peninsula, there is a series of small volcanic cones which are younger than this, but there is no evidence of volcanic activity sufficiently recent as to be contemporaneous with any of the fossil deposits. The Desertas are the same age as the peninsula, whereas the youngest rocks on Porto Santo are at least 12 Ma old. It is therefore possible that Porto Santo was a source for colonizations of Madeira after periods of vulcanism.

The island of Madeira is for the most part steep and rugged, with the low-lying peninsula of São Lourenço, containing the fossil deposit, extending to the east. Rainfall is high on the north side, which supports endemic associations of laurel and *Erica* forest. The mean annual precipitation at Encumeada (altitude 950 m), is 2340 mm. The south side is drier (645 mm rainfall on the coast at Funchal), with xerophytic scrub formations up to about 700 m altitude. Plantations of pine, eucalyptus and mimosa have been introduced. The eastern peninsula is drier than the south coast, with an annual rainfall of about 400 mm. It is eroded and treeless. Vegetation types for the island are described by Sjögren (1972) and for the peninsula by Hampshire (1984). Kämmer (1982) and Ribeira (1985) provide data on climate.

Human occupation of the islands brought about great changes in the ecology and could be expected to have resulted in introduction of mollusc species. There was no aboriginal population, and the island group is reported to have been first colonized by the Portuguese in 1419, with the establishment of a settlement on Porto Santo. This was supposed to be the result of accidental discovery at that time, although it is possible that the island was visited for some decades before settlement (see, for example, Freitas Ferraz (1986); Guerreira & Albuquerque (1989)). The exploitation of Porto Santo is reported to have rapidly degraded the habitat there, with the result that expeditions were made to Madeira in 1420, the eastern peninsula being one of the first parts to be developed. After that, change was very rapid, and over the next thirty years the island became a thriving and productive colony (Freitas Ferraz 1986; Machado 1947; Monod 1986; Peres 1960).

3. MATERIALS AND METHODS

A visit by the three authors was made in 1989 to establish the stratigraphy and to collect material for analysis. An exposure has been visible for many years along a road cut on the east side of the deposit (figure 2*e*). Quarrying to the south and west has now revealed the sedimentary sequence in the other parts of the deposit, and further exposures are accessible down the sea cliff on the north side. Although they are less obvious there, the sand deposits also overly the volcanic rocks both on the hill to the east and southwards along the gully towards the Prainha, a small sandy beach (figure 1). In figure 1 sample sections are numbered.

All the material of the main and east hills is of aeolian origin whereas the sediments from lower down the slope consist largely of colluvial redeposited material. Three basic types of sediment can be recognized: (i) black and white medium to coarse sands, usually bedded, the black grains being basaltic and the white biogenic marine carbonates which comprise 5–15% of the sediments; (ii) black medium sands, unbedded; and (iii) clays. In the black and white sands there are extensive fossil root systems produced by replacement of the original organic material in trees and shrubs by carbonate (Ziehen 1981). In some horizons there are impressions of trunks and roots, and in places these have weathered out on the surface to indicate graphically the pattern of afforestation which occurred from time to time through the sequence. Snail shells were found only in the black and white sand units. Figure 3 indicates the observed pattern of sand, clay and indurated units in the sections, and the approximate position of the samples. Dissolved and redeposited carbonates have resulted in the layers containing casts of root systems and in calcrete slabs and indurated sand layers. These, and the clay–sand mixtures, indicate periods of comparative stabilization, while some of the intervening sands are mobile dune deposits.

Sequences were studied and sampled at 12 locations. In each, the stratigraphy was recorded, samples of deposits were collected to examine sedimentation pattern, and shells and soil carbonates were collected for dating studies. A visit was made by Cook and Goodfriend in 1990 to complete the survey. For faunal analysis, a cube of material of approximately 500 mm side was removed and passed through a series of sieves. It was felt that standardization by volume, rather than by weight, would provide sufficiently accurate quantities for comparison between samples. Material passing through 0.5 mm mesh was discarded; other fractions were searched for shells in the laboratory. The sandy matrix varied considerably in the ease with which it could be sieved, and in some cases smaller samples had to be taken. When this occurred, the volume of the sample was estimated and an adjustment made to the numbers recorded. This necessarily reduces precision; the figures nevertheless give a reasonable indication of relative abundance of shells both within and between samples.

In some places, material was also picked from the matrix, to get a more complete, although non-quantitative, record. The resulting shells were identified and the number in each taxon counted. Final determinations were made in all cases by Cameron. Nomenclature follows Waldén (1983), who gives the authorship of the names, except for *Geomitra watsoni* (Johnson 1897), which is not included in his list. It is clearly distinct from the commoner *G. tiarella*. Problems in identification were resolved as far as possible by reference to collections at the Natural History Museum, London (BMNH), and the National Museum of Wales (Cardiff, Melville-Tomlin collection). The following reservations should be noted.

1. Individuals referred to *Craspedopoma mucronatum* are very close in appearance to that modern species. It is

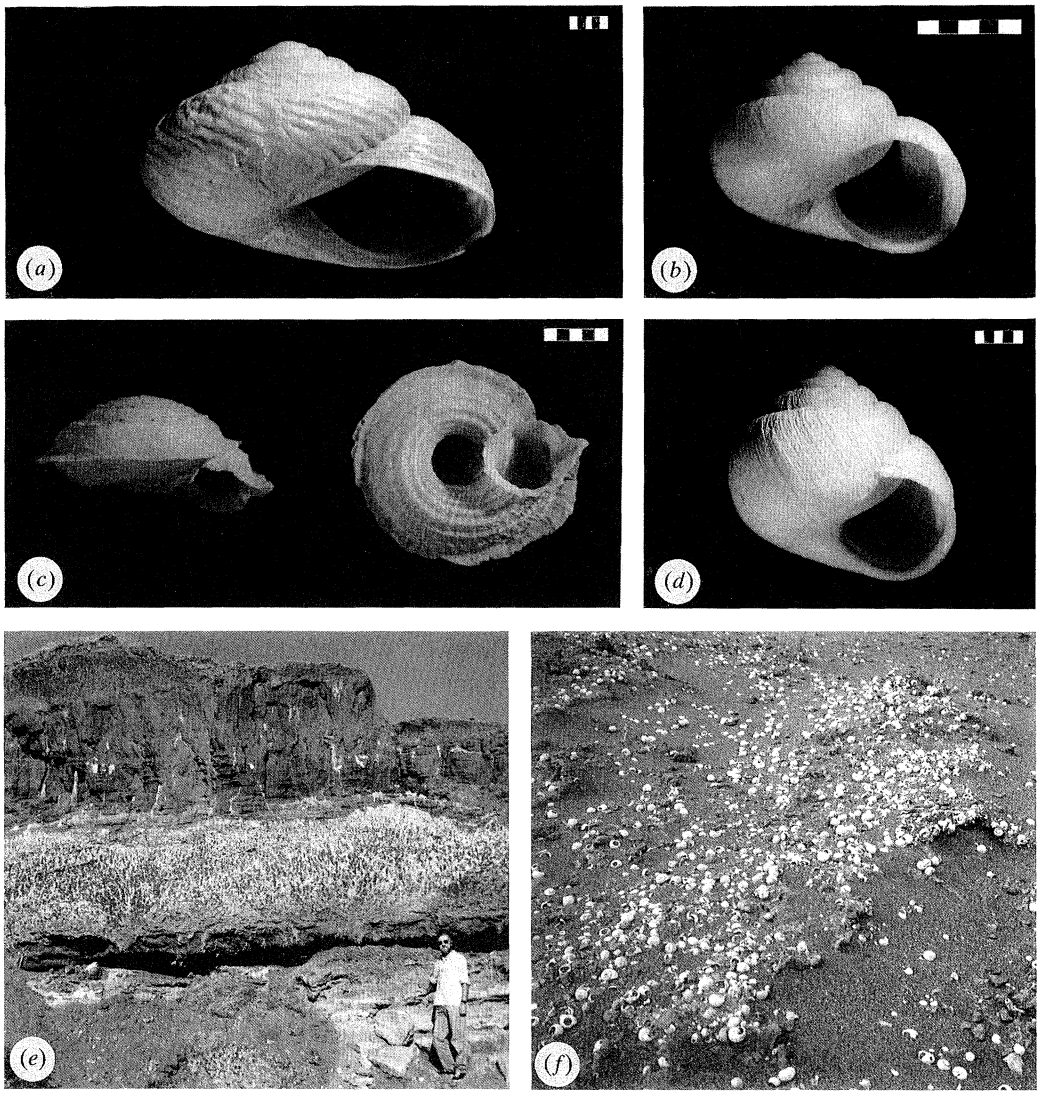

Figure 2. Fossil shells and aeolian deposits, Madeira. (*a*) *Leptaxis undata*; (*b*) *Actinella nitidiuscula*; (*c*) *Geomitra delphinula* (extinct); (*d*) *Caseolus bowdichianus* (extinct); (*e*) view of the road cut. The person is 1.83 m high. Above his head can be seen the thick clay unit with carbonate concretions. At the top of the section is the base of the Holocene sand unit containing abundant *C. bowdichianus*. The lower left part of the section is covered by sediments slumped from above; (*f*) a lag deposit of land snail shells (mostly *C. bowdichianus*) on top of the deflated surface of the main hill.

possible, however, that the fossils are another, as yet undescribed, species.

2. The status of *Truncatellina linearis* is doubtful (M. Seddon, personal communication). It closely resembles the European *T. callicratis*, and if conspecific, would not be endemic.

3. *Amphorella* specimens segregate clearly into two taxa, one of which (*A. grabhami*) is known only fossil. The other closely resembles the modern *A. tornatellina minor*, and thus confirms the conclusion of Cook *et al.* (1990) that it is a species distinct from *A. tornatellina* (*sensu stricto*). With this exception, we have not used subspecific epithets, although some have been given to forms known only as fossils (Waldén 1983).

4. *Caseolus punctulatus* is the best fit we can make to large *Caseolus* from the older samples, but *C. solidus* cannot be excluded. The specimens differ from the more recent *C. bowdichianus* in smaller size, smaller protoconch, characteristic shell sculpture, and in having brown spiral bands visible on larger shells. Representative lots of all species have been deposited in the National Museum of Wales.

Because of the long time span covered by the deposits a variety of dating methods were used. These are as follows.

1. Radiocarbon analysis of land snail shell carbonate, by conventional decay counting methods and by accelerator mass spectrometry (AMS). Results are corrected for isotopic fractionation but are not calibrated or corrected for the small age anomaly (*ca.* 600 years) which occurs in some samples (Goodfriend *et al.* 1993).

2. U–Th analysis of land snail shells and of fissure-fill carbonates. Results presented are from Goodfriend *et al.* (1993). The relatively large error terms result from uncertainties of the corrections for detrital Th.

3. Amino acid epimerization analysis of land snail shells. The uniformity of D-alloisoleucine:L-isoleucine

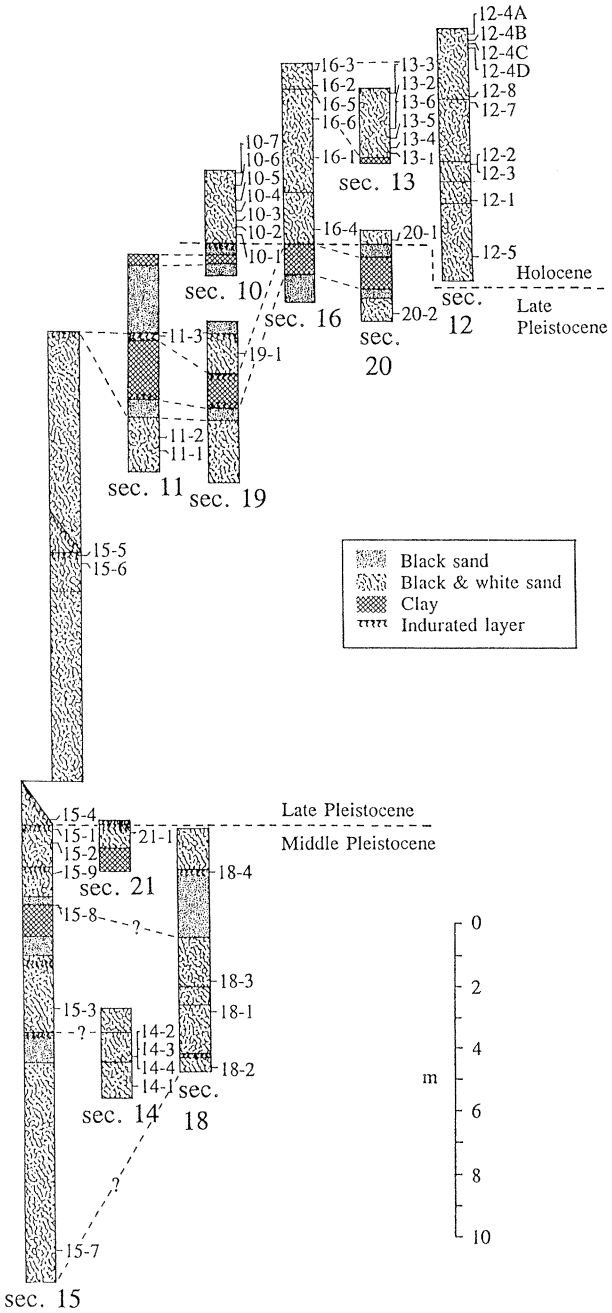

Figure 3. Diagram of stratigraphic sections of the Madeira aeolianite sequence, with positions of land snail samples indicated. See figure 1 for locations of the sections. The Holocene–Pleistocene and Late Pleistocene–Middle Pleistocene boundaries are indicated.

(A:I) values among individual shells within a stratum was used to determine the age uniformity of fauna (whether some shells may have been redeposited from older deposits (Goodfriend 1989)). Age determination of late Holocene shells was also made by calibration of the epimerization rate against the Holocene radiocarbon dates. A:I values were also used to correlate various strata in different sections.

The results of these procedures are used here to provide dates for the strata; the full details will be presented elsewhere (Goodfriend *et al.* 1993).

4. CHRONOLOGY

The oldest units in the Madeiran sequence occur in the lower part of the west side of the main hill (samples 15–8 and 15–7) and the colluvium in section 18 (18–3, 18–1 and 18–2)(table 1 and figure 1). Fissure-fill carbonates occurring in the same unit as sample 15–8 have a U–Th age in excess of 220 ka BP. Samples 18–1 and 18–2 have higher A:I ratios than 15–8 and may be older, whereas 18–3 is probably close in age to 15–8. Because the mean A:I value of the snails in 15–8 (0.53) does not greatly exceed that of the overlying units, which contains snails with a mean A:I ratio of 0.42–0.45 and a U–Th age of *ca.* 137 ka BP, we suggest that the younger end of this age limit (*ca.* 200–300 ka BP) is probably correct (but see further discussion of this age below). Epimer ratios indicate that 14–2, from the north face of the main hill, is of similar age to 15–8 on the west side.

The three U–Th dates based on analysis of land snails cannot be taken literally, due to the well-known unreliability of U–Th dates on molluscs (e.g. Kaufman *et al.* 1971). Based on their relation to the A:I data, the 95 (15–4) and 137 ka BP dates seem reasonable. The 65 ka BP date for 11–2 seems a little too young; the amino acid data indicate that it should be only a little younger than 15–4. It is, however, within 2 standard deviations of the mean age estimate of 15–4. All of the snail samples from this part of the sequence (15–4, 15–5, 17–1 and 11–2) show similar A:I values (0.37–0.41) and thus are of similar age, despite the significant vertical distances between them. Small differences among samples may relate to temperature differences resulting from different exposures (e.g. 17–1 from the north face shows a lower A:I value). Epimer ratios indicate that 20–2, the only Pleistocene sample from the east hill, is similar in age to 11–2 and 17–1 from the main hill. The next youngest snail-containing unit is represented by samples 19–1 and 11–3. Separate AMS radiocarbon analyses of two shells indicates that these samples are near the limit of radiocarbon, but both dates show measurable radiocarbon activity while, in contrast, there is no measurable radiocarbon activity in the shell from the next older unit. Combining the two analyses, we calculate an age of 46 380 years BP for this fauna, with a 1 s.d. range of 44 500 to 48 800.

Non-fossiliferous units overlie the unit containing the 19–1 and 11–3 faunas. The next faunas above this in the sequence (10–1 on the main hill, east side, 16–4 on the east hill, and 12–5 in the south slope colluvium) are already of Holocene age, *ca.* 7–8 ka BP. On the main hill, this Holocene unit has been actively eroded, so that the sequence is truncated at *ca.* 6 ka BP (10–7). On the east hill, the sequence continues to 4 ka BP, and is capped with recent aeolian clayey sands which contain a cultural midden of limpet shells (*Patella aspera* Röding and *P. candei* Drouët). Limpets are a favourite food on the island even today. Radiocarbon analysis indicates that this midden is no older than A.D. 1640, and thus post-dates settlement of the island. The Holocene colluvial sequence of section 12 covers nearly the same early to middle Holocene time range

Table 1. *Data on the chronology of Madeira land snail samples from analysis of amino acid epimer ratios (D-alloisoleucine: L-isoleucine, or A:I), and radiocarbon (^{14}C) and U–Th dates*

(The sections are grouped geographically and the samples within each section are listed in stratigraphic order. Where sections from the same area overlap in time, the samples are listed in chronological order, based on the A:I values. Radiocarbon laboratory sample numbers are given in parentheses.)

sample no.	A:I analyses of land snail shells				radiometric dates
	$\bar{x}$ (±s.d.)	range	species[a]	n	
			main hill – east side		
10–7	0.115 (±0.007)	0.105–0.125	*C. b.*	6	^{14}C: 6160 (±100) years BP (RT-1479)[b]
	0.104 (±0.003)	0.100–0.108	*G. d.*	4	
10–2	0.145 (±0.016)	0.135–0.173	*A. n.*	6	^{14}C: 8260 (±85) years BP (RT-1474)[b]
	0.139 (±0.012)	0.124–0.154	*C. b.*	6	
10–1	0.140 (±0.022)	0.114–0.167	*C. b.*	4	
11–3	0.258 (±0.024)	0.232–0.291	*A. n.*	4	
19–1	0.297 (±0.036)	0.235–0.325	*A. n.*	5	^{14}C: 45 640 (±2600) years BP (AA-6118)[c] 47 640 (±3400) years BP (AA-6120)[c]
11–2	0.399 (±0.050)	0.342–0.432	*A. n.*	3	^{14}C: >47 300 years BP (AA-6117)[c]
	0.447 (±0.064)	0.390–0.537	*L. u.*	6	U–Th: 65 000 (±11 000) years BP[d]
17–1	0.369 (±0.038)	0.301–0.408	*A. n.*	6	
14–2	0.549 (±0.017)	0.530–0.567	*A. n.*	6	
			main hill – west side		
15–5	0.407 (±0.049)	0.335–0.478	*A. n.*	8	
	0.494 (±0.034)	0.470–0.532	*L. u.*	3	
15–4	0.410 (±0.016)	0.381–0.422	*A. n.*	6	U–Th: 95 000 (±12 000) years BP[e]
	0.433 (±0.039)	0.406–0.461	*G. d.*	2	
15–1A					U–Th: 137 000 (±10 000) years BP[e]
15–2	0.452 (±0.049)	0.394–0.512	*A. n.*	5	
15–9	0.432 (—)	—	*A. n.*	1	
	0.432 (—)	—	*C. p.*	1	
21–1	0.424 (±0.051)	0.347–0.490	*A. n.*	5	
15–8	0.531 (±0.050)	0.477–0.592	*A. n.*	4	U–Th: >220 000 years BP[f]
15–7	0.558 (±0.065)	0.512–0.604	*A. n.*	2	
			east hill		
20–1	0.0108 (±0.0023)	0.0090–0.0133	*T. p.*	3	
	0.0120 (±0.0015)	0.0100–0.0133	*T. p.*	4	
16–3	0.110 (±0.041)	0.078–0.190	*C. b.*	6	
	0.0129 (±0.0023)	0.0104–0.0153	*T. p.*	6	
16–2	0.0209 (±0.0005)	0.0204–0.0212	*T. p.*	2	^{14}C: 97.8 (±0.7) PMC (RT-1504)[g]
16–5	0.086 (±0.006)	0.077–0.090	*C. b.*	7	
16–6	0.088 (±0.006)	0.081–0.094	*C. b.*	6	^{14}C: 3960 (±70) years BP (RT-1446)[b] 3800 (±70) years BP (RT-1464)[b] 4220 (±70) years BP (Beta-42915)[b]
16–1	0.127 (±0.011)	0.113–0.139	*C. b.*	6	
	0.108 (±0.010)	0.094–0.121	*G. d.*	9	
16–4	0.163 (±0.009)	0.150–0.176	*C. b.*	5	^{14}C: 7320 (±90) years BP (RT-1527)[b]
20–2	0.364 (±0.044)	0.301–0.416	*A. n.*	6	
			colluvium – south side		
12–4A	0.0128 (±0.0034)	0.0099–0.0177	*T. p.*	4	
12–4D	0.0117 (±0.0005)	0.0111–0.0121	*T. p.*	3	
12–8	0.077 (±0.037)	0.034–0.126	*C. b.*	6	
	0.075 (±0.035)	0.035–0.131	*G. d.*	6	
	0.0183 (±0.0030)	0.0148–0.0218	*T. p.*	7	
13–3	0.0188 (±0.0050)	0.0124–0.0244	*A. n.*	4	
	0.0177 (±0.0065)	0.0123–0.0298	*T. p.*	6	
13–2	0.0246 (±0.0029)	0.0211–0.0264	*T. p.*	14	
	0.074 (—)	—	*G. d.*	1	
13–5	0.034 (±0.004)	0.031–0.038	*A. n.*	3	
13–4	0.031 (±0.005)	0.0244–0.036	*A. n.*	4	
	0.034 (±0.004)	0.0271–0.042	*C. b.*	8	^{14}C: 1500 (±60) years BP (AA-6122)[h]
13–1	0.0270 (±0.0015)	0.0260–0.0288	*A. n.*	3	
12–7	0.077 (±0.016)	0.063–0.103	*A. n.*	5	
	0.071 (±0.004)	0.066–0.078	*C. b.*	6	
	0.049 (±0.015)	0.0232–0.067	*G. d.*	7	
12–2	0.085 (±0.002)	0.084–0.088	*C. b.*	4	^{14}C: 4460 (±70) years BP (RT-1601)[b]

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Table 1 (*Continued*)

sample no.	A:I analyses of land snail shells				radiometric dates
	$\bar{x}$ (±s.d.)	range	species[a]	*n*	
12–1	0.151 (±0.022)	0.125–0.166	*A. n.*	3	
	0.173 (±0.033)	0.123–0.219	*C. b.*	6	^{14}C: 9620 (±160) years BP (OxA-3526)[i]
12–6	0.183 (±0.009)	0.176–0.189	*C. b.*	2	
12–5	0.156 (±0.015)	0.137–0.171	*A. n.*	5	
	0.231 (—)	—	*C. b.*	1	
	0.152 (±0.028)	0.134–0.184	*G. d.*	3	
18–3	0.515 (±0.048)	0.445–0.567	*A. n.*	6	
18–1	0.575 (±0.043)	0.516–0.610	*A. n.*	5	
18–2	0.579 (±0.074)	0.466–0.666	*A. n.*	5	

[a] *A. n.* = *Actinella nitidiuscula*; *C. b.* = *Caseolus bowdichianus*; *C. p.* = *Caseolus punctulatus*; *G. d.* = *Geomitra delphinula*; *L. u.* = *Leptaxis undata*.
[b] Conventional radiocarbon analysis of bulk samples of *C. bowdichianus*.
[c] AMS radiocarbon analysis of individual shell of *A. nitidiuscula*.
[d] Conventional U–Th analysis of bulk sample of *L. undata*.
[e] Mass spectrometric U–Th analysis of bulk sample of *L. undata*.
[f] Conventional U–Th analysis of calcite vein.
[g] Conventional radiocarbon analysis of bulk sample of a midden consisting of the marine mollusks. *Patella aspera* and *P. candei*. Calibrated age (for ±2 S. D.) is AD 1642–1955.
[h] AMS radiocarbon analysis of individual shell of *C. bowdichianus*, with A:I = 0.035.
[i] AMS radiocarbon analysis of individual shell of *C. bowdichianus* with A:I = 0.219.

as the east hill sequence from 12–5 up to 12–2, but some of these faunas are of mixed age (see below). Late Holocene deposits occur above this and also in section 13.

The uniformity of the A:I values among the individual shells within a unit can be used to determine the age uniformity of the fauna (Goodfriend 1987, 1989). The analytical error of A:I measurements is about 5%, except at very low values (less than 0.02), where it increases to about 10%. A comparison of the variability of A:I values within the middle and early Holocene deposits of the main hill, east hill and south face colluvium is presented in table 2. For the main hill and east hill, where the sediments are of aeolian origin, the variability of A:I values within a species averages 7.4%, which is only slightly greater than the variability expected from the analytical error alone. These deposits can thus be considered

Table 2. *Variability of amino acid epimer ratios (A:I values) within Madeiran snail samples, expressed as the coefficient of variation [(100 × s.d.)/mean]*

Early – middle Holocene samples				Pleistocene samples		
sample number	variability within species[a]			sample number	variability within species[a]	
	A. n.	*C. b.*	*G. d.*		*A. n.*	*L. u.*
			main hill			
10–7		6.6	3.1	11–3	9.3	
10–2	10.7	8.5		19–1	12.0	
				11–2		14.3
				17–1	10.4	
				14–2	3.2	
				15–5	12.0	
				15–4	3.8	
				15–2	10.9	
				21–1	12.0	
				15–8	9.4	
			east hill			
16–6		6.5		20–2	12.1	
16–1		9.2	8.9			
16–4		5.7				
			south-face colluvium			
12–7	20.3	5.8	35.1	18–3	9.2	
12–2		2.3		18–1	7.4	
12–1	14.6	19.0		18–2	12.7	
12–5	9.8					

[a] *A. n.* = *Actinella nitidiuscula*; *C. b.* = *Caseolus bowdichianus*; *G. d.* = *Geomitra delphinula*; *L. u.* = *Leptaxis undata*.

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to be of nearly uniform age. On the other hand, samples 12–7 and 12–1 (but not 12–2) from the colluvial deposits show high levels of variability in most of the species, thus indicating a mixed-age assemblage. These age mixtures are presumably the result of redeposition of shells when the colluvium was laid down. The age when the sediments were deposited in their present positions is indicated by the age of the youngest shells within the unit; shells with higher A:I values represent redeposited shells.

Species used in age determination are shown in figure 2. Differences in A:I values among species are in part due to differences in rates of epimerization. *Caseolus bowdichianus* and *Actinella nitidiuscula* epimerize at about the same rate, whereas *Geomitra delphinula* and *Theba pisana* epimerize more slowly and *Leptaxis undata* epimerizes more rapidly (considered in more detail in Goodfriend *et al.* (1993)). Many of the late Holocene samples contain a mixed-age faunal assemblage. For example, 16–3 contains near-modern *T. pisana* (table 1), but middle to early Holocene specimens of *C. bowdichianus*. A similar pattern is seen in the colluvial assemblages 12–8 and 13–2. The earliest records of *Caseolus bowdichianus* (highest A:I values) occur as redeposited shells within younger colluvial deposits (12–1 and 12–5). AMS radiocarbon analysis of a *C. bowdichianus* shell with A:I = 0.219 from 12–1 gave an age of 9600 years BP. Thus, the earliest record of this species is in the early Holocene. The species does not occur in 19–1, dated to 46 ka BP. No fossiliferous deposits occur between these times, so the time of appearance of *C. bowdichianus* on Madeira could be anywhere within the intervening period.

The mixtures in Pleistocene assemblages are more difficult to assess, because it is not known exactly how much natural variation in A:I values may occur among individuals of the same age. Diagenetic alteration of the shell organic matter (e.g. loss of amino acids) may induce some variation in A:I values which does not reflect variation in ages. Variability of A:I values within the Pleistocene samples on the main and east hill (average 9.9%) only slightly exceeds that of the early to middle Holocene deposits (7.4%) (table 2). Much of this variability is accounted for by the analytical error (5%). Thus, all of these samples are considered to be of nearly uniform age, including the 18-series samples from colluvial deposits.

5. FAUNAL ANALYSIS

The molluscs obtained from the samples are enumerated in Appendix 1. Sites are arranged in order of increasing age, based on dating and stratigraphic position. Some samples are, however, of mixed age, as noted above. Numbers of species and individuals are given for each sample. Where non-standard quantities of matrix were searched, these numbers are corrected to give the number per 50 cm cube. Interpretation of the data has to take into account three factors. First, differential preservation of species may occur, which is particularly important if different kinds of deposit favour preservation of different species. Second, there may be reworking of deposits. Thirdly, shells may sometimes be worked into deposits older than themselves, either by burrowing while alive, or by falling down holes. Where such mixing was obvious, the specimens have been excluded from the samples. The samples were analysed in several ways to try to detect temporal changes in the fauna while making allowance for accidental mixing. The results of these tests are now described.

The Madeira sequence (Appendix 1) contains 43 taxa, of which 38 are endemic to the archipelago, one is found on other Atlantic islands and four are European species. Twelve are extinct, two more are extinct on Madeira proper, and only 12 are to be found living within 3 km of the site. Excluding slugs, six endemics and seven non-endemics now occur within 3 km of the site but are not represented in the fossil record (Cook *et al.* 1990).

Even cursory examination of Appendix 1 shows that the species composition varies consistently from one sample to another. In particular, there are some mutually exclusive sets of species in the younger samples at the left of the table compared with the oldest samples at the right. These differences indicate transitions in the habitat types represented, or evolutionary changes, or both. Changes could have been abrupt or progressive, and the patterns are rendered more complicated by the possibility of redeposition of shells. If we look at the relation of number of species to position in the series there is a slight indication that the samples are richer in the centre than in the oldest or youngest. The linear regression has a coefficient of -0.008, which is not significant ($F = 0.02$), but the quadratic has a positive mode and explains a significant amount of the variation ($F = 7.41$, $p < 0.05$). One possible way to examine the composition of the samples is to calculate the Shannon diversity, H, for each sample and the evenness, J, which is the diversity expressed as a fraction of the maximum value it could attain for a given number of species (Pielou 1975). It has been shown that empirically communities tend to follow log normal distributions of species abundance; this may be because species interact with each other in some way, or it may arise simply because of canonical effects of sampling (May 1981). Whatever the origin, the evenness may be calculated from the relative abundances of the species comprising the sample of the community. If data from different communities were mixed, the J values would, on average, be higher than if they were not. Similarly, a community consisting of subsets of species, each of which is lognormally distributed but which do not interact, should have a higher J value than one with the same number of species forming a single lognormal distribution. The relation of J to species number therefore indicates something about the pattern in the assemblage.

As an example, we have examined the data for modern samples of molluscs from the eastern peninsula of Madeira and the Deserta islands presented by Cook *et al.* (1990) and discussed by Cook (1984). These consisted of 68 samples containing endemic species only, and 33 samples which had a mixture of endemics and non-endemics. Because the latter contain proportionally more species, we suggested that

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non-endemics, and particularly introduced ones, were simply added to the endemic fauna and did not displace it. In that case, the average value of J should go up. Calculated mean values are 0.714 ± 0.029 for samples of mixed origin and 0.654 ± 0.019 for samples with endemics only. The difference is in the expected direction ($t = 1.83$). It is not significant at the 5% level using a 2-tailed test although it is using a 1-tailed test. To make a parallel calculation for the fossil data, the 51 samples were arranged in ascending order of species number, and J values calculated for the third with the fewest species per sample to compare with values for the third with the greatest number of species. Calculated values are 0.742 ± 0.018 for species-poor samples and 0.742 ± 0.009 for species-rich samples. Fossil samples therefore show greater evenness than extant ones, but there is no difference related to species number. So far as it goes, this test provides no evidence of mixing of faunas, either before or after death.

The location of faunal changes in the sequence has also been examined by plotting the cumulative number of species on site number, starting from one end of the sequence. If there were n species in all, and on average a fraction p of these are present per site, then if the species were distributed at random the cumulative fraction present at the ith site would be $1 - e^{-pi}$. Variation in species number per site can be accommodated by finding $1 - \Pi q_i$, where q_i is the probability of a species not being present at that site, estimated as the fraction of the n which are absent. If there are sharp breaks in the actual cumulative curve compared with this expectation, then a faunal transition has occurred. The result of this procedure is shown in figure 4. Samples are accumulated from the oldest to the youngest. The distribution is nonrandom, the data curve being displaced from the expectation over most of its length. Proceeding from right (oldest) to left (youngest) there is an increase in species present from sample 49 to 48 (18–3 to 14–1), a stabilization to sample 43 (15–2) and thereafter a progressive increase to sample 26 (12–1). After that, total species number is again stable until sample 12 (13–5) is reached, after which numbers rise to the final total of 43 species. The main sections defined by these breaks correspond to a recent period up to *ca.* 300 years old, a central period back to 8 ka BP and a long section of 45 ka or older.

Another way to examine the changes in faunal composition is to calculate similarity coefficients for presence or absence of species before or beyond a given point. Data may be accumulated so that, progressively, sample 1 is compared with samples 2–51, samples 1 and 2 with samples 3–51, and so on. Transitions will then show up as minima in the sequence of similarity estimates. The change in species composition of modern taxa along a geographical transect on the peninsula was examined in this way by Cook (1984), and the resulting values are also illustrated in Cook *et al.* (1990), where the index used is described. An abrupt change in the fauna was apparent along the geographic sequence. The equivalent calculation for the time sequence considered here is shown in figure 5. The upper line is based on all the data at each site. It may be that single specimens are more likely than larger numbers of individuals to be accidentally redeposited, and the lower line shows the comparisons when species represented by a single specimen are excluded. The earliest seven and the latest four samples show uniform composition, and the largest changes in composition take place between samples 15 (13–4) and 17 (12–2) and between samples 40 (15–6) and 45 (14–2) respectively. These changes are, however, less marked than in the modern geographical sequence examined before.

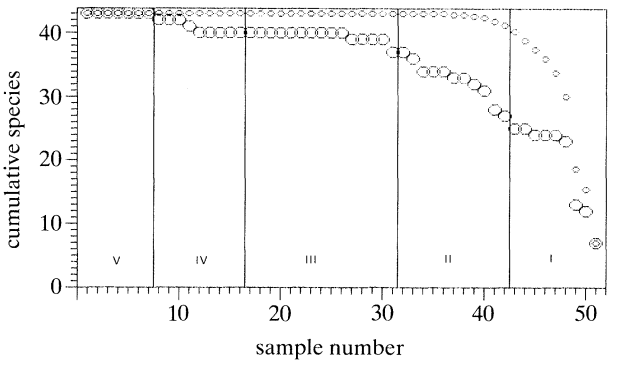

Figure 4. Number of species represented in the samples in Appendix 1, accumulated from oldest sample (at right) to youngest (at left). Large circles, observed numbers; small circles, numbers expected if species were randomly distributed. Roman numbers indicate the five suggested age groups.

These comparisons involve presence or absence of species but do not take abundance into account. The recorded abundances cannot give the true proportions of living faunas, and are sometimes biassed between samples by the method of sampling. However, differences between large numbers and single, or very few, shells are likely to be meaningful. In particular, small numbers of misplaced shells may minimize differences between samples, and some reckoning of abundance will counteract this. Accordingly, we have clustered the data using the cosine method available on SPSS,

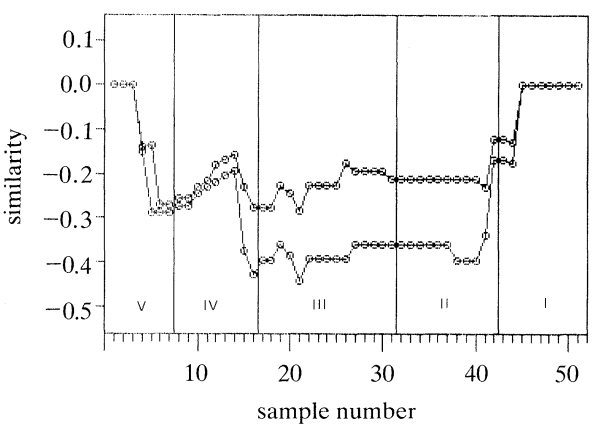

Figure 5. Similarity in species composition between sections when the samples in Appendix 1 are divided into two parts successively from youngest (at left) to oldest (at right). Minima indicate discontinuities in species composition. Roman numbers indicate the five suggested age groups.

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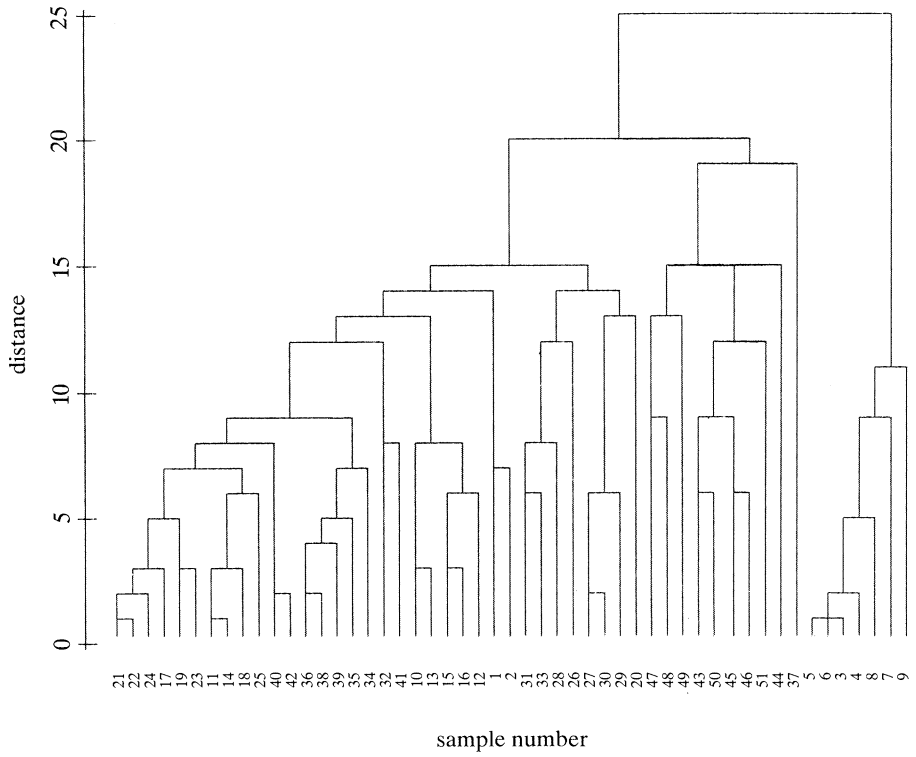

Figure 6. Cluster diagram showing distance between samples in terms of species composition, using the cosine method applied to logarithms of numbers of species present and UPGMA grouping. Sample numbers are from 1 (most recent) to 51 (oldest).

based on the logarithms of the numbers of individuals of each species. The logarithmic scaling reduces the effect of large numbers of some of the smaller species obtained in many samples. The calculated matrix has been clustered on the basis of average linkage between groups, or UPGMA (Norušis 1986). The result is shown in figure 6. Again, groups of sites at the start and the end of the sequence separate out. Among the younger samples, sites 3 to 9 (12–4a to 13–6) form a well defined group, as do 43 to 51 (15–2 to 18–2), which are linked to 37 (17–1). The rest form less consistent clusters. As a check on the effect of including relative abundance of species the data were then reanalysed giving equal weight to every species present, i.e. another presence–absence classification. The changes produced are minor; sites 1 and 2 are still separated and 51 is in the same group as before while the central sections are somewhat reorganized. The classification is therefore not sensitive to variations in recorded abundance.

6. FAUNAL GROUPINGS

Consideration of the three grouping procedures used, and of the dates which can be attached to samples, has led us to divide the sequence into five groups for comparison, as follows.

(V) Samples 1–7 (20–1 to 13–3). These are the most recent samples, all of which post-date the Portuguese colonization.
(IV) Samples 8–16 (13–2 to 13–1). These are of late Holocene age. Sample 16–2 (no. 10) is post 1640 A.D.
(III) Samples 17–31 (12–2 to 12–5). Early to middle Holocene age (8–4 ka BP).
(II) Samples 32–42 (11–3 to 15–1). Late Pleistocene age (135–45 ka BP).
(I) Samples 43–51 (15–2 to 18–2). Middle Pleistocene age (300–135 ka BP).

In all of these the dates and the faunal changes agree, except that there is some uncertainty about the exact positioning of the division between Group I and Group II. The division chosen is based on the fauna. The stratigraphy suggests, however, that 15–1 and 15–2, where the split has been made, have similar ages of *ca.* 137 ± 10 ka BP. Possibly the transition was very rapid. There is no doubt, however, that the fauna separates into two group at about here, one predominantly middle Pleistocene and the other predominantly late Pleistocene. At the younger end of the whole sequence, Group V is separated from Group IV at the point of first entry of *Cochlicella barbara*. The duration of both groups is relatively very short, but dated samples in Group V are younger than those of Group IV. Numbers of individuals have been summed within each of the five groups and the totals are presented in table 3. Most species show considerable change in abundance between one or other of the groups.

Table 4*a* shows the breakdown of species and individuals by present status in each group. In terms of occurrence alone, the only substantial difference between groups lies in the absence from Group V of species now found elsewhere, but this group is not

Table 3. *Total number of individuals of each species in the five age groups*

(W, species with woodland affinities; G, species with grassland affinities; +, extinct; (+), extinct in Madeira; n, non-endemic. The ages of the groups are: V, post-colonization; IV, 1600–200 years BP; III, 7000–3500 years BP; II, 150–45 ka BP; I, 300–200 ka BP.)

Group					habitat		
V	IV	III	II	I	type	species	
10	245	112	206	2	W	1. *Craspedopoma mucronatum*	
0	0	0	2	0	W	2. *C. trochoideum*	
39	626	1305	759	351	G	3. *Truncatellina linearis*	+
1	113	157	585	102	G	4. *Staurodon saxicola*	
0	0	0	0	2	W	5. *Leiostyla laurinea*	
0	1	1	1	0		6. *L. sphinctostoma*	
1	0	4	24	1		7. *L. wollastoni*	+
5	708	203	37	1	G	8. *L. millegrana*	
0	0	8	1	0		9. *L. abbreviata*	
0	337	20	55	17	W	10. *L. cassida*	
1	92	8	7	0		11. *L. gibba*	
0	2	0	1	0	W	12. *Plagyrona placida*	n
0	31	8	26	0	W	13. *Punctum pygmaeum*	n
0	0	0	8	0	W	14. *Phenacolimax marcidus*	
2	8	13	15	4	W	15. *P. crassus*	+
0	32	1	0	11		16. *Janulus stephanophora*	
2	197	217	107	2		17. *J. bifrons*	
0	47	1	4	3		18. *Amphorella t. minor*	
4	259	134	134	9		19. *A. grabhami*	+
26	98	138	25	5		20. *Cylichnidia cylichna*	+
0	0	1	0	0		21. *Boettgeria lorenziana*	+
41	10	4	0	0	G	22. *Heterostoma paupercula*	
61	654	540	319	6	W	23. *Geomitra tiarella*	
0	0	1	4	103		24. *G. watsoni*	+
2	11	141	44	0		25. *G delphinula*	+
2	26	19	45	0		26. *Spirorbula squalida*	
78	318	70	81	60	G	27. *Caseolus compactus*	
0	0	2	24	61	G	28. *C. sphaerulus*	+
0	0	0	19	11		29. *C. subcalliferus*	(+)
0	0	0	0	14		30. *C. punctulatus*	(+)
4	268	430	0	0		31. *C. bowdichianus*	+
4	36	68	33	9		32. *Actinella actinophora*	
4	12	8	51	51	G	33. *A. arcinella*	+
0	2	0	0	0		34. *A. obserata*	
3	73	40	2	0	W	35. *A. promontoriensis*	+
13	550	239	108	98		36. *A. nitidiuscula*	
2	126	123	179	45	W	37. *Lemniscia calva*	
219	95	29	1	0	G	38. *Discula polymorpha*	
3	0	0	0	0	G	39. *Cochlicella barbara*	n
0	96	118	93	6		40. *Leptaxis erubescens*	
0	5	23	45	9	W	41. *L. furva*	
3	48	62	12	0		42. *L. undata*	
420	36	0	0	0	G	43. *Theba pisana*	n

deficient in extinct species, especially considering that it represents sites less than 400 years old (see below).

By contrast, abundance gives a different picture (table 4*b*). Group V sites are dominated by individuals of species still living in the area, and despite the limitations of using abundances, this difference from the other groups is clearly real. Group IV sites have an intermediate appearance; the youngest of them may be just within the period of human colonization.

Some species, such as the two *Craspedopoma* species, are characteristic of woodland habitats, whereas others, such as *C. compactus* and *D. polymorpha* are grassland species (Cook *et al.* 1990). Others are catholic in their preferences or, being extinct, cannot be put into a habitat category. The changes in relative frequencies probably indicate, to some extent, changes in the type of habitat present. Table 3 also shows which species are extinct and distinguishes those of grassland from those of woodland habitats. Using species which can be classified as grassland or woodland dwellers we have calculated for each site the ratio of logarithms of the numbers in the two classes, to provide an index of habitat types represented. The result is illustrated in figure 7. Grassland species predominate in the two most recent groups. The next

Table 4. *Patterns of distribution of species between the five time groups*

(*a*) Present status of species in each group

Group	V	IV	III	II	I	total
number of species						
species living within 3 km	11	11	10	9	7	12
other extant species	5	13	13	18	18	20
extinct species	9	8	11	9	9	11
percentage of total individuals						
species living within 3 km	83.7	47.4	26.1	34.9	27.7	
other extant species	7.5	26.4	21.7	26.0	18.0	
extinct species	8.8	26.2	52.2	39.1	54.3	
total	950	5162	4248	3053	983	

(*b*) Species composition and abundance in different habitat categories

Group	V	IV	III	II	I	total
number of species						
woodland affinities	5	9	8	11	7	12
intermediate or unknown	11	15	18	16	12	21
grassland affinities	9	8	8	7	6	10
total	25	32	34	34	25	43
percentage of individuals						
woodland affinities	8.1	28.7	20.7	28.1	8.6	
intermediate or unknown	6.6	34.1	37.4	21.5	27.7	
grassland affinities	85.3	37.7	41.9	50.4	63.7	
total	950	5162	4248	3053	983	

two groups tend towards woodland, while the oldest indicates grassy conditions. Sample 34 (20–2), which shows a stronger grassland character than the other samples of Group II, is the only Pleistocene sample we have from the east hill. This difference may be related to environmental differences between the two hills, e.g. poorer water storage capacity of the east hill sequence due to the much thinner sand unit. The ecology has also undoubtedly changed through time, and until the recent period these changes were probably climatically mediated.

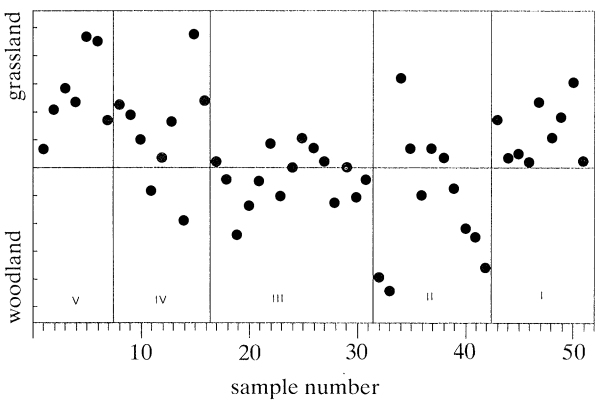

Figure 7. Relative representation of grassland and woodland species in samples. Samples are arranged from youngest (at left) to oldest (at right). Roman numbers indicate the five suggested age groups. The index on the vertical scale is the logarithm of the number of individuals in grassland species as a fraction of those in woodland species. Horizontal line represents equal numbers in the two categories.

Species composition and abundance in the different habitat categories are summarized in table 4. A similar result is obtained to that of figure 6. A shift in proportion of individuals from woodland and intermediate to grassland species occurs in Group V and in Group I, compared with the rest. This is a relative, rather than an absolute, phenomenon; not only do errors of sampling and preservation affect the numbers, but the biomass of individuals of different species differs by orders of magnitude.

These general shifts are not always reflected in the distribution of individual species, and there is, of course, considerable variation in occurrence and abundance between sites in the same group. Species restricted to one group tend to occur in such small numbers that chance may play a part in their discovery. Nevertheless, five species are confined to Groups II and I, but only one each to the others. The species represented only in Group V is the non-endemic *Cochlicella barbara*, certainly introduced. Other species which predominate in that group, both absolutely and relatively, are *Discula polymorpha* and *Heterostoma paupercula* and the non-endemic *Theba pisana*, all of which can be found alive nearby. Nevertheless, there are many species in Group V not found locally today.

Many species are common in Group IV sites but are rare or absent in Group V. These comprise *Truncatellina linearis*, *Staurodon saxicola*, *Leiostyla millegrana*, *Phenacolimax crassus*., *Janulus stephanophora*, *J. bifrons*, *Amphorella tornatellina minor*, *A. grabhami*, *Geomitra tiarella*, *Caseolus bowdichianus*, *Actinella actinophora*, *A. promontoriensis*, *A. nitidiuscula*, *Lemniscia calva*, *Leptaxis*

erubescens and *L. undata*. In some cases their presence in Group V may be the result of mixing. The large number of species which have changed in abundance, indicates a massive change in ecology over the last few hundred years, and almost certainly this is the result of human activity.

At the other extreme, there is a group of species present only in the early samples (Groups I and II). These are *Craspedopoma trochoideum*, *Leiostyla laurinea*, *Phenacolimax marcidus*, *Caseolus subcalliferus* and *C. punctulatus*. Of these, *L. laurinea* and *C. punctulatus* are only in Group I. It is possible that *Caseolus sphaerulus* and *Geomitra watsoni* also belong to this category, each being represented by a very few individuals in Group III. They indicate a fauna displaced well before the end of the Pleistocene.

Replacement species which come into the fauna with Group III are *Heterostoma paupercula* and *C. bowdichianus*. *Leiostyla abbreviata* and *Actinella promontoriensis* may also belong to this category, although in each case there are one or two earlier specimens. There is a single specimen of *D. polymorpha* in Group II (in sample 40, (15–6)). *C. punctulatus* and *C. bowdichianus* are very similar species, *C. punctulatus* being extant and fossil on Porto Santo and the southern Deserta island (Bugio) but extinct on Madeira, while *C. bowdichianus* is an extinct species from Madeira and Porto Santo which has not been found on the Desertas. The transition represented here indicates that *C. punctulatus* disappeared from this part of Madeira at an early date and later *C. bowdichianus* came in. Group III is dominated by *Truncatellina linearis*, *G. tiarella* and *C. bowdichianus*, which together form 52 per cent of total collected.

7. DISCUSSION

Taking into account both faunal considerations and dates we have divided the data in Appendix 1 into five groups. Two of these are recent, dating to the post-settlement period, and the separation of Group V from Group IV may be a recognition of the later effect of human colonization on the ecology of the area. Group III is early to middle Holocene in age (8–4 ka BP). The next group is late Pleistocene in age (135–45 ka BP), and the oldest is Middle Pleistocene (300–135 ka BP). The amount of variation between samples within groups is similar. In the short-duration groups it probably indicates sampling error and small scale ecological differences, so that we should be cautious about attributing differences between samples in the long-duration groups to climatic or other changes. Nevertheless, it is worth trying to reconstruct the environmental changes which occurred during deposition of the sequence.

There have been profound climatic changes in the north Atlantic region over the period concerned, associated with the successive phases of glaciation and recession. In Madeira, these will have resulted in fluctuation in average temperature and humidity. Glaciation also caused a lowering of sea level, which, in the Madeiran archipelago, altered the size of the territory available to be occupied and the likelihood of colonization of Madeira from the Desertas or vice versa. In addition, the north coast of Madeira is an area of marine erosion, which has probably altered the topography, and hence the local climate, of the locality. Finally, although the effect is almost instantaneous compared with the others, the coming of man must have brought about very significant changes. Grazing by domestic animals and rabbits began and much of the present vegetation consists of typical introductions (Hampshire 1984). These various factors are discussed in more detail in the following sections.

(i) *Relation to global patterns of climate and sea level change during the Quaternary*

The faunal samples from the Madeiran aeolianite sequence cover only discrete slices of the Quaternary. The present Holocene interglacial (warm) period is well represented, with the main period of aeolian accumulation spanning *ca.* 8–4 ka BP. But extensive late Holocene colluvial deposits occur, as well as a recent aeolian sand unit capping the east hill (top of section 16). The next earliest fossiliferous deposits date to *ca.* 45 ka BP. Missing from the sequence are snail samples covering the last glacial maximum (peaking at *ca.* 18 ka BP), and the subsequent deglaciation period that was associated with global warming (*ca.* 14–8 ka BP). Some shells in the Holocene colluvial deposits pre-date 8 ka BP; these represent redeposited shells (see chronology section above). However, no complete faunal sample is available for the intervening period. The samples dating to *ca.* 45 ka BP represent an interstadial (moderately warm) phase within isotope stage 3 (Stuiver *et al.* 1978; Chappell & Shackleton 1986). The thick unit containing samples 11–2, 17–1, 15–5 and 15–4 on the main hill and 20–2 on the east hill is thought to date to *ca.* 85 ka BP. This places it within the latest phase of the last interglacial (isotope stage 5), which ended *ca.* 80–75 ka BP (Edwards *et al.* 1987; Bard *et al.* 1990). The samples associated with the U–Th date of *ca.* 137 ka BP (15–2, 15–9 and 21–1), and also the older samples, cannot be placed in a definite palaeoclimatic context, due to the uncertainties of the dating. Pushing the date towards the younger end of the range of the error would place these samples in the early part of the last interglacial (stage 5A, *ca.* 130–125 ka BP), whereas the middle of older end of the range would place them in the glacial phase of stage 6.

Thus, all of the samples which can be dated with reasonable accuracy turn out to belong to interglacial or interstadial phases. It seems likely that the older deposits also represent warmer climatic phases. The colder phases of the Pleistocene appear to be represented by the clay–silt and black sand units, which are non-fossiliferous (Goodfriend *et al.* 1993).

Despite the fact that only a limited range of palaeoclimates is represented in the faunal sequence, the changes in these faunas over time are quite dramatic. They are comparable to changes seen over the same periods in continental land snail faunas near regions subject to glaciations (e.g. for Europe: Kerney 1971; Preece 1990; Rousseau 1987; for North Amer-

ica: Leonard 1952; Leonard *et al.* 1971). The varying ecological affinities of the various species comprising the Madeiran fossil faunas (table 3) indicate that significant changes in vegetation, from grassland to woodland, occurred at the site. These must have been the result of significant variations in effective moisture conditions over time, most probably as a result of changes in rainfall amounts, although temperature variations, and local geographical changes (see below) may also have played a role. Faunal changes between interglacial and glacial periods must have been even more dramatic, but the sequence unfortunately provides no records of the latter.

(ii) *Erosion and topography*

The highest part of the sand bed (103 m) is at its northern edge. Beyond this, the basalt and lava bedrock terminates in a sea cliff; the sand above has been eroded and the calcreted sheets have collapsed down the mound and into the sea. The whole north coast of the island is an area of intense erosion. Along the peninsula the greatest altitudes occur as the summits of northern sea cliffs, and it is evident that what were once its highest parts have now disappeared to compose the shallow northern submarine shelf. Differences in altitude have a marked effect on climate in Madeira (Sjögren 1972). Four kilometres to the west, between Caniçal and Machico, the ridge of high land which rises to 626 m is heavily wooded. This woodland consists of introduced trees, but laurel woods, which are outliers of the main indigenous forest of the island, occur to the north of Machico at 600 m, and probably once occupied the ridge. The gastropod fauna is very different from that of the peninsula (Cook *et al.* 1990). The change from perennial to annual vegetation as one proceeds eastward along the peninsula (Cook 1984; Hampshire 1984) is associated with a lower level of rainfall. The progressive removal of the northern side of the peninsula, coupled with the periodic fluctuation in sea level, may have resulted in local climatic changes with an overall trend towards decline in humidity and more xeric vegetation. It is not known, however, whether significant erosion has occurred within the period represented by the fossil faunal sequence.

(iii) *Colonization by man*

The conspicuous species *Caseolus bowdichianus* and *Geomitra delphinula* are very abundant in Group III sites, 8–4 ka old; *Theba pisana* is absent. *T. pisana*, along with *Cochlicella barbara*, may well have been introduced by man. The decline in the two extinct species which were such a feature of Group III associations, appears to have begun before human colonization, but there are some Group IV samples in which they are present. The coming of man, and the resultant ecological disturbance, may have hastened the extinction of these two species. The precise dating, and the effect of colonization, are the subject of another paper (Goodfriend *et al.* 1993).

(iv) *Faunal changes in the sequence*

Considering Groups IV and V as representing the same period, most of the species (29 in 43) are present throughout the sequence. These include two European species (*Punctum pygmaeum* and *Plagyrona placida*). Two species (*Cochlicella barbara* and *Theba pisana*) are non-endemic recent arrivals, while five (*Craspedopoma trochoideum*, *Leiostyla laurinea*, *Phenacolimax marcidus*, *Caseolus subcalliferus* and *C. punctulatus*) are present only in the oldest group. The first three of these are woodland species extant elsewhere in Madeira; the other two live in drier habitats and are extinct in Madeira but present on other islands. The pattern of species composition was therefore established by the middle Pleistocene.

The presence of European species as fossils and the existence of species common to Madeira and Porto Santo show that occasional colonizations must have occurred from one land mass to another across considerable stretches of ocean. At the other extreme, the difference in the fauna of Madeira and the Desertas and of Porto Santo and its offshore islets indicates that short distances present significant barriers. Presumably there can be few species in common unless an extended time scale is involved. The common features of the fauna of the Madeiran islands and Europe arise from the cumulative effect of accidental colonizations over a period of 10 million years or more, whereas endemic taxa which have only been in existence for some tens of thousands of years are likely to be confined to a single island. This makes it interesting to consider the possible effect of a land connection between Madeira and the Desertas.

The possible locations of such bridges in the sequence are between Group I and Group II and between Group II and Group III. The evidence of contact is ambiguous. *Heterostoma paupercula* is a Desertan species which first appears on Madeira in Group III and is today found mainly in the eastern part of Madeira. It also occurs on Porto Santo, but study of the morphology and genetics indicates that the Madeiran and Desertan populations are more closely related to each other than to those of Porto Santo (Lace 1990, 1992). *Discula polymorpha* is represented by one specimen only in Group II, but is certainly established in Group III. It, too, occurs on the Desertas, where living representatives are morphologically distinct from their nearest neighbours on the eastern islets of Madeira (Cook *et al.* 1990). Like *H. paupercula*, there is a closely related taxon on Porto Santo (*D. calcigena*), in this case distinct but originally considered to be the same species (Waldén 1983). *Leptaxis undata* is a Madeiran species, absent from the earliest samples but present in Group II. It occurs on this island only, but has a sister species, *L. vulcania*, on the Desertas while there are fossil *Leptaxis* species on Porto Santo similar to it in appearance.

Contact between the Deserta islands and Madeira could have played a part in determining the distributions but movements between Porto Santo and the other islands are also implicated. In the early period, *Caseolus punctulatus* (or a similar species) is established in the sequence. It dies out, and considerably later its place is taken by *C. bowdichianus*. This is a fossil species occurring on Madeira and Porto Santo, while *C.*

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punctulatus occurs living and fossil on Porto Santo and the southern Deserta island (Bugio). Transport over the ocean barrier between Porto Santo and the other islands must have taken place in each species, and contact between the Desertas and Madeira is not suggested. While some of these distributions may be a consequence of the periodic development of land bridges, there are sufficient species common to Porto Santo and the other islands for this effect to be masked.

Although the pre-colonization faunas described here contain a number of extinct species, and are very unlike those currently living in the immediate vicinity, they show closer resemblances to other living faunas further west along the north coast of Madeira. These living faunas differ amongst themselves in the balance of species with grassland or woodland affinities, and these differences correlate with topography, vegetation and local moisture régime. The shifts in species composition between pre-colonization fossil faunas can be considered as temporal analogues of the spatial (and environmentally influenced) shifts found in modern faunas further west. The pattern of climate and sea level changes discussed above will have influenced environments elsewhere in Madeira. They will have occurred throughout the Pleistocene, and imply repeated movement and fragmentation of environments suitable for particular snail species, thus creating, at least near sea level, ideal circumstances for allopatric differentiation and speciation. The fossil sequence reported here provides some evidence of the scale and nature of local changes involved, which will help us to interpret present patterns of distribution in a historical context.

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APPENDIX 1.

Distribution of molluscan species between samples

The samples are arranged in order as far as possible from youngest (and highest in sequence) to oldest (and lowest in sequence). Sample numbers and section references are given at the head of each column. Dates and locations in the sequence can be seen by reference to table 1 and figure 3. The foot of each column shows the type of sample (R: random, bedded; P: picked, so that some species are under-represented; C: colluvial), the number of species, number of individuals and the evenness (J) of the sample. Groups shown below are derived from faunal similarity. In the list of species names, n indicates non-endemics, + extinct species and (+) species extinct on Madeira but extant on other islands. In the body of the table > indicates that the species is not present in the sample or in any to the left (younger).

species		1 20–1	2 16–3	3 12–4a	4 12–4b	5 12–4c	6 12–4d	7 13–3	8 13–2	9 13–6	10 16–2	11 12–8	12 13–5
1. *Craspedopoma mucronatum*		5	1	0	4	0	0	0	0	0	5	206	1
2. *C. trochoideum*		>	>	>	>	>	>	>	>	>	>	>	>
3. *Truncatellina linearis*	+	16	21	1	1	0	0	0	0	0	35	307	3
4. *Staurodon saxicola*		>	1	0	0	0	0	0	0	0	0	78	0
5. *Leiostyla laurinea*		>	>	>	>	>	>	>	>	>	>	>	>
6. *L. sphinctostoma*		>	>	>	>	>	>	>	>	>	>	1	0
7. *L. wollastoni*	+	>	1	0	0	0	0	0	0	0	0	0	0
8. *L. millegrana*		>	2	1	0	2	0	0	1	2	7	568	1
9. *L. abbreviata*		>	>	>	>	>	>	>	>	>	>	>	>
10. *L. cassida*		>	>	>	>	>	>	>	>	>	>	306	0
11. *L. gibba*		>	>	>	1	0	0	0	0	0	0	78	0
12. *Plagyrona placida*	n	>	>	>	>	>	>	>	>	>	>	2	0
13. *Punctum pygmaeum*	n	>	>	>	>	>	>	>	>	>	>	13	0
14. *Phenacolimax marcidus*		>	>	>	>	>	>	>	>	>	>	>	>
15. *P. crassus*	+	>	>	>	>	2	0	0	0	0	1	2	0
16. *Janulus stephanophora*		>	>	>	>	>	>	>	>	>	>	32	0
17. *J. bifrons*		2	0	0	0	0	0	0	0	0	0	173	0
18. *Amphorella t. minor*		>	>	>	>	>	>	>	1	1	0	22	2
19. *A. grabhami*	+	1	2	1	0	0	0	0	0	1	1	223	0
20. *Cylichnidia cylichna*	+	24	2	0	0	0	0	0	0	0	0	81	0
21. *Boettgeria lorenziana*	+	>	>	>	>	>	>	>	>	>	>	>	>
22. *Heterostoma paupercula*		>	>	4	4	14	19	0	7	0	0	3	0
23. *Geomitra tiarella*		40	10	2	4	5	0	0	1	0	14	538	2
24. *G. watsoni*	+	>	>	>	>	>	>	>	>	>	>	>	>
25. *G. delphinula*	+	1	0	0	0	1	0	0	0	0	0	7	0
26. *Spirorbula squalida*		2	0	0	0	0	0	0	0	0	3	19	0
27. *Caseolus compactus*		2	1	4	6	44	21	0	0	8	4	233	4
28. *C. sphaerulus*	+	>	>	>	>	>	>	>	>	>	>	>	>
29. *C. subcalliferus*	(+)	>	>	>	>	>	>	>	>	>	>	>	>
30. *C. punctulatus*	(+)	>	>	>	>	>	>	>	>	>	>	>	>
31. *C. bowdichianus*	+	3	1	1	0	1	0	0	0	0	1	203	1
32. *Actinella actinophora*		4	0	0	0	0	0	0	0	0	0	31	1
33. *A. arcinella*	+	3	0	0	0	1	0	0	0	0	0	4	0
34. *A. obserata*		>	>	>	>	>	>	>	>	>	>	2	0
35. *A. promontoriensis*	+	2	1	0	0	0	0	0	0	0	0	70	0
36. *A. nitidiuscula*		4	1	0	2	1	0	5	3	2	1	366	1
37. *Lemniscia calva*		1	1	0	0	0	0	0	0	0	0	118	0
38. *Discula polymorpha*		>	14	7	10	145	41	2	5	6	1	75	0
39. *Cochlicella barbara*	n	1	0	0	0	0	0	2	0	0	0	0	0
40. *Leptaxis erubescens*		>	>	>	>	>	>	>	>	>	>	66	0
41. *L. furva*		>	>	>	>	>	>	>	>	>	1	1	1
42. *L. undata*		>	>	1	1	1	0	0	5	0	0	0	2
43. *Theba pisana*	n	31	17	36	61	126	121	28	32	2	2	14	0
sample type		R	R	C	C	C	C	C	C	C	R	C	C
number of species		17	15	10	10	12	4	4	8	7	13	30	11
number of individuals		142	76	58	94	343	202	37	55	22	76	3842	19
evenness (J)		0.73	0.74	0.60	0.58	0.54	0.79	0.57	0.67	0.85	0.70	0.80	0.94
faunal group		Group V							Group IV				

Appendix 1 (*Continued*)

species		13 16–5	14 12–7	15 13–4	16 13–1	17 12–2	18 12–3	19 10–7A	20 10–7B	21 10–7	22 10–6	23 10–5	24 10–4
1. *Craspedopoma mucronatum*		1	28	1	3	11	15	14	1	8	43	3	9
2. *C. trochoideum*		>	>	>	>	>	>	>	>	>	>	>	>
3. *Truncatellina linearis*	+	92	77	98	14	56	1	3	0	250	675	13	253
4. *Staurodon saxicola*		0	13	20	2	6	0	2	0	8	126	2	0
5. *Leiostyla laurinea*		>	>	>	>	>	>	>	>	>	>	>	>
6. *L. sphinctostoma*		0	0	0	0	0	1	0	0	0	0	0	0
7. *L. wollastoni*	+	0	0	0	0	0	0	0	0	0	0	0	0
8. *L. millegrana*		24	17	76	12	1	36	0	0	14	57	3	19
9. *L. abbreviata*		>	>	>	>	>	>	>	>	>	>	>	>
10. *L. cassida*		0	31	0	0	0	19	0	0	0	0	0	0
11. *L. gibba*		0	13	1	0	0	8	0	0	0	0	0	0
12. *Plagyrona placida*	n	0	0	0	0	0	0	0	0	0	0	0	0
13. *Punctum pygmaeum*	n	0	18	0	0	3	0	0	0	0	0	0	0
14. *Phenacolimax marcidus*		>	>	>	>	>	>	>	>	>	>	>	>
15. *P. crassus*	+	1	4	0	0	0	0	0	1	1	1	2	0
16. *Janulus stephanophora*		0	0	0	0	0	1	0	0	0	0	0	0
17. *J. bifrons*		1	24	1	3	27	15	29	7	37	33	8	14
18. *Amphorella t. minor*		0	1	10	10	0	1	0	0	0	0	0	0
19. *A. grabhami*	+	0	34	0	0	21	22	6	0	12	17	0	38
20. *Cylichnidia cylichna*	+	0	7	9	1	0	3	0	0	0	5	0	0
21. *Boettgeria lorenziana*	+	>	>	>	>	>	>	>	>	>	>	>	>
22. *Heterostoma paupercula*		0	0	0	0	1	1	0	0	0	1	0	0
23. *Geomitra tiarella*		21	45	10	23	29	73	137	7	57	50	17	42
24. *G. watsoni*	+	>	>	>	>	>	>	>	>	1	0	0	0
25. *G. delphinula*	+	0	4	0	0	18	1	23	40	25	12	7	9
26. *Spirorbula squalida*		2	2	0	0	5	0	0	0	0	1	0	0
27. *Caseolus compactus*		6	13	27	23	4	29	11	0	0	2	9	5
28. *C. sphaerulus*	+	>	>	>	>	>	>	>	>	>	>	>	>
29. *C. subcalliferus*	(+)	>	>	>	>	>	>	>	>	>	>	>	>
30. *C. punctulatus*	(+)	>	>	>	>	>	>	>	>	>	>	>	>
31. *C. bowdichianus*	+	20	23	5	15	96	51	82	36	10	16	15	20
32. *Actinella actinophora*		1	3	0	0	1	0	16	0	3	15	3	3
33. *A. arcinella*	+	0	0	6	2	0	1	0	0	0	0	0	0
34. *A. obserata*		0	0	0	0	0	0	0	0	0	0	0	0
35. *A. promontoriensis*	+	0	3	0	0	2	2	11	0	8	13	3	0
36. *A. nitidiuscula*		11	13	43	110	16	36	75	14	4	20	7	4
37. *Lemniscia calva*		0	8	0	0	2	3	34	4	18	23	7	16
38. *Discula polymorpha*		0	2	2	4	2	7	7	3	2	3	0	0
39. *Cochlicella barbara*	n	0	0	0	0	0	0	0	0	0	0	0	0
40. *Leptaxis erubescens*		0	7	3	20	3	6	18	11	13	14	8	9
41. *L. furva*		0	2	0	0	0	0	2	1	2	4	6	3
42. *L. undata*		0	6	5	30	1	1	5	43	2	6	0	0
43. *Theba pisana*	n	0	0	0	0	0	0	0	0	0	0	0	0
sample type		R	C	C	C	C	C	R	P	R	R	R	R
number of species		11	25	16	15	20	23	17	12	19	22	16	14
number of individuals		180	398	317	272	305	333	475	168	475	1137	113	444
evenness (J)		0.65	0.85	0.73	0.76	0.73	0.78	0.78	0.77	0.62	0.54	0.93	0.63
faunal group		Group IV				Group III							

Appendix 1 (*Continued*)

species		25 16–1	26 12–1	27 10–3	28 16–4	29 10–2	30 10–1	31 12–5	32 11–3	33 19–1	34 20–2	35 11–2	36 11–1
1. *Craspedopoma mucronatum*		7	0	0	1	0	0	0	23	6	1	46	20
2. *C. trochoideum*		>	>	>	>	>	>	>	2	0	0	0	0
3. *Truncatellina linearis*	+	45	2	1	1	5	0	0	1	0	243	45	252
4. *Staurodon saxicola*		12	0	1	0	0	0	0	0	3	468	24	48
5. *Leiostyla laurinea*		>	>	>	>	>	>	>	>	>	>	>	>
6. *L. sphinctostoma*		0	0	0	0	0	0	0	0	0	0	0	0
7. *L. wollastoni*	+	2	0	0	2	0	0	0	0	0	5	0	18
8. *L. millegrana*		32	2	3	0	36	0	0	3	0	6	26	1
9. *L. abbreviata*		8	0	0	0	0	0	0	0	1	0	0	0
10. *L. cassida*		1	0	0	0	0	0	0	35	4	0	0	0
11. *L. gibba*		0	0	0	0	0	0	0	3	0	0	0	0
12. *Plagyrona placida*	n	0	0	0	0	0	0	0	0	0	0	0	1
13. *Punctum pygmaeum*	n	5	0	0	0	0	0	0	0	2	0	5	6
14. *Phenacolimax marcidus*		>	>	>	>	>	>	>	>	>	>	>	3
15. *P. crassus*	+	1	4	0	0	3	0	0	1	0	3	5	0
16. *Janulus stephanophora*		0	0	0	0	0	0	0	0	0	0	0	0
17. *J. bifrons*		27	18	0	2	0	0	0	3	7	0	28	10
18. *Amphorella t. minor*		0	0	0	0	0	0	0	0	0	0	0	1
19. *A. grabhami*	+	13	2	0	2	1	0	0	30	1	2	10	10
20. *Cylichnidia cylichna*	+	130	0	0	0	0	0	0	1	0	0	0	0
21. *Boettgeria lorenziana*	+	>	>	>	>	>	1	0	0	0	0	0	0
22. *Heterostoma paupercula*		0	1	0	0	0	0	0	0	0	0	0	0
23. *Geomitra tiarella*		8	2	22	52	26	13	5	6	63	35	32	79
24. *G. watsoni*	+	0	0	0	0	0	0	0	0	0	0	0	0
25. *G. delphinula*	+	4	0	0	0	0	1	1	1	4	3	7	9
26. *Spirorbula squalida*		0	4	0	6	0	0	3	8	25	0	0	0
27. *Caseolus compactus*		3	5	2	0	0	0	0	0	0	3	20	1
28. *C. sphaerulus*	+	>	>	>	>	>	>	2	0	0	0	20	0
29. *C. subcalliferus*	(+)	>	>	>	>	>	>	>	>	>	>	>	>
30. *C. punctulatus*	(+)	>	>	>	>	>	>	>	>	>	>	>	>
31. *C. bowdichianus*	+	18	6	27	13	22	18	0	0	0	0	0	0
32. *Actinella actinophora*		12	0	1	5	8	1	0	1	1	0	0	0
33. *A. arcinella*	+	1	4	0	2	0	0	0	0	1	29	1	4
34. *A. obserata*		0	0	0	0	0	0	0	0	0	0	0	0
35. *A. promontoriensis*	+	0	0	0	0	0	1	0	0	2	0	0	0
36. *A. nitidiuscula*		6	17	2	27	5	2	4	7	33	0	20	7
37. *Lemniscia calva*		14	1	0	1	0	0	0	20	25	3	12	32
38. *Discula polymorpha*		4	0	0	1	0	0	0	0	0	0	0	0
39. *Cochlicella barbara*	n	0	0	0	0	0	0	0	0	0	0	0	0
40. *Leptaxis erubescens*		3	5	12	2	7	5	2	0	23	21	3	7
41. *L. furva*		0	1	0	2	1	0	1	2	21	2	3	1
42. *L. undata*		3	1	0	0	0	0	0	0	0	0	3	3
43. *Theba pisana*	n	0	0	0	0	0	0	0	0	0	0	0	0
sample type		R	R	R	R	R	R	R	R	R	R	R	R
number of species		23	16	9	15	10	8	7	17	17	14	18	20
number of individuals		359	75	71	119	114	42	18	147	222	824	310	513
evenness (J)		0.74	0.84	0.70	0.66	0.79	0.71	0.92	0.77	0.77	0.46	0.89	0.61
faunal group		Group III							Group II				

Appendix 1 (*Continued*)

species		37 17–1	38 15–5	39 21–1	40 15–6	41 15–4	42 15–1	43 15–2	44 15–3	45 14–2	46 14–3	47 14–4	48 14–1
1. *Craspedopoma mucronatum*		0	3	5	34	39	20	1	0	0	0	0	10
2. *C. trochoideum*		0	0	0	0	0	0	0	0	0	0	0	0
3. *Truncatellina linearis*	+	0	114	39	22	42	1	5	1	0	0	231	63
4. *Staurodon saxicola*		0	17	22	3	0	0	1	0	0	0	0	98
5. *Leiostyla laurinea*		>	>	>	>	>	>	>	>	>	>	>	2
6. *L. sphinctostoma*		0	0	0	1	0	0	0	0	0	0	0	0
7. *L. wollastoni*	+	0	0	0	1	0	0	0	0	0	0	0	1
8. *L. millegrana*		0	1	0	0	0	0	0	1	0	0	0	0
9. *L. abbreviata*		0	0	0	0	0	0	0	0	0	0	0	0
10. *L. cassida*		0	0	0	2	11	3	0	0	0	0	0	17
11. *L. gibba*		0	0	0	4	0	0	0	0	0	0	0	0
12. *Plagyrona placida*	n	0	0	0	0	0	0	0	0	0	0	0	0
13. *Punctum pygmaeum*	n	0	0	2	3	8	0	0	0	0	0	0	0
14. *Phenacolimax marcidus*		2	3	0	0	0	0	0	0	0	0	0	0
15. *P. crassus*	+	2	1	2	0	1	1	0	0	0	0	0	1
16. *Janulus stephanophora*		0	0	0	0	0	0	0	10	0	0	1	0
17. *J. bifrons*		1	3	16	16	3	20	0	0	0	0	0	2
18. *Amphorella t. minor*		2	0	1	0	0	0	0	0	0	0	0	3
19. *A. grabhami*	+	0	2	14	22	23	20	0	3	0	0	2	4
20. *Cylichnidia cylichna*	+	0	2	0	7	0	10	1	0	0	0	1	3
21. *Boettgeria lorenziana*	+	0	0	0	0	0	0	0	0	0	0	0	0
22. *Heterostoma paupercula*		0	0	0	0	0	0	0	0	0	0	0	0
23. *Geomitra tiarella*		0	41	21	21	1	20	2	1	0	0	0	0
24. *G. watsoni*	+	4	0	0	0	0	0	2	1	4	1	71	24
25. *G. delphinula*	+	1	2	0	6	4	7	0	0	0	0	0	0
26. *Spirorbula squalida*		0	0	12	0	0	0	0	0	0	0	0	0
27. *Caseolus compactus*		53	2	0	1	1	0	12	1	16	1	18	1
28. *C. sphaerulus*	+	2	1	0	1	0	0	5	0	4	1	7	4
29. *C. subcalliferus*	(+)	18	0	0	0	0	1	0	0	0	0	0	0
30. *C. punctulatus*	(+)	>	>	>	>	>	>	>	>	>	1	4	8
31. *C. bowdichianus*	+	0	0	0	0	0	0	0	0	0	0	0	0
32. *Actinella actinophora*		0	1	0	17	0	13	2	0	1	1	4	1
33. *A. arcinella*	+	1	5	9	0	0	1	17	4	1	1	1	7
34. *A. obserata*		0	0	0	0	0	0	0	0	0	0	0	0
35. *A. promontoriensis*	+	0	0	0	0	0	0	0	0	0	0	0	0
36. *A. nitidiuscula*		1	21	13	1	2	3	6	9	27	1	20	10
37. *Lemniscia calva*		1	9	39	12	6	20	4	2	11	1	16	10
38. *Discula polymorpha*		0	0	0	1	0	0	0	0	0	0	0	0
39. *Cochlicella barbara*	n	0	0	0	0	0	0	0	0	0	0	0	0
40. *Leptaxis erubescens*		1	2	7	8	1	20	1	0	0	1	0	3
41. *L. furva*		1	2	1	6	1	5	1	1	2	1	1	0
42. *L. undata*		0	1	1	1	1	2	0	0	0	0	0	0
43. *Theba pisana*	n	0	0	0	0	0	0	0	0	0	0	0	0
sample type		P	R	R	R	R	P	R	R	R	P	R	R
number of species		14	20	16	22	15	17	14	11	8	10	13	20
number of individuals		90	233	204	190	144	167	60	34	66	10	377	272
evenness (J)		0.55	0.60	0.85	0.83	0.72	0.86	0.83	0.82	0.76	1.00	0.51	0.70
faunal group		Group II							Group I				

Appendix 1 (*Continued*)

species		49 18–3	50 18–1	51 18–2
1. *Craspedopoma mucronatum*		0	0	0
2. *C. trochoideum*		0	0	0
3. *Truncatellina linearis*	+	44	7	0
4. *Staurodon saxicola*		0	3	0
5. *Leiostyla laurinea*		0	0	0
6. *L. sphinctostoma*		0	0	0
7. *L. wollastoni*	+	0	0	0
8. *L. millegrana*		0	0	0
9. *L. abbreviata*		0	0	0
10. *L. cassida*		0	0	0
11. *L. gibba*		0	0	0
12. *Plagyrona placida*	n	0	0	0
13. *Punctum pygmaeum*	n	0	0	0
14. *Phenacolimax marcidus*		0	0	0
15. *P. crassus*	+	2	0	0
16. *Janulus stephanophora*		0	0	0
17. *J. bifrons*		0	0	0
18. *Amphorella t. minor*		0	0	0
19. *A. grabhami*	+	0	0	0
20. *Cylichnidia cylichna*	+	0	0	0
21. *Boettgeria lorenziana*	+	0	0	0
22. *Heterostoma paupercula*		0	0	0
23. *Geomitra tiarella*		0	1	2
24. *G. watsoni*	+	0	0	0
25. *G. delphinula*	+	0	0	0
26. *Spirorbula squalida*		0	0	0
27. *Caseolus compactus*		0	11	0
28. *C. sphaerulus*	+	1	19	20
29. *C. subcalliferus*	(+)	0	11	0
30. *C. punctulatus*	(+)	0	1	0
31. *C. bowdichianus*	+	0	0	0
32. *Actinella actinophora*		0	0	0
33. *A. arcinella*	+	10	9	1
34. *A. obserata*		0	0	0
35. *A. promontoriensis*	+	0	0	0
36. *A. nitidiuscula*		7	14	4
37. *Lemniscia calva*		0	0	1
38. *Discula polymorpha*		0	0	0
39. *Cochlicella barbara*	n	0	0	0
40. *Leptaxis erubescens*		0	0	1
41. *L. furva*		0	1	2
42. *L. undata*		0	0	0
43. *Theba pisana*	n	0	0	0
sample type		C	C	C
number of species		5	10	7
number of individuals		64	77	31
evenness (J)		0.60	0.86	0.63
faunal group			Group I	

gure 2. Fossil shells and aeolian deposits, Madeira. (*a*) *Leptaxis undata*; (*b*) *Actinella nitidiuscula*; (*c*) *Geomitra delphinula* xtinct); (*d*) *Caseolus bowdichianus* (extinct); (*e*) view of the road cut. The person is 1.83 m high. Above his head can seen the thick clay unit with carbonate concretions. At the top of the section is the base of the Holocene sand unit ntaining abundant *C. bowdichianus*. The lower left part of the section is covered by sediments slumped from above;) a lag deposit of land snail shells (mostly *C. bowdichianus*) on top of the deflated surface of the main hill.