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Results of palaeofaunal research

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Introduction

In this chapter, we describe the results of identifications of the faunal remains described in Chapter 2. We restrict the results to data from the fossil sites rather than the archaeological sites, which are described in Chapter 10. Analyses were carried out by Worthy using the reference collections noted in Chapter 10, which include relatively modern material in order to examine changes in the Fiji fauna.

The following abbreviations have been used for both single and plural reference to the elements: cmc, carpometacarp; cor, coracoids; fem, femora; fib, fibulae; hum, humeri; pt, part; quad, quadrates; rad, radii; scap, scapulae; stern, sterna; tmt, tarsometatarsi; and tib, tibiotarsi. When listing material, bones are sometimes identified as left (L) or right (R) elements. L or R prefixed by 'p', 's' or 'd' indicates 'proximal', 'shaft' or 'distal' part of the element respectively, e.g. pR fem means the proximal part of a right femur. Anatomical nomenclature for specific bone landmarks follows Baumel and Witmer (1993), but terms are Anglicised after first mention. Some common terms are abbreviated as follows: *proc.* for *processus*; *artic.* for *articularis*.

Owl middens – insights into modern faunas

In many of the sites described in the preceding chapter, middens accumulated by the barn owl (*Tyto alba*) were present (Table 1). In several cases, the bone deposits were relatively thin (<10 cm) and generally they overlay archaeological deposits, indicating initiation of deposition after human use of the site. At Nabalabalagita Cave, the test pit indicated abundant bones of *Rattus exulans* to 45 cm depth. They are probably derived from owl midden, but human use of the cave is indicated by archaeological material to 62 cm depth. At the Tavuni site near Toga, the sediment containing owl-derived fauna and *Tyto* bone extended to 45 cm depth, and there, also, human influence in the site extended to about 60 cm depth. While still dominated by *Rattus exulans*, bones of *R. praetor*, *Gallicolumba stairii* and *Porphyrio porphyrio* are probably several hundred years old. In no case was there evidence of owl-midden deposits in sediments older than the period of human colonisation.

Table 1. Faunas from barn owl (*Tyto alba*) sites showing NISP.

Species	Common name	VVS	Buk	Tav	Q2	Nab
<i>*Rattus exulans</i>	Pacific rat	100s	100s	100s	100s	100s
<i>*Mus musculus</i>	Mouse		21	73	88	6
<i>*Rattus rattus/norvegicus</i>	Rat	64		17		5
<i>*Rattus ?praetor</i>	Rat			4		
<i>Emballonura semicaudata</i>	Microbat		54	2	4	
<i>Tyto alba</i>	Barn owl	5	4	4	8	1
<i>Egretta sacra</i>	Reef heron		24	100		
<i>Halcyon chloris</i>	White-collared kingfisher				1	3
<i>Collocalia spodiopygia</i>	White-rumped swiftlet		127	9	158	
<i>Gallicolumba stairii</i>	Friendly ground dove			1		
<i>Ptilinopus perousii</i>	Many-coloured fruit dove dove		2			
<i>Ptilinopus luteovirens</i>	Golden dove					?1
<i>Poliolimnas cinereus</i>	White-browed crake	8				
<i>Porzana tabuensis</i>	Spotless crake	5				
<i>Porphyrio porphyrio</i>	Purple swampphen			1		
<i>Foulehaio carunculatus</i>	Wattled honeyeater					2
<i>*Acridotheres fuscus</i>	Indian myna			13		4
<i>*Pycnonotus cafer</i>	Bulbul		58		1	45
<i>Aplonis tabuensis</i>	Fiji starling	1				
<i>Turdus poliocephalus</i>	Island thrush		2			
<i>Zosterops ?lateralis</i>	Fiji white-eye	5	25			30
<i>Erythrura cyanovirens</i>	Parrot bill finch					1
Undetermined passerines			7	6		Y
<i>Gehyra oceanica</i>	Gecko	2	5	7		18
<i>Nactus pelagicus</i>	Gecko	1		2		
Gecko sp. indet	Gecko	17			2	
Skink sp. indet	Skink	6				
<i>Brachylophus ?vitiensis</i>	Banded iguana				1	

VVS – Volivoli Swamp site, Buk – Bukusia, Tav – Tavuni at Toga, Q2 – Qararioso #2 at Tau, Nab – Nabalabalagita Cave. 'Y' indicates the taxon was present.

* means taxon is introduced. While rats appear to dominate these assemblages there is a consistent high diversity of birds and other vertebrates present.

The owl middens are observed as large surface deposits of rat bones. While most bones appeared to be whole, bulk samples show many are fragmented. Most are of the Pacific rat (*Rattus exulans*), but large numbers of geckos and a lesser number of birds are always present. Samples from such sites were collected to compare to the older fossil sites and provide indications of modern deposition in caves. It was hoped these could be compared to prehistoric owl-accumulated faunas, but none of those were found.

In all sites, rodents dominated the faunas (Table 1), with *Rattus exulans* most common. However, larger rats were also present, with *Rattus praetor* at deeper levels in one site, and *Rattus rattus/norvegicus* in surface deposits with *Mus musculus*. The small bat *Emballonura semicaudata* was common in some sites, where suitable roosting caves were present nearby. At least 17 species

of birds plus other undetermined passerines were recorded from these owl middens. Two geckos and the banded iguana complete the fauna.

The fauna in each site appear to have been highly influenced by the local environment and the availability of prey species. For example, the small bat *Emballonura* and the swiftlets *Collocalia* were only present when there were caves near the sites, and then their bones were common, indicating they were favoured owl prey. The Volivoli Swamp site was the only one near a wetland and it was also the only one that had wetland birds such as white-browed crake *Poliolimnas cinereus* and spotless crake *Porzana tabuensis*. Fish bones were also present and, together with the crake bones, indicate the owl foraged over the wetland. The modern deposits often contained historically introduced birds, such as Indian myna *Acridotheres fusca* and bulbul *Pycnonotus cafer*, which, together with white-eyes *Zosterops lateralis*, were often the most common birds in the site. These taxa indicate that the owls were hunting in open grassland–shrubland habitats rather than in closed forest. One species notable by its absence among these faunas was the long-tailed cuckoo *Eudynamis taitensis*. Its bones were common in owl middens on Vatulele Island (see below), and this observation bears out the observations of local ornithologists (D. Watling, pers. comm., Environment Consultants, Fiji) that the long-tailed cuckoo is rare or absent on Viti Levu, yet common on smaller islands.

The most important conclusion from these data is that humans were already present in Viti Levu, and had been for some time, before barn owls *Tyto alba* arrived. The presence of suitable rodent prey introduced by people presumably at or near colonisation about 3000 years ago (Anderson and Clark, 1999; White et al. 2000) was probably the prerequisite that allowed barn owls, which are specialist predators of small mammals and specifically rodents, to self-colonise, presumably from the Solomon Islands.

The fossil faunas

Fossil vertebrate faunas were obtained from five main sites: Volivoli #1, Qaranivokai, Wainibuku Cave, Udit Tomo and Vatumu. Isolated finds were made at Delaniqara at Wailotua, Bukusia and Qaranioso. The fossil faunas available from these sites reveal a minimum of 11 herpetofaunal species, 24 birds plus at least four undetermined passerines, and four bats (Table 2) (Worthy and Anderson 1999; Worthy et al. 1999; Molnar et al. 2002; Pregill and Worthy 2003; Worthy 2000a, 2001a, b, 2003, 2004). Of great significance, this fossil fauna revealed the presence of some extinct taxa, of which several are sufficiently large to be termed megafauna. Foremost among these were herpetofaunal species: a terrestrial crocodilian, a giant iguana, a giant frog and a tortoise. Among the birds were a giant flightless megapode and an equally large flightless pigeon, rivalling the dodo in size. Other extinct species include another megapode, a large fruit pigeon, and another large rail, in addition to the historically extinct barred-wing rail *Gallirallus* (= *Nesoclopeus*) *poicilopterus*, a snipe and a duck.

Herpetofauna

Three species of frog are represented. Bones of the two extant species, *Platymantis vitiensis* and *P. vitianus*, are present, with those of a newly discovered extinct species named *Platymantis megabotoniviti* (Worthy 2001a). Growing to about 150 mm snout–vent length, the latter was a very much larger and more robust ground frog than *P. vitianus*. *Platymantis megabotoniviti* was found in most fossil sites in Viti Levu (Figure 19).

Iguana fossils include some attributable to one of the extant species, but many are of a new, extinct giant iguana up to 1.5 m long (Worthy et al. 1999), recently named *Lapitiguana impensa* (Pregill and Worthy 2003). This iguana has been found in four sites (Volivoli #1, Qaranivokai,

Table 2. A list of taxa and NISP recorded from the main fossil sites in Viti Levu.

Species	Common Name	Volivoli I	Qaranivokai	Wainibuku Cave	Udit Pitfall Cave	Vatumu	Wailotua	Joskes Thumb
† <i>Platymantis megabotoniviti</i>	Giant ground frog	36	795	53	6	11	1	
<i>Platymantis vitiensis</i>	Fiji tree frog		15			2		
<i>Platymantis vitianus</i>	Fiji ground frog	4	375			3		
<i>Gehyra</i> aff. <i>G. vorax</i>	Large gecko		9			1		
Gecko sp.			13					1
Skink large sp.			2					
† <i>Lapitiguana impensa</i>	Giant iguana	35	134					
<i>Brachylophus ?vitiensis</i>	Modern iguana	1	3					
<i>Candoia</i> sp.	Boa	1		157				
† <i>Volia athollandersoni</i>	Land crocodilian	13		112				
†Tortoise nsp	Tortoise	1						
?†Tortoise nsp fragments	?Tortoise	13						
<i>Pseudobulweria rostrata</i>	Tahiti petrel					6		
<i>Pterodroma ?brevipes</i>	Collared petrel					2		180
<i>Pterodroma leucoptera</i>	New Caledonian petrel							1
<i>Pterodroma externa</i> or <i>Pt. cervicalis</i>	Juan Fernandez petrel							5
<i>Nesofregatta albigularis</i>	White-throated storm petrel							4
<i>Puffinus lherminieri</i>	Audubon's shearwater							20
<i>Sterna fuscata</i>	Sooty tern							4
† <i>Vitrallus watlingi</i>	Viti Levu rail	7	544		1			
<i>Gallirallus philippensis</i>	Banded rail		5					
† <i>Nesoclopeus poecilopterus</i>	Barred-wing rail			2	2		18	
†Rail indet sp. 1	?Gallinule			1	2			
† <i>Megavitiornis altirostris</i>	Giant megapode	7	6	17	200		5	
† <i>Megapodius amissus</i>	Viti Levu scrubfowl	2	2		89			
† <i>Anas</i> sp. indet.	Fiji teal					1		
<i>Natunaornis gigoura</i>	Giant pigeon	10	16	13	29			
<i>Columba vitiensis</i>	White-throated pigeon		2					
<i>Ducula latrans</i>	Peale's pigeon		3			3		53
† <i>Ducula</i> sp. cf. <i>D. lakeba</i>	Large fruit pigeon	1		1	1	2		
<i>Gallicolumba stairii</i>	Friendly ground dove					24		
<i>Ptilinopus ?lutiovitrens</i>	Golden dove		1					
<i>Ptilinopus perousii</i> or <i>P. luteovirens</i>	Many-coloured or golden dove					7		
<i>Ptilinopus</i> sp. indet	Indet dove sp.							3
<i>Prosopeia personata</i>	Musk parrot		31			2		6
<i>Vini solitarius</i>	Collared lory					1		8
† <i>Coenocorypha miratropica</i>	Fiji snipe					17		
<i>Accipiter rufoptorques</i>	Fiji goshawk							39
<i>Halcyon chloris</i>	White-collared kingfisher							1
<i>Aplonis tabuensis</i>	Polynesian starling	1	3					2
<i>Rhipidura cf spilodera</i>	Spotted fantail		1					
<i>Zosterops</i> sp.	White-eye		1					
<i>Foulehaio carunculata</i>	Wattled honeyeater		1					
<i>Gymnomyza viridis</i>	Giant forest honeyeater							5
<i>Collocalia spodiopygia</i>	Swiftlet					1		
<i>Turdus poliocephalus</i>	Island thrush	1	7		?1			
Passerine sp.	Small perching birds		10			7 (4 sp)		
<i>Pteropus tonganus</i>	Large fruit bat	2			?1	?1		204
<i>Notopteris macdonaldi</i>	Small fruit bat		10	647		34	209	
<i>Emballonura semicaudata</i>	Small bat	3	98	2		14		
<i>Chaerephon bregullae</i>	Fijian mastiff bat			6				

† Species globally extinct. Joskes Thumb is attributed to falcon predation, and is after Worthy (2000b) with addition of new material collected.

Bukusia, Qaranioso), all in western Viti Levu (Worthy and Anderson 1999). Its large size is unrivalled in the Pacific, and also indicates that it was a terrestrial species (Figure 20). It has not been found in the wetter rainforest regions of the east despite the presence there of suitable fossil sites, indicating it favoured drier habitats. Banded iguanas in Fiji have recently been shown to comprise three distinct species, with *Brachylophus bulabula* erected for populations formerly known as *B. fasciatus* in the wet forests of Viti Levu, Vanua Levu and Kadavu (Keogh et al. 2008). Populations in the dry vegetation zones of the northwestern side of Viti Levu and offshore islands are *B. vitiensis*, and *B. fasciatus* is now restricted to populations in the Lau Group. We follow this nomenclature here, but note that the referral of iguana bones from Vatulele or Sigatoka to either *B. vitiensis* or *B. bulabula* is problematic, as extant populations, if present, have not been identified (Keogh et al. 2008).

The new species (and genus) of extinct terrestrial crocodilian *Volia athollandersoni* and the tortoise were both found in Volivoli #1 on the first investigation (Worthy et al. 1999). Remains of the tortoise have not been identified with certainty from any other site. The only identifiable bone, although there are several fragments with internal turtle osteological morphology, is an ungual, which is similar to that of the meiolaniids, or terrestrial horned turtles, known from, for example, New Caledonia and Lord Howe Island.

Figure 19. Selected bones of *Platymanitis megabotoniviti*. A, femur MNZ S37094. B–D, adult left humeri in ventral view: S37027, S37068 and S37065. E, right maxilla S37061 in lingual view. F, left tibiofibula S37027 in anterior view. G, right radioulna S37027 in lateral view. H–I, left ilia S37057C and S37057A in lateral view. Reproduced from Worthy (2001a) with the permission of *Palaeontology*.

Figure 20. Giant iguana (*Lapitiguana impensa*) remains. Bottom, right maxilla (MNZ S37015) lingual view. Middle and top, pelvis (left side) of modern *B. vitiensis* and *Lapitiguana impensa* (MNZ S37034).

The crocodilian *Volia athollandersoni* is represented by material from Volivoli #1 and Wainibuku Cave in the west and east of Viti Levu respectively (Figure 21). The better-preserved remains found in Wainibuku Cave have enabled the species to be described (Molnar et al. 2002). It is a terrestrial species most similar to *Mekosuchus inexpectatus* (Balouet and Buffetaut 1987) from New Caledonia and *M. kalpokasi* from Vanuatu (Mead et al. 2002), as well as fossil mekosuchine taxa from Australia (Molnar et al. 2002). *Volia athollandersoni* grew to at least 3 m in length.

The remaining fossil herpetofauna includes remains of a boid snake, presumably the extant *Candoia bibronii*, and undetermined skinks and geckos, including large (ca. 20–30 cm long) species of each.

Avifauna

The 24 taxa of birds so far known from these fossil faunas, even when augmented by at least four undetermined passerines, is a considerably smaller total than the 47 known historically from Viti Levu (Watling 1982). However, eight of the fossil taxa are newly discovered, extinct taxa. Most of the fossil species are ground-dwelling species, with canopy-dwelling forest species under-represented, and wetland taxa virtually absent.

Megapodes are one of the most characteristic ground birds of the South Pacific, with either extant or extinct species spread from Indonesia across the Pacific to Western Samoa (Jones et al. 1995; Steadman 1999, 2006a). The largest and most unusual species is *Sylviornis*

Figure 21. Terrestrial crocodilian (*Volia athollandersoni*) remains. Top left, coalesced parietals (MNZ S37342) dorsal view. Top right, humerus (right) (MNZ S37348). Middle, mandible (MNZ S37332) lateral view. Bottom, mandible (MNZ S37332) dorsal view.

neocaledoniae from New Caledonia (Poplin and Mourer-Chauviré 1985; Balouet 1991), but the fossils discovered in Viti Levu reveal a smaller, but still very large species. Recently described as *Megavitiornis altirostris* (Worthy 2000a), this flightless species was perhaps up to 15 kg in weight and stood near 1 m tall. Its bones were found in Volivoli #1, Qaranivokai, Udit Cave and Delaniqara at Wailotua, so the species lived in both wet and dry habitats (Figures 22–

Figure 22. Top, Tarsometatarsi and phalanges of the giant megapode *Megavitiornis altirostris* from Viti Levu. A, paratype MNZ S37369; B–D, holotype MNZ S37362. Reproduced from Worthy (2000a) with the permission of the Royal Society of New Zealand. Bottom, the incredibly stout mandible of *Megavitiornis altirostris*, MNZ S37017 in A, medial, B, lateral, and C, dorsal, aspects. Reproduced from Worthy (2000a) with the permission of the Royal Society of New Zealand.

Figure 23. Reconstruction of the skull of *Megavitiornis altirostris* based on MNZ S37455 and MNZ S37017. Reproduced from Worthy (2000a) with the permission of the Royal Society of New Zealand.

23). A smaller extinct megapode was also found in Volivoli #1, Qaranivokai and Udit Cave, a flightless or weakly volant form of the widespread genus *Megapodius* (Jones et al. 1995) named *Megapodius amissus* (Worthy 2000a). It was larger than all its congeners except *M. reinwardt* in Australia and *M. molistructor* (Balouet and Olson 1989) extinct of New Caledonia.

The second giant flightless species of bird was a pigeon. Large flightless pigeons are rare in insular faunas (Goodwin 1967): they are otherwise unknown in the Pacific and represented in the Indian Ocean by the dodo *Raphus cucullatus* and solitaire *Pezophaps solitaria*. The giant extinct species from Fiji was nearly the same size as the dodo and has been recently described as the new genus and species *Natunaornis gigoura* (Worthy 2001b), allied to the crowned pigeons *Goura* of Papua New Guinea. Its genus name honours Kiniviliame Natuna, the senior chief of Volivoli in Nadroga, while its specific name reflects its likeness to a gigantic *Goura* species. A few bones indicate the presence of a large fruit pigeon, which may be *Ducula lakeba*, described recently by Worthy (2001b) from Lakeba Island. This species is a larger pigeon than the extinct *Ducula david* of Wallis Island (Balouet and Olson 1987) and *Ducula harrisoni* of Henderson Island (Wragg and Worthy 2006), but Viti Levu bones are of either undiagnostic parts or elements not shared with the Lakeba assemblage, precluding a certain referral. However, both the Viti Levu species and *Ducula lakeba* are larger than any other *Ducula* so far described.

As might be expected from their remarkable radiation elsewhere in the Pacific (Steadman 1987, 1995, 2006a; Steadman et al. 2000), there are several rails in the Viti Levu fauna, of which three are extinct, and only one was historically known. One is a very distinctive form, recently described as *Vitirallus watlingi* (Worthy 2004), the long bill of which approaches the proportions of that in *Aphanapteryx* in the Mascarene Islands, but the bird was the size of the weka *Gallirallus australis* of New Zealand. Three bones attest to the probable presence of a gallinule, which would not be unexpected given the presence of *Gallinula pacifica*, historically known from Samoa, and *Gallinula silvestris*, from the Solomon Islands, both listed in the genus *Pareudiastes* by Steadman (2006a). Last and rarest of the extinct taxa within the fossil record is the historically extinct *Gallirallus* (= *Nesoclopeus*) *poicilopterus*, of which few bones have been

found. Four extant rails are also present in the fossil fauna: the banded rail *Gallirallus philippensis*, the spotless crane *Porzana tabuensis*, the purple swamphen *Porphyrio porphyrio*, and the white-browed crane *Poliolimnas cinereus*.

An unexpected discovery was that of a new species of extinct snipe *Coenocorypha miratropica*, found at Vatumu, near Nadi (Worthy 2003). This genus is otherwise not known from Fiji, but has been recorded in New Caledonia (Balouet and Olson 1989) outside its stronghold in the New Zealand archipelago (Holdaway et al. 2001; Worthy and Holdaway 2002).

Also at Vatumu, a single bone of a small duck *Anas* sp. was recovered. This is the only anatid fossil so far recovered from Fiji. It is not referable to *Dendrocygna arcuata*, which is a small, highly vagile species, reported historically from Fiji (Watling 1982). The single scapula is not differentiable from the New Zealand brown teal *Anas chlorotis*, and so it is possible Fiji had a member of the Australasian radiation to which this species belongs. A teal that is very like *Anas gracilis* has been recorded from New Caledonia (Balouet and Olson 1989; Worthy unpubl. data).

Fossil sea birds are so far known only from the one fossil site at Vatuma near Nadi. Two petrels, *Pterodroma brevipes* and *Pseudobulweria rostrata*, are present in this fauna, which was probably accumulated by a predator, assumed to be the peregrine falcon *Falco peregrinus*. Clunie (1972) and Worthy (2000b) studied a recent fauna, accumulated by peregrine falcons, found at Joskes Thumb a few kilometres west of Suva. It was dominated by numerous species of birds, including canopy dwellers like *Ducula*, *Vini* and *Foulehaio*, and sea birds such as *P. brevipes* and *Sterna fuscata*, and fruit bats, and so was similar to the fauna found at Vatumu. The modern prey faunas of peregrines from Joskes Thumb (Clunie 1972) and downtown Suva (Clunie 1976) clearly show that the peregrine captures prey both over the ocean, outside the reef, and within forests.

Only the sites of Qaranivokai and Vatumu provide data on the volant and canopy species component of the prehuman avifauna. These sites have fossils of three fruit pigeons, a ground dove, one or two fruit-doves, the musk parrot, the collared lory and several passerines (Table 2). Only one of these, the largest fruit pigeon, is extinct.

Mammals

Four species of bats are represented in the fossil faunas (Table 2). These include the large fruit bat *Pteropus tonganus*, the endemic smaller fruit bat *Notopteris macdonaldi*, and the small sheath-tailed bat *Emballonura semicaudata*. A surprise was the discovery of the Fijian mastiff bat *Chaerephon bregullae* in the Wainibuku site, as this species is now known in the Fiji archipelago only from Vanua Levu and Taveuni (Flannery 1995; Palmeirim et al. 2007), but it is also known from Vanuatu, and a congener *Chaerephon solomonis* is known from the Solomon Islands (Flannery 1995:406).

No rodents were found in the fossil deposits, but in the archaeological site of Qaraniiso #2 and in the barn owl site at Tavuni (Worthy and Anderson 1999), *Rattus praetor* was found with *R. exulans*. *Rattus praetor* is a Western Pacific species, occurring nearest in Vanuatu, and recorded recently from Mago Island in the Lau Group, Fiji, to which it was presumably taken by human colonisers about 2800 years ago (White et al. 2000). It is now extinct and has been replaced in upper layers of owl sites by *Rattus rattus*.

Significance of the faunas

The fossil record of birds throughout the Pacific has revealed many extinct species, and range reductions of others (Steadman 2006a, and references therein). In the New Zealand geographic region, 66, or 26.9%, of the original 245 breeding species are now globally extinct (Holdaway et al. 2001; Worthy and Holdaway 2002: where New Zealand was defined as North, South

and Stewart Island and associated islets; Chatham Islands; the subantarctic Snares, Bounty, Antipodes, Auckland, Campbell and Macquarie Islands; and the tropical Norfolk Island and Kermadec Islands). At least 41% of the endemic species from the New Zealand region are extinct. On main islands, losses are even higher, e.g. the North Island lost 51% of its original fauna (Holdaway et al. 2001; Worthy and Holdaway 2002), and total losses have only been reduced because of the presence of small refuge islands adjacent to larger ones (Holdaway 1999). Gigantism and flightlessness have been significant evolutionary trends on mammalian predator-free islands, as shown in New Zealand by the 10 species of moa (Dinornithiformes, Tennyson and Martinson 2006), large rail-like birds (Aptornithidae), *Aptornis* (two species) and waterfowl (Anatidae), *Cnemiornis* (two species) (Olson and James 1991; Quammen 1996). The Hawaiian archipelago lost more than half its bird diversity (James and Olson 1991; Olson and James 1991), including at least four species of large, flightless, browsing anatids, called moa-nalos. Elsewhere in the Pacific, often up to half the fossil species were found to be extinct (Steadman 2006a), as in the Marquesas (Steadman 1989a; Steadman and Rolett 1996), Easter Island (Steadman 1995), Henderson Island (Wragg and Weisler 1994; Wragg and Worthy 2006; Worthy and Wragg 2003, 2008), Society Islands (Steadman 1989a), Samoa (Steadman 1994), and on the Tongan and Cook Island groups (Steadman 1989a, 1993, 1995). Among the extinct taxa are many species of rails, megapodes, columbids and parrots (Balouet and Olson 1987; Kirchman and Steadman 2005, 2006a, 2006b, 2007; Steadman 1987, 1989b, 1992, 2006a, 2006b, 2006c; Steadman and Zarriello 1987; Wragg and Worthy 2006; Worthy and Wragg 2003, 2008). A similar history of extinction has also been found in New Caledonia (Balouet and Olson 1989) and there are indications of them in Micronesia (Steadman and Intoh 1994; Steadman 2006a). Throughout the Pacific, most of the documented species diversity that has been lost is among the birds, but bats (Koopman and Steadman 1995), lizards (Pregill 1993) and iguanas (Pregill and Dye 1989; Pregill and Steadman 2004) all suffered losses prehistorically.

The recent palaeontological investigations have contributed substantially to knowledge of the prehuman terrestrial fauna of Viti Levu in the Fiji group. A remarkable fauna of large herpetofaunal species (crocodilian, tortoise, iguana and frog) has been revealed (Worthy et al. 1999). The tortoise and the crocodilian (Molnar et al. 2002) have their parallels in *Mekosuchus* and *Meiolania* on New Caledonia, Vanuatu and Lord Howe Island. The iguana *Lapitiguana impensa* (Pregill and Worthy 2003) and the extinct frog *Platymantis megabotoniviti* (Worthy 2001a) are both substantially larger than the extant taxa in each group, and together consolidate the notion of a long evolutionary history in Fiji for each of these groups. They also typify the phenomenon of island taxa having a tendency to evolve large terrestrial forms that are more at risk of extinction when new animals enter their habitats (Quammen 1996).

To the 47 historically known land birds (Watling 1982), eight more extinct species can be added. These include two of the most remarkable species known from the Central Pacific. Of these, the giant megapode *Megavitiornis altirostris* was exceeded in size only by *Sylviornis* of New Caledonia (Poplin and Mourer-Chauviré 1985). The giant, flightless pigeon *Natunaornis gigoura* represents a unique evolutionary course in the Pacific, but has its parallel in the Mascarene Islands with the solitaire and dodo. While considerably derived, this giant pigeon has several resemblances to *Goura* from Papua New Guinea (Worthy 2001b). The other extinct species, such as the smaller megapode *Megapodius amissus*, the large fruit pigeon *Ducula* cf. *lakeba*, the duck *Anas* sp., the three rails, and the snipe *Coenocorypha miratropica*, all have parallels elsewhere in the Pacific and were to be expected, in view of palaeontological research on other islands (Steadman 1995, 2006a).

Before these discoveries, Fiji was unique among larger Pacific islands in seemingly having lost only two taxa historically, with none known to be lost prehistorically. The new palaeontological

data show the all-too-familiar pattern seen in insular faunas, that after humans and their commensals colonise an island for the first time there are numerous changes in the fauna, commonly with the large flightless birds and other ground-dwelling taxa becoming extinct (e.g. Olson and James 1991; Quammen 1996; Steadman 1995, 1999, 2006a; Worthy and Holdaway 2002). The large extinct taxa doubtless fell victim to over-hunting by the first humans (Anderson 1996; Quammen 1996). The evidence for this in Viti Levu is still largely lacking, but there is no other plausible reason why large taxa should persist for millennia through many climatic cycles then drop from the record about the time of human arrival. To date, no significant archaeological bone middens of extinct fauna have been recovered from Viti Levu. But *Lapitiguana* was present in the basal layers of a test pit in the archaeological deposit in Qaranioso near Tau, which is the only inland archaeological site dating to the first contact period of humans with the fauna. A test pit in Volivoli II has revealed one of the extinct rails and small petrels. The archaeological site VL 21/5 on Naigani (Best 1981) contained remains of a giant megapode, as first reported by van Tets (1985) and later by Jones et al. (1995). These bones were identified as *Megavitiornis altirostris* by Worthy (2000a). There are also bones of the giant iguana *Lapitiguana* and the crocodilian *Volia* present in this fauna (Irwin and Worthy in prep). The archaeological record would be immensely enhanced by the discovery of first-contact faunas from sites on Viti Levu. The very small faunas available from these few early sites do attest, however, to the use of some of the extinct taxa by humans, suggesting they had a significant hand in that process.

On Viti Levu, extinction is not just a prehistorical or a historical phenomenon. Viti Levu has the usual range of rodents (*Rattus exulans*, *R. rattus*, *R. norvegicus*, *Mus musculus*) found on many islands. These are disastrous enough on their own, but in addition to cats and dogs, Viti Levu has a mustelid, the mongoose, which is a highly efficient predator. The mongoose *Herpestes auropunctatus* was introduced in 1883 (Pernetta and Watling 1979), and the barred-wing rail *Gallirallus* (= *Nesoclopeus*) *poecilopterus* was probably extinct soon after: the only specimens were collected in the mid-19th century. Since then, the purple swamp hen *Porphyrio porphyrio* has become extinct on Viti Levu and other islands with mongoose. Moreover, no colonies of petrels are known to survive on Viti Levu, yet *Pterodroma brevipes*, *Pseudobulweria rostrata*, *Nesofregatta albigularis*, *Puffinus pacificus* and *P. lherminieri*, at least, are likely to have had breeding populations in the past. The large ground frog *Platymantis vitianus* is very rare and seemingly headed for extinction on Viti Levu, while remaining common on mongoose-free parts of its former range. Similarly, banded iguanas (*Brachylophus* spp.) are rare now on Viti Levu, yet can be abundant on predator-free islands. In New Zealand, birds like kaka *Nestor meridionalis*, kokako *Callaeas cinerea*, parakeets *Cyanoramphus* sp. and yellowheads *Mohoua ochrocephala* are unable to maintain populations in the presence of the stoat *Mustela ermina* without management of stoat numbers. It is probable that the same is true of several species in Viti Levu, and that the true predatory effects of the mongoose may not yet have been realised. Several birds, notably the pink-billed parrot-finch *Erythrura kleinschmidti*, the greater forest warbler *Trichocichla rufa* and the friendly ground dove *Gallicolumba stairii* are very rare and are likely headed for extinction.

Even bats are not immune from extinction. The fauna from Wainibuku revealed that the Fiji mastiff bat *Chaerephon bregullae* was formerly on Viti Levu, though presently it is only known from Vanua Levu and Taveuni in Fiji (Palmeirim et al. 2007). While fossils indicate the sheath-tailed bat was widespread in Viti Levu even recently, we only saw one individual in Volivoli cave, and since then the species has not been found at all and is now considered extinct on Viti Levu (Palmeirim et al. 2007). Thus, extinction is an ongoing phenomenon on Viti Levu.

These new discoveries shed some light on the origin of the Fiji fauna, and that of Viti Levu in particular. As noted above, the affinities of the Fijian avifauna are generally held to be with Samoa and Tonga (Watling 1982; Steadman and Franklin 2000; Steadman 2006a). However,

the former presence of the crocodilian, tortoise and three frogs, along with the megapodes and the giant pigeon, all indicate a western relationship for the older, endemic component of the fauna of Viti Levu, as centres of abundance of these taxa and/or their nearest relatives lie to the west. The duck and the snipe probably have an Australasian derivation.

The fossil fauna of Vatulele

Most of the fossil faunas located in caves on Vatulele arise from predation by the barn owl *Tyto alba* so most species are its preferred prey. Reptiles were very common in these prey assemblages, with hundreds of geckos present, represented mainly by *Gehyra oceanicus* and some *Nactus pelagicus*. Also present were some skinks large enough to be the green tree skink *Emoia concolor*, rare banded iguanas *Brachylophus ?bulabula*, and rarely, small boas *Candoia bibroni*. However, the most obvious component of the owl faunas were rats. Three species were present, with the Pacific rat *Rattus exulans* most common. The larger, European species *R. norvegicus* and *R. rattus* were always present, clearly indicating that these owl deposits mainly post-dated European arrival. Even the subsurface deposits at Ganilao had large rat bones attributed to *R. rattus* or *R. norvegicus*, and therefore were post-European in age. However, in the small sample from the subsurface deposits, we found a single lower mandible, referred to the Fijian mastiff bat *Chaerephon bregullae*, now known only from Taveuni.

Only in sites associated with Big Cave entrances 2A and 2B and at Muremure were deposits found that could conceivably pre-date human occupation on the island. In all cases, these were small deposits attributed to single individuals on cave floors.

A total of at least 25 species of birds were recorded as fossil bones from the caves of Vatulele (Table 3). Most of these were in the owl sites. The main birds hunted by the owls were the swiftlet *Collocalia spodiopygia*, small *Ptilinopus* doves, Polynesian starling *Aplonis tabuensis* and wattled honeyeater *Foulehaio carunculata*. Other regular prey species were kingfishers *Halcyon chloris* and long-tailed cuckoos *Eudynamis taitensis*. The common presence of the latter species is interesting, as bones from the species have been not been found on mainland Viti Levu, despite several owl sites having been investigated. Moreover, it is seen only rarely on the main islands of Fiji (D. Watling, pers. comm.). Perhaps it avoids the main islands when it migrates to Fiji. The doves could be either *Ptilinopus porphyraceus* or *P. perousii*, both of which are extant on the island. They are of similar size, and the size range of the fossil bones, illustrated by humerus length in Figure 24, has an apparently normal distribution, with a few small individuals. The available reference specimens of *P. perousii* and *P. porphyraceus* fall within the size range of the fossils, which thus could be either. Other than these taxa, the owl preyed on a range of smaller passerines (undetermined) and some coastal species.

Big Cave entrances 2A and 2B and Muremure Cave provided pitfall faunas, which were dominated by bones of the purple swamp hen *Porphyrio porphyrio*, typical of the small, slender Pacific races *P. p. vitiensis* and *P. p. samoensis*, with the banded rail *Gallirallus philippensis* also common. No bones of megapodes or those of any other flightless bird were found. No bones of the frog *Platymantis* spp. were found.

Extinctions on Vatulele

Few species have demonstrably gone extinct on Vatulele. It seems likely the Fijian mastiff bat lived on the island in the past, and it is presumed extinct there. Of the birds, the swamp hen has gone extinct on Vatulele in living memory, as on Viti Levu. On Vatulele, the mongoose is absent, but the marshy areas are now cultivated, and the swamp hen population may have relied on the mainland population to offset declines in bad seasons. Now that the Viti Levu

Table 3. A list of the birds, reptiles and mammals from Vatulele Island at present and recorded here as fossils. Data for extant birds is from Dick Watling.

	Taxon	Common Name	Extant Status	Fossil
Reptiles	<i>Brachylophus ?bulabula</i>	Banded iguana	B	Y
	Skink, cf. <i>Emoia concolor</i>	Green tree skink	B	Y
	<i>Gehyra oceanicus</i>	Oceanic gecko	B	Y
	<i>Nactus pelagicus</i>	Pacific slender-toed gecko	B	Y
	<i>Candoia bibroni</i>	Pacific boa	B	Y
Birds	<i>Puffinus ?lherminieri</i>	Shearwater sp.	V	Y
	<i>Puffinus pacificus</i>	Wedge-tailed shearwater	V	Y
	<i>Pterodroma ?brevipes</i>	Gadfly petrel ?Collared	V	Y
	<i>Phaethon lepturus</i>	White-tailed tropic bird	B	Y
	<i>Sula dactylatra</i>	Masked booby	B	
	<i>Sula leucogaster</i>	Brown booby	V	
	<i>Sula sula</i>	Red-footed booby	B	
	<i>Fregata ariel</i>	Lesser frigate bird	V	
	<i>Ardea novaehollandiae</i>	White-faced heron	?B, V	
	<i>Egretta sacra</i>	Reef heron	B	
	<i>Anas superciliosa</i>	Pacific black duck	B	
	<i>Circus approximans</i>	Swamp harrier	B	
	<i>Gallus gallus</i>	Jungle fowl	B	Y
	<i>Gallirallus philippensis</i>	Banded rail	B	Y
	<i>Porphyrio porphyrio</i>	Purple swamphen	Locally extinct	Y
	<i>Porzana tabuensis</i>	Sooty crane	?	Y
	<i>Poliolimnas cinereus</i>	White-browed crane	?	Y
	<i>Pluvialis fulva</i>	Pacific golden plover	V	Y
	<i>Tringa incana</i>	Wandering tattler	V, common	Y
	<i>Tringa brevipes</i>	Siberian tattler	V, rare	
	<i>Arenaria interpres</i>	Ruddy turnstone	V	
	<i>Limosa lapponica</i>	Bar-tailed godwit	V	
	<i>Sterna bergii</i>	Crested tern	V	
	<i>Sterna sumatrana</i>	Black-naped tern	B	
	<i>Sterna anaethetus</i>	Bridled tern	V	
	<i>Anous minutus</i>	Black noddy	?B	Y
	<i>Anous stolidus</i>	Common noddy	B	Y
	<i>Gygis alba</i>	White tern	B	
	<i>Columba vitiensis</i>	White-throated pigeon	B	
	<i>Ducula pacifica</i>	Pacific pigeon	B	Y
	<i>Ptilinopus porphyraceus</i>	Crimson-crowned fruit-dove	B	Y
	<i>Ptilinopus perousii</i>	Many-coloured fruit dove	B	
	<i>Gallicolumba stairii</i>	Friendly ground dove	?locally extinct	Y
	<i>Streptopelia chinensis</i>	Spotted turtle dove	I	
	<i>Vini solitarius</i>	Collared lory	B	
	<i>Cacomantis pyrrhophanus</i>	Fan-tailed cuckoo	?	Y

Continued on next page

Table 3 continued

	Taxon	Common Name	Extant Status	Fossil
Birds	<i>Eudynamys taitensis</i>	Long-tailed cuckoo	?	Y
	<i>Tyto alba</i>	Barn owl	B	Y
	<i>Collocalia spodiopygia</i>	White-rumped swiftlet	B	Y
	<i>Hirundapus caudacutus</i>	Spine-tailed swift/White-throated needletail	V	
	<i>Halcyon chloris</i>	Kingfisher	B	Y
	<i>Mayrornis lessoni</i>	Slaty monarch	B	
	<i>Clytorhynchus vitiensis</i>	Lesser shrikebill	B	?Y
	<i>Myiagra vanikorensis</i>	Vanikoro broadbill	B	
	? <i>Zosterops lateralis</i>	Grey-backed white-eye	B	Y
	<i>Aplonis tabuensis</i>	Polynesian starling	B	Y
	<i>Foulehaio carunculata</i>	Wattled honeyeater	B	Y
	Passerine sp. indet.			Y
	<i>Acridotheres tristis</i>	Common mynah	I	
	<i>Acridotheres fuscus</i>	Jungle mynah	I	
Mammals	? <i>Chaerephon bregullae</i>	?Fijian mastiff bat	Locally extinct	Y
	<i>Emballonura semicaudata</i>	Sheath-tailed bat	B, rare	Y
	<i>Pteropus</i> cf. <i>tonganus</i>	Fruit bat	B	Y
	<i>Rattus exulans</i>	Pacific rat	B	Y
	<i>Rattus rattus</i>	Black rat	B	Y
	<i>Rattus norvegicus</i>	Norway rat	B	Y

B, breeding; V, visitor; I, introduced species.

Figure 24. A frequency distribution of humerus length for *Ptilinopus humeri* from Ganilao plotted with measurements for modern specimens of two *P. perousii* and one *P. porphyraceus*.

population has gone, so has that on Vatulele. The sooty crane probably still lives on the island, though no record exists for it. At least two small rails are seen in the forest near the resort (M. Livingston, pers. comm.), and these are likely to be the banded rail and sooty crane.

The only other possibly extinct bird is the friendly ground dove. This is a shy bird of the forest and it may still be extant in the western forests of the island: Dick Watling's observations of extant fauna were mainly around the resort in the north (D. Watling, pers. comm.). However, the presence of abundant mammalian predators (cats, black rats and Norway rats) militates against this possibility, as this dove has been found to be susceptible to these predators in many other places.

The absence of fossils suggest megapodes were absent from Vatulele, as these ground-frequenting birds surely would have been in the deposits if they were present on the island. Two species of megapodes have been found on Viti Levu, and a further species was present on islands in the Lau Group (Worthy et al. 1999; Worthy 2000a).

Differences from the Viti Levu fauna

The fossil faunas from Viti Levu include a number of distinctive extinct endemic species. These include a crocodilian, a giant iguana, a new giant frog to add to the two species already known (Worthy 2001a; Worthy et al. 1999), a giant megapode, and another weakly flightless one (Worthy 2000a), a giant flightless pigeon and a new large *Ducula* species (Worthy 2001b), a new flightless rail *Vitirallus watlingi* (Worthy 2004), a small duck, and a snipe *Coenocorypha miratropica* (Worthy 2003). The terrestrial giants and the frogs appear to be or have been restricted to Viti Levu and nearshore islands that were connected to it during low sea levels of the Pleistocene. None of these taxa were recorded from Vatulele, which is about 30 km distant. The deep intervening water (>250 m) would have ensured Vatulele was an island throughout the Pleistocene glacial–interglacial cycles.

The species that constitute the fauna on Vatulele are all good dispersers. The arboreal iguana, boa, skinks and geckos, for example, could easily have arrived on trees washed down the Sigatoka River during cyclones. Large trees remained on the Vatulele reef in November 1999 from the last cyclone, and Worthy was told they arrived only two days after the storm. The birds are all highly volant taxa, and characteristic of the many small atoll islands in Fiji and elsewhere in the South Pacific (Steadman 2006a). However, the terrestrial species from Viti Levu have not populated Vatulele, so presumably 30 km of water was an effective barrier.

The lack of any distinct species on Vatulele suggests this island has not been isolated for any great length of time in a form capable of supporting a fauna. In comparison, Henderson Island in the southeast Pacific first emerged only 380 kyr ago (Blake 1995), yet three endemic pigeons and a sandpiper have evolved in that period (Wragg 1995; Wragg and Worthy 2006; Worthy and Wragg 2003, 2008). The lack of any distinct species, particularly of flightless forms, on Vatulele suggests that its subaerial history may be quite short indeed. This provides some support for the relatively recent history of rising land suggested by (Nunn 1998). However, if the true age of Vatulele lies somewhere between the contrasting scenarios outlined above, it is possible that during the last interglacial high stand of sea level, the island was mostly, if not entirely, inundated. Only a small area of the present Naura cliff may have been emergent, an area insufficient to support a diverse terrestrial fauna. Moreover, such a small and low island could have had its fauna periodically removed by storm events. Thus, the present fauna may have a history no older than 70–80 kyr BP. Investigations to better date the antiquity of Vatulele, such as dating the speleothems in the wave-cut notches or in caves, are needed to test this suggestion.

Appendix: Vatulele fauna from Big Cave, Ganilao, Korolamalama and Muremure

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Appendix: Table 4. Faunas from the fossil sites on Vatulele. Big Cave System. This cave system comprises two discrete sections of cave now separated by collapsed rockfalls. Fossils were found mainly associated with entrances 2A and 2B. The faunas are listed by the sites they were collected from. All fossils were on the surface. Values are NISP/MNI.

Taxon	Name	Entrance 2A area	SW passage off 2A	2B, Gavin's Site	2B, Talus slope	2B, Isolated sites	2B, Dry rim-stone pool	2B, Dry sandy pool	Big Cave main Ent.
<i>Brachylophus fasciatus</i>	Banded iguana			9/1					
<i>Candoia bibroni</i>	Boa			2/1				6 vert	
Skink, cf <i>Emoia concolor</i>	Green skink			1 bone					
Gecko sp. indet	Gecko								Y
<i>Puffinus pacificus</i>	Wedge-tailed shearwater	17/1							
<i>Porphyrio porphyrio</i>	Purple swamp hen		1/1, 30/1	90/4	45/2	1/1	3/1	62/1, x/1	
<i>Gallirallus philippensis</i>	Banded rail		6/1, 16/1, 2/1	75/5	29/3		45/2	34/2, x/1	
<i>Porzana tabuensis</i>	Sooty crane			5/1					
<i>Gallus gallus</i>	Chicken				7/1				
<i>Tyto alba</i>	Barn owl				2/1				
<i>Ptilinopus porphyraceus</i>	Crimson-crowned fruit-dove				3/2				
<i>Gallicolumba stairii</i>	Friendly ground-dove	1/1	2/1	2/1		7/1, 1/1			
<i>Eudynamys taitensis</i>	Long-tailed cuckoo								21/1
<i>Aplonis tabuensis</i>	Polynesian starling		4/1						1/1
<i>Foulehaio carunculata</i>	Wattled honeyeater								1/1
Passerine sp. indet.				Yes	Yes				Yes
<i>Pteropus tonganus</i>	Fruit bat	1 dentary							
<i>Emballonura semicaudata</i>	Sheath-tailed bat			7 bones				20 bones	28 bones
<i>Rattus exulans</i>	Pacific rat		Y	74 bones	196 bones		53 bones		Skeleton
<i>Rattus rattus</i>	Black rat		Y						
<i>Rattus rattus /norvegicus</i>	Norway rat	Y		12 bones	30 bones		5 bones		

Appendix: Table 4 *continued*. List of species from the Ganilao barn owl midden. Faunas are listed here from the five separate samples. Values are NISP/MNI.

Taxon	Common name	Surface	Test pit 0–5 cm	Test pit 5–10 cm	Test pit 10–15 cm	Damp alcove
<i>Brachylophus fasciatus</i>	Banded iguana	28/1				9 bones
Skink, cf <i>Emoia concolor</i>	Green tree skink	34 bones			1 bone	1 bone
<i>Gehyra oceanicus</i>	Oceanic gecko	100s/94	30 bones	10 bones	8 bones	68/6
<i>Nactus pelagicus</i>	Pacific slender-toed gecko	X/26				3 bones
Gecko species						X/2
<i>Puffinus</i> sp. ? <i>lherminieri</i>	?Audubon's shearwater					1/1
<i>Pterodroma</i> ? <i>brevipes</i>	White-winged petrel	5/2			4/1	
<i>Phaethon lepturus</i>	White-tailed tropic bird	7/2				
<i>Pluvialis fulva</i>	Lesser golden plover	4/1				
<i>Anous minutus</i>	Black noddy	5/1		2/1	1/1	1/1
<i>Anous stolidus</i>	Common noddy	8/4			2/1	14/4
<i>Tringa incana</i> .	Wandering tattler	2/1		1/1		
<i>Gallirallus philippensis</i>	Banded rail	25/6				7/2
<i>Porzana tabuensis</i>	Sooty crane					2/1
<i>Poliolimnas cinereus</i>	White-browed crane	4/1				
<i>Tyto alba</i>	Barn owl	2/1				
<i>Ducula pacifica</i>	Pacific pigeon	9/2	1/1			
<i>Ptilinopus porphyraceus</i>	Crimson-crowned fruit-dove	447/33	11/2	1/1		46/5
<i>Gallicolumba stairii</i>	Friendly ground dove	54/6				12/3
<i>Cacomantis pyrrhophanus</i>	Fan-tailed cuckoo		3/2			
<i>Eudynamis taitensis</i>	Long-tailed cuckoo	66/7	4/1			13/3
<i>Halcyon chloris</i>	Kingfisher	31/5	1/1		2/1	9/2
<i>Collocalia spodiopygia</i>	Swiftlet	451 bones	20 bones	9 bones	8 bones	81 bones
<i>Aplonis tabuensis</i>	Polynesian starling	158/15	3/1	2/1	2/1	13/3
<i>Foulehaio carunculata</i>	Wattled honeyeater	87/8				3/1
? <i>Zosterops lateralis</i>	Grey-backed white-eye	4/1				6/2
? <i>Clytorhynchus vitiensis</i>	Lesser shrikebill					1/1
Passerine sp.		2 spp.	Yes			Yes
? <i>Chaerephon bregullae</i>	?Fijian mastiff bat			R dentary		
<i>Emballonura semicaudata</i>	Sheath-tailed bat	120 bones	7 bones	1 bone	4 bones	11 bones
<i>Rattus exulans</i>	Pacific rat	X/100s	100s/20	100s/5	X/1	100s
<i>Rattus rattus</i>	Black rat	X/23				X/1
<i>Rattus norvegicus</i>	Norway rat	X/10				X/3
<i>Rattus rattus/norvegicus</i>	Black or Norway rat		30 bones	6 bones		

Appendix: Table 4 *continued*. List of specimens from Korolamalama Cave owl midden. Values are NISP/MNI.

Taxon	Common name	Specimens
<i>Gehyra oceanicus</i>	Oceanic gecko	100+
<i>Nactus pelagicus</i>	Pacific slender-toed gecko	1
<i>Gallirallus philippensis</i>	Banded rail	2/1
<i>Gallus gallus</i>	Chicken	9/1
<i>Tyto alba</i>	Barn owl	8/1 juv
<i>Ptilinopus porphyraceus</i>	Crimson-crowned fruit-dove	90/11
<i>?Cacomantis pyrrhophanus</i>	?Fan-tailed cuckoo	4/1
<i>Aplonis tabuensis</i>	Polynesian starling	75/7
<i>Foulehaio carunculata</i>	Wattled honeyeater	51/6
Passerine sp.		Yes
<i>Emballonura semicaudata</i>	Sheath-tailed bat	30 bones
<i>Rattus exulans</i>	Pacific rat	100s
<i>Rattus rattus</i>	Black rat	X/16
<i>Rattus norvegicus</i>	Norway rat	Nil

Appendix: Table 4 *continued*. List of faunas from Muremure Cave. Fossils are listed under each discrete site they were found in. Values are NISP/MNI.

Taxon	Common name	Site 1	Site 2	Site 3	Site 4	Site 5	Owl site
<i>Brachylophus fasciatus</i>	Banded iguana		1/1				
<i>Porphyrio porphyrio</i>	Purple swamp hen	27/2		30/1	3/1, 1/1	22/1	
<i>Gallirallus philippensis</i>	Banded rail	7/2				4/1	
<i>Porzana tabuensis</i>	Sooty crane			3/1			
<i>Tyto alba</i>	Barn owl						12/2
<i>Ptilinopus porphyraceus</i>	Crimson-crowned fruit-dove						9/2
<i>Gallicolumba stairii</i>	Friendly ground dove		5/1				
<i>Eudynamys taitensis</i>	Long-tailed cuckoo						3/1
<i>Aplonis tabuensis</i>	Polynesian starling						4/1
<i>Foulehaio carunculata</i>	Wattled honeyeater						3/2
<i>Rattus exulans</i>	Pacific rat						40 bones
<i>Rattus rattus/norvegicus</i>	Black or Norway rat						23 bones

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