

Changes in the terrestrial molluscan fauna of Miti‘āro, southern Cook Islands

Fred J. Brook*, Richard K. Walter** and Jacqueline A. Craig***

* PO Box 3123, Onerahi, Whangarei, New Zealand (fjb@igrin.co.nz)

** Department of Anthropology, University of Otago, PO Box 56, Dunedin, New Zealand (richard.walter@otago.ac.nz)

*** 31 Yeovil Rd, Te Atatu Peninsula, Auckland, New Zealand (jacqui.craig@gmail.com)

ABSTRACT: Thirty-seven species of terrestrial molluscs (36 landsnails and one slug) are recorded from Miti‘āro, a low-lying makatea island in the southern Cook Islands. The fauna was found to consist predominantly of non-indigenous and cryptogenic species, and lacked local endemics. Comparison of fossil and modern assemblages indicates declines and extirpation/extinction of some species, including three species of Endodontidae, over the last several hundred years. There have also been synanthropic introductions of many non-indigenous species, beginning in the prehistoric period, and including a major influx over the last 100 years or so of species ultimately derived from source areas outside the Pacific basin.

KEYWORDS: Pacific Ocean, landsnail fauna, fossil landsnails, non-indigenous species, extinctions, Holocene faunal changes.

Introduction

Miti‘āro (latitude 19° 52'S, longitude 157° 42'W) in the Cook Islands archipelago, southeastern Polynesia, is in a group of four islands collectively known as Ngaputoru. One of these islands (Takūtea) is a sand cay, but Miti‘āro (Fig. 1) and the other two (Ātiu, Ma‘uke) are makatea islands that have central areas of deeply eroded and weathered volcanic rocks surrounded by swampy depressions and an encircling rim of emergent reef limestone (Stoddart *et al.* 1990).

The earliest published information on landsnails of the southern Cook Islands was a series of species descriptions by Pease (1865a,b, 1866, 1867, 1868a,b, 1871) and Garrett (1872, 1874), based largely on collections made by Andrew Garrett during brief visits to Aitutaki, Ātiu, Mangaia and Rarotonga in 1865, and a six-month stay on Rarotonga in 1869. Garrett (1881) subsequently published a comprehensive overview of the fauna of these four islands. The

earliest known collections of landsnails from Miti‘āro were made by Sir Peter Buck in 1929 and are held by the Bernice P. Bishop Museum, Honolulu. Craig (1995) produced the first account of the landsnail fauna of Miti‘āro, describing modern assemblages collected by Amanda Brooks and Tutere Taia at a series of sites across the island in 1994, and fossil material collected by Richard Walter from a sixteenth-century AD archaeological site at Paraoa on the eastern coast in 1993. A small number of additional collections were made on Miti‘āro in 2007 by Fred Brook and David Winter.

This paper describes the composition and biogeographical relationships, and evidence of changes over the last several hundred years, of the landsnail fauna of Miti‘āro. It forms part of a wider study of the composition and conservation status of the landsnail faunas of the southern Cook Islands being undertaken for the Cook Islands Natural Heritage Trust.

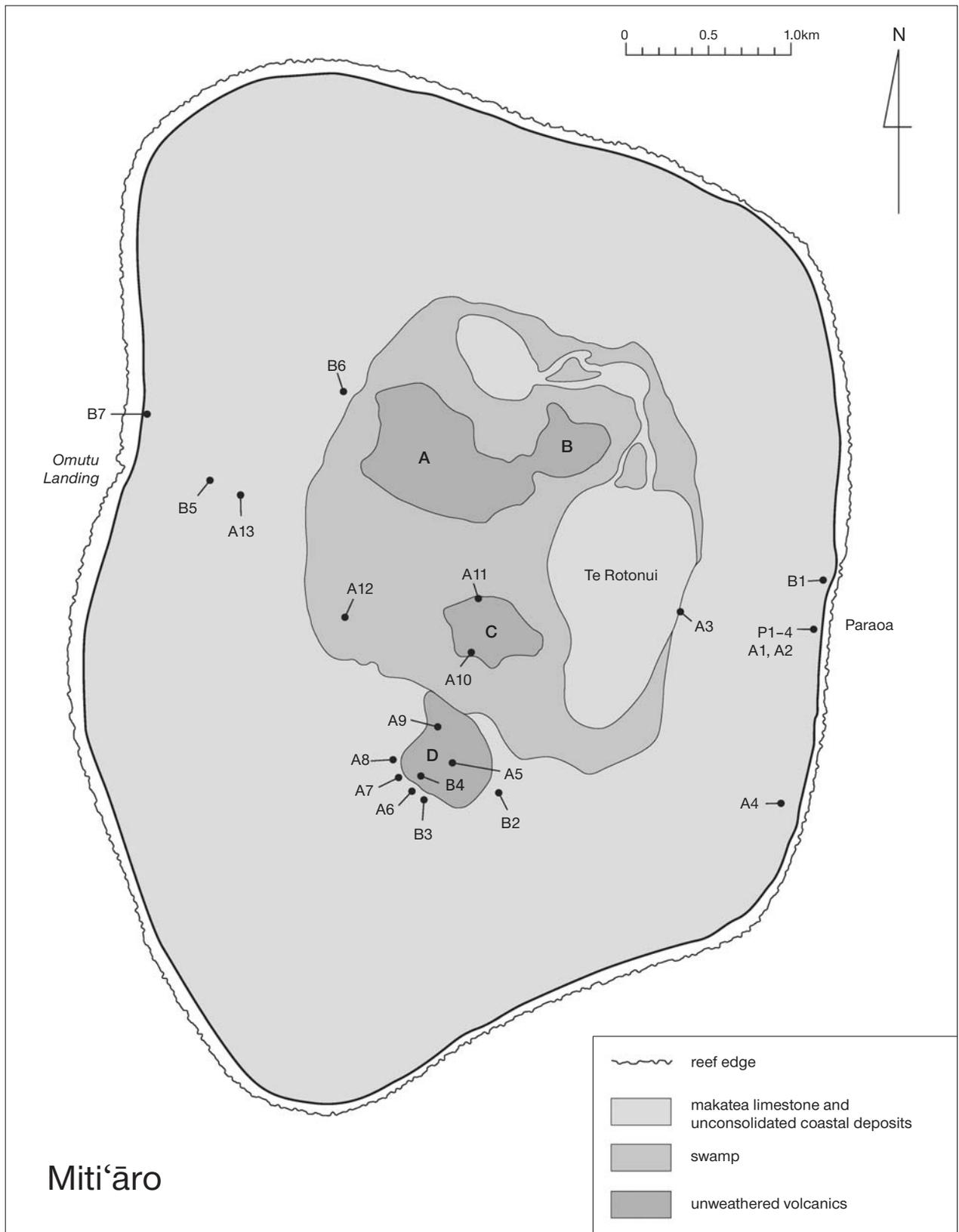


Fig. 1 Miti'āro, showing the distribution of makatea, weathered volcanics and wetland, and the location of the fossil sample sites (P1–4) and the modern sample sites (A1–13; B1–7). A, Atai-Auta foodland; B, Taurangi foodland; C, Mangarei foodland; D, Takaue foodland.

Physical setting

The island of Miti'āro is the emergent summit of an irregularly shaped volcanic edifice that rises steeply from a surrounding ocean depth of *c.* 4000–4500 m (Summerhayes & Kibblewhite 1969). It is part of a chain of islands and seamounts extending between Aitutaki, 240 km to the west-northwest, and Ma'uке, 45 km to the east-southeast (Kroenke *et al.* 1983; Stoddart *et al.* 1990: fig. 1; Mamerickx 1992). The closest island to Miti'āro is Ātiu, 40 km to the west-southwest.

Miti'āro has maximum dimensions of 6.3 × 4.5 km, a total area of *c.* 2300 ha, and consists of a peripheral rim of makatea limestone (covering *c.* 1745 ha) surrounding a central depression that contains deeply weathered volcanic remnants and a large wetland (Wood & Hay 1970; Stoddart *et al.* 1990). There are three weathered volcanic remnants, known as the Atai-Auta-Taurangi, Mangarei and Takaue foodlands (Fig. 1). The first two of these form small, low islands (72.5 ha and 17.5 ha, respectively, with maximum elevations of *c.* 6–7 m), surrounded by an extensive wetland (*c.* 430 ha) of swamps and associated brackish lakes with water levels at or slightly above sea-level. The third volcanic remnant, the Takaue foodland (22.5 ha, maximum elevation *c.* 9 m), is located at the southwestern edge of the central depression, bounded on three sides by the belt of makatea that encircles the central depression. Turner & Jarrard (1982) reported a K-Ar age of $\geq 12.3 \pm 0.42$ Ma for olivine basalt cobbles from regolith in the Takaue foodland, indicating that the emergent part of the Miti'āro volcano is of Middle Miocene age or older.

The surrounding belt of makatea limestone has a broadly horizontal upper surface with a maximum elevation of *c.* 11 m, and a moderately rugged, eroded surface topography of pinnacles, slots and sinkholes with up to *c.* 2 m relief. The makatea belt is 800–1700 m wide, being narrowest in the east and widest in the northwest and southwest. This limestone unconformably overlies weathered volcanics on the Takaue foodland, and outlying erosional remnants also overlie the volcanics on the Atai-Auta and Mangarei foodlands (Wood & Hay 1970; Stoddart *et al.* 1990; Brook, pers. obs. 2007). The makatea limestone has not been dated directly, but the stratigraphic relationships with the volcanic remnants suggest it is possibly largely of Late Miocene to Pliocene age. The seaward margin of the makatea is younger reef limestone of Pleistocene age that extends up to a few hundred metres inland from the coastal cliffs encircling

the island (Stoddart *et al.* 1990; Woodroffe *et al.* 1991). The latter are highest on the eastern, southern and south-western coasts (*c.* 6–7 m), and lowest on the western and northern coasts (*c.* 2.5–3.5 m). Exposures in coastal cliffs indicate that the Pleistocene limestone comprises two super-imposed reef units separated by a sharp disconformity. The lower reef unit contains recrystallised corals and has not been dated, but is inferred to be of penultimate interglacial age (i.e. oxygen isotope stage 7; *c.* 190–240 ka) by comparison with dated sequences on Ātiu and Ma'uке (Woodroffe *et al.* 1991). The upper reef unit attains a maximum elevation of 9.8 m above sea-level, with well-preserved emergent spurs, grooves and hummocky abrasion platforms up to *c.* 6–7 m above sea-level. In its upper part, this unit includes fields of acroporid corals that extend inland and form a thin veneer over the older makatea. Corals in the upper reef unit gave uranium-series ages of 116–128 ka and are thus of last interglacial age – i.e. oxygen isotope substage 5e (Woodroffe *et al.* 1991).

Holocene storm deposits of unconsolidated bioclastic sand and coral rubble form a belt *c.* 100–500 m wide and up to a few metres thick, perched on top of Pleistocene and older makatea inland from the coastal cliffs along the western and northern sides of the island, and are present as narrow, laterally discontinuous, perched lenses on the seaward makatea immediately inland from the eastern coast. Modern storm-tossed boulders of reef rock are also present locally up to *c.* 250 m inland around the island, and are particularly common along the eastern coast. These perched sediments and scattered boulders were presumably deposited by storm waves during severe cyclones like that described by Gill (1876: 168). Similarly, unconsolidated coral sand underlying the brackish wetland in the central depression (Grange & Fox 1953; Wood & Hay 1970) is probably also of Holocene age, carried inland by storm waves that overtopped the makatea rim. The coastal cliffs around Miti'āro are bounded to seaward by a laterally continuous, erosional, intertidal platform up to 120 m wide, with an algal ridge and surge channels at the outer edge. Small pocket beaches of bioclastic sand and coral gravel are present locally at the back of this platform (Stoddart *et al.* 1990).

The early geological history of Miti'āro is poorly known. The elevation of the makatea rim relative to the volcanic remnants, and the presence of makatea outliers overlying the volcanics, indicates that a cap of reef limestone formerly extended right across the area now occupied by the central depression (Grange & Fox 1953; Wood & Hay 1970;

Stoddart *et al.* 1990). Lateral and vertical accretion of this limestone presumably took place during a period of regional tectonic subsidence in the Late Miocene and/or Pliocene, but no details of the history of reef development and topography at this time are known. Whether the limestone formed over the eroded summit of a drowned former high island, or an ephemeral volcanic shoal, is also unknown. In Plio-Pleistocene time, subsidence was evidently replaced by tectonic uplift, leading to the emergence of Miti'āro. This uplift has been attributed to lithospheric flexure resulting from crustal loading by Rarotonga, Aitutaki and Manuae (McNutt & Menard 1978), or by Rarotonga alone (Lambeck 1981). However, the magnitude of this uplift, and the extent to which the former limestone cap on Miti'āro has been worn down by erosion, have not been determined. The timing of uplift is also unknown, although at least some was evidently of Late Pleistocene age. The presence of *in situ* corals of last interglacial age up to 9.8 m elevation indicates uplift of at least 3 m since 120 ka (i.e. ≥ 0.025 mm/yr), assuming the last interglacial highest sea-level in this region was c. 6 m above the present level (Woodroffe *et al.* 1991). The present sub-horizontal surface on the makatea rim on Miti'āro possibly corresponds to the original accretionary surface of this limestone unit, but more likely formed as a result of marine and/or sub-aerial erosion during the Pleistocene (Stoddart *et al.* 1990; Woodroffe *et al.* 1991). The central depression presumably formed after uplift as a result of solutional erosion of emergent limestone.

The geomorphological history of Miti'āro during Mid-Late Pleistocene time was presumably analogous to that of present-day atolls, existing as a high limestone island during glacial periods when sea-level fell by as much as c. 140 m below the present level (Rohling *et al.* 1998), and being largely or entirely submerged during interglacial periods when sea-level rose to as much as 20 m higher than at present (e.g. Howard 1997; Kindler & Hearty 2000).

Climate

The southern Cook Islands have a tropical climate. No long-term temperature records are available for Miti'āro, but average monthly temperatures recorded on nearby Ma'uke over the period 1968–82 ranged from c. 27°C in January–March, to 23°C in July and August (Thompson 1986: fig. 20). There is marked seasonality in the rainfall regime, with a wet season from November to April, and a dry season from May to October. During the dry season Miti'āro

generally lies within the South Pacific trade-wind zone, and southeasterly winds predominate. By contrast, during summer the South Pacific Convergence Zone (SPCZ), an area of convergence between equatorial easterly winds and higher-latitude southeasterly trades, commonly moves south to lie over the southern Cook Islands, bringing unsettled weather. On average, Miti'āro receives 65% of its rain in the wet season and 35% in the dry season. Mean monthly rainfall during the period 1958–82 ranged from 273 mm in February to 83 mm in July, but actual monthly and seasonal rainfall varied markedly from year to year (Thompson 1986).

From time to time, Miti'āro is affected by tropical cyclones that form on the SPCZ between November and April (Thompson 1986), and these storms can cause extensive damage. For example, a severe cyclone in 1865 reportedly had storm waves that 'rose upwards of 30 feet', and that swept away dwellings and trees in a settlement on the western coast of the island, and deposited 'a vast expanse of sand and shingle' on the coastal makatea (Gill 1876: 168).

Vegetation

The modern vegetation of Miti'āro differs markedly between sedimentary and volcanic substrata. The vegetation on makatea limestone and perched Holocene bioclastic sediments is generally dominated by indigenous species, except in the villages on the western side of the island and the airstrip at the northern tip, where introduced species predominate. Low forest is present around the leeward western and northern sides of the island, around the edge of the central depression, and as scattered groves around the exposed eastern and southeastern coasts, but dense, tangled shrubland is the most widespread vegetation type elsewhere on the makatea.

The western and northern coasts of Miti'āro typically have a narrow belt of supralittoral shrubland containing *Pemphis acidula*, *Scaevola taccada*, *Suriana maritima*, *Timonius polgamus* and *Tournefortia argentea*, backed by low forest of *Casuarina equisetifolia* and coconut (*Cocos nucifera*). By contrast, the exposed eastern and southeastern coast has a wide band of prostrate to low-growing open shrubland containing *Chamaesyce fosbergi*, *Heliotropium anomalum*, *Pandanus tectorius*, *Pemphis acidula*, *Sophora tomentosa*, *Suriana maritima* and *Timonius polygamus*, grading back into taller shrubland with scattered groves of *Casuarina equisetifolia*, *Guettarda speciosa* and coconut.

Dominant woody species in shrubland and scrubby forest on the inland makatea include *Casuarina equisetifolia*, *Guettarda speciosa*, *Pandanus tectorius* and *Pisonia grandis*, with frequent *Geniostoma sykesii*, *Ixora bractea*, *Myrsine cheesmanii* and *Planchonella grayana*, and less common *Cyclophyllum barbatum*, *Glochidion ramiflorum*, *Morinda citrifolia*, *Pipturus argenteus* and *Xylosma suaveolens*. *Casuarina equisetifolia* also forms stands on the inner edge of the makatea bordering the central wetland, growing locally in riparian areas that are periodically flooded. The palm *Pritchardia mitiaroana* is present as scattered trees and small stands in inland makatea shrubland in the southwestern part of island, and *Hernandia moerenhoutiana* and coconut are locally dominant tree species within inland makatea forest in the western part of the island (Sykes 1981; Franklin & Merlin 1992; Brook, pers. obs. 2007).

The vegetation of the deeply weathered volcanic remnants that make up the Atai-Auta-Taurangi, Mangarei and Takaue foodlands is highly modified and generally dominated by non-indigenous species. It includes horticultural plots under cultivation and lying fallow, coconut plantations, and groves of secondary forest of predominantly introduced tree species, including breadfruit (*Artocarpus altilis*), candlenut (*Aleurites moluccana*), mango (*Mangifera indica*) and Polynesian chestnut (*Inocarpus fagifer*), along with coconut palms and *Hibiscus tiliaceus*. This secondary forest is contiguous with disturbed makatea forest around the western, southern and southeastern margins of the Takaue foodland.

Swamp vegetation in the central depression of Miti'āro is dominated by the native sedge *Cladium jamaicense*, with the fern *Acrostichum aureum* common locally (Sykes 1981).

Human history

The timing of first settlement in the southern Cook Islands is presently the subject of debate. The oldest archaeological remains reported from the region are from an occupation site on Mangaia dated to the period *c.* 930–680 yrs BP (Steadman & Kirch 1990; Kirch *et al.* 1991, 1992, 1995; Allen & Wallace 2007). Elsewhere, occupation sites as old as *c.* 700–650 yrs BP have been recorded on Rarotonga, Aitutaki and Ma'uke (Bellwood 1978; Allen & Steadman 1990; Allen 1994; Walter & Sheppard 1996: table 1; Walter 1998; Allen & Wallace 2007). Ellison (1994), Kirch & Ellison (1994), and Kirch (1996) have argued on the basis of palynological, geochemical and sedimentological

evidence that people first arrived on Mangaia *c.* 2500 yrs BP and extensively modified the island's vegetation and hydrology after *c.* 1400 yrs BP. Similarly, Parkes (1997) reported palynological and sedimentological evidence of major and sustained environmental changes of inferred anthropogenic origin at *c.* 1310 yrs BP on Ātiu. However, the paleoenvironmental case for early settlement on Mangaia has been disputed (Anderson 1994, 1995). Until corroborative material of unambiguous cultural origin is identified, a conservative model of southern Cook Island settlement would see occupation occurring after 1000 yrs BP, as suggested by the archaeological record.

All the islands in the southern Cook Islands would have been discovered and settled relatively quickly, probably over a period of years rather than decades. Currently, the earliest dated archaeological material from Miti'āro is from the Paraoa site, which provided radiocarbon dates indicating occupation in the sixteenth century AD (Walter & Campbell 1996). On nearby Ma'uke, the Anai'o village site was occupied in the fourteenth century AD and contained evidence for the operation of extensive exchange networks that would certainly have included Miti'āro (Walter & Campbell 1996; Sheppard *et al.* 1997; Walter 1998; Walter & Sheppard 2001).

Although the archaeological record from Miti'āro is not as well known as those from other islands in the southern Cook group, it is likely that land use and settlement patterns followed a similar trajectory. Most of the early sites in the southern Cook Islands were located on the leeward (i.e. western or northern) coastlines adjacent to major reef passages, and included nucleated villages or hamlets (e.g. Bellwood 1978; Allen 1994; Walter 1996, 1998, 2004). Archaeological analysis shows an early reliance on inshore fishing coupled with the use of domestic pig, dog and fowl. Horticulture and arboriculture of synanthropically introduced crop species were practised from first settlement, but during the first centuries of occupation the habitation zones were coastal while the gardens were located some distance inland (Walter 1996). The archaeological evidence suggests that a shift towards a more dispersed settlement pattern based on inland occupation had occurred by the fifteenth century. On the makatea islands, the villages broke up and settlement dispersed over the pockets of dry and wetland soils that supported taro and other root and tree-crop production (Walter 1996, 1998). This is consistent with the reports of the first European visitors to the southern Cook Islands, which described small household units distributed across the inland

garden zones and, on Rarotonga, well up into the valleys (Williams 1838; Bellwood 1971).

The earliest known European contact with Miti'āro was in July 1823, when the missionaries Robert Bourne and John Williams from the schooner *Endeavour* made a brief visit ashore (Coppell 1973). A mission was established on Ma'uke during the same trip, and its influence in Ngaputoru grew quickly (Williams 1838: 84–90). This included changes in settlement patterns as the mission teachers persuaded the people to re-establish villages around the new churches on the leeward coast near Omutu Landing (Walter 1996), and the introduction of new crop species to the island. In July 1865, following the move back to the coast, the missionary W.W. Gill described walking from Takaue village to the interior of the island: 'The pathway is execrable, the entire surface of the island being sharp coral rock, sprinkled with small patches of soil, which sustain a growth of orange, bread-fruit, and cocoa-nut trees, besides plantains, bananas, and guavas' (Gill 1876: 170).

Since the nineteenth century, the sandy coastal soils, especially those on the perched Holocene sediments of the northern and western coasts, have supported some arboriculture, principally coconuts. However, the foodlands inland of the makatea belt have probably always been the main areas of cultivation on Miti'āro. The principal crops today are cassava, taro, sweet potato, banana and breadfruit.

Methods

Information on composition and recent changes in the landsnail fauna of Miti'āro was obtained from four sources: a small collection of landsnails made by Sir Peter Buck in 1929; fossil landsnail assemblages collected by Richard Walter in 1993 from a buried soil at Paraoa; collections made by Amanda Brooks and Tutere Taia at 13 sites across the island in 1994; and collections made by Fred Brook and David Winter at seven sites in June 2007.

The fossil fauna from Paraoa (P1–4; Appendix 1) was collected from a single buried sandy soil that contained cultural material dating to the early sixteenth century AD (Fig. 2; i.e. Layer 2 of Walter & Campbell 1996). Four bulk sediment samples of *c.* 1 litre volume were collected from sections exposed in archaeological excavations within, and adjacent to, a stone enclosure (see Walter & Campbell 1996: fig. 2). Snail shells were extracted in the laboratory by placing each sample in a 5-litre container of water, stirring the water, and hand-picking shells that floated to the surface. The process of

stirring and removing shells was repeated several times for each of the four samples. All snail shells collected were dried and later sorted under a binocular microscope.

Landsnails collected from Miti'āro by Sir Peter Buck in 1929 are held at the Bishop Museum, Honolulu. This material was examined by one of us (Fred Brook) and a species list was compiled.

The locations of the 13 modern sites sampled in 1994 (A1–13) are shown in Fig. 1, and site details are given in Appendix 1. At each site, a bulk sample of *c.* 5–6 litres of soil, litter and herbaceous ground-layer plants was collected from a representative selection of the terrestrial microhabitat types present. Snail shells were extracted in the laboratory by sieving. The samples were air-dried and shaken through a 1 cm screen to separate out larger gravel, twigs, leaves and snail shells. The remainder of the sample was then washed through nested sieves with mesh sizes of 2 mm, 1 mm and 0.5 mm. The resulting fractions were air-dried and sorted under a hand lens and binocular microscope. Three sites were in coastal vegetation on the eastern side of the island (A1, A2, A4). Four sites were in horticultural plots and secondary forest on volcanic soils in the Mangarei and Takaue foodlands (A5, A9–11). Three sites were in disturbed broadleaved-coconut forest on makatea along the southwestern edge of Takaue foodland (A6–8). Two sites were in *Casuarina* groves on the inner edge of the makatea in recently flooded, low-lying areas (A3, A12), and one site was in a recent clearing in scrubby forest on the inland makatea (A13).

The locations of the seven modern sites sampled in 2007 (B1–7) are also shown in Fig. 1, and site details are likewise given in Appendix 1. At four sites, bulk samples (*c.* 2 litres volume) of litter and soil were collected from a range of microhabitat types, then later air-dried and sorted under a binocular microscope for live snails and empty shells. One site was in coastal shrubland on makatea (B7), another was in open coastal shrubland on a substratum of sandy soil and storm-tossed coral boulders (B1), and two sites were in inland makatea forest (B5, B6). At the other three sites, visual searches only were carried out. One of these sites was in a grove of secondary forest on volcanic soil in the Takaue foodland (B4), and the other two were in modified makatea forest on the margins of this foodland (B2, B3). At each of the last three sites, *c.* 30 minutes was spent looking for snails and shells in the litter, under coral rubble, fallen wood and coconut fronds, on the leaves of ground-layer plants, and on the leaves, trunks and branches of shrubs and trees. Snails

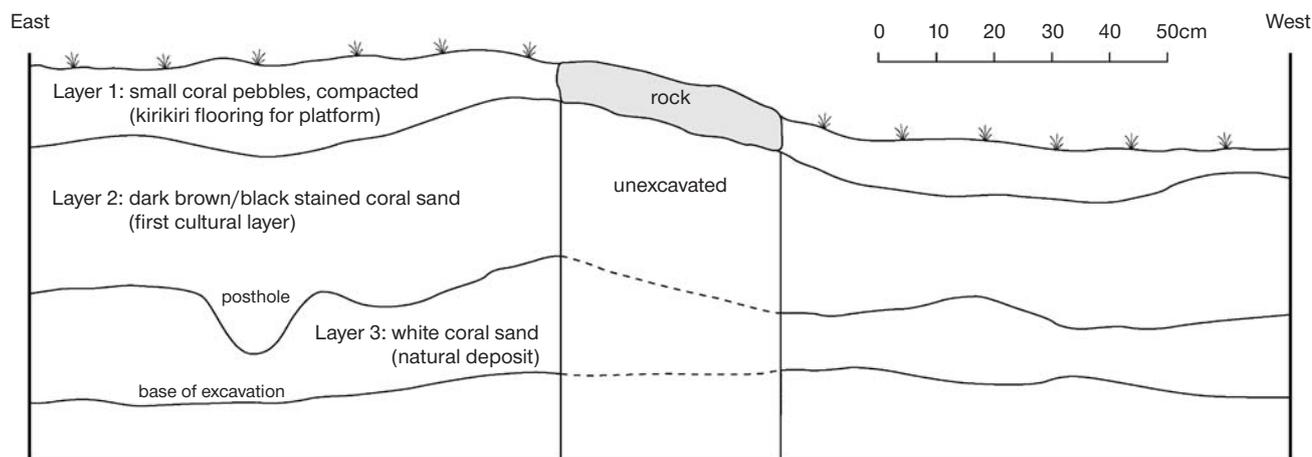


Fig. 2 Stratigraphy at the Paraoa site, eastern Miti'āro.

found were collected, preserved in 98% ethanol, and subsequently identified using a binocular microscope.

Faunal analysis

A faunal list was compiled based on species records from the Paraoa fossil collection, and on the 1929, 1994 and 2007 collections (Appendix 2). Species populations on Miti'āro were classified as 'probably extinct' if known from old empty shells only, or 'extant' if live snails or fresh empty shells were found during the 1994 and 2007 surveys. Patterns of local extirpation on the island were assessed by comparing distributions of old empty shells and live snails/fresh empty shells among the sites sampled in 1994 and 2007. Species richness of modern assemblages was determined for sites and habitat types sampled in 1994 and 2007, based on the presence of live-collected or fresh empty shells in bulk litter/soil samples. The habitat categories were: supralittoral shrubland (B7); coastal shrubland and forest (A1, A2, A4, B1); scrubby forest on makatea (A7, A13, B5); broadleaved-coconut forest on makatea (A6, A8, B6); riparian *Casuarina* groves (A3, A12); tree gardens on volcanic soils (A5, A9); and horticultural plots on volcanic soils (A10, A11). Sites sampled by hand-collecting only in 2007 (i.e. B2–4) were excluded from this analysis.

The biogeographic affinities of the fully terrestrial component of the Miti'āro landsnail fauna (i.e. excluding supralittoral species in families Assimineidae, Truncatellidae and Ellobiidae) were categorised in terms of the following four distribution groups, following Brook (2010): 1. Cook

Islands species (present on two or more islands in the Cook archipelago but not known elsewhere); 2. Polynesian species (present in two or more island groups in the tropical central and eastern Pacific); 3. tropical Pacific species (distributions extending from the tropical western Pacific eastward to Polynesia); and 4. extra-Pacific species (not indigenous to the Pacific region). The number and percentage of species in each of these biogeographical categories were determined for the Paraoa fossil fauna. The biogeographical composition of the modern fauna was assessed based only on the presence of live-collected or fresh empty shells in samples.

Faunal changes at Paraoa between the early sixteenth century AD and the present day were examined by comparing the composition of the fossil landsnail assemblage at sites P1–4 with those of modern assemblages at sites A1, A2 and B1.

Taxonomy and collection data

Snail identifications were based on comparison with taxonomic literature, and with reference material in the Bishop Museum, Honolulu, and the Museum of New Zealand Te Papa Tongarewa, Wellington.

The fossil material from the Paraoa archaeological excavation, and material obtained during the 1994 and 2007 field surveys, has been lodged in the mollusc collection at the Museum of New Zealand Te Papa Tongarewa (registration numbers prefixed by NMNZ M.). Details of this material, and the collection from Miti'āro in the Bishop Museum (registration numbers prefixed by BPBM), are listed in Appendix 2.

Results

Paraoa stratigraphy and fossil fauna

The Paraoa site is located on the dry, windward eastern coast of Miti'āro, and there are no soils suitable for agricultural production in the vicinity. The archaeological evidence indicates this site was used mainly as a sea-fishing camp (Walter & Campbell 1996). It consisted of a low, stone-lined enclosure about 12×4 m in area, on flat sandy soil directly above the slope running down to the reef. The perimeter of the enclosure was defined by a line of coral rocks, and the entire interior was paved with a thick layer of fine coral pebbles (kirikiri), which was, on average, about 8 cm thick. The enclosure itself was a small example of a late-prehistoric or early-historic platform that probably served as the foundation for a structure, or as a ceremonial site. Archaeological excavations were undertaken both within the structure and beyond the perimeter. The stratigraphy of the site varied across the excavation units, but consisted of two occupation levels, as shown in Fig. 2.

Samples containing fossil landsnails were collected from a charcoal-stained, bioclastic sandy buried soil (18–27 cm thick) directly underlying the enclosure and adjacent ground soil (6–10 cm thick). This buried soil (i.e. Layer 2 of Walter & Campbell 1996) was deposited during the period of initial human occupation of the site. The sediment was probably derived mainly from oven rake-out, and contained abundant burnt marine shell and coral fragments, along with fish bones, crab shell, landsnail shells and worked artefacts (Walter & Campbell 1996). The buried soil was underlain by unweathered storm deposits of weakly consolidated white coral sand and boulders, which in turn rested on emergent reef limestone (makatea) of Pleistocene age.

Radiocarbon dates on two samples of *Turbo setosus* marine shell midden from the buried soil gave calibrated ages at one standard deviation of AD 1491–1603 and AD 1461–1565, indicating human occupation at the site in the early sixteenth century AD (Walter & Campbell 1996). These calibrations were determined using CALIB Version 3.0 (Stuiver & Reimer 1986), with a delta-R value of 45 ±30 following Stuiver *et al.* (1986). Soil formation and accumulation of landsnail shells presumably began sometime before this.

A total of nine landsnail species in eight families was recorded in the Paraoa fossil fauna. The four samples collected all contained similar species assemblages (Appendix 2). Five of the nine species recorded as fossils were present in all four samples (*Orobophana pacifica*, *Lamellidea pusilla*,

Gastrocopta pediculus, *Allopeas gracile*, *Libera fratercula*), and two other species were present in three samples each (*Omphalotropis variabilis*, *Discocharopa aperta*). The other two fossil species (*Truncatella guerinii*, *Lamellidea oblonga*) were present in two samples each. Rare modern shells of *G. pediculus* and *Gastrocopta servilis*, present in two samples (P1, P3), had presumably been derived from the overlying ground soil.

Modern sites

A total of 37 landsnail species in 15 families was recorded, including four presumed extinct species known from old empty shells only (Appendix 2). Two species in the latter group (*Libera fratercula*, *Discocharopa aperta*) were formerly widely distributed on Miti'āro, being represented in the Paraoa fossil fauna and in ground soils on coastal sand and makatea substrata elsewhere on the island (Appendix 2). Records of these two species at modern sample sites were mostly based on old shells preserved *in situ* in calcareous ground soils. However, fossil shells of *L. fratercula* (plus *Georissa striata* and *Sinployea atiensis*) collected from a taro plot beside a road in the Mangarei foodland (A10), and at a road junction in the Takaue foodland (A9), had probably been eroded from calcareous sand used for road construction at these sites. The other two presumed extinct landsnail species on Miti'āro were apparently rare. Old shells of *Mautodontha rarotongensis* were found at a single site (A8), in broadleaved-coconut forest on makatea inland from the Takaue foodland. *Minidonta* sp. was found at two sites: under broadleaved-coconut forest in a sandy ground soil on makatea (B6), and in *Casuarina* litter beside the road to Lake Te Roto (A3). The single shell found at the latter site was a fossil and had probably been eroded from calcareous sand brought in from elsewhere on the island for road construction.

Several species still extant on Miti'āro evidently had wider distributions on the island in the past. This group included *Georissa striata*, *Orobophana pacifica*, *Assimineia parvula*, *Truncatella guerinii* and *Sinployea atiensis*, all of which were found as old shells only at some sites (Appendix 2). For example, snails of the last species were locally abundant in secondary forest and disturbed forest in, and adjacent to, the Takaue foodland in 1994 and 2007 (i.e. A5, A6, A8, A9, B2–4), but at other forest sites sampled this species was represented by old shells only and had evidently died out (i.e. A7, A13, B5, B6). Similarly, *T. guerinii* had evidently

Table 1 Species richness of modern landsnail assemblages on Miti'āro.

Habitat type	Sites	Total number of extant species	Species per site	
			Range	Mean \pm SD
Supralittoral shrubland	B7	4		
Coastal shrubland and forest	A1, A2, A4, B1	10	4–9	6.25 \pm 2.2
Scrubby makatea forest	A7, A13, B5	20	14–19	16.7 \pm 2.5
Broadleaved-coconut makatea forest	A6, A8, B6	27	11–24	18.0 \pm 6.6
Riparian <i>Casuarina</i> groves	A3, A12	13	8–9	8.5 \pm 0.7
Tree gardens	A5, A9	14	9–13	11 \pm 2.8
Horticultural plots	A10, A11	12	7–8	7.5 \pm 0.7

died out at some coastal sites on eastern Miti'āro where it was represented by old empty shells only (e.g. Paraoa, A4, B1).

Species richness of modern landsnail assemblages in the habitat types sampled on Miti'āro is summarised in Table 1. Scrubby forest and broadleaved-coconut forest on inland makatea contained the highest overall numbers of species, and supralittoral shrubland contained the fewest species. The richest assemblages were found at sites in scrubby forest (A7, A13, B5) and broadleaved-coconut forest (A6, A8, B6), and in a tree garden on volcanic soil in the Takaue foodland (A9). Assemblages at sites in supralittoral shrubland, coastal shrubland and forest, riparian *Casuarina* groves, and horticultural plots all contained fewer species. The richest modern assemblages were at sites B6 (24 species); A8 and B5 (19 species each); A13 (17 species); A7 (14 species); A9 (13 species); and A6 (11 species).

The most frequent species found in the modern assemblages sorted from bulk samples (i.e. 17 sites, excluding B2–4) were *Allopeas gracile* and *Gastrocopta pediculus* (14 sites each); *Allopeas micra* (13 sites); *Lamellidea pusilla* (10 sites); *Pacificella variabilis* and *Liardetia samoensis* (9 sites each); *Orobophana pacifica*, *Omphalotropis variabilis*, *Tornatellides oblongus* and *Subulina octona* (8 sites each); and *Georissa striata*, *Assimineea parvula*, *Gastrocopta servilis* and *Opeas hannense* (7 sites each). All these species were found across a wide range of habitat types. By contrast, some scarcer species had narrow ecological distributions,

being found only in supralittoral shrubland (i.e. *Assimineea lucida*, *Truncatella guerinii*, *Melampus luteus*), makatea forest (*Lamellidea micropleura*, '*Microcystina*' *gerritsi*, *Quickia concisa*), or foodlands (*Allopeas clavulinum*, *Paropeas achatinaceum*). Most species in the modern landsnail fauna on Miti'āro were ground-dwelling, but two species were arboreal (*Elasmias apertum*, *Pupisoma orcula*), and several were semi-arboreal, being found on the ground as well as on ferns, trees and shrubs (e.g. *Orobophana pacifica*, *Omphalotropis variabilis*, *Pacificella variabilis*, *Tornatellides oblongus*, *Liardetia samoensis*).

Biogeography

The overall biogeographical composition of the Miti'āro terrestrial landsnail fauna ($n = 34$ species) is shown in Table 2. The fauna was dominated by extra-Pacific species (12 species; 35%), with fewer Polynesian species (8; 24%), tropical Pacific species (7; 20.5%) and Cook Island species (7; 20.5%). The last group included three endodontid species thought to be extinct on this island (i.e. *Libera fratercula*, *Mautodontia rarotongensis*, *Minidonta* sp.), and four other species still extant on Miti'āro and elsewhere in the southern Cook Islands (i.e. *Nesopupa dentifera*, *Nesopupa rarotonga*, *Nesopupa* sp. 1, *Sinployea atiensis*). *Libera fratercula* is also still extant elsewhere in the group (Solem 1976; Brook 2010), but the other two endodontids are probably globally extinct.

Table 2 Biogeographical composition of the Miti'āro landsnail fauna. Species marked with an asterisk are thought to be extinct on this island.

Cook Islands species	<i>Nesopupa dentifera</i> , <i>Nesopupa rarotonga</i> , <i>Nesopupa</i> sp. 1, <i>Libera fratercula</i> *, <i>Mautodontha rarotongensis</i> *, <i>Minidonta</i> sp.*, <i>Sinployea atiensis</i>
Polynesian species	<i>Georissa striata</i> , <i>Orobophana pacifica</i> , <i>Assimineea parvula</i> , <i>Omphalotropis variabilis</i> , <i>Lamellidea micropleura</i> , <i>Lamellidea oblonga</i> , <i>Tornatellides oblongus</i> , <i>Nesopupa armata</i>
Tropical Pacific species	<i>Elasmias apertum</i> , <i>Lamellidea pusilla</i> , <i>Pacificella variabilis</i> , <i>Gastrocopta pediculus</i> , <i>Discocharopa aperta</i> *, <i>Liardetia samoensis</i> , <i>'Microcystina' gerritsi</i>
Extra-Pacific species	<i>Vaginulus plebeius</i> , <i>Gastrocopta servilis</i> , <i>Pupisoma orcula</i> , <i>Allopeas clavulinum</i> , <i>Allopeas gracile</i> , <i>Allopeas micra</i> , <i>Opeas hannense</i> , <i>Paropeas achatinaceum</i> , <i>Subulina octona</i> , <i>Streptostele musaecola</i> , <i>Quickia concisa</i> , <i>Bradybaena similaris</i>

Mautodontha rarotongensis was formerly present on Ātiu and Aitutaki, and *Minidonta* sp. on Ātiu (Brook, unpublished data).

The biogeographical composition of the Paraoa fossil fauna and modern faunas in various habitat types is summarised in Table 3. The Paraoa fauna was dominated by tropical Pacific and Polynesian species, and included a single extra-Pacific species (*Allopeas gracile*) that is inferred to have been synanthropically introduced to Polynesia (Appendix 2). By contrast, extra-Pacific species were a significant component of faunas in all the modern habitat types sampled, and were dominant in riparian *Casuarina* groves, tree gardens and horticultural plots (i.e. the most modified and disturbed habitats). Extra-Pacific and Polynesian species predominated in broadleaved-coconut forest on makatea; Polynesian, tropical Pacific and extra-Pacific species predominated in coastal shrubland and forest; and Polynesian species predominated in scrubby forest on makatea. Cook Islands species formed a minor component in the Paraoa fauna and in faunas of modern shrubland, forest and tree-garden habitats.

The western Pacific species *'Microcystina' gerritsi*, and the extra-Pacific species *Vaginulus plebeius*, *Gastrocopta servilis*, *Allopeas clavulinum*, *Allopeas micra*, *Opeas hannense*, *Paropeas achatinaceum*, *Subulina octona*, *Streptostele musaecola*, *Quickia concisa* and *Bradybaena similaris*, were probably all introduced to Miti'āro after European contact. *Subulina octona* was evidently widespread by the late 1920s. The locality information on a Bishop Museum collection made in 1929 (BPBM 95671) notes that this species was present: 'everywhere ... under stones or logs, and coconut husks'.

The timing of introduction and establishment of the other listed species on Miti'āro is not known. Most were present by 1994, but *V. plebeius* and *Q. concisa* were first recorded in 2007.

Faunal changes at Paraoa

The Paraoa fossil assemblage contained nine species of land-snails. Modern assemblages in coastal shrubland and forest at Paraoa (i.e. species represented by live-collected snails or fresh empty shells in bulk samples from sites A1, A2, B1) had a combined total of 11 species, with between five and nine species present at individual sites (Appendix 2). The modern local fauna included four species common to all three sites (*Orobophana pacifica*, *Lamellidea pusilla*, *Gastrocopta pediculus*, *Allopeas gracile*); two species present at two sites each (*Pacificella variabilis*, *Tornatellides oblongus*); and five species present at one site each (*Assimineea parvula*, *Gastrocopta servilis*, *Allopeas micra*, *Subulina octona*, *Sinployea atiensis*). Old empty shells in ground soils indicate *Truncatella guerinii*, *Nesopupa armata*, *Libera fratercula* and *Discocharopa aperta* also formerly lived at one or more of these sites but have since died out. Similarly, *Sinployea atiensis* formerly lived in the vicinity of site B1 but is no longer extant there.

Species richness of the fossil fauna at Paraoa was thus the same as, or higher than, that of modern landsnail assemblages, and four species represented in the fossil fauna were also present at all the modern sites sampled at Paraoa. However, the other five fossil species have apparently subsequently died out at Paraoa, and several other species not known from the fossil fauna have become established in the

Table 3 Biogeographical composition of modern and fossil landsnail assemblages on Miti'āro, showing numbers of species and percentage of total within each habitat type.

	Sites	Cook Islands species	Polynesian species	Tropical Pacific species	Extra-Pacific species
Coastal shrubland and forest	A1, A2, A4, B1	1 (9%)	3 (27%)	3 (27%)	4 (36%)
Scrubby makatea forest	A7, A13, B5	3 (15%)	7 (35%)	5 (25%)	5 (25%)
Broadleaved-coconut makatea forest	A6, A8, B6	4 (15%)	8 (30%)	6 (22%)	9 (33%)
Riparian <i>Casuarina</i> groves	A3, A12	0	3 (23%)	4 (31%)	6 (46%)
Tree gardens	A5, A9	2 (14%)	4 (29%)	2 (14%)	6 (43%)
Horticultural plots	A10, A11	0	3 (27%)	2 (18%)	6 (55%)
Paraoa fossil assemblage	P1–4	1 (13%)	3 (37%)	3 (37%)	1 (13%)

area. The timing of these extinctions/extirpations and arrivals is not directly known. The fact that shells of *Omphalotropis variabilis* and *Lamellidea oblonga* were found only in the buried soil suggests that these two species may have died out some time before *Truncatella guerini*, *Liberia fratercula* and *Discocharopa aperta*, which were present in both the buried soil and overlying ground soil. Whether these species died out in late prehistoric time or after European contact is presently unknown.

Three of the new arrivals at Paraoa (*Gastrocopta servilis*, *Allopeas micra*, *Subulina octona*) are extra-Pacific species that were probably synanthropically introduced to Miti'āro after European contact. The other arrivals (*Assimineea parvula*, *Pacificella variabilis*, *Tornatellides oblongus*, *Nesopupa armata*, *Sinployea atiensis*) were probably all present on Miti'āro before European contact, so potentially could have established at Paraoa anytime after the early sixteenth century. Fossil shells of the last-named species were present in the ground soil at site B1, indicating that it at least has a long history at Paraoa.

Discussion Biogeography

No endemic landsnails are known from Miti'āro. This is in marked contrast to the landsnail faunas of Aitutaki, Ātiu, Mangaia, Manuae and Rarotonga, which contain(ed) local endemics in families Assimineidae, Charopidae, Endodontidae, Euconulidae and Partulidae (Garrett 1881; Solem 1976, 1983; Brook 2010, unpublished data). If this absence of endemics on Miti'āro is real, it supports the contention of Stoddart *et al.* (1990) and Woodroffe *et al.* (1991) that the island was largely or completely submerged during Mid–Late Pleistocene highest sea-levels, including during the last interglacial maximum at *c.* 120 ka. If correct, this would also indicate that all the species in the Miti'āro landsnail fauna must have colonised either by natural dispersal since the time of last submergence, or by synanthropic introduction within the last 1000 years or so.

No fossil deposits older than the sixteenth century AD were found on Miti'āro during this study. As a result, the

composition and diversity of the landsnail fauna before human settlement is not known, but the original fauna was undoubtedly very different from that reported here. At least 37 landsnail species are known to have been, or have become, established on Miti'āro since the early sixteenth century. This total includes a mix of Cook Islands, Polynesian, tropical Pacific and extra-Pacific species. The 12 extra-Pacific species listed in Table 2 were almost certainly all synanthropic introductions. One is known to have been established on Miti'āro by the early sixteenth century (i.e. *Allopeas gracile*). *Pupisoma orcula* was not present in the Paraoa fossil fauna but it does occur in prehistoric occupation horizons elsewhere in the southern Cook Islands (Rarotonga, Aitutaki) (Brook 2010, unpublished data), and may have been introduced to Miti'āro before European contact. The other 10 extra-Pacific species and '*Microcystina*' *gerritsi* are inferred to have been introduced since European contact (below).

At present, it is not possible to determine conclusively whether the other species in the Miti'āro fauna are indigenous or non-indigenous on this island (i.e. these are all cryptogenic species, *sensu* Carlton 1996), but some inferences can be drawn on the basis of known distributions and histories elsewhere. The widely distributed supralittoral species *Assiminea lucida*, *Truncatella guerinii* and *Melampus luteus* are probably all indigenous to Miti'āro. Conversely, some or many of the fully terrestrial tropical Pacific, Polynesian and Cook Islands species may be non-indigenous. Many of these cryptogenic species (e.g. *Omphalotropis variabilis*, *Elasmias apertum*, *Lamellidea oblonga*, *Lamellidea pusilla*, *Pacificella variabilis*, *Tornatellides oblongus*, *Gastrocopta pediculus*, *Discocharopa aperta*, *Liardetia samoensis*) are thought to have been synanthropically dispersed among eastern Polynesian islands in prehistoric time (Pilsbry 1916–18; Baker 1938; Cooke & Kondo 1961; Kirch 1973; Allen 1997, 1998; Preece 1998; Walter 1998; Brook 2010), and may well have been introduced to Miti'āro. Five species in the latter group are represented in the Paraoa fossil fauna, so have been present on Miti'āro since at least the early sixteenth century AD. This fossil fauna presumably contained only a subset of the contemporary landsnail fauna on Miti'āro, but the presence of *Allopeas gracile* and probable synanthropic adventives like *Lamellidea pusilla*, *G. pediculus* and *D. aperta* indicates coastal landsnail assemblages were already highly modified by the early sixteenth century. Whether the subsequent establishment of *Assiminea parvula*, *P. variabilis*, *Tornatellides oblongus*, *Nesopupa armata* and

Sinployea atiensis in the vicinity of the Paraoa site was owing to habitat-mediated expansion of pre-existing populations on Miti'āro, and/or further new synanthropic introductions to this island, is not known at present.

As noted, '*Microcystina*' *gerritsi*, along with all the extra-Pacific landsnails on Miti'āro except *Allopeas gracile* and possibly *Pupisoma orcula*, are inferred to have been introduced to the island after European contact. This component of the Miti'āro fauna represents a subset of the extra-Pacific faunas of other islands in the southern Cook group (Brook 2010, unpublished data; Appendix 2), and may have been derived in part from secondary sources on one or more of these islands. *Subulina octona* is the only extra-Pacific species represented in a landsnail collection made on Miti'āro in 1929 (BPBM), and was evidently widespread and abundant on the island at this time. However, comparison with the better known faunal histories of other islands suggests that some other post-European species may also have been established by the early 1900s, whereas some were probably more recent arrivals. For example, *Gastrocopta servilis*, *Allopeas clavulinum*, *Allopeas micra*, *Opeas hannense* and '*Microcystina*' *gerritsi* were all established elsewhere in the Cook Islands by the early 1900s; *Vaginulus plebeius*, *Paropeas achatinaceum* and *Bradybaena similis* by the mid-1900s; and *Streptostele musaecola* and *Quickia concisa* by the late 1900s (Brook 2010). Establishment of these species on Miti'āro, as on other southern Cook Islands, presumably resulted from inadvertent introductions on foliage or in soil around the roots of crop and ornamental plants, or as stowaways in imported cargo.

Extirpation and extinction

The landsnail fauna of Miti'āro, in common with those of many other tropical Pacific islands, was modified by the local extirpation and probably also extinctions of some species in late-Holocene time. As noted, four species are known from fossils only on Miti'āro and are thought to be extinct on this island, and several other species have evidently died out locally within the last few hundred years. The causes of these declines and inferred extinctions are not known directly, but potentially could include modification and loss of habitat, predation by introduced species, competition with introduced species, or mortality from introduced pathogens (e.g. Solem 1976, 1983, 1990; Hadfield 1986; Hadfield *et al.* 1993; Cowie 2000, 2001a,b; Bouchet & Abdou 2003; Brook 2010).

Since human settlement began on Miti'āro there have been substantial anthropic habitat changes as a result of vegetation clearance for settlements and horticulture, and the introduction of new plant species. The original vegetation on volcanic-derived soils of the four foodlands was evidently completely cleared for horticulture and settlements in prehistoric time, and cultivated trees and other dryland crops have probably also been grown in clearings on Holocene coastal sediments, and in pockets of soil on the makatea, since then. These habitat changes undoubtedly affected the local distribution and abundance of the various landsnail species present to a greater or lesser degree, depending on particular tolerances to, and the nature and frequency of, the disturbance. However, the greater portion of the makatea on Miti'āro is unsuitable for horticulture and settlement, and was presumably never used for these purposes. Whether the original vegetation of this undeveloped part of the island has survived intact and relatively unmodified throughout the period of human occupation, or has been substantially altered by plants introduced by Polynesians (e.g. possibly including *Casuarina equisetifolia* – see Whistler 1991), recruitment failure of some tree or shrub species (below), or catastrophic events such as fires, cyclones and tsunamis, has not been determined. Palynological, sedimentological and geochemical analyses of swamp and lacustrine deposits in the central depression could potentially provide considerable information on the late-Holocene vegetation history of Miti'āro.

Two species of introduced rats are present on Miti'āro (McCormack 2007): the Pacific rat (*Rattus exulans*), which was probably introduced prehistorically; and the ship rat (*Rattus rattus*), which arrived after European contact (Atkinson 1985). Both species are known to prey on landsnails (e.g. Daniel 1973; Brook 1999, 2000) and may have contributed to declines of some species on Miti'āro. Furthermore, seed predation by the Pacific rat has been identified as an agent of prehistoric lowland forest collapse in Hawai'i and Easter Island (Athens *et al.* 2002; Hunt 2007). Whether or not this species had a similar influence on vegetation communities on Miti'āro is unknown, though the possibility that it may have contributed to the present highly restricted distribution of the palm *Pritchardia mitiarioana* warrants further investigation.

Solem (1976: 100–101; 1983: 97) argued that predation of snails and their eggs by introduced ants was an important cause of recent declines and extinctions of species of ground-dwelling endodontoid snails on tropical Pacific islands.

At least 11 species of ants are known from Miti'āro (McCormack 2007), all or most of which were probably introduced since European contact. They include three highly invasive and ecologically damaging species (i.e. *Anoplolepis gracilipes*, *Paratrechina longicornis*, *Pheidole megacephala*) that have been implicated in declines and extinction of native invertebrates on other tropical Pacific islands (e.g. Perkins 1913; Zimmerman 1948; Nafus 1993; Reimer 1994; Wetterer 1997, 2007; Holway *et al.* 2002). Predation by ants may well have contributed to the extirpation/extinction of various landsnail species on Miti'āro over the last 150 years or so, although a lack of direct evidence means this is only speculation.

The actual history of landsnail decline, extirpation and extinction on Miti'āro is poorly known at present. The only stratified sequence examined was at Paraoa, where five landsnail species are known as fossils only. The causes of the species losses at this site are not known directly. Habitat changes may have been a key factor in the loss of *Omphalotropis variabilis* and *Libera fratercula*. In modern coastal habitats elsewhere in the southern Cook Islands, these two species typically inhabit broadleaved forest and closed-canopy shrubland (Brook 2010, unpublished data). This suggests that the Paraoa area may have supported taller broadleaved vegetation in the sixteenth century, rather than the open, stunted shrubland and *Casuarina*-coconut groves present today. The presence of rare old shells of *Libera fratercula* at sites A4 and B1 suggests that similar vegetation changes occurred there as well, and may have been widespread along the exposed eastern coast of Miti'āro. However, vegetation changes alone do not provide an adequate explanation for the extirpation of *Truncatella guerinii* and *Lamellidea oblonga* at Paraoa and elsewhere on the eastern coast. In the modern faunas of Miti'āro and other southern Cook Islands, these two species inhabit a variety of coastal habitats, ranging from low, open shrubby and herbaceous vegetation, to closed shrubland and forest (Brook 2010, unpublished data).

Similarly, other factors presumably contributed to the apparent island-wide extinctions of *Libera fratercula* and *Discocharopa aperta*, and the local extirpation of *Sinployea atiensis*, as these species died out not only in coastal habitats, but also in inland areas that presently support forest and closed shrubland. In 1994 and 2007, *S. atiensis* was actually most abundant in non-indigenous forest (i.e. tree gardens) on the Takaue foodland and in highly modified forest on the adjoining makatea, was scarce and extirpated in shrubland

and forest groves on the east coast, and had died out in makatea forest southeast and northeast of Mangarei village. In these cases, the declines and extirpation/extinction may have been caused by predation and/or disease, although the possibility that they resulted from habitat changes caused by catastrophic events in late prehistoric time cannot be discounted at present.

Conclusions

The broad pattern of faunal change on Miti'āro in the last few hundred years, namely the decline and extirpation/extinction of some landsnail species, and the establishment of a diverse suite of non-indigenous species, is common to other islands in the southern Cook group, and elsewhere in the tropical Pacific (e.g. Solem 1976, 1983, 1990; Cowie 2001a,b; Cowie & Robinson 2003; Brook 2010). As on other islands, many habitats on Miti'āro are now dominated by alien landsnail species ultimately derived from sources outside the Pacific region. The majority of the known non-indigenous species on Miti'āro have been introduced since European contact, and probably most in the last 100 years or so. However, the extent to which the landsnail fauna of Miti'āro was modified by synanthropic introductions in prehistoric time is still largely unknown. The extra-Pacific species *Allopeas gracile* was almost certainly introduced by Polynesians, but it is possible that many, or even most, of the cryptogenic Cook Islands, Polynesian and tropical Pacific species in the fauna (e.g. including *Omphalotropis variabilis*, *Elasmias apertum*, *Lamellidea oblonga*, *Lamellidea pusilla*, *Pacificella variabilis*, *Tornatellides oblongus*, *Gastrocopta pediculus*, *Discocharopa aperta* and *Liardetia samoensis*) were also introduced synanthropically before European contact. As already noted, at present it is not possible to distinguish indigenous from non-indigenous species reliably, because the composition of the native fauna on Miti'āro prior to human settlement is not known. This problem will be resolved only if pre-settlement fossil assemblages can be found. The extensive deposits of perched calcareous sand and coral rubble on the eastern and northern sides of Miti'āro were not examined during the present study, but offer the greatest potential for preservation of stratified fossil sequences of pre- and post-settlement age on this island.

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Appendix 1:

Details of sites sampled for landsnails on Miti'āro in 1994 and 2007

Paraoa archaeological site

- P1 Cook Islands, Miti'āro, Paraoa, Dec. 1993, R. Walter. Cultural layer to 30 cm thick of black sand containing burnt marine shell, coral fragments and fine charcoal [Sample 1 – Test pit 1, Layer 2 (Craig 1995: 87; Walter & Campbell 1996: 49–50)].
- P2 Cook Islands, Miti'āro, Paraoa, Dec. 1993, R. Walter. Shallow fire scoop, probably base of an umu [Sample 2 – Area 1, Feature 1 (Craig 1995: 87; Walter & Campbell 1996: 49–50)].
- P3 Cook Islands, Miti'āro, Paraoa, Dec. 1993, R. Walter. Cultural layer to 30 cm thick of black sand containing marine shell, stones and fine charcoal [Sample 3 – Test pit 2, Layer 2 (Craig 1995: 88; Walter & Campbell 1996: 49–50)].
- P4 Cook Islands, Miti'āro, Paraoa, Dec. 1993, R. Walter. Cultural layer to 25 cm thick containing burnt marine shell, stones and charcoal [Sample 4 – Area 1, Layer 2 (Craig 1995: 88; Walter & Campbell 1996: 49–50)].

Modern sites 1994

- A1 Cook Islands, Miti'āro, Paraoa, 1994, A. Brooks & T. Taia. Under *Casuarina equisetifolia* needles and leaf litter, c. 10–20 m inland of the road [site 1–A (Craig 1995: 83, fig. 4-2)].
- A2 Cook Islands, Miti'āro, Paraoa, 1994, A. Brooks & T. Taia. Under *Casuarina equisetifolia* trees and leaf litter, near the house platform on the coastal side of the road [site 1–B (Craig 1995: 83, fig. 4-2)].
- A3 Cook Islands, Miti'āro, Te Rotonui, 1994, A. Brooks & T. Taia. Recently flooded area under *Casuarina equisetifolia* trees at road end on E side of lake [site 6 (Craig 1995: 83, fig. 4-2)].
- A4 Cook Islands, Miti'āro, eastern coast, 1994, A. Brooks & T. Taia. Clearing in shrubland on coastal makatea c. 1300 m S of Paraoa [site 7 (Craig 1995: 84, fig. 4-2)].
- A5 Cook Islands, Miti'āro, Takaue foodland, 1994, A. Brooks & T. Taia. Leaf litter under banana, breadfruit, *Cordyline terminalis* and *Inocarpus fagifer* [site 3 (Craig 1995: 83, fig. 4-2)].
- A6 Cook Islands, Miti'āro, Takaue foodland, 1994,

- A. Brooks & T. Taia. Inland makatea edge forest, with leaf litter and ferns [site 2 (Craig 1995: 83, fig. 4-2)].
- A7 Cook Islands, Miti'āro, Takaue foodland, Rimapere Pool, 1994, A. Brooks & T. Taia. Scrub in makatea at entrance to pool [site 4 (Craig 1995: 83, fig. 4-2)].
- A8 Cook Islands, Miti'āro, Takaue foodland, 1994, A. Brooks & T. Taia. Leaf litter and ferns under *Cocos nucifera* palm [site 8 (Craig 1995: 84, fig. 4-2)].
- A9 Cook Islands, Miti'āro, Takaue foodland, 1994, A. Brooks & T. Taia. Under mango (*Mangifera indica*) tree [site 5 (Craig 1995: 83, fig. 4-2)].
- A10 Cook Islands, Miti'āro, Mangarei foodland, 1994, A. Brooks & T. Taia. Under wetland taro (*Colocasia esculenta*) plants beside road [site 10 (Craig 1995: 84, fig. 4-2)].
- A11 Cook Islands, Miti'āro, Mangarei foodland, 1994, A. Brooks & T. Taia. Under *Cordyline fruticosa* plants in an open area surrounded by wetland taro (*Colocasia esculenta*) [site 9 (Craig 1995: 84, fig. 4-2)].
- A12 Cook Islands, Miti'āro, road to Mangarei and Takaue foodlands, 1994, A. Brooks & T. Taia. Recently flooded area under *Casuarina equisetifolia* trees at edge of swamp [site 11 (Craig 1995: 84, fig. 4-2)].
- A13 Cook Islands, Miti'āro, road to Mangarei and Takaue foodlands, 1994, A. Brooks & T. Taia. Under limestone blocks in recently cleared area of inland makatea, formerly covered in scrub and forest [site 12 (Craig 1995: 84, fig. 4-2)].
- Modern sites 2007**
- B1 Cook Islands, Miti'āro, E coast N of Paraoa, 19° 52.095'S, 157° 40.857'W, 10/06/2007, F. Brook & D. Winter. Open *Pandanus-Suriana-Timonius* shrubland on rubble-strewn sandy soil.
- B2 Cook Islands, Miti'āro, SE of Takaue foodland near inner edge of makatea, 19° 52.797'S, 157° 41.968'W, 9/06/2007, F. Brook & D. Winter. Litter, fallen wood and ferns in disturbed mixed broadleaved-coconut forest on makatea.
- B3 Cook Islands, Miti'āro, SW of Takaue foodland near inner edge of makatea, 19° 52.778'S, 157° 42.248'W, 9/06/2007, F. Brook & D. Winter. Litter, fallen wood and ferns in disturbed mixed broadleaved-coconut forest on makatea.
- B4 Cook Islands, Miti'āro, Takaue foodland, 19° 52.710'S, 157° 42.237'W, 8/06/2007, F. Brook & D. Winter. Leaf litter and fallen wood on volcanic soil under mango and other exotic broadleaved trees.
- B5 Cook Islands, Miti'āro, S side of road SE of Takaue village, 19° 51.740'S, 157° 42.969'W, 10/06/2007, F. Brook & D. Winter. Mixed *Casuarina-Pandanus*-broadleaved low forest on pocket of fine sandy soil in hollow on makatea.
- B6 Cook Islands, Miti'āro, N side of road ENE of Mangarei village, 19° 51.452'S, 157° 42.492'W, 11/06/2007, F. Brook & D. Winter. Mixed broadleaved-*Cocos nucifera* forest on makatea with pockets of sandy soil.
- B7 Cook Islands, Miti'āro, W coast N of Omutu Landing, 19° 51.512'S, 157° 43.201'W, 9/06/2007, F. Brook & D. Winter. Litter under *Casuarina equisetifolia* and *Scaevola-Pemphis* shrubland on coastal makatea.

Appendix 2:

Annotated list of landsnail species recorded from Miti'āro

Information on species distributions among the southern Cook Islands was obtained from Garrett (1881), Cooke & Kondo (1961), Solem (1976, 1983), Allen & Christensen (1992), and Brook (2010, unpublished data), and from examination of the mollusc collection in the Bishop Museum (Honolulu), and the Museum of New Zealand Te Papa Tongarewa (Wellington). Distribution records from the southern Cook Islands are listed as follows: Aitutaki (AK), Manuae (MA), Ātiu (AT), Ma'uke (MK), Miti'āro (MT), Mangaia (MG), Palmerston (PA) and Rarotonga (RR).

Miti'āro site designations are as follows: P1–4 are archaeological samples from Paraoa, with ^ denoting species represented by modern shells only; A1–13 are soil and litter samples collected in 1994; B1–7 are modern samples collected in 2007, with * denoting species present in modern samples as old shells only. Site details are listed in Appendix 1.

Collection numbers with BPBM and NMNZ M. prefixes refer to material in the Bishop Museum and the Museum of New Zealand Te Papa Tongarewa, respectively.

Status of species on Miti'āro is listed as 'extant' if live individuals or fresh empty shells were found in 1994 and/or 2007, or 'probably extinct' if old empty shells only were found.

Class GASTROPODA

Order NERITOPSINA

HYDROCENIDAE

Georissa striata (Pease, 1871) AK, AT, MK, MT, RR

SITES: A3, A6–8, A9*, A10*, A12*, A13; B2, B3, B5, B6.
COLLECTIONS: NMNZ M.282150, 282172, 282191,
282208, 282224, 282256, 282269, 282282, 282306,
282314, 282330, 282352.

DISTRIBUTION: southeastern Polynesia (Garrett 1879, 1881,
1884, 1887; Cooke 1934).

STATUS: extant; inland makatea forest.

HELICINIDAE

Orobophana pacifica (Pease, 1865) AK, MA, AT, MK,
MT, MG, RR

SITES: P1–4; A1–4, A7, A8*, A11*, A13; B1, B5*, B6.

COLLECTIONS: BPBM 95673–8; NMNZ M.282099,
282106, 282114, 282123, 282131, 282142, 282173,
282209, 282217, 282225, 282246, 282283, 282323,
282331, 282353, 282379.

DISTRIBUTION: southeastern Polynesia (Garrett 1881, 1884;
Brook 2010).

STATUS: extant; coastal shrubland and forest, and inland
makatea forest.

Order SORBEOCONCHA

ASSIMINEIDAE

Assiminea lucida Pease, 1869 MA, AT, MK, MT, MG, RR
SITE: B7.

COLLECTION: NMNZ M.282319.

DISTRIBUTION: southern Polynesia (Brook 2010).

STATUS: extant; coastal shrubland.

Assiminea parvula (Mousson, 1865) AK, AT, MT, MG, RR
SITES: A1, A6*, A7*, A8–10, A11*, A12; B6.

COLLECTIONS: NMNZ M.282132, 282151, 282174,
282192, 282218, 282226, 282247, 282257, 282270,
282354.

DISTRIBUTION: southern Polynesia (Brook 2010).

STATUS: extant; coastal shrubland and forest, inland makatea
forest, and foodlands.

Omphalotropis variabilis Pease, 1865 AK, MA, AT, MK,
MT, MG, RR

SITES: P1–3; A5, A6, A7*, A8–10, A11*, A12*, A13; B2–6.
COLLECTIONS: NMNZ M.282100, 282107, 282115,
282152, 282163, 282175, 282193, 282227, 282248,
282258, 282271, 282284, 282302, 282307, 282315,
282332, 282355.

DISTRIBUTION: southern Cook Islands, and Raivavae in the
Austral Islands (Garrett 1881; Brook 2010). Fossil faunas
indicate this species was introduced to Aitutaki, Ātiu,
Ma'uke and Mangaia in prehistoric time (Brook 2010,

unpublished data), and the population on Raivavae probably
also resulted from a synanthropic introduction.

STATUS: extant; inland makatea forest and foodlands.

TRUNCATELLIDAE

Truncatella guerinii A. Villa & J. Villa, 1841 MA, AT,
MT, MG, RR

SITES: P3, P4; A4*; B1*, B7.

COLLECTIONS: NMNZ M.282116, 282124, 282219,
282320.

DISTRIBUTION: tropical Indo-Pacific (Clench & Turner
1948).

STATUS: extant; coastal shrubland.

Order PULMONATA

VERONICELLIDAE

Vaginulus (Sarasinula) plebeius P. Fischer, 1868 AK, AT,
MT, MG, RR

SITES: B3, B4.

DISTRIBUTION: native to the Caribbean and South America,
but with a wide anthropogenic distribution in the tropical
Pacific (Grimpe & Hoffmann 1925; Baker 1931; Solem
1959, 1964; Cowie 1997, 2000, 2001b; Brook 2010).

STATUS: extant; inland makatea forest and foodlands.

ELLOBIIDAE

Melampus luteus (Quoy & Gaimard, 1832) AK, AT, MK,
MT, MG, RR

SITE: B7.

COLLECTION: NMNZ M.282321.

DISTRIBUTION: tropical Pacific.

STATUS: extant; coastal shrubland.

ACHATINELLIDAE

Elasmias apertum (Pease, 1865) AK, AT, MT, MG, RR
SITES: A7, A13; B3, B5, B6.

COLLECTIONS: BPBM 95679–82, 97413; NMNZ
M.282176, 282285, 282308, 282333, 282356.

DISTRIBUTION: widely distributed among islands in the
tropical South Pacific (Cooke & Kondo 1961).

STATUS: extant; inland makatea forest.

Lamellidea micropleura Cooke & Kondo, 1961 AK, AT,
MT

SITES: B5, B6.

COLLECTIONS: NMNZ M.282334, 282357.

DISTRIBUTION: Society Islands (Moorea) (Cooke & Kondo
1961), Pitcairn Island and Henderson Island (Preece 1995),
and southern Cook Islands (this study; Brook, unpublished
data).

STATUS: extant; inland makatea forest.

Lamellidea oblonga (Pease, 1865) AK, AT, MK, MT,
MG, RR

SITES: P2, P4; A8; B5, B6.

COLLECTIONS: NMNZ M.282108, 282125, 282228,
282335, 282358.

DISTRIBUTION: widely distributed in Polynesia; probably spread among central Pacific islands on food plants transported by humans in prehistoric time (Cooke & Kondo 1961).

STATUS: extant; inland makatea forest.

Lamellidea pusilla (Gould, 1847) AK, MA, AT, MK,
MT, MG, PA, RR

SITES: P1–4; A1–4, A7, A8, A13; B1, B5, B6.

COLLECTIONS: NMNZ M.282101, 282109, 282117,
282126, 282133, 282143, 282177, 282210, 282220,
282229, 282286, 282324, 282336, 282359.

DISTRIBUTION: widely distributed among islands in the tropical northwestern and southern Pacific; this species is thought to have originated west of the Marshall Islands in Micronesia, and been carried eastwards to islands in the central Pacific by humans in prehistoric time (Cooke & Kondo 1961).

STATUS: extant; coastal shrubland and forest, and inland makatea forest.

Pacificella variabilis Odhner, 1922 AK, MA, AT, MK,
MT, MG, RR

SITES: A2, A4, A7, A12; B1, B3, B5–7.

COLLECTIONS: BPBM 95672, 95683, 97414; NMNZ
M.282144, 282178, 282221, 282272, 282287, 282309,
282322, 282325, 282337, 282360.

DISTRIBUTION: widely distributed in the Pacific, from Micronesia to southeastern Polynesia (Cooke & Kondo 1961; Preece 1995; Bauman 1996).

STATUS: extant; coastal shrubland and inland makatea forest.

Tornatellides oblongus (Anton, 1839) AK, AT, MK, MT,
MG, RR

SITES: A1, A2, A6, A8, A9, A11; B2–6.

COLLECTIONS: BPBM 97415; NMNZ M.282134, 282145,
282153, 282194, 282230, 282249, 282310, 282316,
282338, 282361.

DISTRIBUTION: widely distributed among islands in the tropical southeastern Pacific (Cooke & Kondo 1961).

STATUS: extant; coastal shrubland and forest, inland makatea forest and foodlands.

VERTIGINIDAE

Gastrocopta pediculus (Shuttleworth, 1852) AK, MA, AT,
MK, MT, MG, PA, RR

SITES: P1–4; A1–8, A9*, A11–13; B1, B5, B6.

COLLECTIONS: NMNZ M.282102, 282110, 282118,
282127, 282135, 282146, 282154, 282164, 282179,
282195, 282211, 282222, 282231, 282250, 282273,
282288, 282326, 282339, 282362.

DISTRIBUTION: widely distributed among tropical Pacific islands; probably native to the southwestern Pacific (Pilsbry 1916–18; Cooke 1934; Solem 1959, 1964, 1978, 1989; Kirch 1973, 1993; Christensen & Kirch 1981, 1986; Hunt 1981; Rollett 1992; Cowie 1997, 1998a,b, 2000, 2001b; Preece 1998; Brook 2010).

STATUS: extant; coastal shrubland, inland makatea forest and foodlands.

Gastrocopta servilis (Gould, 1843) AK, MA, AT, MT,
MG, RR

SITES: P1[^], P3[^]; A1, A5, A8–10, A12; B6.

COLLECTIONS: NMNZ M.282103, 282119, 282136,
282165, 282196, 282232, 282259, 282274, 282363.

DISTRIBUTION: probably native to the Caribbean, central America and Brazil, with a wide synanthropic distribution among islands in the tropical Pacific (Pilsbry 1916–18; Solem 1964, 1978, 1989; Christensen & Kirch 1986; Cowie 1997, 1998b, 2000, 2001b; Brook 2010).

STATUS: extant; coastal shrubland and forest, inland makatea forest and foodlands.

Nesopupa armata (Pease, 1871) AK, AT, MT, MG, RR

SITES: A1*, A6, A8, A9, A13; B5, B6.

COLLECTIONS: NMNZ M.282137, 282155, 282197,
282233, 282289, 282340, 282364.

DISTRIBUTION: Society Islands and southern Cook Islands (Pilsbry & Cooke 1918–20; Brook 2010).

STATUS: extant; inland makatea forest and foodlands.

Nesopupa dentifera (Pease, 1871) AK, AT, MT, RR

SITES: A7–9, A13; B5.

COLLECTIONS: NMNZ M.282180, 282198, 282234,
282290, 282341.

DISTRIBUTION: southern Cook Islands (Pilsbry & Cooke 1918–20; Brook 2010).

STATUS: extant; inland makatea forest and foodlands.

Nesopupa rarotonga Brook, 2010 AK, AT, MT, MG, RR

SITES: A7, A8, A9*, A13; B5, B6.

COLLECTIONS: NMNZ M.282181, 282199, 282235,
282291, 282342, 282365.

DISTRIBUTION: southern Cook Islands (Brook 2010).

STATUS: extant; inland makatea forest.

Nesopupa sp. 1 AT, MT, MG

SITES: A6, A7, A13; B5.

COLLECTIONS: NMNZ M.282156, 282182, 282292, 282343.

DISTRIBUTION: southern Cook Islands (Brook, unpublished data).

STATUS: extant; inland makatea forest.

Pupisoma orcula (Benson, 1850) AK, AT, MK, MT, MG, RR

SITES: A7, A13; B5, B6.

COLLECTIONS: NMNZ M.282183, 282293, 282344, 282366.

DISTRIBUTION: a tropical species known from southeastern Africa, India, Indonesia, Japan, Philippines, New Guinea, Australia, and many Pacific islands (Pilsbry 1920–21; Cooke 1934; Solem 1964, 1989; Preece 1995, 1998; Cowie 1997, 1998b, 2000, 2001b; Brook 2010).

STATUS: extant; inland makatea forest.

SUBULINIDAE

Allopeas clavulinum (Potiez & Michaud, 1838) AK, AT, MT, MG

SITE: A12.

COLLECTION: NMNZ M.282275.

DISTRIBUTION: probably native to Asia, with a wide tropical synanthropic distribution that includes many Pacific islands (Pilsbry 1906–07; Cooke 1934; Solem 1978, 1989; Preece 1995; Cowie 1997, 1998b, 2000, 2001b; Brook 2010).

STATUS: extant; foodlands; known from a single empty juvenile shell collected in 1994.

Allopeas gracile (Hutton, 1834) AK, MA, AT, MK, MT, MG, PA, RR

SITES: P1–4; A1, A2, A5–13; B1, B4–6.

COLLECTIONS: NMNZ M.282104, 282111, 282120, 282128, 282138, 282147, 282157, 282166, 282184, 282200, 282236, 282251, 282260, 282276, 282294, 282303, 282327, 282345, 282367, 287359.

DISTRIBUTION: probably native to Asia, with a very wide synanthropic distribution that includes many tropical Pacific islands (e.g. Pilsbry 1906–07; Cooke 1934; Solem 1964; Preece 1995; Cowie 1997, 1998a, 2000, 2001b; Boyko & Cordeiro 2001; Brook 2010).

STATUS: extant; coastal shrubland and forest, inland makatea forest and foodlands.

Allopeas micra (d'Orbigny, 1835) MT, MG, RR

SITES: A2, A3, A5–13; B3, B5, B6.

COLLECTIONS: NMNZ M.282148, 282158, 282167, 282185, 282201, 282212, 282237, 282252, 282261, 282277, 282295, 282311, 282346, 282368.

DISTRIBUTION: native to central and southern America and the Caribbean, with a wide synanthropic distribution that includes several tropical Pacific islands (Pilsbry 1906–07; Solem 1964; Cowie 2001a,b; Brook 2010).

STATUS: extant; coastal shrubland and forest, inland makatea forest and foodlands.

Opeas hannense (Rang, 1831) AK, AT, MT, MG, RR

SITES: A3, A7, A8, A12, A13; B5, B6.

COLLECTIONS: NMNZ M.282186, 282213, 282238, 282278, 282296, 282347, 282369.

DISTRIBUTION: native to the American tropics, with a wide synanthropic distribution that includes many tropical Pacific islands (Solem 1959, 1978, 1989; Christensen & Kirch 1981; Preece 1995; Cowie 1997, 1998a,b, 2000, 2001b; Brook 2010).

STATUS: extant; inland makatea forest.

Paropeas achatinaceum (Pfeiffer, 1846) AT, MT, MG, RR

SITES: A5, A9; B4.

COLLECTIONS: NMNZ M.282168, 282202.

DISTRIBUTION: native to Southeast Asia, with a wide synanthropic distribution among tropical Pacific islands (Solem 1978, 1989; Naggs 1994; Cowie 1997, 1998b, 2000, 2001b; Brook 2010).

STATUS: extant; foodlands.

Subulina octona (Bruguière, 1792) AK, AT, MK, MT, MG, RR

SITES: A1, A5, A6, A8–11; B6.

COLLECTIONS: BPBM 95671, 97416; NMNZ M.282139, 282159, 282169, 282203, 282239, 282253, 282262, 282370, 287360.

DISTRIBUTION: thought to be native to the American tropics, with a wide synanthropic distribution that includes many tropical Pacific islands (Pilsbry 1906–07; Cooke 1928, 1934; Solem 1964, 1978; Preece 1995; Cowie 1997, 1998a,b, 2000, 2001b; Brook 2010).

STATUS: extant; coastal shrubland and forest, inland makatea forest and foodlands.

STREPTAXIDAE

Streptostele (Tomostele) musaecola (Morelet, 1860) AK, AT,
MT, MG, RR

SITES: A3, A10, A12, A13; B5, B6.

COLLECTIONS: NMNZ M.282214, 282263, 282279,
282297, 282348, 282371.

DISTRIBUTION: native to West Africa, with a wide syn-
anthropic distribution in the tropics. Adventive populations
have been recorded from Vanuatu, Samoa, Cook Islands,
Society Islands, central America, Bermuda, and several
islands in the Caribbean (Solem 1989; Cowie 1998a, 2001a;
Hausdorf & Bermúdez 2003; Brook 2010).

STATUS: extant; inland makatea forest and foodlands.

ENDODONTIDAE

Libera fratercula (Pease, 1867) AK, MA, AT, MK,
MT, MG, RR

SITES: P1–4; A4*, A7*, A9*, A10*, A13*; B1*, B5*, B6*.

COLLECTIONS: NMNZ M.282105, 282112, 282121,
282129, 282187, 282204, 282223, 282264, 282298,
282328, 282349, 282372.

DISTRIBUTION: southern Cook Islands (Garrett 1881;
Solem 1976).

STATUS: probably extinct on Miti'āro.

Mautodontha (Garrettoconcha) rarotongensis (Pease, 1870)
AK, AT, MT

SITE: A8*.

COLLECTION: NMNZ M.282240.

DISTRIBUTION: southern Cook Islands (Garrett 1881; Solem
1976; Brook, unpublished data).

STATUS: probably extinct on Miti'āro.

Minidonta sp. AT, MT

SITES: A3*; B6*.

COLLECTIONS: NMNZ M.282215, 282373.

DISTRIBUTION: southern Cook Islands (Brook, unpublished
data).

STATUS: probably extinct on Miti'āro.

CHAROPIDAE

Discocharopa aperta (Mollendorff, 1888) AK, AT, MK,
MT, MG, RR

SITES: P2–4; A1*, A2*, A6*, A7*, A8*, A13*; B6*.

COLLECTIONS: NMNZ M.282113, 282122, 282130,
282140, 282149, 282160, 282188, 282241, 282299,
282374.

DISTRIBUTION: Philippines, Indonesia, Australia, and many
Pacific islands (Solem 1983; Brook 2010).

STATUS: probably extinct on Miti'āro.

Sinployea atiensis (Pease, 1870) AK, AT, MK, MT, MG, RR
SITES: A1, A5, A6, A7*, A8, A9, A10*, A13*; B1*, B2–4,
B5*, B6*.

COLLECTIONS: NMNZ M.282141, 282161, 282170,
282189, 282205, 282242, 282265, 282300, 282304,
282312, 282317, 282329, 282350, 282375.

DISTRIBUTION: southern Cook Islands (Garrett 1881; Solem
1983; Brook 2010).

STATUS: extant; coastal shrubland and forest, inland makatea
forest, and foodlands.

EUCONULIDAE

Liardetia (Liardetia) samoensis (Mousson, 1865) AK, MA,
AT, MK, MT, MG, RR

SITES: A3, A6–9, A11, A13; B2–6.

COLLECTIONS: NMNZ M.282162, 282190, 282206,
282216, 282244, 282254, 282301, 282305, 282313,
282318, 282351, 282377.

DISTRIBUTION: possibly native to Indonesia (Solem 1959),
with a wide and probably synanthropic distribution among
islands in the tropical Pacific (Baker 1938; Solem 1959,
1964, 1978; Christensen & Kirch 1981; Kirch 1993; Cowie
1998a, 2000, 2001b; Brook 2010).

STATUS: extant; inland makatea forest and foodlands.

Microcystina gerritsi Benthem Jutting, 1964 AK, AT, MT,
MG, RR

SITES: A8; B6.

COLLECTIONS: NMNZ M.282243, 282376.

DISTRIBUTION: probably native to northern New Guinea
and adjacent islands (Benthem Jutting 1964), with an
inferred synanthropic distribution in the Cook Islands
(Brook 2010).

STATUS: extant; inland makatea forest.

SUCCINEIDAE

Quickia concisa (Morelet, 1848) AK, AT, MT, MG, RR
SITE: B6.

COLLECTION: NMNZ M.282378.

DISTRIBUTION: native to western Africa and/or western
Indian Ocean islands, with a synanthropic distribution in
Polynesia (Brook 2010).

STATUS: extant; inland makatea forest.

BRADYBAENIDAE

Bradybaena similaris (Rang, 1831) AT, MT, MG, RR
SITES: A5, A8–11.

COLLECTIONS: NMNZ M.282171, 282207, 282245,
282255, 282266.

DISTRIBUTION: probably native to Asia and Indonesia, with a very wide synanthropic distribution in the tropics, including many Pacific islands (Pilsbry 1893–95; Solem 1959, 1964, 1978; Cowie 1997, 1998a,b, 2000, 2001b; Brook 2010).

STATUS: extant; inland makatea forest and foodlands.