Impact of early Polynesian occupation on the land snail fauna of Henderson Island, Pitcairn group (South Pacific)

R. C. Preece

Phil. Trans. R. Soc. Lond. B 1998 **353**, 347-368
doi: 10.1098/rstb.1998.0214

The Royal Society

Impact of early Polynesian occupation on the land snail fauna of Henderson Island, Pitcairn group (South Pacific)

R. C. Preece

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

CONTENTS

	pages
1. Introduction	347
2. The nature of Henderson Island	348
3. The sites and their stratigraphy	349
4. Sampling and analyses	351
5. Preservation and problems of identification	351
6. Land snail analyses	352
7. Radiocarbon dates	353
8. Systematic review	354
9. Discussion	363
References	367

Henderson Island, an uninhabited raised coral atoll in the Pitcairn group, has recently been designated a World Heritage Site because of its unique and relatively undisturbed ecosystem. The island is believed to have been uplifted and subaerially exposed during the last 275 kyr. This therefore provides the maximum age for the terrestrial biota that includes several endemic taxa. Henderson today supports 16 strictly terrestrial species of snails, about half of which are endemic. Analyses of sediments beneath Polynesian occupation horizons dated between the eleventh and seventeenth centuries AD, have yielded 11 species of land snail present in the modern fauna, together with at least six (and possibly as many as eight) further species that no longer occur on the island. These extinct taxa are illustrated and formal descriptions provided for five (*Pleuropoma hendersoni*, *Orobophana carinacosta*, *Minidonta macromphalus*, *Philonesia pyramidalis*, *P. weisleri*); a sixth, known only from broken shells, appears to belong to the genus *Hiona*. The two remaining taxa are 'tornatellinids' that have not been recognized among the modern fauna. Radiocarbon dates from bones of associated extinct land birds confirm their occurrence on Henderson before the first signs of Polynesian settlement. The extinction of these taxa seems to coincide with the Polynesian occupation and evidence for large-scale burning, at least around parts of the plateau margin, suggests that their demise can be linked with habitat destruction. At least three species, *Gastrocopta pediculus*, *Lamellidea oblonga* and *Pupisoma orcula*, first appear in Polynesian occupation horizons. Their status as prehistoric introductions is therefore confirmed, but *G. pediculus* no longer lives on Henderson. *Pacificella variabilis*, *Tornatellides oblongus parvulus* and *Elasmias* sp., all previously thought to have been other prehistoric introductions to Henderson, were recovered from pre-Polynesian levels and are therefore native.

Keywords: land snail extinctions; Polynesian impact; endemic land snails; Henderson Island; Pitcairn Islands; fossil land snails

1. INTRODUCTION

Faunal histories of remote oceanic islands have furnished much of the raw data that underpin theories of island biogeography and evolution. For many groups of organisms the prospects of gaining insights into the history of colonization and evolutionary events following successful establishment are extremely slim. Land snails, on the other hand, leave shells that can provide good fossil records. As many oceanic islands have volcanic origins, they frequently lack calcareous sediments suitable for the preservation of shells. It is consequently difficult to obtain data that relate to these important biogeographical and evolutionary issues. Conclusions about the status of species on different islands have mostly had to rely on circumstantial evidence, such as wide geographical distributions, anthropophilic associations and unrelatedness to other taxa in the area, rather than on direct evidence from the fossil record. There are some noteworthy exceptions. Thick aeolianite deposits on Madeira, for example, have yielded sequences of land snail assemblages from the Middle Pleistocene to the present day. These have provided a geological perspective on patterns of endemism and rates of faunal turnover, as well as allowing an assessment of the

Phil. Trans. R. Soc. Lond. B (1998) **353**, 347–368
Received 7 October 1996 *Accepted* 25 February 1997

effects of introduced taxa during the historical period (Cook *et al.* 1990, 1993; Goodfriend *et al.* 1994, 1996; Cameron & Cook 1997). Nearly all the other information on fossil land snail assemblages on oceanic islands relates to work undertaken at or close to archaeological sites of more recent date (e.g. Christensen & Kirch 1981, 1986).

Almost every remote oceanic island in the Pacific supports an endemic fauna of land snails. Only atolls, which have had emergent land only during the past 8000 years, lack rich endemic faunas. Moreover, any evolutionary novelties that may have arisen during this time are likely to have been eliminated by tropical storms, which regularly cause inundation of the entire surfaces of low-lying atolls. Atoll endemics appear to be restricted to the few known exceptions to this rule, where Pleistocene outcrops occur (Paulay 1991*a*).

Crustal disturbances resulting from the formation of new islands by active volcanism can cause uplift of neighbouring atolls at critical distances from the volcanic centres by the process of lithospheric flexure (McNutt & Menard 1978; Spencer 1995). Even an uplift of only a few metres can render these newly raised atolls relatively immune from washovers, and endemic faunas can begin to develop. Such islands potentially offer enormous opportunities for studying patterns of colonization and rates of faunal turnover (cf. Taylor *et al*. 1979). First, because they are composed of limestone, they are more likely than volcanic islands to furnish good fossil records. Second, it might be possible to obtain more accurate estimates of the maximum age of the terrestrial faunas by high-precision uranium–thorium (U-Th) dating of the now subaerially exposed fossil corals. Such dates will be able to constrain the time-scale for the development of the terrestrial biota far better than, for example, radiometric dates of surface basalts, a common way of deriving the age of an oceanic island. Such ages may relate only to the latest episode of volcanic activity, rather than dating rocks from the main constructional phase, which may be deeply buried. Regrettably, these possibilities have been wasted for almost all such islands in the Pacific because they have been severely disturbed by human activity, both recently and by Polynesian voyagers in the past. This has resulted in the widespread extinctions of endemic taxa, as well as the dispersal and introduction of alien species. Consequently, it is difficult to appreciate the original composition and diversities of land snail communities in natural habitats or even to fully comprehend the scale of humanly induced extinctions.

This paper presents data on fossil land snail assemblages from Henderson Island in the Pitcairn group. This remote uninhabited island stands alone as probably the last essentially pristine elevated limestone island in the world (Fosberg *et al.* 1983) and was the main reason for its designation by UNESCO as a World Heritage Site. Compared with almost all other Pacific islands, Henderson is indeed relatively undisturbed and retains a significant endemic biota (Paulay 1991*b*). Recent archaeological work, however, has shown that Henderson was settled by early Polynesians between 800 and 1050 AD and deserted sometime in the seventeenth century, following an abrupt end to inter-island voyaging at about 1450 AD (Weisler 1994, 1995). The island was discovered by Europeans in 1606, but no landing was attempted and no signs of human settlement were reported. The fossils, reported on here, were recovered not only from radiocarbon-dated Polynesian occupation horizons but also from levels beneath, so that it has been possible to assess the impact that may have resulted from the 600-year period of human occupation. It has also been possible to establish from the fossil record the status of various species, as either native or introduced. These fossil assemblages include a number of apparently undescribed taxa that no longer occur on Henderson (cf. Preece 1995*a*). Formal descriptions are provided for these extinct land snails and details of the associated fauna are given. The specimens have been deposited in the University Museum of Zoology, Cambridge (UMZC), England, UK.

2. THE NATURE OF HENDERSON ISLAND

The Pitcairn Islands are the easternmost islands on the Pacific Plate and are located towards the south-eastern margin of the Indo-Pacific province, some 390 km east of their nearest neighbour, Temoe Atoll in the Tuamotu-Gambier Islands, and 1570 km west of Easter Island (figure 1). The four islands that comprise the Pitcairn group appear to result from two volcanic hotspots. One, located near Pitcairn, gave rise to that island during two phases of volcanism, the main constructional phase at 0.95–0.76 Myr and a second between 0.63 and 0.45 Myr (Duncan *et al.* 1974). It may have given rise to others islands on the same alignment in the southern Tuamotus. Another appears to have been responsible for Oeno, Henderson and Ducie, estimated to be 16, 13 and 8 Myr, respectively (Spencer 1995), which lie on a parallel line of weakness. The dates for these islands are inferred, based on a number of assumptions, so they must be regarded as first approximations (Spencer 1995).

Henderson (24°22′ S 128°20′ W) with maximum dimensions of 9.6×5.1 km is the largest island in the Pitcairn group with an area of 37 km^2. It is an uplifted atoll with peripheral rims reaching about 33 m above sea level, surrounding a central depression with an elevation of 22 m, interpreted as a fossil lagoon (Paulay & Spencer 1988; Pandolfi 1995). Henderson is therefore extremely flat, with more than 80% of its land surface above 20 m. About half the coastline is bordered by fringing reef, particularly in the north, and the south coast is bounded by sheer vertical cliffs.

The uplift of Henderson is thought to result from loading following the emplacement of Pitcairn, that lies 200 km west-south-west, through the process of lithospheric flexure. U-Th dates obtained from *in situ* fossil corals from Henderson span the period 404–225 kyr (Blake 1995). As mean sea level in this part of the Pacific is believed to have been several metres higher between 440–380 kyr ago, it is thought that Henderson would have become emergent and subaerially exposed for a period from 380 kyr. The island was submerged again during the next high sea level phase at about 280 kyr, and corals of this age have been found in the fossil lagoon (Blake 1995). Subsequently, the island again became emergent, perhaps about 275 kyr. This date therefore provides a maximum age for the modern terrestrial biota. The younger corals, which formed up to 18 m above the present sea level on the margin of Henderson 230–215 kyr,

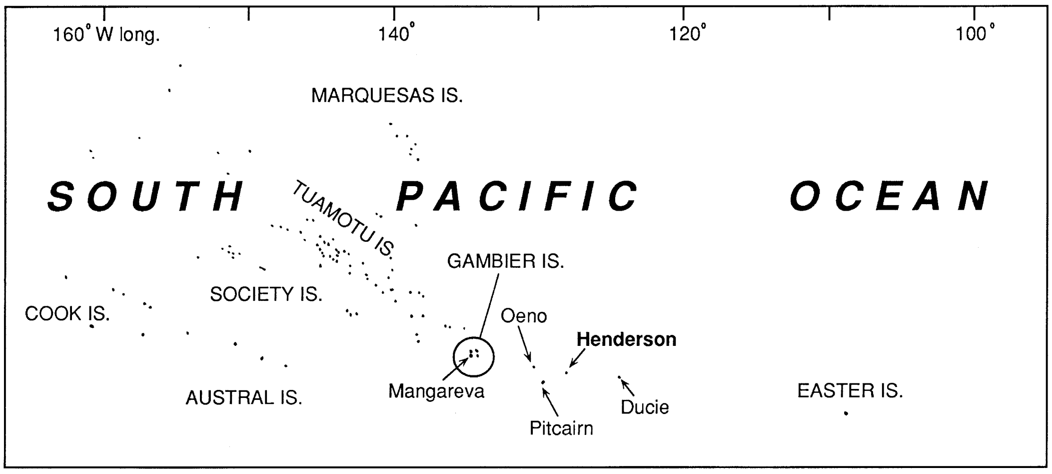

Figure 1. Islands of south-eastern Polynesia showing the location of Henderson and other islands mentioned in the text.

are direct evidence that this high sea level phase occurred after uplift, as the sea did not cover the surface of the island as it had done previously.

The limited meteorological data from Henderson (Spencer 1995) suggest that it receives an annual rainfall of about 1600 mm, about 30% less than Pitcairn. It has a clear seasonal pattern of temperature. For the one-year period for which there are records, the mean monthly maximum temperature varied between 29.6 °C (February 1991) and 24.2 °C (June 1991); the comparable minimum temperatures were 22.2 °C (February) and 15.7 °C (June). The maximum temperature recorded was 31.4 °C, on three occasions in February and March, and the absolute minimum 12.0 °C (September).

Much of the surface of Henderson is composed of raised coral limestone ('makatea'), now heavily dissected and karstified, with pinnacles and crevasses up to 7 m deep (Paulay & Spencer 1988; Spencer & Paulay 1989; Pandolfi 1995). There are no streams or bodies of standing water and, consequently, no wetland habitats. Soils are generally thin and patchy, although more extensive areas of soil cover occur towards the south. Sixty-three native vascular plants are known, nine of which are endemic (Florence *et al.* 1995). Much of the plateau supports a dense cover of closed-canopy woodland dominated by *Pisonia grandis*, but with a number of other species, including several endemics. The general canopy height is 7–10 m. Areas of more open vegetation occur towards the south of the island. The herb layer of the plateau forest is usually well-developed, consisting of *Peperomia hendersonensis*, *Procris pedunculata*, *Asplenium nidus* and *Phymatosorus scolopendria* (Waldren *et al.* 1995). The vegetation is relatively undisturbed and only six species of introduced plants have been recognized (Florence *et al.* 1995).

3. THE SITES AND THEIR STRATIGRAPHY

Archaeological excavations under the direction of Marshall Weisler were undertaken at a number of sites on Henderson during the Sir Peter Scott Commemorative Expedition (1991–1992). A number of caves and rock-shelters were studied, as well as a large coastal midden behind the North Beach (Weisler 1994, 1995). Each major site was given a number (prefixed Hen-) and every trial pit (TP) excavated at each one was also numbered sequentially. Although small samples were collected for fossil land snails from a number of locations, attention is here focused on two of the most critical sites.

(a) *Hen-6*

The most important site to provide evidence of the land snail fauna of Henderson before the arrival of humans was a cave (Hen-6) behind the eastern end of the North Beach (figure 2). The cave extended about 15 m in from the dripline, and had an entrance about 12 m wide. It had been cut into the fossil cliff about halfway up the slope, approximately 18 m above sea level. A water drip was located at the back of the cave and ferns grew along the base of the walls where the light penetrated.

Samples containing the fossil snails were obtained from TP 1 (dimensions 1 m × 2 m), excavated in the centre of the cave about 5 m inside the dripline. Trial pit 2 was located adjacent to TP 1, and was subsequently extended to join the two pits. The cave sediments reached a maximum thickness of 108 cm and rested on an irregular surface of limestone bedrock. Figure 3 is a sketch of the stratigraphy showing the positions of samples taken for land snail analysis. The individually numbered spits, coarsely screened for shells and artefacts, are also shown. In places, pockets of shelly sand (sample 7) were found filling fissures in the limestone surface.

The sediments are predominantly fine-to-medium sands with small comminuted marine shells, especially in the lower levels. The lower unit (5) is a fine, cream-to-white sand lacking any appreciable organic component, but the sands in the upper units (1–4) are stained black and contain many small charcoal fragments. Bones of birds, shells of land snails, and the remains of terrestrial hermit crabs (*Coenobita* spp.) were frequent throughout. Bones of Pacific rat (*Rattus exulans*) were frequent only in the upper Polynesian levels (units 1–4).

(b) *Hen-5*

Sixteen trial pits were excavated in the large coastal midden, measuring 9900 m^2 behind the North Beach (Weisler 1995; figure 2). The stratigraphy was simple and relatively uniform across the whole area of the midden (figure 4). Trial pit 1, from which the analysed samples

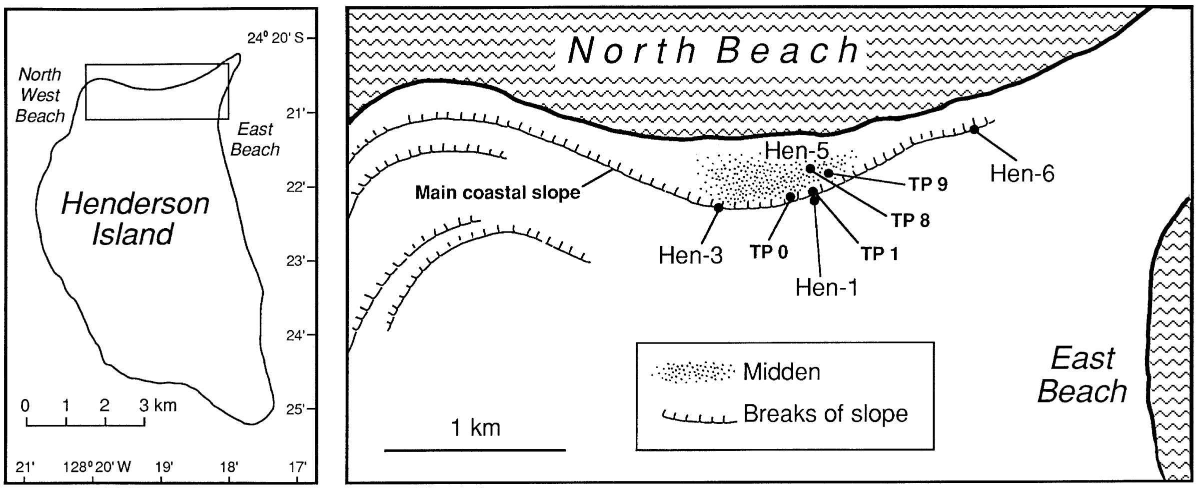

Figure 2. Maps of Henderson Island showing the locations of Hen-5, Hen-6, and other sites mentioned in the text.

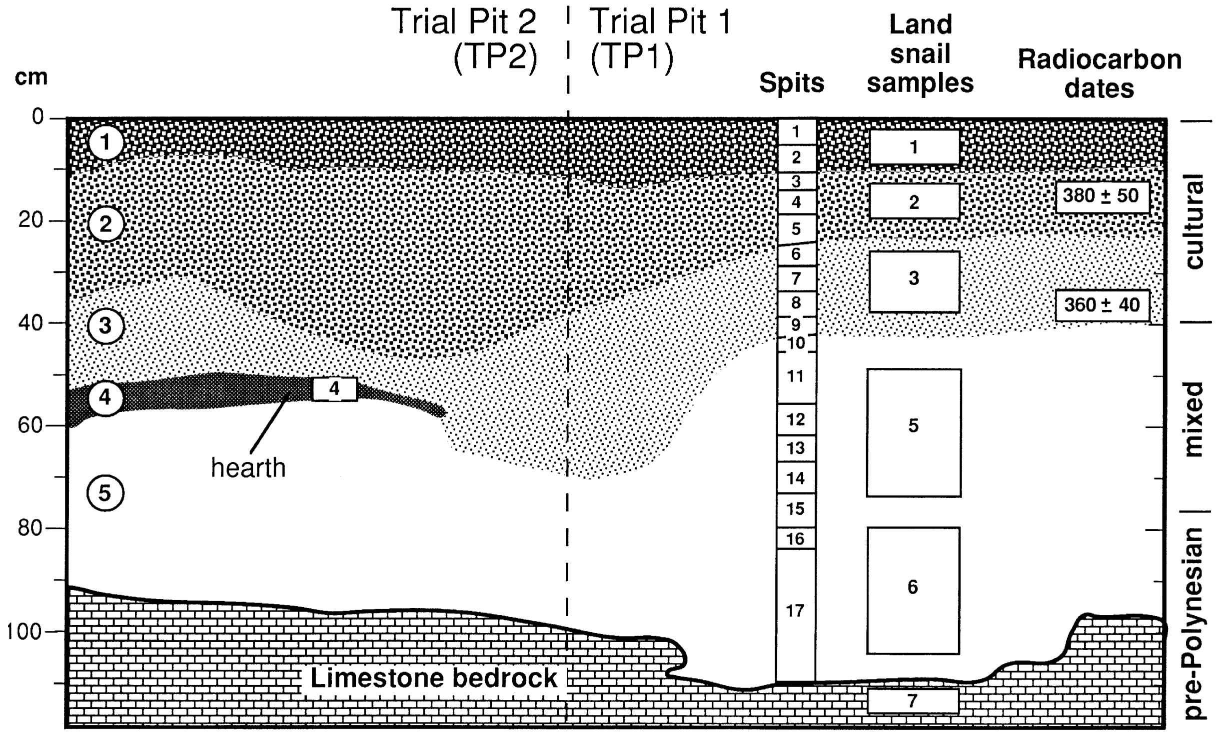

Figure 3. Schematic section through TP 1 and TP 2 in Hen-6 showing the major stratigraphical units, sampled spits and the positions of samples taken for land snail analysis and radiocarbon dating (only charcoal dates shown; for details of AMS dates on bone, see text). Stratigraphical/archaeological units: 1, humus layer (A horizon); 2, powdery sediment with much charcoal; 3, light grey powdery sediment with some charcoal; 4, hearth with abundant charcoal; 5, pale yellowish fine sand, occasional small limestone fragments.

were taken, was located at the base of the slope in front of a cave (Hen-1). A basal medium-to-coarse white sand (about 120 cm thick) rested on large slabs of limestone at a depth of about 180 cm below the ground surface. Although devoid of artefacts, this sand did yield the remains of extinct birds, especially bones of pigeons (*Ducula* sp. and *Gallicolumba* sp.). A thick, dark cultural horizon (25–30 cm thick), rich in charcoal and Polynesian artefacts, occurred directly above and graded into an upper white sand devoid of artefacts. Radiocarbon dates of 380 ± 70 years BP and 660 ± 110 years BP were obtained from charcoal from the top and base of the cultural horizon, respectively (see below for complete details).

An initial trial pit (TP 0) had previously been excavated about 50 m west of TP 1, revealing the first signs of the important Polynesian midden described above. This trial pit is mentioned here for two reasons. First, it was from the cultural horizon of this pit that a large sample of *Orobophana carinacosta* n. sp. was collected and measured (see below). Second, associated charcoal yielded a radiocarbon date of 1120 ± 50 years BP), the oldest 'Polynesian' date yet obtained for the whole island.

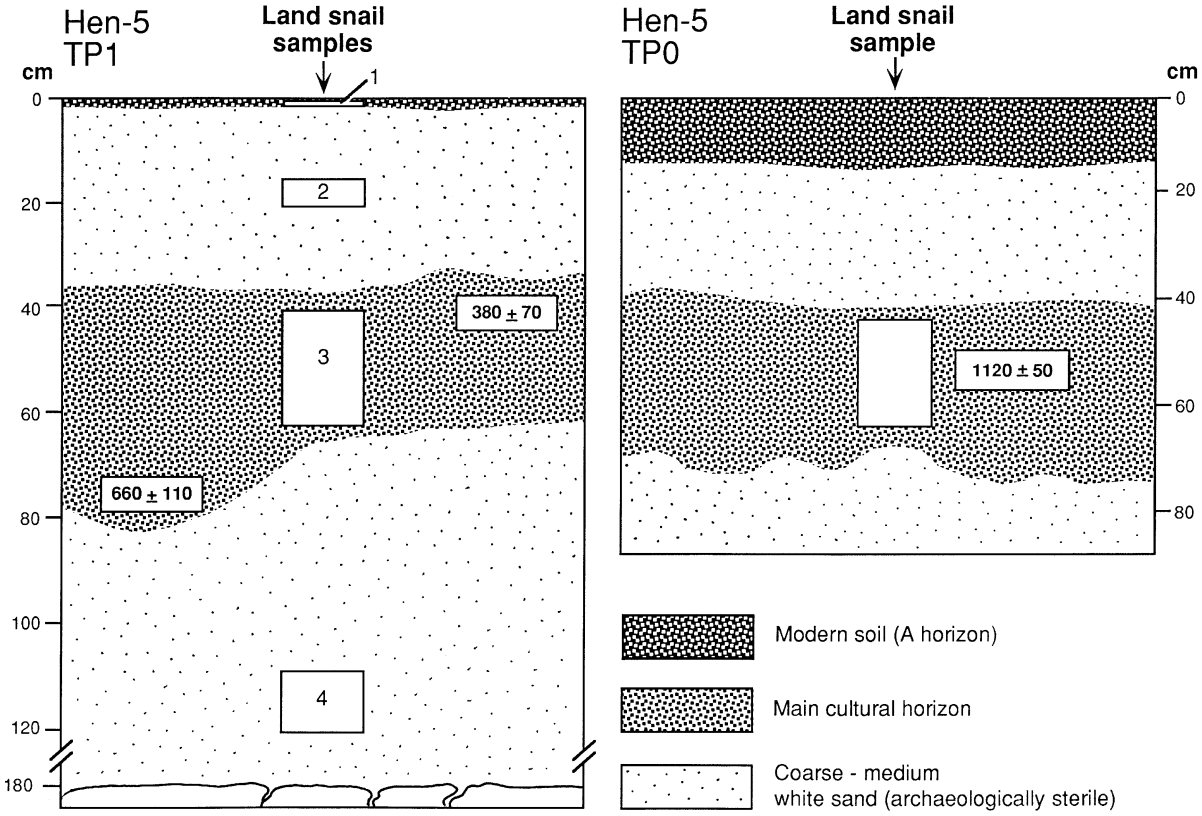

Figure 4. Schematic stratigraphical sections through two trial pits excavated through the coastal midden (Hen-5). TP 1 is on the left, and TP 0 is on the right. The positions of samples taken for land snail analysis and radiocarbon dating are also shown.

Mention should be made of two further trial pits (TP 8 and TP 9), as these have also provided radiocarbon dates relevant to the present study (see below). TP 8 was located approximately halfway between TP 1 and the shore; TP 9 was dug about 50 m east of TP 8 and 20 m closer to the main coastal slope (figure 2). Here a bone of *Ducula* sp. from sand beneath the cultural horizon provided a radiocarbon date of 2065±55 years BP, confirming the 'pre-Polynesian' age of the unit. Full details of all the radiocarbon dates are given below.

4. SAMPLING AND ANALYSES

The samples were collected in two ways. As part of the archaeological work, bulk samples of sediment carefully excavated from different spits in the trial pits were routinely sieved on site. Most were screened over a 6 mm or a 3 mm mesh but very occasionally a 1.6 mm mesh was used. This obviously retained the larger snails (especially *Orobophana*), but failed to recover any of the more numerous smaller taxa. These were recovered from a series of small samples of raw sediment taken from the main stratigraphical units and returned to Britain for laboratory analyses. Larger samples of raw sediment were obtained from Hen-5, but these lacked most of the extinct taxa recovered from the older sediments in Hen-6. All the sediment samples were analysed in the standard way by wet-sieving (Evans 1972); a small quantity of hydrogen peroxide was used on sediment from the 'cultural horizons' to clean shells stained black. This treatment was only partly successful. Minimum totals for each species present were derived by counting every shell or apex retained on a 0.5 mm sieve. To avoid counting specimens twice, non-apical fragments were not counted unless they represented species otherwise unrepresented in the analysis (tables 1 and 2).

5. PRESERVATION AND PROBLEMS OF IDENTIFICATION

The preservation of shells throughout the Hen-6 sequence was generally excellent. The surface ornament was still preserved in most specimens and many shells were translucent and had not become opaque with age. Even traces of colour banding remained on some of the specimens of *Philonesia*. Preservation of shells in the Hen-5 sequence was inferior, and many specimens from the Polynesian cultural horizons were covered with a black encrustation that generally resisted treatment in hydrogen peroxide. The preservation was nevertheless reasonably good.

The excellent preservation meant that identification of many of the specimens was reasonably straightforward, but two problems were encountered. First, the assemblages were dominated by 'tornatellinid' members of the Achatinellidae. Identification of adult or even half-grown shells could be achieved relatively satisfactorily once the sediment obscuring the diagnostic apertural barriers had been carefully removed with a fine paint-brush. Most of the specimens, however, were very small juveniles at what Cooke & Kondo (1961) call the ananeanic stage. These could often not be split into species with any confidence and are listed in the tables under 'unidentified achatinellids'. This is a well-known problem with Pacific island land snail analyses (e.g. Christensen & Kirch 1986). Brief notes on identification characters, particularly for immature

Table 1. *Land snail analyses from Hen-6*

sample number (see figure 3)	6	5	4	3	2	1
dry mass of sample (g)	72.6	74.6	3.7	138.5	118.3	89.7
Georissa hendersoni	46	86	5	36	3	1
Orobophana solidula	9	17	2	3	1	1
[a]*Pleuropoma hendersoni* n. sp.	5	5	—	2	—	—
Assiminea sp.	6	7	1	6	5	—
Tubuaia hendersoni	21	32	—	7	1	—
Lamellidea sp.	3	13	—	1	—	—
Elasmias sp.	47	62	2	12	4	1
Pacificella variabilis without palatals	11	3	—	4	—	—
form with spiral palatal folds	71	107	9	39	2	—
Tornatellides oblongus parvulus	4	4	—	—	—	—
unidentified achatinellids	86	92	11	30	8	—
[a]tornatellinid with pointed apex	2	2	1	—	—	—
[a]unknown without teeth	2	2	—	—	—	—
Pupisoma orcula	—	—	—	1	—	—
Nesopupa n. sp.	—	5	1	1	—	—
Minidonta hendersoni	60	89	5	22	7	1
[a]*Minidonta macromphalus* n. sp.	—	1	—	—	—	—
Diastole glaucina	4	—	—	1	—	—
[a]cf. *Hiona* sp.	1	—	—	—	—	—
[a]*Philonesia* sp.	3	5	1	1	—	—

[a]Extinct taxa.

Table 2. *Land snail analyses from Hen-5*

sample (see figure 4)	4	3	2	1
stratigraphical level	120 cm	main cultural horizon	layer 2	surface sample
dry mass of sample (g)	250	500	250	250
Georissa hendersoni	—	—	13	498
Orobophana solidula	—	5	15	40
[a]*Orobophana carinacosta* n. sp.	16	14	—	2[b]
Orobophana spp. (immature/broken)	—	41	—	—
Assiminea sp.	—	2	—	—
Tubuaia hendersoni	?1	5	77	491
Lamellidea oblonga	—	40	51	252
Lamellidea cf. *micropleura*	—	—	1	—
Lamellidea sp.	1	9	4	20
Elasmias sp.	2	7	—	1
Pacifecella variabilis without palatals	—	10	7	109
form with spiral palatal folds	12	26	2	5
Tornatellides oblongus parvulus	—	—	—	6
unidentified achatinellids	22	113	31	458
Pupisoma orcula	—	—	2	9
Nesopupa n. sp.	—	—	1	8
Gastrocopta pediculus	—	10	—	—
Pronesopupa sp.	—	—	—	1
Minidonta hendersoni	35	110	77	95

[a]Extinct taxa.
[b]Probably derived from lower levels.

specimens, are given below under the relevant species, and detailed *camera lucida* drawings are provided. All measurements were made using a binocular microscope with a graticule eye-piece. Second, a number of taxa were recovered which no longer occur on Henderson (Preece 1995*a*). These could not be matched with any species described in the literature (e.g. Baker 1938, 1940, 1941; Solem 1976, 1982; Wagner 1905, 1907–1911), or with specimens in the Bernice P. Bishop Museum, Honolulu (BPBM), the National Museum of Wales, Cardiff (NMW), or the Natural History Museum, London (BMNH). They would therefore appear to be extinct endemic taxa, for which formal descriptions are given below.

6. LAND SNAIL ANALYSES

(a) *Hen-6*

Seven small samples, all less than 150 g dry mass, were analysed through this profile (table 1). These samples were supplemented by other larger shells screened from the bulk samples, although these were not included in the quantitative analyses. Some of the larger shells were only recovered from these screened bulk samples. A specimen of *Melampus flavus* was recovered from spit 13, and the most complete specimens of *Philonesia*, including the holotypes of *P. pyramidalis* and *P. weisleri*, were all recovered in this way (see below).

The basal sample (sample 7) from fissures in the limestone bedrock proved to be a sand containing an interesting assemblage of small marine gastropods and bivalves. This is likely to date from the late Middle Pleistocene and is not considered further here. The lowermost levels of cave sediment (samples 5 and 6) yielded the richest and most diverse land snail assemblages. At least 18 species of land snail were recovered from these levels. Eleven of these still occur in the modern fauna (Preece 1995*a*), but at least five (and possibly as many as seven) no longer occur on Henderson. These are described in §8.

Sample 4 was taken near a hearth in TP 2. Only 3.7 g of sediment were available and not surprisingly the count was low. The remaining three samples were also taken from the cultural horizons. Of these, only sample 3 produced reasonable numbers of snails. Several of the extinct taxa were present, which could imply that they persisted up to the period of human occupation. However, given the disturbed nature of these sediments, it is also possible that they may just have been derived from lower pre-Polynesian levels. Unfortunately, there is not yet enough evidence to distinguish between these alternatives. Amino acid epimerization ratios (D-alloisoleucine/L-isoleucine) of individual shells of the extinct species, that have been calibrated against radiocarbon-dated samples, would be an obvious method of addressing this problem (Goodfriend 1989). However, there is currently insufficient material of the extinct species to warrant sacrifice for this purpose.

The two uppermost samples (samples 1 and 2) yielded very low numbers of snails, even though somewhat larger quantities of sediment were processed. Radiocarbon dates of 380 ± 50 years BP and 360 ± 40 years BP were obtained from charcoal from levels 2 and 3, respectively (see below for complete details). It would appear that the rate of sediment accumulation rapidly increased after humans began to use the cave.

(b) *Hen-5, TP 1*

Four samples were analysed from this profile, one from the sand below the 'main cultural horizon', one from the cultural horizon itself, one from the sand above it, and one from the modern soil (table 2). The basal sand appeared to be largely of marine origin, perhaps blown against the base of the coastal slope. Various species of land snail were recovered from this unit, most notably *Orobophana carinacosta* n. sp., which occurred here to the exclusion of *O. solidula*. The 'main cultural horizon' yielded two further species of interest, namely *Lamellidea oblonga* and *Gastrocopta pediculus*. As these species are absent from all pre-Polynesian sediments examined (e.g. lower levels of Hen-6 and from the previous sample), they appear to be Polynesian introductions.

There were some significant differences between the two assemblages above the 'main cultural horizon' and those from earlier levels. First, the number of land snails recovered was considerably higher. The surface sample, for example, was extremely rich, yielding over 2000 shells in only 250 g of sediment. No trace of *Gastrocopta pediculus* was detected in either of the two upper samples, whereas *Georissa hendersoni*, absent in levels below, dramatically increased in frequency to dominate the surface sample. *Orobophana solidula* now completely outnumbered *O. carinacosta*; the two shells of the latter from the surface sample are most probably derived from levels beneath. The frequency of *Pacificella* shells with two strong palatal lamellae also declined markedly. In the two upper samples, only a very small proportion possess these apertural barriers and even in these they are much less strongly developed than in specimens from earlier levels. *Pupisoma orcula*, *Lamellidea* cf. *micropleura*, *Pronesopupa* sp. and *Tornatellides oblongus parvulus*, were also present in the two upper samples, the last two species being recovered only in the modern soil.

Some of these trends probably relate to changes of habitat. *O. carinacosta* may have been unable to survive the habitat disturbances associated with Polynesian activity in the area of the North Beach. Perhaps clearance and disturbance of coastal vegetation, the death-knell for *O. carinacosta*, did create habitats suitable for species such as *Orobophana solidula*, *Tubuaia hendersoni* and *Georissa hendersoni*, which all show significant increases.

7. RADIOCARBON DATES

A series of radiocarbon dates have been obtained from both Hen-6 and Hen-5 to provide detailed chronologies for the sites. The cultural horizons were rich in charcoal and conventional dates had already been obtained from these levels (Weisler 1995). The obvious question that had to be addressed was the age of the sediments beneath the Polynesian occupation horizons containing most of the extinct land snails (described below) and to test (i) whether extinction of these species occurred long before the period of Polynesian occupation and was therefore a 'natural' part of the faunal turnover characteristic of so many oceanic islands; or (ii) that the extinct species survived up to the period of Polynesian occupation but not beyond. Charcoal was not present beneath the cultural horizons and an alternative material was therefore needed. Although the bones of seabirds were abundant, they were not used for dating because they are likely to show a marine reservoir effect (cf. Shackleton *et al.* 1988). Instead, attention was focused on the much rarer bones of land birds that would be free from this complication. Several of the bird species chosen for dating were themselves extinct species and direct dates on their bones would obviously be of considerable interest (Wragg 1995). All the bone samples were extremely small and were dated by accelerator mass spectrometry (AMS) at the Research Laboratory for Archaeology, University of Oxford. The dates are given in table 3.

These dates fall into two groups. The earliest dates, namely OxA-5910, OxA-6018, OxA-5911 from Hen-6 and OxA-5453 from Hen-5, all relate to pre-Polynesian contexts. The rest are all from Polynesian occupation horizons. The earliest of these (B-45596) is actually the oldest date associated with Polynesian artefacts known from

Table 3. *Radiocarbon dates from bird bones and charcoal associated with the fossil land snail assemblages from Hen-6 and Hen-5*

(The dates are uncalibrated in radiocarbon years before present (BP) using the half-life of 5568 years. Isotopic fractionation has been corrected for, using the measured δ^{13}C values quoted (to ±0.5–1.0 per mil relative to PDB).)

site	trial pit/horizon	species	material	lab. no.	δ^{13}C‰	date (years BP)
Hen-6	TP1/4	unidentified	charcoal	B-59009	−25.1	380±50
Hen-6	TP1/9	unidentified	charcoal	B-59010	−25.6	360±40
Hen-6	TP1/7	*Ducula* sp.	sternum	OxA-5452	−19.0	800±50
Hen-6	TP1/10+11	*Gallicolumba* n. sp.	toe/leg bones	OxA-5910	−23.8	13 420±340
Hen-6	TP1/15+16	*Gallicolumba* n. sp	toe/leg bones	OxA-6018	−20.1	2320±60
Hen-6	TP1/16	*Pluvialis fulva*	various bones	OxA-5911	−24.6	9020±220
Hen-5	TP0/3	unidentified	charcoal	B-45596	−25.3	1120±50
Hen-5	TP8/1	*Ducula* sp.	various bones	OxA-6015	−19.1	860±55
Hen-5	TP8/3	*Ducula* sp.	various bones	OxA-6016	−19.8	755±55
Hen-5	TP8/4	*Ducula* sp.	various bones	OxA-6017	−20.4	900±55
Hen-5	TP9/8	*Ducula* sp.	tarsomet.	OxA-5453	−17.9	2065±55
Hen-5	TP1/6	*Ducula* sp.	sternum	OxA-5454	−19.4	1295±50
Hen-5	TP1/6	unidentified	charcoal	B-59003	−26.1	380±70
Hen-5	TP1/12	unidentified	charcoal	B-59984	−27.2	660±110

Henderson (Weisler 1994, 1995). The earlier date of 2065±55 years BP (OxA-5453) came from a level immediately beneath the dark, charcoal-rich horizon representing the Polynesian cultural horizon in TP 9. The difference in age between these two dates suggests the presence of a hiatus, but many more dates would be needed to establish this. The date of 1295±50 years BP (OxA-5454) from the *Ducula* sternum from the cultural horizon in TP 1, a horizon that has also provided charcoal dated at 380±70 years BP, implies derivation of the sternum from older deposits, although the date itself falls close to the earliest period of Polynesian occupation.

In Hen-6 it has not been possible to establish whether a hiatus exists between the cultural horizons and the levels below because the dates obtained are severely inverted. This implies that the lower sediments have been mixed, perhaps by burrowing gadfly petrels or terrestrial hermit crabs. Bird burrows were certainly evident in some of the trial pits.

8. SYSTEMATIC REVIEW

The following review covers all fossil land snail taxa recovered from the analysed deposits on Henderson. Descriptions of modern species not encountered as fossils are given by Preece (1995*a*).

(a) *Family Hydrocenidae*

(i) *Genus* Georissa *Blanford, 1864*

Georissa hendersoni *Preece, 1995*

The shell of this distinctive endemic species is minute (height 1.1–1.3 mm, breadth 0.96–1.08 mm) and often tinged with pink when fresh. This species is abundant on Henderson, where it occurs under fragments of coral limestone, under fallen branches, or among ground litter over the whole of the island.

(b) *Family Helicinidae*

(i) *Genus* Orobophana *Wagner, 1905*

Orobophana solidula (*Sowerby in Gray, 1839*) (*figures 5a–c*)

This species is common on Henderson today, where it occurs under stones or climbing on trees and other plants. It is polymorphic with respect to shell colour, and may be yellow (the most common colour morph), orange-brown, or have a single peripheral orange-brown band (Preece 1995*a*). Although *O. solidula* is variable in size (breadth 6.4–7.6 mm, height 4.1–4.8 mm), specimens from pre-Polynesian levels show considerably greater variation in shape and size than modern populations from the North Beach area. Some of the fossils are extremely small (figure 5, 1*c*) and not unlike some modern populations from leaf-litter behind the beach-ridge on the North Beach. Other specimens are remarkably tall (figure 5, 1*a*) and are quite unlike any modern population. Measurements of specimens from the basal pre-Polynesian levels (spits 16 and 17) show this clear bimodal pattern (figure 6). This probably reflects the mixing of populations of *O. solidula* from two distinct micro-habitats. Modern populations from the North Beach area, other than those from the beach-ridge, are intermediate in size and shape between these two fossil groups (figure 6).

Orobophana carinacosta *n. sp.* (*figures 5d–f*)

Material examined. Holotype (UMZC I20425a); 25 measured paratypes (UMZC I20425b–z) plus several hundred referred specimens in UMZC from Polynesian occupation horizons of Hen-5. Duplicate specimens lodged with the Bishop Museum (BPBM 250783).

Description. Shell solid, moderately large (breadth 9.15–10.16 mm, height 5.33–6.16 mm), flattened above and below with low, obtuse spire of 4.5–5 slightly convex whorls. Sutures shallow. Periphery with strong keel developed as a rib with rounded edge. Base rather flattened, often covered with callous extending from parietal region. Umbilicus absent. Aperture roughly triangular, peristome sometimes thickened with callous. Inner whorls completely resorbed. Shell with moderately coarse, irregular growth ridges. Traces of spiral microsculpture sometimes visible on apical whorls.

Etymology. Carina (latin), keel; *costa* (latin), rib.

Remarks. This species of *Orobophana* occurs commonly in the Polynesian occupation levels in the North Beach area, where it is associated with *O. solidula*. It is also abundant in

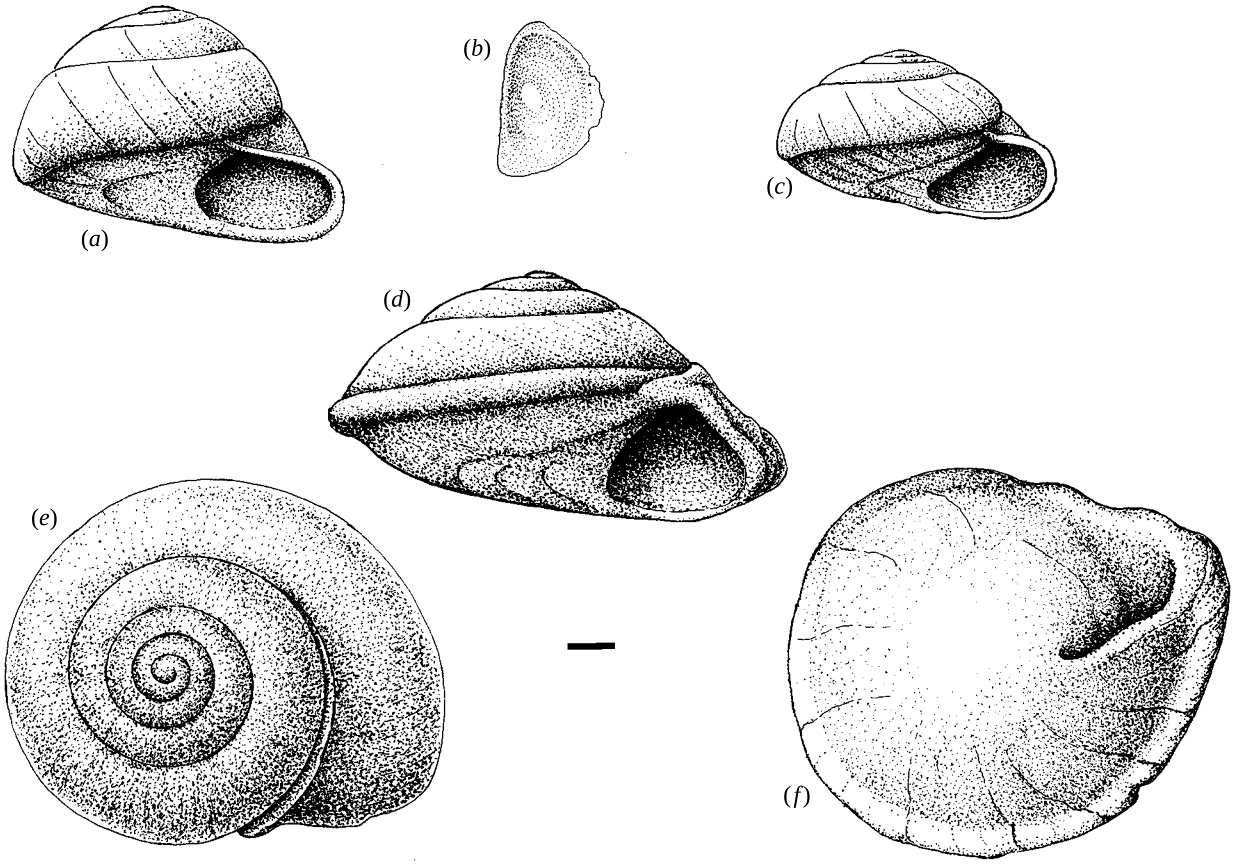

Figure 5. *Orobophana solidula*: (*a*) tall form, Hen-6, TP 1, spit 15; (*b*) operculum from same shell; (*c*) small form with depressed spire, Hen-6, TP 1, spit 7; (*d–f*) *Orobophana carinacosta* n. sp., three views of holotype, Hen-5, TP 1, 'main cultural horizon'. Scale bar represents 1 mm.

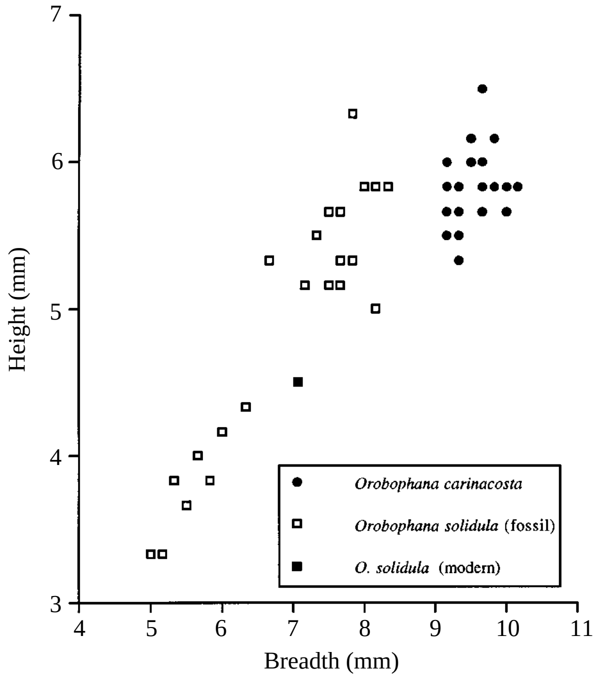

Figure 6. Plot of height versus breadth of shells of *Orobophana solidula* from pre-Polynesian levels in Hen-6 (spits 15–17) and *Orobophana carinacosta* n. sp. from the 'main cultural horizon' of Hen-5 (TP 0). The mean size of a modern population ($n=20$) of *O. solidula* from the North Beach area (habitats other than beach-ridge) is also shown.

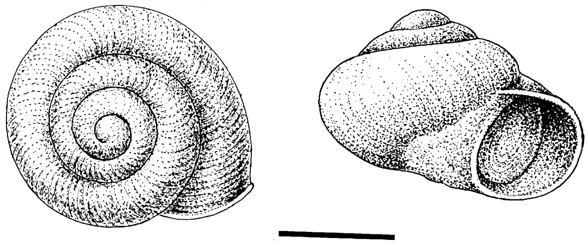

Figure 7. *Pleuropoma hendersoni* n. sp., Holotype. Hen-6, TP 1, sample 5. Scale bar represents 1 mm.

the pre-Polynesian levels. It has a thicker shell and is much larger than *O. solidula* and is more lenticular in shape (figure 5, 2*a–c*). The peripheral keel is also more strongly developed. The two species can easily be distinguished on size, especially shell breadth (figure 6). Mean measurements of 25 shells from the 'main cultural horizon' in Hen-5 (TP 0) were 9.56 ± 0.30 mm (breadth) and 5.85 ± 0.24 mm (height), compared with 7.00 ± 1.05 mm and 4.97 ± 0.86 mm for *O. solidula* from pre-Polynesian levels in Hen-6 ($n=25$).

This species does not match any specimens held either by the BMNH or the BPBM in Hawaii. Specimens in the BPBM labelled '*fulgora*' from Samoa and '*albolabris*' from Tahiti are similar in size and shape but they lack the distinctive keel. Neither does it match any of the helicinid species illustrated by Wagner (1905, 1907–1911) and is here described as new.

O. carinacosta was obviously extremely common at a number of sites in the North Beach area up to and apparently during the period of human occupation. However, it does not appear to have spread beyond this immediate area and failed to extend even as far as Hen-6. This would suggest that it was a strictly coastal species with more exacting ecological requirements than *O. solidula*, a species that was able to survive the Polynesian occupation and which occurs some way inland.

(ii) *Genus* Pleuropoma *Möllendorff, 1893*

Pleuropoma hendersoni *n. sp.* (*figures 7 and 8*)

Material examined. One complete shell with operculum *in situ* from Hen-6, TP 1, sample 5 (holotype: UMZC I.20420a); second complete shell without operculum from Hen-6, sample 6 (paratype: UMZC I.20420b). Referred specimens: ten apical fragments from Hen-6 (see table 1 for details); four apical fragments from Hen-3, W2SO, layer 4a (see Weisler (1994) for site details).

Description. Shell small (breadth 2.1 mm, height 1.6 mm), with 3–3.25 rounded and evenly expanding whorls separated by a moderately deep suture, last whorl slightly descending. Spire low and obtuse. Shell pale, translucent, surface slightly glossy and covered with fine irregular growth-lines, which in places are crossed by spiral microsculpture in a complex chevron pattern (figure 8*b*,*c*). Inner whorls completely resorbed. Protoconch relatively smooth, large and bulbous. Teleoconch with up to four spiral ribs that extend for less than half a whorl (figure 8*a*). Aperture semicircular in outline, columellar lip nearly vertical, forming rather angular base to the aperture. Outer lip thin and very delicately reflected. Umbilical area depressed and covered with thin callous which extends into the parietal area. Operculum semicircular, calcareous and concentric with nucleus lying slightly towards the columellar region. Dimensions: shell breadth 2.16 mm, shell height 1.60 mm (holotype); shell breadth 2.12 mm, shell height 1.64 mm (paratype).

Etymology. hendersoni, named after the type locality.

Remarks. Similar species have been described from Mangareva in the Gambier Islands (French Polynesia). In the BMNH there are specimens in the Hugh Cuming collection (accession no. 1829) labelled '*Helicina vestita* Gould' and '*Helicina antoni* Pfeiffer' from the 'Gambier', and further specimens in the E. R. Sykes collection from Mangareva labelled '*Helicina pazi* Crosse'. These all seem to be very similar and are probably conspecific. The name *H. vestita* was validated by Sowerby (1847) for shells from North America, which were said to be 'concentrically ribbed'. This taxon is clearly different. Likewise, according to Crosse (1865), *Helicina antoni* Pfeiffer, 1849, also relates to shells from an entirely different region, this time from Honduras. Crosse (1865), on the other hand, actually described *H. pazi* from the Gambier and this is clearly the correct name for these shells. Wagner (1907–1911, p. 222) referred to this species as '*Aphanoconia* (*Sphaeroconia*) *pazi*', but Wenz (1938–1940) regarded both *Aphanoconia* Wagner, 1905 and *Sphaeroconia* Wagner, 1909 as subgenera of *Pleuropoma*. Cowie *et al.* (1995) also regarded *Aphanoconia* as a subgenus of *Pleuropoma*, but pointed out that *Sphaeroconia* is a junior objective synonym of *Aphanoconia*. This position is followed here.

Shells of *Pleuropoma pazi* comb. nov. are slightly larger, more loosely coiled and thicker than those of *P. hendersoni*. They are also brownish rather than colourless, and have a more conical spire. Relatively strong spiral ribs are visible on some of the juvenile shells of *P. pazi*, as they are on some specimens of *P. hendersoni*. Both species share similar bulbous apices (larger in *P. pazi*) and delicately reflected lips; and they are clearly congeneric.

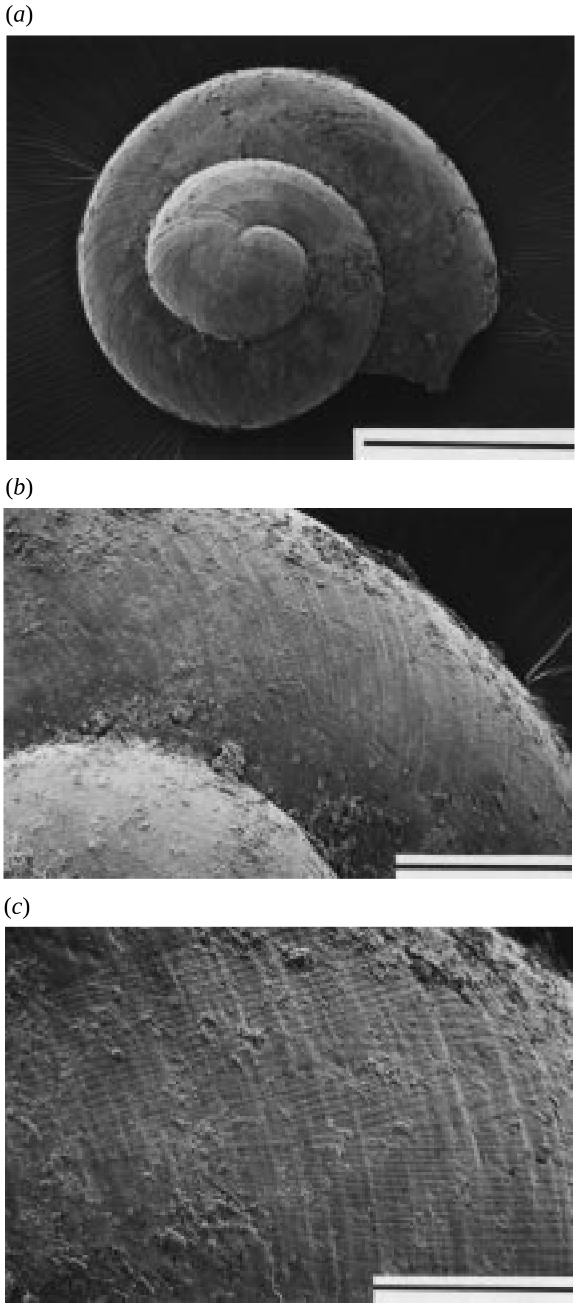

Figure 8. Scanning electron micrographs of *Pleuropoma hendersoni* n. sp. Hen-6, TP 1, sample 3. (*a*) apical view: note bulbous protoconch and spiral ribs on early part of teleoconch; (*b*, *c*) chevron microsculpture. Scale bars (*a*) 0.5 mm; (*b*) 0.1 mm; (*c*) 0.05 mm.

(c) *Family Assimineidae*

(i) *Genus* Assiminea *Fleming, 1828*

Assiminea *sp.*

The specific identity of this species (Preece 1995*a*, fig. 3G–I) remains unknown, but it is likely to belong to a widespread Indo-Pacific species. On Henderson, it occurs in coastal areas under stones and under fallen branches of *Pandanus* and *Argusia* (often with *Melampus flavus*). It also occurred in damp recesses in the rock face of the fossil reef slope behind the North Beach. Near the South Point, it dominated communities under stones among *Scaevola sericea* on the cliff top.

(d) *Family Ellobiidae*

(i) *Genus* Melampus *Montfort, 1810*

Melampus flavus (*Gmelin, 1791*)

On Henderson, this widespread Indo-Pacific species lives among shingle or under wood and leaves of *Pandanus* and *Argusia* on the seaward edge of the embayment forest behind the beach-ridge along the North Beach. Although not recovered from the small samples analysed quantitatively, a specimen of *M. flavus* was recovered from the bulk sampling (Hen-6, spit 13).

(e) *Family Achatinellidae*

(i) *Genus* Pacificella *Odhner, 1922*

Pacificella variabilis *Odhner, 1922* (*figures 9n,o,p,q and 10c*)

Cooke & Kondo (1961) included this species in the genus *Tornatellinops*, but *variabilis* is the type species of *Pacificella* and must therefore revert to this genus (Preece 1995*a*). As the specific name suggests, shells of this species are extremely variable. On Henderson at least two forms occur. The first has a bulbous apex, loosely coiled shell with pronounced spiral microsculpture, large body-whorl and a moderate-to-weak parietal lamella (figure 9*n*,*o*). The second has a more pointed apex, more generally slender shell, which lacks strong spiral microsculpture, a moderate to strong parietal lamella folded downwards and two strong spiral palatal folds (figures 9*p*,*q* and 10*c*). The first form is very similar to shells of *variabilis* illustrated by Cooke & Kondo (1961, fig. 76) from other Pacific islands, which are typically 3.8 mm in height and 1.5 mm in breadth, slightly larger than the Henderson fossils. The two forms are commonly associated on Henderson. Juvenile shells are equally variable. Many have one, or more usually two, spirally entering palatal lamellae, which are continuous and, unlike *Tubuaia*, never beaded (figure 9*p*,*q*). Other juvenile specimens, apparently belonging to the first form (above), have simple parietal lamellae and lack any trace of palatal barriers (figure 9*o*).

These differences raise the possibility that two taxa are being confused. Odhner (1922), in his original description of *variabilis* from Easter Island, states that in young specimens there are sometimes faint traces of 1–2 palatal plicae, whereas Cooke & Kondo (1961, pp. 164–165) deny seeing these plicae 'in any of the juvenile specimens from the many other islands of the Pacific which we have referred to *T. variabilis*'. In specimens from Henderson the two spiral lamellae are hardly 'faint traces', but are strongly developed and extend into the shell for about a quarter of a whorl (figures 9*p*,*q*, 10*c*). In the BPBM there are modern shells (BPBM 149646, 149648) from Henderson showing these well-developed spiral lamellae, the lower one invariably being the more prominent. These have clearly been examined and some even dissected by Kondo, who has labelled them '*Lam.dea* (*per.* group) n. sp.'. Similar forms are known from Pitcairn (BPBM 141918). No mention of these specimens was made in Cooke & Kondo (1961) and their systematic position remains uncertain. The two forms have been distinguished in the analyses of the fossils and separate totals are given for each. Forms with two spiral palatal lamellae are more common as fossils than at the present day. This is particularly striking in the case of the Hen-5 sequence, where about half of the *Pacificella* shells in the Polynesian deposits possess strong lamellae, whereas only a small fraction of those from the surface sample contain any trace of such structures.

'*Pacificella variabilis*' has a wide range in the Pacific, different forms being recorded not only between islands but also within a single island. It is a climbing species and occurs abundantly on leaves of ferns and other plants, particularly in coastal areas. *P. variabilis* is commonly assumed to have been widely dispersed by humans and this is certainly largely true. However, on Henderson it occurred in pre-Polynesian levels, and here it therefore appears to be native.

(ii) *Genus* Tubuaia *Cooke & Kondo, 1961*

Tubuaia hendersoni *Kondo, 1962* (*figure 9h–k* and *figure 10d*)

An adult specimen of *Tubuaia hendersoni* is easily recognized by virtue of its small, slender, fusiform shell (height 2.5 mm, breadth 1.2 mm), strong parietal fold and outer lip, which frequently has a distinct central indentation (figure 9*h*). Immature shells of *Tubuaia* can be distinguished from those of *Lamellidea* because they lack a vertical palatal rib and instead have one or two rows of spirally entering, oblong denticles, which are usually connected by a thin thread, giving a beaded appearance (Cooke & Kondo 1961, p. 145). Juvenile shells of *T. hendersoni* (figures 9*i*–*k*) can easily be confused with those of some forms of *Pacificella*, which have two continuous spiral palatal folds (figures 9*p*,*q*, 10*c*). In the latter, the whorls are wider (measured suture to suture), the last whorl larger, parietal lamella uneven and flaring outward and upper palatal continuous, sometimes interrupted once or twice, but never beaded (Kondo 1962). In juvenile specimens of *T. hendersoni* the parietal lamella is often strongly folded for about half a whorl (figure 10*d*).

This Henderson endemic is ground-dwelling and may occur at high densities under dead *Pandanus* leaves or under coral limestone. It appears to be most common in coastal areas and is rare towards the centre of the island.

(iii) *Genus* Lamellidea *Pilsbry, 1910*

Lamellidea *cf.* micropleura *Cooke & Kondo, 1961*

Shells of this species are readily recognized by virtue of their small size and cylindrical shape (Preece 1995, fig. 5F and G). Typical adult shells measure 2 mm in length and 0.8 mm in breadth. Uncertainty in specific attribution stems from the fact that few adult shells of *L. micropleura* are available from its type locality (Faatoai Valley, Moorea) for comparison, although the few specimens from here (BPBM 150531) do match Henderson shells reasonably well. On Moorea and on the Pitcairn Islands, this species was found under loose bark or behind clumps of lichen growing on trees (Cooke & Kondo 1961; Preece 1995*a*). Only occasionally was it found living under stones on the ground.

The status of this species on Henderson is uncertain. It was not recovered either from pre-Polynesian levels or

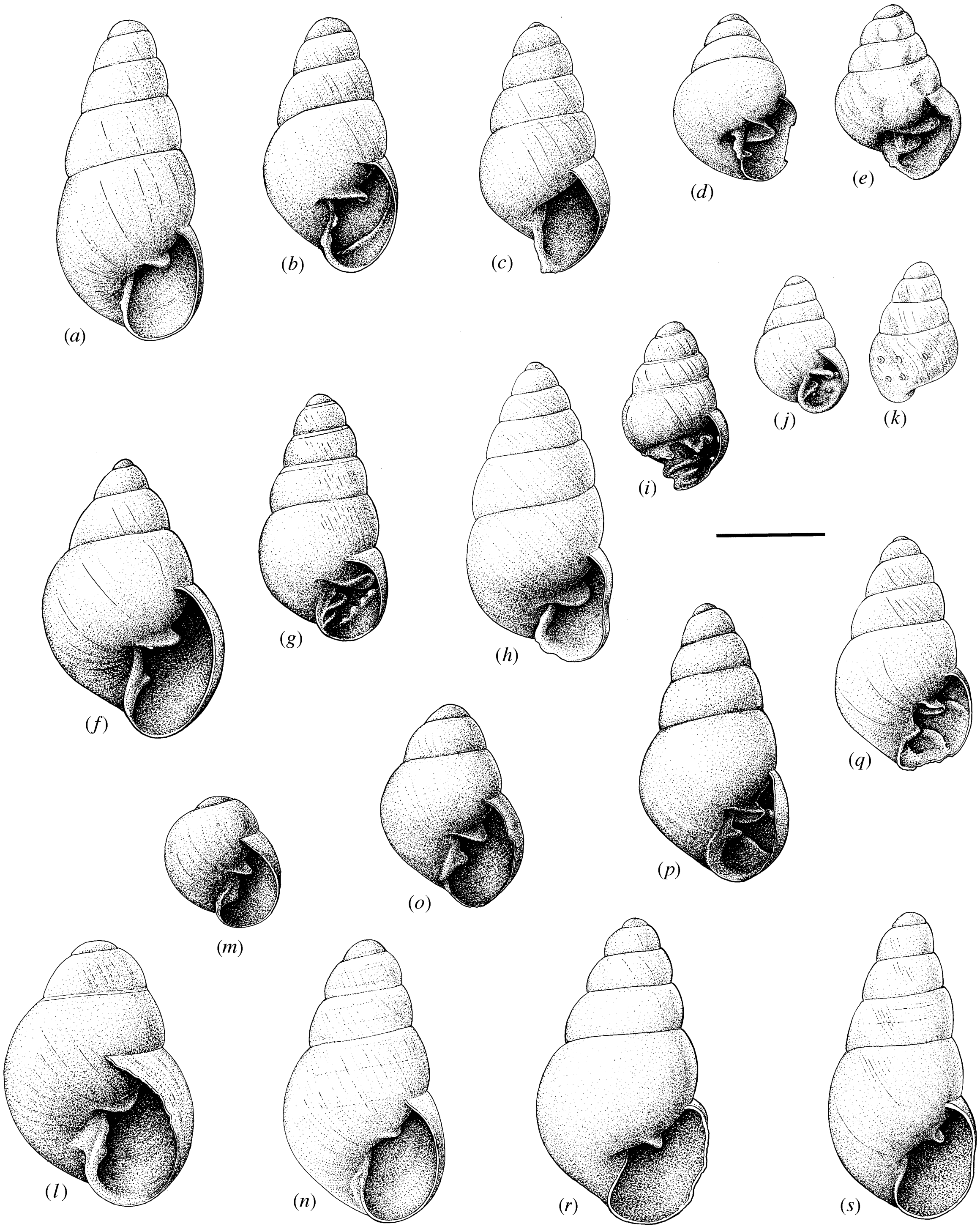

Figure 9. Achatinellidae. *Lamellidea oblonga*, Hen-5, TP 1, surface sample, (*a*) adult shell; (*b*) immature shell with vertical palatal rib; (*c*) unknown species, Hen-6, sample 5. Note absence of apertural barriers. (*d* and *e*) *Tornatellides oblongus parvulus*, Hen-6, sample 5. Two views of the same immature shell: (*d*) tilted back to show umbilicus; (*e*) rotated to show form and size of the parietal fold. (*f*) Unidentified achatinellid, Hen-6, TP 1, sample 5: note pointed apex and absence of palatal folds. (*g*) *Lamellidea* sp. Hen-6, sample 6: note shoehorn-like form of parietal fold and vertical palatal rib with serrate margin. (*h–k*) *Tubuaia hendersoni*, Hen-6, sample 6: (*h*) adult shell, note strong parietal fold and pronounced central indentation of outer lip; (*i*) immature shell showing strongly folded form of parietal (slightly broken in this specimen); (*j* and *k*) two views of another immature shell showing beaded form of palatal barriers (Hen-6, sample 5). (*l* and *m*) *Elasmias* sp. Hen-6, sample 5: (*l*) subadult; (*m*) immature shell. (*n* and *o*) *Pacificella variabilis*, form without palatal folds: (*n*) adult shell with weak parietal fold, Hen-6, TP 1, sample 5; (*o*) immature shell, Hen-6, sample 6. (*p* and *q*) Form with two strong palatal folds, Hen-6, sample 5. (*r* and *s*) *Lamellidea* sp. Hen-6, sample 5. (*r*) Form identical with specimens living on Henderson (cf. Preece 1995*a*, fig. 5D). (*s*) Form approaching *L. oblonga* (cf. *a*), but with more slender spire and traces of spiral microsculpture. Scale bar represents 1 mm.

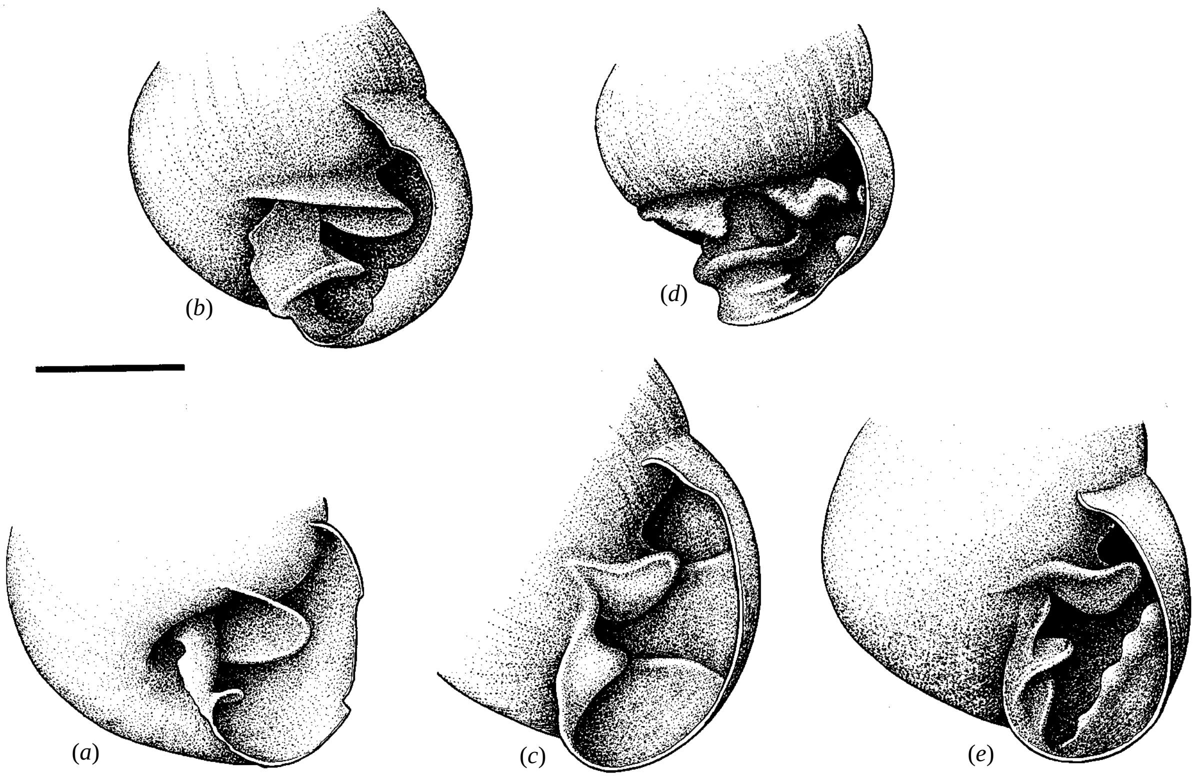

Figure 10. Detailed views of the apertural barriers of selected species of Achatinellidae. (*a* and *b*) *Tornatellides oblongus parvulus*, Hen-6, sample 5. Two views of same specimen showing the form of the strong parietal fold. (*c*) *Pacificella*, Hen-6, sample 5. Form with two strong palatal folds. (*d*) *Tubuaia hendersoni* (immature shell), Hen-6, sample 6. Note strongly folded parietal (slightly broken) and beaded palatals. (*e*) *Lamellidea* sp. Hen-6, sample 6. Note shoehorn-like form of parietal fold and vertical palatal rib with serrate margin. Scale bar represents 0.5 mm.

from the 'main cultural horizon', but a single shell was present in the sand above the latter, beneath the modern soil. This suggests that it is not a modern introduction.

Lamellidea oblonga (*Pease, 1865*) (*figure 9a,b*)

Adult specimens of *L. oblonga* are distinguished from similar species with which they may occur by their slender, more elongate shells (height 3.2 mm, breadth 1.2 mm) and relatively taller spires (figure 9*a*). Many juveniles have one or more vertical palatal ribs, which are usually plain and blade-like (figure 9*b*).

Specimens belonging to the genus *Lamellidea*, were recovered from the pre-Polynesian levels. These shells appear to be somewhat smaller than typical *L. oblonga*, and in some specimens the vertical palatal rib was not plain but minutely serrate and the parietal lamella resembled a shoehorn (figures 9*g*, 10*e*). According to Cooke & Kondo (1961), *L. oblonga* is extremely variable not only with regard to the occurrence and nature of the palatal ribs, but also the size of the embryonic whorls, convexity of the upper portion of the spire and in the strength of the parietal lamella. The specific identity of these pre-Polynesian fossils is uncertain. One shell from Hen-6 (sample 5), does approach *L. oblonga* in general form, but the spire is more slender (figure 9*s*) and there are faint traces of spiral microsculpture that are absent in typical *L. oblonga*. Without further material it would be unwise to identify this specimen as *L. oblonga*. The earliest positively identified specimens came from the Polynesian occupation horizon in the coastal midden (Hen-5).

L. oblonga is widespread in islands in the north-central and south-central Pacific, where it is assumed to have been dispersed by Polynesian voyagers (Cooke & Kondo 1961). It reaches the easternmost limit of its range on Henderson, where it is abundant under logs and on trunks of *Pandanus* and other plants in the coastal areas. *L. oblonga* is a lowland species 'usually found under moist conditions, near or at no great distance from occupied or deserted human habitations' (Cooke & Kondo 1961, p. 200). It is therefore noteworthy that on Henderson *L. oblonga* has spread into the plateau forest and even occurs in the centre of the island (Preece 1997).

Lamellidea *sp.* (*figure 9r*)

This species differs from *L. oblonga*, with which it commonly occurs, by its small shell (height 2.7 mm, breadth 1.4 mm), shorter spire composed of less than five whorls (compared with a whorl number of 5.25–7 in *L. oblonga*), and proportionately larger body-whorl, typically representing about 65% of the total height (Preece 1995*a*, fig. 5D and E). This species was found not only on Henderson but also on Pitcairn and Oeno, where it occurred on ferns and other plants. Fossils matching this species were present in pre-Polynesian levels in Hen-6 (figure 9*r*), indicating that this species has a long pedigree on Henderson.

(iv) *Genus* Elasmias *Pilsbry, 1910*

Elasmias *sp.* (*figure 9l,m*)

This genus is easy to identify by virtue of its relatively large, loosely coiled, globose shells (height 3 mm, breadth 2 mm), which have a blunt apex, characteristic columellar plate, strong parietal lamella but no palatal teeth. In juvenile specimens the apertural armature is more complex than in the adult stage. The species has not been identified but the fossils recovered seem to belong to the recent species from Henderson figured by Preece (1995*a*, fig. 5X and Y).

Elasmias is an arboreal genus, which can be found on Henderson on the underside of leaves of plants such as *Pisonia* and *Nesoluma*. According to Cooke & Kondo (1961), *Elasmias* is the most widespread of the 'tornatellinid' genera, a fact which they attribute to human dispersal on cultivated plants. It is therefore noteworthy that *Elasmias* was recovered from sediments well below the Polynesian occupation horizon in Hen-6, demonstrating its native status.

(v) *Genus* Tornatellides *Pilsbry, 1910*

Tornatellides oblongus parvulus *Cooke & Kondo, 1961*
(*figures 9d,e and 10a,b*)

Specimens belonging to this genus are readily separated from other local 'tornatellinids' because they are umbilicate (figures 9*d*, 10*a*). Shells of *Tornatellides oblongus* from Henderson are much smaller (height 2.5 mm, breadth 1.5 mm) than typical specimens (height 3.0 mm, breadth 1.8 mm) from elsewhere (Preece 1995*a*), and this was one reason why Cooke & Kondo (1961) distinguished it as a distinct subspecies (*parvulus*). As the Henderson specimens represent the only record of *Tornatellides* from a non-volcanic island in the Southern Hemisphere, Cooke & Kondo (1961) did wonder whether the size difference might be ecophenotypic. Size, however, is not the only difference between the subspecies. Juvenile specimens of *parvulus* also possess longer and much stronger parietal lamellae and more prominent columellar folds than those of *T. o. oblongus* (figures 9*d*,*e*, 10*a*,*b*). The fossil examples are small and match specimens of *T. oblongus parvulus*. This subspecies lives among leaf-litter, under fallen branches of *Pandanus* and under fragments of coral limestone.

Tornatellides oblongus has a wide distribution in the Pacific, occurring on virtually all the high islands, although seldom at elevations above about 150 m. Cooke & Kondo (1961) recorded a range from Nukuhiva (latitude 8°52′ S) in the north, to Rapa (latitude 27°36′ S) in the south, and from Pitcairn (longitude 130°06′ W) in the east, to Rarotonga (longitude 159°46′ W) in the west. They regarded it as a lowland species that has been disseminated accidently with food plants. From the similarity of shells from different islands, they suggested that 'the distribution from its original home has been comparatively recent, probably since the advent of the Polynesians' (Cooke & Kondo 1961, p. 251). The occurrence of *T. oblongus parvulus* in pre-Polynesian levels on Henderson is therefore significant, suggesting a longer and more isolated existence from its parent stock.

(vi) *Unidentified achatinellid* (*figure 9f*)

Material examined. Four shells from levels 5 and 6, Hen-6. Specimen figured (UMZC I.22871).

Description. Shell small, pale, glossy, composed of four whorls. Sutures moderately impressed and whorls slightly rounded. Body whorl relatively broad; spire acute tapering to a distinctly pointed apex. Faint spiral microsculpture visible. Aperture ear-shaped and lip simple. Columella twisted and thickened in upper part. Weak columellar lamella present. Parietal lamella strongly developed, inflected slightly downward and extending for about a quarter of a whorl. Palatal barriers absent.

Dimensions of illustrated specimen. Height 2.56 mm; breadth 1.64 mm. Apertural breadth 0.8 mm, apertural height 1.32 mm. Height of body whorl 1.68 mm.

Remarks. There are some modern shells from Henderson in the BPBM that also have this general form, but none of them has an apex quite so pointed. These shells appear to fall outside the range of variability shown by '*Pacificella variabilis*', and may prove to be another undescribed species. A final decision must await the discovery of further material.

(vii) *Unidentified Achatinellidae*

As most of the specimens recovered from the analysed samples consist of small juvenile shells, it has not been possible to identify them as particular species with any degree of confidence. Likewise, apical fragments that lack the diagnostic apertural characters are also not identifiable. The specimens listed under this heading are likely to include very small specimens of several taxa, particularly '*Pacificella variabilis*' and species of *Lamellidea*. The systematics of the modern representatives of this family on Henderson cannot be regarded as finally settled and it is likely that one or two other species may be distinguished (Preece 1995*a*). It is therefore possible that species, as yet unrecognized among the modern fauna, or even extinct species, may be represented in the fossil material. A final verdict must await the analysis of larger samples, which should recover more adult shells.

(viii) *Unknown species* (*figure 9c*)

Material examined. Four shells from levels 5 and 6 in Hen-6.

Description. Shell tall, slender, composed of about 4.5 somewhat convex whorls. Sutures moderately impressed. Apex rather pointed. Shell rather glassy and translucent. Traces of spiral microsculpture visible on upper whorls below suture. Columella straight and slightly thickened. Apertural barriers completely absent.

Dimensions of illustrated specimen. Shell height 2.28 mm, breadth 1.16 mm.

Remarks. All specimens are immature, so the form of the complete adult shell is unknown. These might be examples of aberrant achatinellids that have failed to produce apertural barriers. A less likely alternative is that they could be subulinids, but members of this family are commonly regarded as being introduced to all islands in this part of the Pacific, whereas the present specimens were all from pre-Polynesian levels. The shells are much smaller than those of *Allopeas gracile*, a subulinid widely disseminated by the Polynesians. Without more material that includes adult specimens, it is not possible to distinguish between these alternatives.

(f) *Family Pupillidae*

(i) *Genus* Pupisoma *Stoliczka, 1873*

Pupisoma orcula (*Benson, 1850*)

This is an arboreal species that occurs on the trunks and branches of various trees and shrubs. Specimens tend to cluster on the underside of branches where the branch divides from the trunk, or on the underside of small twigs. They prefer semi-rough to smooth bark trees and are most abundant on the sheltered side. On Henderson it is not confined to the coastal area but occurs in the plateau forest, even in the centre of the island (Preece 1998).

This species has a wide distribution and is known from South Africa, India, Japan, Indonesia, New Guinea, Hawaii, Australia and Polynesia. It was not found in the pre-Polynesian levels in Hen-6, but a single very broken shell tentatively attributed to this species was recovered from the 'cultural horizon' (sample 3) in Hen-6, suggesting that it is a prehistoric introduction. Shells undoubtedly belonging to this species were recovered from Hen-5 (sample 2), a level above the 'main cultural horizon', but beneath the modern soil.

(ii) *Genus* Nesopupa *Pilsbry, 1900*

Nesopupa *n. sp.*

This species was illustrated by Preece (1995*a*, fig. 3N–P) but has not yet been formally named. On Henderson it was common under blocks of coral limestone and also occurred in leaf-litter. The fossil material consists of juvenile shells that are strictly indeterminate, but they almost certainly belong to this taxon.

(iii) *Genus* Gastrocopta *Wollaston, 1878*

Gastrocopta pediculus (*Shuttleworth, 1852*) (*figure 11a,b*)

Several specimens of this species were recovered, but only in the Polynesian occupation horizon of Hen-5 behind the North Beach. It seems to have flourished for a brief time during the period of human occupation, but does not live on Henderson today. Its wide distribution throughout the Pacific, occurring on nearly every inhabited atoll and high island of Polynesia, Micronesia and Melanesia (Pilsbry 1916–1918), has long been assumed to result from human dispersal. This assumption received support from its discovery in well-dated archaeological contexts on the Marquesas (Kirch 1973) and Solomon Islands (Christensen & Kirch 1981), but at neither of these sites was it possible to demonstrate its absence in pre-Polynesian levels. This new record from Polynesian contexts on Henderson, above pre-Polynesian levels where it was absent, provides evidence for this assumption.

(g) *Family Endodontidae*

(iii) *Genus* Minidonta *Solem, 1976*

Minidonta hendersoni *Cooke & Solem in Solem, 1976* (*figure 12a–c*)

A distinctive ground-dwelling endemic found under blocks of coral limestone and under fallen branches. Although dead shells were widespread over the whole island, including the area around the South Point, live specimens have recently been found only in the vicinity of the North Beach (Preece 1995*a*).

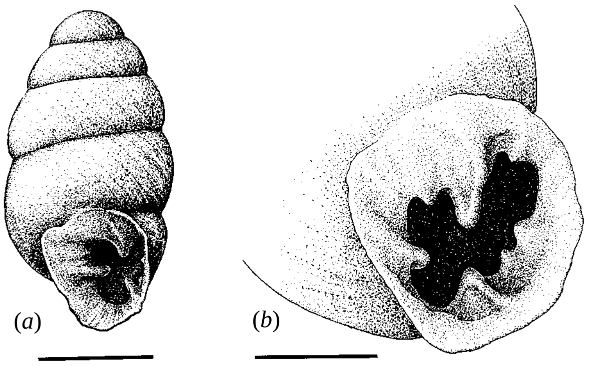

Figure 11. *Gastrocopta pediculus*, Hen-5, 'main cultural horizon'; (*a*) whole shell, scale bar represents 1 mm; (*b*) detail of apertural barriers. Scale bar represents 0.5 mm.

Minidonta macromphalus *n. sp.* (*figure 12d–f*)

Material examined. Unique holotype (UMZC I.22455) from Hen-6, sample 5.

Description. Shell small, with 4.25 normally coiled whorls. Apex slightly impressed but spire moderately elevated, last whorl descending more rapidly. Height/diameter ratio is 0.57. Apical whorls 1.5, sculpture of fine radial riblets. Post-nuclear whorls with high, prominent radial ribs, about 74 on the body whorl, whose interstices are about three times their widths. Microsculpture of fine radial riblets, about 4–6 between each pair of major ribs. Sutures moderately deep and whorls rounded above, slightly compressed laterally. Colour is light reddish-brown with irregularly spaced, narrow-to-wide, reddish flammulations. Umbilicus very wide, regularly decoiling, about a third of the width of the diameter. Aperture ovate and laterally compressed. Three parietal barriers, extending and expanding for about a quarter of a whorl, plus one accessory trace above the upper tooth. Upper parietal barrier, blade-like and slightly less prominent; second and third roughly equal in size with blade-like lamella showing strong anterior descension. All three lamellae become thread-like anteriorly. Columellar barrier a thin, straight, horizontal blade, less prominent than parietals. A very indistinct threadline accessory basal lamella also present. Palatal barriers: four, extending for about an eighth of a whorl, lower basal in position, smaller than others, which rapidly expand posteriorly. Two accessory thread-like traces above upper palatal and single accessory traces between each of the other palatals.

Dimensions. Shell diameter (*D*) 2.52 mm (lip slightly damaged), shell height (*H*) 1.44 mm, spire protrusion 0.24 mm, body whorl width 0.8 mm, umbilical width (*U*) 0.84 mm.

Etymology: makros (Greek), large; *omphalos* (Greek), navel.

Remarks. This species is similar to *M. hendersoni*, with which it was associated (table 1), but is slightly larger, more loosely coiled, has fewer ribs on the body whorl and a much wider umbilicus. The apertural margin of the specimen of *M. macromphalus* has been broken, so that the figures given for the diameter represent minimum dimensions. Even so, its diameter of 2.52 mm falls outside the range cited by Solem (1976) for *M. hendersoni* (1.85–2.45 mm). Similarly, the rib count (74) falls just outside the lower limit for

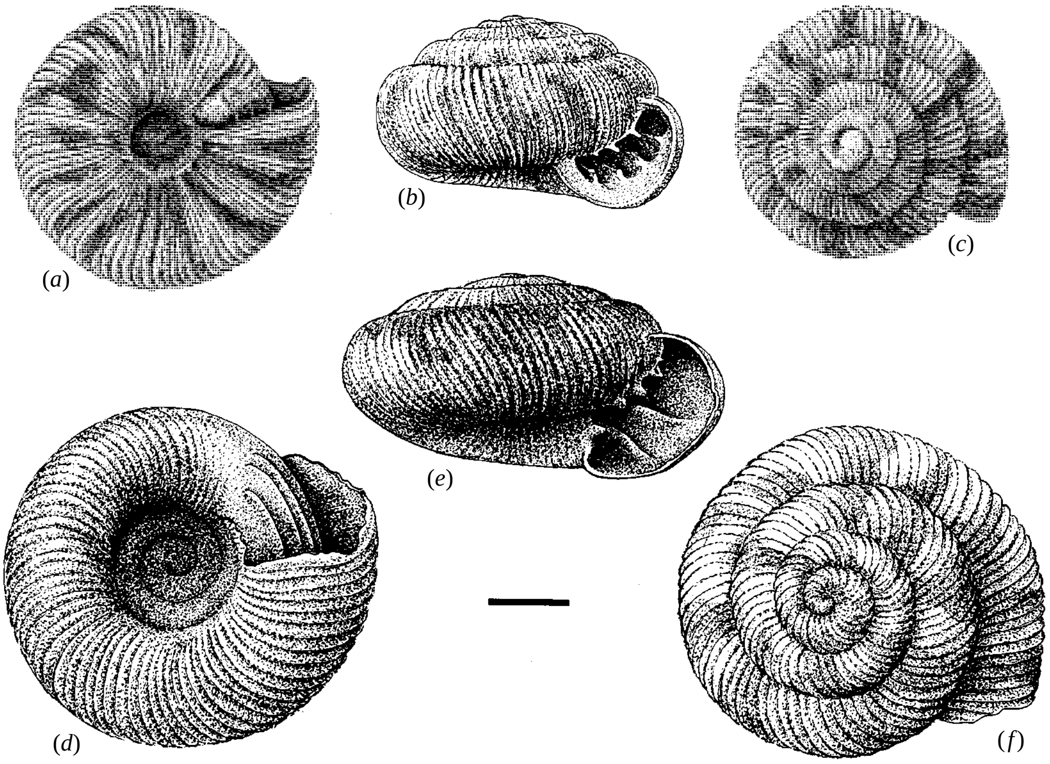

Figure 12. (*a–c*) *Minidonta hendersoni*, modern shell, from coastal area behind North Beach; (*d–f*) *Minidonta macromphalus*, holotype, Hen-6, sample 5. Scale bar represents 0.5 mm.

M. hendersoni (75–95) and the umbilical width also lies just outside the range cited for *M. hendersoni*; for the latter, Solem cites the range of *D*/*U* ratios as 3.09–4.35, whereas the *D*/*U* ratio for *M. macromphalus* is 3.0. The patterning of the shell of both species, however, does appear to have been similar. Solem (1976) describing fresh, live-collected shells, states that *M. hendersoni* lacks darker markings. However, in dead and fossil shells that have faded, irregular darker patterns are apparent (figure 12*a–c*), so that this character cannot be used to distinguish the species.

(h) ***Family Helicarionidae***

(i) *Genus* Philonesia *Sykes, 1900*

Philonesia pyramidalis *n. sp.* (*figure 13a–c*)

Material examined. All known specimens come from pre-Polynesian levels in Hen-6. Holotype (UMZC I.22530a) from TP 1 (spit 13); paratype 1 (UMZC I.22530b) from TP 1 (spit 17); paratype 2 (UMZC I.22530c) from TP 2 (spit 10). Referred material: apical fragments from TP 1 in spits 10, 11, 13, 14, 15, 16 and 17.

Description. Shell moderately large with broad conical spire and somewhat flattened base conferring pyramidal shape. Whorls 4–4.25. Apex flat and shield-like. Periphery bluntly angulated (more sharply keeled when young). Suture shallow, scarcely impressed; whorls rather flattened. Shell pale, white surface slightly glossy with irregular wrinkled growth-lines; faint traces of spiral microsculpture also visible. Traces of a moderately broad darker band are apparent towards the upper half of the whorls on the paratypes, especially UMZC I.22530b. Aperture width greater than apertural height. Lip thin and simple. Columella margin nearly vertical and thickened in upper half. No umbilicus.

Dimensions. Shell breadth 10.83 mm, shell height 9.00 mm (holotype); 9.83 mm, 8.83 mm (I.22530b); 10.50 mm, 8.33 mm (I.22530c).

Etymology. Pyramis (Greek), pyramid; *al*, English suffix meaning 'belonging to'. Refers to the shape of the shell.

Remarks. This distinctive species is known only from three adult shells and about a dozen apical fragments. Both the paratypes have a relatively taller spire than the holotype and also have distinct shell colour banding. As with some other species of *Philonesia* it is likely that this species was polymorphic with respect to banding. This species is completely unlike the two (or three) congeneric species known from Pitcairn (Preece 1995*a*) or *P. mangarevae* Baker from the Gambier Islands. It also appears to be quite different from any other species of *Philonesia* described by Baker (1938, 1940). It is similar in shape to *Microcystis saintjohni* Baker from the Austral Islands, but this species is larger, has shallower sutures with a distinctive blackish-brown subsutural band and a less pointed spire.

Philonesia weisleri n. sp. (*figure 13d*)

Material examined. Unique holotype (UMZC I.22531), Hen-6, spit 17.

Description. Shell thin, subglobose and moderately large with only a suggestion of angulation at the periphery. Whorls four. Sutures scarcely impressed and whorls rather flattened. Apex somewhat flat, dome-like and relatively smooth. Shell surface pale and polished with weak, irregular, wrinkled growth-lines and faint traces of spiral microsculpture. A distinct thin brownish band occurs towards the upper half of the whorls. Aperture narrowly lunate, evenly rounded; peristome

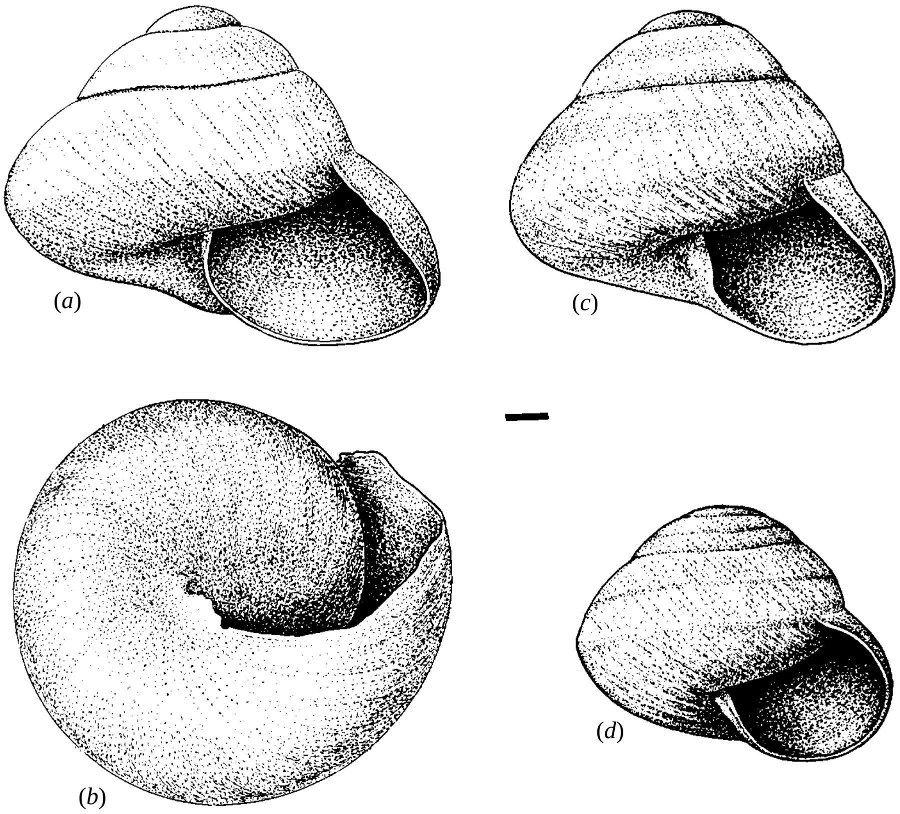

Figure 13. (*a–b*) *Philonesia pyramidalis* n. sp. holotype, Hen-6, spit 13; (*c*) *P. pyramidalis*, paratype 1, Hen-6, TP 1, spit 11; (*d*) *Philonesia weisleri* n. sp. holotype, Hen-6, TP 1, spit 17. Scale bar represents 1 mm.

thin and simple. Columella almost vertical, becoming thicker towards top.

Dimensions. Shell breadth 8.33 mm, shell height 7.16 mm.

Etymology. Weisleri, named after Dr Marshall Weisler, the archaeologist who directed the excavations on Henderson.

Remarks. This species appears to be closely related to *Philonesia pyramidalis*, but can be distinguished from this species, with which it was associated, by its smaller size, subglobose shape and more rounded whorl profile. The base of the shell is also less flattened and more evenly rounded.

(ii) *Genus* Hiona *Baker, 1940*
Hiona *sp.* (*figure 14a–c*)

Material examined. One broken specimen from Hen-6, spit 12 (UMZC I.22535). Other minute fragments from pre-Polynesian levels in Hen-6 may also belong to this species.

Description. Shell small, thin, glassy and translucent with five closely coiled whorls, gradually increasing in size. Spire depressed, almost flat. Sutures relatively shallow. Body-whorl rather rounded but much of the upper part of this has become detached. Lip apparently simple and not thickened internally. Umbilicus entirely closed.

Dimensions. Minimum breadth 3.32 mm (shell damaged), height 2.04 mm.

Remarks. The fragmentary nature of this material precludes any detailed comparisons with other species. It is similar to *H. angustivoluta* (Garrett) from Moorea but is smaller and not horn-coloured. It does not match any of the species of *Hiona* in the BPBM, and it may represent another extinct endemic species. Formal description is deferred until better material becomes available.

(iii) *Genus* Diastole *Gude, 1913*
Diastole glaucina *Baker, 1938*

The shell (breadth 5–6 mm, height 4 mm) is strongly keeled and superficially similar to immature shells of *Orobophana*, but differs in being thinner, more tightly coiled and in its distinctive apical microsculpture (Preece 1995*a*, fig. 4D–F). This Henderson endemic has been found living only in the area of the North West Beach, where it was found at the bases of tree trunks (Preece 1995*a*). Its occurrence in pre-Polynesian levels in Hen-6 shows that it once lived in the area of the North Beach and so had a much wider range on Henderson.

9. DISCUSSION

Despite the limited sampling programme and the small size of some of the samples, a number of important conclusions can be drawn from the analyses. The land snail fauna that inhabited Henderson before the arrival of early Polynesians differed significantly both from that which occurred during the period of occupation and from that which persists today.

Nothing is known of the land snail fauna that colonized Henderson after its emergence during the Middle Pleistocene. The earliest evidence comes from fossiliferous cave sediments in Hen-6 behind the North Beach. From its

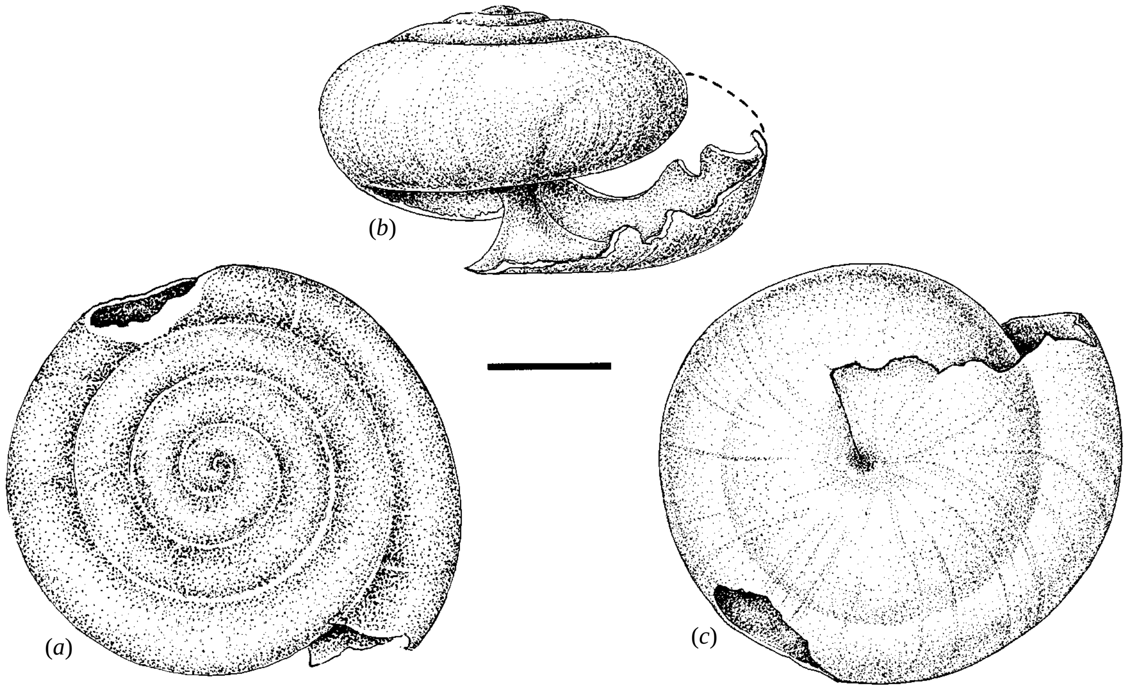

Figure 14. (*a–c*) *Hiona* sp. Hen-6, TP 1, spit 12. Three views of same shell (*a*) and (*c*) were drawn before a portion of the body whorl became detached (*b*). Scale bar represents 1 mm.

Table 4. *History of land snail taxa on Henderson Island*

		pre-Polynesian	Polynesian	modern
E	*Georissa hendersoni* Preece, 1995	+	+	+
†	*Pleuropoma hendersoni* n. sp.	+	$+^{*}$	−
E	*Orobophana solidula* (G. B. Sowerby in Gray, 1839)	+	+	+
†	*Orobophana carinacosta* n. sp.	+	+	−
	Assiminea sp.	+	+	+
	Melampus flavus (Gmelin, 1791)	+	−	+
E	*Tubuaia hendersoni* Kondon, 1962	+	+	+
PI	*Lamellidea oblonga* (Pease, 1865)	−	+	+
	Lamellidea cf. *micropleura* Cooke & Kondo, 1961	−	−	+
	Lamellidea sp.	+	+	+
	Elasmias sp.	+	+	+
	Pacificella variabilis (Odhner, 1922) without palatals	+	+	+
	form with spiral palatal folds	+	+	+
E	*Tornatellides oblongus parvulus* Cooke & Kondo, 1961	+	−	+
?†	tornatellinid with pointed apex	+	−	−
?†	tornatellinid without teeth	+	−	−
PI	*Pupisoma orcula* (Benson, 1850)	−	+	+
PI	*Gastrocopta pediculus* (Shuttleworth, 1852)	−	+	−
	Nesopupa cf. *pleurophora* (Shuttleworth, 1852)	−	−	+
E	*Nesopupa* n. sp.	+	+	+
?	*Pronesopupa* sp.	−	−	+
E	*Minidonta hendersoni* Cooke & Solem in Solem, 1976	+	+	+
†	*Minidonta macromphalus* n. sp.	+	−	−
E	*Diastole glaucina* Baker, 1938	+	$+^{*}$	+
†	*Philonesia pyramidalis* n. sp.	+	$+^{*}$	−
†	*Philonesia weisleri* n. sp.	+	−	−
†	*Hiona* sp.	+	−	−

+, present; −, absent/not known; *, possibly derived; E, endemic; PI, prehistoric introduction; †, extinct; ?, status uncertain.

geomorphological context and from available U-Th dates, it seems likely that this cave was formed by marine processes during a late Middle Pleistocene interglacial period (Blake 1995). Indeed, the basal sediments have yielded a marine fauna that probably dates from this period and contains species absent from the modern one (cf. Preece 1995*b*). The fossil land snail fauna, from cave deposits immediately above the marine sediments, consists of a minimum of 18 species, plus one semi-terrestrial pulmonate (*Melampus flavus*). Like many indigenous land snails on Pacific islands, most of these species are small (less than 4 mm), a feature that aids natural dispersal to remote islands by aerial means (Vagvolgyi 1976; Preece 1998). The fauna does, however, include two species of *Philonesia* which exceed 8 mm in breadth. Eleven species present in this fauna, together with *Melampus flavus*, still live on Henderson but at least five (and possibly as many as seven) apparently did not survive beyond the period of human occupation (table 4). These taxa, formally described in this paper, are thought to represent extinct and, most likely, endemic species. This fossil fauna is therefore more diverse than the modern one, composed of just 16 strictly terrestrial species that includes adventive taxa absent as fossils (Preece 1995*a*). Ecological studies of the modern fauna have shown that between two and eight species of land snail may occur together in any micro-habitat (Preece 1998), so it is clear that the fossil taxa did not all live together, particularly as the assemblages include both ground-dwelling and arboreal taxa. The ground-dwellers probably lived in leaf-litter on the floor of the cave, whereas the arboreal taxa may have lived on ferns growing along the sides of, or on foliage overhanging, the cave entrance.

Associated with these fossil land snails were the bones of birds, including three undescribed extinct species (Wragg 1995): Henderson sandpiper (*Prosobonia* n. sp.), Henderson archaic pigeon (Columbidae n. g.) and Henderson ground dove (*Gallicolumba* n. sp.). Although rare in the pre- Polynesian levels in Hen-6, the remains of a fourth extinct bird, a ducula pigeon (*Ducula* n. sp.), were recovered in large numbers in cultural (and earlier) horizons elsewhere, particularly those forming the coastal midden (Hen-5). Shells of *Orobophana carinacosta*, an extinct land snail absent from Hen-6, were also common in the 'main cultural horizon' and earlier levels of Hen-5. A number of species of extant birds that do not breed today on Henderson were also recovered from the pre-Polynesian levels of Hen-6 (Wragg 1995). These included black-winged petrel (*Pterodroma nigripennis*), Christmas shearwater (*Puffinus nativitatis*) and Polynesian storm petrel (*Nesofregetta fuliginosa*). The last two species were also present in pre-Polynesian levels of Hen-5 (Wragg 1995). The high proportion of immature bones of the Pacific swallow (*Hirundo tahitica*) in Hen-6 provides conclusive evidence that this species did once breed on Henderson.

The radiocarbon dates obtained from some of the bird bones in Hen-6 are seriously inverted and obviously raise doubts about the stratigraphical integrity of the sequence. The lower sediments have clearly been bioturbated, perhaps by burrowing seabirds or terrestrial hermit crabs (*Coenobita* spp.). Such burrows were actually observed in some of the trial pits. Wragg (1995), who has undertaken a thorough study of the fossil bird remains from this site, concluded that only spits 15–17 can be considered purely 'pre-Polynesian', spits 10–14 contain mixed faunas and levels above spit 9 are primarily cultural, although occasional derived elements may occur. The limited land snail analyses support this view. The radiocarbon dates nevertheless confirm the 'pre-Polynesian' age of the lower sediments and indicate that some of the fossils date from the end of the last cold stage. It is possible that some of the fossils from the basal levels are even older.

The cause of these extinctions is clearly a fundamental question. It appears from charred remains in hearths, and from characteristic patterns of breakage of bone (Weisler & Gargett 1993), that at least some of the ground doves formed part of the diet of the early Polynesians during their 600 years of occupation from the eleventh century AD. This would seem to provide a *prima facie* case that their extinction can be attributed directly to human activity (cf. Steadman & Olson 1985; Schubel & Steadman 1989; Wragg & Weisler 1994; Wragg 1995).

The extinction of some of the land snails, which includes some very small species, is not so readily explained. It is most unlikely that any of these land snails were eaten by the Polynesians, but their disappearance might be linked to the destruction of natural habitats to make way for the cultivation of food-plants. In contrast to lowland areas on volcanic islands, the vegetation of karstic islands seems to be more resilient to human disturbance (Paulay 1994). It is therefore most unlikely that vast areas of the plateau vegetation on Henderson were cleared by burning. Nevertheless, Weisler (1995, p. 399) found evidence for 'large-scale burning of the northern and eastern margins of the plateau immediately inland of the habitation sites'. This habitat destruction, even if confined to areas around the plateau margin, must have had serious consequences for endemic land snails, particularly for those that had restricted distributions.

The precise dating of this disturbance has proved problematic as it is very difficult, because of plateaux in radiocarbon production, to obtain accurate age estimates for events during the medieval period. Consequently, it is hard to interpret a mean radiocarbon age of 200 ± 55 years BP (B-45597), obtained from dispersed charcoal from soil from the plateau margin above the North Beach (Weisler 1994, 1995), as its calibrated age of 1659 AD falls close to the date that Henderson is believed to have been finally abandoned. An AMS date from the east plateau suggests that burning here was initiated as early as 1174 AD (Weisler 1995).

The Polynesians were also responsible for the introduction of the Pacific rat (*Rattus exulans*) to Henderson, as elsewhere in the Pacific (Roberts 1991). A radiocarbon date of 670 ± 60 years BP (B-45599), calibrated age 1283 ± 60 AD, dates the earliest known occurrence of the Pacific rat on Henderson (Weisler 1994). The Pacific rat is now known to be a significant predator of gadfly petrels (Brooke 1995) and may well have contributed to the range reductions on Henderson of Christmas shearwater, black-winged petrel and Polynesian storm petrel. It may also have eaten some of the larger species of land snail. *Orobophana solidula*, for example, is certainly eaten by rats today, as indicated by small piles of broken shells outside their holes. *O. carinacosta* is likely to have been another item of prey in the recent past.

At least seven species of ant are now known from Henderson, all of them believed to have been introduced by early Polynesians (Wilson & Taylor 1967; Benton 1995). Some species of ant are known to prey on land snails and possibly to have seriously affected some snail populations (e.g. Solem 1976), but none of those recorded from Henderson are known to eat live snails.

The impact of human occupation did not just result in the extinctions of some vulnerable endemic taxa but, as with some birds, also seems to have caused contraction of the ranges of a few species that did survive. For example, *Diastole glaucina*, an endemic species currently known only from the area of the North West Beach, was recovered from pre-Polynesian levels in Hen-6 behind the North Beach, indicating a much wider distribution. Similarly, *Minidonta hendersoni* could only be found living in the vicinity of the North Beach, although dead shells were found over the whole island, including the area around the South Point (Preece 1995*a*). It is tempting to attribute these distributional changes to human impact but other factors may be involved. For example, in the North Beach area, *M. hendersoni* was recovered from the 'main cultural horizon' and clearly survived here through the episode of maximum anthropogenic disturbance.

To sustain an existence on Henderson the early Polynesians introduced a range of animals and plants. The introduction of the Pacific rat (*Rattus exulans*), the bones of which are abundant in the archaeological deposits, has already been mentioned. Remains of pigs (*Sus scrofa*) were also recovered from two sites, including the coastal midden behind the North Beach (Weisler 1995). Only six apparently introduced plants are known amongst the modern flora (Florence *et al*. 1995). Some, such as the newly recorded *Solanum americanum*, may have dispersed to Henderson relatively recently. Others, such as *Cordyline fruticosa*, a useful plant providing leaves for thatching houses, making clothing and for wrapping food for cooking in earth ovens, were clearly introduced by the early Polynesian settlers. Remains of this plant have been found in the archaeological excavations on Henderson (Weisler 1995), together with remains of swamp taro (*Cyrtosperma chamissonis*), banana (*Musa*sp.), coconut (*Cocus nucifera*), candlenut (*Aleurites moluccana*) and possibly taro (*Colocasia*sp.) and *Hibiscus*.

The early Polynesians also seem to have inadvertently introduced a number of land snails, possibly on or in soil adhering to the roots of some of these plants. At least three species, *Gastrocopta pediculus*, *Lamellidea oblonga* and *Pupisoma orcula* appear for the first time in Polynesian occupation horizons. Although the records for the last are slightly equivocal, the other two species seem to have been common during the period of occupation, but *G. pediculus* no longer lives on Henderson. Both *G. pediculus* and *L. oblonga*are commonly regarded as being humanly dispersed to many islands throughout the Pacific. These assertions are based largely on modern distribution patterns and their absence in Pleistocene and early Holocene sediments in places like Hawaii (Pilsbry 1916–1918; Cooke & Kondo 1961). Firm evidence for the occurrence of these adventive species in a securely dated prehistoric context was provided by Kirch (1973) in the northern Marquesas. Rolett (1992), working on an archaeological site on Tahuata in the southern Marquesas, also recovered *L. oblonga* and *Allopeas* (=*Lamellaxis*) *gracile*, another anthropophilic species, but not *G. pediculus*. The last species was, however, found in a Polynesian context on Tikopia in the south-eastern Solomon Islands, although its absence in sediments predating the arrival of humans could not been demonstrated there (Christensen & Kirch 1981).

The occurrence of both *G. pediculus* and *L. oblonga* in similar contexts on Henderson provides further evidence of their dispersal by early Polynesians. On Henderson, in contrast to Tikopia, it has been possible to demonstrate their absence in pre-Polynesian contexts. There is no evidence to indicate that *G. pediculus* or *Orobophana carinacosta* occurred beyond the coastal area behind the North Beach. For example, both species were absent in cultural horizons sampled from the area of the East Beach. This might help to explain why these species, unlike *L. oblonga*, which has spread into the plateau forest (Preece 1998), should have failed to become permanently established on Henderson.

Some species that have previously been regarded as possible prehistoric introductions, such as *Pacificella variabilis*, *Tornatellides oblongus parvulus* and *Elasmias* sp., have now been recovered from pre-Polynesian levels and their native status established. Just three species, *Lamellidea* cf. *micropleura*, *Nesopupa* cf. *pleurophora* and *Pronesopupa* sp., were not recovered from either the pre-Polynesian or cultural horizons, so their status still requires clarification. A single specimen of *L.* cf. *micropleura* was recovered from the sand above the 'main cultural horizon' of Hen-5, implying that it is not a modern introduction. Interestingly, these are all species that live on the trunks of trees, under loose bark or behind clumps of lichen (Preece 1998), and their virtual absence from the fossil record might be due to taphonomic reasons.

On Pitcairn, a number of other species of land snail occur which are thought to be modern, rather than prehistoric, introductions. Four species of subulinids (*Subulina octona*, *Opeas pumilum*, *Allopeas clavulinum* and *Allopeas gracile*), *Zonitoides arboreus*, *Deroceras* sp. and *Hawaiia minuscula* have all been found (Preece 1995*a*). The last species even occurs on Oeno, an uninhabited but frequently visited atoll in the Pitcairn group (Preece 1995*a*). All these species have now been widely distributed throughout the world and are common in greenhouses, especially hot-houses, in botanical gardens, even in north-west Europe (Kerney & Cameron 1979). *Allopeas gracile* has been found in prehistoric contexts on Tikopia and in the Marquesas (Christensen & Kirch 1981; Rolett 1992), but it was not found in the Polynesian cultural horizons on Henderson. It would appear that the species of prehistoric snails spread by the early Polynesians differ in several respects from those commonly dispersed by modern commerce (cf. Cooke 1934; Harry 1966).

This limited number of analyses have given an important historical perspective on the land snail fauna of Henderson. They have not only helped to clarify the status of various species that remain on Henderson, but have also provided a glimpse of the fauna both before and during the period of Polynesian settlement. Henderson still retains a reasonable endemic biota, but at least 40% of its land snail fauna appears to have become extinct as a result of the Polynesian occupation. This loss is moderate when compared to other Pacific islands, such as the Hawaiian archipelago, which is estimated to have lost about 75% of its land snail fauna (Hadfield 1986; Solem 1990; Cowie *et al*. 1995), or the Ogasawara Islands, south of Japan, where nearly 40% of their endemic fauna has become extinct since 1945 alone (Tomiyama & Kurozumi 1992). Habitat destruction and the introduction of predators and competitors have been the primary cause of these losses.

It is clear, therefore, that not even Henderson, cherished as one of the last 'pristine' islands of the world, has remained completely immune from the effects of humans. Extinctions here are not simply confined to a few vulnerable bird species that formed part of the Polynesian diet, but are now shown to include a range of land snails. Destruction of natural habitats was clearly involved and the occurrence of charcoal in soil in the vicinity of Polynesian habitation sites indicates that this was achieved by burning. It is likely that other invertebrates that have not left a fossil record were also casualties of the Polynesian occupation. The dangers of using data based solely on modern faunas to correlate, for example, island size with species richness, which underlie much of the work in island biogeography (e.g. MacArthur & Wilson 1967; Steadman 1995), are obvious. Larger samples from pre-Polynesian sediments are likely to furnish yet more extinct species and a more comprehensive sampling programme of sites elsewhere on Henderson should provide data on the former ranges of various species. Further specimens of extinct species could be sacrificed to improve the chronology of extinction by means of amino acid epimerization analyses, coupled with AMS measurements, which would allow direct dating of individual shells (e.g. Goodfriend 1989; Goodfriend *et al*. 1994). Only when such results become available will the full scale of the human impact become apparent.

I thank Michael Brooke for his invitation to join the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands (1991–1992), which was made possible by the generous support of the following major sponsors: The Royal Society, International Council for Bird Preservation, British Ornithologists' Union, Foreign and Commonwealth Office UK and UNESCO. My own participation was made possible by grants from the Leverhulme Trust and Percy Sladen Memorial Fund. Sediment samples and specimens of fossil land snails were collected on my behalf by Marshall Weisler and Graham Wragg, who have both contributed much discussion relating to the prehistory of Henderson. The new radiocarbon dates were measured at the Oxford Accelerator Laboratory. I thank Dr Robert Cowie and Fred Naggs for discussion and for access to the collections in the Bishop Museum, Honolulu, Hawaii, and the Natural History Museum, London, respectively. Professor Robert Cameron, Dr Robert Cowie and Dr Gustav Paulay kindly read earlier drafts of the paper and additional information was provided by Dr Carl Christensen and Dr T. Spencer. Special thanks are due to John Rodford for his illustrations. This is paper no. 59 of the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands.

REFERENCES

Baker, H. B. 1938 Zonitid snails from Pacific Islands. I. Southern genera of Microcystinae. *Bernice P. Bishop Mus. Bull.* **158**, 1–102.

Baker, H. B. 1940 Zonitid snails from Pacific Islands. II. Hawaiian genera of Microcystinae. *Bernice P. Bishop Mus. Bull.* **165**, 105–201.

Baker, H. B. 1941 Zonitid snails from Pacific Islands. III. Genera other than Microcystinae. IV. Distribution and indexes. *Bernice P. Bishop Mus. Bull.* **166**, 205–370.

Benton, T. G. 1995 Biodiversity and biogeography of Henderson Island's insects. *Biol. J. Linn. Soc.* **56**, 245–259.

Blake, S. G. 1995 Late Quaternary history of Henderson Island, Pitcairn group. *Biol. J. Linn. Soc.* **56**, 43–62.

Brooke, M. de L. 1995 The breeding biology of the gadfly petrels *Pterodroma*spp. of the Pitcairn Islands: characteristics, population sizes and controls. *Biol. J. Linn. Soc.* **56**, 213–231.

Cameron, R. A. D. & Cook, L. M. 1997 Diversity and durability: responses of the Madeiran and Porto-Santan snail faunas to natural and human-induced environmental change. *Am. Malacological Bull.* **12**, 3–12.

Christensen, C. C. & Kirch, P. V. 1981 Nonmarine mollusks from archaeological sites on Tikopia, southeastern Solomon Islands. *Pacific Sci.* **35**, 75–88.

Christensen, C. C. & Kirch, P. V. 1986 Nonmarine mollusks and ecological change at Barbers Point, O'ahu, Hawai'i. *Bishop Mus. Occasional Papers* **26**, 52–80.

Cook, L. M., Cameron, R. A. D. & Lace, L. A. 1990 Land snails of eastern Madeira: speciation, persistence and colonization. *Proc. R. Soc. Lond.*B **239**, 35–79.

Cook, L. M., Goodfriend, G. A. & Cameron, R. A. D. 1993 Changes in the land snail fauna of eastern Madeira during the Quaternary. *Phil. Trans. R. Soc. Lond.* B **339**, 83–103.

Cooke, C. M. 1934 Land shells of Makatea. *Bernice P. Bishop Mus. Occasional Papers* **10**, 3–11.

Cooke, C. M. & Kondo, Y. 1961 Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). *Bernice P. Bishop Mus. Bull.* **221**, 1–303.

Cowie, R. H., Evenhuis, N. L. & Christensen, C. C. 1995 *Catalog of the native land and freshwater molluscs of the Hawaiian Islands*. Leiden: Backhuys Publishers.

Crosse, H. 1865 Description d'espèces nouvelles provenant des îles Gambier. *J. Conchyliologie* **13**, 217–224.

Duncan, R. A., McDougall, I., Carter, R. M. & Coombs, D. S. 1974 Pitcairn Island—another Pacific hotspot? *Nature* **251**, 679–682.

Evans, J. G. 1972 *Land snails in archaeology.* London and New York: Seminar Press.

Florence, J., Waldren, S. & Chepstow-Lusty, A. J. 1995 The flora of the Pitcairn Islands: a review. *Biol. J. Linn. Soc.* **56**, 79–119.

Fosberg, F. R., Sachet, M.-H. & Stoddart, D. R. 1983 Henderson Island (southeastern Polynesia): summary of current knowledge. *Atoll Res. Bull.* **272**, 1–47.

Goodfriend, G. A. 1989 Complementary use of amino acid epimerization and radiocarbon analysis for dating of mixed-age fossil assemblages. *Radiocarbon* **31**, 1041–1047.

Goodfriend, G. A., Cameron, R. A. D. & Cook, L. M. 1994 Fossil evidence of recent human impact on the land snail fauna of Madeira. *J. Biogeogr.* **21**, 309–320.

Goodfriend, G. A., Cameron, R. A. D, Cook, L. M., Courty, M.-A., Federoff, N., Livett, E. & Tallis, J. 1996 The Quaternary eolian sequence of Madeira: stratigraphy, chronology, and palaeoenvironmental interpretation. *Palaeo. Palaeo. Palaeo.* **120**, 195–234.

Hadfield, M. G. 1986 Extinction in Hawaiian achatinelline snails. *Malacologia* **27**, 67–81.

Harry, H. A. 1966 Land snails of Ulithi Atoll, Caroline Islands: a study of snails accidently distributed by man. *Pacific Sci.* **20**, 212–223.

Kerney, M. P. & Cameron, R. A. D. 1979 *A field guide to the land snails of Britain and north-west Europe.* London: Collins.

Kirch, P. V. 1973 Prehistoric subsistence patterns in the northern Marquesas Islands, French Polynesia. *Archaeol. Physical Anthropol. Oceania* **8**, 24–40.

Kondo, Y. 1962 The genus *Tubuaia* (Pulmonata, Achatinellidae). *Bernice P. Bishop Mus. Bull.* **224**, 1–49.

MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography.* Princeton University Press.

McNutt, N. K. & Menard, H. W. 1978 Lithospheric flexure and uplifted atolls. *J. Geophys. Res.* **83**, 1206–1212.

Odhner, N. H. 1922 Mollusca from Juan Fernandez and Easter Island. *Nat. Hist. Juan Fernandez and Easter Island* **3**, 219–265.

Pandolfi, J. M. 1995 Geomorphology of the uplifted Pleistocene atoll at Henderson Island, Pitcairn group. *Biol. J. Linn. Soc.* **56**, 63–77.

Paulay, G. 1991*a* Late Cenozoic sea level fluctuations and the diversity and species composition of insular shallow water marine faunas. In *The unity of evolutionary biology* (ed. E. C. Dudley), pp. 184–193. *Proc. 4th Int. Congr. Syst. Evol. Biol.*, vol. 1. Portland, OR: Dioscoroides Press.

Paulay, G. 1991*b* Henderson Island: biogeography and evolution at the edge of the Pacific Plate. In *The unity of evolutionary biology* (ed. E. C. Dudley), pp. 304–313. *Proc. 4th Int. Congr. Syst. Evol. Biol.*, vol. 1. Portland, OR: Dioscoroides Press.

Paulay, G. 1994 Biodiversity on Oceanic islands: its origin and extinction. *Am. Zool.* **34**, 134–144.

Paulay, G. & Spencer, T. 1988 Geomorphology, palaeoenvironments and faunal turnover, Henderson Island, S.E. Polynesia. *Proc. 6th Int. Coral Reef Symp.* **3**, 461–466.

Pilsbry, H. A. 1916–1918 *Manual of conchology. Second series: Pulmonata*, vol. XXIV. *Pupillidae* (*Gastrocoptinae*). Philadephia: Academy of Natural Sciences.

Preece, R. C. 1995*a* Systematic review of the land snails of the Pitcairn Islands. *Biol. J. Linn. Soc.* **56**, 273–307.

Preece, R. C. 1995*b* The composition and relationships of the marine molluscan fauna of the Pitcairn Islands. *Biol. J. Linn. Soc.* **56**, 339–358.

Preece, R. C. 1998 Endemic land snail assemblages from the Pitcairn Islands (South Pacific). (In preparation.)

Roberts, M. 1991 Origin, dispersal routes, and geographic distribution of *Rattus exulans*, with special reference to New Zealand. *Pacific Sci.* **45**, 123–130.

Rolett, B. V. 1992 Faunal extinctions and depletions linked with prehistory and environmental change in the Marquesas Islands (French Polynesia). *J. Polynesian Soc.* **101**, 86–94.

Schubel, S. E. & Steadman, D. W. 1989 More bird bones from archaeological sites on Henderson Island, Pitcairn group, South Pacific. *Atoll Res. Bull.* **325**, 1–13.

Shackleton, N. J., Duplessy, J.-C., Arnold, M., Maurice, P., Hall, M. A. & Cartlidge, J. 1988 Radiocarbon age of last glacial Pacific deep water. *Nature* **335**, 708–711.

Solem, A. 1976 *Endodontoid land snails from Pacific Islands* (*Mollusca: Pulmonata: Sigmurethra*). *1. Family Endodontidae.* Chicago, IL: Field Museum of Natural History.

Solem, A. 1982 *Endodontoid land snails from Pacific Islands* (*Mollusca: Pulmonata: Sigmurethra*). *2. Families Punctidae and Charopidae, zoogeography.* Chicago, IL: Field Museum of Natural History.

Solem, A. 1990 How many Hawaiian land snails are left? and what we can do for them *Bishop Museum Occasional Papers* **30**, 27–40.

Sowerby, G. B. II 1847 *Thesaurus Conchyliorum, or monographs of genera of shells*, vol. 1. London: Sowerby.

Spencer, T. 1995 The Pitcairn Islands, South Pacific Ocean: plate tectonic and climatic contexts. *Biol. J. Linn. Soc.* **56**, 13–42.

Spencer, T. & Paulay, G. 1989 Geology and geomorphology of Henderson Island. *Atoll Res. Bull.* **323**, 1–50.

Steadman, D. W. 1995 Prehistoric extinctions of Pacific birds: biodiversity meets zooarchaeology. *Science* **267**, 1123–1131.

Steadman, D. W. & Olson, S. L. 1985 Bird remains from an archaeological site on Henderson Island, South Pacific: man-caused extinctions on an 'uninhabited' island. *Proc. Natn. Acad. Sci. USA* **82**, 6191–6195.

Taylor, J. D., Braithwaite, C. J. R., Peake, J. F. & Arnold, E. N. 1979 Terrestrial faunas and habitats of Aldabra during the late Pleistocene. *Phil. Trans. R. Soc. Lond.* B **286**, 47–66.

Tomiyama, K. & Kurozumi, T. 1992 Terrestrial mollusks and conservation of their environment in the Ogasawara Islands. *Regional Views* **5**, 39–81. (In Japanese with English summary.)

Vagvolgyi, J. 1976 Body size, aerial dispersal, and origin of the Pacific land snail fauna. *Syst. Zool.* **24**, 465–488.

Wagner, A. J. 1905 Helicinenstudien. *Denkschriften der* Kaiserlichen Akademie der Wissenschaften. Wein. Mathematisch-Naturwissenschaften Klasse **77**, 357–450.

Wagner, A. J. 1907–11 Die Familie der Helicinidae. In *Systematisches Conchylien-Cabinet von Martini und Chemnitz. Neu herausgegeben und vervollständigt* (ed. H. C. Küster), Band I. Neue Folge. Nürnberg: von Bauer & Raspe.

Waldren, S., Florence, J. & Chepstow-Lusty, A. J. 1995 A comparison of the vegetation communities from the islands of the Pitcairn group. *Biol. J. Linn. Soc.* **56**, 121–144.

Weisler, M. I. 1994 The settlement of remote Polynesia: new evidence from Henderson Island. *J. Field Archaeol.* **21**, 83–102.

Weisler, M. I. 1995 Henderson Island prehistory: colonization and extinction on a remote Polynesian island. *Biol. J. Linn. Soc.* **56**, 377–404.

Weisler, M. I. & Gargett, R. 1993 Pacific islands avian extinctions: the taphonomy of human predation. *Archaeol. Oceania* **28**, 85–93.

Wenz, W. 1938–1940 Gastropoda. In *Handbuch der Paläozoologie. Teil I. Allgemeiner Teil und Prosobranchia* (ed. O. H. Schindewolf). Berlin: von Gebrüder Borntraeger.

Wilson, E. O. & Taylor, R. W. 1967 The ants of Polynesia (Hymenoptera: Formicidae). *Pacific Insects Monogr.* **14**, 1–109.

Wragg, G. M. 1995 The fossil birds of Henderson Island, Pitcairn group: natural turnover and human impact, a synopsis. *Biol. J. Linn. Soc.* **56**, 405–414.

Wragg, G. M. & Weisler, M. I. 1994 Extinctions and new records of birds from Henderson Island, Pitcairn group, South Pacific Ocean. *Notornis* **41**, 61–70.