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Holocene distribution, ecology and local extinction of the endemic New Zealand dune snail Succinea archeyi Powell (Stylommatophora: Succineidae)

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Holocene distribution, ecology and local extinction of the endemic New Zealand dune snail *Succinea archeyi* Powell (Stylommatophora: Succineidae)

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The Holocene fossil record indicates that the prehistoric distribution of *Succinea archeyi* Powell was restricted to coastal and near coastal sites in the northern and eastern North Island, New Zealand The species was formerly widely distributed in northern and eastern Northland, and from the Hauraki Gulf to western Bay of Plenty with geographically-disjunct outlier populations near Cape Kidnappers in southern Hawke Bay Paleoenvironmental evidence indicates that in prehistoric time *S archeyi* occupied a variety of sandfield, grassland and shrubland habitat types on dunefields, coastal flats and, locally, coastal hills

The prehistoric *S archeyi* populations in Hawke Bay apparently became extinct long before human settlement of New Zealand, whereas at most if not all of the more northern sites, the species coexisted with early Maori However, in historic time *S archeyi* declined at many sites between Northland and the Bay of Plenty, resulting in the contraction, fragmentation and extinction of many local populations This decline is inferred to have begun in about the mid 19th century, mainly as a consequence of the impacts of European pastoral farming practices on the coastal habitats occupied by the snail In the 20th century, other types of coastal development, including residential subdivisions and establishment of exotic forestry plantations, have also adversely affected *S archeyi* populations The species is known to have survived at 15 dunefield locations, including ten in Northland and five on eastern Coromandel Peninsula

Keywords *Succinea archeyi* Succineidae landsnail New Zealand Holocene sand dunes biogeography habitat extinction

INTRODUCTION

Succinea archeyi Powell, 1933 is a species of small terrestrial snail (max shell height 12 mm) endemic to New Zealand (Powell 1950, 1979) Extant populations have previously been recorded from a few coastal dune sites in the northern and northeastern North Island (Powell 1950, 1979, Thomson 1952, 1959, Thomson & Jones 1954) However, Holocene fossil records indicate that the species was formerly much more widely distributed in northern New Zealand (e g , Powell 1950, Willan 1974, Climo 1980), and Pleistocene fossil succineids identified as *S archeyi* have been recorded from near Marton in the southwestern North Island, and near Cromwell in the southern South Island (Climo 1980, Fig 1)

The present study was undertaken as part of an investigation aimed at determining the distribution and conservation status of extant populations of *S archeyi*, and assessing evidence for the nature and causes of changes in distribution patterns during Holocene time Results of surveys of the extant populations, along with recommendations for conservation

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management of the populations, are given in a separate report (Brook 1999e). The present paper records the prehistoric and historic distributions of *S. archeyi*, assesses temporal variation in the ecology of the species in terms of changes to associated landsnail faunas and habitats, and discusses the timing and causes of local extinctions.

METHODS

Existing information on prehistoric and historic distributions of *S. archeyi* was obtained from published and unpublished literature, landsnail collections of the Auckland War Memorial Museum and the Museum of New Zealand, Wellington, and from discussions with Norman Gardner, Andrew Jeffs and Bruce McFadgen. Additional information on the distribution of extant populations was obtained from reconnaissance surveys of a number of dunefields in northern and eastern Northland, and eastern Coromandel Peninsula, carried out between 1994 and 1998 (see Brook 1999e for details). New information on the geographic and stratigraphic distribution of *S. archeyi* was collated from the findings of contemporaneous studies on fossil landsnail faunas and paleoenvironmental histories of a number of Northland dunefields, and from a reconnaissance paleontological survey of dunefields near Cape Kidnappers in southern Hawke Bay (Brook 1999b–d, Brook & Goulstone 1999, F. J. Brook unpubl. data).

Patterns of long-term temporal variation in ecological relationships of *S. archeyi* were assessed on the basis of observed changes in coexisting landsnail faunal diversity, comparison between present-day and prehistoric landsnail faunal diversities, and comparison between present-day dune habitat types and prehistoric habitats occupied by *S. archeyi*, as determined from landsnail paleoecology.

Geographic patterns of extinction of *S. archeyi* were determined from comparison of the distributions of prehistoric, historic and extant populations. Where possible, the stratigraphic distribution of *S. archeyi* or historical records were used to determine an extinction chronology for sites. For prehistoric fossil sites, a stratigraphic distinction was made where possible between those pre-dating human settlement of New Zealand by Polynesians, and post-settlement sites. Present evidence suggests that permanent Maori settlements were established no earlier than about 900–700 years B.P. (Anderson 1991, McFadgen et al. 1994, McGlone et al. 1994, Elliot et al. 1995, Higham & Hogg 1997, Newnham et al. 1998). The end of the prehistoric period is taken as the date of Captain James Cook's first visit to New Zealand in 1769 AD (Davidson 1984).

Informal identifier names for undescribed native landsnail species referred to in this paper (i.e., *Phrixgnathus* sp. "marshalli", punctid sp. 24) follow the useage of Brook (1999a–d) and Brook & Goulstone (1999).

RESULTS

Distribution

The known prehistoric and historic Holocene distributions of *S. archeyi* are shown in Fig. 1 and 2 respectively, and locality information is listed in Appendix 1.

Fossils indicate that *S. archeyi* had a prehistoric Holocene distribution that included coastal areas of northern and eastern Northland, the Hauraki Gulf to western Bay of Plenty, and outliers in Hawke Bay on the eastern coast of the North Island. The majority of the fossil sites recorded from Northland and Coromandel Peninsula to the western Bay of Plenty date from the period of Maori occupation prior to European contact (i.e., c. 900–180 years B.P.; above). However, fossil *S. archeyi* are also known from a number of pre-Maori sites, including Cape Maria van Diemen-Te Werahi, Tom Bowling Bay, Whareana Beach, Tokerau Beach and Smugglers Bay (Appendix 1). By contrast, there are no records of *S. archeyi*

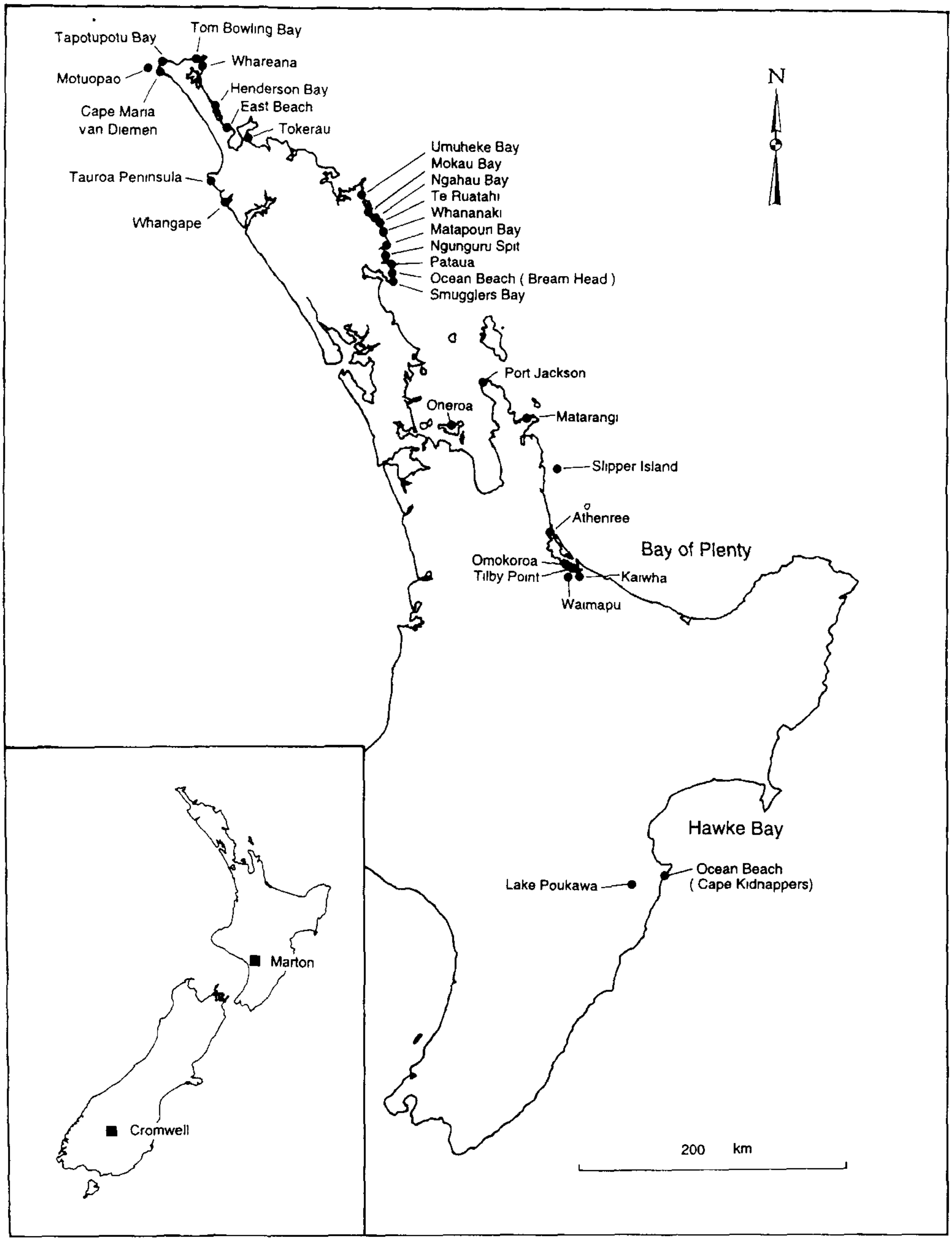

Fig. 1 Location of prehistoric Holocene *Succinea archeyi* Powell fossil sites, northern New Zealand Location of Pleistocene *Succinea* fossil sites shown on inset map for comparison

younger than Polynesian settlement in Hawke Bay *S archeyi* fossils recorded from a site at Lake Poukawa were from a stratigraphic interval with an estimated age of 8–5 ka (Climo 1980) The exact location and age of fossil *S archeyi* recorded by Powell (1950) from Ocean Beach, south of Cape Kidnappers, are not known However, a recent survey of fossil

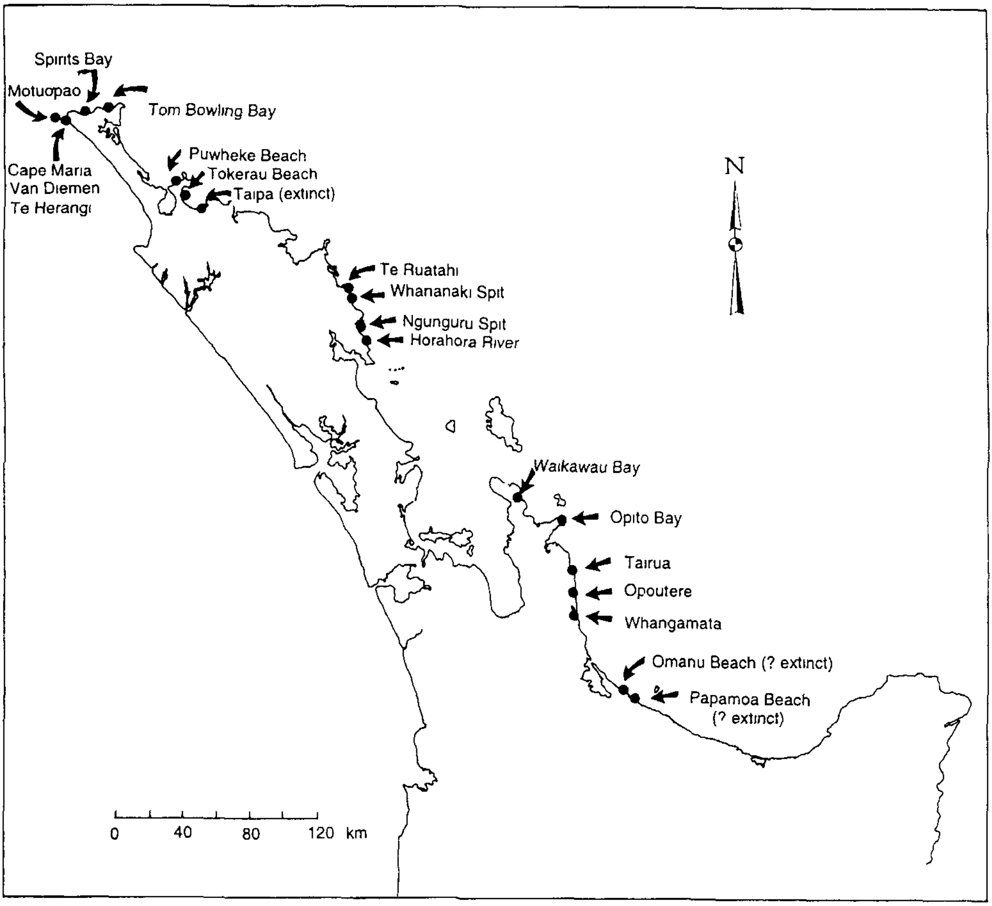

Fig. 2 Location of historic *Succinea archeyi* Powell populations, North Island, New Zealand.

landsnail faunas from stratigraphically above Taupo Pumice (i.e., younger than 1.7 ka), in dune sequences between Cape Kidnappers and Ocean Beach, failed to turn up any *S. archeyi* (F. J. Brook unpubl. data), suggesting that the species probably became extinct there well before human settlement.

The historic distribution of *S. archeyi* (Fig. 2) parallels the late prehistoric distribution described above, albeit with far fewer sites overall and none on the west coast south of Cape Maria van Diemen. During the historical period, *S. archeyi* has been recorded from a total of 18 locations and is known to be extant at 15 of these, including six in northern Northland, four in eastern Northland, and five in eastern Coromandel Peninsula (Appendix 1; Brook 1999e).

Associated landsnail faunas

Lists of landsnail species present at 19 sites with surviving *S. archeyi* populations are given in Table 1, and species richness data for some fossil landsnail faunas incorporating *S. archeyi* are given in Table 2.

Diversities of the present-day native landsnail faunas were consistently low, ranging from 3–7 species per site. Two native species (*Tornatellinops novoseelandica*, *Paralaoma*

Table 1 Landsnail faunal composition at dune sites with extant *Succinea archeyi* Powell Non-native species are denoted by an asterisk Locations are 1 Motuopao, 2 Cape Maria van Diemen, 3 Paraspiritus headland, 4 Herangi summit, 5 NW Herangi, 6 Te Kohatu Point, 7 Spirits Bay, 8 Tom Bowling Bay, 9 Puwheke Beach, 10 Tokerau Beach, 11 Te Ruatahi, 12 Whananaki Spit, 13 Ngunguru Spit, 14 Horahora River, 15 Waikawau Bay, 16 Opito Bay, 17 Tairua, 18 Opoutere, 19 Whangamata

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Delouagapia cordelia (Hutton)			x																
Paralaoma caputspinulae (Reeve)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Phenacohelix tholoides (Suter)		x	x	x															
Placostylus ambagiosus Suter		x	x																
Succinea archeyi Powell	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Tornatellinops novoseelandica (Pfeiffer)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
punctid sp 24		x	x	x	x	x													
**Candidula intersecta* (Poiret)							x												
**Cantareus aspersus* (Muller)	x	x	x				x	x	x	x	x	x	x	x	x	x	x	x	x
**Cochlicopa lubrica* (Muller)		x								x								x	x
**Lauria cylindracea* (da Costa)																	x		x
**Oxychilus alliarius* (Miller)									x	x	x	x		x	x	x	x	x	x
**Prietocella barbara* (Linnaeus)							x			x	x	x		x					
**Vallonia excentrica* Sterki											x				x	x			
No of native landsnail species	3	6	7	5	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3
No of non-native landsnail species	1	2	1	0	0	0	3	1	2	4	4	3	1	3	3	3	3	3	4

caputspinulae) coexisted with *S archeyi* at all 19 sites The five sites in the Cape Maria van Diemen area were the only ones that contained additional native species, namely punctid sp 24 (5 sites), *Phenacohelix tholoides* (3 sites) *Placostylus ambagiosus* (2 sites) and *Delouagapia cordelia* (1 site)

All of the sites with *S archeyi* except those between Herangi and Te Kohatu Point, also had between one and four introduced landsnail species, of which the most widely distributed were *Cantareus aspersus* (16 sites) and *Oxychilus alliarius* (10 sites) *Prietocella barbara* was present at several Northland sites but none on Coromandel Peninsula and, conversely, *Lauria cylindracea* was present at two of the Coromandel sites but none in Northland

The very low diversities of native landsnail faunas at sites with surviving *S archeyi* populations were paralleled in some prehistoric faunas As few as 2–3 species have been recorded from some pre-Maori sites at Tokerau, and from some post-settlement sites at Tauroa Peninsula, Cape Maria van Diemen-Te Werahi, Tokerau and Ngahau (Table 2) However, *S archeyi* was also associated with landsnail faunas that had higher diversity prehistorically than at the present-day, as highlighted by range and mean data in Table 2 for pre-Maori sites at Cape Maria van Diemen Te Werahi, and post-settlement fossil sites at Ngahau and Whananaki

Landsnail species commonly associated with *S archeyi* in Northland fossil faunas included *Tornatellinops novoseelandica* (Pfeiffer), *Cavellia buccinella* (Reeve), *Mocella eta* (Pfeiffer), *Phenacohelix tholoides* (Suter), *Paralaoma caputspinulae* (Reeve), *Phrixgnathus* sp "marshalli" and punctid sp 24 (Brook 1999b d, Brook & Goulstone 1999, F J Brook unpubl data) Three of those species (*Cavellia buccinella*, *Mocella eta*, *Paralaoma caputspinulae*), along with *Climocella prestoni* (Sykes), were also commonly associated with *S archeyi* in fossil landsnail faunas from around Tauranga Harbour (B G McFadgen unpubl data)

Habitat

Modern populations of *S archeyi* inhabit sandfield vegetation and mosaics of sandfield and prostrate shrubland on coastal sand dunes The sandfield habitats range from low diversity floras characterised by the native spinifex (*Spinifex sericeus*) and rush *Isolepis nodosa*, to richer floras that also include shore bindweed (*Calystegia soldanella*), scattered prostrate shrubs (e g , *Coprosma acerosa*, *Muehlenbeckia complexa*, *Pimelia arenaria*) and taller shrub-layer species such as *Cassinia leptophylla*, flax (*Phormium tenax*) and toetoe (*Cortaderia splendens*) Prostrate shrubland habitats typically include the same native plant species, but

Table 2 Species richness in prehistoric (pre-Polynesian and post-settlement) landsnail faunas containing *Succinea archeyi* Powell Data from Brook (1999b–d) and Brook & Goulstone (1999)

	Pre Polynesian landsnail faunas			Post-settlement landsnail faunas		
	no of sites	no of species per site: range	no of species per site: mean ± SD	no of sites	no of species per site: range	no of species per site: mean ± SD
Tauroa Peninsula				10	2–10	4 8 ± 2 3
Cape Maria van Diemen-Te Werahi	9	6–27	15 1 ± 6 9	25	3–12	4 7 ± 1 9
Tokerau	11	3–15	7 6 ± 3 4	5	2 7	3 6 ± 2 1
Ngahau				5	3–18	12 2 ± 7 3
Whananaki				7	8–23	12 9 ± 5 6

Table 3 Native plant species present at dune sites with extant *Succinea archeyi* Powell Locations as for Table 1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Calystegia soldanella (Linnaeus)	x	x	x	x			x	x		x	x				x	x	x	x	x
Cassinia leptophylla (Forst f)		x	x	x	x	x	x	x		x			x			x		x	
Coprosma acerosa A Cunn	x	x	x	x	x	x	x		x	x					x			x	x
Coriaria arborea Lindsay				x															
Cortaderia splendens Connor			x	x		x	x												
Isolepis nodosa Rottb	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Muehlenbeckia complexa (A Cunn)	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x		x
Phormium tenax J R et G Forst	x	x	x	x	x	x	x	x		x					x				
Pimelia arenaria A Cunn	x			x	x				x	x									x
Pimelea ?urvilleana (A Rich)				x		x													
Pteridium esculentum (Forst f)										x									
Spinifex sericeus R Br	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Tetragonia ?trigyna Banks et Sol	x				x	x													

differ from the more open sandfield vegetation in having a dense, prostrate plant cover dominated by *Coprosma acerosa* and/or *Muehlenbeckia complexa* Native plant species present at extant *S archeyi* population sites are listed in Table 3 In addition to the native flora, sandfield and prostrate shrubland habitats at these sites typically include adventive grasses and small dicotyldonous herbs introduced into New Zealand following European settlement and some sites have also been invaded by adventive shrubs and large herbs (Brook 1999e)

Paleoenvironmental interpretations of fossil landsnail faunas by Brook (1999b–d) and Brook & Goulstone (1999), indicate that in prehistoric times, coastal dunes in Northland supported a wide range of vegetation types including sandfield, prostrate shrubland, tall flax-broadleaf shrubland and forest *S archeyi* fossils are common in prehistoric coastal dune landsnail faunas characteristics of sandfield and shrubland habitats, and are also rarely present in landsnail faunas indicative of coastal forest settings, suggesting that the species formerly occupied not only low open sandfield and prostrate shrubland habitats as at the present day, but also taller shrubland and ecotones on forest margins

There is insufficient paleontologic information at present to determine whether *S archeyi* occupied a comparably wide range of dune habitat types in the eastern Coromandel region during prehistoric time However, the richness of fossil landsnail faunas associated with *S archeyi* at sites at Port Jackson and Slipper Island (Goulstone 1979, Willan 1974) do indicate the former existence of tall shrubland and forest on those dunefields, suggesting that the overall structure and patterns of dune vegetation there were probably similar to those in Northland

All the existing fossil records of *S archeyi* from Northland and eastern Coromandel are from dunefields in open coastal settings, with no sites being more than one kilometre inland from the coast By contrast, the fossil distribution of *S archeyi* in the western Bay of Plenty includes sites on supratidal flats and low headlands around the shores of Tauranga Harbour, as well as on dissected hillcountry up to 3 km inland from the harbour (Appendix 1) Fossil landsnail faunas at these sites are suggestive of open shrubland and grassland vegetation (B G McFadgen unpubl data)

The Hawke Bay fossil records of *S archeyi* comprise one coastal dune site of unknown paleoenvironmental setting, and the Lake Poukawa site The latter is within an alluvial basin in hill country, 25 km inland from the present coast Palynological evidence indicates that *S archeyi* at that site lived in an open sparsely vegetated landscape comprising a mosaic of grassland and shrubland (Climo 1980)

Population declines and extinctions

The recorded Holocene distribution of *S archeyi* comprises a total of 41 locations, but the snail has become extinct in at least 25 (61%) of these (Appendix 1) Further, many of the surviving populations are very small, occupying total areas of less than 0 5 ha each (Brook 1999e) In two locations with small modern populations, at Cape Maria van Diemen-Te Werahi and Tom Bowling Bay, fossil evidence clearly shows that *S archeyi* was more widespread in prehistoric time than at present (Fig 3)

As described above, there are no records of *S archeyi* from post-1 7 ka deposits in the Lake Poukawa and Cape Kidnappers areas, suggesting that the Hawke Bay outlier populations probably became extinct in prehistoric time, well before human settlement of New Zealand By contrast, there is no evidence that any *S archeyi* populations in the Northland and Coromandel Peninsula to Bay of Plenty regions became extinct before human settlement Rather, the stratigraphic distribution of *S archeyi* in sediments deposited during the period of prehistoric Maori occupation, indicates that the species was widespread in coastal areas

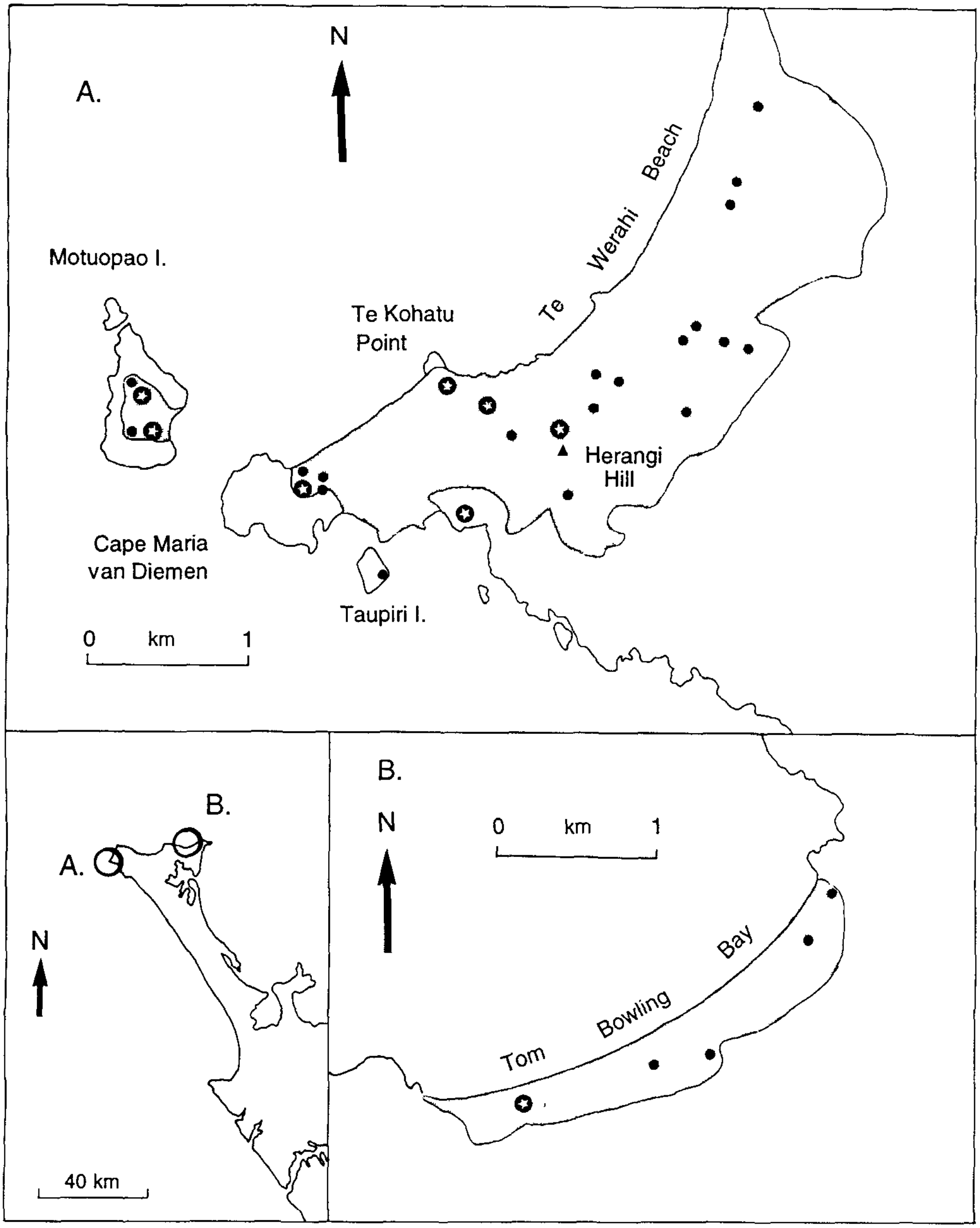

Fig. 3 Location of prehistoric Holocene *Succinea archeyi* Powell fossil sites (filled circles) and extant populations (stars) at Cape Maria van Diemen-Te Werahi and Tom Bowling Bay, showing changes in geographic distributions. Stippled areas on maps denote Holocene dunefields.

inhabited by Maori. It is generally not possible to determine extinction dates of *S. archeyi* at locations between Northland and the Bay of Plenty, but from available stratigraphic evidence it seems likely that most local extinctions took place since late prehistoric time. At least one Northland population is definitely known to have become extinct in historic time. Powell (1950) recorded the existence of abundant *S. archeyi* at Taipa (Doubtless Bay), in 1949–50, but that population became extinct at some time before the early 1990s (Brook 1999e). A series of small, fragmented *S archeyi* populations recorded in 1947 1953 from Omanu and Papamoa beaches in the Bay of Plenty (Thomson 1952, Thomson & Jones 1954), are possibly now also extinct (Brook 1999e)

DISCUSSION

Distribution and habitat

Succinea archeyi had a Holocene distribution extending from northern Northland to the western Bay of Plenty, with outliers near Cape Kidnappers in southern Hawke Bay The species distribution as mapped in Fig 1 and 2 shows three main clusters of populations in the northern North Island between Cape Maria van Diemen and Doubtless Bay in northern Northland, between the Bay of Islands and Whangarei Harbour in eastern Northland, and between the inner Hauraki Gulf and western Bay of Plenty It is not known whether the distribution gaps between these three clusters are real, or simply reflect inadequate sampling or a lack of suitable exposed fossiliferous deposits on intervening coasts However, the distribution gap between the Cape Maria van Diemen and Tauroa Peninsula populations does appear to represent an actual biogeographic disjunction, in that *S archeyi* is absent from prehistoric (post-settlement) fossil landsnail faunas from dune sequences along western Aupouri Peninsula (R T Wallace unpubl data) Similarly, *S archeyi* has not been found in any fossil landsnail faunas from Holocene dunes north or south of Cape Kidnappers (B G McFadgen pers comm 1998, F J Brook unpubl data), suggesting that the distribution gap between Bay of Plenty and Hawke Bay populations is also real

Modern populations of *S archeyi* are restricted to spinifex sandfield and sandfield-prostrate shrubland mosaics on coastal dunes, but in prehistoric time the species clearly occupied a much wider range of habitats Coastal dunes in northern New Zealand formerly supported diverse mosaics of sandfield and prostrate to tall shrubland, where ecotones graded landwards into coastal forest Paleoecological evidence suggests that *S archeyi* occupied a range of these sandfield, shrubland and forest-edge habitats There is presently no indication that *S archeyi* lived anywhere other than on coastal dunes in Northland, whereas the species was clearly not so restricted further south in the Bay of Plenty and Hawke Bay Since *S archeyi* fossils recorded from harbour margins and coastal hills in the Tauranga district were all associated with prehistoric Maori occupation sites, it is possible that anthropic land clearance increased the area of suitable habitat for snails at some coastal sites, and favoured their spread inland into areas that were presumably formerly forested Palynological evidence indicates that widespread anthropic deforestation in this region began at c 700 years B P (Newnham et al 1995, 1998)

A different explanation is clearly required to account for the existence of *S archeyi* at the Lake Poukawa site in early-mid Holocene time, several thousand years before human settlement The limited amount of paleoenvironmental information available for this site indicates that it was under shrubby grassland vegetation when *S archeyi* was living there, but was forested later in prehistoric time up until clearance by early Maori (McGlone 1978, Climo 1980, see also McGlone et al 1993) McGlone (in Climo 1980) suggested that the existence of a grassland-shrubland mosaic at the Lake Poukawa site in early-mid Holocene time resulted from decreased rainfall and temperatures c 4–5°C cooler than at present, which prevented the establishment of forest That climatic hypothesis may be correct, but needs to be tested against Holocene climatic and vegetation histories for other North Island east coast sites New Zealand regional climatic and vegetation histories (e g , McGlone et al 1993) show no supporting evidence for substantial cooling and forest retreat in early-mid Holocene time An alternative explanation for the former presence of grassland-shrubland at Lake Poukawa is suggested by the Holocene history of seismic tectonic uplift in southern Hawke

Bay Hull (1987) and Ota et al (1990) described Holocene coastal terraces uplifted to 12 m above present-day sea level in the Cape Kidnappers area The Lake Poukawa basin is presently at c 20 22 m above sea level but the *S archeyi* fossils were obtained from a depth of c 14 m below present ground surface (i e 6 8 m above present sea level) That suggests the possibility that the basin may have been temporarily occupied by the upper reaches of an estuary following the maximum post-glacial sea level rise at c 6 5 ka and that *S archeyi* at the site may consequently have lived in open vegetation on an estuarine fringe, as at Tauranga Harbour

Climo (1980) argued, on the basis of fossil distribution and paleoecological associations, that *S archeyi* is a cold-adapted, ice-age relictual species He also considered that the life-cycle of *S archeyi*, in which breeding and egg-laying take place in autumn and early winter, rather than in spring and summer as for many other terrestrial snail species, represents an adaptation to cold climates Contrary to that, I suggest that the Holocene distribution of *S archeyi*, restricted to coastal areas of the northern North Island, provides clear evidence that the species is instead adapted to warm temperate climates Further, as Powell (1950) has shown, the life history of *S archeyi* is closely tied to seasonal variation in rainfall, with annual recruitment of juveniles taking place during the winter wet season, rather than during the generally drier periods with less predictable rainfall at other times of the year

The paleoecological evidence for cold climate adaptation cited by Climo (1980) related to the Holocene site at Lake Poukawa, and Pleistecene fossil sites at Marton in the southwestern North Island (40°05′S Lat 175°23′E Long) and near Cromwell in the southern South Island (44°59′S Lat, 168°53′E Long) As noted above, the evidence for a markedly cooler climate at the Lake Poukawa site in early-mid Holocene time is uncorroborated, and needs to be tested against climate and vegetation histories from other sites The Middle Pleistocene *S archeyi* fossils from Marton were collected from coastal facies of the Waiomio Shellbed, a unit dated at c 700 ka, and correlated with the interglacial period of isotope stage 17 (Naish et al 1998) It was not deposited during a glacial period, as stated by Climo (1980) The climate at Marton during that interglacial may have been slightly cooler than at present, as suggested by A G Beu (pers comm in Climo 1980), but clearly would have been considerably warmer than during any of the Pleistocene glacial periods

The best evidence linking New Zealand *Succinea* to cold climates is the record of fossils from calcareous lake deposits of presumed last glacial age from the Crown Terrace near Cromwell (Climo 1980, D H Bell & K M Swanson unpubl data) The occurrence of *Succinea* at that locality is noteworthy on several counts Firstly, it represents the only record of the genus from the South Island Secondly, the Crown Terrace site is located 750 km (c 5° latitude) south of the closest known North Island site with *Succinea* Thirdly, it is located c 100 km inland from the nearest coast Fourthly, it represents the only New Zealand record of *Succinea* from sediments deposited in a periglacial environment On the basis of shell morphology, the Crown Terrace fossils are indistinguishable from North Island *S archeyi* However, Succineidae in general have very conservative shell morphology, and the family includes cryptic species that are distinguishable only on anatomical and genetic characters That, combined with the considerable geographic disjunction and markedly different paleoenvironmental setting from other New Zealand *Succinea*, suggests the possibility that the Crown Terrace fossils represent an endemic southern taxon

Putting aside the issue of climatic adaption, Climo (1980) correctly identified that habitats suitable for *S archeyi*, and particularly coastal dunefields, would have been far more extensive around the New Zealand coast at times of lowered sea level during Pleistocene glacial periods, than during interglacials This contrast would have been pronounced in eastern Northland and Coromandel Peninsula where, during past interglacials and since the post-glacial maximum sea level rise at 6 5 ka, much of the coastline comprised rocky headlands and embayments One of the consequences of these glacio-eustatic changes in sea level is that *S archeyi* would have existed as large and laterally extensive coastal populations during glacial periods, and would have been fragmented into smaller genetically isolated local populations during interglacial periods and the Holocene The effect of this cyclical history on genetic variation within the species is unknown

One noteworthy feature concerning the Holocene distribution of *S archeyi* is the scarcity of records from the western North Island coast Sandy beaches backed by dunefields occupy much of the coastline north of the Waikato River mouth (37(24′ Lat) on the west coast, but *S archeyi* is known only between Whangape and Tauroa Peninsula, and from the Cape Maria van Diemen area in the far north (Fig 1, 2) The west coast dunefields differ from those in northeastern New Zealand in being considerably larger, and having had long histories (Early Pleistocene-Holocene) of extensive landwards dune transgression under the influence of strong prevailing westerly quarter winds By contrast, the dunefields inhabited by *S archeyi* on the more sheltered east coast mostly comprise relatively narrow belts of accretionary, beach-parallel foredunes of Late Pleistocene and Holocene age (Isaac et al 1994) The contrasts between east and west coast distributions of *S archeyi* are thus possibly linked to overall differences in dunefield environments between the two coasts, with respect to the relative effects of inshore sand supply and wind regime on dune stability and the spatial-temporal distribution of dune vegetation available for snails to inhabit Alternatively, *S archeyi* might have been more widely distributed on the North Island west coast during Holocene time, but lacks a fossil record as a result of widespread erosion and remobilisation of coastal dunes in the late prehistoric-historic period The record of Middle Pleistocene *S archeyi* from near Marton hints at a former extensive west coast distribution of the species

Causes of Holocene population decline and extinction

The modern distribution of *S archeyi* in northern New Zealand is considerably reduced from the situation in prehistoric time, as a result of the widespread decline and local extirpation of populations As noted above, there is insufficient information available to determine the chronology of these declines in *S archeyi* abundance at most sites, other than to place them in latest prehistoric to historic time Exceptions are the two Hawke Bay populations that I infer became extinct well before Polynesian settlement of New Zealand, and the population at Taipa that became extinct some time after 1950 AD

Two lines of evidence suggest that the main overall decline in *S archeyi* distribution took place following the European settlement of New Zealand The first concerns patterns of *S archeyi* distribution during the period of prehistoric Maori occupation, and the second concerns the impacts of environmental changes associated with European settlement

Succinea archeyi was widely distributed in northeastern New Zealand during the late prehistoric period, and inhabited coastal sites that were also utilised and modified by Maori Probably the main environmental change wrought by Maori that influenced *S archeyi*, was the widespread clearance of lowland forest after c 900–700 years B P (e g , McGlone et al 1994, Elliot et al 1995, Newnham et al 1998) Paleoecological evidence from the Te Werahi dunefield in northernmost Northland indicates that anthropic land clearance there actually increased the area of sandfield and prostrate shrubland habitat available for *S archeyi* to occupy (Brook 1999c) The same kinds of vegetation changes, involving the replacement of forest and tall shrubland by more open shrub sandfield/grassland mosaics, presumably benefited *S archeyi* at other coastal sites as well

The kiore (*Rattus exulans*), a human commensal that was present in New Zealand throughout the period of prehistoric Maori occupation, is a known predator of landsnails (Campbell et al

1984, Meads et al 1984, Atkinson 1986, Parrish & Sherley 1993, Brook 1999a) There is circumstantial historical evidence from Motuopao Island that the kiore may have been an important predator of that *S archeyi* population (Brook 1999e) However, the declines and local extinction of *S archeyi* populations at mainland North Island sites cannot be correlated with the coexistence of kiore The fact that the main overall decline in *S archeyi* distribution within northern New Zealand took place at least several hundred years, and possibly more than 1500 years, after the arrival of kiore (cf Holdaway 1996, 1999, Anderson 1996), suggests that predation by kiore was probably not a decisive factor

European settlement of northern New Zealand led to considerably more profound environmental changes in coastal areas than had already happened in late prehistoric time Probably the most important changes affecting *S archeyi* were those relating to the establishment of pastoral farming from the mid-19th century Impacts on dunefield habitats would have been cumulative, and included the modification and loss of native vegetation by firing, browsing and trampling by livestock, overplanting with exotics, and invasion by adventive weed species In addition, loss of vegetation cover through firing and livestock damage contributed to extensive erosion of some dunefields In the 20th century, some *S archeyi* dunefield habitats were further modified or destroyed as a result of residential development and the establishment of exotic plantation forests

The introduction of exotic (European) invertebrate and small mammal species to New Zealand during historic time, has also caused profound ecological changes in dunefield ecosystems, but the full extent of these impacts on *S archeyi* abundance and distribution is not known as yet Adventives that became established in northern New Zealand between the late 18th and early 20th centuries, and which are known to eat small landsnails, include gastropod molluscs (e g , *Oxychilus alliarius*), European rats (*Rattus norvegicus*, *Rattus rattus*), mice (*Mus musculus*), hedgehogs (*Erinaceus europeaus*) and possums (*Trichosurus vulpecula*) (King 1990, Barker 1999)

The lack of evidence for significant adverse anthropic or other environmental impacts on *S archeyi* distribution during the period of prehistoric human occupation of New Zealand, coupled with the known history of widespread and substantial modification and destruction of native coastal vegetation in the historic period, suggest that most of the decline of *S archeyi* in northern New Zealand followed European settlement I infer that the distribution of *S archeyi* contracted rapidly from the mid-19th century onwards, mainly as a consequence of the impacts of pastoral farming on native coastal shrubland, grassland and sandfield vegetation From at least the mid 20th century onwards, residential subdivisions, associated land development, and the establishment of *Pinus radiata* plantations on coastal dunefields have also contributed to the diminution, fragmentation, and extinction of some *S archeyi* populations (Brook 1999e)

The same anthropic ecological impacts now threaten the continued survival of some known relict populations of *S archeyi* in Northland and Coromandel Peninsula Elsewhere (Brook 1999e), I have identified immediate threats to present-day *S archeyi* populations These include the replacement of native plant communities on dunes by invasive exotic weed species, or by deliberate plantings of native and exotic tree and shrub species, and loss of habitat through livestock damage, land development and dune erosion Most of the modern *S archeyi* populations on Coromandel Peninsula, and the populations at Tom Bowling Bay, Whananaki Spit, Ngunguru Spit and Horahora River in Northland, are seriously threatened by one or more of the impacts listed above (Brook 1999e) Conservation action (habitat management) is required to prevent these populations becoming extinct By contrast, the *S archeyi* populations at Motuopao, Cape Maria van Diemen-Te Werahi, Spirits Bay, Puwheke Beach, Tokerau Beach and Te Ruatahi in Northland, and that at Waikawau Bay on

Coromandel Peninsula, occupy dune habitats that do not appear to be under any serious threat at present However, even at those dune sites, long-term eradication of invasive exotic weed species, and possibly also animal pest control, will be necessary to preserve the ecological integrity of the native sandfield and prostrate shrubland floras, and to ensure the continued survival of the *S archeyi* populations

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APPENDIX 1

Prehistoric and historic Holocene distribution of *Succinea archeyi*

For each location, the status (extant or extinct) is given, and reference is made to data sources Fossil sites are categorised as pre-Maori (i e, prehistoric, pre-Polynesian settlement) or post-settlement (i e, prehistoric Maori occupation period) Identifier numbers quoted refer to New Zealand Fossil Record File catalogue numbers (with NZMS 260 map code followed by site number with f prefix), archaeological site numbers (with NZMS 260 map code), and collections held at the Auckland War Memorial Museum (AIM) and the Museum of New Zealand (NMNZ), indicated by AK and M prefixes respectively

Whangape (extinct)
Fossil post-settlement (N05/f57, f59) (F J Brook unpubl data)
Tauroa Peninsula (extinct)
Fossil post-settlement (N02/f33, f36–38, f41, f42, f45, f49–51) (Brook 1999d)

Motuopao Island (extant: Brook 1999c, 1999e)
Fossil: pre-Maori (M02/f146, f148); post-settlement (M02/f145) (Brook 1999c).
Cape Maria van Diemen-Te Werahi (extant at five sites between Cape Maria van Diemen and Herangi Hill: Brook 1999c, 1999e)
Fossil: pre-Maori (M02/f76, f77, f80, f89, f95, f102, f112, f128, f142); post-settlement (M02/f87, f90, f93, f98, f101–104, f108–110, f113, f116–122, f129, f131, f134, f136, f139–141, f143) (Brook 1999c).
Tapotupotu Bay (extinct)
Fossil: pre-Maori (M02/f29); post-settlement (M02/f154–158) (Millener 1981; F. J. Brook unpubl. data).
Spirits Bay (extant: Powell 1950; Brook 1999e).
Tom Bowling Bay (extant: Brook 1999e)
Fossil: pre-Maori (M02/f50, f211); post-settlement (M02/f209, f216, f221) (Millener 1981; F.J.Brook unpubl.data).
Whareana Beach (extinct)
Fossil: pre-Maori (N02/f55, f222, f224–226); post-settlement (N02/f223, f227–230) (Millener 1981; F.J.Brook unpubl.data).
Henderson Bay (extinct)
Fossil: ? pre-Maori (N03/f11) (Millener 1981).
East Beach (extinct)
Fossil: ? pre-Maori (O03/f8) (Millener 1981).
Puwheke Beach (extant: Brook 1999e).
Tokerau Beach (extant: Powell 1950; Brook 1999e)
Fossil: pre-Maori (O03/f10; O04/f22, f24, f25, f136, f138, f141, f142, f146, f149, f150, f152, f155, f156, f158–160, f162, f164, f165, f166–171); post-settlement (O04/f135, f140, f147, f175, f177) (Millener 1981; Brook 1999b).
Taipa Beach (extinct: Powell 1950; Brook 1999e).
Umuheke Bay (extinct)
Fossil: post-settlement (Q05/f9, f12, f13) (Brook & Goulstone 1999)
Mokau (extinct)
Fossil: post-settlement (Q05/f10) (Brook & Goulstone 1999)
Ngahau Bay (extinct)
Fossil: post-settlement (Q06/f50, f51, f53, f65, f73) (Brook & Goulstone 1999).
Te Ruatahi (extant: Powell 1950; Brook & Goulstone 1999; Brook 1999e).
Fossil: post-settlement (Q06/f60, f61) (Brook & Goulstone 1999).
Whananaki (extinct)
Fossil: post-settlement (Q06/f49, f68–70, f78–80) (Brook & Goulstone 1999).
Whananaki Spit (extant: Brook & Goulstone 1999; Brook 1999e).
Matapouri (extinct)
Fossil: post-settlement (Q06/f81, f82, f89) (F. J. Brook unpubl. data).
Ngunguru Spit (extant: Powell 1950; Brook 1999e).
Horahora River (extant: Brook 1999e).
Pataua (extinct)
Fossil: stratigraphic distribution not recorded (Thomson 1959).
Ocean Beach, Bream Head (extinct)
Fossil: stratigraphic distribution not recorded (AIM AK33632, AK90780; NMNZ M.4884, M.37716, M.84649: Powell 1950).
Smugglers Bay (extinct)
Fossil: pre-Maori (Q07/f139); post-settlement (Q07/f140, f141) (F. J. Brook unpubl. data).
Oneroa, Waiheke Island
Fossil: stratigraphic distribution not recorded (AIM AK30602: Powell 1950).
Port Jackson (extinct)
Fossil: stratigraphic distribution not recorded (AIM AK90776: Goulstone 1979).
Waikawau Bay (extant: Thomson 1959; Brook 1999e).
Matarangi
Fossil: post-settlement (F. J. Brook unpubl.data).
Opito Bay (extant: Brook 1999e).
Tairua (extant: Brook 1999e).

Slipper Island (extinct)
  Fossil post-settlement (Willan 1974)
Opoutere (extant Brook 1999e)
Whangamata (extant Thomson & Jones 1954, Brook 1999e)
Athenree (extinct)
  Fossil post-settlement (archaeological sites U13/79, U13/966, NMNZ M 85922, 86241 B G McFadgen unpubl data)
Omokoroa (extinct)
  Fossil post-settlement (archaeological site U14/967, NMNZ M 85867 B G McFadgen unpubl data)
Tilby Point (extinct)
  Fossil post-settlement (archaeological site U14/2683, NMNZ M 85971 B G McFadgen unpubl data)
Waimapu (extinct)
  Fossil post-settlement (archaeological site U14/1927, NMNZ M 87556 B G McFadgen unpubl data)
Kaiwha (extinct)
  Fossil post-settlement (archaeological sites U14/2472, 2527, NMNZ M 86001, M 86086 B G McFadgen unpubl data)
Omanu-Papamoa Beach (? extinct Powell 1950, Thomson 1952, Thomson & Jones 1954, Brook 1999e)
Lake Poukawa (extinct)
  Fossil pre-Maori (NMNZ M 57754 Climo 1980)
Ocean Beach, Cape Kidnappers (extinct)
  Fossil ? pre-Maori (Powell 1950)