

Coastal landsnail fauna of Rarotonga, Cook Islands: systematics, diversity, biogeography, faunal history, and environmental influences

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ABSTRACT: The prehistoric (pre-AD 1800) landsnail fauna of the Rarotongan coastal plain comprised at least 43 species. Seventeen of these were probably endemic to this island; the remainder of the fauna consisted of species with wider distributions in the tropical Pacific, including several species probably introduced by Polynesians. By contrast, the modern coastal landsnail fauna as surveyed in 2005–07 contained 48 species and was dominated by non-indigenous species that were mostly introduced to Rarotonga in the last 100 years or so; most of the Rarotongan and Cook Island endemics are either extinct or verging on extinction. Loss and modification of native shrubland and forest habitats in the lowlands during the historic period was undoubtedly a key factor in the declines and extinctions of many native Rarotongan snail species. However, the introduction and establishment of a suite of non-indigenous predators during the historic period was probably also a significant contributing factor, and is inferred to have been the main cause of the declines and extinctions of native snail species in inland Rarotonga over the last 140 years.

Descriptions of 13 new species of landsnails, thought to be endemic to Rarotonga, are given: *Atropis rarotongana* n.sp. (Assimineidae); eight species of *Minidonta* (Endodontidae) – *Minidonta aroa* n.sp., *Minidonta arorangi* n.sp., *Minidonta iota* n.sp., *Minidonta kavera* n.sp., *Minidonta matavera* n.sp., *Minidonta ngatangia* n.sp., *Minidonta pue* n.sp. and *Minidonta rutaki* n.sp.; and four species of *Sinployea* (Charopidae) – *Sinployea muri* n.sp., *Sinployea taipara* n.sp., *Sinployea titikaveka* n.sp. and *Sinployea tupapa* n.sp. *Nesopupa rarotonga* n.sp. (Vertiginidae) from the southern Cook Islands is also described.

KEYWORDS: Pacific Ocean, Cook Islands, Rarotonga, landsnail fauna, new species, fossil species, endemic species, non-indigenous species, extinctions, Holocene faunal changes.

Introduction

Rarotonga (21°14'S, 159°47'W) in the southern Cook Islands, southeastern Polynesia, is a high oceanic island bordered by a narrow coastal plain, lagoon and fringing coral reef (Fig. 1). It has a land area of 67 km² and a circumference of c. 30 km.

Andrew Garrett made extensive collections of landsnails on Rarotonga in 1865 and 1869, and documented a rich fauna with many local endemics, including noteworthy radiations in genera now included in the families Charopidae

and Endodontidae (Garrett 1872, 1874, 1881; Solem 1978, 1983). However, most of the endemic species recorded by Garrett were not found during subsequent surveys in the early to mid-1900s, leading Solem (1983: 45) to conclude that they had gone extinct. Since the mid- to late 1800s, declines and extinctions of endemic and indigenous landsnails have also been reported from many other tropical oceanic islands (e.g. Solem 1976, 1983, 1990; Chambers & Steadman 1986; Hadfield 1986; Cowie 1992, 2001a; Goodfriend *et al.* 1994; Baumann 1996; Dye & Tuggle 1998; Bieler & Slapcinsky 2000; Burney *et al.* 2001;

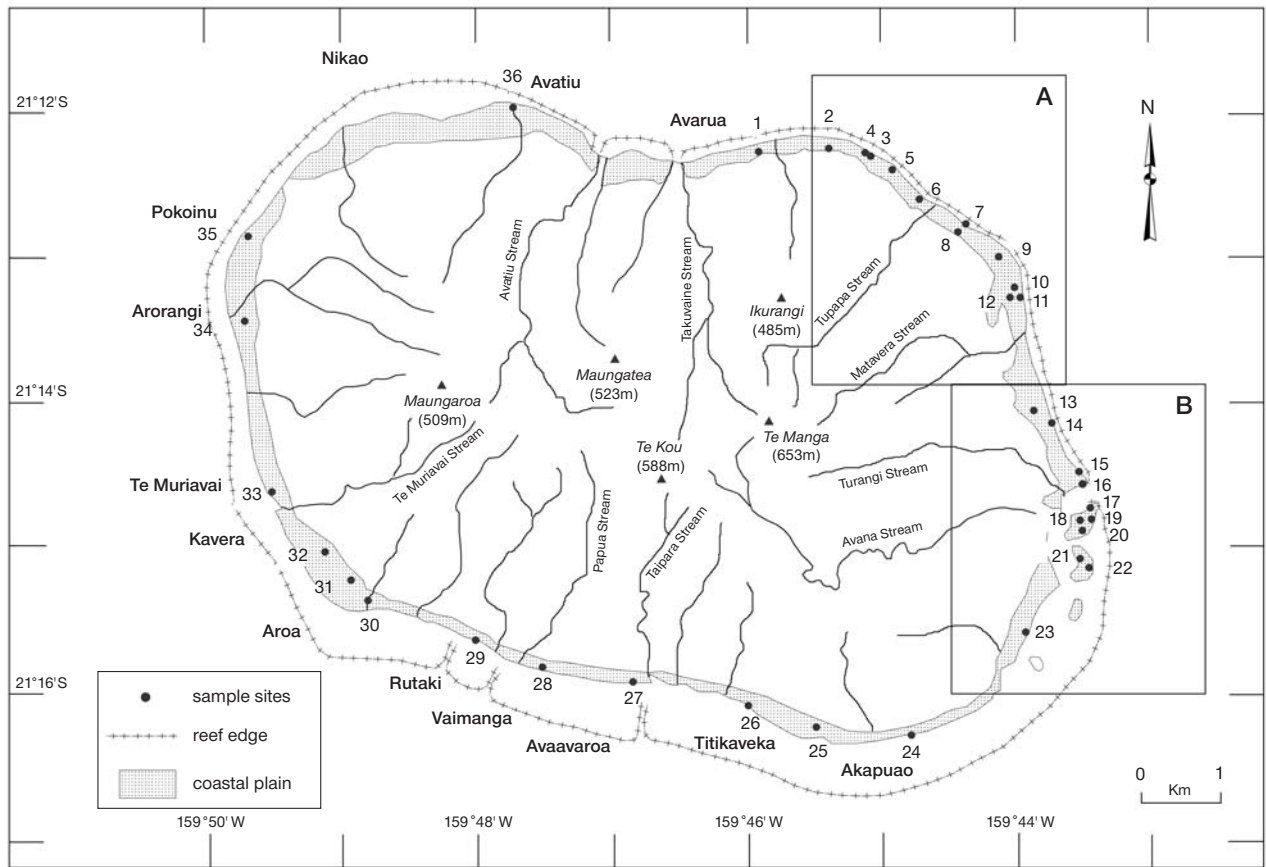


Fig. 1 Rarotonga, showing location of survey sites 1–36 on the coastal plain. Detailed maps of insets A and B given in Fig. 2. Stipple denotes the distribution of calcareous sediments on the coastal plain and motu. The peripheral crinkly line marks the location of the outer edge of the fringing reef.

Bouchet & Abdou 2003; Cowie & Robinson 2003), and have generally been attributed to habitat modification and destruction, and/or predation by non-indigenous vertebrates and invertebrates.

In addition to suffering loss of species through extinction, the faunas of most tropical Pacific islands, including Rarotonga, have also been altered by inadvertent or intentional synanthropic introductions of landsnails and slugs. Some species were probably spread throughout the tropical Pacific on food plants in prehistoric time (e.g. Cooke 1928; Baker 1938; Cooke & Kondo 1961; Christensen & Kirch 1981), but the majority have evidently been introduced to Pacific islands since European contact in the late 1700s to early 1800s (e.g. Solem 1964; Cowie 1998b). The landsnail faunas of some tropical and subtropical Pacific islands have been modified to such an extent that they are now dominated by adventive species (e.g. Easter Island: Kirch *et al.* 2009).

In the case of Rarotonga, information on the history of landsnail extinctions and invasions can be drawn from several sources. Of primary importance are Garrett's publications, and the landsnail collections made by him, which are dispersed among several museums, including the Academy of Natural Sciences of Philadelphia, the Bernice P. Bishop Museum, Honolulu, and the Museum of Comparative Zoology, Harvard University, Massachusetts. Other important collections of landsnails from Rarotonga include those made by Thomas Cheeseman in 1899 (held in the Auckland War Memorial Museum, and the Museum of New Zealand Te Papa Tongarewa, Wellington); by E.S. Handy in 1923, Gerrit Wilder in 1925–29, Sir Peter Buck in 1929–30 and Noel Krauss in 1964 (all in the Bishop Museum); by William Tailby, probably between 1943 and 1951 (Museum of New Zealand Te Papa Tongarewa); by Laurie Price in 1964–65 (Field Museum of Natural History, Chicago); and by Jacqui Craig in 1994 (Museum of New Zealand Te Papa

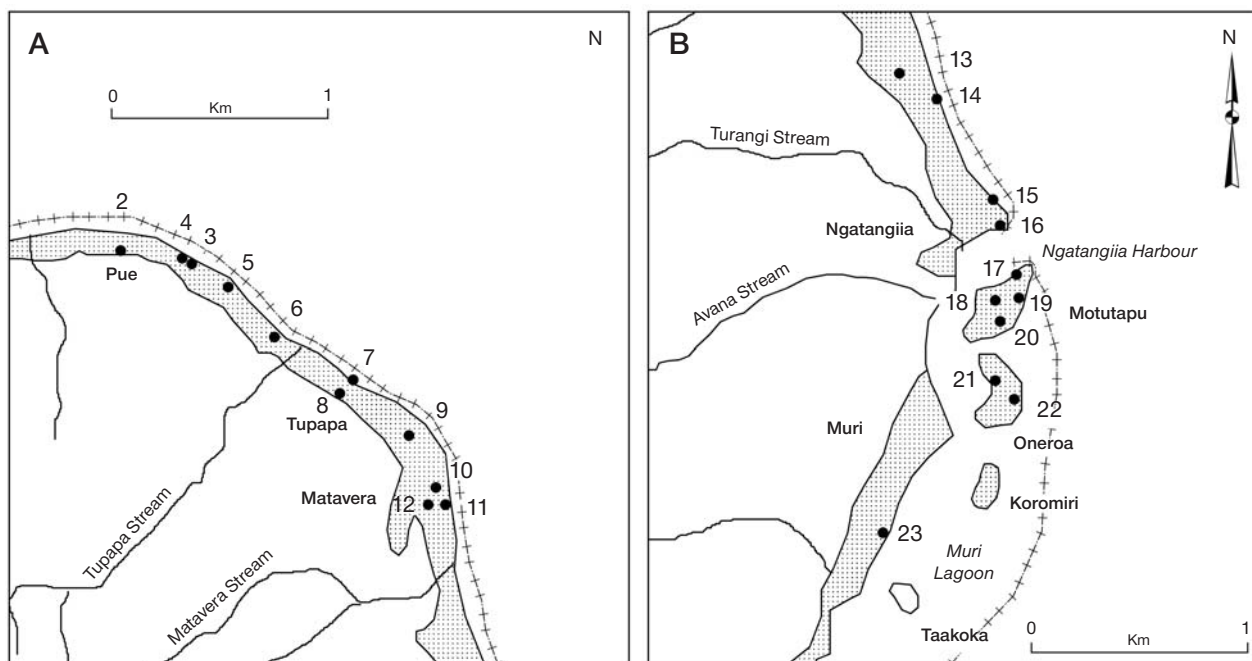


Fig. 2 Location of coastal survey sites on eastern Rarotonga between Pue and Matavera (A), and between Ngatangiia and Muri (B). Map symbols as for Fig. 1.

Tongarewa). In addition to these sources of historical information, fossil landsnail assemblages in calcareous soils on the coastal plain of Rarotonga provide a faunal record spanning the last several hundred years or more.

The main aim of the present study was to determine the composition and history of the coastal landsnail fauna of Rarotonga, based on information obtained from field surveys of fossil and present-day faunal assemblages, existing museum collections, and historical records. This study is part of a wider survey of the landsnail faunas of the southern Cook Islands being undertaken for the Cook Islands Natural Heritage Trust.

Physical setting

Rarotonga is the only high volcanic island in the southern Cook Islands, and is also the largest island in this group. The other southern Cook Islands include four makatea islands with deeply eroded volcanic cores ringed by uplifted reefal limestone (Mangaia, Ātiu, Ma'uke, Miti'āro); one 'almost atoll' with eroded, low volcanic islands set in a large lagoon surrounded by a fringing reef (Aitutaki); two true atolls (Palmerston, Manuae); and a platform reef capped by a sand cay (Takūtea) (Marshall 1927, 1930; Wood & Hay 1970;

Stoddart *et al.* 1985; Stoddart *et al.* 1990). The closest islands to Rarotonga are Mangaia, 180 km to the east-southeast; Ātiu, Miti'āro and Ma'uke, respectively situated 187 km, 228 km and 241 km to the northeast; Manuae, 200 km to the north-northeast; and Aitutaki, 257 km to the north.

The southern Cook Islands are located at the north-western end of the Cook–Austral chain, which comprises a 2600 km-long, northwest–southeast-trending group of islands and seamounts extending between Palmerston Atoll (18.045°S, 163.165°W) and McDonald Seamount (29°S, 140.2°W). Radiometric dates give ages of *c.* 2.4–1.0 Ma for the volcanics on Rarotonga; *c.* 1.9–0.7 Ma and 8.0–8.4 Ma for Aitutaki; *c.* 8.0–10.0 Ma for Ātiu; ≥ 12.3 Ma for Miti'āro; ≥ 6.0 Ma for Ma'uke; and *c.* 18.0–19.4 Ma for Mangaia (Dalrymple *et al.* 1975; Turner & Jarrard 1982; Matsuda *et al.* 1984). Islands and seamounts in the Austral group to the southeast range are aged from *c.* 0.6– ≥ 21.2 Ma and 0–55 Ma, respectively (Turner & Jarrard 1982; Clouard & Bonneville 2005). All the volcanoes in the Cook–Austral chain formed in an intraplate setting, on oceanic crust with an age range of *c.* 40–120 Ma (Mueller *et al.* 1993). The lithosphere in this part of the south-central Pacific forms a 'superswell', with shallower seafloor depths and unusually thin, elastic thicknesses compared to oceanic lithosphere elsewhere; the

intraplate volcanics in this region are characterised by strongly radiogenic isotopes (Calmant & Cazenave 1986, 1987; McNutt & Fischer 1987; McNutt & Judge 1990; Staudigel *et al.* 1991). Various hotspot models based on putative northwest-directed age progressions along volcanic alignments have been proposed to account for the origin of the Cook–Austral chain (e.g. Duncan & McDougall 1976; Turner & Jarrard 1982; Chauvel *et al.* 1997; Dickinson 1998; Bonneville *et al.* 2002). However, the known spatial distribution and ages of the constituent islands and seamounts (e.g. Clouard & Bonneville 2005: fig. 3, table 1), and evidence of temporally disjunct volcanism on some (e.g. Aitutaki, Rurutu, Marotiri, Arago – Turner & Jarrard 1982; Chauvel *et al.* 1997; McNutt *et al.* 1997; Bonneville *et al.* 2006), is not consistent with a history of formation over one or more fixed, deep-seated, long-lived and continuously active mantle plumes. Instead, bathymetric and age data suggest the Cook–Austral chain most likely resulted from volcanism at a series of short-lived, discontinuous hotspots, with products ranging from single, isolated volcanic edifices to relatively short (<500 km) volcanic chains showing northwest-directed age progressions (e.g. MacDonald Seamount–Marotiri–Rapa chain; *c.* 0–5.1 Ma – Clouard & Bonneville 2005: table 1). Volcanic alignments oriented northwest–southeast but showing no consistent age progression (e.g. such as that between Aitutaki and Ma‘uke) may have formed along extensional lithospheric fractures and flexures (e.g. McNutt *et al.* 1997; Koppers *et al.* 2003; Jordahl *et al.* 2004). The Rarotonga hotspot was relatively young and short-lived, having produced this island only (Clouard & Bonneville 2001).

Rarotonga is the eroded and deeply dissected summit of a volcano that rises steeply from a surrounding ocean depth of *c.* 4000–4500 m (Kroenke *et al.* 1983; Mammerickx 1992), to a maximum elevation of 653 m. The emergent part of this volcano formed during two distinct eruptive phases: an initial period of basaltic volcanism; and a later period of phonolitic eruptions (Marshall 1930; Wood 1967; Wood & Hay 1970; Thompson *et al.* 1998). The first sub-aerial eruptive phase built a composite basaltic volcano formed mostly of pyroclastic material with subordinate intercalated lava flows, all cut by numerous dykes. Wood (1967) and Wood & Hay (1970) thought this basaltic volcano had a central caldera *c.* 3 km in diameter during the latter part of its history, but as pointed out by Thompson *et al.* (1998), there is no convincing structural or volcanological evidence for the existence of such a feature. Rather, successive basaltic

eruptions apparently built a large, polygenetic cone, with small parasitic cones of ash and fine breccia present locally on the lower flanks.

The maximum height attained by the main cone is not known directly, but seaward dips of constituent lava flows and layering in volcanic breccia indicate it probably reached >900 m above present sea-level (Wood 1967; Wood & Hay 1970). However, at the end of this eruptive phase, the upper several hundred metres of the main cone were removed, creating a stepped, north-facing, horseshoe-shaped depression *c.* 4 km long and 3 km wide atop the volcano. The western and eastern sides of this depression were bounded by a rim of seaward-dipping basaltic volcanics in the vicinity of the present Maungaroa–Maungapiko and Te Manga–Ikurangi ridges, respectively, and the lower northern flank of the original volcanic cone was breached in the Avatiu–Avarua area. The southern and central parts of the depression, now preserved beneath younger volcanics at Maungatea, Te Ko‘u and Maungatapu Ridge, sloped northwards from *c.* 400–200 m above present sea-level. Stratigraphic relationships and a lack of associated eruptive products indicate this depression formed as a result of catastrophic gravitational collapse and avalanching of material down the northern flank of the volcano. An indentation on the northern coastline of Rarotonga indicates that a portion of the northern submarine flank of the volcano also collapsed, but whether this occurred at the same time or earlier than the summit collapse has not been determined.

The second and final phase of volcanic activity on Rarotonga involved the eruption of relatively small volumes of phonolitic lava, breccia and ash from multiple vents within, and on the margins of, the central depression. Pyroclastic breccia, cinder cones and lava flows produced by these eruptions are presently exposed as erosional remnants between Maungatea and Maungatea Bluff, on Maungatapu Ridge, and at Te Ko‘u. Phonolitic lava locally also flowed out of the central depression and down the flanks of the volcano towards the coast, forming the Tuakata, Black Rock, Raemaru and Muri flows (Wood & Hay 1970; Thompson *et al.* 1998).

Available radiometric (K/Ar) dates give age ranges of *c.* 2.4–1.9 Ma (i.e. Late Pliocene) for the subaerial basaltic volcanics on Rarotonga, and *c.* 1.4–1.0 Ma (Early Pleistocene) for the overlying phonolitic eruptives (Turner & Jarrard 1982). However, basaltic volcanism must have continued for some time after 1.9 Ma. Wood & Hay (1970:

19, fig. 10) noted that phonolite flows exposed in the eastern cliffs of Maungaroa concordantly overlie thick beds of basaltic tephra 'without any obvious weathering zone between'. Eroded basaltic volcanics exposed on the floor of the central depression were slightly weathered prior to emplacement of the overlying phonolitic eruptives, but no intervening soil horizons are known (Wood & Hay 1970; Thompson *et al.* 1998). Thus the earliest phonolitic eruptions at *c.* 1.4 Ma must have occurred soon after cessation of basaltic volcanism and cone collapse, which suggests basaltic eruptions continued until *c.* 1.5 Ma.

The radiometric dates indicate volcanism on Rarotonga had ceased by *c.* 1.0 Ma. Since then, the volcano has been extensively eroded, producing a topographically complex, rugged interior of deep, amphitheatre-headed valleys separated by knife-edge ridges that rise to a series of peaks *c.* 400–653 m in elevation. Most of the streams that arise on the former flanks of the volcano are relatively short (<3 km in length), and generally have a radial distribution. Three larger stream systems arise in the interior of the island, dissecting the former collapse depression and overlying phonolitic volcanics (i.e. the Avatiu, Takuvaine and Avana streams). Downcutting of valleys by fluvial erosion and slope failures during the latter part of the Pleistocene produced large amounts of poorly sorted volcanoclastic sediment, which was transported downstream and deposited on alluvial fans at the valley mouths. Multiple depositional and erosional cycles are represented within these fans, presumably resulting from changes in stream base level and sediment supply during glacial–interglacial cycles. The eroded and deeply weathered alluvial fan remnants underlie a series of seaward-dipping surfaces up to *c.* 50 m in elevation and 800 m wide, bordering the eroded lower seaward flanks of the volcano. These fan remnants commonly have marine eroded scarps on their seaward sides, and are bounded laterally and to seaward by Holocene alluvial and swamp deposits, respectively. These in turn are bounded to seaward by a circum-peripheral belt, *c.* 50–500 m in width, of mid- to late-Holocene beach ridges and swales that form a low (*c.* 2–7 m above high-water mark) coastal plain bordering the lagoon (Wood & Hay 1970; Leslie 1980; Moriwaki *et al.* 2006). Around most of Rarotonga, the coastal plain sediments are predominantly bioclastic calcareous sand with or without minor coral rubble, but seaward beach ridges on the northern and northeastern coasts, where the lagoon is narrowest, are formed predominantly of coral rubble. The three northernmost motu in Muri Lagoon (Motutapu,

Oneroa, Koromiri), which are also formed of bioclastic sand and coral rubble, are stable islets of late-Holocene age. By contrast, the southernmost islet in the lagoon (Ta'akoka) is formed of phonolite lava, and this rock type also crops out on the mainland shore nearby, and on the northwestern coast at Black Rock. Erosional remnants of Pleistocene makatea reefal limestone, probably of last interglacial age, are present on the coast bordering the outlet of Muri Lagoon at Ngatangia and on the northern tip of Motutapu (Wood & Hay 1970; Moriwaki *et al.* 2006).

The coastal plain on Rarotonga formed in mid- to late-Holocene time, after the maximum post-glacial sea-level rise. According to Moriwaki *et al.* (2006), sea-level attained its present level *c.* 6500–6000 cal. BP on Rarotonga, and rose gradually until *c.* 4500 cal. BP, when it was *c.* 1.5 m above the present level. From *c.* 6500 cal. BP to *c.* 4500 cal. BP there was evidently a deeply indented coastline around Rarotonga, with lagoonal embayments extending into the mouths of stream valleys, and intervening promontories of mainly weakly consolidated Pleistocene alluvial sediments, which were cut back into cliffs by wave erosion. Sea-level then remained more or less stable from *c.* 4500 cal. BP until *c.* 800–500 cal. BP, after which time it fell to, or slightly below, its present level. Sandy and coral rubble sediments forming the present coastal plain began to accumulate *c.* 4500 cal. BP, and prograded seaward through late-Holocene time to form either a single broad ridge, or a series of ridges with intervening swales (Moriwaki *et al.* 2006). In some areas, notably Matavera, Muri and Titikaveka, peaty mud accumulated locally in swales between sand ridges (Wood & Hay 1970; Leslie 1980; Moriwaki *et al.* 2006).

The oldest reef limestones exposed on Rarotonga reach 3.5 m in elevation (Schofield 1970) and are probably of last interglacial age. However, the weakly consolidated Mid- to Late Pleistocene alluvial fan deposits around the periphery of the former volcano probably built out over reef and lagoon deposits, and Wood & Hay (1970: 16) suggested the phonolite flow at Muri was 'emplaced over a reef flat a little lower than the present one'. If correct, this indicates a fringing reef has existed since at least *c.* 1.1 Ma.

Climate

Rarotonga has a tropical climate, with average monthly air temperatures recorded at the airport over the period 1930–82 ranging from *c.* 26°C in February to *c.* 22°C in August (Thompson 1986). There are two main seasons: a wet

season from November to April; and a dry season from May to October. During the dry season, Rarotonga 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, Rarotonga receives 64% of its rain in the wet season and 36% in the dry season, but actual monthly and seasonal rainfall varies markedly from year to year. Rainfall and air temperatures are generally higher than average during La Niña events, when the Southern Oscillation Index (SOI) is strongly positive and the SPCZ intensifies. Conversely, during El Niño events, when the SOI is strongly negative, the SPCZ is located north and east of its mean position, and the southern Cook Islands generally have lower than average rainfall and air temperatures (Thompson 1986; Salinger *et al.* 1995).

The mean position of the SPCZ also varies on a decadal timescale according to the polarity of the Interdecadal Pacific Oscillation (IPO), shifting northeast when the IPO is positive and southeast when it is negative (Folland *et al.* 2002). El Niño events tend to be enhanced and more frequent when the IPO is positive (Salinger *et al.* 2001). Proxy sea-surface temperature (SST) records, obtained from Sr/Ca isotope variability in long-lived corals, point to a pattern of decadal and interdecadal climate variability at Rarotonga extending back for at least the last few hundred years, which is inferred to be related mainly to variability in the IPO and associated changes in the strength and frequency of El Niño and La Niña events (Linsley *et al.* 2000, 2004). Coral oxygen isotope records suggest there has also been a gradual change to warmer, more La Niña-like long-term mean conditions in this region of the South Pacific over the last few centuries (Linsley *et al.* 2006), and historical records indicate there has been an overall increase in air temperatures at Rarotonga since the early 1900s, consistent with global warming trends (Salinger *et al.* 1995).

On Rarotonga, the distribution of rainfall varies according to elevation and exposure to prevailing easterly-quarter winds, with the southeastern part of the island typically having the highest rainfall. Records from 1951 to 1980 indicate that mean annual rainfall over the period was highest around the central peaks of Te Manga, Te Atukura and Te Ko'u (*c.* 4000–4500 mm/yr), and lowest on the

lowlands and foothills around the northern half of the island (*c.* 2000–2500 mm/yr). On the coastal plain, mean annual rainfall was highest between Aroa and Muri (*c.* 2500–3000 mm/yr), and lowest between Arorangi and Nikao (*c.* 2000 mm/yr) (Thompson 1986: fig. 16).

Tropical cyclones that form on the SPCZ between November and April affect Rarotonga from time to time, and can cause extensive damage. They tend to be most frequent during El Niño events (Thompson 1986; de Scally 2008). In historical time, storm surges and waves during severe cyclones have overtopped the coastal plain, eroding and depositing sand- to boulder-size sediment, killing vegetation and destroying buildings. Strong winds have caused extensive tree-throw in the lowlands and the mountains, and standing trees in exposed sites have been defoliated as a result of wind shear and salt spray. Heavy rain during cyclones has caused flooding in the lowlands, and slips on steep hill slopes in the interior of the island (e.g. Williams 1838: 386; Gill 1856: 87; Buzacott 1866: 85, 93; Marshall 1930: 19, 27).

Human history

The oldest archaeological remains known from Rarotonga are human skeletons on Motutapu islet, dated to 720 ± 50 ¹⁴C yrs BP (Moriwaki *et al.* 2006), and a settlement site on the inner edge of the coastal plain at Avarua, dated to *c.* 700–500 yrs BP (Bellwood 1978; Walter & Sheppard 1996: table 1). Archaeological sites of similar age have also been recorded from Aitutaki and Ma'uke (Bellwood 1978; Allen & Steadman 1990; Allen 1994; Walter 1998; Allen & Wallace 2007). The oldest cultural remains discovered so far in the southern Cook Islands were in a stratified 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). By contrast, Ellison (1994), Kirch & Ellison (1994), and Kirch (1996) have argued, on the basis of palynological, geochemical and sedimentological evidence obtained from cores drilled in lacustrine and swamp deposits, that anthropogenic disturbance began on Mangaia as early as 2500 ¹⁴C yrs BP, with widespread and sustained forest clearance after *c.* 1650 ¹⁴C yrs BP. Similarly, Parkes (1997) reported palynological and sedimentological evidence of major and sustained environmental changes of inferred anthropogenic origin at *c.* 1310 ¹⁴C yrs BP on Ātiu.

At present, the issue of whether the southern Cook Islands were first colonised as early as *c.* 2500 ¹⁴C yrs BP or as late as *c.* 1000 yrs BP, as suggested by the paleoenvironmental

and archaeological evidence, respectively, is unresolved. However, whereas the existing archaeological evidence is unambiguous, the paleoenvironmental evidence is not. The key areas of uncertainty with the latter are the accuracy of the radiocarbon chronology, and the interpretation of natural versus anthropogenic paleoenvironmental changes. The radiocarbon chronologies of Ellison (1994), Kirch & Ellison (1994), Kirch (1996) and Parkes (1997) were based on dating of bulk samples of lake and swamp sediments, which can potentially yield anomalously old dates as a result of hard-water contamination, and in-washing of old carbon, such as soil humics, relict charcoal, or contemporary charcoal particles derived from burning of long-lived trees (e.g. McGlone & Wilmshurst 1999). Thus there is a possibility that the major paleoenvironmental changes dated to *c.* 1650 ¹⁴C yrs BP and 1310 ¹⁴C yrs BP on Mangaia and Ātiu, respectively, actually occurred much later, close to the beginning of the archaeological record. By contrast, the paleoenvironmental changes dated to *c.* 2500 ¹⁴C yrs BP in three stratigraphic cores from two separate drainage basins on Mangaia (Kirch & Ellison 1994: 317) are undoubtedly much older than the earliest archaeological remains. In this case, the key issue is whether these changes, which included burning of vegetation, forest destruction and soil erosion, were natural or anthropogenic in origin. They are certainly entirely consistent with the kinds of ecological disturbances attributed to anthropogenic land clearance following human settlement elsewhere in Polynesia (e.g. Flenley & King 1984; Flenley *et al.* 1991; McGlone & Wilmshurst 1999; Kennett *et al.* 2006; Mann *et al.* 2008). However, the possibility that they were climate-induced natural events (e.g. possibly related to a marked increase in the frequency, persistence and strength of El Niño events at *c.* 2000 yrs BP: see Moy *et al.* 2002; Rein *et al.* 2005; Conroy *et al.* 2008) requires investigation. Given the potential ambiguity of the paleoenvironmental record, and drawing on present archaeological evidence, the interpretation preferred here is that the southern Cook Islands were settled over a relatively short period soon after 1000 yrs BP.

Prehistoric settlement and land utilisation on Rarotonga was mainly concentrated within a zone of fertile lowland soils, located on Pleistocene and Holocene alluvial and colluvial deposits inland from the coastal plain and along stream valleys (Grange & Fox 1953; Crocombe 1964; Bellwood 1971; Leslie 1980; Campbell 2001, 2003), but settlements and gardens were established locally in the foothills, and probably also on sandy sediments of the coastal

plain (e.g. the Maungaroa Valley and Ngati Tiare sites described by Bellwood 1978). There were apparently no villages as such in late-prehistoric time, with households and clusters of households mostly sited close to a circum-island road, the Ara Metua, which ran around the inland border of the lowlands (Gilson 1980: 7). The island's population probably subsisted mainly on plant crops and seafood, but domesticated pig and chicken, wildfowl, eels (*Anguilla* spp.) and land crabs were also eaten (Williams & Barff 1830; Buzacott 1866: 240; Gill 1885: 216; Crocombe 1964; Campbell 2003).

The earliest known European contact with Rarotonga was a brief visit by HMS *Bounty*, under the command of Fletcher Christian, in May 1789. A few European ships stopped by or sailed past the island in the early 1800s, including the trading schooner *Cumberland* in 1814 (Gosset 1940; Maude & Crocombe 1962; Coppell 1973), but there was no permanent contact until 1823, when the Reverend John Williams of the London Missionary Society landed Papeiha, a native Tahitian missionary teacher, on Rarotonga. Williams returned to Rarotonga in 1827, installed the first of several English missionaries to settle on the island, and instituted a series of major social and economic changes. Mission stations were established on the coastal plain at Avarua, Arorangi, Titikaveka, Ngatangiia and Matavera, and households that had converted to Christianity were encouraged to move from their former inland dwellings to new villages that were built up around the mission stations (Gilson 1980: 26). At the same time, there was an increase in horticultural production, with a shift from a self-sufficient subsistence economy to a dependence on cash crops and overseas trade. A coastal circum-island road – the Ara Tapu – was constructed between 1857 and the 1860s (Maretu 1983: 192), and this contributed to increased residential and horticultural development on the coastal plain, with the ‘spread of villages from closely packed clusters of houses, ... to lines of houses spread out along either side of a newly formed road’ (Crocombe 1964: 66). From the 1870s onwards, there was also an increasing population shift to Avarua, which became the main residential and commercial centre on the island (Gilson 1980: 39).

As on many other Polynesian islands, the population of Rarotonga fell dramatically after European settlement. In 1823, it was estimated to comprise between 6000 and 7000 people (Williams 1838: 19), and it remained at about this level until *c.* 1830 (Gilson 1980: 37). However, the population declined markedly over the next few decades, primarily

as a result of disease epidemics, to *c.* 3000 people in 1845 and fewer than 2000 in the late 1860s (Beaglehole 1957; McArthur 1967; Curson 1973; Gilson 1980). The decline began to level off in the late 1800s, partly because of immigration of people from other islands in the group, but sustained population recovery did not begin until the early twentieth century (McArthur 1967; Curson 1973; Gilson 1980).

From the time of European settlement until 1888, there was no central government in Rarotonga. Instead, as in pre-contact time, the three main tribal districts on the island (i.e. Arorangi, Avarua, and Takatimu) were each governed by a supreme chief (*ariki*). In 1888, a British Protectorate was established over the Cook Islands, and a Rarotongan and federal government was established. In 1901, the Cook Islands was annexed to New Zealand. The group was then largely governed from Wellington until 1965, when it became an independent, self-governing nation in free association with New Zealand.

Horticultural produce was the main export from Rarotonga (and the other southern Cook Islands) from the 1830s until the 1980s. Trade with whaling ships was the most important market for exports of fresh foodstuffs until the early 1860s, but from the 1830s onwards there was also extensive commerce with merchants from Tahiti in the Society Islands (Crocombe 1964: 87; Gilson 1980: 43). Crop species that were grown on Rarotonga for trade during the first few decades of European settlement included cassava (*Manihot esculenta*), coffee (probably Arabian coffee, *Coffea arabica*), Polynesian arrowroot (*Tacca leontopetaloides*), rice (*Oryza sativa*?) and sweet potato (*Ipomoea batatas*) (Buzacott 1866: 91). Foreign traders and planters first settled on Rarotonga in significant numbers in the 1860s, and Auckland (New Zealand) became the main export destination for horticultural produce from this time onwards. However, trade with Tahiti remained important until the end of the 1800s, comprising up to a quarter of recorded exports from the Cook Islands (i.e. shipped through Rarotonga), and about a third of the import trade, in the 1890s (Gilson 1980: 43, 79). The main exports from Rarotonga in the late 1800s were coffee, copra, cotton, lime juice and oranges (Johnston 1951; Gilson 1980: 43, appendix 2). Plantations of sea-island cotton (*Gossypium barbadense*) were established on the lowlands from the 1880s until the mid-1890s, when the export market failed (Crocombe 1964: 87; Davis 1968: 6; Gilson 1980: 79,

appendix 2). Arabian coffee was widely planted on the lowlands and lower hill slopes by the 1870s (e.g. see 1893 illustration of Avarua by John Pearse, reproduced in endpapers of Scott 1991), but commercial production collapsed soon after 1900 as a result of economic factors and disease (McCormack 2007). The citrus industry was largely based on semi-wild trees scattered through the 'bush and undergrowth' on the lowlands and lower hill slopes (Crocombe 1964: 143).

In 1902, the government introduced land tenure reforms with the aim of encouraging production of horticultural exports, and over the next few years the area of cultivated land on the island increased substantially (Crocombe 1964; Gilson 1980: 148, 150, 154). The main commercial crops on Rarotonga during the early to mid-twentieth century were bananas (*Musa* hybrids), citrus (mostly *Citrus sinensis*) and tomatoes (*Lycopersicon esculentum*), with copra of lesser importance. The first three were grown on alluvial and colluvial soils on the lowlands, and bananas were grown also in swidden clearings on lower hill slopes. Coconuts were grown on the coastal plain and on alluvial and colluvial soils (Johnston 1951, 1953, 1959). Loss of export markets led to a collapse in production of all these crops by the mid- to late twentieth century (Crocombe 1964; Gilson 1980; McCormack 2007). Subsequently there has been patchy utilisation of arable lowland soils on Rarotonga for commercial crops grown mostly for local sale, as well as continued planting of household plots for domestic consumption. The main crops grown during the last few decades have been taro (*Colocasia esculenta*), cassava, sweet potato, pawpaw (*Carica papaya*), banana, passion-fruit (*Passiflora edulis*), tomatoes, cabbages (*Brassica* spp.), eggplant (*Solanum melongena*), long beans (*Vigna unguiculata*), and capsicum (*Capsicum annuum* var.) (Gerald McCormack, pers. comm. 2009).

The population of Rarotonga has increased substantially over the last hundred or so years, from just over 2000 people in 1902, to *c.* 5500 in 1950 and >14 000 in 2006 (Curson 1973: table 2; Gilson 1980: 3). There has also been a substantial increase in the numbers of tourists visiting Rarotonga since 1973, when the present international airport opened. These increases in the resident population and visitor numbers have contributed to extensive commercial development in the Avarua–Avatiu area, and to residential, tourism and horticultural development over much of the rest of the coastal plain on Rarotonga.

Vegetation changes

Before humans arrived, Rarotonga was probably largely forested except for a narrow fringe of littoral shrubland, freshwater wetlands on the inner edge of the coastal plain, and ephemeral clearings resulting from treefall and wind-throw, slips, fluvial erosion and storm waves. Natural wildfires were probably also important agents of forest disturbance from time to time. For example, in the 1830s Williams (1838: 397) reported ‘the highest mountain was set on fire in a thunder storm, and it burnt ... fiercely for nearly a fortnight’.

The mountainous interior of the island probably retained much of its forest cover over the centuries of human occupation, and is still composed predominantly of native species. The present simple vegetation pattern probably existed throughout late Holocene time, with slope forests dominated by *Homalium acuminatum* on steep hillsides below c. 400 m, and cloud forest dominated by *Metrosideros collina* or *Ascarina diffusa* on hillsides and ridge tops at higher elevations (Merlin 1985). Palynological samples from Karekare Swamp on northeastern Rarotonga described by Peters (1994) indicate that tree and shrub species present in the indigenous lowland forest before human settlement included coconut (*Cocos nucifera*), pandanus (*Pandanus tectorius*), *Barringtonia asiatica*, *Cyclophyllum barbatum*, *Elaeocarpus floridanus*, *Fagraea berteriana*, *Hibiscus tilliaceous*, *Homalium acuminatum* and *Ixora trifolia*, and probably also *Macropiper latifolium* and *Pipturus argenteus*. Other tree and shrub species recorded in the modern lowland flora, which are probably also native to Rarotonga, include *Calophyllum inophyllum*, *Celtis pacifica*, *Cerbera odollum*, *Ficus prolixa*, *Ficus tinctoria*, *Guettarda speciosa*, *Hernandia moerenhoutiana*, *Hernandia nymphaeifolia*, *Macaranga harveyana*, *Morinda citrifolia*, *Pisonia grandis*, *Scaevola taccada*, *Schleinitzia insularum*, *Sophora tomentosa*, *Thespesia populnea* and *Tournefortia argentea* (Cheeseman 1903; Wilder 1931; McCormack 2007).

Human settlement of Rarotonga led to profound environmental changes in lowland habitats with the patchwork clearance of native vegetation on the alluvial and colluvial soils of fans and valley floors for horticultural plots, pond fields, tree gardens and settlements. The composition of the island’s flora also changed dramatically, with the prehistoric introduction by Polynesians of at least 30 new species of herbs, shrubs and trees (Cheeseman 1903; Whistler 1991; McCormack 2007). Five of the six most important crop

species were introduced: taro was grown in wetlands bordering the coastal plain and in constructed pond fields along stream valleys; giant taro (*Alocasia macrorrhizos*), banana and breadfruit (*Artocarpus altilis*) were grown mainly on lowland, volcanic-derived, alluvial and colluvial soils inland from the coastal plain and along stream valleys; and mountain plantains (*Musa troglodytarum*) grew semi-wild in large groves at valley heads and ‘in damp shady places on the higher slopes of the mountains’ (Williams & Barff 1830; Williams 1838: 205; Gill 1885: 216; Cheeseman 1903: 268; Campbell 2003). The other main crop species, the coconut palm, was native to Rarotonga and was probably originally largely restricted to the coastal plain. However, a domesticated variety with a spherical, thin-husked fruit is thought to have been introduced by Polynesians (Harries 1978, 1992) and was probably widely planted in clearings in the lowlands. In addition to a reduction in forest cover, the composition and structure of lowland and mid-elevation forest remnants and secondary growth forests on Rarotonga presumably also changed during late-prehistoric time, as introduced tree species such as breadfruit, candlenut (*Aleurites moluccana*), Polynesian chestnut (*Inocarpus fagifer*), *Casuarina equisetifolia* and *Cordyline fruticosa* became established in the wild.

At the time of European settlement in the early 1800s, the coastal plain and mountainous interior of Rarotonga were predominantly forested, and the lowlands to landward of the coastal plain supported a mosaic of settlements and gardens interspersed with forest and shrubland. In 1828, Buzacott (1866: 25) made the following observations: ‘The lowlands revealed cultivated spots amid stately trees and forests. The very hills and mountains, from base to summit, were covered with dense wood of varied growth and colour. ... A vegetation of wondrous luxuriance grew down to the seashore’. Gill (1856: 1–2) noted that ‘A comparatively level tract of land surrounds the island, richly covered with fruitful groves of chestnut, cocoa-nut, breadfruit, and banana trees. Beyond this is marshy ground, cultivated as “tara” swamps; thence rise hills, then deep, wild, rugged fertile valleys’. Williams & Barff (1830) described the country alongside the Ara Metua between Avarua and Ngatangiia as being ‘under cultivation almost all the way with bananas, mountain plantains etc’. Williams (1838: 207) noted that both sides of the Ara Metua were ‘lined with bananas and plantains; and these, with the *Barringtonia*, chestnut and other trees of wide spreading foliage, protect you from the rays of the tropical sun, and afford even in

midday the luxury of cool, shady walks of several miles in length'. Elsewhere, Williams (1838: 210) noted that buffer zones of 'uncultivated land, generally about half a mile in width' were present along the lowland boundaries of the Arorangi, Avarua and Takatimu tribal districts. There were probably tree gardens (e.g. of coconut, pandanus and breadfruit), and swidden cultivation of dryland tubers such as Polynesian arrowroot and yams (*Dioscorea* spp.) on the less fertile, free-draining, sandy soils of the coastal plain. However, shrubland and forest probably persisted over much of the seaward part of coastal plain throughout the prehistoric and early contact periods.

The European settlers introduced many new crop and ornamental plants to Rarotonga from the late 1820s onwards, some of which subsequently became naturalised on the island (below). Changing patterns of horticultural production and the introduction of cash-cropping resulted in the clearance of forest and shrubland on the Rarotongan lowlands after European settlement (e.g. Williams 1838: 210; Buzacott 1866: 91; Gilson 1980: 40), while on the coastal plain, forest and shrubland was also cleared for the establishment of mission stations and villages. For example, William Gill noted that the site of Aorangi village, on the western side of Rarotonga, was on 'a level piece of ground two miles long' that was formerly 'densely covered with trees and brushwood, the growth of many generations' (1856: 39). In the mid- to late 1800s, construction of the Ara Tapu around the coastal plain led to further clearance of forest and shrubland (Maretu 1983: 192), and vegetation on the lowlands and lower hill slopes was cleared for plantations of sea-island cotton, Arabian coffee and food crops. Gill (1876: 11) described 'immense chestnut trees ... marking off the actual domain of man; miles of breadfruit groves intermingled with cocoa-nut palms, shading plantations of coffee. Nearer the beach are plantains, bananas, sweet potatoes, and lastly, growing to the water's edge, are graceful ironwood [i.e. *Casuarina equisetifolia*] trees.' In the Avarua District, Gill (1876: 161) noted 'Near the sea are numerous spots where the primeval forest has yielded to the hand of man, and plantations of sweet potato, coffee, and cotton flourish. Extensive groves of cocoa-nut trees give a pleasing variety to the scene.'

The trend of increasing development of the lowlands was reversed in the later part of the nineteenth century as a result of population decline and movement of people to Avarua. By the end of the century as much as half the arable land on the island was uncultivated, with shrubland and secondary

forest widely established in areas of former cultivation (Cheeseman 1903; Gilson 1980: 93, 149). The latter author (1980: 39) noted that 'large areas of land were left uncultivated, especially along the south coast where the soil was less suitable and the people farthest from the harbours'. In 1902, there were large areas of vacant land 'between Avatiu and Black Rock, and in Titikaveka, where some lands had not been cultivated since the epidemics of 1830–1845' (Gilson 1980: 149). Cheeseman (1903: 264) noted:

it can roundly be said that the whole island is covered with forest. Here and there a bare rocky face shows out on the sides of the mountains, and the slopes of a few hills are free of trees, but the total area of open land is quite insignificant. Even the cultivations of the natives – their orange groves and coffee plantations, their Banana and Taro patches – are either part and parcel of the forest, or are sheltered and almost overshadowed by it.

Dicranopteris fernland was present on 'dry open hills' (Cheeseman 1903: 306), but was evidently far less extensive than at the present day. Referring to alluvial soils inland of the coastal plain and up stream valleys, Cheeseman (1903: 265) noted: 'At one time or another the whole of this has been under cultivation, but the portion at present tilled is small. The vegetation is thus more or less a second growth, and in places that have been recently cultivated is often largely composed of naturalised plants ... The cultivations are usually patches of small size some distance apart.'

Cheeseman (1903: 265) described the vegetation of the coastal plain as follows:

The first vegetation seen on the sea shore is usually one of three plants: *Ipomoea biloba* [= *I. pes-caprae*], with its prostrate stems often 30 feet or more in length, broad fleshy leaves and purplish flowers; *Triumfetta procumbens*; and *Thuarea sarmentosa* [= *T. involuta*], a creeping grass ... *Heliotropium anomalum* and a few other species sometimes accompany them. All of these grow vigorously in pure coral sand, and in situations where they must be often drenched with salt spray. In open places they are followed by *Vigna retusa* [= *V. marina*] and *Canavalia sericea*; but usually they are backed by shrubs and trees. On the northern and western coasts *Scaevola koenigii* [= *S. taccada*] is the first shrubby plant to appear, usually forming a close growing belt a few yards wide and from 4 to 8 feet high. On the eastern shore it is replaced by *Pandanus odoratissimus* [= *P. tectorius*] or *Hibiscus tiliaceus*. Immediately behind these are *Casuarina equisetifolia*, *Hernandia peltata* [= *H. nymphaeifolia*], cocoa-nut palms, *Leucaena forsteri* [= *Schleinitzia insularum*], *Morinda citrifolia*, *Barringtonia butonica* [= *B. asiatica*], and a tall

tree called pukatea [= *Pisonia grandis*] ... Of less common occurrence are *Calophyllum inophyllum*, *Thespesia populnea*, *Cerbera odollum*, and *Tournefortia argentea*. Growing under the shade of the trees are *Lepidium piscidium* [= *L. bidentatum*], *Sophora tomentosa*, *Euphorbia chamissonis* [= *Chamaesyce fosbergii*], *Wedelia aristata* [= *Wollastonia biflora*], *Stenotaphrum subulatum* [= *S. micranthum*], *Polypodium phymatodes* [= *Microsorium grossum*], *Nephrolepis acuta* [= *N. hirsutula* and possibly also *N. biserrata*], and *Asplenium nidus* [probably = *A. australasicum*].

In 1899, Cheeseman (1903) recorded more than 85 species of exotic plants known or inferred to have become naturalised on the Rarotongan lowlands since European settlement began. The majority were introduced crop or ornamental plants, but about one-quarter of them were weeds that presumably had been introduced by accident. Many of the economic species, including avocado (*Persea americana*), cassava, coffee, custard apple (*Annona squamosa*), granadilla (*Passiflora quadrangularis*), common guava (*Psidium guajava*), kapok (*Ceiba pentandra*), lime (*Citrus aurantifolia*), mango (*Mangifera indica*), orange (*Citrus sinensis*), pawpaw and *Melia azedarach*, were common in secondary growth forest on the lowlands, along with abundant *Hibiscus tiliaceus*, and less common breadfruit, candlenut, coconut, pandanus, Polynesian chestnut, *Barringtonia asiatica*, *Cananga odorata*, *Elaeocarpus floridanus*, *Hernandia nymphaeifolia*, *Homalium acuminatum*, *Macaranga harveyana* and *Pipturus argenteus* (Cheeseman 1903: 265). Whether or not any areas of predominantly native forest remained on lowland alluvial-colluvial soils at this time is unknown.

Marshall (1930: 15) made brief observations on the vegetation of the Rarotongan coastal plain during a visit in 1926:

On the coastal strip *Ipomoea* and *Triumfetta* are prominent, while the first trees to be encountered are *Pandanus* and *Casuarina*. The widely distributed *Hibiscus* soon succeeds them and with it the coconut palm. At a short distance from the sea front are noble trees of *Barringtonia* ... Here, too, grows the tamanu (*Calophyllum inophyllum*) used generally for canoe making, the banyan [= *Ficus prolixa*], orange trees and many coffee bushes. There is a thick undergrowth of ferns, and *Asplenium nidus* grows everywhere on the trees.

Marshall (1930: 22) also noted that *Dicranopteris* fernlands with scattered trees of *Casuarina equisetifolia* were present on Raemaru and 'a smaller flat-topped hill, which rises directly behind the village of Arorangi', but that all the surrounding hills were covered with mixed forest.

By the late 1920s, more than 110 exotic plant species introduced since European settlement were naturalised on Rarotonga (Wilder 1931). The majority of these were found in the lowlands only, but some had invaded forests of the coastal hills and interior valleys. The latter group included trees (*Carica papaya*, *Citrus sinensis*, *Psidium guajava*, *Syzygium cumini*), shrubs (*Ardisia elliptica*, *Coffea arabica*, *Solanum mauritanium*), vines (*Epipremnum pinnatum*, *Passiflora maliformis*, *Passiflora quadrangularis*), and herbs (*Alpinia zerumbet*, *Capsicum frutescens*, *Commelina diffusa*, *Conyza bonariensis*, *Elephantopus mollis*, *Hedychium coronarium*, *Paspalum scrobiculatum*, *Stachytarpheta cayennensis*) (Marshall 1930: 15; Wilder 1931; McCormack 2007).

Land reforms and increased horticultural production on Rarotonga in the early to mid-twentieth century led to clearance of substantial areas of secondary shrubland and forest on the coastal plain, mainly for coconut plantations, and on lowland alluvial and colluvial soils for bananas, citrus and tomatoes (e.g. Johnston 1959). Forest was also cleared from many inner valleys and lower hill slopes for banana plantations, and trees in low- to mid-elevation forest were milled for boxwood and building material (Grange & Fox 1953: 7; Johnston 1953, 1959). During the rest of the twentieth century, all but a few tiny remnants of the formerly extensive lowland forests and shrublands described by Cheeseman (1903) were cleared for horticultural and residential development. By the latter part of the century there was no native forest left anywhere on the fertile lowland alluvial-colluvial soils inland from the coastal plain. The vegetation here was dominated by cultivated plants, and by thickets of *Hibiscus tiliaceus* and weedy associations of predominantly exotic herbaceous and woody plants in areas of former cultivation (Philipson 1971; Sykes 1983; Merlin 1985). Burnoffs associated with clearance of this arable land for horticulture had extended onto coastal hills and up valley sides, resulting in the widespread replacement of native slope forest by grassland and *Dicranopteris* fernland, and locally by secondary mixed forest dominated by exotic species, or by dense thickets of *H. tiliaceus* (Johnston 1953; Philipson 1971; Sykes 1983; McCormack & Künzlé 1995). Between the mid-1980s and early 1990s, some fernland areas were planted with *Pinus caribaea*, *Acacia auriculiformis* and *Acacia mangium* (McCormack & Künzlé 1995: 95; McCormack 2007).

Many exotic plant species have become serious invasive weeds in lowland and hill country habitats on Rarotonga. These include the trees *Cecropia pycnostachya*, *Eugenia*

uniflora, *Falcataria molluccana*, *Leucaena leucocephala*, *Psidium cattleianum*, *Psidium guajava*, *Spathodea campanulata*, *Syzygium cumini*, *Syzygium jambos*; shrubs *Ardisia elliptica*, *Cestrum nocturnum*, *Lantana camara*, *Solanum mauritianum*; perennial herb *Hedychium coronarium*; and vines *Cardiospermum grandiflorum*, *Mikania micrantha*, *Passiflora maliformis* and *Passiflora rubra* (Johnston 1953; Sykes 1983; Merlin 1985; McCormack & Künzle 1995; Meyer 2000; McCormack 2007).

On the coastal plain, areas of forest and shrubland existed between villages until the mid-1960s (e.g. Johnston 1959: fig. 8; Solem 1978: 425; Sykes 1983: 1; Peters 1994: 141), but these have since been almost entirely replaced by a patchwork of residential dwellings and domestic gardens, tourism and other commercial developments, horticultural plots, and cleared, uncultivated areas dominated by naturalised weedy herbs and woody plants. The species composition of forest and shrubland remnants on the coastal plain also changed during the twentieth century, with the loss of some native species, and invasions of adventive weed species. Present-day coastal forest remnants generally lack the native ground-layer ferns and other herbs recorded by Cheeseman (1903) and Marshall (1930), and there are no longer any 'wild' populations of *Calophyllum inophyllum* and pandanus on the coastal plain. The latter species was formerly locally common in coastal shrubland, but died out in the early twentieth century, probably as a result of disease (Johnston 1953; Philipson 1971: 49, 51; Peters 1994: 145). Invasive exotic weed species that had become widely established in coastal forest and shrubland remnants included the shrub *Ardisia elliptica* and the vine *Epipremnum pinnatum* (pers. obs. 2007).

Previous work on Cook Islands landsnails

The earliest known collection of landsnails in the Cook Islands was made by a Dr Dean, on Mangaia, in 1861 (Garrett 1881). This material, along with numerous new species of landsnails collected by Garrett on Rarotonga and other islands in the southern Cook group in 1865 and 1869, was described by Pease (1865a,b, 1866, 1867, 1868a,b, 1871), Garrett (1872, 1874, 1881) and Heynemann (1871). A list of the species recorded from the Cook Islands was compiled by Kobelt (1879), and Garrett (1881) gave the first overview of the fauna. Cockerell (1891) recorded the introduced slug *Limacus flavus* (Linnaeus, 1758) from

Rarotonga, based on specimens collected by the missionary William Wyatt Gill. The distribution and biogeographic relationships of *Partula hyalina* Broderip, 1832 on Mangaia and Ma'uke were described by Crampton (1916) and Lee *et al.* (2007), and the phylogenetic relationships of *Partula assimilis* Pease, 1867 were mentioned briefly by Johnson *et al.* (1986) in an electrophoretic analysis of *Partula* from the Society Islands. Achatinellidae from the Cook Islands were included in taxonomic monographs by Pilsbry & Cooke (1915–16), Cooke & Kondo (1961) and Kondo (1962), and the endemic achatinellid *Tekoulina pricei*, restricted to the summit basin of Te Ko'u on Rarotonga, was described by Solem (1972). Baker's (1938, 1940, 1941) monographs on zonitoid snails from Pacific islands covered the Euconulidae known from the Cook Islands, and the morphology and taxonomy of some Cook Islands taxa in family Assimineidae were outlined by Cooke & Clench (1943), Kondo (1944) and Abbott (1958). Solem (1969) described the ecology of *Libera fratercula* Pease, 1867 on Rarotonga, and compiled taxonomic monographs on Pacific Endodontidae and Charopidae, which included descriptions of species from the Cook Islands (Solem 1976, 1983). Fossil landsnails have been recorded from archaeological sites on Aitutaki (Allen 1992, 1997, 1998; Allen & Christensen 1992), Miti'aro (Craig 1995) and Ma'uke (Craig 1995; Walter 1998). Craig (1995) described modern landsnail assemblages from Rarotonga and Miti'aro, based on collections made in 1994, and Cowie (2001b: table 1) listed non-indigenous species recorded from the Cook Islands.

Methods

Field survey

Landsnail assemblages were qualitatively sampled at 36 sites on the coastal plain around Rarotonga, during visits in September–October 2005, May–June 2006, and June 2007. The geographic coordinates (WGS 1984) of each site were determined using a Garmin Etrex GPS unit. The distribution of sites is shown in Figs 1 and 2, and site details are listed in Appendix 1.

Two sites were in open shrubland in the supratidal zone (i.e. sites 16, 17), one site spanned an ecotone from coastal forest to herbaceous strand vegetation (site 7), and 15 sites were in littoral shrubland and forest remnants (i.e. sites 4, 5, 8, 9, 11, 12, 14, 15, 18–22, 30, 35A). At most of these sites, the sampling protocol involved spending *c.* 30 minutes searching for snails and empty shells by eye over an

area up to 20 m in diameter, and collecting a series of spot samples of litter and soil with a combined volume of *c.* 4 litres, which were later sorted under a binocular microscope for live snails and empty shells. The searches by eye involved looking for snails and shells in the litter, under coral rubble, fallen wood and coconut fronds, and on the leaves of ground-layer plants, and the leaves, trunks and branches of shrubs and trees. This sampling regime was aimed at qualitatively covering as great a variety of microhabitats at each site as possible. Sites in two forest remnants on the northeastern coast were searched by eye for *Libera fratercula* and *Orobophana pacifica* only (i.e. sites 4, 5). Brief vegetation descriptions were compiled at each of the forest and shrubland sites.

The other 18 sites were all in highly modified vegetation, and soil samples only were collected. Seven sites were in open grassy areas beneath isolated old trees or small groves of *Barringtonia asiatica*, with or without *Hernandia nymphaeifolia* and *Hibiscus tiliaceus* (i.e. sites 6, 24, 26–29, 33), one site was in a horticultural plot bordered by a small grove of old *B. asiatica* trees (site 10), and another site was in grass below *Casuarina equisetifolia* trees (site 23). The remaining eight sites were in grassland and weedy herbaceous vegetation in residential and commercial areas, or in horticultural plots. At five sites, soils were exposed in natural, wave-eroded coastal sections (i.e. sites 23, 24, 26, 29, 33). Elsewhere, sections were fortuitously exposed in holes dug for septic tanks (sites 2, 36), coral-gravel extraction (site 35), sand extraction (sites 25, 31, 32), and a trench for utility cables (site 34). Stratigraphic and sedimentologic descriptions were compiled for sequences exposed in these sections. Sediment samples of *c.* 4 litres volume were collected from the ground soil 'A' horizons at all the modified sites, and sediment samples of *c.* 4 litres volume were collected also from paleosols underlying the present ground soils at three sites (i.e. 23B, 35B, 36B). Snail shells in these samples were later separated and concentrated by flotation in water, sieving, and hand-sorting under a binocular microscope.

At each site, individual specimens of each landsnail species found were arbitrarily categorised as 'modern' if they were live snails or fresh, empty shells, and 'fossil' if they were old, bleached, empty shells. Fossils were recovered from 28 ground-soil samples (i.e. all sites except 4, 5, 7, 14–17, 22) and three paleosols. The composition of fossil species assemblages and modern species assemblages at each site was then determined, and from this the fossil and modern species distributions on the coastal plain were determined.

The distributions of species among the coastal sites sampled during the present study are listed in the Systematics section below.

Faunal analysis

Geographic distributions of landsnail species represented in the Rarotongan coastal fauna were determined from a variety of sources, including: published literature; examination of collections at the Auckland War Memorial Museum, Bishop Museum and Museum of New Zealand Te Papa Tongarewa; online databases at the Field Museum of Natural History, Florida Museum of Natural History (Gainesville), and United States National Museum of Natural History (Washington, DC); and material collected by the author in the southern Cook Islands and on Niue. This information is summarised for each species under the heading 'Distribution' in the Systematics section below.

The biogeographic affinities of the fully terrestrial component of the Rarotongan coastal landsnail fauna (i.e. excluding littoral and supralittoral species in families Assimineidae, Truncatellidae and Ellobiidae) were categorised in terms of the following five distribution categories: (1) endemic to Rarotonga (known from Rarotonga only); (2) Cook Islands species (present on two or more islands in the Cook archipelago but not known elsewhere); (3) Polynesian species (present on two or more island groups in the tropical central and eastern Pacific); (4) tropical Pacific species (distributions extending from the tropical western Pacific eastward to Polynesia); and (5) extra-Pacific species (not indigenous to the Pacific region). Changes in biogeographic composition between the fossil and modern coastal faunas sampled in 2005–07 were assessed on the basis of differences in species composition within each of these five distribution categories, and the differences in species richness within and between categories. It should be noted that whereas categories 1 and 5 consist exclusively of indigenous and non-indigenous species, respectively, each of the categories 2–4 is inferred to include a mix of both indigenous and non-indigenous species (below).

Information on changes in landsnail faunal composition on Rarotonga from the 1860s onwards was compiled from published records (mainly Garrett 1881; Baker 1938; Cooke & Kondo 1961; Solem 1976, 1983; Craig 1995), and from examination of mollusc collections in the Auckland War Memorial Museum, Bishop Museum, Field Museum of Natural History, and the Museum of New Zealand Te Papa

Tongarewa. The information obtained is summarised in the Systematics section and Table 5 below. It provides a very incomplete record of the timing of changes in faunal composition on the coastal plain itself, as there are very few historical collections from coastal sites. However, it is useful for determining the last recorded appearance of some indigenous lowland species, and the first appearance of some adventive species on Rarotonga.

Information on the timing of establishment of extra-Pacific species in the Cook Islands and on other tropical Pacific islands since the mid-1800s was determined from published records, examination of collections at the Bishop Museum, and from museum database records, and is summarised in the Systematics section below.

Taxonomy and collection data

The landsnail species identifications in this study were based on published literature, examination of type specimens or images of types loaned or provided by various museums (mentioned in the text below), and examination of type and reference material in the collection of the Bishop Museum. The landsnail material collected on Rarotonga during this study has been deposited in the Museum of New Zealand Te Papa Tongarewa. This and the other specimen lots of Rarotongan landsnails examined are listed in the Systematics section below under the heading 'Material', along with some records from Rarotonga obtained from database listings by the United States National Museum of Natural History, the Field Museum of Natural History and the Florida Museum of Natural History.

Several new species of landsnail were discovered on Rarotonga during this study, in the families Assimineidae, Vertiginidae, Endodontidae, Charopidae and Euconulidae. Shell measurements reported below were obtained using a binocular microscope with a calibrated eyepiece graticule. The shell dimensions and ratios for species of *Minidonta* and *Sinployea* follow Solem (1976, 1983): namely, shell height; shell diameter; umbilical width; spire protrusion; whorl number; shell height/shell diameter ratio; shell height/spire protrusion ratio; and shell diameter/umbilical width ratio. Additional dimensions recorded for other taxa (i.e. Assimineidae, Vertiginidae, Euconulidae) included aperture height parallel to shell axis, and spire height relative to aperture height. Nomenclature of apertural processes follows Solem (1976) for Endodontidae and Pilsbry & Cooke (1918–20: fig. 1) for Vertiginidae. Holotypes of the species

in this paper were photographed at the Museum of New Zealand Te Papa Tongarewa using Auto-Montage software.

Plant nomenclature in the introduction and below follows McCormack (2007). A list of equivalent names by Cheeseman (1903) and Wilder (1931) is given in Appendix 2.

Abbreviations used in the text

- AIM – Auckland War Memorial Museum
- ANSP – Academy of Natural Sciences of Philadelphia
- BMNH – Natural History Museum, London
- BPBM – Bernice P. Bishop Museum, Honolulu
- FLMNH – Florida Museum of Natural History, Gainesville
- FMNH – Field Museum of Natural History, Chicago
- MCZH – Museum of Comparative Zoology, Harvard University
- MNHN – Muséum national d'Histoire naturelle, Paris
- NMNZ – Museum of New Zealand Te Papa Tongarewa, Wellington
- NZAC – New Zealand Arthropod Collection, Landcare Research, Auckland
- SMF – Senckenberg Naturmuseum, Frankfurt
- USNM – National Museum of Natural History, Washington, DC
- ZMB – Museum für Naturkunde, Humboldt-Universität zu Berlin
- ZMZ – Zoological Museum, Zurich

Results

Stratigraphic sections and soil horizons

Seaward parts of the coastal plain around northern and northeastern Rarotonga consisted of one or more broad, low, beach-parallel ridges of unconsolidated, poorly sorted, clast-supported coral rubble, comprising predominantly subrounded clasts in the pebble- to boulder-size range. In places, the rubble had an open framework to depths of 50 cm or more, but elsewhere a matrix of fresh, unweathered, bioclastic sand was present at, or close to, the ground surface. Where broadleaved litter was ponded on the rubble, there were generally associated small pockets of humus trapped on and between coral blocks. The gravel ridges extended locally to the inner edge of the coastal plain, but were more commonly bounded by, or graded into, moderately or slightly gravelly sand to landward. Similarly, Motutapu and Oneroa islets had beach ridges of coral rubble on the exposed northern and eastern coasts, and a lower,

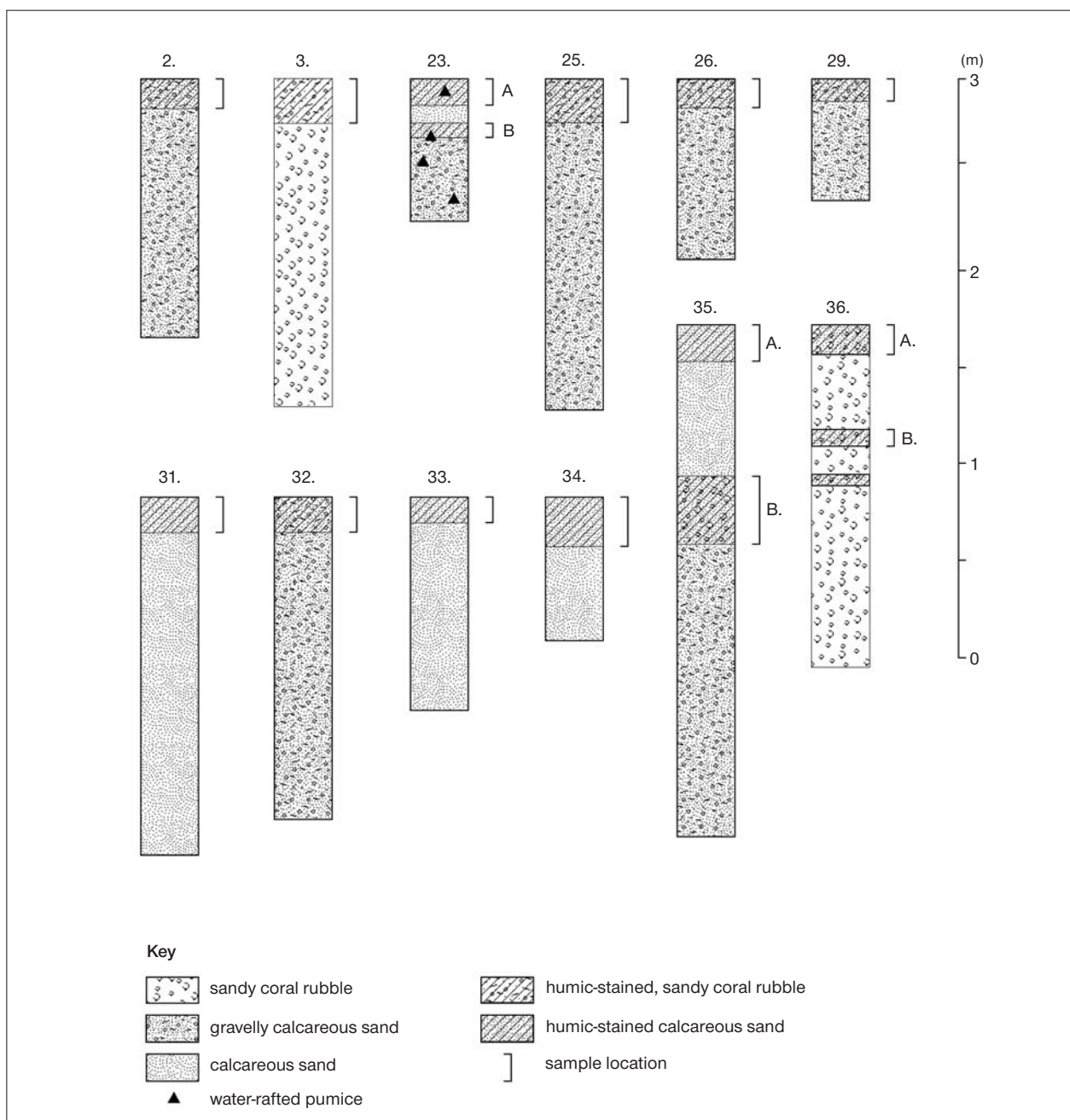


Fig. 3 Stratigraphic columns for sections exposed in coastal banks (sites 23, 26, 29, 33), and in sand and gravel pits (sites 2, 3, 25, 31, 32, 34–36).

hummocked surface underlain by calcareous sand and coral gravel to landward.

Stratigraphic columns of gravelly sequences exposed in pits at Pue (sites 2, 3) are shown in Fig. 3. The section at site 2 was *c.* 140 m from the coast on the inner, landward-sloping part of the coastal plain. It had a 15 cm-thick ground soil of dark brown, strongly humic-stained, bioclastic, gravelly

sand, overlying >1.2 m of unweathered, bioclastic, gravelly, coarse sand to sandy gravel. The section at site 3 was *c.* 15 m from the coast, behind a steep, gravelly beach ridge on the outer, seaward-sloping part of the coastal plain. It had a 25 cm-thick ground soil of clast-supported pebble–cobble gravel with a matrix of dark brown, humic-stained, granular, coarse, fossiliferous, bioclastic sand. This soil horizon was

underlain by >1.5 m of crudely stratified, clast-supported, pebble-cobble gravel with a matrix of granular, coarse sand.

The coastal plain around western and southern Rarotonga was predominantly underlain by sand (Fig. 3). Ground soils typically had a 12–25 cm-thick, dark brown, humic-stained, sandy 'A' horizon, directly underlain by unweathered bioclastic sand containing scattered coral clasts and shells of marine molluscs. In sand quarries at Titikaveka, Aroa and Kavera (sites 25, 31, 32), the unweathered sand unit beneath the ground soil was >1.5 m thick, and it was >0.5–1.0 m thick beneath ground soils in coastal sections at Titikaveka, Rutaki and Te Muriavai (sites 26, 29, 33). This unit was generally massive, but paleobeach deposits of thinly intercalated, subplanar layers of finer and coarser sand dipping seaward at *c.* 6° were present in a sand quarry at Aroa.

Stratified sequences containing ground soils and buried soils were seen at three sites (Fig. 3). A section exposed in a low coastal bank at Muri (site 23) incorporated a strongly humic-stained, fine- to medium-grained, sandy ground soil and an underlying weakly humic-stained, fine- to medium-grained, sandy paleosol, separated by an 8 cm-thick interval of unweathered bioclastic sand. The paleosol was underlain by >40 cm of unweathered bioclastic sand containing common pumice clasts. A section exposed in a pit excavated at Pokoinu (site 35) was *c.* 75 m inland from the coast. It had a 20 cm-thick ground soil of dark brown, humic-stained, fine bioclastic sand containing scattered coral clasts, underlain by 40–80 cm of unweathered, weakly stratified, bioclastic coarse sand. Below this was a 50–60 cm-thick unit of clast-supported, poorly sorted, pebble-boulder coral gravel, with a matrix of dark brown, humic-stained, bioclastic sand. This gravelly layer was presumably a storm (or possibly tsunami) deposit, on which a soil subsequently developed. It overlies >1.5 m of unweathered, coarse bioclastic sand containing scattered coral fragments. A sequence exposed in a pit at Avatiu (site 36), *c.* 80 m inland from the coast, incorporated three soil-capped sandy gravel units deposited during separate storm (or possibly tsunami) events. The uppermost unit consisted of a 15 cm-thick ground soil of dark brown, strongly humic-stained, bioclastic, gravelly sand overlying a 25–40 cm-thick layer of sandy coral rubble. Below this was a 7 cm-thick, moderately humic-stained, sandy gravel paleosol overlying a 15 cm-thick layer of sandy coral rubble. The lowest stratigraphic unit consisted of a 5 cm-thick, moderately humic-stained, sandy gravel paleosol overlying a >1 m-thick layer of sandy coral rubble.

The ages of the soils sampled during the present study are not known directly. The ground soils and paleosols exposed in coastal sections at Muri, Akapuao, Titikaveka, Rutaki and Te Muriavai (i.e. sites 23, 24, 26, 29, 33) were between 1.0 m and 2.0 m above present high-water mark (hwm), and so presumably formed after the mid- to late-Holocene highstand when sea-level was 1.5 m above the present level. On the basis of the sea-level curve determined by Moriwaki *et al.* (2006), these soils are all inferred to be younger than *c.* 800–500 cal. BP. Similarly, Motutapu, Oneroa and Koromiri islets in Muri Lagoon, which are stable motu composed of coral rubble and sand, probably did not form until late in Holocene time, after ambient high-tide levels fell below mid-Holocene low-tide levels (Dickinson 2003). Dated human remains from Motutapu indicate that this island formed before 720 ±50 ¹⁴C yrs BP (Moriwaki *et al.* 2006). By contrast, ground soils at the sample sites on inland parts of the Rarotongan coastal plain presumably started forming much earlier in the mid- to late-Holocene emergence, sometime after *c.* 4500 cal. BP (Moriwaki *et al.* 2006). Soil formation may have begun as much as a few thousand years ago on the earliest-formed, inner parts of the coastal plain.

No cultural material was found in any of the paleosols examined on Rarotonga. However, these soils are all inferred to post-date human settlement because of the ubiquitous presence of fossil shells of two non-indigenous species thought to have been synanthropically introduced to Polynesia in prehistoric time (i.e. *Allopeas gracile* and *Gastrocopta pediculus*; below).

Coastal shrubland and forest remnants

In 2005–07, forest and shrubland were very scarce on the coastal plain of Rarotonga, comprising scattered, small remnant patches within highly modified, developed landscapes. The smallest patches were *c.* 0.14–0.3 ha in area (i.e. at sites 4, 5, 8, 9, 14, 15, 16), and the largest were in the range 0.5–1.0 ha (i.e. at sites 7, 11, 12, 30, 35). Most of these forest and shrubland remnants were on coral rubble substrata along the coast between Pue and Ngatangia. There were only two small patches of forest left on sand substrata: one at Aroa, which has since been largely cleared (site 30); and the other at Pokoinu, which was also under threat from land development (site 35). The largest areas of coastal forest and shrubland remaining were on Motutapu and Oneroa

islets in Muri Lagoon (c. 11.5 ha and 9.5 ha, respectively), on coral rubble and sand substrata. Coastal shrubland was also present on makatea limestone karst at the northern and southern headlands of Ngatangiia Harbour (e.g. site 16).

Intact vegetation sequences in the supratidal zone on coral rubble substrata had herbaceous strand vegetation of *Wollastonia biflora*, and sprawling vines of *Canavalia sericea*, *Ipomoea pes-caprae*, and *Vigna marina*, with *Ipomoea macrantha* and *Triumfetta procumbens* present locally. Behind this was a wind-shorn shrubland of *Scaevola taccada*, with or without *Hibiscus tiliaceus* and rare *Tournefortia argentea*, which graded back into low forest. Between Pue and Ngatangiia, the two commonest tree species in this coastal forest were *Barringtonia asiatica* and *Hernandia nymphaeifolia*, with coconut palms, *Guetarda speciosa*, *Hibiscus tiliaceus* and *Pisonia grandis* present locally. The invasive adventive vine *Epipremnum pinnatum* was abundant in several of these forest remnants, sprawling on the ground and climbing trees. The exposed seaward coast of Motutapu had a band of forest containing coconut palms, *G. speciosa*, *Hernandia nymphaeifolia*, *Hibiscus tiliaceus*, *Morinda citrifolia* and *Schleinitzia insularum*, with groves of *B. asiatica* present locally. Secondary forest in a former coconut plantation behind this was dominated by *Hibiscus tiliaceus*, with common coconut palms and scattered emergent *Hernandia nymphaeifolia*. *Casuarina equisetifolia* trees were common on sandy substrata around the western coast of Motutapu. Tree species present in forest on Oneroa included coconut palms, *Casuarina equisetifolia*, *G. speciosa*, *Hernandia nymphaeifolia*, *Hibiscus tiliaceus*, *M. citrifolia* and *P. grandis*.

The Pokoinu remnant on the northwestern coast of Rarotonga (site 35) had an intact sequence from strand vegetation to a small patch (c. 0.5 ha) of coastal forest. Sprawling vines of *Canavalia sericea*, *Ipomoea pes-caprae* and *Vigna marina* were present on the upper strand, along with scattered small shrubs of *Scaevola taccada*. There was no littoral shrubland, with the strand vegetation passing straight into, and overlapping with, a mixed forest remnant of coconut palms, *Casuarina equisetifolia*, *Guetarda speciosa* and *Hernandia nymphaeifolia*. The Aroa remnant (site 30) was a small, isolated patch of *Barringtonia asiatica*–*Hibiscus tiliaceus* forest.

Systematics

Class GASTROPODA

Order NERITOPSINA

Family HYDROCENIDAE

Georissa striata (Pease, 1871)

Chondrella striata Pease, 1871: 477 [Rarotonga, Cook Islands]; Garrett, 1879: 28; Garrett, 1881: 408; Garrett, 1884: 106; Johnson, 1994: 25.

Georissa sp. Craig, 1995: 100, fig. 6–3c; Walter, 1998: 88.

DISTRIBUTION: Southeastern Polynesia, including the southern Cook Islands (Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro), Austral and Society islands, Makatea in the Tuamotu group, and Nuku Hiva, Marquesas Islands (Garrett 1879, 1881, 1884, 1887; Cooke 1934; Allen & Christensen 1992; Craig 1995; Walter 1998; Brook *et al.* 2010).

MATERIAL: MCZH 187917 (holotype); BPBM 8592–3, 54390, 79786, 79807, 94359, 94366, 94371, 94392, 94403, 94415, 94419, 95346, 95383, 95390–2, 95400, 95422, 95449, 97694; FMNH 144542, 144543, 144570, 144598, 144612, 144620, 144642, 144644; NMNZ M.208825, 282395, 282448, 282472, 282482, 282504, 282553, 282582, 282608, 282632, 282674, 282690, 282757, 282782, 282802, 282823, 282854, 282880, 282904, 282951, 282976, 283002, 283023, 283044, 283075, 283104, 283132, 283157, 283184, 283213, 283242, 283262, 283284.

SITES: 1, 2, 6, 8–10, 12, 13, 18–21, 23A, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of *Georissa striata* were found at most of the coastal sites examined around Rarotonga, indicating that this species was formerly widely distributed on sand and coral rubble substrata of the coastal plain. Garrett (1879: 28) noted that *G. striata* inhabited 'dry localities in forests ... adhering to rocks, dead wood, and the under surface of loose stones'. He reported that this species was 'plentiful' on Rarotonga in the 1860s (Garrett 1881: 410). Collections made in the 1920s (BPBM), 1964–65 (FMNH) and 1994 (NMNZ) indicate that *G. striata* occupied native and disturbed forest habitats from near sea-level to c. 350 m elevation. During the present survey, extant populations of *G. striata* were found at two coastal sites at Tupapa and Matavera on Rarotonga (sites 8 and 9, respectively), and fresh, empty shells were found at another site near Matavera (site 10), and on Motutapu and Oneroa islets (sites 20 and 21, respectively). The distribution and abundance of this species further inland was not determined.

Family HELICINIDAE

Orobophana pacifica (Pease, 1865)

Helicina pacifica Pease, 1865b: 291 [Mangaia, Cook Islands – Pease 1871: 467]; Tryon, 1866: 82, pl. 5, fig. 7; Johnson, 1994: 19, pl. 2, fig. 3.

Helicina flavescens Pease, 1868a: 228, pl. 15, fig. 25 [Mangaia]; Pease, 1871: 467; Garrett, 1881: 407.

Helicina brazieri Pease, 1870: 397 [Niue]; Johnson, 1994: 8, pl. 5, fig. 11.

Helicina tabitensis Pease, 1871: 466 [Society Islands].

Orobophana flavescens.– Wagner, 1905: 417, pl. 8, fig. 21a–c; Craig, 1995: 99, fig. 6–3a.

NOMENCLATURE: No locality information was given in the original description of *Helicina pacifica* Pease, 1865, and the reference to Oulan Island by Tryon (1866: 82) was erroneous according to Garrett (1881: 407). Pease (1868a: 228) listed *Helicina flavescens* from Mangaia, and later listed this species from ‘Rorotonga’ (*sic*), and *H. pacifica* from Mangaia (1871: 476). Comments by Pease (1871: 467) suggest that the descriptions of these two species were based on the same material, presumably collected by Garrett in 1865 from Mangaia or one of the other southern Cook Islands. Garrett (1881: 407) noted that *Helicina tabitensis* was a junior synonym of *H. pacifica*. A carinate morphotype from Niue, *Helicina brazieri* Pease, 1870, is here considered to be a synonym of *H. pacifica*. On Niue, the ‘*brazieri*’ morphotype and a non-carinate form indistinguishable from the typical *pacifica* form are present on the western (leeward) and eastern (windward) sides of the island, respectively (Brook, pers. obs.).

DISTRIBUTION: Southeastern Polynesia, including the southern Cook Islands (Rarotonga, Aitutake, Manuae, Ātiu, Ma‘uke, Miti‘āro, Mangaia), Society Islands (Tahiti, Moorea, Huahine, Raiatea, Taha‘a, Borabora, Maupiti), Austral Islands (Rimatara, Rurutu, Tubuai, Raivavae) and Niue (Garrett 1881, 1884; Craig 1995; Walter 1998; Brook *et al.* 2010; Brook, unpub. data; BPBM).

MATERIAL: AIM AK111668; BPBM 95349–55, 95361, 95372, 95376, 95423–4, 190312; FMNH 144513, 144555, 144617; NMNZ M.208751, 211810, 282390, 282392, 282483, 282505, 282528, 282549, 282551, 282554, 282570, 282583, 282609, 282633, 282658, 282675, 282691, 282704, 282719, 282729, 282748, 282753, 282758, 282783, 282803, 282824, 282845, 283214, 283243, 283263, 283285.

SITES: 1–22, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of *Orobophana pacifica* were common in soils around the northern and eastern coasts of Rarotonga between Pokoinu and Ngatangia, and on Motutapu and Oneroa islets. In 2005–07, this species was still extant on Motutapu and Oneroa, and was patchily distributed in forest and shrubland remnants on the northeastern coast of Rarotonga between Pue and Ngatangia (sites 4, 5, 7–12, 14–16). *Orobophana pacifica* evidently had (e.g. Garrett 1881), and still has, a relatively narrow ecological range on Rarotonga, restricted to coral rubble, gravelly sand and makatea limestone substrata within *c.* 150 m of the coast. The extant populations occupied vegetation sequences extending from mats of herbaceous creeping vines on the upper shore of rubble beaches, through wind-shorn littoral shrubland, to broadleaved forest. Snails were found on the trunks, stems and leaves of living plants, and on the ground beneath rubble, fallen wood, and leaves.

Sturanya parvula (Pease 1868)

Helicina parvula Pease, 1868b: 156, pl. 12, fig. 10 [Ātiu, Cook Islands]; Garrett, 1881: 406; Johnson, 1994: 20.

Sturanya parvula.– Wagner, 1905: 385, pl. 3, figs 10a–c.

Orobophana parvula.– Craig, 1995: 99, fig. 6–3b.

DISTRIBUTION: Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Mangaia (Garrett 1881; Brook, unpub. data; NMNZ).

MATERIAL: BPBM 8594, 79774, 79785, 94315–9, 94348–50, 94357, 94360, 94364, 94370, 94381, 94388, 94417, 95425; FMNH 144539; NMNZ M.208775, 228465, 232900, 282396, 282407, 282484, 282506, 282555, 282610, 282634, 282692, 282759, 282784, 282804, 282825, 282846, 282855, 282881, 282905, 282952, 282977, 283003, 283024, 283045, 283076, 283105, 283133, 283158, 283185, 283215, 283244, 283264, 283286.

SITES: 1, 2, 6, 9, 10, 13, 18–22, 23A, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells indicate that *Sturanya parvula* was formerly widely distributed on sandy and gravelly sand substrata on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets, albeit with a patchy distribution on the northeastern coast of Rarotonga. Garrett (1881: 407) noted that in the 1860s this species was ‘exceedingly abundant on all the islands, where it occurs on the ground in forest’. *Sturanya parvula* was evidently still locally common on Rarotonga in the mid- to late 1920s, with collections in the BPBM from the coastal plain at

Muri, Titikaveka and Nikao; and in valleys and on lower hill slopes to *c.* 180 m elevation near Avarua, Maungaroa, Muri, Titikaveka and Arorangi. By contrast, the FMNH contains a single collection made in 1964–65 from the northern slopes of Maungatea in the upper Vaikapuangi Valley, and in 1994, this species was collected on Motutapu and Oneroa islets only (NMNZ). In 2005–07, extant populations were found at two locations only: in a small, remnant grove of *Barringtonia asiatica*–*Hernandia nymphaeifolia*–*Hibiscus tiliaceus* forest at Matavera (site 9), and in mixed broadleaved *Casuarina equisetifolia*–coconut forest on Oneroa (sites 21, 22). A few fresh, empty shells but no live snails were found in a recently cleared horticultural plot on the site of a former *B. asiatica* grove at Matavera (site 10).

Order SORBEOCONCHA Family ASSIMINEIDAE

Genus *Assiminea* Fleming, 1828

Garrett (1881: 408) recorded *Assiminea nitida* (Pease, 1865) from Rarotonga, Aitutaki, Ātiu and Mangaia, noting that it was ‘generally distributed throughout southern Polynesia, and ranges from near the seashore to about two thousand feet above sea-level’. The type locality of this species is Huahine in the Society Islands (Pease 1869b). Abbott (1958: 255) suggested that there were two morphologically similar species in some early collections labelled *A. nitida* from the Cook Islands. He considered that shells with a fine, subsutural spiral thread and a narrowly open umbilicus belonged to *A. nitida*, and he tentatively attributed shells that lacked a subsutural thread and umbilical chink, and that had two very weak, brown spiral bands on the last adult whorl, to *Assiminea lucida* Pease, 1869. The latter species, originally described from Anaa in the Tuamotu Islands, was incorrectly listed as a junior synonym of *A. nitida* by Garrett (1879, 1881, 1884). Cowie (1998a) noted that *A. nitida* (Pease, 1865) is a junior synonym of *Assiminea parvula* (Mousson, 1865), described from Samoa.

Three species of small brown assimineids were found on Rarotonga during the present survey. One was fully terrestrial and widely distributed across the island. Shells of this species typically have a narrowly open umbilicus, with or without a fine subsutural spiral thread; they are morphologically indistinguishable from the type material of *Hydrocena parvula* Mousson, 1865 (i.e. based on examination of an image of ZMZ 528685, sent by Eike Neubert), *Hydrocena nitida* Pease, 1865 (e.g. ANSP 14237; BPBM 170997; MCZH 139120;

MNHN – syntype), and *Hydrocena similis* Baird, 1873 (i.e. based on examination of an image of BMNH 20090244, sent by Jonathan Ablett). The Rarotongan species is provisionally listed here as *Assiminea parvula* (Mousson, 1865) following Cowie (1998a), but anatomical and/or genetic studies are required to determine whether this represents a single widely distributed Polynesian species or a species complex. The other two species of *Assiminea* on Rarotonga were apparently restricted to supratidal habitats on coral rubble and makatea limestone substrata along the eastern coast of the island. Shells of one species had the umbilicus completely closed by columellar callus, whereas those of the other had a narrowly open umbilicus. The former species closely matches the type material of *Assiminea lucida* Pease, 1869 (e.g. BPBM 171001; MCZH 74952; MNHN – syntype), and is provisionally listed under this name pending further study. The umbilicate intertidal–supratidal species is listed below as *Assiminea* sp. 1.

Abbott (1958) tentatively assigned *Assiminea lucida* to *Paludinella*, but the type species of the latter genus (*Helix litorina* Delle Chiaje, 1825), which lives in the intertidal habitats in the Mediterranean Sea, differs in having a globose, thick, opaque shell, with spiral cords on the early teleoconch whorls (Fukuda & Ponder 2003: 2019). Fukuda & Ponder (2003: 2015) also noted that although hundreds of species have been assigned to *Assiminea*, most bear little morphological resemblance to the type species, *Assiminea grayana* Fleming, 1828, which lives in brackish waters in northwestern Europe. All the Rarotongan species reported here fall into this category, but are retained in *Assiminea* in the meantime, given the absence of reliable information on their phylogenetic relationships.

Assiminea lucida Pease, 1869

Assiminea lucida Pease, 1869b: 166, pl. 7, fig. 10 [Anaa, Tuamotu Islands]; Johnson, 1994: 16.

Assiminea nitida. – Garrett, 1879: 29 (in part); Garrett, 1881: 408 (in part).

DISTRIBUTION: This species was described from Anaa in the Tuamotu group; morphologically similar shells have been collected from several other island groups in southern Polynesia, including the southern Cook Islands (Rarotonga, Manuae, Ātiu, Ma‘uke, Miti‘āro, Mangaia), Austral Islands (Rurutu), Niue and Samoa (Upolu) (Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ). However, genetic and/or anatomical information is required to determine whether or not these populations are all conspecific.

MATERIAL: NMNZ M.282531, 282571, 282586, 282749, 282754.

SITES: 3, 7, 8, 16, 17.

REMARKS: In 2005–07, this species was found at a few sites on the northeastern coast of Rarotonga and on Motutapu. Snails were present beneath mats of herbaceous creeping vines and in contiguous littoral shrubland, in hollows on makatea limestone, and among coral rubble on the modern storm berm. Fossil shells were present locally in ground soils on coral rubble.

Assimineea parvula (Mousson, 1865)

Hydrocena parvula Mousson, 1865: 184 [Upolu, Samoa].

Hydrocena nitida Pease, 1865a: 674 [Huahine, Society Islands]; Johnson, 1994: 18.

Assimineea (Hydrocena) nitida.– Pease, 1869b: 165, pl. 7, fig. 11.

Hydrocena similis Baird, 1873: 440, pl. 39, figs 1, 2 [Samoa].

Assimineea nitida.– Garrett, 1881: 408 (in part); Abbott, 1958: 254 (in part).

Syncera nitida.– Abbott, 1949: 272, fig. 7.

Omphalotropis sp. a Craig, 1995: 102, fig. 6–4b.

Assimineea parvula.– Cowie, 1998a: 29.

DISTRIBUTION: Southern Polynesia, including Samoa (Savai'i, Tau, Tutuila, Upolu), Wallis Island/Uvea, southern Cook Islands (Rarotonga, Aitutaki, Ātiu, Miti'āro, Mangaia), Society Islands (Borabora, Huahine, Mehitia, Tahiti, Raiatea) and Marquesas Islands (Eiao) (Brook *et al.* 2010; Brook, unpub data; BPBM; NMNZ).

MATERIAL: BPBM 8591, 95345, 95388–9, 97693; NMNZ M.208818, 232927, 282438, 282449, 282473, 282486, 282509, 282530, 282558, 282585, 282637, 282677, 282696, 282762, 282786, 282806, 282828, 282956, 282980, 283026, 283048, 283080, 283109, 283135, 283160, 283188, 283217, 283247, 283266, 283288, 283335, 283339, 283343, 283386, 283402, 283446, 283669.

SITES: 1–3, 6, 8, 10, 12, 13, 18–21, 25, 26, 28–34, 35A, 35B, 36A, 36B.

REMARKS: The presence of fossil shells in sandy soils and coral rubble indicates that *Assimineea parvula* was formerly widely distributed on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets. No extant populations were found at any of the coastal sites surveyed in 2005–07; a similar lack of records from lowland sites in the BPBM and FMNH collections suggests that this species had died out on the coastal plain by the early 1900s. BPBM records

indicate that *A. parvula* had a sparse distribution and was comparatively rare in inland Rarotonga in the late 1920s. By contrast, this species was widespread and locally abundant in disturbed forest and slope forest in the interior of Rarotonga in 2005–07, living on the ground in leaf litter, and under stones and fallen wood (Brook, pers. obs.).

Assimineea sp. 1

DISTRIBUTION: The identity and regional distribution of this species is not known. In the Cook Islands, it is present on Rarotonga and Mangaia (Brook, unpub. data).

MATERIAL: NMNZ M.282572.

SITE: 7.

REMARKS: In 2005–07, this species was found at one site on the east coast of Rarotonga, living among coral rubble, beneath mats of herbaceous creeping vines, on the modern storm berm.

Genus *Atropis* Pease, 1871

Atropis rarotongana new species

(Fig. 4A)

DESCRIPTION: Shell small, 3.9–5.4 mm high, narrowly cyrtocooid, higher than wide (height/width ratio 2.05–2.33), spire 1.91–2.29 times as high as aperture. Whorls 4.75–5.75, roundly convex, suture strongly impressed, spire whorls expansion rate slowing during growth. Protoconch of two whorls (0.7–0.8 mm wide), smooth, glossy, lacking sculpture. Teleoconch has microsculpture of very fine, collabral growth lines, and even finer spirals. Base rounded, smoothly and tightly curved into umbilical chink. Aperture ovate, rim thickened within, inner margin moderately reflexed. Colour of fresh shells pale yellowish brown or reddish brown.

TYPE MATERIAL: Holotype NMNZ M.290132 and paratypes M.290133 (12), BPBM 274755 (5): Cook Islands, Rarotonga, Muri, fossils from sandy paleosol exposed in coastal bank (21°15.600'S, 159°43.941'W), 29 Sep. 2005.

OTHER MATERIAL: NMNZ M.282507, 282529, 282556, 282584, 282611, 282635, 282676, 282693, 282856, 282882, 282906, 282953, 283077, 283106, 283186, 283245.

SITES: 2, 3, 6, 8–10, 12, 13, 23A, 23B, 24, 25, 30, 31, 34, 35B.

DISTRIBUTION: Cook Islands – Rarotonga; probably endemic to this island.

REMARKS: This is the first record of this genus and species from Rarotonga. Fossil shells were locally common in sandy soils and coral rubble around Rarotonga, indicating a former

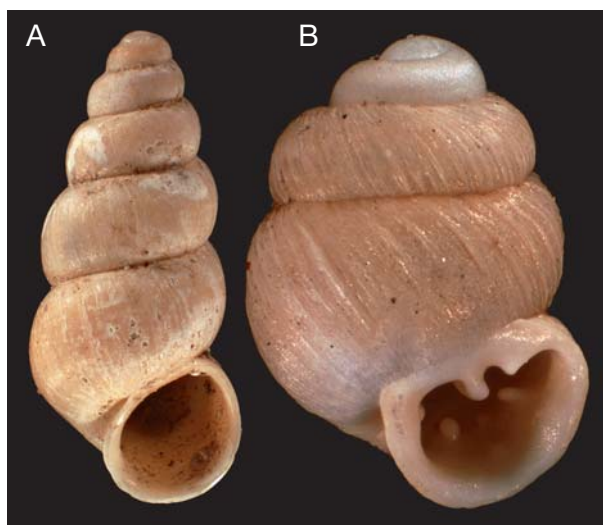


Fig. 4 A, *Atropis rarotongana* n.sp., Muri, holotype, M.290132 (4.55 × 2.05 mm); B, *Nesopupa rarotonga* n.sp., Matavera, holotype, M.290125 (1.60 × 0.65 mm).

wide distribution on the coastal plain. No live snails were found in 2005–07, but a few relatively fresh, empty shells were found in a remnant grove of *Barringtonia asiatica* on coral rubble at Matavera (site 12). *Atropis rarotongana* n.sp. may have been extant at this site in 2005–07, but everywhere else it was almost certainly extinct. The fact that this species was not recorded by Garrett (1881) suggests it was probably already in decline and rare by the 1860s.

Garrettia rotella (Pease, 1868)

Diadema rotella Pease, 1868b: 158, pl. 12, fig. 13 [Rarotonga, Cook Islands – Pease 1871]; Garrett, 1881: 404; Johnson, 1994: 22.

Garrettia rotella. – Cooke & Clench, 1943: 257, fig. 6.

DISTRIBUTION: Cook Islands – Rarotonga (Garrett 1881), Aitutaki (Brook, unpub. data).

MATERIAL: BPBM 2117, 8616, 10115, 188859; NMNZ M.228474, 282612, 282694, 282760, 282826, 282857, 282907, 282954, 282978, 283046, 283078, 283107.

SITES: 9, 13, 18, 21, 23A, 24–26, 29–31.

REMARKS: The presence of fossil shells in ground soils indicates that *Garrettia rotella* formerly had a patchy distribution on sand and coral rubble substrata of the coastal plain around eastern and southern Rarotonga, and on Motutapu and Oneroa islets. Garrett (1881: 405) noted that in the 1860s this species was ‘not uncommon on the ground in forests’ on Rarotonga. However, no live snails or fresh empty shells were found at any of the sites surveyed in

2005–07, and no live specimens or empty shells are represented in snail collections made in the 1920s (BPBM) or 1960s (BPBM, FMNH). This suggests that the species underwent serious decline between the 1860s and 1920s, and is probably now extinct.

Omphalotropis variabilis (Pease, 1865)

Realia variabilis Pease, 1865b: 288 [Ātiu, Cook Islands – Pease 1871: 476]; Tryon, 1866: 82, pl. 5, fig. 2; Johnson, 1994: 27.

Omphalotropis variabilis. – Pease, 1869a: 148; Garrett, 1881: 405.

Omphalotropis cf. *variabilis*. – Craig, 1995: 101, fig. 6–4a; Walter, 1998: 88.

NOMENCLATURE: Garrett (1881) found two species of *Omphalotropis* in the Cook Islands: *Omphalotropis ochrosotoma* (Pease, 1865) on Aitutaki; and *Omphalotropis variabilis* (Pease, 1865) on Rarotonga, Aitutaki, Ātiu and Mangaia. He also listed a third species, *Omphalotropis ovata* (Pease, 1865), on the ‘authority of Mr Pease, who found it in a small lot of land shells collected by Dr Dean at Mangaia’ (Garrett 1881: 406; see also Pease 1869a, 1871). Extensive landsnail collections made on Mangaia in the 1920s (BPBM), and fossil and modern material collected on this island by the author in 2007, contain a single species of *Omphalotropis* that varies from weakly to strongly carinate, and which is morphologically indistinguishable from populations attributed to *O. variabilis* on other islands in the southern Cook group (Brook, unpub. data).

The location of the type material of *Omphalotropis ovata* (originally placed in *Hydrocena*) is not known (Johnson 1994: 19). Pease’s original description (1865a: 674) indicates that the shell was 5 mm high and 3 mm wide, with roundly convex whorls lacking a peripheral carina. Whether *O. ovata* (Pease) represents a non-carinate form of *Omphalotropis variabilis*, which would make the latter a junior synonym, or is a miss-localised taxon from somewhere other than the Cook Islands, is presently unknown. Given this confusion, the name *O. variabilis* is retained here for the Cook Islands species, following Garrett (1881).

DISTRIBUTION: Southern Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Ma’uke, Miti’āro, Mangaia (Garrett 1881; Craig 1995; Walter 1998; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ); and one location on Raivavae, Austral Islands (Vaiaunana Point: BPBM 146744–5, 146749). Fossil faunas indicate that this species was introduced to Aitutaki, Ātiu, Ma’uke and Mangaia in pre-historic time (Brook, unpub. data), and the population on

Raivavae probably also resulted from a synanthropic introduction. Pease (1872) listed *Omphalotropis variabilis* from Tonga, but this record was probably based on carinate specimens of the morphologically similar *Omphalotropis vallata* (Gould, 1847).

MATERIAL: BPBM 8590, 54389, 79630–1, 79773, 79778, 79784, 79791, 94335–9, 94343, 94346–7, 94352, 94365, 94369, 94373, 94379–80, 94387, 94391, 94402, 94418, 95333–6, 95341–4, 95371, 95377–82, 95387, 95396–9, 95405, 95412, 95420–21, 95441–3, 95470, 97687–92; NMNZ M.208756, 232917, 282439, 282450, 282458, 282467, 282474, 282485, 282508, 282557, 282613, 282636, 282695, 282761, 282785, 282805, 282827, 282858, 282883, 282908, 282955, 282979, 283004, 283025, 283047, 283079, 283108, 283134, 283159, 283187, 283216, 283246, 283265, 283287, 283307, 283314, 283346, 283358, 283365, 283387, 283431.

SITES: 1, 2, 6, 9, 10, 13, 18–21, 23A, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells were widely distributed and common in coastal sandy soils and coral rubble around Rarotonga, and on Motutapu and Oneroa islets, albeit with a patchy distribution on the northeastern coast of Rarotonga. Garrett (1881) noted that *Omphalotropis variabilis* was abundant on Rarotonga in the 1860s, and collections in the BPBM indicate that it was common also in the 1920s. This species was still abundant and widespread in native and disturbed forest in the interior of Rarotonga in 2005–07 (Brook, unpub. data), but had evidently died out across almost all of its former range on the coastal plain. Extant colonies were found at two coastal sites only, in small, remnant forest groves at Matavera and Aroa (sites 9, 30), the latter of which has since been cleared for a tourist development.

Family TRUNCATELLIDAE

Truncatella guerinii A. Villa & J. Villa, 1841

Truncatella guerinii Villa & Villa, 1841: 59 [Réunion, Mascarene Islands]; Clench & Turner 1948: 167, pl. 23, figs 12, 13.

Truncatella rustica.— Craig, 1995: 100, fig. 6–3d.

DISTRIBUTION: Widely distributed in the tropical Indo-Pacific (Clench & Turner 1948). Cook Islands—Rarotonga, Manuae, Ātiu, Miti'āro, Mangaia (Brook *et al.* 2010; Brook, unpub. data; NMNZ).

MATERIAL: BPBM 206442; NMNZ M.232908, 282532, 282573, 282660, 282678, 282721, 282730, 282750, 282755, 282847.

SITES: 3, 7, 11, 12, 14–17, 22.

REMARKS: Restricted to the eastern coast of Rarotonga. Fossil shells were found in ground soils on coral rubble at Pue and Matavera (sites 3 and 12, respectively). In 2005–07, this species was found living at a few sites between Tupapa and Ngatangia, and on Motutapu and Oneroa islets (i.e. sites 7, 11, 14–17, 22); snails were present in littoral shrubland remnants on coral rubble and makatea limestone substrata.

Order PULMONATA

Family VERONICELLIDAE

Vaginulus (Sarasinula) plebeius P. Fischer, 1868

Vaginulus plebeius Fischer, 1868: 145 [New Caledonia].

Veronicella brunnea Collinge, 1900a: 435 [Vanuatu].

Veronicella gilsoni Collinge, 1900b: 179 [Fiji].

Veronicella agassizi Cockerell, 1901: 835 [Tahiti, Society Islands].

Vaginula samoana Simroth, 1918: 290 [Samoa].

Vaginulus (Sarasinula) plebeius.— Baker 1931: 134, pl. 8, figs 1, 2.

DISTRIBUTION: This species is native to the Caribbean and South America, but has become widely distributed among tropical Pacific islands since European contact (Grimpe & Hoffmann 1925; Baker 1931; Solem 1959, 1964; Cowie 1997, 2000, 2001b; Cowie & Robinson 2003). *Vaginulus plebeius* was established in New Caledonia by 1863; in Vanuatu, Fiji and Tahiti by 1900; and in Samoa by 1918 (Fischer 1868; Collinge 1900a,b; Cockerell 1901; Simroth 1918; Grimpe & Hoffmann 1925; Solem 1964). In the Cook Islands, it is present on Rarotonga, Aitutaki, Ātiu, Miti'āro and Mangaia (Brook *et al.* 2010; Brook, unpub. data).

MATERIAL: BPBM 206441; NMNZ M.283327.

REMARKS: *Vaginulus plebeius* was not recorded by Garrett (1881), and is not represented in terrestrial mollusc collections made on Rarotonga between 1899 and 1930 (BPBM, NMNZ). The earliest record was from Avarua in 1964 (BPBM 206441), which suggests that this species was probably introduced to Rarotonga sometime between 1930 and the early 1960s. *Vaginulus plebeius* was not found at any of the coastal sites surveyed in 2005–07, but individuals were seen crawling at night on the walls of houses in open, anthropogenic habitats on the coastal plain. It was also widely but patchily distributed in native and modified habitats in inland Rarotonga, up to at least 450 m elevation (Brook, pers. obs.).

Family ELLOBIIDAE

Allochroa layardi (H. Adams & A. Adams, 1855)

Ophicardelus (Laimodonta) layardi Adams & Adams, 1855: 30 [Sri Lanka].

Laimodonta conica Pease, 1863: 242; Garrett, 1881: 403.

Allochroa layardi.— Martins, 1995: 8.

DISTRIBUTION: Widely distributed in the tropical Indo-Pacific (Martins 1995). Cook Islands – Rarotonga.

MATERIAL: USNM 721509.

REMARKS: Garrett (1881) found a single example of *Allochroa layardi* on Rarotonga in the 1860s, and the Smithsonian collection includes a single specimen collected near Tupapa (USNM 721509). No specimens of *A. layardi* were found in 2005–07. This species was evidently a rare vagrant, with no established population on Rarotonga.

Melampus castaneus Megerle von Mühlfeld, 1816

Melampus castaneus Megerle von Mühlfeld, 1816: 4 [Indonesia].

DISTRIBUTION: Widely distributed in the tropical Pacific. Cook Islands – Rarotonga, Ātiu, Ma'uke (NMNZ; USNM).

MATERIAL: NMNZ M.283919.

REMARKS: This species is recorded from Rarotonga on the basis of two shells collected by R.J. Dashwood in 1937 (NMNZ M.283919). Like *Allochroa layardi* (above), it is presumably a rare vagrant on this island, with no established population.

Melampus fasciatus (Deshayes, 1830)

Auricula fasciatus Deshayes, 1830: 90 [New Guinea and Philippines].

Melampus fasciatus.— Garrett, 1881: 402.

DISTRIBUTION: Widely distributed in the tropical Pacific. Cook Islands – Rarotonga, Aitutaki, Ātiu, Ma'uke, Mangaia (Garrett 1881; USNM).

MATERIAL: NMNZ M.201791, 212962, 282574, 282661, 282751, 283887; USNM 889135, 889136.

SITES: 7, 11, 16.

REMARKS: In 2005–07, this species was found under coral rubble in open littoral shrubland and *Scaevola taccada* shrubland on the northeastern coast of Rarotonga.

Melampus luteus (Quoy & Gaimard, 1832)

Auricula lutea Quoy et Gaimard, 1832: 163, pl. 13, figs 25–27 [Vanikolo, Solomon Islands].

Melampus luteus.— Garrett, 1881: 402; Craig, 1995: 107, fig. 6–5g.

DISTRIBUTION: Widely distributed in the tropical Pacific. Cook Islands – Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro,

Mangaia (Garrett 1881; Craig 1995; Brook *et al.* 2010; USNM).

MATERIAL: BPBM 206448; NMNZ M.212964, 217680, 282393, 282575, 282731, 282752, 282756, 283666; USNM 889137, 889138, 889142.

SITES: 7, 14–17.

REMARKS: Present locally on Motutapu and the north-eastern coast of Rarotonga in 2005–07, living in littoral shrubland and beneath mats of herbaceous creeping vines, on coral rubble and makatea limestone substrata.

Family ACHATINELLIDAE

Elasmias apertum (Pease, 1865)

Tornatellina aperta Pease, 1865a: 673 [Tahiti, Society Islands – Pease 1871: 473]; Johnson, 1994: 6, pl. 2, fig. 18.

Elasmias apertum.— Pilsbry, 1910: 122; Cooke & Kondo, 1961: 222, fig. 97; Craig, 1995: 105, fig. 6–4f.

DISTRIBUTION: Widely distributed among islands in the tropical South Pacific (Cooke & Kondo 1961). Cook Islands – Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro, Mangaia, Pukapuka (Brook *et al.* 2010; Brook, unpub. data; BPBM). Cooke & Kondo (1961) considered that the wide distribution of *Elasmias apertum* in the South Pacific was attributable to synanthropic introductions by Polynesians in prehistoric time, but circumstantial evidence suggests that this species was introduced to some Polynesian islands in historic time (e.g. Iredale 1913: 386).

MATERIAL: BPBM 94384, 94406–7, 94423, 95409, 95465; FMNH 144526, 144571, 144573, 143574, 144643, 144668, 144682, 144689; NMNZ M.282418, 282942, 283348, 283364.

REMARKS: This species was not present in fossil assemblages on Rarotonga, and was not recorded by Garrett (1881), which suggests that it was introduced to this island sometime after 1860. Collections in the BPBM and FMNH indicate that it was widely distributed in inland parts of Rarotonga in the 1920s and 1960s, respectively. Craig (1995) collected a single individual of *Elasmias apertum* in coastal forest on Oneroa in 1994 (NMNZ M.282418), but none was found at any of the coastal sites sampled in 2005–07.

Lamellidea oblonga (Pease, 1865)

Tornatellina oblonga Pease, 1865a: 673 [Tahiti, Society Islands – Pease 1871: 473]; Garrett, 1881: 398; Pilsbry & Cooke, 1915–16: 162; Johnson, 1994: 18, pl. 4, fig. 6.

Lamellidea oblonga.— Cooke & Kondo, 1961: 196, figs 86–91; Craig, 1995: 104, fig. 6–5b.

DISTRIBUTION: Widely distributed among islands in

Polynesia (Cooke & Kondo 1961: fig. 85; Preece 1995). Cook Islands – Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro, Mangaia, Nassau (Garrett 1881; Cooke & Kondo 1961; Allen & Christensen 1992; Craig 1995; Allen 1997, 1998; Walter 1998; Brook *et al.* 2010; Brook, unpub. data; BPBM). Cooke & Kondo (1961) noted that *Lamellidea oblonga* was generally found at, or close to, areas of human habitation and cultivation, and was often common on the leaves of plant species cultivated by Polynesians. They concluded that this species was originally native to eastern Polynesia, and was spread among central Pacific islands on food plants transported by humans in prehistoric time. On Aitutaki, *L. oblonga* has been recorded from prehistoric human occupation sites dating back to *c.* 700 yrs BP (Allen 1997, 1998; Allen & Wallace 2007).

MATERIAL: BPBM 54385, 94313, 94329, 94344, 94356, 94385, 94416, 95415–7; NMNZ M.282409, 282419, 282476, 282487, 282510, 282533, 282559, 282587, 282614, 282638, 282662, 282679, 282697, 282732, 282763, 282787, 282807, 282829, 282848, 282859, 282884, 282910, 282981, 283005, 283027, 283049, 283110, 283161, 283189, 283218, 283248, 283289.

SITES: 1–3, 6, 8–13, 15, 18–22, 23A, 23B, 24, 26–29, 31, 33, 34, 35A, 35B, 36B.

REMARKS: Fossil shells of this species were widely distributed in ground soils and paleosols on the coastal plain of Rarotonga, and on Motutapu and Oneroa islets. In 2005–07, extant colonies were present on Rarotonga in some coastal forest and shrubland remnants, and beneath old relict broadleaved trees, and on Motutapu and Oneroa islets in forest. Live snails were found on plant stems and on the ground among fallen leaves and dead wood.

Lamellidea pusilla (Gould, 1847)

Partula (Auriculella) pusilla Gould, 1847: 197 [Makatea, Tuamotu Islands].

Lamellina laevis Pease, 1865a: 672; Johnson, 1994: 16, pl. 2, fig. 16 [Cook Islands].

Tornatellina conica.– Garrett, 1881: 399.

Tornatellina serrata.– Garrett, 1881: 399; Pilsbry & Cooke, 1915–16: 164, pl. 33, figs 4, 5.

Tornatellina impressa.– Pilsbry & Cooke, 1915–16: 173.

Tornatellina pusilla.– Pilsbry & Cooke, 1915–16: 176, pl. 34, fig. 3.

Lamellidea pusilla.– Cooke & Kondo, 1961: 184, figs 82–83; Craig, 1995: 103, fig. 6–5c.

DISTRIBUTION: Widely distributed among islands in the

tropical northwestern and southern Pacific (Cooke & Kondo 1961: fig. 81). Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Ma'uke, Miti'āro, Mangaia, Nassau, Rakahanga, Penrhyn (Garrett 1881; Cooke & Kondo 1961; Allen & Christensen 1992; Craig 1995; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ). Cooke & Kondo (1961) thought *Lamellidea pusilla* probably originated west of the Marshall Islands in Micronesia, and was carried eastwards to islands in the central Pacific by humans in prehistoric time.

MATERIAL: BPBM 8587, 98804; NMNZ M.282488, 282511, 282560, 282588, 282615, 282639, 282663, 282698, 282733, 282788, 282808, 282830, 282849, 282860, 282885, 282911, 282957, 282982, 283006, 283028, 283050, 283111, 283136, 283162, 283190, 283219, 283249, 283267, 283290.

SITES: 1, 2, 6, 8–11, 13, 15, 19–22, 23A, 23B, 24–29, 31–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of this species were widely distributed in ground soils and paleosols on the coastal plain of Rarotonga, and on Motutapu and Oneroa islets. *Lamellidea pusilla* was collected by Garrett in the 1860s (BPBM 8587, 98804), but is not represented in BPBM collections made on Rarotonga in the 1920s. In 2005–07, extant colonies were present on northeastern Rarotonga in a few coastal forest and shrubland remnants, and beneath old relict broadleaved trees, and on Motutapu and Oneroa islets in forest. Snails were found living on the ground among fallen leaves and dead wood.

Pacificella variabilis Odhner, 1922

Pacificella variabilis Odhner, 1922: 249, pl. 8, figs 15–17 [Easter Island].

Tornatellinops variabilis.– Cooke & Kondo, 1961: 172, fig. 76.

DISTRIBUTION: Widely distributed in the Pacific, from Micronesia to southeastern Polynesia (Cooke & Kondo 1961: 173; Preece 1995; Bauman 1996; Kirch *et al.* 2009). Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Miti'āro, Mangaia, Nassau, Penrhyn (Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ). Cooke & Kondo (1961) suggested that the wide distribution of *Pacificella variabilis* in the Pacific, and particularly its presence on atolls and low islands, is at least partly attributable to synanthropic dispersal among islands in prehistoric time. However, fossil shells of this species are present in sedimentary deposits pre-dating human settlement on Henderson Island (Preece 1998), indicating that southeastern Polynesia forms part of its natural range.

MATERIAL: BPBM 8588–9; NMNZ M.282534, 282576, 282589, 282616, 282640, 282664, 282680, 282699, 282722, 282734, 282764, 282789, 282809, 282831, 282850, 282861, 282886, 282912, 282983, 283007, 283051, 283081, 283137, 283163, 283191, 283220, 283291.

SITES: 3, 7–15, 18–22, 23A, 23B, 24, 26, 27, 29, 30, 32–34, 35A, 36B.

REMARKS: Fossil shells of *Pacificella variabilis* were widely but sparsely distributed in ground soils and paleosols on the coastal plain of Rarotonga, and on Motutapu. This species was collected by Garrett in the 1860s (BPBM 8588–9), but is not represented in BPBM collections made on Rarotonga in the 1920s. In 2005–07, it was widespread in coastal habitats on Rarotonga, and on Motutapu and Oneroa islets. The modern population occupied a wide variety of ecological settings, including herbaceous strand vegetation, coastal forest and shrubland remnants, and highly modified, open, anthropogenic habitats. Snails were found on the trunks, stems and leaves of shrubs and trees, and on the ground among fallen leaves and dead wood. On the east coast of Rarotonga, they were also found living in coral rubble beneath mats of creeping herbaceous vines on the upper strand.

***Tornatellides oblongus* (Anton, 1838)**

Strobilus oblongus Anton, 1838: 46 [Rapa, Austral Islands].

Tornatellina simplex.– Garrett, 1881: 398.

Tornatellides simplex.– Pilsbry & Cooke, 1915–16: 197, pl. 44, fig. 10.

Tornatellides oblongus.– Cooke & Kondo, 1961: 248, fig. 105; Craig, 1995: 105, fig. 6–5a.

DISTRIBUTION: Widely distributed among islands in the tropical southeastern Pacific (Cooke & Kondo 1961: fig. 107). Cook Islands – Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro and Mangaia (Garrett 1881; Cooke & Kondo 1961; Allen & Christensen 1992; Brook *et al.* 2010; Brook, unpub. data; BPBM). Cooke & Kondo (1961) noted that this species, like *Lamellidea oblonga* (above), was typically found in disturbed lowland areas associated with human cultivation, and had possibly been spread among islands by Polynesians in prehistoric time.

MATERIAL: BPBM 54386, 79775, 79788, 94314, 94330–2, 94342, 94351, 94363, 94367, 94378, 94386, 94389, 94397–9, 94408, 94414, 95330, 95339, 95348, 95386, 95418, 95466–9; NMNZ M.208803, 232925, 282386, 282512, 282561, 282590, 282617, 282641, 282665, 282700, 282735, 282765, 282810, 282862, 282887,

282913, 282984, 283008, 283052, 283082, 283138, 283164, 283192, 283221, 283292.

SITES: 2, 6, 8–11, 13, 15, 18, 20, 23A, 23B, 24, 26, 27, 29, 30, 32–34, 35A, 35B, 36B.

REMARKS: Fossil shells of *Tornatellides oblongus* were present in ground soils and paleosols on the coastal plain of southern and western Rarotonga but were scarce elsewhere around the island. This species was reported as plentiful by Garrett (1881), and is common in BPBM collections made on Rarotonga in the 1920s. In 2005–07, the modern population was widely distributed in coastal habitats around Rarotonga, and on Motutapu. Snails were found on the ground among fallen leaves and dead wood in forest and shrubland remnants, and in highly modified, open, anthropogenic habitats, including residential gardens and horticultural plots.

Family VERTIGINIDAE

***Costigo saparuana* (Boettger, 1891)**

Vertigo (*Costigo*) *saparuana* Boettger, 1891: 270, pl. 3, figs 12, 12a [Saparua, Moluccas Islands].

Costigo saparuana.– Pilsbry & Cooke, 1918–20: 366, pl. 31, fig. 12; Benthem Jutting, 1953: 301; Schileyko, 1998: fig. 180; Vermeulen & Raven, 1998: 273, fig. 2.

Gastrocopta sp. a Craig, 1995: table 5.3 (in part).

DISTRIBUTION: Indonesia – Moluccas Islands (Saparua) and Tanimbar group (Boettger 1891; Benthem Jutting 1953; Vermeulen & Raven 1998); Cook Islands – Rarotonga, Ātiu and Mangaia; Niue (Brook, unpub. data). *Costigo saparuana*, which is the type species of this genus, is probably native to Indonesian islands on the eastern margins of the Banda Sea, and has not previously been recorded from the Pacific region. The populations in the Cook Islands and Niue are inferred to be of anthropogenic origin; the presence of rare fossil shells in ground soils on Rarotonga (below) and Niue (Brook, unpub. data), suggests *C. saparuana* was introduced to both of these islands in prehistoric time.

MATERIAL: NMNZ M.282459, 282478, 282835, 283056. **SITES:** 21, 29.

REMARKS: The Cook Islands shells are slightly larger (shell height 2.25–2.50 mm) than the type material of *Costigo saparuana*, but otherwise closely match the description and illustrations of this species (Pilsbry & Cooke 1918–20: 366; Schileyko 1998: fig. 30). *Costigo saparuana* was extremely rare in the fossil fauna of Rarotonga, with a single shell found in a sandy ground soil at Rutaki (site 29). This

species is not represented in BPBM collections made on Rarotonga in the early 1900s, but rare fresh, empty shells are present in collections made in lower- to mid-elevation hill forest in the upper Avatiu Valley in 1994 (i.e. NMNZ M.282459, 282478), and in 2005–07 a single fresh, empty shell was found in forest litter on Oneroa (site 21).

***Gastrocopta pediculus* (Shuttleworth, 1852)**

Pupa pediculus Shuttleworth, 1852: 296 [Marquesas Islands and Tahiti]; Neubert & Gosteli, 2003: 42, pl. 3, fig. 5.

Vertigo pediculus.– Garrett, 1881: 400.

Gastrocopta pediculus.– Pilsbry, 1917: 145, pl. 25, figs 1–3, 5–8, 12–15, pl. 26, fig. 1; Craig, 1995: 108, fig. 6–5f.

DISTRIBUTION: Widely distributed among tropical Pacific islands; probably native to Indonesia and the tropical western Pacific (Garrett 1881, 1884, 1887; 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). Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Ma‘uke, Miti‘āro, Mangaia, Palmerston, Nassau, Penrhyn (Garrett 1881; Allen & Christensen 1992; Craig 1995; Allen 1997, 1998; Walter 1998; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ). *Gastrocopta pediculus* is thought to have been dispersed eastwards among central and eastern Pacific islands by humans in prehistoric time (e.g. Pilsbry 1916–18; Kirch 1973; Christensen & Kirch 1981; Preece 1998). It was present on at least some of the southern Cook Islands well before European contact, as indicated by fossil shells in archaeological sites on Aitutaki and Ma‘uke dating from the thirteenth and fourteenth centuries, respectively (Allen 1997, 1998; Walter 1998; Allen & Wallace 2007).

MATERIAL: BPBM 8586; NMNZ M.282384, 282400, 282411, 282421, 282489, 282513, 282535, 282562, 282591, 282618, 282642, 282666, 282701, 282736, 282766, 282790, 282811, 282832, 282851, 282863, 282888, 282914, 282958, 282985, 283009, 283029, 283053, 283083, 283112, 283139, 283165, 283193, 283222, 283251, 283268, 283293.

SITES: 1–3, 6, 8–11, 13, 15, 18–22, 23A, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of this species were widely distributed in ground soils and paleosols on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets. The species was recorded by Garrett (1881), but is not represented in BPBM collections made on Rarotonga in the 1920s. In

2005–07, the modern population had a scattered distribution on Rarotonga in coastal shrubland and forest remnants, and in highly modified, open, anthropogenic habitats, and on Motutapu and Oneroa islets in forest and shrubland.

***Gastrocopta servilis* (Gould, 1843)**

Pupa servilis Gould, 1843: 16, fig. 14 [Cuba].

Pupa lyonsiana Ancey, 1892: 713 [O‘ahu, Hawaiian Islands].

Gastrocopta servilis.– Pilsbry, 1916: 70, pl. 14, figs 4–7.

Gastrocopta lyonsiana.– Pilsbry, 1917: 141, pl. 24, figs 1–4.

Gastrocopta servilis.– Solem, 1960: 8.

Gastrocopta cf. lyonsiana.– Craig, 1995: 108, fig. 6–5e.

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; Kirch *et al.* 2009). Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Miti‘āro, Mangaia, Penrhyn (Craig 1995; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ). This species was evidently widely distributed in the Pacific by the early 1900s. The earliest published records are from New Guinea (1883 – Solem 1989); O‘ahu, Hawai‘i (1892 – Solem 1989; Cowie 1998b), the Philippines (1893 – Solem 1989); New Caledonia (1928 – Solem 1964), and Makatea, Tuamotu Islands (1930 – Cooke 1934). However, collections in the BPBM indicate that this species was also present on Ua Huka, Marquesas Islands, by 1921 (BPBM 54322); Fanning Island/Tabuaeran and Christmas Island/Kiritimati, Line Islands, by 1924 (BPBM 77777, 79479); Hull Island/Orona, Kiribati, by 1924 (BPBM 77284, 77299); and Guam and Saipan, Marianas, by 1923–25 (BPBM 75176, 82589, 82590). In the Cook Islands, *Gastrocopta servilis* was present on Manuae by c. 1900 (NMNZ M.232893); Rarotonga by 1923 (below); Penrhyn by 1924 (BPBM 79506, 79518, 79529); Ātiu by 1929 (BPBM 94960, 94999, 95018–9); and Mangaia by 1929 (BPBM 97456, 97515, 97601).

MATERIAL: BPBM 54383, 94394; NMNZ M.282385, 282433, 282490, 282514, 282536, 282563, 282577, 282592, 282619, 282643, 282667, 282702, 282737, 282864, 282915, 282959, 282986, 283010, 283030, 283054, 283113, 283140, 283166, 283194, 283223, 283269.

SITES: 1–3, 6–11, 13, 15, 23A, 24–29, 31–34, 35A, 36A.

REMARKS: This species is not represented in fossil assemblages from ground soils and paleosols on the coastal plain, and was not recorded by Garrett (1881). However, collections in the BPBM indicate that it had become

established on Rarotonga by 1923 (BPBM 54383). In 2005–07, *Gastrocopta servilis* was widely distributed around the coastal plain in shrubland and forest remnants, and in highly modified, open, anthropogenic habitats. It was present also in forest on Oneroa.

Genus *Nesopupa* Pilsbry, 1900

Nesopupa armata (Pease, 1871)

Vertigo armata Pease, 1871: 461 [Borabora, Society Islands]; Johnson, 1994: 7.

Vertigo tantilla.—Garrett, 1881: 400 (in part); Garrett, 1884: 84 (in part).

Nesopupa armata.—Pilsbry & Cooke, 1920: 327, pl. 30, figs 9, 12, 13; Gargominy, 2008: 535, fig. 6D.

Gastrocopta sp. a Craig, 1995: table 5.3 (in part), fig. 6.5h.

DISTRIBUTION: Southeastern Polynesia. Presently known from Borabora, Society Islands (Garrett 1881; Pilsbry & Cooke 1918–20); Rarotonga, Aitutaki, Ātiu, Miti'āro and Mangaia, Cook Islands; and Niue (Brook *et al.* 2010; Brook, unpub. data). *Pupa tantilla* var. *tongana* Boettger, 1881, which was described from Tongatapu, Tonga, is probably a junior synonym of *Nesopupa armata*, based on examinations of an image of the lectotype from the SMF (SMF 1803) and a syntype from the ZMB (ZMB 111982). If this is correct, the distribution of *N. armata* extends at least as far west as Tonga.

MATERIAL: BPBM 54384, 79628–9, 79781; NMNZ M.282401, 282477, 282491, 282515, 282564, 282593, 282620, 282644, 282767, 282791, 282812, 282833, 282865, 282889, 282939, 282960, 282987, 283011, 283031, 283055, 283084, 283167, 283195, 283224, 283252, 283294.

SITES: 1, 2, 6, 8, 9, 10, 18–21, 23A, 23B, 24–30, 33, 34, 35A, 35B, 36B.

REMARKS: *Nesopupa armata* had a scattered fossil distribution in ground soils and paleosols around the coastal plain of Rarotonga. In 2005–07, the modern population was sparsely distributed in forest and shrubland remnants and relict broadleaved groves on the coastal plain, and was present in forest on Motutapu and Oneroa islets. The inland distribution of this species was not surveyed during the present study, but collections made in 1994 (NMNZ) indicate that it occurred in forest to at least 125 m elevation.

Nesopupa dentifera (Pease, 1871)

Vertigo dentifera Pease, 1871: 462, 474 [Aitutaki, Cook Islands – Garrett 1881: 401]; Johnson, 1994: 11.

Vertigo tantilla.—Garrett, 1881: 400 (in part).

Nesopupa dentifera.—Pilsbry & Cooke, 1920: 329, pl. 30, fig. 14; Gargominy, 2008: 535, fig. 6A.

Gastrocopta sp. a Craig, 1995: table 5.3 (in part).

DISTRIBUTION: Presently known from the Cook Islands (Rarotonga, Aitutaki, Ātiu, Miti'āro) only (Garrett 1881; Pilsbry & Cooke 1918–20; Brook *et al.* 2010; Brook, unpub. data), but is possibly more widely distributed in Polynesia.

MATERIAL: NMNZ M.282402, 282834, 283225, 283253. SITES: 21, 35A, 35B.

REMARKS: Fossil shells of this species were present in a ground soil on Oneroa and a paleosol at Pokoinu, and empty modern shells were also found in forest remnants at these two locations in 2005–07.

Nesopupa pleurophora (Shuttleworth, 1852)

Pupa pleurophora Shuttleworth, 1852: 296 [Marquesas Islands and Tahiti]; Neubert & Gosteli, 2003: 44, pl. 3, fig. 6.

Nesopupa pleurophora.—Pilsbry & Cooke, 1920: 326, pl. 30, figs 5, 6; Gargominy, 2008: fig. 6C.

DISTRIBUTION: Marquesas Islands; Society Islands (Tahiti); Pitcairn Islands (Henderson, Pitcairn); Cook Islands (Rarotonga); and Niue (Shuttleworth 1852; Preece 1995; Brook, unpub. data).

MATERIAL: NMNZ M.282703.

SITE: 13.

REMARKS: Two fossil shells found in a sandy ground soil at a site near Ngatangia, southeastern Rarotonga, match descriptions and illustrations of this widespread Polynesian species (Pilsbry & Cooke 1918–20). This is the first and only record of *Nesopupa pleurophora* from Rarotonga. This species evidently had a highly restricted distribution on the coastal plain, and the absence of modern records indicates it has probably died out there. Whether or not it is still extant further inland on this island is unknown.

Nesopupa rarotonga new species

(Fig. 4B)

DESCRIPTION: Shell minute, 1.45–1.80 mm high, dextral, ovate, higher than wide (height/width ratio 1.25–1.60), aperture 0.56–0.80 mm high, spire 1.20–1.75 times as high as aperture, umbilicate. Colour yellowish brown. Whorls 3.8–4.25, moderately convex, suture deeply impressed. Protoconch of 1.3–1.5 whorls (0.50–0.55 mm wide), smooth, without visible sculpture; teleoconch whorls densely and minutely pitted, with irregularly spaced,

oblique, narrow, axial riblets (commonly worn off), and very fine growth lines in interstices. Aperture subrhomboidal, prosocline, lip slightly reflexed and moderately thickened within, shallow sinus above periphery on the outer margin. Apertural processes consist of a small, curved, angular lamella; a strong, thick, curved, parietal lamella; a very small, recessed, infraparietal lamella; a short, thick, curved, columellar lamella; a very small subcolumellar lamella rarely present; subequal, small, lower and upper palatal lamellae, the former more deeply recessed, basal in position; and generally a very small interpalatal. All except the infraparietal and subcolumellar are visible in frontal view, but only the apertural lamella reaches the apertural edge. Umbilicus tiny.

TYPE MATERIAL: Holotype NMNZ M.290125 and paratypes M.290127 (10), BPBM 274764 (3): Cook Islands, Rarotonga, Matavera, fossils in sandy coral rubble (21°13.236'S, 159°44.014'W), 22 Sep. 2005.

OTHER MATERIAL: Rarotonga – NMNZ M.282492, 282516, 282537, 282645, 282681, 282738, 282792, 282813, 282890, 283295, 283665; Ātiu – NMNZ M.290811; Miti'āro – NMNZ M.282181, 282199, 282235, 282291, 282342, 282365.

SITES: 1–3, 10–12, 15, 19, 20, 23B, 36B.

DISTRIBUTION: Cook Islands – Rarotonga, Ātiu, Miti'āro.

REMARKS: This species is of similar size and form to the Samoan *Nesopupa goddefroyi* (Boettger, 1881), but the latter has a more conical spire, and stronger palatal lamellae. Fossil shells of *Nesopupa rarotonga* n.sp. were present in ground soils and paleosols around the northern and eastern coasts of Rarotonga, and on Motutapu. This species was not recorded by Garrett (1881), and is not represented in later collections from Rarotonga in the BPBM and FMNH. No live snails were found on Rarotonga in 2005–07, but rare fresh, empty shells were present in forest remnants and relict broadleaved groves at Matavera (site 10), Ngatangia (site 15), and on Motutapu islet (sites 19, 20), so it is possible that a few small colonies were still extant. The lack of previous collections is probably attributable to the scarcity and very small size of this species.

***Pupisoma orcula* (Benson, 1850)**

Helix orcula Benson, 1850: 251 [India].

Pupisoma orcula.– Pilsbry, 1920: 31, pl. 2, figs 1–5.

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). Southern Cook Islands – Rarotonga,

Aitutaki, Ātiu, Ma'uke, Miti'āro, Mangaia (Brook *et al.* 2010; Brook, unpub. data; BPBM). *Pupisoma orcula* is thought to have been introduced to some Pacific islands after European contact (e.g. Cooke 1934; Cowie 1998b), but it was apparently first introduced to Polynesia in prehistoric time. Preece (1998) reported a tentative identification of this species from a seventeenth-century occupation horizon on Henderson Island in southeastern Polynesia, and it is present in prehistoric occupation horizons on Aitutaki (Brook, unpub. data). There is also a possible prehistoric record from O'ahu, Hawaiian Islands (Pilsbry 1922–26: 228).

MATERIAL: NMNZ M.282594, 282793, 282836, 283057, 283085, 283226.

SITES: 8, 19, 21, 29, 30, 35A.

REMARKS: A single fossil shell was found in a sandy ground soil at Rutaki (site 29). The species was not recorded by Garrett (1881), and is not represented in later collections from Rarotonga in the BPBM, FMNH or NMNZ. In 2005–07, *Pupisoma orcula* was present in a few coastal forest remnants on Rarotonga, and on Motutapu and Oneroa islets. Snails were arboreal, living on the underside of leaves of young coconut palms, and on the trunks and branches of broadleaved trees and shrubs. The fossil shell was slightly taller and proportionately narrower than the modern shells (i.e. height/width ratios of 1.11 and 0.89–0.96, respectively). Whether these morphological differences were ecophenotypic or genetic (i.e. possibly resulting from more than one introduction of this species to Rarotonga) is unknown.

Family FERUSSACIIDAE

***Cecilioides (Geostilbia) aperta* (Swainson, 1840)**

Achatina (Macrospira) aperta Swainson, 1840: 335, fig. 97e, f.

Cecilioides (Geostilbia) aperta.– Pilsbry, 1946, fig. 89b; Solem, 1964: 134.

Cecilioides sp. Allen & Christensen, 1992: 494.

Cecilioides aperta.– Cowie 1997: 19.

DISTRIBUTION: Reportedly native to the Caribbean, but with a wide tropical synanthropic distribution (Pilsbry 1946; Solem 1964), including published records from the Hawaiian Islands (Cowie 1997, 1998b, 2000, 2001b), New Caledonia (Solem 1964), and Guam (B.D. Smith 1992 *in* Cowie 2000). In the Cook Islands, it is present on Rarotonga, Aitutaki and Mangaia (Allen & Christensen 1992; Brook, unpub. data). The earliest Pacific records of this species are from New Caledonia (1867 – Solem 1964) and Hawai'i (1892 – Cowie

1998b). Collections in the BPBM indicate that it was present on Guam, Marianas, by 1923 (BPBM 75207); Hull Island/Orona, Kiribati, by 1924 (BPBM 77282); Mangareva, Gambier Islands, by 1934 (BPBM 136638); Truk/Chuuk, Federated States of Micronesia, by 1935 (BPBM 153227); and Ovalau, Fiji, by 1938 (BPBM 178291).

MATERIAL: NMNZ M.282517, 282739, 282891, 282916, 283032, 283058, 283114, 283141, 283168, 283196, 283270, 283296.

SITES: 2, 15, 23B, 24, 28, 29, 31–34, 36A, 36B.

REMARKS: This species was not recorded by Garrett (1881), and is not represented in later collections from Rarotonga in the BPBM or FMNH. In 2005–07, empty modern shells of *Cecilioides aperta* had a scattered distribution in sandy soils and coral rubble on the coastal plain around Rarotonga. This species was evidently at least partly subterranean in habit, with fresh, empty shells present locally to depths of 0.6 m below the ground surface (e.g. site 36B).

Family SUBULINIDAE

Allopeas clavulinum (Potiez & Michaud, 1838)

Bulimus clavulinus Potiez & Michaud, 1838: 136, pl. 14, figs 9, 10 [Réunion, Mascarene Islands].

Opeas clavulinum.—Pilsbry, 1906: 135, pl. 23, figs 17, 21, 22.

Lamellaxis gracilis.—Craig, 1995: table 5–3 (in part).

Allopeas clavulinum.—Cowie, 1998a: 56.

DISTRIBUTION: Probably native to Asia, where it locally has a pre-human fossil record (e.g. Marui *et al.* 2004), but with a wide tropical synanthropic distribution, including the Mascarene Islands, Australia, Japan and many Pacific islands (Pilsbry 1906–07; Cooke 1934; Solem 1978, 1989; Preece 1995; Cowie 1997, 1998b, 2000, 2001b; Kirch *et al.* 2009). In the Cook Islands, it is known from Rarotonga, Aitutaki, Ātiu, Miti'āro and Mangaia (Brook *et al.* 2010; Brook, unpub. data). This species was widely distributed in the Pacific by the early 1900s. The earliest published records are from Hawai'i (1900 – Cowie 1998b) and Makatea (1932 – Cooke 1934), but collections in the BPBM indicate that it was also present on Rapa, Austral Islands, by 1921 (BPBM 53191, 53193, 53250, 53262, 53267); Upolu, Samoa, by 1923 (BPBM 54369); Viti Levu, Fiji, by 1924 (BPBM 79651); Tahiti, Moorea and Borabora, Society Islands, by 1925–26 (BPBM 79584, 79586, 79607, 79830); Rarotonga, Cook Islands, by 1925 (below); and Tongatapu, Tonga, by 1928 (BPBM 87767, 87781, 87806).

MATERIAL: BPBM 79776; NMNZ M.282441, 282468, 282538, 282595, 282682, 282723, 282768, 282961, 283086, 283142, 283169, 283227, 283317, 283320, 283347, 283359, 283440.

SITES: 3, 8, 12, 14, 18, 25, 30, 32, 33, 35A.

REMARKS: This species is not represented in fossil assemblages and was not recorded by Garrett (1881), but was established near Avarua by 1925 (BPBM 79776). In 2005–07, *Allopeas clavulinum* was present in forest on Motutapu, and had a scattered distribution in forest remnants and highly modified, open, anthropogenic habitats on the coastal plain of Rarotonga. It was also widely distributed in disturbed forest, slope forest and cloud forest up to 650 m elevation in the interior of the island (Brook, pers. obs.).

Allopeas gracile (Hutton, 1834)

Bulimus gracile Hutton, 1834: 84, 93 [India].

Bulimus opananus Pfeiffer, 1846a: 34 [Rapa, Austral Islands].

Stenogyra tuckeri.—Garrett, 1881: 393 (not Pfeiffer, 1846).

Opeas gracile.—Pilsbry, 1906: 125, pl. 18, figs 3–6, pl. 22, fig. 4, pl. 23, figs 23–25, pl. 24, figs 40–41.

Opeas opananum.—Pilsbry, 1906: 183, pl. 22, figs 1–3, 12, pl. 24, fig. 39.

Lamellaxis gracilis.—Solem, 1978: 43; Solem, 1989: 521, figs 117–20; Craig, 1995: 112, fig. 6–6b, table 5–3 (in part).

Allopeas gracile.—Cowie *et al.*, 1995: 141; Cowie, 1997: 34; Cowie, 1998a: 56.

DISTRIBUTION: *Allopeas gracile* is probably native to Asia but has a very wide tropical synanthropic distribution that includes many Pacific islands (e.g. Pilsbry 1906–07; Cooke 1934; Solem 1964; Preece 1995; Cowie 1997, 1998a, 2000, 2001b; Boyko & Cordeiro 2001). In the Cook Islands, it is present on Rarotonga, Aitutaki, Manuae, Ātiu, Ma'uke, Miti'āro, Mangaia, Palmerston, Nassau, Pukapuka and Penrhyn (Garrett 1881; Allen & Christensen 1992; Craig 1995; Allen 1997, 1998; Walter 1998; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ). This species was apparently widely distributed throughout the Pacific in pre-historic time, well before European contact (e.g. Kirch 1973, 1993; Christensen & Kirch 1981, 1986; Hunt 1981; Rollett 1992; Orliac 1997). On Aitutaki and Ma'uke in the southern Cook Islands, the earliest recorded shells in archaeological sites date from the thirteenth and fourteenth centuries, respectively (Allen 1997, 1998; Walter 1998; Allen & Wallace 2007).

MATERIAL: BPBM 79790, 94401; NMNZ M.232895, 282493, 282518, 282539, 282621, 282646, 282704,

282740, 282769, 282794, 282814, 282837, 282866, 282892, 282917, 282962, 282988, 283012, 283033, 283059, 283115, 283143, 283170, 283197, 283228, 283254, 283271, 283297.

SITES: 1–3, 6, 9, 10, 13, 15, 18–21, 23A, 23B, 24–29, 31–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of *Allopeas gracile* were widely distributed and locally common in ground soils and paleosols on the coastal plain around Rarotonga, and were also present in soils on Motutapu and Oneroa islets. Garrett (1881) recorded *A. gracile* from Rarotonga but made no comment on its local distribution or abundance. The BPBM contains two collections only from the 1920s, which suggests that the species was rare at that time. In 2005–07, fresh, empty shells were relatively widely distributed albeit scarce on the coastal plain, but no live snails were found. This suggests that the population on Rarotonga, in common with those on many other Pacific islands, was in decline (e.g. Solem 1989: 522–23; Cowie 2000: 152; 2001b: 133).

Allopeas micra (d'Orbigny, 1835)

Helix micra d'Orbigny, 1835: 9 [Chilon, Bolivia].

Opeas micra.– Pilsbry, 1906: 193, pl. 27, figs 49, 56–57.

Lamellaxis (Allopeas) micra.– Solem, 1964: 131.

Lamellaxis gracilis.– Craig 1995: table 5–3 (in part).

DISTRIBUTION: Native to central and southern America and the Caribbean (Pilsbry 1906–07). In the Pacific, adventive populations are known from New Caledonia, Samoa, Niue, and the Cook, Society, Tuamotu, Line and Marquesas islands (Solem 1964; Cowie 2001a,b; Brook, unpub. data; BPBM). In the Cook Islands, the species is present on Rarotonga, Mangaia, Miti'āro and Rakahanga (Brook *et al.* 2010; BPBM). The earliest published records from the Pacific are from New Caledonia (1928 – Solem 1964) and Ofu, Samoa (1998 – Cowie 2001a), but collections in the BPBM indicate that this species was widely distributed in Polynesia by the 1920s. It was present on Tahiti by 1925 (BPBM 79564–6, 79598); Nuku Hiva, Marquesas Islands, by 1929 (BPBM 96192–6); Makatea, Tuamotu Islands, by 1930–32 (BPBM 97719, 115732, 115755, 115766); and Flint Island, Line Islands, by 1934 (BPBM 152567–8). In the Cook Islands, *Allopeas micra* was present on Rarotonga, Mangaia and Rakahanga by 1929 (BPBM 95331, 95369, 95419, 97446, 97451, 95473).

MATERIAL: BPBM 95331, 95369, 95419; NMNZ M.282442, 282451, 282494, 282622, 282705, 282770, 282868, 282918, 283060, 283116, 283144, 283171,

283198, 283229, 283272, 283668, 287366.

SITES: 1, 9, 13, 18, 23A, 24, 29–34, 35A, 36A.

REMARKS: *Allopeas micra* is not represented in fossil assemblages and was not recorded by Garrett (1881), but was present near Tupapa, Ngatipa and Nikao by 1929 (BPBM). In 2005–07, it was widely distributed but generally scarce on the Rarotongan coastal plain.

Opeas hannense (Rang, 1831)

Helix hannensis Rang, 1831: 41, pl. 3, fig. 8 [Cap Vert, Senegal].

Opeas hannensis.– Pilsbry, 1906: 141, pl. 15, fig. 59.

Opeas goodalli.– Pilsbry, 1906: 200, pl. 28, figs 72–74.

Opeas pumilum.– Solem, 1959: 118; Solem, 1978: 43; Christensen & Kirch, 1981: 82; Solem, 1989: 524; Preece, 1995: 294.

Opeas hannense.– Proschwitz, 1994: 184; Cowie, 1997: 35; Cowie, 1998a: 57; Cowie, 2000: 153.

Lamellaxis gracilis.– Craig 1995: table 5–3 (in part).

DISTRIBUTION: Probably native to the American tropics (Pilsbry 1906–07), with a wide tropical synanthropic distribution that includes many Pacific islands (Solem 1959, 1978, 1989; Christensen & Kirch 1981; Preece 1995; Cowie 1997, 1998a, 2000, 2001b). Cook Islands – Rarotonga, Aitutaki, Ātiu, Miti'āro, Mangaia, Nassau, Penrhyn (Brook, unpub. data; BPBM). *Opeas hannense* was probably spread through the Pacific after European contact, and was widely distributed by the early 1900s. The earliest published record is from Hawai'i (present by 1906) (Pilsbry 1906–07: 183 – as *Opeas goodalli*; Cowie 1998b), but the BPBM has material collected by Garrett on the Gambier Islands in the mid- to late 1800s (BPBM 3268). *Opeas hannense* was present on Palmyra Atoll, Line Islands, by 1913 (BPBM 52305); Rapa and Raivavae, Austral Islands, by 1921–22 (BPBM 53190, 53261, 53328, 53364, 53375); Washington Island/Teraina and Fanning Island/Tabuaeran, Line Islands, by 1924 (BPBM 79434, 79435); Tahiti and Moorea, Society Islands, by 1925 (BPBM 79566, 79567, 79608–9); Tutuila, Samoa, by 1926 (BPBM 85448); Tongatapu, Tonga, by 1928 (BPBM 87805, 87815); Viti Levu, Fiji, by 1928 (BPBM 87964, 88530, 88571); Nuku Hiva, Marquesas Islands, by 1929 (BPBM 96226); and Makatea, Tuamotu Islands, by 1932 (BPBM 115757, 115828). In the Cook Islands, it was present on Nassau by 1924 (BPBM 77233, 77247, 77249); Penrhyn by 1924 (BPBM 79515, 79525); Ātiu by 1927 (BPBM 87413); and Mangaia by 1930 (BPBM 97647).

MATERIAL: AIM AK113728; NMNZ M.282423, 282434,

282519, 282540, 282565, 282578, 282596, 282623, 282647, 282668, 282683, 282706, 282724, 282741, 282771, 282795, 282815, 282838, 282852, 282867, 282893, 282919, 282963, 282989, 283013, 283034, 283061, 283117, 283172, 283199, 283230, 283273.

SITES: 2, 3, 7–15, 18–22, 23A, 23B, 24–29, 31, 33, 34, 35A, 36A.

REMARKS: This species was not recorded by Garrett (1881) and is not represented in the BPBM collections made on Rarotonga in the 1920s. However, there is one lot of *Opeas hannense* from Rarotonga in AIM (AK 113728); this was formerly part of the Charles Cooper collection, which was acquired by the Auckland Museum in 1929 (Powell 1932: 211). Collection details are not given, but this material may have been collected by Cheeseman in 1899 (see *Libera subcavernula*, below). In 2005–07, *O. hannense* was widely distributed and locally common in soils on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets, in shrubland and forest remnants, and in highly modified, open, anthropogenic habitats. Fresh, empty shells were present locally to depths of up to 0.25 m below the present ground surface (e.g. site 23B), which suggests that this species was partly subterranean in habit.

***Paropeas achatinaceum* (Pfeiffer, 1846)**

Bulimus achatinaceus Pfeiffer, 1846b: 82 [Java, Indonesia].

Opeas javanicum.—Pilsbry, 1906: 138, pl. 12, figs 14, 16, pl. 16, figs 81, 88, pl. 22, fig. 9.

Prosopias javanicum.—Cooke, 1934: 6.

Paropeas achatinaceum.—Naggs, 1994: 17.

Lamellaxis gracilis.—Craig 1995: table 5–3 (in part).

DISTRIBUTION: Thought to be native to Southeast Asia, with a wide synanthropic distribution among tropical Pacific islands (Pilsbry 1906–07; Solem 1978, 1989; Naggs 1994; Cowie 1997, 1998b, 2000, 2001b). The earliest published Pacific records were from Hawai'i (1904 – Cowie 1998b) and Makatea (1932 – Cooke 1934). Collections in the BPBM indicate that this species was present on Vava'u, Tonga, by 1923 (BPBM 54363); Tutuila and Upolu, Samoa, by 1923 (BPBM 54374, 75518); Viti Levu, Fiji, by 1924 (BPBM 77016, 77027, 87913); Tahiti, Society Islands, by 1925 (BPBM 79568); and Tongatapu, Tonga, by 1928 (BPBM 87814). Cook Islands – Rarotonga, Ātiu, Miti'āro, Mangaia (Brook *et al.* 2010; Brook, unpub. data).

MATERIAL: BPBM 206461; FMNH 144523, 144564–66, 144580, 144585, 144601, 144602, 144608, 144609, 144621, 144627, 144657, 144658, 144665, 144666,

144680; NMNZ M.211812, 282388, 282427, 282443, 282452, 282460, 282469, 282479, 282707, 282964, 283087, 283118, 283145, 283173, 283200, 283311, 283321, 283329, 283349, 283360, 283432, 283670.

SITES: 13, 25, 30–34.

REMARKS: This species was not recorded by Garrett (1881), and is not represented in collections made on Rarotonga in the 1920s (BPBM). It was first collected by Tailby, probably between 1943 and 1951 when he was Resident Commissioner to the Cook Islands, and definitely before 1957–58, when the material was registered at NMNZ (M. 211812). Collections made in the mid-1960s (BPBM, FMNH) indicate that *Paropeas achatinaceum* was widely distributed on this island by this time. In 2005–07, this species had a sparse distribution in highly modified, open habitats around much of the coastal plain, being most common in the southwest between Aroa and Arorangi. It was widely distributed and locally common in disturbed forest, slope forest and cloud forest up to 650 m elevation in the interior of the island (Brook, pers. obs.).

***Subulina octona* (Bruguière, 1789)**

Bulimus octonus Bruguière, 1789: 325 [Les Iles Antilles, Caribbean].

Subulina octona.—Pilsbry, 1906: 72, 222, pl. 12, figs 8, 9, pl. 39, figs 28–37, 39, 40; Craig, 1995: 101, fig. 6–3e.

DISTRIBUTION: Thought to be native to the American tropics, with a wide tropical synanthropic distribution that includes many Pacific islands (Pilsbry 1906–07; Cooke 1928, 1934; Reigle 1964; Solem 1964, 1978; Christensen & Kirch 1981; Preece 1995; Cowie 1997, 1998a, 1998b, 2000, 2001b). In the Cook Islands, it is present on Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro and Mangaia (Allen & Christensen 1992; Craig 1995; Brook *et al.* 2010; Brook, unpub. data; BPBM). The earliest published records from the Pacific were from New Caledonia (1887 or 1888, on plants imported from Réunion – Solem 1964), Vanuatu (1900 – Sykes 1902); Hawai'i (1903 – Cowie 1998b), and Makatea, Tuamotu Islands (1930 – Cooke 1934). Collections in the BPBM indicate that *Subulina octona* was present on Saipan and Guam, Marianas, by 1920 and 1923, respectively (BPBM 75135, 75205); Tutuila and Upolu, Samoa, by 1920 (BPBM 53537, 54396); Tongatapu and Vava'u, Tonga, by 1921 (BPBM 53522, 53527); Hiva Oa and Ua Huka, Marquesas Islands, by 1920 and 1921, respectively (BPBM 54333, 54337, 54340, 54324, 54335); Mangareva, Gambier Islands, by 1921 (BPBM 81664); Raivavae, Rimatara and

Rurutu, Austral Islands, by 1921–22 (BPBM 53363, 53392, 53478); Tahiti, Moorea, Borabora, Maupiti and Raiatea, Society Islands, by 1925–26 (BPBM 79569, 79610–12, 79829, 81732, 87190–3); and Viti Levu, Fiji, by 1928 (BPBM 87912). In the Cook Islands, this species was present on Rarotonga by 1923 (below), Aitutaki and Ma'uke by 1925 (BPBM 79766, 89727), Mangaia by 1926 (BPBM 86038), Ātiu by 1927 (BPBM 87415–6) and Miti'āro by 1929 (BPBM 95671, 97416).

MATERIAL: BPBM 54387–8, 79632, 79770, 79772, 79782–3, 79789, 79806, 94324, 94345, 94358, 94368, 94390, 94400, 95332, 95340, 95370, 95440, 206460; FMNH 144524–5, 144529, 144546, 144549, 144562–3, 144572, 144579, 144587, 144592, 144603–4, 144615–6, 144619, 144626, 144656, 144660–1, 144667, 144679, 144684, 152271; NMNZ M.282428, 282453, 282461, 282470, 282495, 282520, 282624, 282708, 282869, 282920, 282965, 282990, 283035, 283062, 283088, 283119, 283146, 283174, 283201, 283274, 283312, 283318, 283322, 283330, 283350, 283361, 283671.

SITES: 1, 2, 9, 13, 23A, 24–26, 28–34.

REMARKS: This species is not represented in fossil assemblages and was not recorded by Garrett (1881). It was first collected on Rarotonga in 1923 (BPBM 54387–8), and was widely distributed in coastal and inland areas in 1925–29 (BPBM) and 1964 (FMNH). In 2005–07, *Subulina octona* had a patchy distribution on the coastal plain, being most common around the southern and western coasts of Rarotonga, where it inhabited shrubland and forest remnants, and highly modified, open anthropogenic habitats. It was also widely distributed and locally common in disturbed forest, slope forest and cloud forest up to 650 m elevation in the interior of the island (Brook, unpub. data).

Family STREPTAXIDAE

Gulella (Huttonella) bicolor (Hutton, 1834)

Pupa bicolor Hutton, 1834: 86, 93 [India].

Gulella (Huttonella) bicolor.– Benthem Jutting, 1950: 504, figs 106, 107.

DISTRIBUTION: Possibly native to the Indian subcontinent (Naggs 1989), with a wide synanthropic distribution in the tropics that includes several Pacific islands (Clench 1964; Harry 1966; Naggs 1989; Solem 1989; Cowie 2000, 2001b). Cook Islands – Rarotonga (this study) and Aitutaki (Brook, unpub. data). Collections in the BPBM indicate that this species was present on Fanning Island/Tabuaeran, Line

Islands, by 1922 (BPBM 52312); Guam, Marianas, by 1923 (BPBM 75183); Viti Levu, Fiji, by 1926 (BPBM 92356); Tutuila, Samoa, by 1926 (BPBM 83584, 83594, 85126, 85177, 85178); Wallis Island/Uvea, Tonga, by 1932 (BPBM 115605); and Tau, Olosega and Upolu, Samoa, by 1936–37 (BPBM 171257, 171281, 173577, 174584, 174751).

MATERIAL: NMNZ M.282966, 283063, 283275.

SITES: 25, 29, 36A.

REMARKS: *Gulella bicolor* was not recorded by Garrett (1881) and is not represented in later collections from Rarotonga in the BPBM or FMNH. In 2005–07, rare weathered, empty modern shells were found in sandy and rubbly ground soils at sites at Titikaveka, Rutaki and Avatiu. This species was probably introduced to Rarotonga in the late 1800s or early 1900s, and on present evidence was never common. It appears to have died out on the coastal plain, but may be extant elsewhere on the island. *Gulella bicolor* is carnivorous, feeding on soft-bodied invertebrates, including other snails (Benthem Jutting 1950; Naggs 1989; Solem 1989). If it is still living on Rarotonga, it could therefore pose a threat to the native snail species on this island.

Streptostele (Tomostele) musaecola (Morelet, 1860)

Achatina musaecola Morelet, 1860: 190 [Guinea, West Africa].

Streptostele (Tomostele) musaecola.– Pilsbry, 1919: 191, pl. 21, fig. 11; Solem, 1989: 532.

Subulina sp. a. – Craig, 1995: 101, fig. 6–3f.

DISTRIBUTION: Native to West Africa, with a wide synanthropic distribution in the tropics. Adventive populations have been recorded from Vanuatu, Samoa, Society Islands, Central America, Bermuda, and several islands in the Caribbean (Solem 1989; Cowie 1998a, 2001a; Hausdorf & Bermúdez 2003). Cook Islands – Rarotonga, Aitutaki, Ātiu, Miti'āro, Mangaia (Craig 1995; Brook *et al.* 2010; Brook, unpub. data). This species was apparently introduced to the Pacific comparatively recently. It was present on Tahiti, Society Islands, by 1974 (Solem 1989); Tutuila, Samoa, by 1975 (Solem 1989); Moorea, Society Islands, by 1977 (FMNH 201055, 201112); Efate, Vanuatu, by 1984 (Solem 1989); and Rarotonga, Cook Islands, by 1994 (below).

MATERIAL: FLMNH UFM0419079; NMNZ M.282383, 282412, 282496, 282541, 282566, 282579, 282597, 282625, 282648, 282669, 282684, 282709, 282725, 282742, 282772, 282796, 282816, 282839, 282870, 282921, 282991, 283014, 283036, 283064, 283089, 283120, 283147, 283175, 283231, 283276, 283298, 283331.

SITES: 1, 3, 6–15, 18–21, 23A, 24, 26–33, 35A, 36A, 36B.

REMARKS: *Streptostele musaecola* was not recorded by Garrett (1881), and is not represented in later collections from Rarotonga in the BPBM or FMNH. It was first collected on Rarotonga in 1994, at a coastal site near Pokoinu, on Motutapu, and in the lower Avana Valley (FLMNH UFMO419079; NMNZ M.282383, 282412). It is thus likely that this species was introduced to Rarotonga sometime between the 1960s and early 1990s. In 2005–07, *S. musaecola* was widely distributed and locally common on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets, inhabiting shrubland and forest remnants, and highly modified, open, anthropogenic habitats. It was evidently partly subterranean in habit, as fresh, empty shells were present locally up to 0.6 m below the ground surface (e.g. site 36B). A few individuals were found in secondary forest and disturbed slope forest in the lower parts of some inland valleys, but the overall distribution of this species in the interior of Rarotonga is unknown. *Streptostele musaecola* is carnivorous, preying on soft-bodied invertebrates, and is therefore a potential threat to small native snail species on Rarotonga.

Family ENDODONTIDAE

Libera fratercula (Pease, 1867)

Helix sculptilis Pease, 1865a: 669 (not Bland, 1858) [Mangaia, Cook Islands – Garrett 1881: 392]; Johnson, 1994: 23.

Helix fratercula Pease, 1867: 104 (new name for *sculptilis* Pease, 1865).

Libera fratercula.– Garrett, 1881: 392; Solem, 1969: 10; Craig, 1995: 110, fig. 6–6d.

Libera fratercula fratercula Solem, 1976: 418, fig. 182e–f.

Libera fratercula rarotongensis Solem, 1976: 425 (in part), fig. 182a–d [Rarotonga].

NOMENCLATURE: Garrett (1881: 392) noted differences in shell size and colour pattern between populations of this species from Rarotonga, Ātiu and Mangaia. Solem (1976) thought that the populations from Mangaia, Ātiu, Ma'uke and two motu in Muri Lagoon on Rarotonga (i.e. Motutapu, Oneroa) were all representative of typical *Libera fratercula*, and included populations on the northeastern coast of Rarotonga in a new subspecies – *L.f. rarotongensis*. He differentiated the latter on the basis of larger shell size, the presence of fewer palatal barriers, and the common presence of a prominent columellar barrier. However, the morphological differences between Solem's subspecies are here not

considered taxonomically significant, and all the Rarotongan populations are reassigned to *L. fratercula* (Pease, 1867).

DISTRIBUTION: Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Ma'uke, Miti'āro, Mangaia (Garrett 1881; Solem 1976; Craig 1995; Walter 1998; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ).

MATERIAL: AIM AK118963; BMNH 1962705; BPBM 8584, 95356–60, 95362–68; FMNH 144556–8, 153372–4, 153376–9, 153393, 153418, 153421; NMNZ M.282391, 282394, 282497, 282521, 282542, 282550, 282552, 282567, 282580, 282598, 282626, 282649, 282670, 282685, 282710, 282726, 282743, 282773, 282797, 282817, 282840, 282853, 282871, 282894.

SITES: 1–15, 18–22, 23A, 23B.

REMARKS: Fossil shells of *Libera fratercula* were common in coral rubble and gravelly sand on the northeastern and eastern coasts of Rarotonga between Pue and Muri. In 2005–07, extant colonies were restricted to small remnants of native coastal shrubland and forest growing on coral rubble between Tupapa and Ngatangia, and on Motutapu and Oneroa islets; snails were present on the ground under coral rubble and fallen wood. The population on northeastern Rarotonga has evidently fragmented and declined substantially since the 1960s, when this part of the coast was still relatively undeveloped (below). The continued existence of the surviving colonies is contingent on the preservation of coastal shrubland and forest habitat remnants.

Libera subcavernula (Tryon, 1887)

Pityis cavernula Garrett, 1872: 226, pl. 19, fig. 16 (not Hombron & Jacquinot, 1852).

Libera cavernula.– Garrett, 1881: 392 (not Hombron & Jacquinot, 1852).

Helix (Libera) subcavernula Tryon, 1887: 70, pl. 13, figs 67–69 [Rarotonga, Cook Islands].

Libera subcavernula.– Solem, 1976: 426, fig. 184a–c.

Libera fratercula rarotongensis Solem, 1976: 425 (in part).

DISTRIBUTION: Cook Islands – Rarotonga (Garrett 1872, 1881; Solem 1976).

MATERIAL: AIM AK118767–69, 118772, 118773, 118964, 118965; BPBM 2240, 115348, 167429, 189937; FMNH 144514–5; NMNZ M.208839, 232911, 232913, 232914, 282922, 282945, 282967, 282992, 283015, 283037, 283065, 283090, 283121, 283148, 283176, 283202, 283232, 283255, 283277, 283299, 283662, 283663, 283664, 283667.

SITES: 1, 2, 9, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of *Libera subcavernula* were abundant

in sandy and rubbly soils around the western and southern coast of Rarotonga between Avatiu and Akapua, and uncommon on the northeastern and eastern coast, where this species was locally sympatric with *Libera fratercula* (above; i.e. sites 1, 2, 9, 23B). Garrett (1872: 227; 1881: 392) did not report *L. subcavernula* from coastal habitats, but noted that this species was common in inland ravines on Rarotonga in 1869. Cheeseman collected a large number of live specimens in 1899 (AIM AK118767–69, 118964–65; NMNZ M.208839, 232913, 232914), indicating that *L. subcavernula* was still abundant at this time, but it is not represented at all in the extensive landsnail collections made in coastal and inland Rarotonga in the mid- to late 1920s (BPBM). NMNZ has one large lot (M.232911) of mostly worn but some relatively fresh shells of *L. subcavernula* obtained by Tailby, probably between 1943 and 1951; the presence of humic-stained sand in some shells indicates that they were derived from soils on the coastal plain. Material collected by Price in FMNH indicates that *L. subcavernula* was still extant and abundant at a single coastal site on the west side of Avatiu Harbour in November 1964 (FMNH 144514–5). This population, which was incorrectly identified as *Libera fratercula rarotongensis* by Solem (1976: 425–26), was reportedly living under dead leaves, among coral blocks, a few feet above high-tide level. This site has since been destroyed by wharf development, and the snail population is extinct. Price did not find *L. subcavernula* anywhere else on Rarotonga. In summary, museum records and Garrett's observations indicate that *L. subcavernula* had died out across most of the coastal plain by 1869, but survived locally until at least 1964; it evidently remained common in inland Rarotonga through the latter part of the nineteenth century but subsequently underwent rapid decline, and had become very rare or had died out inland by the 1920s. This species has not been found alive since 1964 and is probably now extinct.

Genus Minidonta Solem, 1976

Nine undescribed species of Endodontidae were found on the coastal plain of Rarotonga during the present study. Solem (1976) assigned morphologically similar taxa elsewhere in southeastern Polynesia to *Minidonta* and *Mautodontha* (*Garrettoconcha*). However, there do not appear to be any clear and consistent morphological criteria for distinguishing between these two taxa, with considerable overlap in terms of shell size (maximum diameters of *c.* 1.6–3.4 mm and 2.6–4.9 mm, respectively), umbilical width,

spire elevation, sculpture, and arrangement of apertural barriers. Further, it is likely that large- and small-shelled morphotypes arose independently on separate islands and archipelagos in Polynesia, and that both of these genera as defined by Solem (1976) may well be polyphyletic. The same probably applies to the larger, low-spired taxa that Solem (1976) assigned to *Mautodontha* (*s. str.*). The undescribed Rarotongan coastal endodontid species all have broadly similar shell morphologies, and in the absence of anatomical and genetic data, there are no compelling reasons for separating them into different genera. Maximum shell diameters of the species described below are in the range *c.* 1.3–3.6 mm, and all are arbitrarily assigned here to *Minidonta*. Two larger but closely related species from inland Rarotonga that were included in the genera *Mautodontha* (*Mautodontha*) and *Mautodontha* (*Garrettoconcha*) by Solem (1976), are provisionally reassigned here to *Minidonta* (Appendix 3).

Minidonta aroa new species

(Fig. 5A–C)

DESCRIPTION: Shell small, 2.5–3.10 mm diameter, wider than high (shell height/shell diameter ratio of 0.49–0.61), apex and early spire whorls slightly to moderately elevated (spire protrusion 10–22% of shell height), last whorl descending a little more rapidly, umbilicus narrow and constricted (16–23% of shell diameter). Whorls 4.6–5.25, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed. Some shells retain a faint colour pattern of irregularly spaced, narrow to wide, wavy, axial reddish-brown streaks, extending onto base. Protoconch *c.* 0.4–0.5 mm wide, sculptured with fine radial ribs. Teleoconch has very closely spaced, extremely fine, weakly sigmoidal radial ribs, with spiral microsculpture in interstices. Aperture subovate, simple, lip thin, thickened within, particularly on the lower margin. Three parietal barriers, blade-like lamellae, extending back about ¼ whorl, high, weakly thickened, rounded above, middle slightly closer to lower than to upper. No columellar lamella. Four palatal barriers, evenly spaced, lower two basal, third subperipheral, uppermost just above periphery; first is a low, rounded, lamellar ridge; second and third are higher, weakly thickened lamellar ridges, rounded above; fourth is a lower, thinner lamellar ridge.

TYPE MATERIAL: Holotype NMNZ M.290086 and paratypes M.290087 (12), BPBM 274756 (4): Cook Islands, Rarotonga, Aroa, fossils in sandy soil exposed in borrow pit (21°15.238'S, 159°48.923'W), 22 June 2007.

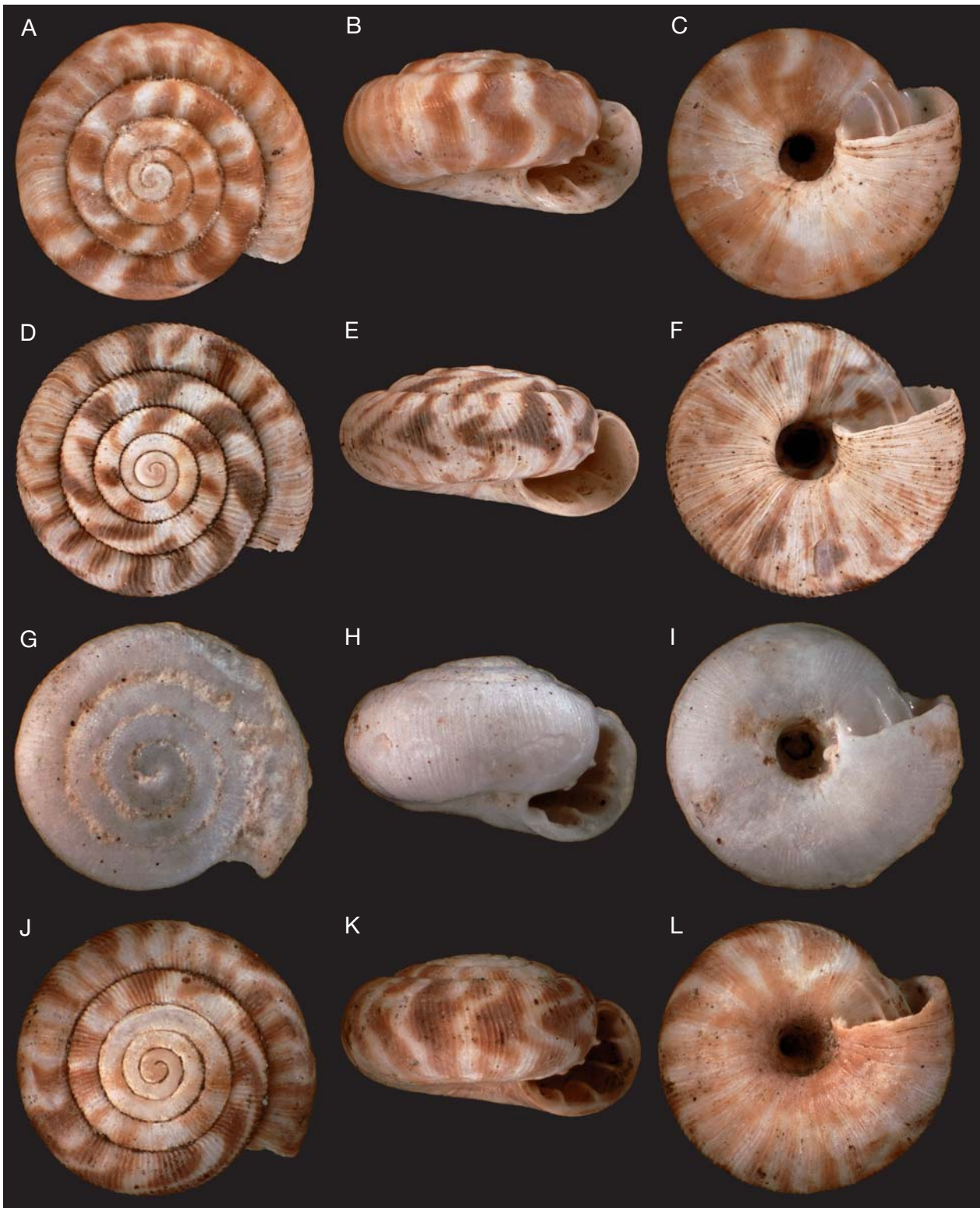


Fig. 5 Shells of *Minidonta* species. A–C, *Minidonta aroa* n.sp., Aroa, holotype, M.290086 (1.65 × 2.95 mm); D–F, *Minidonta arorangi* n.sp., Arorangi, holotype, M.290089 (1.80 × 3.60 mm); G–I, *Minidonta iota* n.sp., Aroa, holotype, M.283122 (0.90 × 1.45 mm); J–L, *Minidonta kavera* n.sp., Kavera, holotype, M.283151 (1.55 × 2.80 mm).

OTHER MATERIAL: NMNZ M.283123, 283149, 283204.
SITES: 31, 32, 34.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: The very fine, closely spaced radial sculpture on the teleoconch is diagnostic for this species. *Minidonta aroa* n.sp. is known only from fossil shells present in sandy soils on the coastal plain of southwestern Rarotonga, between Aroa and Arorangi, and is probably extinct.

Minidonta arorangi new species

(Fig. 5D–F)

DESCRIPTION: Shell small, 3.1–3.6 mm diameter, wider than high (shell height/shell diameter ratio of 0.45–0.53), apex and early spire whorls slightly to moderately elevated (spire protrusion 7–22% of shell height), last whorl descending a little more rapidly, umbilicus narrow and constricted (16–22% of shell diameter). Whorls 4.6–5.5, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed. Colour pattern of widely and irregularly spaced, narrow to wide, wavy, axial reddish-brown streaks, radial on spire, zigzag on sides and base. Protoconch *c.* 0.52–0.55 mm wide, sculptured with closely spaced, fine radial ribs. Teleoconch sculpture of closely spaced, low, narrow, rounded, weakly sigmoidal, radial ribs, *c.* 90–115 on last adult whorl; interstices about twice their width, with microsculpture of very fine radials and spirals. Aperture subovate, simple, lip thin, thickened within. Three parietal barriers, lower shortest, middle closer to lower than to upper, high, thickened, lamellar ridges, rounded above, extending back about ¼ whorl. No columellar barrier. Five palatal barriers: first a low, rounded ridge at baso-columellar margin; second and third basal, low, weakly thickened lamellar ridges; fourth subperipheral, a slightly higher, weakly thickened lamellar ridge; fifth supraparipheral, a lower, thinner lamellar ridge.

TYPE MATERIAL: Holotype NMNZ M.290089 and paratypes M.290090 (8), BPBM 274757 (3): Cook Islands, Rarotonga, Arorangi, fossils in sandy soil exposed in trench (21°13.429'S, 159°49.716'W), 18 June 2007.

OTHER MATERIAL: NMNZ M.283150, 283205, 290088.

SITES: 31, 32, 34.

DISTRIBUTION: Cook Islands–Rarotonga.

REMARKS: This species is most similar to *Minidonta rutaki* n.sp. (below), which occurred syntopically at Arorangi (site 34), but has a lower shell height/shell diameter ratio and more closely spaced ribs on the teleoconch, and lacks a columellar barrier. It is known only from fossil shells present

in sandy soils on the coastal plain between Aroa and Arorangi, southwestern Rarotonga, and is probably extinct.

Minidonta iota new species

(Fig. 5G–I)

DESCRIPTION: Shell minute, 1.3–1.5 mm diameter, wider than high (shell height/shell diameter ratio of 0.58–0.63), apex and early spire moderately and evenly elevated (spire protrusion 16–22% of shell height), last whorl descending a little more rapidly, umbilicus narrow and very constricted (17–19% of shell diameter). Whorls 3.6–4.0, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed. No colour pattern seen. Protoconch *c.* 0.35 mm wide; apical sculpture not seen. Teleoconch sculpture of very closely spaced, low, narrow, rounded, weakly sigmoidal radial ribs, wider than interstices. Aperture ovate, simple, lip thin, thickened within. Two parietal barriers, low lamellar ridges, thickened, rounded above. No columellar lamella. Four palatal barriers: first a low, rounded ridge at baso-columellar margin; second and third basal and subperipheral, respectively, weakly thickened lamellar ridges, rounded above; fourth supraparipheral, a lower, thinner lamellar ridge.

TYPE MATERIAL: Holotype NMNZ M.283122 and paratype M.290094 (1): Cook Islands, Rarotonga, Aroa, fossils in sandy soil exposed in borrow pit (21°15.238'S, 159°48.923'W), 22 June 2007. Additional paratypes NMNZ M.283092 (2), BPBM 274758 (1): Cook Islands, Rarotonga, Aroa, fossils in sandy ground soil (21°15.363'S, 159°48.810'W), 29 May 2006.

SITES: 30, 31.

DISTRIBUTION: Cook Islands–Rarotonga.

REMARKS: This species is distinguished by its minute size, to which the specific epithet refers. It is the smallest known member of the Endodontidae. *Minidonta iota* n.sp. is known only from a few poorly preserved fossil shells found in sandy soils on the coastal plain at Aroa, southwestern Rarotonga, and is probably extinct.

Minidonta kavera new species

(Fig. 5J–L)

DESCRIPTION: Shell small, 2.8–3.0 mm diameter, wider than high (shell height/shell diameter ratio of 0.54–0.57), apex and early spire whorls moderately and evenly elevated (spire protrusion 13–18% of shell height), last whorl descending a little more rapidly, umbilicus narrow and constricted (18–22% of shell diameter). Whorls 4.75–5.50, moderately rounded above, final whorl slightly flattened on

periphery and base, suture deeply impressed. Colour pattern of irregularly spaced, narrow to wide, wavy, axial reddish-brown streaks, extending onto base, sometimes zigzag on sides. Protoconch width and sculpture not determined. Teleoconch sculpture of closely spaced, low, narrow, rounded, weakly sigmoidal radial ribs (one specimen has 130 on last adult whorl), interstices less than twice width of ribs, with very fine radial and spiral microsculpture. Aperture subovate, simple, lip thin, thickened within. Three parietal barriers, middle slightly closer to lower than to upper, blade-like lamellae, extending back about $\frac{1}{4}$ whorl, high, weakly thickened, rounded above. No columellar barrier. Five palatal barriers, evenly spaced: first a low, rounded ridge at baso-columellar margin; second a basal, slightly higher, thickened, rounded lamellar ridge; third and fourth subperipheral, high, thickened lamellar ridges, rounded above; fifth a supraperipheral, lower, thinner lamellar ridge. TYPE MATERIAL: Holotype NMNZ M.283151: Cook Islands, Rarotonga, Kavera, fossil in sandy soil exposed in borrow pit (21°15.041'S, 159°49.112'W), 29 May 2006. Paratypes NMNZ M.283124 (3), BPBM 274759 (1): Cook Islands, Rarotonga, Aroa, fossils in sandy soil exposed in borrow pit (21°15.238'S, 159°48.923'W), 22 June 2007. OTHER MATERIAL: NMNZ M.283124, 283151. SITES: 31, 32.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species is most similar to the allopatric *Minidonta ngatangia* n.sp. (below), but is slightly larger, with finer teleoconch sculpture, a proportionately wider umbilicus, a slightly lower spire, and five rather than four primary palatal lamellae. It is known only from rare, poorly preserved fossil shells present in sandy soils on the coastal plain at Aroa and Kavera, southwestern Rarotonga, and is probably extinct.

Minidonta matavera new species

(Fig. 6A–C)

DESCRIPTION: Shell very small, 2.1–2.7 mm diameter, wider than high (shell height/shell diameter ratio of 0.57–0.63), apex and early spire whorls moderately and evenly elevated (spire protrusion 12–22% of shell height), last whorl descending a little more rapidly, umbilicus narrow and very constricted (13–17% of shell diameter). Whorls 4.8–5.4, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed. Unweathered shells have a ground colour of pale buff, with faint, irregularly spaced, wavy, pale yellowish-brown axial streaks, dying

out on base. Protoconch 0.5–0.6 mm wide, sculptured with closely spaced, fine radial ribs. Teleoconch sculpture of prominent, closely spaced, rounded, weakly sigmoidal radial ribs, c. 80–120 on last adult whorl, interstices generally less than twice their width, with very fine radial and spiral microsculpture. Aperture subovate, simple, lip thin, thickened within. Three major parietal barriers, narrow, blade-like lamellar ridges, middle slightly closer to lower than to upper, all of similar size, extending back approximately $\frac{1}{4}$ whorl. A shorter, accessory thread is sometimes present below the lowest primary parietal lamella. Columellar barrier a low, narrow, rounded ridge. Five major palatal barriers, lowest two are basal, third and fourth subperipheral, and uppermost peripheral, all are narrow and blade-like lamellar ridges, first and fifth are weakest. A short, low, accessory lamellar thread is commonly present between the first and second palatal lamellae.

TYPE MATERIAL: Holotype NMNZ M.290095 and paratypes M.290096 (18), BPBM 274760 (4): Cook Islands, Rarotonga, Matavera, coral rubble in *Barringtonia asiatica* grove (21°13.289'S, 159°43.997'W), 5 June 2006.

OTHER MATERIAL: NMNZ M.282599, 282650, 282686.

SITES: 8, 10, 12.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: The prominent, closely spaced teleoconch ribbing and presence of a columellar barrier distinguish *Minidonta matavera* n.sp. from other Rarotongan species of this genus. Fossil shells were common in sandy and rubbly soils on the northeastern coast of Rarotonga between Tupapa and Matavera. This species was probably extinct at Tupapa, but relatively fresh, empty shells were found in coastal forest remnants at Matavera in 2005–07 (sites 10, 12), suggesting the possibility that these populations were still extant.

Minidonta ngatangia new species

(Fig. 6D–F)

DESCRIPTION: Shell very small, 2.2–2.7 mm diameter, wider than high (shell height/shell diameter ratio of 0.56–0.65), apex and early spire whorls moderately and evenly elevated (spire protrusion 17–21% of shell height), last whorl descending a little more rapidly, umbilicus narrow and very constricted (10–18% of shell diameter). Whorls 4.7–5.0, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed, almost channelised. Some shells retain a colour pattern of irregularly spaced, narrow to wide, wavy, reddish-brown axial streaks, extending onto base. Protoconch c. 0.4–0.5 mm wide,

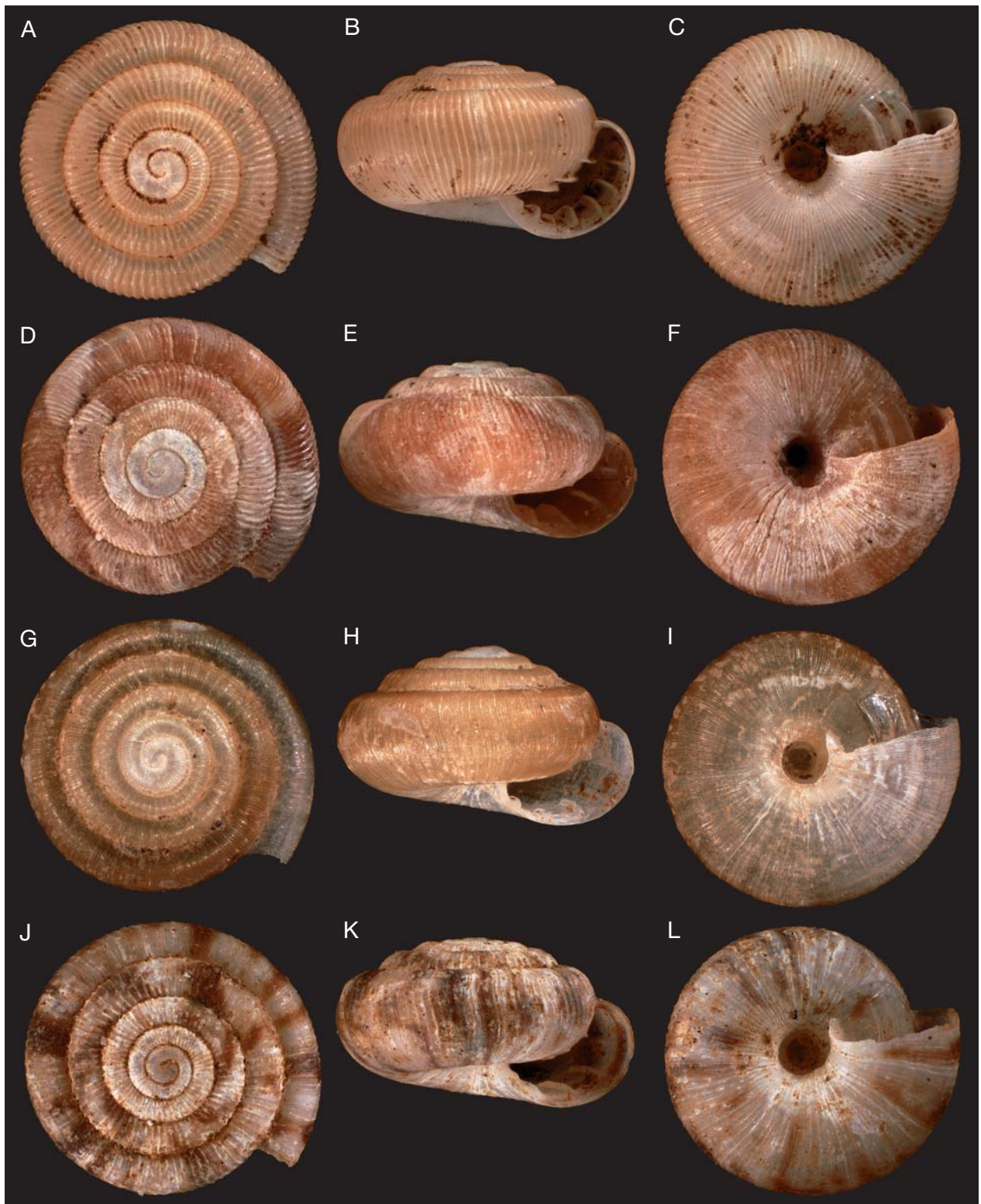


Fig. 6 Shells of *Minidonta* species. A–C, *Minidonta matavera* n.sp., Matavera, holotype, M.290095 (1.35×2.15 mm); D–F, *Minidonta ngatangia* n.sp., Muri, holotype, M.290103 (1.45×2.45 mm); G–I, *Minidonta pue* n.sp., Pue, holotype, M.290118 (1.45×2.40 mm); J–L, *Minidonta rutaki* n.sp., Rutaki, holotype, M.290136 (1.85×3.25 mm).

sculptured with closely spaced, fine radial ribs. Teleoconch sculpture of closely spaced, low, narrow, rounded, sigmoidal, radial ribs, *c.* 95–130 on last adult whorl; interstices slightly wider than ribs, with microsculpture of very fine radials and spirals. Aperture subovate, simple, lip thin, thickened within. Three parietal barriers, subequal and evenly spaced, high, thickened lamellar ridges, rounded above, extending back approximately $\frac{1}{4}$ whorl. No columellar barrier. Four palatal barriers, lowest two are basal, third subperipheral, and uppermost peripheral, second and third are high lamellar ridges, thickened and rounded above, first and fourth are lower and thinner ridges. A short, low, accessory lamellar ridge is rarely present between the first and second or second and third palatal lamellae.

TYPE MATERIAL: Holotype NMNZ M.290103 and paratypes M.290100 (19), BPBM 274761 (5): Cook Islands, Rarotonga, Muri, fossils in sandy paleosol exposed in coastal bank (21°15.600'S, 159°43.941'W), 29 Sep. 2005. Additional paratypes: Cook Islands, Rarotonga, Ngatangia, fossils in sandy ground soil, (21°14.078'S, 159°43.871'W), 9 June 2006, M.290105 (8).

OTHER MATERIAL: NMNZ M.282711, 282872, 282895, 282968.

SITES: 13, 23A, 23B, 25.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species differs from the parapatric *Minidonta matavera* n.sp. (above) in having a slightly smaller protoconch, more strongly sigmoidal axial sculpture on the teleoconch, fewer primary palatal lamellae, and lacking a columellar lamella. It is known only from fossil shells present in sandy soils around the southeastern coast of Rarotonga between Ngatangia and Titikaveka, and is probably extinct.

Minidonta pue new species

(Fig. 6G–I)

DESCRIPTION: Shell very small, 2.15–2.40 mm diameter, wider than high (shell height/shell diameter ratio of 0.57–0.64), apex and early spire whorls moderately and evenly elevated (spire protrusion 20–25% of shell height), last whorl descending a little more rapidly, umbilicus narrow and very constricted (13–19% of shell diameter). Whorls 4.5–4.9, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed. Unweathered shells are a uniform yellowish-brown colour. Protoconch 0.5–0.6 mm wide, sculptured with closely spaced, fine radial ribs. Teleoconch sculpture of widely spaced, low, narrow, rounded, weakly sigmoidal, primary radial ribs, interstices *c.* 3–4 times their width, with closely spaced, fine,

rounded, radial riblets, and very fine spiral microsculpture. Aperture ovate, simple, lip thin, thickened within. Three major parietal barriers, middle closer to lower than to upper, high lamellar ridges, thickened and rounded above, extending back approximately $\frac{1}{4}$ whorl. A shorter accessory thread is rarely present below the lowest primary parietal lamella. No columellar barrier. Five palatal barriers, more or less evenly spaced, extending back *c.* $\frac{1}{8}$ whorl, lowest three are basal, fourth subperipheral, uppermost peripheral. Lower four are high lamellar ridges, thickened and rounded above; uppermost barrier is a narrower and lower ridge.

TYPE MATERIAL: Holotype NMNZ M.290118 and paratypes M.290120 (7), BPBM 274762 (3): Cook Islands, Rarotonga, Pue, fossils in sandy coral rubble in gravel pit (21°12.301'S, 159°45.080'W), 19 June 2007.

OTHER MATERIAL: NMNZ M.282543.

SITE: 3.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species is distinctive in the combination of a relatively high spire, and teleoconch sculpture of widely spaced, primary radial ribs with prominent interstitial riblets. It is known only from fossil shells present in a rubbly soil on the northeastern coast of Rarotonga, at Pue, and is probably extinct.

Minidonta rutaki new species

(Fig. 6J–L)

DESCRIPTION: Shell small, 2.7–3.4 mm diameter, wider than high (shell height/shell diameter ratio of 0.53–0.63), apex and early spire whorls moderately and evenly elevated (spire protrusion 17–27% of shell height), last whorl descending a little more rapidly, umbilicus narrow and very constricted (13–18% of shell diameter). Whorls 5.0–5.8, moderately rounded above, final whorl slightly flattened on periphery and base, suture deeply impressed. Colour pattern of irregularly spaced, narrow to wide, axial, bright reddish-brown streaks, radial on spire, zigzag on sides and base. Protoconch 0.55–0.6 mm wide, sculptured with fine radial ribs. Teleoconch sculpture of low, narrow, weakly sigmoidal, radial ribs, *c.* 95–125 on last adult whorl, interstices approximately three times their width, with microsculpture of very fine radials and spirals. Aperture subovate, simple, lip thin, weakly thickened within. Three, rarely four, parietal barriers, lamellar ridges, thickened, rounded above, extending back about $\frac{1}{4}$ whorl. Columellar barrier a low, rounded ridge. Four palatal barriers, evenly spaced, lower two basal, third subperipheral, uppermost just above periphery. Lower three

are low, thickened lamellar ridges, rounded above, uppermost is a lower and thinner lamellar ridge.

TYPE MATERIAL: Holotype NMNZ M.290136 and paratypes M.290137 (12), BPBM 274763 (3): Cook Islands, Rarotonga, Rutaki, fossils in sandy soil exposed in low coastal bank (21°15.642'S, 159°48.015'W), 29 Sep. 2005.

OTHER MATERIAL: NMNZ M.283038, 283066, 283091, 283203, 283233, 283256, 283278, 283300.

SITES: 28–30, 34, 35A, 35B, 36A, 36B.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: The combination of relatively widely spaced ribs on the teleoconch, presence of a columellar ridge and zigzag colour pattern distinguish this species. It is known only from fossil shells present in sandy soils on the coastal plain around western Rarotonga, between Vaimaanga and Avatiu, and is probably extinct.

Minidonta sp.

The following description is based on a broken specimen, which is too poorly preserved to warrant naming. Shell minute (final whorl broken back, with diameter of 1.5 mm at 3.7 whorls), wider than high, apex and early whorls slightly elevated, umbilicus narrow (c.30% of shell diameter), constricted internally, last whorl decoiling rapidly. Whorls originally c.3.9, moderately rounded, with slightly flattened periphery and base, suture impressed. No colour pattern seen. Protoconch c.0.4 mm wide, sculptured with fine radial ribs. Teleoconch has closely spaced, low, narrow, rounded, weakly sigmoidal radial ribs; interstices slightly wider than ribs, with fine radial and spiral microsculpture. Aperture ovate. Two parietal barriers, short lamellar ridges, lower one thickened and rounded above, upper blade-like. Palatal barriers not preserved.

MATERIAL: NMNZ M.282522

SITE: 2.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species is most similar to *Minidonta iota* n.sp. (above) in terms of size and number of parietal barriers, but is slightly larger, with a proportionately wider umbilicus. It is known from a single poorly preserved fossil shell, found in a sandy ground soil at Pue, northeastern Rarotonga, and is probably extinct.

Family CHAROPIDAE

Seven species of Charopidae were found on the Rarotongan coastal plain, including three new endemic species of *Sinployea*, which are formally described below.

Discocharopa aperta (Möllendorff, 1888)

Patula aperta Möllendorff, 1888: 89 [Philippines].

Discocharopa aperta.– Solem, 1983: 76, figs 5a–f, 34a–d, 35a–b, 36a–c, 37a–d.

Sinployea sp.– Craig, 1995: table 5.3 (in part).

DISTRIBUTION: According to Solem (1983), *Discocharopa aperta* has a wide distribution, including the Philippines, Indonesia, Australia and many Pacific islands. In the Cook Islands, it is present on Rarotonga, Aitutaki, Ātiu, Miti'āro and Mangaia (Brook *et al.* 2010; Brook, unpub. data). If Solem's interpretation is correct, the Pacific island populations, including those on the Cook Islands, probably resulted from synanthropic introductions. However, Solem (1983) also noted that there were morphological differences between geographically separated populations of *D. aperta*, which suggests the possibility that this taxon may comprise a species complex, autochthonous or otherwise.

MATERIAL: NMNZ M.282424, 282498, 282523, 282544, 282600, 282627, 282651, 282671, 282687, 282712, 282727, 282744, 282774, 282798, 282818, 282841, 282873, 282896, 282923, 282969, 282993, 283016, 283039, 283067, 283093, 283125, 283152, 283177, 283206, 283234, 283257, 283279, 283301.

SITES: 1–3, 8–15, 18–21, 23A, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells were widely distributed in ground soils and paleosols on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets. This species was not recorded by Garrett (1881), and is not represented in later collections from Rarotonga in the BPBM and FMNH. No live snails were found in 2005–07, but rare, fresh, empty shells were found at five sites: beneath old *Barringtonia asiatica* trees at Matavera (site 10); in a coastal forest remnant at Ngatangiia (site 15); and in forest on Motutapu and Oneroa islets (sites 19–21). *Discocharopa aperta* was probably still extant on Rarotonga, but had evidently undergone a marked decline since prehistoric time. The lack of previous collections is probably attributable to the rarity and small size of this species.

Genus *Sinployea* Solem, 1983

Sinployea andrewi Solem, 1983

Sinployea andrewi Solem, 1983: 99, figs 42b, 44a–c [Mangaia, Cook Islands].

DISTRIBUTION: Cook Islands – formerly thought to be endemic to Mangaia (Solem 1983), but present also on Rarotonga.

MATERIAL: NMNZ M.282603, 282654, 282672, 282688,

282715, 282800, 282820, 282877, 282899, 282927, 282972, 282997, 283019, 283071, 283096, 283129, 283154, 283179, 283209, 283237, 283259.

SITES: 8, 10–13, 19, 20, 23A, 23B, 24–27, 29, 30–34, 35A, 35B.

REMARKS: The presence of fossil shells in soils indicates that this species was formerly widely distributed and locally common around the coastal plain of Rarotonga, and was also present on Motutapu. Relatively fresh, empty shells were found in coastal forest remnants at Matavera in 2005–07 (sites 10, 11), so there may have been an extant population at this locality, but the species had evidently died out elsewhere on the coastal plain. It was still extant and locally common on Mangaia in 2007 (Brook, pers. obs.).

Sinployea atiensis (Pease, 1870)

Pithys atiensis Pease, 1870: 394 [Ātiu, Cook Islands];

Johnson, 1994: 7, pl. 2, fig. 8.

Pityis atiensis.—Pease, 1871: 453, 474.

Patula atiensis.—Garrett, 1881: 386.

Patula modicella.—Garrett 1884: p. 28.

Sinployea atiensis.—Solem, 1983: 99, fig. 44d–f.

Sinployea sp.—Craig, 1995: table 5.3 (in part).

NOMENCLATURE: Garrett (1881: 386) recorded *Sinployea atiensis* from Ātiu (the type locality), Aitutaki and Rarotonga, noting that shells on Rarotonga attained a larger size, and had variable umbilical width and spire elevation. He considered that *S. atiensis* was morphologically indistinguishable from *Sinployea modicella* (Férussac in Deshayes, 1840) and *Sinployea vicaria* (Mousson, 1871) from the Society Islands and Tonga, respectively, and later (Garrett 1884: 28) synonymised these three species. Solem (1983) resurrected *S. atiensis* as a valid species name for the populations on Ātiu and Aitutaki, and erected a new species, *Sinployea peasei* Solem, 1983, for Rarotongan shells that were slightly larger, with a lower spire, wider umbilicus, and weaker protoconch sculpture than typical *S. atiensis*. Solem (1983) did not record *S. atiensis* from Rarotonga. However, shells matching the latter species are abundant in fossil assemblages on the coastal plain, and an extant population of *S. atiensis* was found in the upper Tupapa Valley during the present study (below).

DISTRIBUTION: Cook Islands – Rarotonga, Aitutaki, Ātiu, Ma'uke, Miti'āro, Mangaia (Garrett 1881; Solem 1983; Brook *et al.* 2010; Brook, unpub. data).

MATERIAL: NMNZ M.208813, 282405, 282413, 282425, 282499, 282524, 282545, 282628, 282713, 282775, 282799, 282819, 282842, 282874, 282897, 282924,

282970, 282994, 283017, 283040, 283068, 283094, 283126, 283153, 283178, 283207, 283235, 283258, 283280, 283302, 283340, 283341, 283344, 283435, 283436, 283438.

SITES: 1–3, 9, 13, 18–21, 23A, 23B, 24–34, 35A, 35B, 36A, 36B.

REMARKS: Fossil shells of *Sinployea atiensis* were present in soils on the coastal plain right around Rarotonga, and on Motutapu and Oneroa islets, indicating that this species was formerly widespread and locally abundant on the Rarotongan lowlands. No extant colonies were found in coastal habitats on Rarotonga in 2005–07, but this species was locally common in slope forest and cloud forest, at *c.* 80–460 m elevation in the upper Tupapa Valley (NMNZ M.283340, 283341, 283344, 283435, 283436, 283438). The snails there were present in leaf litter, under stones and fallen wood, and under moss and foliose lichens on tree trunks up to *c.* 1.5 m above the ground. No live snails or empty shells were found in any other inland areas searched in 2005–07.

Sinployea rudis (Garrett, 1872)

Pityis rudis Garrett, 1872: 227, pl. 19, fig. 18 [Rarotonga, Cook Islands].

Patula rudis.—Garrett, 1872: 387.

Sinployea rudis.—Solem, 1983: 108, fig. 47d–f.

MATERIAL: ANSP 47701; BPBM 2320, 167420–1; NMNZ M.208809, 282500, 282714, 282876, 282926, 282948, 282971, 282996, 283070, 283095, 283127.

SITES: 1, 13, 23A, 24–26, 29–31.

DISTRIBUTION: Cook Islands–Rarotonga.

REMARKS: Fossil shells of this species were widely distributed and locally common in sandy soils of the coastal plain around southern and southeastern Rarotonga, and were present also at a site near Pue on the northern coast. In 1869, *Sinployea rudis* was reportedly abundant in several inland valleys on Rarotonga, living on the ground in forest, but was apparently not found on the coastal plain (Garrett 1872, 1881). The species is not represented in collections at the BPBM or FMNH made in the 1920s and 1960s, respectively, and was not found living anywhere on Rarotonga in 2005–07. It is probably extinct (Solem 1983: 45, 97).

Adult shells of *Sinployea rudis* from the coastal plain were generally smaller than those collected by Garrett at inland sites, with maximum diameters of 2.9–3.7 mm (4.0–4.5 whorls), and 3.50–4.83 mm (3.9–4.6 whorls), respectively (Garrett 1872; Solem 1983; this study). Shells from coastal sites had the last adult whorl flattened laterally above the

periphery but none had a supraproperipheral sulcus, unlike some shells from inland sites (cf. Solem 1983). The coastal population included two colour morphs: shells with irregularly spaced, wavy reddish-brown axial streaks on a pale background; and reddish-brown shells, with or without faint, darker axial streaks. One distinctive conchological feature mentioned by Garrett (1872), but overlooked by Solem (1983), is that the primary teleoconch ribs on modern shells have prominent periostracal lamellar extensions. The latter feature is typical of Society Island species of *Sinployea* (Solem 1983: 86), but has not been reported for any other Cook Island species of this genus.

***Sinployea tenuicostata* (Garrett, 1872)**

Pityis tenuicostata Garrett, 1872: 229, pl. 19, fig. 23 [Rarotonga, Cook Islands].

Patula tenuicostata.— Garrett, 1881: 385.

Sinployea tenuicostata.— Solem, 1983: 117, fig. 50a–c [i.e. not fig. 50d–f as stated in text and caption].

DISTRIBUTION: Cook Islands – Rarotonga.

MATERIAL: BPBM 2325; NMNZ M.208812, 282525, 282601, 282652, 282875, 282898, 282925, 282995, 283018, 283041, 283069, 283208, 283236, 283281.

SITES: 2, 8, 10, 23A, 23B, 24, 26–29, 34, 35A, 36A.

REMARKS: Fossil shells of this species were widely distributed but scarce in sandy soils on the coastal plain around Rarotonga. In 1869, *Sinployea tenuicostata* was reportedly ‘somewhat rare ... having a wide range on the island, and generally found on the ground on the sides of ravines’ (Garrett 1872: 229). Material collected by Cheeseman (NMNZ M.208812) indicates that this species was still extant in 1899, but it has not been found alive since and is probably now extinct.

Fossil shells of *Sinployea tenuicostata* from the coastal plain ranged in size up to a maximum diameter of 4.1 mm (4.2 whorls), which is at the lower limit of the size range reported by Solem (1983) for shells collected by Garrett from inland sites (i.e. 4.08–5.03 mm). A live adult collected by Cheeseman in 1899 was also relatively small (4.0 mm diameter, 4.2 whorls), which suggests it may have come from the lowlands.

***Sinployea muri* new species**

(Fig. 7A–C)

DESCRIPTION: Shell very small, 2.0–2.6 mm diameter, wider than high (shell height/shell diameter ratio 0.52–0.61), apex and early spire whorls moderately and evenly elevated (spire protrusion 13–21% of shell height), last whorl descending more rapidly, umbilicus moderately open (21–30% of shell

diameter). Whorls 3.5–4.0, broadly rounded, final whorl slightly flattened laterally above periphery and on base, suture deeply impressed. Some shells retain a faint colour pattern of irregularly spaced pinkish-brown axial streaks. Protoconch 0.52–0.59 mm wide, sculptured with fine spiral cords. Teleoconch sculpture of closely spaced, low, narrow, sigmoidal radial ribs, 85–110 on last adult whorl, interstices less than twice width of ribs, with very fine radial and spiral microsculpture. Aperture simple, lip thin, weakly and evenly thickened within.

TYPE MATERIAL: Holotype NMNZ M.290097 and paratypes M.290098 (15), BPBM 274765 (3): Cook Islands, Rarotonga, Muri, fossils in sandy paleosol exposed in coastal bank (21°15.600'S, 159°43.941'W), 29 Sep. 2005.

OTHER MATERIAL: NMNZ M.282716, 282900, 282973.

SITES: 13, 23B, 25.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species is distinctive in the combination of its very small size, moderately elevated spire and narrow umbilicus. It is known only from fossil shells present in soils on the coastal plain between Ngatangia and Titikaveka, southeastern Rarotonga, and is probably extinct.

***Sinployea titikaveka* new species**

(Fig. 7G–I)

DESCRIPTION: Shell minute, 1.45–1.65 mm diameter, wider than high (shell height/shell diameter ratio of 0.52–0.57), apex and early spire whorls barely elevated (spire protrusion 6–9% of shell height), last whorl descending more rapidly, umbilicus moderately open (24–29% of shell diameter). Whorls 3.25–3.75, broadly rounded, final whorl slightly flattened laterally above periphery and on base, suture deeply impressed. No colour pattern seen. Protoconch *c.* 0.45 mm wide, sculptured with fine spiral cords. Teleoconch sculpture of closely spaced, low, narrow, sigmoidal radial ribs (holotype has *c.* 120 ribs on last adult whorl), interstices less than twice width of ribs, with very fine radial and spiral microsculpture. Aperture ovate, simple, lip thin, weakly thickened within.

TYPE MATERIAL: Holotype NMNZ M.290145 and paratypes M.290146 (3), BPBM 274766 (1): Cook Islands, Rarotonga, Aroa, fossils in sandy ground soil (21°15.363'S, 159°48.810'W), 29 May 2006. Additional paratype NMNZ M.290143 (2): Cook Islands, Rarotonga, Titikaveka, fossils in sandy soil exposed in borrow pit (21°16.238'S, 159°45.494'W), 29 May 2006.

OTHER MATERIAL: NMNZ M.283097, 283128.

SITES: 25, 30, 31.

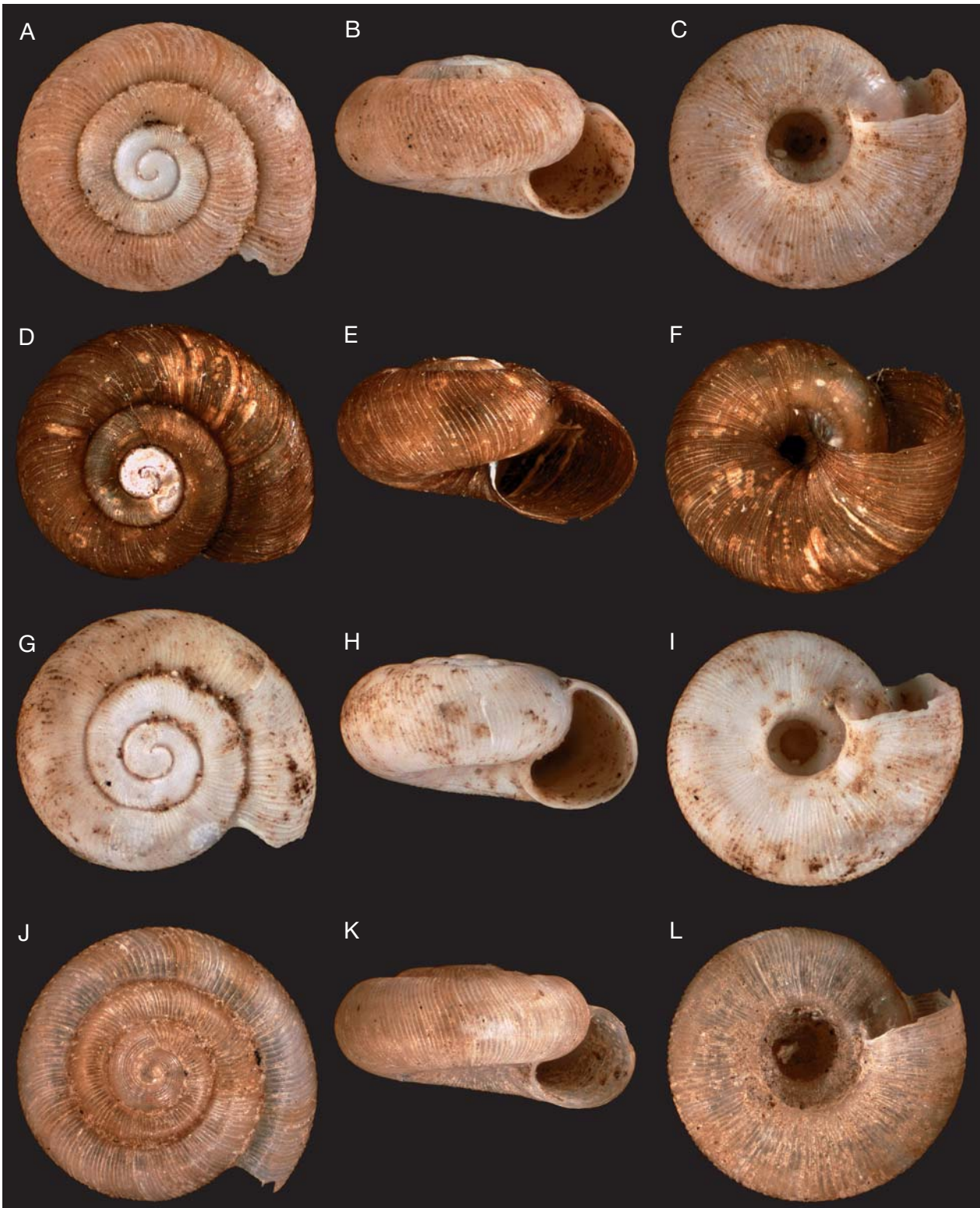


Fig. 7 Shells of *Sinployea* species. A–C, *Sinployea muri* n.sp., Muri, holotype, M.290097 (1.25×2.35 mm); D–F, *Sinployea taipara* n.sp., Taipara Valley, holotype, M.290085 (1.30×2.50 mm); G–I, *Sinployea titikaveka* n.sp., Aroa, holotype, M.290145 (0.82×1.55 mm); J–L, *Sinployea tupapa* n.sp., Pue, holotype, M.290148 (1.05×2.05 mm).

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species is most similar to *Sinployea muri* n.sp. (above), which occurred syntopically at Titikaveka (site 25), but is smaller than that species, and has finer axial ribbing on the teleoconch. *Sinployea titikaveka* n.sp. is known only from fossil shells present in soils on the coastal plain between Titikaveka and Aroa, southern Rarotonga, and is probably extinct.

***Sinployea tupapa* new species**

(Fig. 7J–L)

DESCRIPTION: Shell very small, 1.90–2.25 mm diameter, wider than high (shell height/shell diameter ratio of 0.44–0.53), apex and early spire whorls flat to moderately elevated (spire protrusion 2–14% of shell height), last whorl descending more rapidly, umbilicus widely open (32–36% of shell diameter). Whorls 3.8–4.2, broadly rounded, final whorl slightly flattened laterally above periphery and on base, suture deeply impressed. Well-preserved shells have a buff ground colour, with very faint, irregularly spaced yellowish-brown axial streaks. Protoconch 0.5–0.6 mm wide, sculptured with spiral cords. Teleoconch sculpture of closely spaced, low, narrow, sigmoidal radial ribs, *c.* 110–130 on last adult whorl, interstices one-and-a-half to three times their width, with microsculpture of very fine radials and spirals. Aperture simple, lip thin, weakly and evenly thickened within.

TYPE MATERIAL: Holotype NMNZ M.290148 and paratypes M.290150 (12), BPBM 274767 (4): Cook Islands, Rarotonga, Pue, fossils in sandy coral rubble in gravel pit (21°12.301'S, 159°45.080'W), 19 June 2007.

OTHER MATERIAL: NMNZ M.282546, 282602, 282653.

SITES: 3, 8, 10.

DISTRIBUTION: Cook Islands – Rarotonga.

REMARKS: This species differs from all other Rarotongan *Sinployea* in its combination of small size, low spire and widely open umbilicus. It is known only from fossil shells present in rubbly soils at Pue, Tupapa and Matavera on the northeastern coast of Rarotonga, and is probably extinct.

Family AGRIMOLIMACIDAE

***Deroceras laeve* (Müller, 1774)**

Limax laevis Müller, 1774: 1.

Limax rarotonganus Heynemann, 1871: 43 [Rarotonga, Cook Islands]; Garrett, 1881: 402.

Agriolimax laevis rarotonganus.– Cockerell & Collinge, 1893: 176.

Deroceras laeve.– Barker, 1999: 32.

DISTRIBUTION: This slug is thought to be native to the Palearctic region, and possibly also to North and South America (Barker 1999), but it has a very wide synanthropic distribution. In the tropical Pacific, it has been recorded from New Caledonia, Vanuatu, Fiji, and the Society, Tuamotu and Hawaiian islands (Garrett 1884; Solem 1964; Cowie 1997, 1998b, 2000, 2001b; Barker 1999). In the southern Cook Islands, it is known from Rarotonga (Garrett 1881) and Mangaia (Brook, unpub. data). It was apparently widely distributed in the Pacific by the late 1800s, and present on Rarotonga by the 1860s (below), New Caledonia by the 1870s (Solem 1964), Tahiti and the Gambier Islands before the early 1880s (Garrett 1884), and Hawai'i by 1896 (Cowie 1998b).

MATERIAL: BPBM 206449; FMNH 153390; NMNZ M.273278, 282776, 283308, 283368, 285580, 287342, 287344–6.

SITE: 18.

REMARKS: Garrett (1881: 402) noted that this species was 'very abundant in damp places in the mountain ravines on Rarotonga'. In 2005–07, it was scarce in forest on Motutapu, and was not found at any sites on the coastal plain of Rarotonga. However, it was common and widely distributed in the interior of the island, inhabiting disturbed forest, slope forest and cloud forest up to 650 m in elevation.

Family ZONITIDAE

***Hawaia minuscula* (Binney, 1841)**

Helix minuscula Binney, 1841: 435, pl. 22, fig. 4 [Ohio, United States].

Hawaia minuscula.– Baker, 1941: 322, pl. 61, figs 13–15.

DISTRIBUTION: Native to North America and possibly eastern Asia (Chiba *et al.* 2008), with a wide synanthropic distribution in the tropical Pacific, including New Caledonia, Vanuatu, Tahiti, Pitcairn, and the Hawaiian Islands (Peile 1936; Baker 1941; Solem 1964; Preece 1995; Cowie 1997, 2000, 2001b; FLMNH). Cook Islands – Rarotonga, Aitutaki, Ātiu (Brook, unpub. data). *Hawaia minuscula* was present on Hawai'i by 1850, Lord Howe Island by 1887, New Caledonia by 1888, Norfolk Island by 1913, and Pitcairn and Tahiti by the 1930s (Peile 1936; Solem 1964; Cowie 1998b).

MATERIAL: BPBM 94372, 95384; NMNZ M.282501, 282526, 282655, 282745, 282777, 282821, 282878, 282928, 282998, 283282.

SITES: 1, 2, 10, 15, 18, 20, 23A, 24, 26, 36A.

REMARKS: Not represented in fossil assemblages, and not

recorded by Garrett (1881). The first collections on Rarotonga were made in 1929 near Ngatipa and Muri (BPBM 94372, 95384), which indicates that this species was probably introduced to Rarotonga sometime between the mid-1800s and 1920s. In 2005–07, *Hawaiia minuscula* was widely distributed but uncommon on the coastal plain around Rarotonga and on Motutapu, in forest and shrubland remnants, and highly modified, open, anthropogenic habitats. Its distribution elsewhere on Rarotonga was not determined.

Zonitoides arboreus (Say, 1819)

Helix arboreus Say, 1819: pl. 4, fig. 4 [United States].

Zonitoides arboreus.—Baker, 1941: 327, pl. 61, figs 10–12.

DISTRIBUTION: This species is thought to be native to North and Central America and the Caribbean, but has a wide synanthropic distribution (Baker 1941; Barker 1999). Adventive populations are known from relatively few tropical Pacific islands. *Zonitoides arboreus* was present in Hawai'i by 1928 (Baker 1941; Cowie 1997, 1998b), Rarotonga by 1964 (below), and Pitcairn by 1991 (Preece 1995).

MATERIAL: FMNH 144576, 144577, 144607, 144629, 153382; NMNZ M.283098.

SITE: 30.

REMARKS: *Zonitoides arboreus* was not recorded by Garrett (1881), and is not represented in collections made on Rarotonga during the 1920s (BPBM). However, this species was evidently locally common in upper parts of the Taipara and Avana valleys in 1964–65 (FMNH), which indicates that it was probably introduced to Rarotonga sometime between 1930 and the 1950s. In 2006, rare fresh, empty shells of *Z. arboreus* were found at one site on the coastal plain at Aroa, in a small remnant of *Barringtonia asiatica*–*Hibiscus tiliaceus* forest. No snails or empty shells were found anywhere else on Rarotonga in 2005–07, which suggests that the population had declined since the mid-1960s.

Family EUCONULIDAE

Diastole conula (Pease, 1861)

Helix conula Pease, 1861: 243 [Tahiti, Society Islands]; Johnson, 1994: 9, pl. 3, fig. 6.

Microcystis conula.—Garrett, 1881: 383.

Diastole conula.—Baker, 1938: 46, pl. 17, fig. 3, pl. 5, figs 9–10; Craig, 1995: 111–112, fig. 6–6a.

DISTRIBUTION: Present on many of the Society Islands (Garrett 1884; Baker 1938) and probably native to this

island group. Populations on other Pacific islands, including Rurutu in the Austral Islands, some of the southern Cook Islands (Rarotonga, Ātiu, Ma'uke, Mangaia), and New Caledonia (Baker 1938; Solem 1964), are most likely of synanthropic origin.

MATERIAL: BPBM 54380–1, 79787, 94321, 94326–8, 94340, 94376, 94382, 94405, 94413, 95373–5, 95393–5, 95401, 95406–8, 95410–11, 95444–5, 95450, 95456–8, 95460–1, 95577, 97684–6, 206451; NMNZ M.208829, 282604, 282778, 282999, 283099, 283305, 283309.

SITES: 8, 18, 26, 30.

REMARKS: *Diastole conula* is arboreal, living on the foliage of trees, shrubs and ferns. It was evidently introduced to Rarotonga in the mid-1800s. Garrett (1881: 383) recorded its distribution on Rarotonga in the 1860s as follows: 'Nearly 200 of this species were taken from the foliage of a large shrub, near the seashore at Rarotonga. Though carefully searched for, I failed to detect it in any other part of the island.' By contrast, collections in the BPBM indicate that it was widely distributed and common on Rarotonga by the late 1920s. In 2005–07, *D. conula* was found to be sparsely distributed in coastal forest remnants on Rarotonga and Motutapu, but was widespread and locally abundant in disturbed forest, slope forest, and cloud forest in the interior of the island.

Kororia palaensis (Semper, 1870)

Microcystis palaensis Semper, 1870: 45, pl. 2, fig. 16, pl. 6, fig. 34 [Palau Islands].

Kororia palaensis.—Baker, 1941: 220, pl. 43, figs 10–12, pl. 53, figs 13–15.

Lamprocystis (Avarua) venosa.—Craig, 1995: 112, table 5–3 (in part).

Ovachlamys fulgens.—Cowie, 2001a: 212, tables 2, 3.

DISTRIBUTION: Probably native to Micronesia, but with a wide synanthropic distribution extending east to Polynesia. Known from Palau, Northern Marianas, Caroline Islands, Marshall Islands, Samoa, Cook Islands and Society Islands (Baker 1941; Harry 1966; BPBM; FMNH; NMNZ). In the Cook Islands, this species is present on Rarotonga, Ātiu and Mangaia (Brook, unpub. data). *Kororia palaensis* was apparently a fairly recent introduction to Polynesia, first recorded from the Society Islands in 1974 (FMNH), Rarotonga in 1994 (below), and Samoa in 1998 (Cowie 2001a – as *Ovachlamys fulgens*).

MATERIAL: NMNZ M.282387, 282426, 282446, 282455, 282465, 282481, 282780, 283101, 283310, 283333,

283345, 283362, 283369, 283374, 283381, 283390, 283414, 283422.

SITES: 18, 30.

REMARKS: Not represented in fossil assemblages, and not recorded by Garrett (1881) or present in later collections from Rarotonga in the BPBM and FMNH. However, this species was evidently locally common by 1994, with collections made on Oneroa and in the upper Avatiu Valley (NMNZ M.282387, 282426, 282446, 282455, 282465, 282481). In 2005–07, *Kororia palaensis* was very scarce on the coastal plain of Rarotonga, with fresh, empty shells found in coastal forest at two sites only: near Aroa and on Motutapu. However, it was widely distributed and common from lower hill slopes up to 650 m elevation in disturbed forest, slope forest and cloud forest in the interior of Rarotonga, living on the ground under stones, fallen wood and leaves.

Lamprocystis (Avarua) venosa (Pease, 1866)

Helix venosus Pease, 1866: 290, pl. 21, fig. 2 [Rarotonga, Cook Islands – Pease 1871: 475]; Johnson, 1994: 27.

Microcystis venosa.– Garrett, 1881: 382.

Lamprocystis (Avarua) venosa.– Baker, 1938: 72, pl. 11, figs 1–2, pl. 6, figs 3, 5; Craig, 1995: 112, table 5–3 (in part).

DISTRIBUTION: Cook Islands–Rarotonga.

MATERIAL: BPBM 3189, 11462, 58972; NMNZ M.208857, 282902, 283001, 283073, 283239, 283342, 283354, 283367, 283371, 283375, 283383, 283388, 283392, 283395, 283397, 283399, 283400, 283403, 283404, 283407, 283410, 283411, 283413, 283415, 283416, 283417, 283420, 283424, 283429.

SITES: 23B, 26, 29, 35A.

REMARKS: Garrett (1881: 382) noted that this species was ‘extremely abundant on the foliage of bushes, and is widely diffused throughout the inland ravines of Rarotonga’. In 2005–07, the only specimens found on the coastal plain of Rarotonga were a few fossil shells present in soils at three sites on the southern coast, and one site at Pokoinu on the northwestern coast. This indicates that *Lamprocystis venosa* was never common in coastal habitats, and it has probably died out on the coastal plain. However, in 2005–07 the species was still widely distributed and common across much of the interior of the island (Appendix 3).

Liardetia (Liardetia) samoensis (Mousson, 1865)

Nanina samoensis Mousson, 1865: 165 [Upolu, Samoa].

Microcystis samoensis.– Garrett, 1881: 384.

Liardetia (Liardetia) striolata.– Baker, 1938: 22, pl. 14, fig. 12, pl. 9, figs 5–6, pl. 3, figs 4–5.

Liardetia (Liardetia) samoensis.– Baker, 1940: 190.

DISTRIBUTION: This species is possibly native to Indonesia (Solem 1959), and has 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). Cook Islands – Rarotonga, Aitutaki, Manuae, Ātiu, Ma‘uke, Miti‘āro, Mangaia (Garrett 1881, 1887; Baker 1938; Brook *et al.* 2010; Brook, unpub. data; BPBM; NMNZ).

MATERIAL: BPBM 54382, 94312, 94341, 94362, 94377, 94383, 94393, 95347, 95385, 95451; FMNH 144618; NMNZ M.282569, 282605, 282630, 282844, 283020, 283102, 283181, 283240, 283261, 283304, 283334, 283442, 287371.

SITES: 6, 8, 9, 21, 27, 30, 33, 35A, 35B, 36B.

REMARKS: Rare fossil shells of *Liardetia samoensis* were present in ground soils and paleosols at a few coastal sites around Rarotonga (i.e. sites 6, 30, 35A, 35B, 36B). Garrett (1881: 384) noted that in the 1860s this species was ‘very abundant beneath dead wood and under loose stones in the low-land forests near the seashore’. Collections in the BPBM indicate that *L. samoensis* was widely distributed but uncommon on the coastal plain and lowland valleys and hill slopes of Rarotonga in the late 1920s. In the mid- to late 1900s, it was evidently sparsely distributed on the coastal plain and in forest on lower- to mid-elevation hill slopes (e.g. FMNH 144618; NMNZ M.283334, 283442, 287371). It was also rare on the coastal plain in 2005–07, with fresh, empty shells and rare live snails found in a few forest and shrubland remnants and beneath old relict broadleaved trees on Rarotonga, and in forest on Oneroa.

Liardetia (Liardetia) sculpta (Möllendorff, 1883)

Microcystis sculpta Möllendorff, 1883: 364, pl. 12, fig. 4 [China].

Liardetia (Liardetia) sculpta.– Baker, 1938: 26, pl. 2, figs 19–20, pl. 9, fig. 8, pl. 14, fig. 6.

DISTRIBUTION: Probably native to Asia. In the western Pacific, recorded from Guam, Marianas Islands, and Pohnpei, Caroline Islands (Baker 1938). Cook Islands – Rarotonga.

MATERIAL: NMNZ M.283021.

SITE: 27.

REMARKS: Not represented in fossil assemblages, and not recorded by Garrett (1881) or present in later collections from Rarotonga in the BPBM, FMNH and NMNZ. In 2006, fresh, empty shells of this species were found under an old *Barringtonia asiatica* tree on the coast at Avaavaroa.

Liardetia sculpta is not known elsewhere on Rarotonga, and is probably a recent introduction to this island.

Liardetia (Oceania) discordiae (Garrett, 1881)

Microcystis discordice Garrett, 1881: 383 [Cook Islands].

Liardetia (Oceania) discordiae.— Baker, 1938: 19, pl. 8, figs 11–12, pl. 2, figs 11–13.

DISTRIBUTION: This species has been recorded from the southern Cook Islands (Rarotonga, Aitutaki, Ātiu, Ma‘uke, Mangaia); Rurutu, Austral Islands; several of the Society Islands; Makatea, Tuamotu group; and Nuku Hiva, Marquesas Islands (Garrett 1881, 1884, 1887; Baker 1938); according to Baker (1941: 347, 349), it was spread among the Polynesian islands by humans.

MATERIAL: BPBM 95413–4, 170874 (ex MCZH 11518); NMNZ M.208828, 282903, 283211.

SITES: 23B, 34.

REMARKS: Rare fossil shells of *Liardetia discordiae* were present in a ground soil at Arorangi and a paleosol at Muri; the scarcity of fossils suggests that this species was neither common nor widespread on the coastal plain in prehistoric time. Garrett (1881: 383) noted that *L. discordiae* was ‘found in great abundance beneath rotting wood and among decaying leaves’, but he may have been referring to a population(s) on one or more of the other southern Cook Islands. Museum records indicate that this species was extant but scarce on Rarotonga in 1899 (NMNZ M.208828) and 1929 (BPBM 95413–4). No live snails or fresh, empty shells of *L. discordiae* were found anywhere on Rarotonga in 2005–07, and the local population is probably extinct.

‘Microcystina’ gerritsi Benthem Jutting, 1964

Microcystina gerritsi Benthem Jutting, 1964: 57, figs 45–47 [New Guinea].

NOMENCLATURE: The anatomy and phylogenetic relationships of this minute, discoidal, colourless, spirally sculptured ‘euconuloid’ species are presently unknown. In terms of shell characters, it does not appear to be closely related to, and may not be congeneric with, the type species of the genus, *Microcystina rinki* Morch, 1872, from the Nicobar Islands (Bay of Bengal). It is provisionally listed here as ‘*Microcystina*’ pending further study.

DISTRIBUTION: Probably native to coastal areas of northern New Guinea and adjacent islands (Benthem Jutting 1964). In the eastern Pacific this species is presently known only from the Cook Islands (Rarotonga, Aitutaki, Ātiu, Miti‘āro, Mangaia, Nassau, Penrhyn: Brook *et al.* 2010; Brook, unpub. data; BPBM). The latter populations presumably

all resulted from synanthropic introductions after European contact. The earliest records in this group were from Nassau and Penrhyn in 1924 (BPBM 77223, 77239, 79516, 79527).

MATERIAL: NMNZ M.282406, 282414, 282527, 282547, 282568, 282581, 282629, 282656, 282673, 282689, 282728, 282746, 282779, 282801, 282822, 282843, 282879, 282901, 282929, 282975, 283000, 283042, 283072, 283100, 283180, 283210, 283238, 283260, 283283, 283303.

SITES: 2, 3, 6, 7, 9–12, 14, 15, 18–21, 23A, 23B, 24–26, 28–30, 33, 34, 35A, 35B, 36A, 36B.

REMARKS: Not represented in fossil assemblages, and not recorded by Garrett (1881) or present in later collections from Rarotonga in the BPBM and FMNH. However, the early records from Nassau and Penrhyn suggest that it may have been present also on Rarotonga by the 1920s. The first Rarotongan collection was from Motutapu in 1994 (NMNZ M.282406, 282414). In 2005–07, fresh, empty shells of ‘*Microcystina*’ *gerritsi* were uncommon but widely distributed in shrubland and forest remnants, and in highly modified, open, anthropogenic habitats on the coastal plain of Rarotonga, and in forest on Motutapu and Oneroa islets. Shells were present to depths of at least 1 m in soils (e.g. sites 23B, 35B, 36B), suggesting that this species was at least partly subterranean in habit.

Family SUCCINEIDAE

Quickia concisa (Morelet, 1848)

Succinea concisa Morelet, 1848: 351 [Gabon, West Africa]; Quick, 1936: 39.

Quickia concisa.— Odhner, 1950: 206; Patterson, 1975: 182.

Physastra nasutu.— Craig, 1995: table 5–3 (in part).

Succinea manuana.— Cowie, 2001a: tables 2, 3 (in part); Rundell *et al.* 2004: table 1, figs 3, 4.

Succinea modesta.— Cowie, 2001a: tables 2, 3 (in part); Cowie & Rundell, 2002: table 1; Cowie & Robinson, 2003: table 1 (in part); Rundell *et al.* 2004: table 1, figs 3, 4.

TAXONOMY: A single species of Succineidae is known from Rarotonga; anatomical characters match Quick’s (1936) and Patterson’s (1975) descriptions of *Quickia concisa* from western Africa and western Indian Ocean islands (G.M. Barker, pers. comm. 2009). Unpublished gene sequences indicate that the same species is present also in Samoa, the Austral Islands and the Marquesas Islands (R.H. Cowie & B. Holland,

pers. comm. 2006). Examination of material in the BPBM indicates that the Samoan populations were incorrectly referred to *Succinea manuana* Gould, 1846 and *Succinea modesta* Gould, 1846 by Cowie (2001a), Cowie & Rundell (2002), Cowie & Robinson (2003), and Rundell *et al.* (2004). Shells of *Q. concisa* differ from those of *S. manuana* and *S. modesta* in having a proportionately taller spire, less inflated last adult whorl, and smaller adult size. The two last mentioned species are endemic to Samoa, whereas *Q. concisa* is a recent introduction to Polynesia (below).

DISTRIBUTION: *Quickia concisa* is native to tropical Africa and islands in the western Indian Ocean. It has been recorded from tropical West Africa, southeastern Africa, Madagascar, and the Seychelles and Mascarene islands (Quick 1936; Odhner 1950; Patterson 1975). In the Pacific, this species is presently known from Samoa (Savai'i, Upolu, Tutuila, Ta'u, Ofu, Olosega, Aunu'u), Niue, Cook Islands (Rarotonga, Aitutaki, Ātiu, Miti'āro, Mangaia), Austral Islands (Rimatara), and Marquesas Islands (Nuku Hiva, Fatu Hiva, Ua Huka) (R.H. Cowie & B. Holland, pers. comm. 2006; Brook *et al.* 2010; Brook, unpub. data; BPBM). *Quickia concisa* was apparently introduced into Polynesia relatively recently; the earliest records are from Savai'i, Upolu, Ofu, Tau and Tutuila in 1992–94 (Cowie 2001a; Cowie & Robinson 2003; BPBM), and Rarotonga in 1994 (below).

MATERIAL: NMNZ M.273279, 282429, 282502, 282548, 282606, 282631, 282657, 282717, 282747, 282781, 283022, 283043, 283074, 283130, 283155, 283182, 283241.

SITES: 1, 3, 8–10, 13, 15, 18, 27–29, 31–33, 35A.

REMARKS: *Quickia concisa* is not represented in fossil assemblages, and was not recorded by Garrett (1881) or present in later collections from Rarotonga in the BPBM and FMNH. This species was first collected from Rarotonga in 1994, from grass at the edge of a swamp near Tikioki (NMNZ M.282429). In 2005–07, it was widely distributed and locally common on the coastal plain around Rarotonga in shrubland and forest remnants, and in highly modified, open, anthropogenic habitats. It was present also in forest on Motutapu.

Family BRADYBAENIDAE

Bradybaena similaris (Rang, 1831)

Helix similaris Rang, 1831: 15 [Réunion, Mascarene Islands].

Eulota similaris.–Pilsbry, 1894: 202, pl. 55, fig. 19.

Lamprocystis (Avarua) venosa.–Craig, 1995: 112, fig. 6–6b, table 5–3 (in part).

DISTRIBUTION: This species is probably native to Asia and Indonesia, but has 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). Cook Islands – Rarotonga, Aitutaki, Ātiu, Miti'āro, Mangaia (Brook *et al.* 2010; Brook, unpub. data; NMNZ). *Bradybaena similaris* had become widely distributed by the late 1800s, possibly in part associated with shipping of sugarcane plants (Pilsbry 1893–95: 204). In the Pacific, it was first recorded from Hawai'i in 1893 (Pilsbry 1893–95; Cowie 1998b), and New Caledonia in 1911 (Solem 1964). Collections in the BPBM indicate that it was present on Upolu, Samoa, by 1923 (BPBM 75556, 75626); Viti Levu, Fiji, by 1924 (BPBM 77028, 77037, 77038); and Moorea, Society Islands, by 1934 (BPBM 141866).

MATERIAL: BPBM 206450; FMNH 144690, 144693, 144695, 144696; NMNZ M.282430, 282456, 282503, 282607, 282718, 283103, 283131, 283156, 283183, 283212, 283306, 283328, 283456, 285529, 285528.

SITES: 1, 8, 13, 30–34.

REMARKS: This species was not recorded by Garrett (1881), and is not represented in collections made on Rarotonga in the 1920s (BPBM), but was evidently widely distributed on this island by the early 1960s (BPBM; FMNH). It was probably introduced to Rarotonga sometime between c. 1930 and the 1950s. In 2005–07, *Bradybaena similaris* was present between Aroa and Arorangi, and at a few other sites on the coastal plain, in shrubland and forest remnants, and in highly modified, open, anthropogenic habitats. It was more widely distributed in the interior of the island, occurring up to 650 m elevation in disturbed forest, slope forest and cloud forest (Brook, pers. obs.). The Rarotongan population was polymorphic, including individuals with a dark brown animal and plain brown shell, and others with a light brown animal and cream-coloured shell with a circum-peripheral brown band.

Composition of the coastal fauna

A total of 68 species of terrestrial molluscs is recorded here from the coastal plain of Rarotonga, including 43 species in the fossil fauna and 48 species in the modern fauna. The last total includes one species seen on the coastal plain but not found at any of the sampling sites in 2005–07 (i.e. *Vaginulus plebeius*), and three species recorded previously from coastal

Table 1 Biogeographic composition of the fossil and modern terrestrial molluscan fauna of the Rarotongan coastal plain (i.e. excluding littoral and supralittoral species in families Assimineidae, Truncatellidae and Ellobiidae).

Distribution category	Fossil	Modern
Rarotongan endemics	<i>Atropis rarotongana</i> n.sp., <i>Libera subcavernula</i> , <i>Minidonta aroa</i> n.sp., <i>Minidonta arorangi</i> n.sp., <i>Minidonta iota</i> n.sp., <i>Minidonta kavera</i> n.sp., <i>Minidonta matavera</i> n.sp., <i>Minidonta ngatangiia</i> n.sp., <i>Minidonta pue</i> n.sp., <i>Minidonta rutaki</i> n.sp., <i>Minidonta</i> sp., <i>Sinployea muri</i> n.sp., <i>Sinployea rudis</i> , <i>Sinployea tenuicostata</i> , <i>Sinployea titikaveka</i> n.sp., <i>Sinployea tupapa</i> n.sp., <i>Lamprocystis venosa</i>	<i>Atropis rarotongana</i> n.sp., <i>Minidonta matavera</i> n.sp.
Cook Island species	<i>Sturanya parvula</i> , <i>Garrettia rotella</i> , <i>Nesopupa dentifera</i> , <i>Nesopupa rarotonga</i> n.sp., <i>Libera fratercula</i> , <i>Sinployea andrewi</i> , <i>Sinployea atiensis</i>	<i>Sturanya parvula</i> , <i>Nesopupa dentifera</i> , <i>Nesopupa rarotonga</i> n.sp., <i>Libera fratercula</i> , <i>Sinployea andrewi</i>
Polynesian species	<i>Georissa striata</i> , <i>Orobophana pacifica</i> , <i>Assiminea parvula</i> , <i>Omphalotropis variabilis</i> , <i>Lamellidea oblonga</i> , <i>Tornatellides oblongus</i> , <i>Nesopupa armata</i> , <i>Nesopupa pleurophora</i> , <i>Liardetia discordiae</i>	<i>Georissa striata</i> , <i>Orobophana pacifica</i> , <i>Omphalotropis variabilis</i> , <i>Lamellidea oblonga</i> , <i>Tornatellides oblongus</i> , <i>Nesopupa armata</i> , <i>Diastole conula</i>
Tropical Pacific species	<i>Lamellidea pusilla</i> , <i>Pacificella variabilis</i> , <i>Gastrocopta pediculus</i> , <i>Discocharopa aperta</i> , <i>Liardetia samoensis</i>	<i>Elasmias apertum</i> , <i>Lamellidea pusilla</i> , <i>Pacificella variabilis</i> , <i>Gastrocopta pediculus</i> , <i>Discocharopa aperta</i> , <i>Kororia palaensis</i> , <i>Liardetia samoensis</i> , <i>'Microcystina' gerritsi</i>
Extra-Pacific species	<i>Costigo saparuana</i> , <i>Pupisoma orcula</i> , <i>Allopeas gracile</i>	<i>Vaginulus plebeius</i> , <i>Costigo saparuana</i> , <i>Gastrocopta servilis</i> , <i>Pupisoma orcula</i> , <i>Cecilioides aperta</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>Gulella bicolor</i> , <i>Streptostele musaecola</i> , <i>Deroceras laeve</i> , <i>Hawaiiia minuscula</i> , <i>Zonitoides arboreus</i> , <i>Liardetia sculpta</i> , <i>Quickia concisa</i> , <i>Bradybaena similis</i>

habitats but not found during the present survey (i.e. *Allochroa layardi*, *Melampus castaneus*, *Elasmias apertum*).

The biogeographic composition of the fully terrestrial component of the fossil and modern molluscan faunas of the Rarotongan coastal plain (i.e. excluding the supralittoral species in families Assimineidae, Ellobiidae, Truncatellidae) is summarised in Table 1. Note that some species listed here as Rarotongan endemics and Cook Islands species (e.g. in *Nesopupa* and *Sinployea*) may prove to have wider distributions within the Cook Islands and Polynesia, respectively.

Allopeas clavulinum is listed in the table as an extra-Pacific species, but is possibly indigenous to the northwestern Pacific region (e.g. Marui *et al.* 2004).

The fossil and modern terrestrial molluscan faunas of the Rarotongan coastal plain differed markedly in taxonomic and biogeographic composition, as shown in Table 1. The fossil fauna was strongly dominated by Rarotongan endemics (17 species, 41% of fauna, $n = 41$), and contained three extra-Pacific species only (7%). By contrast, the modern fauna was strongly dominated by extra-Pacific

species (19 species, 46% of fauna, $n = 41$), and included two Rarotongan endemics only (5%), both of which were either verging on extinction or already extinct in 2005–07. The modern fauna also contained more tropical Pacific species (8, 20%) than the fossil fauna (5, 12%), as a result of the simple addition of species. Numbers and proportions of Cook Island species and Polynesian species were slightly lower in the modern fauna than in the fossil fauna as a result of the local extinction of some species, partly offset by the addition of one Polynesian species to the modern fauna (i.e. *Diastole conula*).

Fossil fauna

Fossil landsnail shells were collected from 28 ground soils and three paleosols. Species richness of fossil assemblages ranged from 11–23 species per site ($n = 31$; mean = 16.2 \pm 3.8 SD). The richest fossil assemblages were at sites 23A and 23B (23 and 22 species, respectively); sites 34 and 35A (21 species each); site 29 (20 species); sites 13, 31, 35B and 36A (19 species each); and sites 2, 10, 24, 26 and 36B (18 species each).

Fifteen species (35%, $n = 43$) were present at >50% of sites ($n = 31$); 12 species (28%) were present at 10–50% of sites; and 16 species (37%) were present at <10% of sites (including five species each found at a single site only: *Costigo saparuana*, *Nesopupa pleurophora*, *Pupisoma orcula*, *Minidonta pue* n.sp., *Minidonta* sp.). The most frequent species in fossil assemblages were *Discocharopa aperta* (30 sites); *Georissa striata* (29 sites); *Sturanya parvula*, *Omphalotropis variabilis* and *Lamellidea oblonga* (27 sites each); *Lamellidea pusilla*, *Gastrocopta pediculus*, *Allopeas gracile* and *Sinployea atiensis* (26 sites each); *Assimineia parvula* (25 sites); *Sinployea andrewi* (21 sites); *Libera subcavernula* (19 sites); *Orobophana pacifica* (18 sites); *Atropis rarotongana* n.sp. (17 sites); and *Libera fratercula* (16 sites). Fossil shells of the last-named species and *Orobophana pacifica* were found only in coral rubble and gravelly sand on the seaward coastal plain of northern and eastern Rarotonga (including Motutapu and Oneroa islets), and were absent from sandy soils on southern and western coasts. Conversely, fossils of *Sturanya parvula*, *Omphalotropis variabilis* and *Libera subcavernula* had sparse distributions in coral rubble on northern and eastern Rarotonga, but were widespread in sandy soils around the rest of the island. The lowland distribution of the last-named species was largely parapatric with respect to *Libera fratercula*, but the two occurred together locally (e.g. sites 1, 2, 9, 23B).

The various Rarotongan species of *Minidonta* all had locally restricted distributions on the coastal plain. Four species on the eastern side of Rarotonga apparently had allopatric distributions: *Minidonta pue* n.sp. and *Minidonta* sp. were found at different sites near Pue; *Minidonta matavera* n.sp. was found between Tupapa and Matavera; and *Minidonta ngatangia* n.sp. was found between Ngatangia and Titikaveka. By contrast, five other species on the coastal plain of western Rarotonga had partly overlapping distributions: *Minidonta rutaki* n.sp. had the widest distribution, occurring between Vaimaanga and Avatiu; *Minidonta aroa* n.sp. and *Minidonta arorangi* n.sp. were found between Aroa and Arorangi; *Minidonta kavera* n.sp. was found at Aroa and Kavera; and *Minidonta iota* n.sp. was at Aroa only. Two to three species of *Minidonta* were present syntopically at some sites between Aroa and Arorangi on southwestern Rarotonga (i.e. sites 30, 31, 32, 34).

Four species of *Sinployea* had wide distributions on the coastal plain. *Sinployea atiensis* was widespread and frequent, albeit with a patchy distribution on the northeastern coast; *Sinployea tenuicostata* was scarce with a scattered distribution right around Rarotonga; *Sinployea rudis* was widely distributed and locally common around southern and south-eastern Rarotonga, and was present also at a site near Pue on the northern coast; and *Sinployea andrewi* had a patchy distribution around eastern, southern and western Rarotonga. Three other species of *Sinployea* had more restricted distributions: *Sinployea pue* n.sp. was found only on the northeast coast between Pue and Matavera; *Sinployea muri* n.sp. was present on the southeastern coast between Ngatangia and Titikaveka; and *Sinployea titikaveka* n.sp. was found on the southern coast between Titikaveka and Aroa. A few fossil assemblages contained a single species of *Sinployea* (i.e. *S. atiensis* or *S. andrewi*), but most had between two and five syntopic species. The most diverse assemblages, containing four or five species, were all on the south coast between Muri and Aroa (i.e. sites 23A, 23B, 24–26, 29–31).

Modern fauna

Species richness of modern landsnail assemblages (excluding sites 4, 5) was in the range of 4–18 species per site ($n = 34$, mean = 11.5 \pm 3.5 SD). The richest modern assemblages were at site 15 (18 species); sites 10 and 21 (17 species each); sites 8, 9, 30, 33 and 35 (16 species each); site 20 (15 species); and site 11 (14 species). Of the 45 species found in modern assemblages, six species (13%) were present at >50% of

sites; 24 species (53%) were present at 10–50% of sites; and 15 species (33%) were present at <10% of sites (including five species each found at one site only: *Atropis rarotongana* n.sp., *Costigo saparuaana*, *Deroceras laeve*, *Zonitoides arboreus*, *Liardetia sculpta*). The most frequent species in the modern assemblages were *Opeas hannense* and *Streptosteles musaecola* (28 sites each), *Gastrocopta servilis* and '*Microcystina*' *gerritsi* (24 sites each), and *Pacificella variabilis* (21 sites).

Landsnail species richness in the four main habitat types sampled is summarised in Table 2. The richest assemblages were found at sites in shrubland and forest remnants, and beneath relict trees, whereas the most impoverished assemblages were in littoral open shrubland. Overall, more species were found in the shrubland–forest habitat type (i.e. with correspondingly greater faunal heterogeneity between sites) than beneath old, relict trees in highly modified, open, anthropogenic habitats. In turn, the latter habitat type supported a higher total number of snail species, and sites generally also had slightly higher species richness than those in open grassland habitats without trees.

The two littoral open shrubland sites had distinctive snail assemblages characterised by the presence of *Orobophana pacifica*, *Assimineea lucida*, *Truncatella guerinii* and *Melampus luteus*, with or without *Melampus fasciatus*. The last four of these littoral species, along with *Assimineea* sp. 1, had narrow ecological distributions, restricted to littoral shrubland and herbaceous strand vegetation on coral rubble and makatea limestone substrata on the northeastern and eastern coast of Rarotonga. Their ecological distributions overlapped with those of *Orobophana pacifica* and *Pacificella variabilis*, which extended seaward into herbaceous strand vegetation, and with *Gastrocopta servilis*, *Opeas hannense*, *Streptosteles musaecola* and *Libera fratercula*, which extended seaward into littoral *Scaevola taccada* shrubland. *Orobophana pacifica* was restricted to coral rubble, gravelly sand and makatea limestone substrata within c. 150 m of the coast, in forest, littoral shrubland, and herbaceous strand vegetation dominated by mats of creeping vines. Extant populations of *L. fratercula* (12 sites) were also restricted to coral rubble substrata within c. 150 m of the coast, in forest and littoral shrubland.

Many landsnail species in the modern fauna had distributions restricted to forest and shrubland remnants and relict groves of old trees, and were absent from open, grassy, tree-less habitats (Table 3). In particular, this included all the extant Rarotongan endemics and Cook Islands species on the coastal plain (see Table 1). Assemblages in forest and shrubland remnants and relict groves of old trees typically

Table 2 Species richness of modern landsnail assemblages on the Rarotongan coastal plain in 2005–07.

Habitat type	Number of sites	Species per site		
		Total number of species	Range	Mean \pm SD
Littoral open shrubland	2	5	4–5	4.5 \pm 0.7
Forest and shrubland remnants	14	42	9–18	13.9 \pm 2.9
Relict trees	9	31	9–17	11.7 \pm 3.0
Open anthropogenic habitats	9	17	7–11	9.1 \pm 1.5

contained mixtures of Polynesian, tropical Pacific and extra-Pacific species, with or without rare Cook Islands and Rarotongan endemics, whereas assemblages in disturbed open habitats were strongly dominated by extra-Pacific species, with rare Polynesian and tropical Pacific species. *Orobophana pacifica* and *Libera fratercula* were frequent in shrubland and forest remnants, scarce beneath old relict trees, and absent from modified open habitats; *Lamellidea oblonga* and *Nesopupa armata* were moderately frequent in shrubland–forest and relict tree habitats, but absent from open habitats; *Pacificella variabilis* was most frequent in shrubland–forest and least frequent in open habitats; and several species (*Tornatellides oblongus*, *Gastrocopta pediculus*, *Opeas hannense*, *Streptosteles musaecola*, '*Microcystina*' *gerritsi*) were more frequent in shrubland–forest and relict tree habitats than in open habitats (Table 3). By contrast, several other species (*Gastrocopta servilis*, *Ceciloides aperta*, *Allopeas gracile*, *Allopeas micra*, *Quickia concisa*, *Subulina octona*) were more frequent in relict tree and open habitats than in forest–shrubbyland remnants; and *Paropeas achatinaceum* and *Bradybaena similis* were most frequent in open habitats. All the species found in highly modified, open habitats on the coastal plain were also present in forest and shrubland.

The presence of fossil shells of *Allopeas gracile*, *Gastrocopta pediculus* and *Lamellidea oblonga* in archaeological sites on Pacific islands has generally been assumed to be indicative of open habitats in anthropologically disturbed landscapes (e.g. Christensen & Kirch 1981; Hunt 1981: 263; Rollett 1992: 92; Kirch 1993; Allen 1998: 20). However, the

Table 3 Percentages of sites occupied by selected landsnail species within different habitat types on the Rarotongan coastal plain: A, littoral open shrubland (2 sites); B, shrubland and forest remnants (14 sites); C, relict trees (9 sites); D, open anthropogenic habitats (9 sites).

	A	B	C	D
<i>Orobophana pacifica</i>	100	86	22	0
<i>Assimineea lucida</i>	100	7	0	0
<i>Truncatella guerinii</i>	100	36	0	0
<i>Melampus fasciatus</i>	50	14	0	0
<i>Melampus luteus</i>	100	21	0	0
<i>Lamellidea oblonga</i>	0	57	44	0
<i>Pacificella variabilis</i>	0	93	67	22
<i>Tornatellides oblongus</i>	0	50	56	33
<i>Gastrocopta pediculus</i>	0	57	44	22
<i>Gastrocopta servilis</i>	0	43	100	100
<i>Nesopupa armata</i>	0	57	44	0
<i>Ceciloides aperta</i>	0	7	56	56
<i>Allopeas gracile</i>	0	29	56	67
<i>Allopeas micra</i>	0	29	44	67
<i>Opeas hannense</i>	0	93	89	78
<i>Paropeas achatinaceum</i>	0	7	11	56
<i>Subulina octona</i>	0	14	67	89
<i>Streptostele musaecola</i>	0	93	100	67
<i>Libera fratercula</i>	0	64	11	0
' <i>Microcystina</i> ' <i>gerritsi</i>	0	79	89	56
<i>Quickia concisa</i>	0	36	56	56
<i>Bradybaena similaris</i>	0	14	11	56

findings of the present study clearly indicate that these three species inhabit native forest and shrubland, as well as more open, disturbed habitats. *Allopeas gracile* was more frequent in modified habitats than in shrubland–forest, whereas *G. pediculus* was most frequent in intact shrubland and forest. As already mentioned, *L. oblonga* was found in shrubland–forest and relict tree habitats only on the Rarotongan coastal plain, suggesting that this species is intolerant of cleared, open habitats.

Most of the species recorded here in the modern coastal landsnail fauna were ground-dwelling, but some were arboreal or semi-arboreal. The arboreal taxa included *Pupisoma orcula* and *Diastole conula*, and semi-arboreal

species, which were found on the ground as well as on trees and shrubs, included *Orobophana pacifica*, *Lamellidea oblonga*, *Pacificella variabilis*, *Nesopupa armata* and *Quickia concisa*. *Liardetia sculpta* was not found alive, but was probably arboreal. Four ground-dwelling species (i.e. *Ceciloides aperta*, *Opeas hannense*, *Streptostele musaecola*, 'Microcystina' *gerritsi*) were evidently partly subterranean in habit, with fresh, empty shells locally present to depths of 0.3–1.0 m in soils on the coastal plain.

Species declines and extinctions

Comparison of the fossil and modern distributions of species on the Rarotongan coastal plain indicates that many species that were formerly widely distributed have undergone marked decline or become extinct. Species with narrower modern distributions on the coastal plain included *Georissa striata*, *Orobophana pacifica*, *Sturanya parvula*, *Atropis rarotongana* n.sp., *Omphalotropis variabilis*, *Lamellidea oblonga*, *Lamellidea pusilla*, *Gastrocopta pediculus*, *Nesopupa rarotonga* n.sp., *Allopeas gracile*, *Libera fratercula*, *Minidonta matavera* n.sp., *Discocharopa aperta* and *Sinployea andrewi*. This group included three species with highly restricted modern distributions, present at one or two sites only (i.e. *Atropis rarotongana* n.sp., *Minidonta matavera* n.sp., *Sinployea andrewi*).

Twenty species have apparently died out on the coastal plain. Two of these are still extant in inland Rarotonga (i.e. *Assimineea parvula*, *Lamprocystis venosa*). The status of *Nesopupa pleurophora* is presently unknown, but the remainder of this group, including *Garrettia rotella*, *Libera subcavernula*, eight species of *Minidonta*, six species of *Sinployea*, and *Liardetia discordiae*, are probably extinct.

The chronological history of landsnail species declines and extinctions on the Rarotongan coastal plain is poorly known. Some extinct species are known only from fossils in ground soils that began forming sometime after c. 4500 cal. BP (Moriwaki *et al.* 2006). This group includes *Nesopupa pleurophora*, *Minidonta aroa* n.sp., *Minidonta arorangi* n.sp., *Minidonta iota* n.sp., *Minidonta kavera* n.sp., *Minidonta pue* n.sp., *Minidonta* sp. and *Sinployea titikaveka* n.sp. However, the majority of the extinct species are present as fossils in near-coastal ground soils and paleosols that are inferred to have formed after the mid- to late-Holocene high sea-level stand (i.e. younger than c. 800–500 cal. BP – Moriwaki *et al.* 2006). This suggests that most, if not all, the species declines and extinctions reported here probably took place within the last few hundred years.

Table 4 Stratigraphic distributions of selected landsnail species in paleosols and ground soils of Holocene sequences on the Rarotongan coastal plain.

	Muri (site 23)		Pokoinu (site 35)		Avatiu (site 36)	
	paleosol	ground soil	paleosol	ground soil	paleosol	ground soil
<i>Georissa striata</i>	x	x	x	x	x	x
<i>Orobophana pacifica</i>			x	x	x	x
<i>Sturanya parvula</i>	x	x	x	x	x	x
<i>Assimineea parvula</i>			x	x	x	x
<i>Atropis rarotongana</i> n.sp.	x	x	x			
<i>Garrettia rotella</i>		x				
<i>Omphalotropis variabilis</i>	x	x	x	x	x	x
<i>Gastrocopta pediculus</i>	x	x	x	x		x
<i>Nesopupa armata</i>	x	x	x	x	x	
<i>Nesopupa dentifera</i>			x	x		
<i>Nesopupa rarotonga</i> n.sp.	x				x	
<i>Allopeas gracile</i>	x	x	x	x	x	x
<i>Libera fratercula</i>	x	x				
<i>Libera subcavernula</i>	x		x	x	x	x
<i>Minidonta ngatangia</i> n.sp.	x	x				
<i>Minidonta rutaki</i> n.sp.			x	x	x	x
<i>Discocharopa aperta</i>	x	x	x	x	x	x
<i>Sinployea andrewi</i>	x	x	x	x		
<i>Sinployea atiensis</i>	x	x	x	x	x	x
<i>Sinployea muri</i> n.sp.	x					
<i>Sinployea rudis</i>		x				
<i>Sinployea tenuicostata</i>	x	x		x		x
<i>Lamprocystis venosa</i>	x			x		
<i>Liardetia discordiae</i>	x					

There are no consistent patterns of species turnover in fossil assemblages from the three stratified sequences examined on the Rarotongan coastal plain. Stratigraphic distributions of selected species in the sequences at Muri (sites 23A, 23B), Pokoinu (sites 35A, 35B) and Avatiu (sites 36A, 36B) are shown in Table 4. Several species were ubiquitous in paleosols and ground soils at all three sites (*Georissa striata*, *Sturanya parvula*, *Omphalotropis variabilis*, *Allopeas gracile*, *Discocharopa aperta*, *Sinployea atiensis*). Eleven species (*Orobophana pacifica*, *Assimineea parvula*, *Atropis rarotongana* n.sp., *Nesopupa armata*, *Nesopupa dentifera*, *Libera fratercula*, *Libera subcavernula*, *Minidonta ngatangia* n.sp., *Minidonta rutaki* n.sp., *Sinployea andrewi*, *Sinployea tenuicostata*) were

present in both the paleosol and the ground soil at one or two sites, and *Lamprocystis venosa* was sparsely distributed, but similarly showed no consistent stratigraphic trends. By contrast, *Liardetia discordiae*, *Nesopupa rarotonga* n.sp. and *Sinployea muri* n.sp. were found in paleosols only at the three sites. The absence of the first two species from ground soils at these sites is possibly a reflection of rarity, rather than evidence of decline. However, *Sinployea muri* n.sp. was common in the paleosol at the Muri site, and therefore its absence from the overlying ground soil may be indicative of local extirpation, if not extinction. The same applies to the absence of *Libera subcavernula* in the ground soil at Muri. Two other species (*Garrettia rotella*, *Sinployea rudis*) showed the reverse

trend, being found in ground soils only; and *Sinployea tenuicostata* was more frequent in ground soils than paleosols at the three sites. Whether this reflects actual local range expansions of *Garrettia rotella* and the two endemic *Sinployea* in late-Holocene time, or a patchy fossil record, is unknown. The fact that *Garrettia rotella* is present on both Rarotonga and Aitutaki suggests a further possibility that this species may have been a late-prehistoric introduction to Rarotonga.

Garrett (1881) gave a detailed account of the Rarotongan landsnail fauna, based on field visits in 1865 and 1869. He made few specific references to coastal habitats, but noted that *Orobophana pacifica* was 'strictly confined to the lowlands near the seashore, where they occur in prodigious numbers on stony ground' (p. 407); *Sturanya parvula* was 'exceedingly abundant' (p. 407); *Garrettia rotella* was 'not uncommon on the ground in forest' (p. 405); *Libera fratercula* was 'confined to low-lands near the seashore, where it occurs in great numbers in forest' (p. 392); *Liardetia discordiae* was 'found in great abundance beneath rotten wood and among decaying leaves' (p. 383); and *Liardetia samoensis* was 'very abundant beneath dead wood and under loose stones in low-land forests near the seashore' (p. 384). Garrett found five species of endodontids and nine species of charopids living in inland parts of Rarotonga (Garrett 1881; Solem 1976, 1983; Appendix 3), including three of the species reported here from coastal fossil assemblages (i.e. *Libera subcavernula*, *Sinployea rudis*, *Sinployea tenuicostata*). However, he evidently found only *Libera fratercula*, and possibly also *Sinployea atiensis*, living in the lowlands on Rarotonga in the 1860s. This suggests that most of the coastal endodontid and charopid species had become extinct, or at least extremely rare, sometime before 1869. Similarly, he did not find any *Atropis rarotongana* n.sp., which indicates that this species was probably already in decline and had a restricted distribution by 1869.

The BPBM has collections of snails made by Buck in 1929 at coastal sites at Tupapa, Muri, Titikaveka and Nikao on Rarotonga. This material indicates that *Georissa striata* (BPBM 94359, 94419, 95422), *Sturanya parvula* (BPBM 94357, 94360, 94417, 95425) and *Omphalotropis variabilis* (BPBM 94346, 94347, 94418, 95371, 95420, 95421) were still fairly widely distributed on the coastal plain in the late 1920s. *Orobophana pacifica* was present at Nikao and at Tupapa (BPBM 94349–55, 95423, 95424), and *Libera fratercula* was collected at Tupapa only (BPBM 95356–60, 95362–95368). *Liardetia discordiae* evidently had a

restricted distribution, as it was collected at a single site near Nikao (BPBM 95413–4). Buck did not collect any *Garrettia rotella*, which indicates that this species was either scarce or already extinct by the late 1920s. Similarly, a lack of collections of *Assiminea parvula* and *Sinployea atiensis* suggests that these species were probably also scarce or extinct in lowland habitats by the 1920s.

Collections made by Price in 1964–65 indicate that *Libera fratercula* was present along the northeastern coast between Pue and Matavera, and on Motutapu and Oneroa islets. Solem (1976: 425) noted that

a particularly large colony of *Libera fratercula rarotongensis* is found 1.6–2.8 miles east of Avarua on both sides of the main road. Except for scattered houses, where the coral boulders and part of the undergrowth have been cleared away, the colony is continuous. It starts just inside the vegetation above the storm high-tide mark and continues through the coral boulder zone, fading out about 150 yd. inland, congruent with the end of the boulders. The vegetation consists of typical lowland scrub, coconut palms, and a few large trees.

Price also found an extant population of *Libera subcavernula* in dry, scrubby vegetation on the west side of Avatiu Harbour (FMNH 144514–5), and collected *Orobophana pacifica* at Avatiu Harbour, Tupapa, and at Black Rock on the northwestern coast of Rarotonga (FMNH 144513, 144555, 144617).

Collections made on Rarotonga in 1994 by Craig (1995; NMNZ) indicate that *Georissa striata* was present in coastal forest on Motutapu (and in secondary forest and slope forest in the upper Avatiu Valley); *Orobophana pacifica* was present at Tupapa, and on Motutapu and Oneroa islets; *Sturanya parvula* was present on Motutapu and Oneroa; and *Libera fratercula* was present at Tupapa.

In summary, most of the coastal endodontids and *Sinployea* on Rarotonga had probably declined or become extinct before Garrett's visits in the 1860s, and *Atropis rarotongana* n.sp. was probably also in decline by that time. *Garrettia rotella* was reportedly moderately common in the 1860s, but had evidently declined markedly, or was already extinct, by the late 1920s. Fossil assemblages indicate that *Liardetia discordiae* was rare on the Rarotongan coastal plain in late-prehistoric time; this species was still extant in the late 1920s but died out subsequently. Whether *Assiminea parvula* and *Sinployea atiensis* died out on the coastal plain before or after the 1920s is not known. *Libera subcavernula* had probably become rare on the coastal plain by 1869; a small

population survived on the west side of Avatiu Harbour until 1964, but subsequently died out. *Georissa striata*, *Sturanya parvula* and *Omphalotropis variabilis* were apparently relatively common on the coastal plain in the late 1920s, but coastal populations of all three species have declined markedly since then. *Libera fratercula* evidently had a restricted distribution on Rarotonga by the late 1920s, and the population has declined further since the mid-1960s. The same is probably true for *Orobophana pacifica*. By 2005–07, coastal populations of three other species (*Atropis rarotongana* n.sp., *Minidonta matavera* n.sp., *Siployea andrewi*) had declined to the point where they were critically endangered, if not already extinct.

Introduced species

No stratified fossil deposits pre-dating human settlement have been found on Rarotonga, and so the composition of the former 'native' landsnail fauna is not known directly. Clearly, the original fauna must have included all the known Rarotongan endemics listed in Table 1 and Appendix 3, and it probably also included the littoral assimineids (i.e. *Assimineea lucida*, *Assimineea* sp. 1), ellobiids and *Truncatella guerinii*. The non-endemic component of the terrestrial fossil fauna probably includes a mix of indigenous species and non-indigenous synanthropic adventives. *Gastrocopta pediculus*, and the extra-Pacific species *Allopeas gracile* and *Pupisoma orcula*, were introduced to Polynesia in prehistoric time (e.g. Pilsbry 1916–18; Kirch 1973; Preece 1998). In the Cook Islands, the first two of these were introduced to Aitutaki, Ma'uke and Miti'āro well before European contact, as indicated by fossil shells in archaeological sites ranging in age from the thirteenth to sixteenth centuries AD (Craig 1995; Allen 1997, 1998; Walter 1998; Allen & Wallace 2007; Brook *et al.* 2010), and the fossil record indicates that they have probably also been present on Rarotonga for several centuries or more. The presence of single fossil shells of *Costigo saparuaana* and *Pupisoma orcula* in a ground soil at Rutaki (site 29) suggests that these species, which are native to Indonesia and the Old World tropics, respectively, were also introduced to Rarotonga in prehistoric time. *Lamellidea pusilla* and *Liardetia samoensis* have also been identified as possible human commensals, thought to have been carried eastwards across the Pacific in prehistoric time (e.g. Baker 1938; Cooke & Kondo 1961). Similarly, if *Discocharopa aperta* is a single widespread species, as suggested by Solem (1983), then it too may have been a human commensal,

introduced to central and eastern Pacific islands in pre-historic time. Cooke & Kondo (1961: 173) suggested that the Polynesian distribution of *Pacificella variabilis* was largely due to synanthropic introductions. However, fossils of this species have been reported from sedimentary deposits pre-dating human settlement on Henderson Island in southeastern Polynesia (Preece 1998), indicating that it is indigenous to the southeastern Pacific. Whether or not *Lamellidea pusilla*, *Pacificella variabilis*, *D. aperta* and *Liardetia samoensis* are indigenous or non-indigenous on Rarotonga is presently unknown.

At present, there is insufficient information to determine if the other Polynesian species and Cook Islands species in the fossil fauna listed in Table 1 – all of which are fully terrestrial and known from two or more widely separated oceanic islands – are indigenous or non-indigenous on Rarotonga. Their widespread distribution in late-Holocene fossil deposits indicates that these species were probably all present on Rarotonga well before European contact, but whether they were also present before initial human settlement is unknown. All these species, along with *Lamellidea pusilla*, *Pacificella variabilis*, *Discocharopa aperta* and *Liardetia samoensis*, are cryptogenic species *sensu* Carlton (1996).

The modern landsnail fauna on Rarotonga contains many species that were certainly not part of the original fauna, and most of which were introduced to Rarotonga after European contact. This group includes all the extra-Pacific species listed in Table 1, the tropical Pacific species *Elasmias apertum*, *Kororia palaensis* and '*Microcystina*' *gerritsi*, and the Polynesian species *Diastole conula*.

Historical records of non-indigenous species from the 1860s onwards are summarised in Table 5. Garrett (1881: 402) noted that the slug *Deroceras laeve* was 'very abundant in damp places in the mountain ravines on Rarotonga' in 1865–69. This species was most likely introduced to Rarotonga following European settlement in the early 1800s, but a prehistoric introduction cannot be ruled out on present evidence (below). *Diastole conula* was apparently introduced to Rarotonga sometime in the mid-1800s. Garrett (1881: 383) recorded its distribution on Rarotonga in the 1860s as follows: 'Nearly 200 of this species were taken from the foliage of a large shrub, near the seashore at Rarotonga. Though carefully searched for, I failed to detect it in any other part of the island.'

Collections in AIM and NMNZ known or inferred to have been made on Rarotonga in 1899 by Cheeseman (i.e. mostly ex-Henry Suter collection) contained species

Table 5 Historical records of some non-indigenous landsnail species on Rarotonga, based on the following sources: late-Holocene fossils, present study; 1865–69 (Garrett 1881); 1923–25, Handy and Wilder collections (BPBM); 1929–30, Buck collection (BPBM); 1964, Price collection (FMNH) and Kraus collection (BPBM); 1994, Craig collection (NMNZ); 2005–07, present study. Early records of *Opeas hannense* are based on AIM AK113728. *Gulella bicolor* is not listed as no historical records are known.

	Late Holocene fossils	1865–69	1923–25	1929–30	1964	1994	2005–07
<i>Laevicaulis alte</i>							x
<i>Vaginulus plebeius</i>					x		x
<i>Elasmias apertum</i>			x	x	x	x	x
<i>Costigo saparuana</i>	x					x	x
<i>Gastrocopta pediculus</i>	x	x				x	x
<i>Gastrocopta servilis</i>			x	x		x	x
<i>Pupisoma orcula</i>	x						x
<i>Cecilioides aperta</i>							x
<i>Allopeas clavulinum</i>			x			x	x
<i>Allopeas gracile</i>	x	x	x	x		x	x
<i>Allopeas micra</i>				x		x	x
<i>Opeas hannense</i>			?	x		x	x
<i>Paropeas achatinaceum</i>					x	x	x
<i>Subulina octona</i>			x	x	x	x	x
<i>Streptostele musaecola</i>						x	x
<i>Deroceas laeve</i>		x			x		x
<i>Hawaiiia minuscula</i>				x			x
<i>Zonitoides arboreus</i>					x		x
<i>Diastole conula</i>		x	x	x	x	x	x
' <i>Microcystina</i> ' <i>gerritsi</i>						x	x
<i>Kororia palaensis</i>						x	x
<i>Liardetia sculpta</i>							x
<i>Quickia concisa</i>						x	x
<i>Bradybaena similaris</i>					x	x	x

previously recorded by Garrett (1881), including *Diastole conula*, but no new records. By contrast, collections in the BPBM made between 1923 and 1929 (i.e. by Handy, Wilder, Buck) contain the first records of *Elasmias apertum*, and the extra-Pacific species *Gastrocopta servilis*, *Allopeas clavulinum*, *Allopeas micra*, *Subulina octona* and *Hawaiiia minuscula*. All these species were evidently well established on Rarotonga by the 1920s, and the first two, along with *D. conula*, were widely distributed and common on the island. There is also one lot of *Opeas hannense* from Rarotonga in AIM (i.e. AK113728 – ex-C. Cooper

collection) that was definitely collected before 1929, possibly by Cheeseman, or sometime in the early 1900s.

At least four more non-indigenous species were established on Rarotonga by the early 1960s. Collections in the FMNH indicate that *Paropeas achatinaceum*, *Zonitoides arboreus* and *Bradybaena similaris* were fairly widely distributed in inland parts of the island by 1964, and the BPBM contains a specimen of *Vaginulus plebeius* collected at Avarua in 1964. A further four introduced species were first collected in 1994: *Kororia palaensis*, '*Microcystina*' *gerritsi*, *Quickia concisa* and the carnivorous snail *Streptostele musaecola*

(NMNZ). As noted in the Systematics section, *Microcystina gerritsi* was first recorded from other islands in the Cook group in the early 1900s, and may have been established on Rarotonga by then as well. Several non-indigenous species were first recorded on Rarotonga during surveys for the present study in 2005–07. Of these, *Cecilioides aperta*, *Liardetia sculpta* and *Laevicaulis alte* (see Appendix 3) were probably relatively recent introductions to this island, whereas *Gulella bicolor* is inferred to have been introduced earlier, possibly in the late 1800s or early 1900s (below).

Most of the landsnail species that were introduced to Rarotonga since European contact were widely distributed and common on the island in 2005–07. Many were frequent in forest and shrubland remnants on the coastal plain, and predominated in highly modified, open lowland habitats, where members of the pre-contact snail fauna were absent or very scarce. Many of the modern adventives had wide ecological ranges on Rarotonga: species found from near sea-level to the highest peaks included *Vaginulus plebeius*, *Elasmias apertum*, *Allopeas clavulinum*, *Paropeas achatinaceum*, *Subulina octona*, *Deroceras laeve*, *Diastole conula*, *Kororia palaensis* and *Bradybaena similaris*. Some other modern adventives were widely distributed in lowland habitats but not found in inland parts of the island. This group included *Laevicaulis alte* (see Appendix 3), *Gastrocopta servilis*, *Cecilioides aperta*, *Allopeas micra*, *Hawaiiia minuscula*, *Microcystina gerritsi* and *Quickia concisa*.

Some introduced species appear to have declined on Rarotonga within the last 100 years or so, and at least one species has died out. As already noted, comparison of collections of fossil and modern shells of *Allopeas gracile* and *Gastrocopta pediculus* made during the present study indicates that these species, both of which were introduced in prehistoric time, were formerly more widely distributed and common on the coastal plain around Rarotonga, and on Motutapu and Oneroa islets. *Zonitoides arboreus*, which was probably introduced to Rarotonga in the mid-twentieth century, was evidently also in decline. Collections in the FMNH indicate that this species was locally common in inland parts of Rarotonga in 1964–65, but in 2005–07 it was found at a single coastal site and nowhere else on the island. The carnivorous snail *Gulella bicolor* was probably introduced to Rarotonga sometime after the late 1800s, but subsequently died out. It is known only from rare empty shells in ground soils at Titikaveka, Rutaki and Avatiu (sites 25, 29, 36A). The European slug *Limacus flavus* (Linnaeus, 1758) was recorded from Rarotonga by Cockerell (1891:

222), based on specimens in the BMNH, and this identification has been confirmed by Gary Barker (pers. comm. 2005). The BMNH specimens were collected by William Wyatt Gill, probably between 1877 and 1883, when he was stationed on Rarotonga, but there have been no other records of *L. flavus* from this island, and it was not found during the surveys in 2005–07. Assuming the locality information on the museum label is correct, this suggests that *L. flavus* was present on Rarotonga in the late 1800s and subsequently died out there.

Discussion

Garrett (1872, 1881), Baker (1938) and Solem (1972, 1976, 1983) documented the existence of a rich, endemic landsnail fauna in the interior of Rarotonga. This included one species of Achatinellidae (i.e. the monotypic *Tekoulina pricei*), one of Partulidae (*Partula assimilis*), five species in three genera of Endodontidae (*Libera*, *Minidonta*, *Thaumatodon*), 11 species of Charopidae in the genus *Sinployea*, and three species of Euconulidae in the endemic subgenus *Lamprocystis* (*Avarua*) (Appendix 3). A brief survey of inland habitats carried out during the present study found a further undescribed species of *Sinployea*, and at least four new species of *Lamprocystis* (*Avarua*) (Appendix 3), giving a total of 26 endemic landsnail species known from inland Rarotonga.

The late-Holocene fossil snail fauna described here from the Rarotongan coastal plain contained at least 17 endemic species, comprising 40% of the known pre-European lowland snail fauna. However, it included only four of the endemics recorded previously from the interior of the island (i.e. *Libera subcavernula*, *Sinployea rudis*, *Sinployea tenuicostata*, *Lamprocystis venosa*). The other endemics in the coastal fossil fauna comprised one species of Assimineidae (*Atropis rarotongana* n.sp.), nine species of Endodontidae, and four species of *Sinployea*. Thus the majority of the endemic landsnail species on Rarotonga were evidently restricted to either inland or coastal habitats, with very few species common to both. Further, all but two of the largest species of *Sinployea* were apparently restricted to inland parts of Rarotonga, the exceptions being *S. rudis* and *S. tenuicostata*, which attained a larger adult size in inland habitats than on the coastal plain.

Atropis rarotongana n.sp. was widely distributed around the coastal plain on Rarotonga, but all the other putative lowland endemics had locally restricted distributions. *Minidonta matavera* n.sp., *Minidonta ngatangiia* n.sp.,

Minidonta pue n.sp. and *Minidonta* sp. had allopatric or parapatric distributions on the coastal plain on the eastern side of the island, whereas *Minidonta aroa* n.sp., *Minidonta arorangi* n.sp., *Minidonta iota* n.sp., *Minidonta kavera* n.sp. and *Minidonta rutaki* n.sp. had overlapping distributions on the western side. Similarly, *Sinployea tupapa* n.sp. was restricted to northeastern Rarotonga and had a non-overlapping distribution with respect to *Sinployea muri* n.sp. and *Sinployea titikaveka* n.sp., whereas the last two species (and *Sinployea tenuicostata*) had overlapping distributions.

Habitat information provided by Garrett (1872, 1881) and Solem (1983) indicates the inland-restricted endodontids and *Sinployea* showed a similar variety of distribution patterns, with some species found in one or two valleys only (e.g. *Libera tumuloides*, *Minidonta zebrina*, *Thaumatodon multilamellata*, *Sinployea avanaensis*, *Sinployea canalis*, *Sinployea decorticata*, *Sinployea otareae*, *Sinployea youngi*), and others with wider distributions apparently spanning several valleys (e.g. *Minidonta unilamellata*, *Sinployea peasei*, *Sinployea harveyensis*, *Sinployea proxima*). Similarly, in 2005–07 five of the inland-restricted species of *Lamprocystis (Avarua)* had overlapping, partly sympatric distributions centred on Te Ko‘u and Te Manga, and one had an allopatric or parapatric distribution centred on Maungatea (Appendix 3); the more widely distributed congener *Lamprocystis (Avarua) venosa* (below) was sympatric with all these species.

The known fossil and historical distributions of the four endemic species common to both inland and coastal habitats were as follows. Fossils of *Libera subcavernula* were abundant on the coastal plain around the western and southern coast of Rarotonga between Avatiu and Akapuao, and were patchily distributed and uncommon on the north-eastern and eastern coast between Pue and Muri; snails were reportedly common in mountain ravines in the interior of Rarotonga in 1869 (Garrett 1872, 1881). The fossil distribution of this species on the coastal plain was largely parapatric with respect to the coastal-restricted Cook Islands species *Libera fratercula*, but these two species were locally syntopic. Fossils of *Sinployea rudis* were widely distributed and locally common on the coastal plain around southern and southeastern Rarotonga, and were present also at a site near Pue on the northern coast; this species was reportedly abundant, living on the ground in several inland valleys on Rarotonga, in 1869 (Garrett 1872, 1881). Fossils of *Sinployea tenuicostata* were widely distributed but rare on the coastal

plain; Garrett (1872: 229) described this as a ‘somewhat rare species, having a wide range on the island, and generally found on the ground on the sides of ravines’. Fossils of *Lamprocystis (Avarua) venosa* were rare on the coastal plain, suggesting that this species was uncommon in this habitat. However, it was widely distributed and abundant in inland Rarotonga in 1869 (Garrett 1881), and in 2005–07 was widespread in low- to high-elevation forest (Brook, pers. obs.). These four species formerly had the widest known distributions of any endemic snails on Rarotonga, although *Libera subcavernula*, *S. rudis* and *S. tenuicostata* are now apparently extinct, and *Lamprocystis (Avarua) venosa* has died out on the coastal plain.

The fossil fauna of the Rarotongan coastal plain included several non-endemic species that were apparently restricted to lowland habitats on this island. These included the Cook Island species *Garrettia rotella*, *Nesopupa dentifera*, *Nesopupa rarotonga* n.sp., *Libera fratercula* and *Sinployea andrewi*; the Polynesian species *Orobophana pacifica*, *Lamellidea oblonga*, *Tornatellides oblongus*, *Nesopupa pleurophora* and *Liardetia discordiae*; and the tropical Pacific species *Lamellidea pusilla*, *Pacificella variabilis* and *Discocharopa aperta*. Comparison of fossil and modern distributions indicates that two species (*Sturanya parvula*, *Liardetia samoensis*) inhabited the lowlands and lower hill slopes on Rarotonga. Non-endemic species that were more widely distributed in coastal and inland parts of Rarotonga included *Georissa striata*, *Assimineia parvula*, *Omphalotropis variabilis*, *Costigo saparuaana*, *Nesopupa armata* and *Sinployea atiensis*.

Moriwaki *et al.* (2006) have shown that the Rarotongan coastal plain is a relatively young geomorphologic feature, formed entirely in mid- to late-Holocene time. Their Holocene sea-level curve for Rarotonga indicates that sea-level reached the present level *c.* 6500–6000 yrs BP, and continued rising gradually until *c.* 4500 yrs BP, when it attained a maximum height of *c.* 1.5 m above present level. The mid-Holocene marine transgression from *c.* 6500 to 4500 yrs BP extended inland along former stream valleys, particularly the Avana, Avatiu and Takuvaine valleys, forming an indented rocky coastline with narrow, deep embayments separated by promontories of volcanics and cliffed Pleistocene alluvial fan terraces (Moriwaki *et al.* 2006). It follows that populations of coastal and lowland snails would have been restricted to volcanic or volcanic-derived substrata on lower hill slopes, fan-terrace remnants and valley mouths from *c.* 6500 to 4500 yrs BP, and shifted seaward onto bioclastic sediments of the emerging coastal plain after *c.* 4500 yrs BP.

The fossil distributions of endemic and indigenous snails on the Rarotongan coastal plain, including the sympatric, parapatric and allopatric distributions of the various lowland species of Endodontidae and *Sinployea*, thus represent biogeographic patterns that have arisen within the last few thousand years. However, local endemism and allopatry/parapatry on the coastal plain probably reflected, at least to some degree, biogeographic patterns that existed in adjacent areas prior to, and during, the mid-Holocene maximum transgression.

Populations of endemic and indigenous lowland snail species on Rarotonga presumably had a long history of such distributional changes during successive Quaternary glacial–interglacial cycles, as a result of changes in shoreline position, coastal geomorphology and island circumference caused by glacio-eustatic sea-level fluctuations. Throughout much of Pleistocene time, when sea-level was lower than at present, the coastal geomorphology around Rarotonga was probably broadly similar to the present situation on Mangaia (see Stoddart *et al.* 1985), comprising a narrow fringing reef platform, stepped cliffs of emergent reefal limestone (makatea), and elevated erosional terraces mantled by beach and storm deposits of bioclastic sand and gravel. The vertical and lateral extent of these emergent reefal limestones and associated bioclastic sediments would have varied as sea-level rose and fell by tens of metres or more, to as much as *c.* 140 m below present level (Rohling *et al.* 1998). Coastal geomorphology would also have been affected, albeit to a lesser extent, by subaerial and subterranean erosion of carbonate facies, and deposition of volcanic-derived alluvial sediments. By contrast, during Mid- to Late Pleistocene interglacial periods, when sea-levels rose close to the present level, or as much as *c.* 20 m higher than present (e.g. Howard 1997; Kindler & Hearty 2000), the fringing reef and associated carbonate facies would have been largely or entirely submerged, and the Rarotongan coastline was probably broadly similar to that existing at present or during the mid-Holocene highstand, respectively.

Origins of endemism

Rarotonga has never been connected to other land masses, so as on other isolated oceanic islands, all the endemic terrestrial mollusc species (and populations of indigenous, non-endemic species) must be descended from ancestors that dispersed over water (e.g. Gulick 1932; Zimmerman 1948; Vagvolgyi 1975; Peake 1981; Cowie 1996). As already noted,

the Rarotongan snail fauna contains some genus-level taxa represented by single endemic species (e.g. *Atropis*, *Tekoulina*, *Partula*, *Thaumatodon*), and others represented by multiple endemic species, namely *Libera* (2 species), *Minidonta* (11 species), *Sinployea* (15 species) and *Lamprocystis* (7 species). The endemic species in the first group most likely evolved on Rarotonga by allopatric divergence from ancestral source populations. However, the existence of the multiple endemic congeners in the second group could have resulted from endemic radiations on Rarotonga, a series of colonisation events followed by allopatric divergence, or a combination of both processes. The Rarotongan *Lamprocystis* has been placed in an endemic subgenus on anatomical grounds (Baker 1938), which suggests that the various species of this taxon at least represent an endemic radiation. A molecular genetic investigation presently being carried out by David Winter should indicate whether or not this interpretation is correct, and may provide information on ages of divergence of the various species. Unfortunately, extinctions have precluded a comprehensive investigation of genetic relationships among the Rarotongan Endodontidae and *Sinployea*, although partial phylogenetic histories could be determined from extant taxa, and possibly also from preserved tissue of some extinct species in museum collections.

If the endemism in Rarotongan *Lamprocystis*, and possibly also the endodontids and *Sinployea*, was largely or entirely owing to within-island cladogenesis, levels of congeneric endemic diversity may in part reflect the timing of colonisation of ancestral species, with the modern species-rich taxa possibly having had a longer history on Rarotonga than those taxa represented by few or no endemic species. The existence of a single endemic species of *Partula* on Rarotonga is interesting, given the presence of multiple endemic species of this genus on islands of similar age, such as Moorea and Tahiti (i.e. <2.5 Ma – Clouard & Bonneville 2005: table 1) in the Society Islands (Johnson *et al.* 1986; Johnson *et al.* 1993). Clearly, *Partula* is capable of undergoing relatively rapid radiations on high volcanic islands, which suggests that the ancestor of *Partula assimilis* colonised Rarotonga comparatively recently. The electrophoretic analysis by Johnson *et al.* (1986) indicated that *P. assimilis* is most closely related to *Partula lutea* from Borabora in the leeward Society Islands, but the age of divergence of these two species has not yet been determined.

As outlined in the introduction, Rarotonga has existed as a volcanic island since at least Late Pliocene time, and vegetation and terrestrial molluscs presumably first colonised

relatively soon after permanent land was established. Although only speculative, endemic radiations of snails on Rarotonga could theoretically have occurred at different times and for different reasons during the island's history. Basaltic eruptions from *c.* 2.3 Ma to possibly as late as 1.5 Ma formed a composite volcanic cone that reached a maximum height of at least 900 m above present sea-level. During this eruptive phase, intermittent pyroclastic eruptions and lava flows from the main vent(s) and parasitic cones probably killed off areas of vegetation on the flanks of the volcano, giving rise to a shifting mosaic of vegetation patches of different ages and composition, separated by areas of newly erupted, unvegetated lava and pyroclastic material. In theory, it is possible that such shifting patterns of vegetation destruction and fragmentation could have led to kipuka-type vicariant speciation (Zimmerman 1948) of forest and shrubland-restricted snail taxa, as has been documented on other oceanic islands for arthropods and lizards (e.g. Juan *et al.* 2000; Vandergast *et al.* 2004; Bloor *et al.* 2008).

The collapse of the upper part of the cone at the end of the basaltic eruptive phase clearly would have had a drastic impact on the biota of the volcano's summit and northern flank, but may have had little or no effect on the biota of the lower western, southern and eastern flanks. The central part of the island probably remained largely unvegetated during the subsequent eruptive phase from *c.* 1.4 Ma to 1.1 Ma, when phonolitic lava and pyroclastic material were erupted from vents within and on the margins of the collapse depression. During this period, any pre-existing vegetation and constituent snail populations on the flanks of the volcano would have been fragmented by a series of phonolite lava flows, which were emplaced in the Muri, Raemaru, Black Rocks and Tuakata areas. These flows presumably formed barriers to lateral dispersal of forest and shrubland-dwelling snails until vegetation became established over their upper surfaces. As with the earlier basaltic eruptive phase, this may have created a situation that contributed to vicariant speciation of snail taxa on Rarotonga.

In the last 1 million years since volcanism ended, geomorphology, climate and vegetation cover have probably been the main factors affecting snail distributions on Rarotonga. The effects of cyclical changes in coastal geomorphology caused by glacio-eustatic sea-level fluctuations have already been mentioned. In inland Rarotonga, erosion since *c.* 1 Ma has transformed a truncated volcanic cone into a topographically complex, rugged landscape of deep, steep-walled valleys, separated by knife-edge ridges. As noted, some

inland endemic species of endodontids and *Sinployea* were reportedly restricted to one or two valleys in 1869 (Garrett 1872, 1881), and some lowland endemics had highly restricted fossil distributions on the coastal plain, suggesting that micro-allopatric vicariant speciation may have occurred as a result of isolation of snail populations within separate valleys. At present, there are sparsely vegetated and unvegetated rocky bluffs and escarpments on the sides and at the heads of some valleys that presumably constitute physical barriers to landsnail dispersal, but elsewhere ridges and peaks are, or at least were prior to human modification, forested from valley floor to crest. It is difficult to see how vicariant speciation could have occurred in inland Rarotonga under modern conditions given the extensive forest cover, but the island's vegetation may have been rather different at times in the past. Although there is presently no direct information on ecological changes on Rarotonga during the Pleistocene, some inferences can be drawn from paleoclimatic and palynological data obtained elsewhere in the tropical Pacific.

Paleotemperature estimates derived from Mg/Ca in planktonic foraminifera indicate that sea-surface temperatures (SSTs) in the western and eastern tropical Pacific cooled by *c.* 2–5°C and *c.* 1°C, respectively, during the last glacial maximum (LGM) at *c.* 18 000 yrs BP, then rose rapidly to reach modern values by the start of the Holocene at *c.* 11 000 yrs BP (e.g. Lea *et al.* 2000; Koutavas *et al.* 2002; Stott *et al.* 2002, 2004; Visser *et al.* 2003; Gagan & Thompson 2005). SSTs within the Indo-Pacific warm pool in the tropical western Pacific during early to mid-Holocene time were generally similar or slightly warmer than present, whereas SSTs in the eastern tropical Pacific were slightly cooler than present until *c.* 4000–5000 yrs BP (Koutavas *et al.* 2002; Stott *et al.* 2004; Gagan & Thompson 2005). During the LGM, the zonal and meridional SST gradients in the tropical Pacific are thought to have been analogous to modern El Niño conditions, but by early Holocene time this had changed to a predominantly westward-concentrated La Niña-like state, with warming in the west and cooling in the east (Koutavas *et al.* 2002; Stott *et al.* 2002; Gagan & Thompson 2005; Koutavas & Lynch-Stieglitz 2005). The El Niño/Southern Oscillation variability in the tropical Pacific was apparently reduced throughout much of the early to mid-Holocene period; variance increased after *c.* 5000 yrs BP, and the highest frequency, and some of the most persistent and strongest El Niño events, occurred after *c.* 2000 yrs BP (e.g. Moy *et al.* 2002; Rein *et al.* 2005; Conroy *et al.* 2008).

Paleoclimatic and palynological evidence from terrestrial wetland sequences on subtropical Easter Island in southeastern Polynesia (27°08'S, 109°26'W), spanning the period 38 000 yrs BP to the present, confirm that the climate there was cooler and drier during the latter part of the last glacial period. Tree species persisted through the LGM, but forest cover was much reduced, forests were more open and shrubby, grassland was more common, and the tree-line was depressed below 500 m at times during this period (e.g. Flenley & King 1984; Flenley *et al.* 1991). Post-glacial warming led to the re-establishment of forest dominated by the endemic palm *Paschalococos disperta* (Arecaceae) over much of Easter Island after *c.* 12 000 yrs BP, and this forest persisted up until the period of human occupation beginning at *c.* 750 yrs BP (Flenley *et al.* 1991; Hunt & Lipo 2006; Hunt 2007; Mann *et al.* 2008). A pollen record from a montane swamp (463 m elevation) on O'ahu, Hawai'i, covering the period *c.* 28 100 ¹⁴C yrs BP to *c.* 7000 ¹⁴C yrs BP, indicates the LGM climate there was also drier and cooler than at present, with open-canopy forest and/or shrubland, and common grasses and Grammitidaceae-type ferns (Hotchkiss & Juvik 1999). Rainforest dominated by upland trees, climbers and palms re-established at this site after *c.* 16 200 ¹⁴C yrs BP (Hotchkiss & Juvik 1999).

Pollen records from two sites in Fiji show a rather different pattern, with the persistence of podocarp–broadleaved forest in the LGM at Wainisavulevu (780 m elevation) in central Vitu Levu, and from *c.* 14 000 ¹⁴C yrs BP to the present day at Lake Tagamaucia (820 m elevation) on Taveuni Island (Hope 1996: fig. 6). However, at the latter site there was a marked reduction in the abundance of upland and many lowland forest trees, and a concomitant increase in shrubs, climbers and palms, from *c.* 10 000 ¹⁴C yrs BP to 7000 ¹⁴C yrs BP, indicating that closed-canopy rainforest was replaced by open-canopy forest over this period. Hope (1996) suggested that this could have corresponded to a decline in temperature of a few degrees. A Holocene pollen record from Ātiu in the southern Cook Islands shows some similarities; here, the present lowland rainforest apparently established at *c.* 7500 ¹⁴C yrs BP, replacing open, fern-dominated vegetation that had existed for at least the preceding 1000 years (Parkes 1997). The latter included fern species indicative of a cooler climate than at present (Parkes 1997). Holocene pollen records from Mangaia indicate that rainforest containing broadleaved trees and tree ferns (*Cyathea*) was established by 7200 ¹⁴C yrs BP (Ellison 1994), but nothing is known of the earlier vegetation history of this island.

The differences between pollen records indicate that there was no uniform history of vegetation changes through Late Pleistocene and Holocene time on the islands in this region of the Pacific. The fact that tropical montane rainforest persisted (at least locally) on Vitu Levu suggests that the LGM climate of Fiji was warmer and wetter than at islands in higher latitudes and further east in the Pacific. In the South Pacific, these putative climatic differences were probably at least partly related to the longitudinal extent of the Indo-Pacific warm pool, and the influence of this water mass on the location and activity of the South Pacific Convergence Zone during the LGM. The pollen records from Taveuni and Ātiu suggest that the climate of the tropical south-central Pacific may have been somewhat cooler and/or drier than at present during early to mid-Holocene time (i.e. *c.* 10 000–7000 yrs BP), corresponding to a period when SSTs in the eastern Pacific were also slightly cooler than at present (Koutavas *et al.* 2002).

By extrapolation, it is possible that the forest cover of inland Rarotonga was much reduced during the cold phases of Pleistocene glacial periods and possibly also at times during interglacials. If this was the case, then forest-restricted snail taxa could potentially have undergone vicariant speciation as a result of population fragmentation within disjunct habitat refugia (e.g. within separate valleys), if these remained isolated for long enough. The presence of upland and lowland congeneric endemics in the Rarotongan landsnail fauna suggests speciation occurred not only among valleys, but also along altitudinal gradients. Whether this resulted from vicariant speciation among refugia, adaptive radiation in response to environmental factors (e.g. altitudinal differences in vegetation composition and structure, temperature, precipitation, and physico-chemical properties of the substratum), or a combination of both processes, is not known. However, whereas habitat fragmentation and/or environmental adaptation may have been key drivers of speciation of landsnails in inland Rarotonga during Mid- to Late Pleistocene glacial periods, shrubland and forest most likely persisted in coastal habitats on this island throughout glacial–interglacial cycles, and thus the radiations of endemic coastal landsnails on Rarotonga probably had a different origin. All the endemic coastal species in the genera *Minidonta* and *Sinployea* are known only from calcareous substrata. This suggests the possibility that glacio-eustatic sea-level changes may have driven vicariant speciation, with allopatry occurring predominantly during interglacial sea-level highstands, when limestone and bioclastic sand and

gravel substrata were absent, or of very limited extent (e.g. restricted to valley mouths), around Rarotonga. Variation among local populations of *Libera fratercula* on Rarotonga and the lagoon motu may have a similar origin.

To summarise, within-island cladogenesis of snail taxa on Rarotonga (e.g. *Libera*, *Minidonta*, *Sinployea*, *Lamprocystis* (*Avarua*)) could potentially have occurred as a result of vicariant speciation via population fragmentation on the flanks of the >900 m-high basaltic composite volcano that formed from *c.* 2.3 Ma to 1.5 Ma, and on the seaward flanks of the truncated cone from *c.* 1.4 Ma to 1.1 Ma. Following the cessation of volcanism at *c.* 1.0 Ma, erosion produced a topographically complex landscape of deep valleys and knife-edge ridges, within which vicariant diversification and possibly also adaptive radiation may have occurred, both among valleys, and along altitudinal gradients, in response to changing vegetation patterns and sea-levels during glacial–interglacial cycles. During this period, pulses of vicariant speciation of landsnails in inland Rarotonga may have been largely out of phase with those in coastal habitats, occurring predominantly in glacial and interglacial periods, respectively. The environmental factors thought to have driven landsnail speciation on Rarotonga involved a series of intermittent and cyclical processes, each of relatively short duration (i.e. ranging from hundreds of years in the case of separation by lava flows and pyroclastic deposits, to thousands of years in the case of interglacial sea-level highstands, and possibly as much as tens of thousands of years for climate-related vegetation changes during glacial periods). Environmentally driven cycles of fragmentation (allopatry) and re-expansion (i.e. with potential for parapatry and syntopy) of landsnail populations would have led to shifting mosaic distributions, and may well have resulted in the reticulate evolution of some landsnail clades on Rarotonga.

Non-indigenous species

The fossil and modern faunas of the Rarotongan coastal plain contained non-indigenous species known or inferred to have been introduced to Rarotonga from elsewhere, and non-endemic species of unknown provenance, which may or may not be indigenous to Rarotonga. Most, if not all, the non-indigenous species were probably inadvertent synanthropic introductions on foliage or in soil around the roots of crop and ornamental plants, though some species may have arrived as stowaways in imported cargo on canoes in prehistoric time, or since European contact on ships and, more

recently, on planes. The giant African snail (*Achatina fulica*), which has been introduced to many tropical Pacific islands, is not established on any of the Cook Islands, although individuals have been found on several occasions as stowaways in shipping and aircraft containers imported into Rarotonga from or via other Pacific islands. Nor have there been any known intentional introductions of carnivorous snails as biological control agents on Rarotonga or any of the other Cook Islands, unlike on some other Pacific islands (Civeyrel & Simberloff 1996; Cowie 2000, 2001b).

The fossil fauna of the coastal plain includes two non-indigenous snail species native to Asia (*Allopeas gracile*, *Pupisoma orcula*), one native to the Banda Sea region (*Costigo saparuana*), and one thought to be native to Indonesia and the tropical western Pacific (*Gastrocopta pediculus*). All are inferred to have been introduced to Rarotonga by Polynesians in prehistoric time. Some other non-endemic species in the fossil fauna were probably also introduced synanthropically to Rarotonga in prehistoric time (i.e. cryptogenic species, discussed below). However, the bulk of the exotic species in the modern fauna were evidently introduced after European contact. Published records and material in museum collections indicate that a large number of exotic landsnail species became widely established on tropical Pacific islands between the mid-1800s and early 1900s (e.g. Solem 1964; Cowie 1998b). On Rarotonga, the slug *Deroceras laeve* and the snail *Diastole conula* were established by the late 1860s, but the main influx of exotic species on this island apparently occurred after this time. According to Garrett (1881), *Diastole conula* had a highly restricted distribution on Rarotonga in 1869, which suggests that it had not been present on this island for long. It was presumably introduced to Rarotonga from one of the Society Islands. By contrast, *Deroceras laeve* was reportedly ‘very abundant in damp places in the mountain ravines on Rarotonga’ (Garrett 1881: 402). This species is native to the Palearctic region, and possibly also to North and South America (Barker 1999), and was established on several Polynesian islands by the mid- to late nineteenth century. It was apparently widespread in the interior of several Hawaiian islands by 1896 (Cowie 1997: 21–22), and was present on Tahiti before 1881 and in the Gambier group before 1884 (Garrett 1881, 1884 – as *Limax rarotonganus*). *Deroceras laeve* was most likely introduced to Rarotonga and other tropical Pacific islands through European commerce (e.g. Solem 1964; Cowie 1998b), but there is a remote possibility that it was introduced from South

America in prehistoric time, along with the sweet potato (Yen 1974) – the latter crop species was present on Mangaia by at least 500 yrs BP (Hather & Kirch 1991). Molecular genealogies may provide information on the source(s) and timing of introduction of *Deroceras laeve* to Polynesia.

The fact that so few exotic snail species were established on Rarotonga between the beginning of European settlement in 1827 and the late 1860s is rather surprising, given the diversity of new species and varieties of crop and ornamental plants that were introduced to the island over these four decades. The list of post-contact crop introductions included Arabian coffee, cassava, Cavendish bananas, chilli pepper (*Capsicum frutescens*), citron (*Citrus medica*), cocoa (*Theobroma cacao*), custard apple, granadilla, hop plant (*Humulus lupulus*), indigo (*Indigofera suffruticosa*), lime, loquat (*Eriobotrya japonica*), mango, orange, pawpaw, pineapple (*Ananas comosus*), rice, sea-island cotton, sweet potato and tomatoes (Wheeler 1842: 776; Gill 1856: 61; Buzacott 1866: 241; Cheeseman 1903; Beaglehole 1957: 68–69; Gilson 1980: 27, 40; McCormack 2007). These plant species were ultimately all derived from sources outside the central Pacific (i.e. Africa, Madagascar, Asia, America), but at least some of the cultivars introduced to Rarotonga were reported to have been imported from Tahiti (e.g. Chinaberry tree (*Melia azedarach*), custard apple, granadilla, kapok, orange, pigeon pea (*Cajanus cajan*) and sweet potato – Cheeseman 1903). Most were probably imported as seeds, but any brought in as potted plants, cuttings, fruit or tubers could well have been a vector for the introduction of exotic snails.

There was evidently a higher rate of snail introduction to Rarotonga between the late 1800s and early 1900s, with at least six new exotic species known to have become naturalised on the island by the 1920s. None of these is represented in the mollusc collection made by Cheeseman, which suggests that most, if not all, became established on Rarotonga after 1899. This group included one species native to the tropical South Pacific (*Elasmias apertum*), five species native to the Americas (*Gastrocopta servilis*, *Allopeas micra*, *Opeas hannense*, *Subulina octona*, *Hawaiiia minuscula*), and one species probably native to Asia (*Allopeas clavulinum*). The New Guinea species '*Microcystina*' *gerritsi* was established in the northern Cooks by the 1920s, and may have been introduced to Rarotonga by this time as well, possibly in association with imported plants of *Derris malaccensis* (below).

The cause of the influx of extra-Pacific species to Rarotonga over this period is not known directly. It was

presumably at least partly contingent on the timing and pattern of spread of the various alien species into, and establishment of adventive source populations elsewhere in, the Pacific region. However, it may also have been related in part to an increase in the volume of imported plant materials, or a change in the kinds of materials imported into Rarotonga (e.g. possibly a shift from predominantly seeds to cuttings and potted plants), following the establishment of a regular steamer service between Tahiti, Rarotonga and Auckland in 1885 (Gilson 1980: 52; Scott 1991: 41). Additionally, it may have been associated with horticultural development on Rarotonga following the land tenure reforms in the early 1900s (Crocombe 1964; Gilson 1980: 148, 150, 154).

By the late 1920s, at least 110 species of exotic plants introduced since European contact were naturalised on Rarotonga, and more than 190 other exotic crop and ornamental species were in cultivation in horticultural plots, domestic gardens, along roadsides and in a government nursery at Avarua (Cheeseman 1903; Wilder 1931; Scott 1991: 175–76; McCormack 2007). Plants introduced to Rarotonga between the 1860s and 1920s included species native to America, Africa, Madagascar, Asia, Southeast Asia/western Pacific ('Malesia'), New Caledonia, Australia, New Zealand and the Mediterranean, along with pantropical species of uncertain origin (Cheeseman 1903; Wilder 1931; McCormack 2007). Historical records in Cheeseman (1903) and Wilder (1931) indicate that cultivars of many of these plant species and varieties were imported to Rarotonga from other central Pacific islands, including Tahiti (avocado, *Angelonia salicariifolia*, *Eichhornia crassipes*, *Inga ynga*, *Meiococcus bijugatus*, *Musa* variety, *Phyllanthus acidus*, *Polyscias cumingiana*, *Polyscias guilfoylei*), Hawai'i (*Diospyros digyna*, two varieties of *Ipomoea batatas*), Samoa (*Musa* variety, *Solenostemon scutellarioides*), Fiji (*Alpinia purpurata*, *Musa* variety) and Mangaia (*Myoporum wilderi*). Other recorded sources of plant imports between the 1860s and 1920s included New Zealand (*Canna indica*, *Leptospermum scoparium*, *Leucadendron argenteum*), Australia (*Araucaria bidwilli*, *Brachychiton acerifolium*, *Pleiogyne solandri*), New Guinea (*Derris malaccensis*), India (*Musa* variety, *Zizyphus jujuba*), Sri Lanka (*Delonix regia*) and Jamaica (*Musa* variety) (Cheeseman 1903; Wilder 1931; McCormack 2007).

Elasmias apertum was possibly introduced to Rarotonga on plants imported from the Society Islands, where Garrett (1884: 83) noted that it was widespread and 'not uncommon'. The other species may also have been introduced to Rarotonga from other tropical Pacific islands. As noted in the

Systematics section, *Gastrocopta servilis*, *Allopeas clavulinum*, *Allopeas micra*, *Opeas hannense* and *Subulina octona* were all widely distributed in Polynesia by the early 1900s, and *Hawaiiia minuscula* was present in the Hawaiian Islands by 1850, and in New Caledonia and Lord Howe Island by the late 1800s (Peile 1936; Solem 1964; Cowie 1998b). Some snail species may have been introduced to Rarotonga from more than one secondary source. For example, checks on imports into Hawai'i in the early 1900s found *S. octona* on plants shipped from Singapore, Indonesia, the Philippines and Fiji (Thaanum 1927).

There were further introductions of exotic plant species and cultivars to Rarotonga through the mid- to late twentieth century, involving species and cultivars ultimately derived from a wide variety of sources. At least nine further species of exotic snails and slugs became established on Rarotonga during this period. This group included two species native to Africa (*Laevicaulis alte*, *Streptostele musaecola*), one native to western Africa and/or western Indian Ocean islands (*Quickia concisa*), three native to the Americas (*Vaginulus plebeius*, *Ceciloides aperta*, *Zonitoides arboreus*), and four native to Asia and the western Pacific (*Paropeas achatinaceum*, *Kororia palaensis*, *Liardetia sculpta*, *Bradybaena similaris*). Most of the species native to the Americas, Africa and Asia were already widely distributed in the tropical Pacific by the late 1800s to early 1900s (e.g. *Laevicaulis alte*, *V. plebeius*, *C. aperta*, *P. achatinaceum*, *Z. arboreus*, *B. similaris* – Cooke 1934; Solem 1964; Cowie 1998b), and the Rarotongan populations of these species may well have been derived from other Pacific islands. *Liardetia sculpta* is probably native to China, and was established on Guam and Pohnpei in Micronesia by the early 1900s (Baker 1938). The present record from Rarotonga is the first from Polynesia. *Kororia palaensis* is native to Micronesia (Baker 1941); it was apparently introduced to Polynesia relatively recently, having been first recorded from the Society Islands in 1974 (FMNH), Rarotonga in 1994 (this study), and Samoa in 1998 (Cowie 2001a – as *Ovachlamys fulgens*). *Streptostele musaecola* is native to West Africa but had become widely naturalised in tropical America by the early 1900s (Pilsbry 1930; Hausdorf & Bermúdez 2003). The earliest Polynesian records of this species were from Tahiti in 1974 and Samoa in 1975 (Solem 1989). *Quickia concisa* has also recently become widely established in Polynesia; the earliest records are from Samoa in 1992–94 (i.e. as *Succinea modesta* and *Succinea manuana* – Cowie 2001a; Cowie & Robinson 2003), and Rarotonga

in 1994 (this study), but the source and history of spread of this species within Polynesia are presently unknown.

The suite of extra-Pacific terrestrial molluscs introduced to Rarotonga since European contact comprises a large subset of the more than 55 alien species now established in the tropical Pacific, which are contributing to the homogenisation of Pacific island faunas (Cowie 2001b, 2004). On Rarotonga, as on other Pacific islands, the extra-Pacific species typically predominate in synanthropically modified habitats, and are also common and widespread in native habitats. Most of the extra-Pacific species represented on Rarotonga have global distributions restricted to the tropics; the only exceptions are *Deroceas laeve*, *Hawaiiia minuscula* and *Zonitoides arboreus*, which range from tropical to temperate latitudes. Interestingly, despite extensive trade between New Zealand and Rarotonga since the mid- to late 1800s, *D. laeve* and *Z. arboreus* are the only non-indigenous species common to both faunas. The former species was evidently established in Rarotonga much earlier than in New Zealand (Garrett 1881; Barker 1999), whereas *Z. arboreus* was first recorded in the mid-1900s in both countries (Barker 1999; this study). No native New Zealand species are known to have become established on Rarotonga or elsewhere in the Cook Islands. This includes the globally distributed tramp species *Paralaoma servilis* (Shuttleworth, 1852), which ranges north to the subtropical Kermadec Islands in the New Zealand region, and has recently been recorded from Easter Island (Kirch *et al.* 2009) and Hawai'i (Carl Christensen, pers. comm. 2008). Thus the primary and secondary source populations of alien landsnails and slugs introduced to Rarotonga in historical time were evidently mostly or all in the tropics, with little or no input from temperate sources.

Cryptogenic species

In addition to known and inferred non-indigenous species, the Rarotongan landsnail fauna contained 20 cryptogenic species (*sensu* Carlton 1996), including one species known only from inland Rarotonga (i.e. *Diastole* sp. – Appendix 3), seven known from two or more of the southern Cook Islands, eight with wider Polynesian distributions and four with Pacific-wide distributions. Five species in the second group (*Sturanya parvula*, *Nesopupa dentifera*, *Nesopupa rarotonga* n.sp., *Libera fratercula*, *Sinployea atiensis*) were widely distributed among the southern Cook Islands; *Sinployea andrewi* is known from Rarotonga and Mangaia only; and *Garrettia rotella* is known from Rarotonga and

Aitutaki only (Brook, unpub. data). Four cryptogenic Pacific species (*Lamellidea pusilla*, *Pacificella variabilis*, *Discocharopa aperta*, *Liardetia samoensis*) were ubiquitous on the five main islands in the southern Cooks, and all but one of the cryptogenic Polynesian species were similarly widely distributed among the southern Cook Islands (i.e. *Georissa striata*, *Orobophana pacifica*, *Assimineea parvula*, *Omphalotropis variabilis*, *Lamellidea oblonga*, *Tornatellides oblongus*, *Nesopupa armata*, *Liardetia discordiae*). The exception was *Lamprocystis excrescens*, known from Rarotonga only in the Cook Islands (Garrett 1881).

All the cryptogenic species except *Diastole* sp. and *Lamprocystis excrescens* were represented in late-Holocene fossil faunas on Rarotonga, but whether or not they were present on this island before human settlement is unknown. It is possible that some or all were inadvertently dispersed among islands by Polynesian voyagers, as has been suggested by Baker (1941) for *Lamprocystis excrescens*, *Liardetia discordiae* and *Liardetia samoensis*, and by Cooke & Kondo (1961) for *Lamellidea oblonga*, *Lamellidea pusilla*, *Pacificella variabilis* and *Tornatellides oblongus*. It is also possible that *Libera fratercula* and *Orobophana pacifica*, which have traditionally been used by Cook Islanders for making shell necklaces, may have been intentionally translocated between islands for cultural purposes, as happened with *Partula hyalina* in the Austral and Cook islands (Lee *et al.* 2007). However, without molecular genealogical data, or a longer fossil record, the provenance of these species on Rarotonga remains uncertain.

Patterns of species decline and extinction

Studies of changes in the landsnail faunas of some other Polynesian islands have found evidence of landsnail extinctions following initial human settlement, in the late-prehistoric period, and after European contact (e.g. Christensen & Kirch 1986; Dye & Tuggle 1998; Preece 1998; Burney *et al.* 2001; Conte & Kirch 2004; Kirch *et al.* 2009). As noted, no high-resolution fossiliferous sequences or stratigraphically discrete pre-settlement fossil assemblages were found on the Rarotongan coastal plain during the present study. As a result, it is not possible to determine if any coastal landsnail species died out during the initial settlement period. The limited stratigraphic evidence available does suggest that most of the endemic coastal landsnails found in paleosols and ground soils were extant during the period of prehistoric human occupation of this

island. Garrett did not find any of these endemics in the lowlands during his visits to Rarotonga, which indicates that they had either died out on the coastal plain, or become extremely rare, before 1869. At present, there is insufficient taphonomic resolution to determine if the decline and extinction of these endemic species took place during the late-prehistoric period (i.e. before 1789), in the early post-contact period, or after European settlement in 1827. At least one formerly common non-endemic species (*Sinployea andrewi*) not found by Garrett had probably also undergone a marked decline on Rarotonga before the 1860s. Several non-endemic coastal species that were evidently still common in the 1860s (e.g. *Georissa striata*, *Orobophana pacifica*, *Sturanya parvula*, *Garrettia rotella*, *Omphalotropis variabilis*, *Libera fratercula* – Garrett 1881) are known or inferred to have declined markedly since then, and two species (*Assimineea parvula*, *Liardetia discordiae*) have apparently died out completely in coastal habitats on Rarotonga.

By contrast with the coastal fauna, at least five endemic species of Endodontidae and 12 endemic species of *Sinployea* were still extant in inland parts of Rarotonga in the late 1860s (Garrett 1872, 1874, 1881; Solem 1976, 1983; Appendix 3). Some of these species were reported to be relatively common at that time (e.g. *Libera subcavernula*, *Thaumatodon multilamellata*, *Sinployea harveyensis*, *Sinployea proxima*, *Sinployea rudis*). However, several others were evidently rare (e.g. *Minidonta zebrina*, *Minidonta unilamellata*, *Sinployea canalis*, *Sinployea planospira*, *Sinployea tenuicostata*, *Sinployea youngi*), and one species (*Libera tumuloides*) had a highly restricted geographic distribution (Garrett 1872, 1874, 1881). This suggests that at least some inland snail species were already in decline by the 1860s.

Collections made by Cheeseman indicate that *Libera subcavernula* was abundant, and *Sinployea tenuicostata* was still extant, in 1899. However, there are no endodontids or *Sinployea* in the BPBM collections made in inland parts of Rarotonga between 1925 and 1930, which suggests that most of the species recorded by Garrett (1881) were probably either very scarce or extinct by that time. All the inland endodontids and most of the endemic *Sinployea* are now assumed to be extinct (Solem 1976, 1983; Appendix 3). One non-endemic species, *Lamprocystis excrescens*, apparently also died out in inland Rarotonga between the 1860s and 1920s. Garrett (1881: 381) reported that this species was common ‘under damp rotten wood and beneath moist, decaying leaves on the sides of inland ravines’, but it has not been collected or reported since the 1860s.

Two endemic arboreal species found by Garrett on Rarotonga in the 1860s were still common in 2005–07. One of these, *Partula assimilis*, evidently underwent a marked decline sometime in the early to mid-1800s. Garrett (1881: 395) noted: ‘In some valleys where it was formerly abundant, it appears to have become extinct. My conclusions are based on the profusion of half decomposed shells scattered over the grounds, and not observing any living example.’ According to Garrett (1881), *P. assimilis* had a patchy distribution but was locally common in inland valleys in the 1860s, and the same was true in 2005–07 (Appendix 3). *Lamprocystis (Avarua) venosa* was: ‘Extremely abundant ... and widely distributed throughout the inland ravines on Rarotonga’ in the 1860s (Garrett 1881: 382), and was similarly common and widely distributed in 2005–07 (Appendix 3). Three non-endemic operculate taxa recorded by Garrett (1881) were also still widely distributed and common in inland forest on Rarotonga in 2005–07. These included two ground-dwelling species (*Georissa striata*, *Assimineia parvula*) and one terrestrial to semi-arboreal species (*Omphalotropis variabilis*). By contrast, *Sinployea peasei* was evidently in serious decline or extinct. Garrett (1881: 386) reported taking ‘hundreds of examples in different parts of Rarotonga’ in the 1860s. It was still widely distributed but uncommon at *c.* 120–580 m in inland forests in 1964–65 (Solem 1983), but none was found in 2005–07 (Appendix 3). *Sinployea harveyensis* was thought to be extinct by the early to mid-1900s (Solem 1983: 45, 97), but one empty shell was found in fernland on Te Ko‘u in 2007 (Appendix 3), suggesting the possibility that this species may still be extant. If so, it must be extremely rare and restricted to a tiny remnant of its former distribution.

Solem (1972: 93; 1976: 7; 1983: 290) noted that Garrett’s collections from high islands in Polynesia were mainly from lower elevations, and this appears to have been the case on Rarotonga. Several endemic species have been discovered on Rarotonga since Garrett’s surveys, all at mid- to upper elevations. *Sinployea avanaensis* was discovered in 1964 in forest at *c.* 90–300 m elevation in the mid- to upper Avana Valley, living mainly arboreally, under bark and in crevices on moss- and lichen-covered tree trunks and branches (Solem 1983). The present status of this species is not known. A second species of arboreal *Sinployea*, *Sinployea taipara* n.sp., which is described in Appendix 3, was first found in 1983. It is presently known from forest in the upper Taipara Valley, a spur below Te Manga in the upper Tupapa Valley, and near the summit of Te Ko‘u, over an altitudinal range of

c. 200–560 m. The endemic achatinellid *Tekoulina pricei*, discovered in fernland in the summit basin on Te Ko‘u in 1964–65 (Solem 1972), was rare in 2005–07 and possibly in decline (Appendix 3). *Lamprocystis (Avarua) globosa* was discovered in 1929 in the upper Takuvaine Valley and on Te Ko‘u (Baker 1938). Surveys in 2005–07 found that this species had a patchy distribution at *c.* 400–580 m elevation on Te Ko‘u and Te Manga, but was common locally (Appendix 3). At least five other extant, endemic species of *Lamprocystis (Avarua)* were also found in inland Rarotonga in 2005–07, including two found only above 440–500 m elevation, and three not found below *c.* 90–150 m elevation (Appendix 3). One undescribed species of *Lamprocystis (Avarua)* was terrestrial in montane fernland, but all the other species in this taxon were predominantly arboreal, living on the leaves of trees, shrubs and ferns in forest and shrubland. All were common locally. A new species of *Diastole*, which may be endemic to Rarotonga, was first collected in the mid-1990s; in 2005–07, it was found to be relatively widely distributed in mid- to high-elevation forest (Appendix 3). Significantly, the majority of the endemic species discovered living in inland Rarotonga since the mid-1900s are predominantly arboreal, whereas the extinct endodontids and charopids of inland Rarotonga were evidently all ground-dwelling species (Garrett 1872, 1881; Solem 1976, 1983).

In summary, the available evidence points to an overall pattern of recent species declines and extinctions spreading inland from the coastal plain, and from lower to higher elevations in the interior of the island. The first wave of declines and extinctions took place pre-1860s and affected *Atropis rarotongana* n.sp., *Sinployea andrewi*, endemic lowland species of Endodontidae and *Sinployea*, and coastal populations of *Libera subcavernula*, *Sinployea tenuicostata* and possibly also *Lamprocystis (Avarua) venosa*. The only inland species definitely known to have undergone a decline at this time was *Partula assimilis*, which apparently died out in some valleys, though the highly restricted distributions of some endodontids and *Sinployea* are also suggestive of populations in decline. The first ‘wave’ of coastal extinctions was followed post-1860s by further declines and at least one more extinction (*Garrettia rotella*) in the coastal fauna, and by the extinction of all the inland Endodontidae, most of the inland *Sinployea*, and *Lamprocystis excrescens*, possibly by as early as the 1920s. After this, the coastal populations of many species underwent further declines. Since the mid-1960s, *Libera fratercula* is known to have declined markedly, and *Libera subcavernula* has apparently become extinct. By

2005–07, several coastal species were restricted to tiny forest and shrubland remnants. Some endemic and non-endemic landsnail species recorded by Garrett (1881) were still widely distributed and locally common in inland parts of Rarotonga, but two species (*Tekoulina pricei*, *Sinployea peasei*) had apparently declined since the mid-1960s.

On the coastal plain, the declines and extinctions pre-1860s evidently affected mainly ground-dwelling, non-operculate landsnail species, whereas those after the 1860s affected ground-dwelling and semi-arboreal, and operculate and non-operculate, species alike. In inland Rarotonga, the post-1860s declines and extinctions affected mainly ground-dwelling, non-operculate species.

Interestingly, the endemic snails known to have gone extinct in inland habitats post-1860s were all terrestrial species in families Endodontidae and Charopidae. Taxa in these two families are oviparous (i.e. egg-laying) according to Solem (1976, 1983). By contrast, most of the inland endemics that were still extant in 2005–07 were ovoviviparous (*sensu* Solem 1978: 105). This group included *Tekoulina pricei*, *Partula assimilis* and *Lamprocystis (Avarua)* spp. (Garrett 1881; Baker 1938; Solem 1978; Brook, pers. obs. 2005–07).

Causes of species decline and extinction in Rarotonga

Recent declines and extinctions of landsnails on tropical Pacific islands and elsewhere have been attributed to a variety of causes, including modification and loss of habitat, predation by introduced species (both vertebrates and invertebrates), competition with introduced species, and mortality from introduced pathogens (e.g. Solem 1976, 1983, 1990; Chambers & Steadman 1986; Hadfield 1986; Murray *et al.* 1988; Hadfield *et al.* 1993; Cowie 2000, 2001a,b; Bouchet & Abdou 2003; Cowie & Grant-Mackie 2004). The causes of the documented and inferred declines and extinctions of snail species on Rarotonga are generally not known directly, but the available evidence on the timing and geographic patterning do provide some clues as to possible causal factors. For example, habitat loss must have been a significant factor in the decline and extinction of forest-dwelling lowland species, but presumably not of species living in intact montane forests. Predation by introduced species may have been important in both lowland and montane habitats. The time lag between declines/extinctions of lowland endemics and inland endemics, coupled with the known history of

introduction of adventive snails to Rarotonga, suggests that introduced molluscan diseases or other pathogens are unlikely to have been a key factor in the pre-1860s coastal extinctions. However, it is possible that introduced pathogens contributed to declines and extinctions after the 1860s. Similarly, the pre-1860s declines and extinctions in the Rarotongan fauna presumably were not caused by competition for resources or habitat displacement by introduced snails.

Habitat changes

As previously noted, three main geomorphological environments are represented on Rarotonga: the deeply eroded and weathered remnants of a basaltic volcano forming the mountainous interior of the island; a lowland zone of fertile clay-rich soils formed on volcanic-derived, alluvial and colluvial deposits, which surrounds the central mountains and extends inland along stream valleys; and a coastal plain to seaward composed of unconsolidated sandy and gravelly bioclastic sediments. Before human settlement, the three main environmental zones were probably largely forested, but habitats in each have subsequently been affected, at different times and to varying degrees, by human activities.

As already mentioned, human habitat changes during the prehistoric period affected mainly the lowland zone of alluvial-colluvial deposits inland from the coastal plain and in the lower reaches of stream valleys, where settlements and gardens were concentrated. Nothing is known directly about the effects of these changes on the resident native snail fauna, though it is probable that the distributions of at least some lowland species contracted and fragmented as a result of patchwork forest clearance. Whether or not habitat modification or loss in this environmental zone contributed to any snail extinctions in prehistoric time is unknown.

There is no historical or archaeological evidence of major habitat changes on the coastal plain during the late-prehistoric period and up until the time of European settlement. The presence of rich, diverse fossil landsnail assemblages in coastal ground soils and paleosols clearly shows that forest and shrubland habitats suitable for snails existed in this environmental zone during the pre-contact period. Similarly, there is no evidence of any significant human modification of habitats in the hilly interior of Rarotonga during prehistoric time, although there was limited patchwork clearance of forest on lower hill slopes for settlements and horticulture.

Following European settlement, there was a series of major habitat changes on Rarotonga, which included the extensive clearance of native forest and shrubland on the coastal plain, alluvial-colluvial deposits, and lower hill slopes for horticulture and settlements. These changes undoubtedly affected landsnail assemblages, and presumably contributed to declines and the extinction of some species. As described in the Introduction, there were two main periods of vegetation clearance and loss of native habitat on the coastal plain and alluvial-colluvial deposits: between the late 1820s and the mid-1800s; and from the early 1900s to the present day. Land development after 1827 presumably contributed to the pre-1860s declines of lowland snail species, and possibly contributed to extinctions of some species with highly restricted geographic distributions (e.g. *Minidonta* spp. and *Sinployea* spp.). The adverse effects of land development were probably exacerbated by habitat degradation caused by a series of intense cyclones that struck Rarotonga in the first few decades after European settlement. For example, cyclones in December 1831 and March 1846 caused extensive windthrow of trees in the lowlands, and the coastal plain was locally overtopped by storm waves (Williams 1838: 386–393; Gill 1856: 87–90; Buzacott 1866: 85–89, 93–97). During the second half of the nineteenth century, shrubland and forest evidently re-established in some areas of former lowland cultivation, and this presumably would have benefited surviving populations of native lowland snail species. However, any respite would have been fairly short-lived, as economic developments and human population increase during the twentieth century led to the incremental clearance of almost all the remaining native lowland shrubland and forest, for horticultural, residential and commercial purposes. Habitat loss during the early 1900s may have been a factor in the extinction of *Garrettia rotella* on the coastal plain. Shrubland and forest clearance during the twentieth century was probably also the main agent of decline of at least two coastal landsnail species (*Orobophana pacifica*, *Libera fratercula*), and undoubtedly contributed to declines in lowland populations of many other species (e.g. *Georissa striata*, *Sturanya parvula*, *Omphalotropis variabilis*). Habitat loss probably also caused the extinction of the last known population of *Libera subcavernula*, sometime after 1964.

By contrast with the lowlands, native forest has probably persisted over much of the central part of Rarotonga since European settlement began. Habitat loss caused by clearance of lower hill slopes and valley sides for plantations of coffee and bananas in the late 1800s and the first half of the

twentieth century, respectively, probably contributed to the decline of some of the inland snail species recorded by Garrett (1872, 1874, 1881). However, it is unlikely to have been the main cause of the wave of extinctions of inland species between the late 1860s and the early to mid-1900s (i.e. *Lamprocystis excrescens*, all the inland Endodontidae, most of the inland *Sinployea* spp.).

Predation

Before human settlement, terrestrial anomuran and brachyuran crabs (*Birgus latro*, *Coenobita* spp. *Cardisoma* spp.) were probably important predators of landsnails on the lowlands and lower- to mid-elevation hill slopes of Rarotonga, but may have been scarce or absent in higher-elevation forests in the centre of the island. At the present day, landcrabs are largely restricted to forest and shrubland remnants on the coastal plain and motu of eastern Rarotonga, where they prey on *Orobophana pacifica* and *Libera fratercula* (Brook, pers. obs. 2005–07). None of the native bird species recorded on Rarotonga in historic time is known to prey on snails, although the original fauna may have included ground-feeding rails in the genera *Gallirallus* and *Porzana*, as on Mangaia (Steadman 1986, 2006; Steadman & Kirch 1990).

When Polynesians settled in the southern Cook Islands, they introduced several omnivorous vertebrates, including the domestic chicken (*Gallus gallus*), Pacific rat (*Rattus exulans*), pig (*Sus scrofula*), dog (*Canis familiaris*), and several species of lizards in the genera *Gehyra* and *Lepidodactylus* (Gekkonidae), and *Cryptoblepharus*, *Emoia* and *Lipinia* (Scincidae) (Bellwood 1978; Crombie & Steadman 1986; Allen & Steadman 1990; Steadman & Kirch 1990; Kirch *et al.* 1991, 1995; Steadman 1991, 2006; Walter 1998; McCormack 2007). The chicken, Pacific rat and species of *Gehyra* and *Emoia* are known opportunistic predators of landsnails (e.g. Medway & Marshall 1975; Campbell *et al.* 1984; Meads *et al.* 1984; Brook 1999, 2000; Arshad *et al.* 2000), and snails presumably formed a part of their respective diets on Rarotonga. However, the fossil record shows that diverse assemblages of native snails persisted on the coastal plain into the late-prehistoric period, and at present there is no evidence to suggest that predation by chickens, rats or lizards caused the extinction of any snail species in prehistoric time. Pigs are also known to prey on landsnails (e.g. Penniket 1981; Meads *et al.* 1984; Brook & McArdle 1999), albeit generally not on species with shell diameters <10 mm, such as predominated in the Rarotongan fauna.

However, more importantly, rooting and scratching by pigs and chickens can disturb ground-layer microhabitats to the extent that they become uninhabitable by native ground-dwelling snails (Solem 1983: 45), and habitat disturbance of this kind may well have contributed to localised population declines of lowland snails on Rarotonga during the period of human occupation.

Three species of rodent were introduced to Rarotonga after European contact: the brown rat (*Rattus norvegicus*), ship rat (*Rattus rattus*) and house mouse (*Mus musculus*) (Atkinson 1985; Robertson *et al.* 1994; Atkinson & Atkinson 2000). All three species are omnivorous (Innes 2005a,b; Ruscoe & Murphy 2005), and are known opportunistic predators of snails (e.g. Perkins 1913: 226; Daniel 1973; Meads *et al.* 1984; Moors 1985; Hadfield 1986: 72; Navarrete & Castilla 1993; Efford 1998: 29; Brook & McArdle 1999; Brook 2000; Jones *et al.* 2004). The timing of establishment of these three rodent species on Rarotonga is not known directly. A contemporary report by Andrew Bloxham suggests that the brown rat was common on Ma'uke in 1825, two years after the first European contact with that island (Olson 1986: 199). The brown rat might have arrived on Rarotonga as early as 1814, during the visit of the schooner *Cumberland*, but more likely arrived during or after the 1820s. Contemporary accounts indicate rat densities were extremely high at times on the Rarotongan lowlands during the early years of European settlement (e.g. Williams 1838: 152–53), but whether these irruptions were of Pacific rat, brown rat or a combination of both species is unknown. Nor is it known if such irruptions began post-contact (i.e. following introduction of the brown rat and/or changes in horticultural production and food availability), or whether there were comparable irruptions of the Pacific rat in pre-contact time on Rarotonga. On present evidence, it is impossible to determine whether or not predation by brown rats was a factor in any of the pre-1860s declines and extinctions of lowland snails on Rarotonga, although the rat irruptions on the lowlands in the late 1820s–30s may well have contributed to local declines of some of the larger ground-dwelling snail species (e.g. *Orobophana pacifica*, *Atropis rarotongana* n.sp., *Omphalotropis variabilis*, *Libera fratercula*, *Libera subcavernula*, *Sinployea tenuicostata*). Snail populations living in coral rubble substrata along the northeastern coast and on the motu in Muri Lagoon presumably would have been less susceptible to rat predation than those living on sandy substrata and on fine-grained alluvial soils.

Mice were reportedly established in Fiji and Hawai'i by the mid-1800s and in Samoa by 1865 (Cassin 1858; Brenchley 1873; Atkinson & Atkinson 2000), so it is possible that they were present on Rarotonga by the mid- to late 1800s. Two lines of circumstantial evidence suggest that the ship rat was introduced to Rarotonga between the early 1850s and early 1880s. This species was evidently scarce or absent aboard European and American sailing ships during the first half of the nineteenth century, and did not arrive on other Pacific islands until the second half of that century or later (Atkinson 1985), so is not likely to have arrived on Rarotonga before c. 1850. According to Gill (1885: 153–55), songbirds were common in Rarotongan forests in the early 1850s, but largely disappeared over the next 30 years, and a small endemic landbird, the Rarotonga flycatcher (*Pomarea dimidiata*), had declined almost to extinction by the early 1880s. Gill attributed these declines to the combined effects of human hunters, cyclones and predation by cats. However, Robertson *et al.* (1994) found that ship rats were the main predators affecting breeding success of the Rarotongan flycatcher, which strongly suggests that the declines of this and other native landbird species after the early 1850s were due to an invasion of ship rats. If ship rats were established on Rarotonga by the 1860s, they may well have caused or contributed to the decline of the arboreal snail *Partula assimilis* in montane forest reported by Garrett (1881). The scarcity and highly restricted distributions of some of the ground-dwelling endodontids and *Sinployea* in inland forests in the late 1860s (Garrett 1872, 1874, 1881), and their decline post-1860s, may also have been at least partly owing to predation by ship and/or brown rats. However, the relatively small size and cryptic habits (i.e. sheltering under stones and fallen wood) of many of the inland endodontoids and *Lamprocystis excrescens* presumably afforded these species some degree of protection from predation by rats and mice, and it is unlikely rodents were a primary cause of any post-1860s snail extinctions.

The pre-1860s snail extinctions on the coastal plain and the post-1860s extinctions in inland Rarotonga affected mainly small, ground-dwelling species, with non-operculate species being affected to a greater extent than operculate species. Available information also indicates that oviparous endemics (i.e. Endodontidae, *Sinployea* spp.) were more susceptible to extinction than ovoviviparous endemics (i.e. *Tekoulina*, *Partula*, *Lamprocystis (Avarua)* spp.) in inland habitats post-1860s. This suggests that predation of snails and their eggs by small terrestrial invertebrates was a

significant contributing factor in both the lowland and inland extinctions. The fact that operculate taxa fared better than non-operculate terrestrial species suggests that the predators involved were capable of attacking retracted snails inside the aperture.

Solem (1976: 100–101; 1983: 97) has 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 Rarotonga and other tropical Pacific islands. No native ants are known from Rarotonga (or elsewhere in eastern Polynesia), but 26 exotic species have been recorded on the island, all presumed to have been accidentally introduced as a result of human activities (Taylor 1967; Wilson & Taylor 1967; Morrison 1997; Harris & Rees 2004; Table 6). At least 15 species of ant were established on Rarotonga by the early 1900s (i.e. 1914–37), including one species native to Central and North America (*Solenopsis geminata*), four species of probable African origin (*Cardiocondyla nuda*, *Monomorium destructor*, *Pheidole megacephala*, *Tetramorium simillimum*), one pan-tropical species native to Africa and/or Asia (*Paratrechina longicornis*), five species thought to be native to Asia (*Anoplolepis gracilipes*, *Monomorium floricola*, *Paratrechina bourbonica*, *Paratrechina vaga*, *Pheidole fervens*), and four species probably native to Southeast Asia and/or the western Pacific (*Anochaetus graeffei*, *Pheidole oceanica*, *Technomyrmex albipes*, *Tetramorium pacificum*) (Taylor 1967; Wilson & Taylor 1967; McGlynn 1999: appendix 1; Wetterer 2002: table 3; 2005; 2007; Table 6). The timing of introduction of these species is not known directly. The African and American species were presumably introduced to Rarotonga after European settlement began in the 1820s, and the putative Asian species are also generally thought to have been spread to east Polynesia by European commerce (e.g. Taylor 1967; Wilson & Taylor 1967; Morrison 1997; Wetterer 2002). The Southeast Asian/western Pacific species may have been introduced to Rarotonga in prehistoric time (Morrison 1996: 244) or following European contact. Most of the ant species known to have been present on Rarotonga in the early 1900s (i.e. excluding *M. destructor*, *Paratrechina bourbonica*, *Paratrechina vaga*, *Pheidole fervens*) were recorded elsewhere in Polynesia in the 1860s (Wilson & Taylor 1967), and it is likely that at least some of these species were established on Rarotonga by the mid- to late 1800s. Eleven additional invasive exotic species have been recorded on Rarotonga since the mid-1900s (Taylor 1967; Morrison 1997; Harris & Rees 2004; Table 6).

Table 6 Ant species recorded on Rarotonga, and date of earliest known collection. References: 1, Wilson & Taylor (1967); 2, Taylor (1967); 3, Morrison (1997); 4, Harris & Rees (2004).

	Date of earliest collection	References
<i>Anochaetus graeffei</i> Mayr	1937	1, 2, 3
<i>Anoplolepis gracilipes</i> (F. Smith)	1937	1, 2
<i>Cardiocondyla emeryi</i> Forel	pre-1967	2
<i>Cardiocondyla nuda</i> (Mayr)	1925	1, 2, 3
<i>Hypoponera confinis</i> (Roger)	1996	3
<i>Hypoponera eduardi</i> (Forel)	1975	4
<i>Hypoponera opaciceps</i> Mayr	1996	3
<i>Hypoponera punctatissima</i> (Roger)	1987	4
<i>Monomorium destructor</i> (Jerdon)	1925	1, 2
<i>Monomorium floricola</i> (Jerdon)	1925	1, 2, 3
<i>Paratrechina bourbonica</i> (Forel)	1925	1, 3
<i>Paratrechina longicornis</i> (Latr.)	1925	1, 2
<i>Paratrechina vaga</i> Forel	1937	1, 2, 3
<i>Pheidole fervens</i> F. Smith	1925	1, 2, 3
<i>Pheidole megacephala</i> (Fabr.)	1914	1, 2
<i>Pheidole oceanica</i> Mayr	1925	1, 2
<i>Pheidole umbonata</i> Mayr	1996	3
<i>Rogeria stigmatica</i> Emery	1996	3
<i>Solenopsis geminata</i> (Fabr.)	1914	1, 2, 3
<i>Solenopsis papuana</i> Emery	1996	3
<i>Strumigenys godeffroyi</i> Mayr	1996	3
<i>Tapinoma melanocephalum</i> (Fabr.)	pre-1967	1, 2, 3
<i>Technomyrmex albipes</i> (F. Smith)	1914	1, 2, 3
<i>Tetramorium pacificum</i> Mayr	1927	1, 2, 3
<i>Tetramorium simillimum</i> (F. Smith)	1937	1, 2, 3
<i>Tetramorium tonganum</i> Mayr	1996	3

Nothing is known about the present and historical ecology of ants on Rarotonga. Some of the species represented in the fauna are largely restricted to disturbed habitats on other Pacific islands (e.g. *Monomorium destructor*, *Monomorium floricola*, *Pheidole fervens*, *Solenopsis geminata*, *Tetramorium simillimum* – Wilson & Taylor 1967; Reimer 1994; Morrison 1996), but most are capable of inhabiting a mix of disturbed and undisturbed habitats, including native shrubland and forest (e.g. Wilson & Taylor 1967;

Reimer 1994; O'Dowd *et al.* 2003; Wetterer 2007). Some of the latter group apparently favour lowland habitats on other Polynesian islands, and are scarce or absent in higher-elevation wet forests (e.g. *Anoplolepis gracilipes*, *Paratrechina longicornis*, *Pheidole megacephala* – Wilson & Taylor 1967; Reimer 1994).

The last three species and *Solenopsis geminata* are among the most widespread, abundant and ecologically damaging, invasive ants in the Pacific and worldwide (Wetterer 1997, 2007; Holway *et al.* 2002). They are capable of forming large, polygynous colonies, and can dominate invaded areas through aggressive behaviour, generalist diet and numerical abundance (McGlynn 1999; Holway *et al.* 2002). All these species are implicated in declines and elimination of native invertebrates on Pacific islands (e.g. Perkins 1913: 41–42, 101–02; Zimmerman 1948: 65, 173; Gillespie & Reimer 1993; Nafus 1993; Reimer 1994; Krushelnycky *et al.* 2005; Wetterer 2007) and elsewhere (e.g. Hoffman *et al.* 1999; O'Dowd *et al.* 2003; Wetterer 2005). These invasive ant species, along with three others recorded from Rarotonga (*Pheidole fervens*, *Pheidole oceanica*, *Solenopsis papuana*), are numerical and behavioural dominants in ant communities on other Polynesian islands. *Anoplolepis gracilipes* is locally a dominant ant in Hawai'i, Marquesas Islands, Tuamotu Islands and Tokelau; *Paratrechina longicornis* is locally dominant in the Phoenix Islands and Tokelau; *Pheidole fervens* is locally dominant in Hawai'i and the Society Islands; *Pheidole megacephala* is locally dominant in Hawai'i, Marquesas Islands and Tonga; *Solenopsis papuana* is locally dominant in mesic and wet forests in Hawai'i; and *Pheidole oceanica* and *Solenopsis geminata* are local dominants in the Society Islands (e.g. Perkins 1913: 41–42; Wilson & Taylor 1967; Gillespie & Reimer 1993: 29; Reimer 1994; Morrison 1996; Wetterer 2002; Lester & Tavite 2004).

Most of the ant species that have become established on Rarotonga are opportunistic predators, to a greater or lesser degree, but the extent to which they feed on snails or their eggs is unknown. Solem (1976: 100–101; 1990: 34) noted that endodontid snails were typically absent on Polynesian islands where introduced ants were abundant. He suggested that predation of eggs and juveniles by ants, particularly *Pheidole megacephala*, was probably one of the primary causes of endodontid declines and extinctions in eastern Polynesia. Solem (1983: 97) also suggested that predation by introduced ants may have been a contributing factor in the post-1860s extinctions of ground-dwelling charopids on Rarotonga.

A lack of detailed information on the history of ant invasions on Rarotonga, and on the feeding behaviour of the various ant species involved, means that it is not possible to determine whether or not ants could have caused, or contributed to, the documented declines and extinctions of lowland and montane snails on this island. However, the time lag between declines/extinctions of lowland endemics and inland endemics is certainly consistent with the kind of pattern that would be expected if elimination by invasive ants that established first in the lowlands, and subsequently spread inland, was a key factor. As already mentioned, the majority of ant species present on Rarotonga were probably introduced following European settlement in the 1820s. Although only conjecture, it is possible that one or more species of invasive ants was introduced to the Rarotongan lowlands in the first few decades after settlement, via cargo landed from missionary, trading and whaling ships, and contributed to the pre-1860s extinctions of lowland charopids and endodontids. Similarly, the post-1860s inland snail extinctions may have resulted at least in part from predation by invasive ant species capable of spreading inland from drier and typically disturbed lowland habitats, into relatively undisturbed dry to mesic slope forest and wetter cloud forest on Rarotonga.

Exotic predatory invertebrates other than ants might also have played a role in snail declines and extinctions on Rarotonga. Garrett (1881: 402) noted that the introduced slug *Deroceras laeve* was 'very abundant in damp places in the mountain ravines on Rarotonga' in the 1860s. Barker (1999: 34) described this omnivorous species as being 'opportunistically predaceous on slow-moving animals', and 'highly aggressive towards other molluscs'. According to Naggs (1994), many species of snails in family Subulinidae are also facultative predators. The timing of introduction and spread of *Allopeas clavulinum*, *Allopeas micra*, *Opeas hannense* and *Subulina octona* on Rarotonga corresponds to the period of extinction of inland endodontids and charopids. Whether or not any of these subulinid species are actually predaceous on other snails is unknown, but could be investigated. Naggs (1994) noted that radular features indicate that *Paropeas achatinaceum* is probably a facultative predator. This species was apparently introduced to Rarotonga sometime after the 1920s, and had spread through the interior of the island by the mid-1960s. It was common in inland forests and fernland in 2005–07, so potentially might have contributed to declines of *Sinployea peasei* and *Tekoulina pricei* since the 1960s. Two species of carnivorous snails in family

Streptaxidae have been recorded from Rarotonga. *Streptostele musaecola* was common in native and modified lowland habitats in 2005–07, but was apparently introduced to Rarotonga too late (i.e. post-1960s) to be implicated in the lowland extinctions being considered here. Another species of carnivorous snail (*Gulella bicolor*) was also introduced to the island, probably in the late 1800s or early 1900s, but evidently failed to establish.

Three species of planarians, including *Bipalium kewense* and two unidentified taxa, were seen living on the ground and on mossy tree trunks in native and modified forest on Rarotonga in 2005–07. The first of these is native to South-east Asia, and reportedly feeds exclusively on earthworms (Winsor *et al.* 2004). The other two species have not been identified but are probably both introduced. Many species of terrestrial planarians are known to prey on landsnails and slugs (e.g. Winsor *et al.* 2004: table 5.2), but whether the latter two species come into this category has not yet been determined.

Other factors

At present, there is no evidence as to whether or not introduced molluscan pathogens have caused or contributed to any of the recent declines and extinctions of native landsnails on Rarotonga. The possibility of pathogens being responsible for the pre-1860s lowland snail extinctions can probably be discounted on the basis of the known history of post-contact introductions of exotic snails and slugs. The post-1860s inland snail extinctions may have been contemporaneous with the invasion of inland forests by *Diastole conula*, *Elsasmias apertum* and subulinids, but whether or not any of these species spread diseases or other pathogens to the native snail fauna is unknown.

Competition with introduced snails and slugs cannot have been a factor in the pre-1860s lowland extinctions. Two naturalised species known to have spread through inland Rarotonga between 1869 and 1920s were arboreal (i.e. *Diastole conula*, *Elsasmias apertum*), and presumably had little if any ecological effect on native ground-dwelling snails. The introduced subulinid species are terrestrial and occupy the same types of microhabitat reported for some of the extinct *Sinployea* and endodontids (i.e. leaf litter, and under rotting wood and loose stones), but it is difficult to see how competition for living sites or other resources could have contributed to extinctions of the native species.

It has been suggested that post-contact introductions of subulinids may have been a contributing factor in the decline

of populations of *Allopeas gracile* on tropical Pacific islands. According to Solem (1989: 522–23), ‘on many islands, there are mid-1800s records for *Lamellaxis gracilis* [= *A. gracile*], but by the mid-1900s, *Prosopaeas achatinaceum* seems to have replaced it, except in urban gardens’. Cowie (2000: 152; 2001b: 133) noted that *A. gracile* appeared to be declining on many Pacific islands: ‘it is rarely found alive, even in localities where it was formerly common ... [It is] possible that subulinids that arrived later, transported via western exploration and commerce (notably *Subulina octona* and *Paropeas achatinaceum*) have out-competed *A. gracile*’. Whether the decline of *A. gracile* on Rarotonga was primarily owing to competition with, or predation by, one or more of the more recently introduced subulinid species (i.e. all of which have become widely distributed and locally common within the last 100 years), or to other factors, is unknown. Museum labels in the BPBM indicate that subulinids collected on Samoa in the 1920s and 1930s were heavily parasitised (e.g. *Allopeas clavulinum* – BPBM 84096, 84501; *Paropeas achatinaceum* – BPBM 83301 83834; *Subulina octona* – BPBM 83832, 83943), which suggests the possibility that pathogens introduced with subulinid hosts may have contributed to the recent decline of *A. gracile* on Pacific islands.

In summary, the decline and extinction of native snail species on Rarotonga during the nineteenth and twentieth centuries probably had a variety of causes. Habitat loss and modification, and predation by introduced ants, were the most likely causes of declines and extinctions of lowland species. Predation by introduced invertebrates and rodents was probably a major contributing factor in the post-1860s snail declines and extinctions in montane forests on Rarotonga. Whether or not spread of pathogens by introduced snails and slugs was also a factor is unknown.

At least 25 species of landsnail have become extinct on Rarotonga during the last 200 or so years, including the assimineid *Garrettia rotella*, at least 12 species of Endodontidae, at least 11 species of *Sinployea*, and the euconulid *Lamprocystis excrescens*. Eleven of these species were apparently restricted to the lowlands, and 12 were restricted to inland habitats. All except *Lamprocystis excrescens* were endemic to Rarotonga. In 2005–07, two other inland endemics (*Sinployea harveyensis*, *Sinployea peasei*) were either vanishingly rare or already extinct, and two lowland endemics (*Atropis rarotongana* n.sp., *Minidonta matavera* n.sp.) were restricted to tiny, degraded forest remnants on privately owned land at Matavera, and were either verging on extinction or already extinct. Three other lowland

species (*Orobophana pacifica*, *Sturanya parvula*, *Libera fratercula*) were restricted to a few small remnants of coastal forest and shrubland on privately owned land on eastern Rarotonga and on islets in Muri Lagoon. All three still had thriving local populations, albeit with highly restricted distribution areas. Their continued survival on Rarotonga will be dependent on preservation of the existing forest and shrubland habitats in the face of continuing pressure for land development.

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Appendix 1:

Details of coastal sites sampled for landsnails in Rarotonga during 2005–07

- 1 Pue; 21°12.280'S, 159°45.906'W; 1/6/2006; horticultural plot; disturbed ground soil of unconsolidated calcareous sand with common coral fragments.
- 2 Pue; 21°12.248'S, 159°45.384'W; 6/6/2006; anthropogenic grassland; ground soil of unconsolidated sandy coral rubble exposed in excavation for septic tank.
- 3 Pue; 21°12.301'S, 159°45.080'W; 19/6/2007; weedy, herbaceous vegetation on vacant section; ground soil of unconsolidated sandy coral rubble in gravel pit.
- 4 Pue; 21°12.284'S, 159°45.084'W; 4/6/2006; 0.2 ha relict grove of *Barringtonia asiatica*–*Hibiscus tiliaceus* forest grading seaward into *Scaevola taccada* littoral shrubland on storm berm; unconsolidated cobble–boulder coral rubble.
- 5 Tupapa; 21°12.410'S, 159°44.905'W; 1/6/2006; 0.14 ha relict grove of *Barringtonia asiatica*–*Pisonia grandis* forest; unconsolidated cobble–boulder coral rubble.
- 6 Tupapa; 21°12.618'S, 159°44.724'W; 5/6/2006; anthropogenic grassland beneath old *Barringtonia asiatica* and *Hernandia nymphaeifolia* trees; ground soil of unconsolidated calcareous sand.
- 7 Tupapa; 21°12.792'S, 159°44.411'W; 22/9/2005; 0.6 ha remnant of coastal forest and shrubland; ecotone from low *Barringtonia asiatica*–*Hernandia nymphaeifolia* forest, to *Hibiscus tiliaceus*–*Scaevola taccada* shrubland, to herbaceous strand vegetation of *Canavalia sericea*, *Ipomoea macrantha*, *Vigna marina* and *Wollastonia biflora*; unconsolidated cobble–boulder coral rubble.
- 8 Tupapa; 21°12.825'S, 159°44.422'W; 27/5/2006; *Barringtonia asiatica*–*Hibiscus tiliaceus*–*Pisonia grandis* forest remnant (0.19 ha); ground soil of unconsolidated coral rubble and minor calcareous sand.
- 9 Tupapa; 21°13.012'S, 159°44.125'W; 5/6/2006; *Barringtonia asiatica*–*Cocos nucifera*–*Hernandia nymphaeifolia*–*Hibiscus tiliaceus* forest remnant (0.2 ha); ground soil of unconsolidated calcareous sand with common coral fragments.
- 10 Matavera; 21°13.236'S, 159°44.014'W; 22/9/2005; horticultural plot beneath old *Barringtonia asiatica* trees; disturbed ground soil of unconsolidated coral rubble and calcareous sand.
- 11 Matavera; 21°13.283'S, 159°43.971'W; 5/6/2006; 1 ha remnant of coastal forest and shrubland; *Hernandia nymphaeifolia*–*Hibiscus tiliaceus* low forest grading seaward into *Scaevola taccada* littoral shrubland; unconsolidated coral rubble and minor calcareous sand.
- 12 Matavera; 21°13.289'S, 159°43.997'W; 5/6/2006; *Barringtonia asiatica* grove in 1 ha remnant of coastal forest and shrubland; unconsolidated coral rubble and minor calcareous sand.
- 13 Ngatangia; 21°14.078'S, 159°43.871'W; 9/6/2006; horticultural plot; disturbed ground soil of unconsolidated calcareous sand with common coral fragments.
- 14 Ngatangia; 21°14.163'S, 159°43.743'W; 30/9/2005; *Cocos nucifera*–*Guettarda speciosa*–*Hernandia nymphaeifolia*–*Hibiscus tiliaceus* low forest (0.1 ha); unconsolidated coral rubble and minor calcareous sand.

- 15 Ngatangiia; 21°14.512'S, 159°43.541'W; 22/9/2005; *Cocos nucifera*–*Hernandia nymphaeifolia*–*Guettarda speciosa* low forest (0.28 ha); unconsolidated coral rubble and minor calcareous sand.
- 16 Ngatangiia; 21°14.593'S, 159°43.481'W; 22/9/2005; *Scaevola taccada* open shrubland with *Wollastonia biflora*, and vines of *Canavalia sericea*, *Ipomoea pes-caprae* and *Vigna marina*; makatea limestone karst with pockets of unconsolidated coral rubble and calcareous sand.
- 17 Motutapu Island; 21°14.743'S, 159°43.451'W; 25/6/2007; *Scaevola taccada* open shrubland, with *Wollastonia biflora*, and vines of *Vigna marina*; sandy cobble–boulder coral rubble.
- 18 Motutapu Island; 21°14.823'S, 159°43.531'W; 25/5/2006; *Hibiscus tiliaceus* forest with scattered emergent *Cocos nucifera* and *Hernandia nymphaeifolia*; ground soil of unconsolidated calcareous sand with common coral fragments.
- 19 Motutapu Island; 21°14.831'S, 159°43.457'W; 25/9/2005; *Cocos nucifera*–*Guettarda speciosa*–*Hernandia nymphaeifolia*–*Hibiscus tiliaceus*–*Schleinitzia insularum* forest; ground soil of unconsolidated coral rubble and calcareous sand.
- 20 Motutapu Island; 21°14.923'S, 159°43.514'W; 28/9/2005; *Barringtonia asiatica*–*Guettarda speciosa*–*Hernandia nymphaeifolia*–*Hibiscus tiliaceus*–*Schleinitzia insularum* forest; ground soil of unconsolidated coral rubble and calcareous sand.
- 21 Oneroa Island; 21°15.095'S, 159°43.545'W; 25/9/2005; *Casuarina equisetifolia*–*Cocos nucifera*–*Guettarda speciosa*–*Pisonia grandis* forest; ground soil of unconsolidated calcareous sand.
- 22 Oneroa Island; 21°15.154'S, 159°43.458'W; 25/9/2005; *Casuarina equisetifolia*–*Cocos nucifera*–*Guettarda speciosa*–*Hernandia nymphaeifolia*–*Hibiscus tiliaceus*–*Pisonia grandis* forest grading seaward into *Scaevola taccada* shrubland; unconsolidated coral rubble and minor calcareous sand.
- 23A Muri; 21°15.600'S, 159°43.941'W; 29/9/2005; anthropogenic grassland beneath *Casuarina equisetifolia* trees; ground soil of weakly consolidated calcareous sand exposed in low coastal bank.
- 23B Muri; 21°15.600'S, 159°43.941'W; 29/9/2005; late-Holocene paleosol of weakly consolidated calcareous sand exposed in low coastal bank.
- 24 Akapua; 21°16.308'S, 159°44.809'W; 29/09/2005; old *Barringtonia asiatica* trees and *Hibiscus tiliaceus*; ground soil of weakly consolidated calcareous sand exposed in low coastal bank.
- 25 Titikaveka; 21°16.238'S, 159°45.494'W; 29/05/2006; ground soil of weakly consolidated calcareous sand exposed in sand pit.
- 26 Titikaveka; 21°16.111'S, 159°46.015'W; 5/6/2006; anthropogenic grassland beneath old *Barringtonia asiatica* trees; ground soil of unconsolidated calcareous sand exposed in low coastal bank.
- 27 Avaavaroa; 21°15.941'S, 159°46.866'W; 5/6/2006; anthropogenic grassland beneath old *Barringtonia asiatica* trees; ground soil of unconsolidated calcareous sand.
- 28 Vaimaanga; 21°15.851'S, 159°47.532'W; 2/6/2006; anthropogenic grassland beneath old *Barringtonia asiatica* and *Hernandia nymphaeifolia* trees; ground soil of unconsolidated calcareous sand.
- 29 Rutaki; 21°15.642'S, 159°48.015'W; 29/09/2005; anthropogenic grassland beneath old trees of *Barringtonia asiatica* and *Hernandia nymphaeifolia*, *Hibiscus tiliaceus* and *Cocos nucifera*; ground soil of weakly consolidated calcareous sand exposed in low coastal bank.
- 30 Aroa; 21°15.363'S, 159°48.810'W; 29/5/2006; *Barringtonia asiatica*–*Hibiscus tiliaceus* forest remnant (0.4 ha); ground soil of unconsolidated calcareous sand.
- 31 Aroa; 21°15.238'S, 159°48.923'W; 22/6/2007; ground soil of calcareous medium–coarse sand exposed in sand pit.
- 32 Kavera; 21°15.041'S, 159°49.112'W; 29/5/2006; ground soil of weakly consolidated calcareous sand exposed in sand pit.
- 33 Te Muriavai; 21°14.665'S, 159°49.528'W; anthropogenic grassland beneath old trees of *Barringtonia asiatica* and *Hernandia nymphaeifolia*, and *Hibiscus tiliaceus*; ground soil of unconsolidated calcareous sand exposed in low coastal bank.
- 34 Arorangi; 21°13.429'S, 159°49.716'W; 18/6/2007; anthropogenic grassland; ground soil of calcareous fine sand exposed in trench for utility cables.
- 35A Pokoinu; 21°12.867'S, 159°49.704'W; 29/9/2005; *Casuarina equisetifolia*–*Cocos nucifera*–*Guettarda speciosa*–*Hernandia nymphaeifolia* forest remnant (0.5 ha); ground soil of unconsolidated calcareous sand and minor coral rubble.
- 35B Pokoinu; 21°12.867'S, 159°49.704'W; 6/6/2006; paleosol of weakly consolidated sandy coral rubble exposed in borrow pit.

36A Avatiu; 21°11.981'S, 159°47.732'W; 4/6/2006; anthropogenic grassland; ground soil of unconsolidated calcareous sand with common coral fragments exposed in excavation for septic tank.

36B Avatiu; 21°11.981'S, 159°47.732'W; 4/6/2006; late-Holocene paleosol of weakly consolidated sandy coral rubble exposed in excavation for septic tank.

Appendix 2:

Equivalent species names of Rarotongan plants mentioned in the text in Cheeseman (1903) and Wilder (1931).

Plant nomenclature in this study follows McCormack (2007)

This study	Cheeseman (1903)	Wilder (1931)
<i>Alpinia zerumbet</i>	<i>A. nutans</i>	<i>A. nutans</i>
<i>Ananas comosus</i>	<i>A. sativa</i>	<i>A. comosus</i>
<i>Ardisia elliptica</i>	—	<i>A. humilis</i>
<i>Artocarpus altilis</i>	<i>A. incisa</i>	<i>A. incisa</i>
<i>Barringtonia asiatica</i>	<i>B. butonica</i>	<i>B. butonica</i>
<i>Cajanus cajan</i>	<i>C. indicus</i>	<i>C. indicus</i>
<i>Cardiospermum grandiflorum</i>	—	<i>C. halicacabum</i>
<i>Cecropia pachystachya</i>	—	<i>C. palmata</i>
<i>Ceiba petandra</i>	<i>Bombax malabaricum</i>	<i>Ce. casearia</i>
<i>Celtis pacifica</i>	—	<i>C. paniculata</i>
<i>Chamaesyce fosbergii</i>	<i>Euphorbia chamissonis</i>	<i>E. chamissonis</i>
<i>Citrus aurantifolia</i>	<i>C. medica</i> var. <i>acida</i>	<i>C. limetta</i>
<i>Citrus sinensis</i>	<i>C. aurantium</i>	<i>C. aurantium</i> var. <i>sinensis</i>
<i>Colocasia esculenta</i>	<i>C. antiquorum</i>	<i>C. esculenta</i>
<i>Commelina diffusa</i>	<i>C. nudiflora</i>	<i>C. nudiflora</i>
<i>Conyza bonariensis</i>	—	<i>Erigeron albidus</i>
<i>Cordyline fruticosa</i>	<i>C. terminalis</i>	<i>Taetsia fruticosa</i>
<i>Derris malaccensis</i>	—	<i>D. elliptica</i>
<i>Dicranopteris linearis</i>	<i>Gleichenia dichotoma</i>	<i>G. linearis</i>
<i>Diospyros digyna</i>	—	<i>D. ebenaster</i>
<i>Elaeocarpus floridanus</i>	<i>E. rarotongensis</i>	<i>E. rarotongensis</i>
<i>Elephantopus mollis</i>	—	<i>E. scaber</i>
<i>Epipremnum pinnatum</i>	<i>E. mirabile</i>	<i>E. pinnatum</i> and <i>Pothos aureus</i>
<i>Hedychium coronarium</i>	<i>Hedychium</i> sp.	<i>H. coronarium</i>
<i>Hernandia nymphaeifolia</i>	<i>H. peltata</i>	<i>H. peltata</i>
<i>Indigofera suffruticosa</i>	<i>I. anil</i>	<i>I. suffruticosa</i>
<i>Inga ynga</i>	—	<i>I. edulis</i>
<i>Inocarpus fagifer</i>	<i>I. edulis</i>	<i>I. edulis</i>
<i>Ipomoea pescaprae</i>	<i>I. biloba</i>	<i>I. pes-caprae</i>
<i>Lepidium bidentatum</i>	<i>L. piscidium</i>	<i>L. piscidium</i>
<i>Leucaena leucocephala</i>	<i>L. glauca</i>	<i>L. glauca</i>
<i>Manihot esculenta</i>	<i>M. utilissima</i>	<i>M. utilissima</i>
<i>Melicoccus bijugatus</i>	—	<i>Melicocca bijuga</i>
<i>Microsorium grossum</i>	<i>Polypodium phymatodes</i>	<i>P. scolopendria</i>

<i>Myoporum wilderi</i>	<i>Myoporum</i> sp.	<i>M. sandwicense</i>
<i>Musa</i> hybrids	<i>M. paradisiaca</i>	<i>M. paradisiaca</i> , <i>M. cavendishi</i>
<i>Musa troglodytorum</i>	<i>M. febi</i>	<i>M. febi</i>
<i>Nephrolepis hirsutula</i>	<i>N. acuta</i>	<i>N. hirsutula</i>
<i>Pandanus tectorius</i>	<i>P. odoratissimus</i>	<i>P. tectorius</i>
<i>Persea americana</i>	<i>P. gratissima</i>	<i>P. americana</i>
<i>Phyllanthus acidus</i>	—	<i>Cicca acida</i>
<i>Pipturus argenteus</i>	<i>P. velutinus</i>	<i>P. velutinus</i>
<i>Pisonia grandis</i>	pukatea	<i>Ceodes umbraculifera</i>
<i>Scaevola taccada</i>	<i>S. koenigii</i>	<i>S. frutescens</i>
<i>Schleinitzia insularum</i>	<i>Leucaena forsteri</i>	<i>L. forsteri</i>
<i>Solanum mauritianum</i>	<i>S. auriculatum</i>	<i>S. auriculatum</i>
<i>Solenosternon scutellarioides</i>	<i>Coleus blumei</i>	<i>C. blumei</i>
<i>Stachytarpheta cayennensis</i>	—	<i>S. jamaicensis</i>
<i>Stenotaphrum micranthum</i>	<i>S. subulatum</i>	—
<i>Syzygium cumini</i>	—	<i>Eugenia jambolana</i>
<i>Syzygium jambos</i>	<i>Eugenia jambos</i>	<i>E. jambos</i>
<i>Tacca leontopetaloides</i>	—	<i>T. pinnatifida</i>
<i>Thuarea involuta</i>	<i>T. sarmentosa</i>	<i>T. involuta</i>
<i>Vigna marina</i>	<i>V. retusa</i>	<i>V. marina</i>
<i>Wollastonia biflora</i>	<i>Wedelia aristata</i>	<i>Wedelia biflora</i>

Appendix 3:

Annotated list of landsnails recorded from inland Rarotonga but not found in coastal habitats

(Published records are listed in square brackets; new records are indicated by an asterisk and are in **bold** type.)

VERONICELLIDAE

**Laevicaulis alte* (Férussac, 1822)

MATERIAL: NMNZ M.283326.

This species is probably native to Africa (Solem 1964) but has become widely distributed through Asia, Australia and the tropical Pacific (Solem 1959, 1964; B.J. Smith 1992; Cowie 2000, 2001b; Cowie & Robinson 2003). It was established in Vanuatu, the Loyalty Islands and Hawai'i by 1900 (Collinge 1900a; Grimpe & Hoffman 1925; Cowie 1998b), New Caledonia by 1911 (Solem 1964), Fiji by 1958 (FMNH 160004, 160008), and Samoa by 1965 (Cowie & Robinson 2003). First recorded on Rarotonga in 2005; present in disturbed forest on lower hill slopes, and probably also on the lowlands. Also present on Ātiu and Mangaia (Brook, unpub. data)

ACHATINELLIDAE

Tekoulina pricei Solem, 1972

[Solem 1972]

MATERIAL: FMNH 144590–1, 153389, 153414, 167974; NMNZ M.283316, 283427.

An endemic species apparently restricted to the summit basin on Te Ko'u, at c. 540–580 m elevation. In 1964–65, *Tekoulina pricei* reportedly occupied a total area of c. 4 ha, 'under rotting fern leaves and in matted fern roots on the ground' in 'very dense vegetation of creepers, ferns, and stunted moss-covered trees and shrubs' (Solem 1972: 93). The species must have been reasonably common at this time, judging by the number of specimens collected (Solem 1972). Searches in September 2005, June 2006 and June 2007 failed to find any live snails, but a few fresh, empty shells were found beneath the dead skirts of *Blechnum procerum* ferns at a few sites in a mosaic of montane fernland and cloud forest. This species may be in decline.

PARTULIDAE

Partula assimilis Pease, 1867

[Pease 1867, 1870 – in part as *P. a. virgulata*; Garrett 1881]

MATERIAL: BPBM 1662, 94421, 94424, 95426–39, 95585–8, 206446, 206462–3, 104587–91; FMNH 144691–2, 144694, 144697, 153787; NMNZ M.283315,

283336, 283351, 283394, 283396, 283430, 283433, 283434, 283443, 283447, 283452, 283453, 283455.

This endemic species lives on the leaves of trees, shrubs and ferns in forest. Garrett (1881: 395) noted that it was 'not uncommon in the higher portions of a few valleys on Rarotonga ... In some valleys where it was formerly abundant it appears to have become extinct'. In 2005–07, *Partula assimilis* was very sparsely distributed in inland Rarotonga at c. 60–450 m elevation, but snails were common locally (e.g. upper Tupapa and Takuvaine valleys, lower Te Muriavai Valley, below Maungatea Bluff). This species occupied a wide range of forest types, including non-indigenous secondary forest, slope forest and cloud forest.

ENDODONTIDAE

Libera tumuloides (Garrett, 1872)

[Garrett 1872 – in *Pityis*; Garrett 1881; Solem 1972]

MATERIAL: ANSP 47815, 290098; BPBM 2239, 167427.

This endemic species formerly had a highly restricted distribution of c. 0.2 ha, approximately 3 km inland, high up in a mountain ravine on Rarotonga (Garrett 1872: 226; 1881: 393). No snails or empty shells of *Libera tumuloides* have been found since the mid-1800s, and the species is thought to be extinct (Solem 1976, 430; Solem 1983: 45, 97).

Minidonta unilamellata (Garrett, 1874)

[Garrett 1874 – in *Pityis*; Garrett 1881 – in *Patula*; Solem 1976 – in *Mautodontha* (*Garrettoconcha*)]

MATERIAL: ANSP 47798, 290110; BPBM 2339.

This endemic species was formerly rare, living under decayed vegetation in mountain ravines (Garrett 1874: 235). No snails or empty shells of *Minidonta unilamellata* have been found since the mid-1800s, and the species is thought to be extinct (Solem 1983: 45, 97).

Minidonta zebrina (Garrett, 1874)

[Garrett 1874, 1881 – in *Pityis*; Solem 1976 – in *Mautodontha* (*Mautodontha*)]

MATERIAL: ANSP 47799, 290104; BPBM 2337.

An endemic species that was formerly rare in one valley on Rarotonga (Garrett 1881: 389). No snails or empty shells have been found since the mid-1800s, and it is thought to be extinct (Solem 1983: 45, 97).

Thaumatodon multilamellata (Garrett, 1872)

[Garrett 1872, 1881 – in *Pityis*; Solem 1976]

MATERIAL: ANSP 47792, 290108; BPBM 2316, 167424.

An endemic species that was formerly moderately common in two valleys on Rarotonga (Garrett 1881: 389). No snails

or empty shells have been found since the mid-1800s and it is thought to be extinct (Solem 1976: 451; Solem 1983: 45, 97).

CHAROPIDAE

Sinployea avanaensis Solem, 1983

[Solem 1983]

MATERIAL: AIM AK112271; FMNH 144631–2, 144671, 153381, 153383–5, 155948.

This endemic species was discovered in 1964 in the upper Avana Valley, living mainly arboreally, under moss, lichens and loose bark on tree trunks and branches, in slope forest (Solem 1983: 105). Numerous specimens were collected in 1964–65, indicating that the species was reasonably common at this time. Its present status is not known.

Sinployea canalis (Garrett, 1872)

[Garrett 1872 – in *Pityis*; Garrett 1881 – in *Patula*; Solem 1983]

MATERIAL: BPBM 2328.

An endemic species that was formerly rare on the ground in damp forest in one valley on Rarotonga (Garrett 1872: 227; 1881: 385). No snails or empty shells have been found since the mid-1800s, and it is thought to be extinct (Solem 1983: 45, 97).

Sinployea decorticata (Garrett, 1872)

[Garrett 1872 – in *Pityis*; Garrett 1881 – in *Patula*; Solem 1983]

MATERIAL: ANSP 47754; BPBM 2313, 167422.

This endemic species was formerly present in one mountain ravine on Rarotonga (Garrett 1872: 228; 1881: 387). No snails or empty shells have been found since the mid-1800s, and it is thought to be extinct (Solem 1983: 45, 97).

Sinployea harveyensis (Garrett, 1872)

[Garrett 1872 – in *Pityis*; Garrett 1881 – in *Patula*; Solem 1983]

MATERIAL: ANSP 47756; BPBM 2343, 167423; NMNZ M.283450.

This endemic species was reportedly relatively common under rotten wood in valleys on Rarotonga in 1869 (Garrett 1872: 228; 1881: 387). It is not represented at all in collections made on Rarotonga in the 1920s or 1960s (BPBM; FMNH), and was thought to be extinct (Solem 1983: 45, 97). However, a single, relatively fresh, empty shell of *Sinployea harveyensis* was found among the rhizomes and dead fronds of *Blechnum procerum* in montane fernland near the summit of Te Ko'u in June 2007 (NMNZ M.283450),

which suggests that the species may still be extant at this locality.

Sinployea otareae (Garrett, 1872)

[Garrett 1872 – in *Pitys*; Garrett 1881 – as *Patula decorticata*; Solem 1983]

MATERIAL: ANSP 47755; BPBM 2335, 167418–9; NMNZ M.208811.

An endemic species reported to be abundant under dead wood on the banks of a stream in one valley on Rarotonga in 1869 (Garrett 1872: 229; 1881: 387). No snails or empty shells have been found since 1869, and this species is thought to be extinct (Solem 1983: 45, 97).

Sinployea peasei Solem, 1983

[Garrett 1881 – as *Patula atiensis* (in part); Solem 1983]

MATERIAL: AIM AK112299; BPBM 2331, 8595, 79780; FMNH (see Solem 1983: 102).

An endemic species reported to be widely distributed and common on Rarotonga in 1869 (Garrett (1881: 386), and widely distributed but generally scarce in 1964–65, living on the ground among fallen leaves and under stones and dead wood (Solem 1983: 102). Searches in forest in inland parts of the island in 2005–07 failed to turn up any live snails or empty shells of *Sinployea peasei*. This species has evidently declined markedly since the mid-1960s, and may be extinct.

Sinployea planospira (Garrett, 1881)

[Garrett 1881 – in *Patula*; Solem 1983]

An endemic species reported to be very rare by Garrett (1881: 388). No snails or empty shells have been found since 1869, and it is thought to be extinct (Solem 1983: 45, 97).

Sinployea proxima (Garrett, 1872)

[Garrett 1872 – in *Pitys*; Garrett 1881 – in *Patula*; Solem 1983]

MATERIAL: ANSP 47700; BPBM 2317.

This endemic species was formerly common under stones and among rotting wood in several valleys on Rarotonga (Garrett 1872: 230; 1881: 386). No snails or empty shells have been found since the mid-1800s, and it is thought to be extinct (Solem 1983: 45, 97).

Sinployea youngi (Garrett, 1872)

[Garrett 1872 – in *Pitys*; Garrett 1881 – in *Patula*; Solem 1983]

MATERIAL: BPBM 2315.

This endemic species was formerly rare on the ground in damp woods in one valley on Rarotonga (Garrett 1872: 229;

1881: 388). No snails or empty shells have been found since 1869, and it is thought to be extinct (Solem 1983: 45, 97).

**Sinployea taipara* new species

(Fig. 7D–F)

DESCRIPTION: Shell small, 2.25–2.9 mm diameter, wider than high (shell height/shell diameter ratio 0.52–0.60), apex and early spire whorls slightly elevated (spire protrusion 7–9% of shell height), last whorl descending more rapidly, umbilicus narrow and constricted (12–14% of shell diameter). Whorls 3.4–3.8, broadly rounded, final whorl slightly flattened laterally above periphery, suture deeply impressed. Colour medium to dark yellowish brown. Protoconch 0.50–0.57 mm wide, surface corroded in most examples, but some show faint traces of weak, crowded, spiral sculpture. Teleoconch sculpture of widely and irregularly spaced, low, narrow, rounded, sigmoidal, primary radial ribs; interstices with fine, closely spaced, rounded, spiral cords and axial riblets, forming a lattice. Aperture simple, subcircular, lip thin, weakly and evenly thickened within.

TYPE MATERIAL: Holotype NMNZ M.290085 and paratypes M.283332 (2), BPBM 274777 (1): Cook Islands, Rarotonga, headwater basin of Taipara Stream, 200 m elevation, forest, under lichen on tree trunk (21°14.855'S, 159°46.605'W), 27 Sep. 2005. Additional paratypes: Cook Islands, Rarotonga, spur on NNE flank of Te Manga, 420 m elevation, forest, under moss and lichen on tree trunks (21°13.908'S, 159°45.780'W), 17 June 2007, NMNZ M.283437 (2).

OTHER MATERIAL: FMNH 212842; NMNZ M.283366, 283439.

DISTRIBUTION: Cook Islands, Rarotonga, 200–560 m elevation, in forest.

REMARKS: *Sinployea taipara* n.sp. is distinctive in the combination of its small size, narrow umbilicus, prominent spiral microsculpture on the teleoconch, and very weak apical sculpture. This scarce, predominantly arboreal species was not recorded by Garrett (1881) or Solem (1983). It was first collected in 1983 by Gustav Paulay, in cloud forest in the summit basin of Te Ko'u (FMNH 212842). In 2005–07, a few live snails and empty shells were found under foliose lichens and moss on tree trunks in slope forest in the upper Taipara Valley, and in cloud forest in the upper Tupapa Valley, on a spur leading to Te Manga. *Sinployea taipara* n.sp. is known only from Rarotonga, and is probably endemic to this island.

EUCONULIDAE

**Diastole* sp.

DESCRIPTION: Shell conoid-turbinate, spire angle of 88–90°, convex basally, up to 6.94 mm high, wider than high (height/width ratio 0.77–0.87), spire 1.0–1.4 times as high as aperture, periphery angulate, imperforate, with a shiny yellowish-brown periostracum. Whorls up to 5.7, apex bluntly rounded, spire whorls weakly convex, last adult whorl carinate. Protoconch *c.* 2.2–2.3 mm wide, sculptured with 7–8 rounded, spiral cords, and fine, radial riblets in interstices. Teleoconch sculpture of 6–7 widely and evenly spaced spiral cords crossed by fine growth lines, a narrow, rounded cord on the periphery of the final whorl, and numerous closely spaced, low spirals crossed by fine growth lines on the base. Aperture broad, bluntly angulate, thin at rim and within. Columella thickened, with a low spiral ridge.

MATERIAL: NMNZ M.282454, 282463, 283313, 283323, 283352, 283441, 283672, 283673.

REMARKS: This species is known from empty shells only and placement in *Diastole* is provisional. The shell is similar in size to the sympatric *Diastole conula*, but the spire is more narrowly conical with coarser spiral sculpture. *Diastole* sp. was not recorded by Garrett (1881), and is not represented in collections in the BPBM or FMNH. The first known collections were by Craig in 1994, at 150 m and 275 m elevation in the upper Avatiu Valley (NMNZ M.282454, 282463). In 2005–07, fresh, empty shells were uncommon in slope forest and cloud forest at *c.* 300–580 m elevation on Te Ko‘u and Te Manga, and at one site in slope forest at 100 m elevation in the lower Avana Valley. Most shells were found on the ground, but some were up trees, indicating that this species was at least partly arboreal in habit. The presence of hatchling shells within the spire of one adult shell in NMNZ M.283352 indicates that *Diastole* sp. is probably ovoviviparous. *Diastole* sp. is presently known from Rarotonga only, but whether or not it is native to this island is unclear. The fact that it was relatively widely distributed on Rarotonga in 2005–07, but was not collected in the 1860s, 1920s or 1960s, suggests the possibility that it may be an invasive species of unknown provenance recently introduced to this island. Alternatively, it may be a native species that has become more common over the last few decades.

Lamprocystis (Lamprocystis) excrescens (Mousson, 1870)

[Garrett 1881 – in *Microcystis*; Baker 1938]

MATERIAL: BPBM 3196, 3201.

This Polynesian species has been recorded from Fiji, Tonga,

Samoa and Rarotonga (Baker 1938), but whether this distribution is natural, or has resulted in part from synanthropic introductions as suggested by Baker (1941), is unknown. Garrett (1881: 381) reported that *Lamprocystis excrescens* was common ‘under damp rotten wood and beneath moist, decaying leaves on the sides of inland ravines’. There are no known twentieth-century collections of this species, and no snails or empty shells were seen in 2005–07. The Rarotongan population is probably extinct, and may have died out in the late 1800s or early 1900s.

Subgenus *Lamprocystis (Avarua)* Baker, 1938

This taxon is endemic to Rarotonga (Baker 1938). Three species have been included in it: *Lamprocystis (Avarua) globosa* Baker, 1938; *Lamprocystis (Avarua) venosa* (Pease, 1866); and *Lamprocystis (Avarua) subcircularis* (Garrett, 1881). The first two have distinctive shell morphology, but the identity and status of *L. (A.) subcircularis* is unclear at present (see below). Several undescribed species of *Lamprocystis (Avarua)* were found in inland Rarotonga in 2005–07, as outlined below.

Lamprocystis (Avarua) globosa Baker, 1938

[Baker 1938]

MATERIAL: BPBM 11418, 95581–2, 95584, 95592–3, 206454; NMNZ M.283324, 283337, 283353, 283370, 283382, 283423.

DESCRIPTION: Shell smooth, globose-conical, up to 8.5 mm diameter, wider than high (shell height/shell diameter ratio 0.82–0.86), periphery of final whorl evenly rounded. Animal with cream-coloured foot and tail; optic tentacles black; longitudinal black stripe running from the base of each tentacle back along both sides of top of anterior part of body.

REMARKS: *Lamprocystis (Avarua) globosa* was described from material collected by Buck in 1929 on ferns and shrubs at *c.* 150–300 m in the upper Takuvaine Valley, and at *c.* 550 m elevation on Te Ko‘u (Baker 1938). In 2005–07, this species was found in slope forest and cloud forest at *c.* 400–580 m elevation on Te Ko‘u and Te Manga. It was locally common, living predominantly on ferns and particularly *Asplenium australasicum*, and was syntopic with *Lamprocystis (Avarua) venosa* and *Lamprocystis (Avarua)* spp. 1–4.

Lamprocystis (Avarua) venosa (Pease, 1866)

Synonymy and material listed in Systematics section (p. 206).

DESCRIPTION: Shell smooth, low conical, up to 9.3 mm diameter, wider than high (shell height/shell diameter ratio 0.68–0.74), periphery of final whorl weakly angled. Animal with cream-coloured foot and tail; head and tentacles black

or dark grey, with a longitudinal black or dark grey stripe running from the base of each optic tentacle back along both sides of top of anterior part of body; mantle edge generally speckled with grey flecks, but individuals with pink-flecked mantle locally common in valleys on the western side of the island.

REMARKS: In 2005–07, *Lamprocystis (Avarua) venosa* was widely distributed and common across much of the interior of Rarotonga, living on ferns and the leaves of herbaceous plants, shrubs and trees, and less commonly on the ground, in non-indigenous forest, slope forest and cloud forest, at c. 60–560 m elevation. It was syntopic with *Lamprocystis (Avarua) globosa* and *Lamprocystis (Avarua) spp.* 1–5.

Lamprocystis (Avarua) subcircularis (Garrett, 1881)

[Garrett 1881 – in *Microcystis*; Baker 1938 – as *Lamprocystis (Avarua) venosa subcircularis*]

MATERIAL: ANSP 74330; BPBM 3190, 58973.

Garrett (1881: 381–382) noted that this species was common, and was associated with *Lamprocystis excrescens*, which he recorded as occurring ‘under damp rotten wood and beneath moist, decaying leaves on the side of inland ravines’. Thus *Lamprocystis (Avarua) subcircularis* was evidently a ground-dwelling species, in contrast to *Lamprocystis (Avarua) venosa* (above), which was predominantly arboreal. Garrett (1881) described *L. (A.) subcircularis* as having a smooth shell with a depressed spire, angulate periphery, and maximum diameter of 9 mm. He gave no description of the animal. Baker (1938) re-examined some of Garrett’s unlocalised material, along with low-spined *Lamprocystis* collected near Muri and in the upper Takuvaine Valley in 1929. He noted that spire elevation intergraded with that in *L. (A.) venosa*, and treated *L. (A.) subcircularis* as a subspecies of *L. (A.) venosa*. However, he observed that whereas Buck’s specimens had penial morphology essentially the same as *L. (A.) venosa*, Garrett’s specimens of *L. (A.) subcircularis* differed in having a large diverticulum (Baker 1938: 74, pl. 6, figs 4, 5). There is thus a strong possibility that Garrett’s and Buck’s material represented two different species. The true identity of *L. (A.) subcircularis* is unclear at present. Anatomical and/or genetic comparison is required to determine which, if any, of the five taxa listed below corresponds to *L. (A.) subcircularis*.

**Lamprocystis (Avarua) sp. 1*

DESCRIPTION: Shell smooth, lenticular to low conical, up to 9.8 mm diameter, wider than high (shell height/shell diameter ratio 0.62–0.68), periphery of final whorl weakly angled. Animal with cream-coloured foot and tail; optic

tentacles colour-banded with dark grey tips, pale central part, and dark grey lower part contiguous with longitudinal dark grey stripes running back along both sides of top of anterior part of body.

MATERIAL: NMNZ M.283355, 283376, 283379, 283384, 283389, 283398, 283401, 283405, 283408, 283425.

REMARKS: In 2005–07, *Lamprocystis (Avarua) sp. 1* was widely distributed and locally common in southern and eastern parts of the interior of Rarotonga, at c. 150–650 m elevation. It inhabited slope forest, cloud forest and montane fernland, living on the leaves of ferns, shrubs and trees, and in litter on the ground. This species was syntopic with *Lamprocystis (Avarua) globosa*, *Lamprocystis (Avarua) venosa* and *Lamprocystis (Avarua) spp.* 2–4.

**Lamprocystis (Avarua) sp. 2*

DESCRIPTION: Shell smooth, lenticular to low conical, up to 10.2 mm diameter, wider than high (shell height/shell diameter ratio 0.62–0.65), periphery of final whorl weakly angled. Animal dark grey on tail and lower part of foot, grading to greyish cream on upper part of foot; optic tentacles have black or dark grey tips, or are entirely dark-coloured with contiguous longitudinal dark stripes running back along both sides of top of anterior part of body.

MATERIAL: NMNZ M.283372, 283377, 283380, 283448.

REMARKS: In 2005–07, *Lamprocystis (Avarua) sp. 2* was present on Te Ko‘u and Te Manga at c. 440–560 m elevation in cloud forest and montane fernland. Snails were mostly found on the ground in litter, but some were on the fronds of ferns. This species was syntopic with *Lamprocystis (Avarua) globosa*, *Lamprocystis (Avarua) venosa*, *Lamprocystis (Avarua) sp. 1*, and *Lamprocystis (Avarua) spp.* 3–4.

**Lamprocystis (Avarua) sp. 3*

DESCRIPTION: Shell smooth, lenticular to low conical, up to 10.6 mm diameter, wider than high (shell height/shell diameter ratio 0.61–0.67), periphery of final whorl weakly angled. Animal has blotchy crimson colouring on tail and lower part of foot, grading to cream on upper part of body; optic tentacles with dark grey tips, and longitudinal grey stripes running from base of tentacles back along both sides of top of anterior part of body.

MATERIAL: NMNZ M.283319, 283338, 283356, 283373, 283378, 283385, 283406, 283409, 283412, 283418, 283426.

REMARKS: In 2005–07, *Lamprocystis (Avarua) sp. 3* was present on Te Ko‘u, Te Manga, Te Rua Manga, and in the upper Papua Stream valley, in slope forest and cloud forest

at 150–560 m elevation. Snails were generally found on the leaves of ferns, shrubs and trees, and less commonly in litter on the ground. This species was syntopic with *Lamprocystis (Avarua) globosa*, *Lamprocystis (Avarua) venosa*, *Lamprocystis (Avarua) spp. 1–2*, and *Lamprocystis (Avarua) sp. 4*.

****Lamprocystis (Avarua) sp. 4***

DESCRIPTION: Shell smooth, lenticular to low conical, up to 8.9 mm diameter, wider than high (shell height/shell diameter ratio 0.60–0.67), periphery of final whorl weakly angled. Animal black on tail and lower part of foot, grading to cream flecked with dark grey on sides and top of foot; optic tentacles black, with longitudinal black stripes running from base of tentacles back along both sides of top of anterior part of body.

MATERIAL: NMNZ M.283325, 283363, 283428, 283445, 283449, 283451.

REMARKS: In 2005–07, *Lamprocystis (Avarua) sp. 4* was present on Te Ko‘u and Te Manga, living on the ground in cloud forest and montane fernland at *c.* 500–650 m elevation. This species was syntopic with *Lamprocystis (Avarua) globosa*, *Lamprocystis (Avarua) venosa* and *Lamprocystis (Avarua) spp. 1–3*.

****Lamprocystis (Avarua) sp. 5***

DESCRIPTION: Shell smooth, lenticular to low conical, up to 10.6 mm diameter, wider than high (shell height/shell diameter ratio 0.63–0.75), periphery of final whorl weakly angled. Animal with cream-coloured foot and tail; optic tentacles colour-banded with dark grey tips, pale central part, and dark grey basal part contiguous with longitudinal dark grey stripe running back along both sides of top of anterior part of body.

MATERIAL: NMNZ M.283391, 283393, 283419, 283421, 283444, 283454.

REMARKS: Spire elevation in this species varied with altitude: shells from higher altitudes typically had more elevated spires, resembling those of *Lamprocystis (Avarua) venosa*; shells from lower altitudes were more lenticular, like those of *Lamprocystis (Avarua) spp. 1–4*. Animal coloration in *Lamprocystis (Avarua) sp. 5* appears identical to that of *L. (A.) sp. 1*, but the two species differ anatomically (Gary Barker, pers. comm. 2009) and genetically (David Winter, pers. comm. 2007).

In 2005–07, *Lamprocystis (Avarua) sp. 5* was found inland from Avarua on the northern slopes of Maungatea, and in the upper Avatiu and mid-Takuvaine valleys. It inhabited non-indigenous forest and slope forest at *c.* 90–

450 m elevation, living on the leaves of shrubs, trees and ferns. This species was syntopic with *Lamprocystis (Avarua) venosa* below *c.* 300 m, and it apparently had a parapatric distribution with respect to *Lamprocystis (Avarua) sp. 1*.