Journal of the Royal Society of New Zealand
Volume 34, Number 3, September 2004, pp 295–314

The fossil rails (Aves: Rallidae) of Fiji with descriptions of a new genus and species

Trevor H. Worthy[1]

Abstract A new genus and species of *Gallirallus*-like flightless extinct rail is described from deposits in western Viti Levu, Fiji, south-west Pacific. It is distinguished by having a longer, more decurved bill, than all other rails. Fossils of the barred-wing rail *Nesoclopeus poicilopterus* (Hautlaub, 1866) are reported from eastern parts of Viti Levu and several fossil bones suggest the former presence of a probable gallinule. A total of seven rails in seven genera were, therefore, sympatric on Viti Levu in the immediate prehuman period.

Keywords Fiji; rails; Rallidae; Late Quaternary fossils; new genus; new species

INTRODUCTION

The fossil record throughout the Pacific has revealed many extinct species, and range reductions of others. In New Zealand, 39 species of birds became extinct on the main North and South Islands (Turbott 1990; Worthy 1999), but there are 66 extinct taxa known from the whole New Zealand archipelago (Worthy & Holdaway 2002). Gigantism and flightlessness, as shown in New Zealand by the 11 species of moa (Dinornithiformes), large rail-like birds (Aptornithidae: *Aptornis*, two species), and waterfowl (Anatidae: *Cnemiornis*, two species), are common evolutionary trends on mammalian predator-free islands (Worthy & Holdaway 2002). The Hawaiian archipelago lost more than half its bird diversity (James & Olson 1991; Olson & James 1991), including at least four species of large, flightless, browsing anatids, called moa-nalos. Elsewhere in the Pacific, often up to half the species in the fossil record were found to be extinct, as in the Marquesas (Steadman 1989a; Steadman & Rolett 1996), Easter Island (Steadman 1995), Henderson Island (Wragg & Weisler 1994), Society Islands (Steadman 1989a), Samoa (Steadman 1994), and on the Tongan and Cook Island groups (Steadman 1989a, 1993, 1995). Of the extinct birds, species of rail, megapodes, columbids, and parrots are most common (Balouet & Olson 1987; Steadman 1987, 1989b, 1992; Steadman & Zarriello 1987). A similar history of avifaunal extinction has also been found in the western Pacific in New Caledonia (Balouet & Olson 1989) and there are indications of them in Micronesia (Steadman & Intoh 1994).

[1]Palaeofaunal Surveys, 2A Willow Park Drive, RD 11, Masterton, New Zealand.
Email: twmoa@wise.net.nz
R04005 Received 4 May 2004; accepted 28 July 2004; Online publication date 15 September 2004

Rails (Aves Rallidae) are renowned for their tendency to produce flightless forms in insular situations (Olson 1973, 1977; Slikas et al. 2002). Steadman (1995) estimated that some 2000 extinct species of flightless rails probably lived in islands in the tropical Pacific, of which four species *Gallirallus owstoni* (Rothschild, 1895) on Guam, *G. okinawae* (Yamashina & Mano, 1981) on Okinawa, and *Nesoclopeus woodfordi* (Ogilvie-Grant, 1889) in the Solomons, and *Porzana atra* North, 1908, on Henderson Island, survive today. However, fewer than 40 fossil rail taxa have been reported (Balouet & Olson 1989; Olson & James 1991; Steadman 1987, 1988, 1989a, 1993, 1995; Steadman & Rolett 1996) and only a minority of these have been described. The latest contribution to the record of Pacific rails was the small probably flightless *Gallirallus huiatua* from Niue Island (Steadman et al. 2000).

Rails are still a prominent component of the terrestrial avifauna on islands in the Pacific (Mayr 1945; Watling 1982; Taylor & van Perlo 1998), most notably with species of crakes *Porzana* spp. (Slikas et al. 2002) and the buff-banded rails (Schodde & de Naurois 1982), which latter group is usually placed in *Gallirallus* following Olson (1973). The *Gallirallus philippensis* (Linnaeus, 1766) complex includes at least 22 allopatric subspecies (Taylor & van Perlo 1998). There are several flightless island forms that are generally assumed to be derived from an ancestor like *G. philippensis*, for example, *G. sylvestris* (Sclater, 1869) on Lord Howe Island, *G. owstoni* on Guam, and *G. australis* (Sparrman, 1786) on New Zealand (Olson 1973; Schodde & de Naurois 1982). But there are many more extinct flightless species that belong to the same radiation (Steadman 1987, 1995; Steadman et al. 2000).

The extinct Chatham rails are an interesting case as the three species differ greatly in morphology and size with *Diaphorapteryx hawkinsi* Forbes, 1892 one of the largest rails in the world and *Cabalus modestus* (Hutton, 1872) one of the smallest. *Gallirallus dieffenbachii* (Gray, 1843) is about the same size as a *G. philippensis*, but more heavily built and flightless (Andrews 1896; Trewick 1997a). Olson (1973, 1975, 1977) thought it probable that of the two more aberrant taxa, at least *C. modestus* was derived from a *G. philippensis*-like ancestor. Trewick (1997b) presented limited mt-DNA data that suggested *C. modestus* was the sister taxon of *G. dieffenbachii* and that both fell within a clade of *Gallirallus* species. However, at least two other long billed forms from the New Zealand region were not included in Trewick's analysis, *Trichlolimas lafrayensis* (Verreaux & Des Murs, 1860) from New Caledonia and *Capellirallus karamu* Falla, 1954 from North Island of New Zealand, and previously these have been considered to be so divergent from *Gallirallus* that generic separation was clearly warranted (Olson 1973). Moreover, *Tricholimnas* and *Cabalus* are each sexually dimorphic with respect to bill length (Trewick 1997a; pers. obs.), which is a feature not seen in *G. philippensis* and its near relatives. All the Chatham rails differ from *G. philippensis* in having elongate, down-curved bills. *Diaphorapteryx hawkinsi* was an exceeding large and robust rail with very reduced wings and a large robust skull and bill. In contrast, *C. modestus* was a very small bird with neotonic plumage and a slender *Rallus*-like skull and bill. Because both differ so markedly from *G. philippensis*, I prefer to leave them outside of *Gallirallus* until their relationships within Rallidae can be determined (Livezey 1998; Worthy & Holdaway 2002).

Another group of large barred-wing rails from the tropical south-west Pacific that is perhaps intermediate between *Rallina* and *Gallirallus* (Olson 1973) is *Nesoclopeus*, with Woodford's rail, *Nesoclopeus woodfordi* from the Solomon Islands and the barred-wing rail, *Nesoclopeus poecilopterus* (Hartlaub, 1866) historically extinct from Fiji. This genus is sometimes included in *Gallirallus*, for example, by Steadman (1995). All these taxa have stout straight bills as well as stout legs with a relatively short tarsus. It seems that there was until recently much greater diversity amongst the *Gallirallus*-like rails of the Pacific than is now evident among the surviving taxa, and whether all were the result of a single radiation or rather had a more complex origin is yet undetermined. Until unequivocal relationships are determined it is better to retain the most distinctive forms outside of *Gallirallus* and thus highlight this diversity and encourage its phylogenetic analysis.

The Fijian archipelago (320 islands, 18 270 km^2) has the largest area of land in the central Pacific (Pernetta & Watling 1979). When sea level was more than 100 m lower during Pleistocene glaciations and Viti Levu linked with Vanua Levu, it would have been considerably larger (Watling 1982; Gibbons 1985). Viti Levu is the oldest island in the archipelago, with rocks of late Eocene to early Oligocene age and emergent land certainly present since the late Oligocene-middle Miocene (Chase 1971; Rodda 1994). Fiji therefore has a capacity for a terrestrial biota older than any other Pacific oceanic landmass except New Zealand or New Caledonia and so may be expected to have a well-developed endemic faunal component.

The modern vertebrate fauna of Fiji is characterised by the absence of terrestrial mammals, as in other Pacific islands. Birds dominate the extant fauna but there is also a diverse herpetofauna of frogs (2 sp.), iguanas (2 sp.), geckos (10 sp.; 4 presumed to be introduced by people prehistorically), skinks (12 sp.), and snakes (2 sp.) (Pernetta & Watling 1979; Watling & Zug 1998). Indigenous mammals are restricted to six species of bat (Flannery 1995). Historically, 69 indigenous land bird species are known from the Fijian archipelago (Watling 1982), with the largest island, Viti Levu, having the greatest diversity with 47 land birds. Some 56% of these land birds are endemic (Watling 1982), yet few described species are unusual or aberrant, which is unusual in avifaunas from older islands. It is even more unusual for an oceanic island to apparently have so few historical extinctions, there being only two, the barred-wing rail *Nesoclopeus poecilopterus*, globally extinct, and the wandering whistling-duck *Dendrocygna arcuata* whose population was extirpated in the late 19th century (Watling 1982). Including *Nesoclopeus*, five species of rail are known from Fiji: the ubiquitous *Gallirallus philippensis*, the white-browed crake *Poliolimnas cinereus* (Vieillot, 1819), the spotless crake *Porzana tabuensis* (Gmelin 1789), and the purple swamphen *Porphyrio melanotus* Temminck, 1820 (*sensu* Sangster 1998; Sangster et al. 1999).

Unlike the rich archaeological and palaeontological records from New Zealand and many other places in the Pacific, until recently there have been few indications of the prehistoric fauna from Fiji. Recent palaeontological surveys in Viti Levu have revealed several fossil deposits (Worthy et al. 1999), and together with studies of various archaeological faunas, new species of megapodes (Worthy 2000), pigeons (Worthy 2001a), a snipe (Worthy 2003), a frog (Worthy 2001b), a crocodilian (Molnar et al. 2002), and an iguana (Pregill & Worthy 2003) have been described. The archaeological faunas containing extinct taxa were deposited by Lapita people at about 2900–2600 cal. yr BP and, therefore, date to the earliest colonisation of Fiji by people (Anderson & Clark 1999). Worthy et al. (1999) briefly reported the presence of a new rail about the size of *N. woodfordi* but with a stouter tarsus and longer bill. Several species of rails are now represented in the fossil collections from Viti Levu and the purpose of the present contribution is to describe those fossils attributed to extinct taxa.

Study sites

Fossils were recovered from several cave sites on Viti Levu by me and various helpers during investigations aided by the Fiji Museum, as detailed in Worthy & Anderson (1999). Rail bones were found in Site 1 and Qara-ni-vokai, both within the same entrance doline to Voli Voli Cave, Sigatoka (Map Reference: L29 659713, edition 1, 1992; 18°09′39″S, 177°28′53″E) in western Viti Levu. In eastern areas, deposits were found to contain a few rail bones in Wainibuku Cave (O28 722827, edition 1, 1990; resurgence at 18°03′37″S, 178°29′11″E) and Udit Tomo (18°04′03″S, 178°29′21″E) an upstream entrance feature to Udit Cave (Gilbert 1984) both near Suva (Worthy 2000, Fig. 1). A few bones of a single skeleton of a rail were found in Delai-ni-qara, a cave on the plateau overlying Wailotua Cave (O27 644157, edition

1, 1993). Direct dating has not been possible on bones from any of the fossil sites because of loss of collagen from the bones. However, stratigraphic considerations in conjunction with optical dates, uranium series dates, and radiocarbon dates on sediments, together suggest that all material is of late Pleistocene or Holocene age (Anderson et al. 2001).

METHODS

Institutions

MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand and Colonial Museum); BMNH, Natural History Museum, London [formerly British Museum (Natural History)]; USNM, United States National Museum, Smithsonian Institution, Washington, USA; UWBM, Burke Museum, University of Washington, Seattle, USA.

Skeletal elements and descriptive terms

Anatomical nomenclature follows Baumel & Witmer (1993), and simple English translations are used after the first reference.

ELEMENTAL ABBREVIATIONS: acet, acetabular part of pelvis; cmc, carpometacarpi; cor, coracoids; cran, crania; fem, femora; fib, fibulae; frags, fragments; hum, humeri; imm, immature; juv, juvenile; mand, mandibles; pel, pelves; phal, phalanges; pmx, premaxillae; quad, quadrates; rad, radii; sac, synsacra; scap, scapulae; stern, sterna; tmt, tarsometatarsi; tt, tibiotarsi; and vert, vertebrae. When listing material, bones are sometimes identified as left (L) or right (R) elements. L or R prefixed by "p" or "d" indicates "proximal" or "distal" part of the element, e.g., pR femur means the proximal part of a right femur.

Measurements

Measurements were made with Tesa® dial callipers and rounded to 0.1 mm. TL, greatest length except for the coracoid, which was measured down the medial side; PW, proximal width in the lateromedial plane—femora were measured from the ball through the mid-depth point of the neck to the lateral side; SW, shaft width in a lateromedial plane; SD, shaft width in a dorsoventral plane; DW, distal width; tibiotarsi PW, measured across the articular surface; tibiotarsus PD, proximal depth from between the cnemial crests to the posterior side of the articular surface.

Comparative material

Many species and genera of rails in the MNZ collections were examined during the course of the study, but the following specimens therein or elsewhere are of particular note:

Woodford's rail, *Nesoclopeus woodfordi* (Ogilvie-Grant, 1889): *N. woodfordi immaculatus*, UWBM 58791 male, Isabel Island, Solomon Islands; UWBM 58792 female, Isabel Island, Solomon Islands.

Barred-wing rail, *Nesoclopeus poecilopterus* (Hartlaub, 1866): X-rays of BMNH 1889.11.3.68 male, Fiji; BMNH 1898.12.2.531 female, Fiji.

Weka, *Gallirallus australis* (Sparrman, 1786): *Gallirallus australis greyi*, MNZ 12508 male, Gisborne, North Island; *Gallirallus australis australis*, MNZ 25607 male, Grey Valley, South Island, New Zealand.

Banded rail, *Gallirallus philippensis* (Gray, 1843): *assimilis* MNZ12318, MNZ15138, MNZ23821, MNZ24058 female; *swindellsi* MNZ22842, female; *goodsoni* MNZ25267 female, MNZ25269, MNZ27180.

New Caledonian rail, *Tricholimnas lafresnayanus* (Verreaux, J. & Des Murs, 1860): Skins—BMNH 70.12.3.3, male; 70.12.3.4, female; 98.12.2.540, female; 1889.11.1.375, female. Skeletal material—unregistered fossil bones in MNZ from Pindai Cave, New Caledonia, collected by THW in 2003.
Lord Howe rail, *Gallirallus sylvestris* (Sclater, PL, 1869): MNZ 27218a female, Lord Howe Island.
Snipe rail, *Capellirallus karamu* Falla, 1954: MNZ S34036, Te Urupa Cave, North Island, New Zealand.
Hawkin's rail, *Diaphorapteryx hawkinsi* (Forbes, 1892): MNZ S7968, 27227, Chatham Island.
Chatham rail, *Cabellus modestus* (Hutton, 1872): MNZ S27182, Te Ana-a-moe, Chatham Island.
Bush hen, *Amaurornis olivacea* (Meyen, 1834): USNM 560795 male, Halmahera District, Indonesia; USNM 560797 female, Halmahera District, Indonesia.
Black-tailed native hen, *Gallinula ventralis* Gould, 1837: MNZ 22101.

SYSTEMATIC PALAEONTOLOGY

Class Aves, Order Gruiformes

Family Rallidae Vigors, 1825

Genus *Nesoclopeus* Peters, 1932

Nesoclopeus poicilopterus (Hartlaub, 1866) barred-wing rail

REFERRED MATERIAL: MNZ S38264, R acetabulum, synsacrum, LR fem, LR tib, LR tmt, s hum, 5 vert, phal, part dentary, Delai-ni-qara, Wailotua, Viti Levu.

This associated skeleton is referred to a *Gallirallus*-like rail because of the form of the elongate stout mandible, relatively short leg bones, and a tarsometatarsus on which the hypotarsus is not hooked distally. It is much bigger than *Gallirallus philippensis* but of appropriate size for *Nesoclopeus poicilopterus* (Tables 1–5). The left mandible fragment (*os dentale*) has identical morphology to that of *N. woodfordi* (Fig. 1A,E) and preserves most of the length cranially of the mandible symphysis. The rostral half of this fragment is thin and sharp along its dorsal or occlusal surface, and the lateral surface is flat (Fig. 1B,F) and thus differs markedly from the very elongate, laterally convex, and thicker mandible of the following new species.

The leg bones are well preserved and while very similar to those of *N. woodfordi*, differ as follows: Femur, the angle between the lateral and the ventral facies is less angular, distally the *crista supracondylaris medialis* is more expanded and elevated adjacent to the *condylus medialis*, and most obviously, the *condylus medialis* extends farther up the shaft dorsally than in *N. woodfordi*. The tibiotarsus is very similar but is slightly more elongate relative to the femur, and the tarsometatarsus is slightly more robust than in the *N. woodfordi* specimens examined.

Table 1 Measurements (mm) of leg bones of MNZ S38264 from Delai-ni-qara, Wailotua, Viti Levu. For abbreviations, see Methods; AL, length from proximal articular surface.

	L (AL)	PW	SW	DW
Femur	65.6	c.12.5	5.3	12.4
Tibiotarsus	111.6 (98.7)	10.7	5.6	9.5
Tarsometatarsus	64.7	10.1	4.7	10.7

Both MNZ S38264 and *N. woodfordi* have a marked sulcus mesial of the hypotarsus that is bound by a marked ridge dorsally, as also seen in *Gallirallus australis*. The distal foramen is relatively smaller than in *N. woodfordi*. The bones of MNZ S38264 are smaller than even those of the female *N. woodfordi* (UWBM 58792), which is markedly smaller than the male, but are about the same size as those of *N. poicilopterus* as indicated by the measurements taken from X-rays (Tables 2, 5).

MNZ S37325, R hum, Wainibuku Cave, Wainibuku, Viti Levu (Fig. 2C,F). L (estimated) = 50.8 mm, PW = 10.7 mm, SW = 3.6 mm, distal end is worn. This specimen is referred to *N. poicilopterus* because it is a good match for *N. woodfordi* in proportions and especially in the shape of the *crista bicipitalis* and the relative length to that of the *crista deltopectoralis*, which

Table 2 Measurements (mm) for *Nesoclopeus* taxa: tarsometatarsus. For abbreviations, see Methods.

Species	Cat. no.	TL	PW	Prox depth	SW mid L	SD mid L	DW	Depth lat side T3
N. woodfordi immaculatus	UWBM 58791	77.8	11.1	12.1	4.7	4.2	11.5	6.2
N. woodfordi immaculatus	UWBM 58792	67.9	9.5	10.2	4.3	3.9	9.8	5.1
N. poicilopterus[1]	BMNH 1889.11.3.68	70.0	–	–	–	–	–	–
N. poicilopterus[1]	BMNH 1898.12.2.531	66.6	9.5	–	4.0	–	10.0	–

[1]Measurements from X-rays.

Table 3 Measurements (mm) for *Nesoclopeus* taxa: femur. For abbreviations, see Methods; cond, condyle; med, medial; lat, lateral.

Species	Cat. no.	TL	PW	PD	SW	SD	DW	Depth med cond	Depth lat cond
N. woodfordi immaculatus	UWBM 58791	75.7	13.5	11.9	5.4	6.2	13.4	9.7	11.6
N. woodfordi immaculatus	UWBM 58792	70.4	–	–	5.0	5.3	12.3	9.0	10.1

Table 4 Measurements (mm) for *Nesoclopeus* taxa: tibiotarsus. For abbreviations, see Methods; cond, condyle; med, medial; lat, lateral.

Species	Cat. no.	TL	AL	PW	Mid SW	DW	Depth lat cond	Depth med cond
N. woodfordi immaculatus	UWBM 58791	115.8	112.4	11.9	5.8	10.6	10.4	11.1
N. woodfordi immaculatus	UWBM 58792	102.9	99.8	10.9	5.34	8.9	9.0	9.3

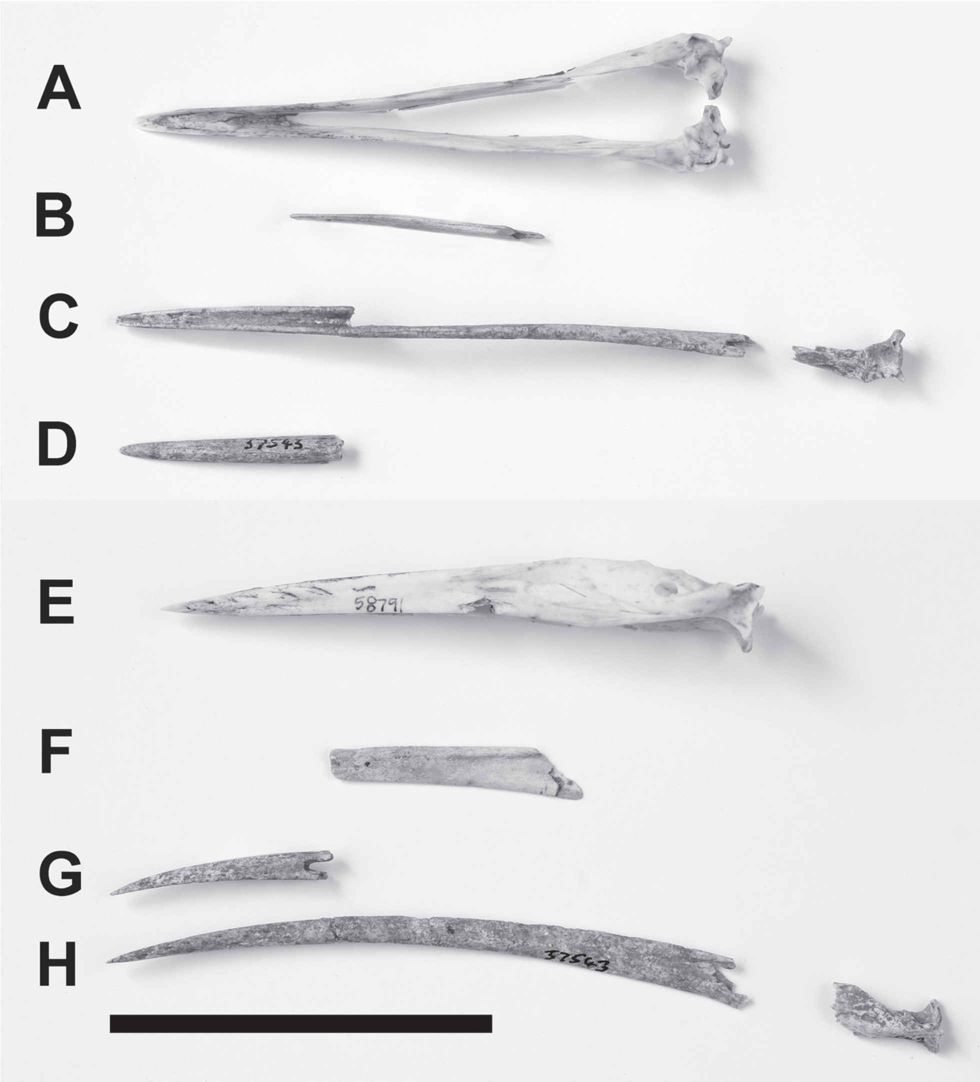

Fig. 1 Bill elements of Fiji rails compared with those of *Nesoclopeus woodfordi* UWBM 58791. **A**, occlusal and **E**, lateral view of mandible of *N. woodfordi*; **B**, occlusal and **F**, lateral view of fossil left ramus mandible of *N. poicilopterus* MNZ S38264; **C**, occlusal and **H**, left lateral view of mandible of *Vitirallus watlingi* MNZ S37543 (Holotype); **D**, dorsal and **G**, left lateral view of premaxilla tip of *V. watlingi* MNZ S37543 (Paratype). Scale bar = 5 cm.

is at right angles to the adjacent cranial facies, not rolled over it as in the following new species. The humerus of *Nesoclopeus* differs from *Gallirallus philippensis* in that the *tuberculum dorsale* is much more offset dorsally above the shaft so that in cranial view the proximal end appears equally expanded either side of the shaft, rather than predominantly medially as in *G. philippensis*. Moreover, the proximal width from the *tuberculum dorsale* to the *tuberculum ventrale* is markedly greater than the distance from the margin of the *crista bicipitalis* to the area between the *caput humeri* and the *tuberculum dorsale* (the latter measurement is greatest in *G. philippensis*). Its size is as expected given the size of elements in the female BMNH 1898.12.2.531.

?*Nesoclopeus poicilopterus* (Hartlaub, 1866) barred-wing rail

MNZ S37315, worn left tibiotarsus with proximal end missing and distal condyles damaged Wainibuku Cave, Wainibuku, Viti Levu. SW = 4.8 mm. MNZ S37480, deformed left tarsometatarsus minus proximal end, Udit Cave, pitfall deposit 4 m into cave in doline 100 m downstream of the submergence, Viti Levu. MNZ S38258, subadult left tarsometatarsus minus trochlea IV, Udit Cave, pitfall deposit 4 m into cave in doline 100 m downstream of the submergence, Viti Levu. L = 65.4 mm, PW = 9.7 mm, SW = 4.2 mm.

These specimens are of appropriate size to be *N. poicilopterus* but lack diagnostic features for certain referral. MNZ S38258 lacks the marked sulcus seen mesial of the hypotarsus in *N. woodfordi* and MNZ S38264, but this absence may be explained by osteological immaturity. The *sulcus extensorius* is also relatively broader with the lateral bounding ridge narrower, but again, this may relate to immaturity.

Vitirallus new genus

GENERIC ATTRIBUTION: The bones described here as *Vitirallus watlingi* are from a species of rail allied to the *Gallirallus-Rallus* complex because of its elongate bill and stout legs with relatively short tarsometatarsus, rather than to gallinules, crakes or coots. The very elongate and decurved bill sets the new taxon apart from *Gallirallus* or *Nesoclopeus* which typically have straight and much shorter bills. In this feature it is similar to a group of extinct flightless south-west Pacific rails, including the New Caledonian rail, *Tricholimnas lafresnayanus*, the snipe rail *Capellirallus karamu* from the North Island of New Zealand, and the Chatham Island rail *Cabellus modestus*. The bill of *Vitirallus* is much more elongate than all of these taxa except *Capellirallus*, which was described by Olson (1977) as one of the most distinctive of the Rallidae.

TYPE SPECIES: *Vitirallus watlingi* sp. nov., by monotypy.

ETYMOLOGY: The generic name is derived from “Viti” referring to the island of origin in Fiji, and “rallus” for rails. Gender is masculine.

DIAGNOSIS: As for the type species.

Table 5 Measurements (mm) of *Nesoclopeus* taxa: wing bones. For abbreviations, see Methods; Ddc, depth distal condyle.

Species	Cat. no.	Hum TL	Hum PW	Hum SW	Hum DW	Hum D dc	Ulna TL	Ulna PW	Ulna SW	Ulna DW	Cmc TL	Cmc PW	Cor med L
N. w. immaculatus	UWBM 58791	62.8	13.1	3.9	9.0	5.6	52.7	6.5	3.1	5.8	34.1	–	33.2
N. w. immaculatus	UWBM 58792	57.2	10.9	3.5	8.5	4.9	–	–		–	–	–	29.5
N. poicilopterus[1]	BMNH 1889.11.3.68	–	–	–	–	–	46.3	–	–	–	31.5	–	–
N. poicilopterus[1]	BMNH 1898.12.2.531	–	–	–	–	–	40.7	–	–	–	29.5	–	–

[1]Measurements from X-rays.

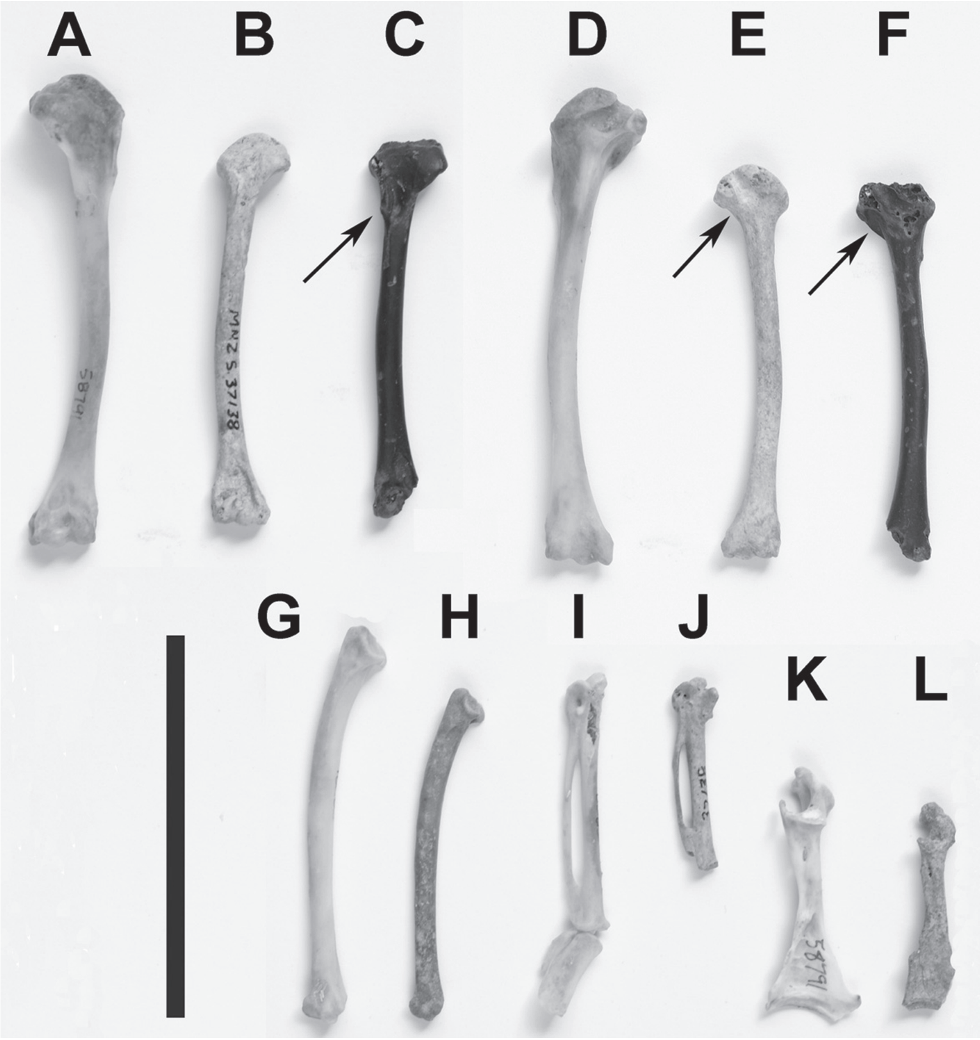

Fig. 2 Wing bones of Fiji rails: *Vitirallus watlingi* MNZ S37138pt (B, E, H, J) and MNZ S37545 (L) and *Nesoclopeus poicilopterus* MNZ S37325 (C, F) compared with those of *N. woodfordi* UWBM 58791 (A, D, G, I, K). Humerus (cranial **A–C**, and caudal **D–F** aspect); A, H left ulna in ventral aspect; **I**, **J**, left carpometacarpus in ventral aspect; **K**, **L**, right coracoid in dorsal aspect. Arrows point to elongate and less rotated deltoid crest in *N. poicilopterus* (C) and differences in the extent of the bicipital crest (E, F). Scale bar = 5 cm.

Vitirallus watlingi new species

(Fig. 1–3; Tables 6–12)

HOLOTYPE: MNZ S37543, the tip and left side of mandible (Fig. 1C,H) with the associated left ramus. Length of symphysis 30.4 mm, width at cranial end of symphysis 3.8 mm, width from articular facet of quadrate to medial process 6.22 mm, maximum depth mandible 6.42 mm, estimated minimum mandible length 108 mm.

TYPE LOCALITY: Square 2, 20–60 cm depth, Qara-ni-vokai, Voli Voli, Viti Levu, Fiji, T. H. Worthy, G. Udy, S. Matararaba, T. Sorovi, 30 September 1998.

PARATYPES: MNZ S37543, pmx associated with Holotype; MNZ S37138, 4dR3pR2pL fem, 1L1dL3dR1pL2pR tmt, 1L2pL1dL1dR ulna, 2 dent frags, 40 phals, 1 stern, 1 vert, 2 pmx, 1 mand tip, 1R ramus, 1 pmx base, 3L2R cmc, 3 tt frags, 1pL1sL2pR5dL4dR tt, 2R3pR1pL2dL4dR hum, 1pR cor, L scap (107 bones); 0–25 cm, Terminal chamber, Qara-ni-vokai, Voli Voli, Viti Levu, Fiji; collected by T. H. Worthy, A. Anderson, S. Matararaba, 28 March 1998.

REFERRED MATERIAL: *Fossil site 1, Voli Voli Cave, Viti Levu*: MNZ S37170, dR tmt; MNZ S37148, pR fem; MNZ S36969, pL cor; MNZ S36968, dR tmt; MNZ S36967, dR tt; MNZ S36966, pL fem; MNZ S36965, d+sL fem.

Qara-ni-vokai, Voli Voli, Viti Levu: MNZ S37572, 1L1pL1dR fem, 1dL2dR1pL hum, 7 phal, 1L cor, 5 frags, 1R2dR1pR2dL tmt, 3pR2dL tt, 1pL cmc, 1pR ulna (33 bones), excavation 4, 1 m on upside of rocks by excavation 2, 0–30 cm; MNZ S37566, L fem, pLpR hum, 4R fib, R ramus, 32 phal, 2dL1dR tmt, 1pL1dL1dR tt, 7 frags (53 bones), excavation at base of entrance slope, 2 × 0.6 m, 0–30 cm; MNZ S37553, R fem, Square 2, 20–60 cm; MNZ S37552, 27 vert, Square 2, 20–60 cm; MNZ S37551, 55 phal, Square 2, 20–60 cm; MNZ S37550, 1L ramus, 1 interorbital area of cran, 2 pmx tips, 3 culmen, 1L mand tip, 1 side mand (9 bones), Square 2, 20–60 cm; MNZ S37549, 2R2dL1p? radius (5 bones), Square 2, 20–60 cm; MNZ S37548, 3L2R scap (5 bones), Square 2, 20–60 cm; MNZ S37547, 2L1R fib (3 bones), Square 2, 20–60 cm; MNZ S37546, 4L6R cmc (10 bones), Square 2, 20–60 cm; MNZ S37545, 1pL1dL1R2pR cor (5 bones), Square 2, 20–60 cm; MNZ S37544, 3L1pL1dL ulnae (5 bones), Square 2, 20–60 cm; MNZ S37542, 1L5dL4pL2R3pR4dR hum (19 bones), Square 2, 20–60 cm; MNZ S37541, 1L2pL1sL2R4pR1sR1dR tmt (12 bones), Square 2, 20–60 cm; MNZ S37540, 3L2pL3dL3R3 pR1dR1s? fem (16 bones), Square 2, 20–60 cm; MNZ S37539, 4L2pL5dL4dR3pR3sR tt (21 bones), Square 2, 20–60 cm; MNZ S37139, 1R1dR4pR2dL tmt, 2dR1sL tt, 1sL1sR fem, 2 pmx, 1 mand tip, 1 syn, 1dL fem, 2pL1R ulna, 2pR1dR hum, 1R1pR cmc, 3 frags mand, 3 vert, 25 phal (57 bones), Square 1, 10–20 cm; MNZ S37137, 1L1dL2dR tmt, 2pR fem, 1dL1dR1sL1sR tt, 1R ramus, 1dR1pR hum, 1pR ulna, 7 phal, 2 vert, 1R acet, 1R fib, 1 pmx, 1 rib (27 bones), Square 2, 0–20 cm; MNZ S37136, cran, pel, 2L1R fem, pL tmt, 8 phal, dR rad, 2R fib, 1 pmx, 1 mand frag, 1L ramus, 1dL ulna, 1L cmc (22 bones), Testpit 2, 0–25 cm; MNZ S37135, L fem, pL tt, 1dL1dR tmt, 2L fib, 1R scap, 1L hum, 1 vert, 6 phal, 1 mand tip (16 bones), Testpit 1 extn, 0–25 cm; MNZ S37134, 2pR fem, 5 phal, 2 vert, 1pR ulna, 1dR tt, 1L fib (12 bones), Square 1, 0–10 cm; MNZ S37132, R tt, sL tt, pL ulna, 3 phal (6 bones), Testpit 4, 0–30 cm; MNZ S37108, pmx, Square 1, 10–20 cm; MNZ S37024, 1L2pL2dL1dR tt, 2sR tt, pR fem, R cmc, L ulna (11 bones), Square 1, 10–20 cm; MNZ S37020, dR tt, rib, phal (3 bones), Testpit 1.

Table 6 Measurements (mm) of *Vitirallus watlingi* bill elements. For abbreviations, see Methods. Cat. no. is catalogue number.

Cat. no. MNZ S	Part	Element	Mandible symphysis length	Mandible width at cranial end symphysis	Length to nasal fossa	Width at nasal fossa
37139	tip	pmx			25.8	3.7
37139	tip	pmx			24.4	3.7
37543	tip	pmx			26	3.8
37135	tip	mand	29.6	3.7		
37139	tip	mand	27.3	3.4		
37543	part	mand	30.4	3.8		

Fig. 3 Leg bones of *Nesoclopeus woodfordi* UWBM 58791 (**A**, **D**, **I**) compared with those of *Vitirallus watlingi*: **B**, **C,** MNZ S37540; **E**, **F**, MNZ S37539; **G**, MNZ S37138 pt; **H**, MNZ S37541. Femora (A, B, left caudal, and C, right cranial aspect), left tibiotarsi (D–F, cranial aspect), left tarsometatarsi (G–I, dorsal aspect). Scale bar = 5 cm.

Udit Cave pitfall deposit 4 m into cave in doline 100 m downstream of the submergence, MNZ S37478, R fem.

DIAGNOSIS: A flightless rail about the size of *Nesoclopeus poicilopterus* with a very elongate and slender decurved bill; humerus very small (~79% femur length) with the *crista bicipitalis* very reduced in size such that in caudal view it does not extend distad of either the *tuberculum ventrale* or the distal end of the *tuberculum dorsale* and on which the *crista deltopectoralis* is rolled over the cranial surface; tarsometatarsus with deep *sulcus extensorius* which passes both mesial and laterad of the *tuberositas musculus tibialis cranialis*.

ETYMOLOGY: The species is named after Dr Dick Watling who has contributed greatly to knowledge of the ornithology of Fiji.

Species description

None of the more diagnostic elements, such as premaxillae, mandibles, wing bones, or tarsometatarsi found in the Qara-ni-vokai deposits, were referable to *Nesoclopeus poicilopterus*, so all large rail bones from this deposit were referred to *Vitirallus*.

Mandible and premaxilla (Fig. 1, Table 6)

The bill of *Vitirallus watlingi* is very elongate and slender with an estimated total length of 108 mm (MNZ S37543), yet a maximum depth at the *angulus mandibulae* of just 6.42 mm. The *os dentale* is laterally convex and quite thick especially along the occlusal margin, unlike in *Nesoclopeus* where the occlusal surface is sharp. Most *Gallirallus*-like rails including *Nesoclopeus* have much shorter straight bills about 105–120% of cranium length. *Vitirallus watlingi* has the unusual feature that the *rostrum maxillare*, which is also elongate, has very robust ventrally flattened *crista tomialis* that enclose a narrow deep groove medially. This groove is less than a third of bill width at any point along it. Most rails, including *Nesoclopeus* and *Gallirallus* species, have bills in which the premaxilla tip has sharp tomial crests that enclose a wide trough-like groove between them. The bill of *Vitirallus watlingi* has relatively few large *foveae corpusculorum nervosorum* in the bill tip, and is similar to most rails in this respect. The bill of *Cabellus modestus* is more elongate (about 135% of cranium length) and down-curved than all *Gallirallus* species, but it has a typical *Gallirallus*-like premaxilla with sharp tomial crests separated by a wide groove, and it has the usual density of sensory foveae. *Capellirallus karamu*, while having bill of a similar length and proportions to that of *V. watlingi*, differs markedly as its bill tip uniquely has abundant sensory foveae over both the mandible and premaxilla, and the tip of the premaxilla has sharp tomial crests separated by a deep groove. The broad tomial crests on the entire premaxilla tip in *V. watlingi* is similar to that seen in *Diaphorapteryx*, but that genus is a very much larger and more robust taxon with a relatively shorter bill, and differs in many other ways.

The *fenestra caudalis mandibulae* are nearly closed. The *cotyla lateralis* bears a small posterior process and the pneumatic foramen in the *processus medialis mandibulae* is small. The anterior width for the quadrate articulation in MNZ S37543 is 4.9 mm and the length of the articular facet on the lateral side is 5.4 mm. In *Nesoclopeus woodfordi* and *Gallirallus australis*, width is greater than lateral length for this articulation.

Table 7 Summary statistics (mm) of *Vitirallus watlingi* humeri measurements. For abbreviations, see Methods. Data from MNZ S 37137, 37139, 37138, 37542, 37572.

	TL	PW	SW	DW
Mean	52.20	9.98	3.20	7.84
Standard error	0.745	0.175	0.057	0.059
Standard deviation	1.490	0.633	0.235	0.230
Minimum	50.8	8.1	2.5	7.4
Maximum	54.3	10.5	3.5	8.3
Count	4	13	17	15

Cranium

Only two fragmentary crania referred to *V. watlingi* are available. The more complete MNZ S37136 has a maximum width (just in front of temporal fossae) of 19.3 mm, width at the zygomatic processes of 18.0 mm, and an interorbital width of 7.5 mm. The postorbital processes are not prominent and ventrally directed and the zygomatic processes of the squamosals are relatively smaller than in *N. woodfordi*. A second cranial fragment MNZ S37550 has an interorbital width of 8.3 mm. These crania are relatively narrow as the distance from mid orbit to the posterior end of the cranium is 28 mm or 1.45 times width. In contrast, for *T. sylvestris* the equivalent length is 1.15 times width, and for *G. australis*, values of about 1.25 are found.

Humerus (Fig. 2B,E, Table 7)

The humerus of *Vitirallus watlingi* is reduced in length like other flightless rails with mean values (Tables 7, 10) suggesting humeri are about 78.6% femur length. *Nesoclopeus woodfordi* has more elongate humeri, 81.2, 82.9% length (Tables 3, 5), but *Gallirallus australis* has much shorter humeri at about 70% femur length. While length does not seem greatly reduced, *V. watlingi* humeri have extreme reduction of their proximal end, such that the *crista bicipitalis* in caudal view does not extend distad of the *tuberculum ventrale* and it joins the shaft level with the distal end of the *tuberculum dorsale*. The *fossa pneumotricipitalis* is shallow and bound by robust margins and proximally is only a little excavated under the ventral tubercle, which therefore is a robust triangular prominence. The *crista deltopectoralis* is robust, short, and strongly rolled over the cranial surface of the bone enclosing a furrow. The change in angle marked by a point on the deltoid crest lies opposite where the bicipital crest joins the shaft. The overall configuration results in the small dorsal tubercle becoming prominent on the end of the *caput humeri* in cranial view. Distally the *fossa brachialis* is deep, and the ligament attachment on the *tuberculum supracondylare ventrale* is poorly developed.

In most other flightless forms, e.g., *Gallirallus australis*, *G. sylvestris*, *Nesoclopeus woodfordi*, and *Cabellus modestus* the deltoid crest is not rolled over the shaft, and generally forms a right angle with the adjacent cranial surface, and the bicipital crest is not so reduced. The bicipital crest in *N. woodfordi* is much larger than in *V. watlingi* with a convex distal margin and the tricipital fossa is deeply excavated under the ventral tubercle. The dorsal tubercle in *Nesoclopeus woodfordi* is larger than that of *V. watlingi* but, because in cranial view the deltoid crest overhangs the shaft dorsally, the dorsal tubercle is not so prominent. In more volant forms, such as *G. philippensis* the deltoid crest is larger and forms a wider angle with the cranial surface, further reducing the prominence of the dorsal tubercle. In *Diaphorapteryx*, whose humeri are amongst the most reduced known in rails, the deltoid crest is rolled over the cranial surface and the bicipital crest is extremely reduced. It is likely that the sample of humeri for *Vitirallus* is biased towards larger specimens and that the humerus femur ratio is less than the means of the available data suggest.

Ulna (Fig. 2H, Table 8)

The ulnae are short, have a relatively thin shaft, and have a very deep *impressio brachialis*, whereas the brachial impression is shallow in *N. woodfordi* and *G. philippensis*. Unlike most rails, the *processus cotyla dorsalis* does not overhang the shaft but rather is buttressed dorsally to enclose a distinct fossa beneath the *cotyla dorsalis*. The *condylus dorsalis ulnaris* is weakly developed such that its maximum diameter is not much greater than that of the shaft. All these features relate to reduction of the bone with loss of flight ability.

Carpometacarpus (Fig. 2J, Table 8)

The carpometacarpi are unremarkable except that they are much shorter than those of the similar sized rail *Nesoclopeus woodfordi* (Table 5), and so too presumably of *N. poicilopterus*.

Coracoid (Fig. 2L, Table 9)

The *processus acrocoracoideus* in *V. watlingi* is reduced to the form of a rounded knob that only just extends past the humeral facet, whereas in *Nesoclopeus woodfordi* and *Gallirallus australis* the tip is narrower than the base and directed medially because of an oblique lateral-medial compression. The *impressio musculus sternocoracoidei* is deepest near the *angulus medialis* and merges with the shaft at mid length without a sharp ridge medially, whereas in *N. woodfordi* and *G. philippensis* the sulcus is deeper and remains so to mid length where it abruptly rises to shaft level adjacent to a sharp medial ridge. In contrast, the sulcus in *G. australis* is shallow as in *V. watlingi* and there is no sharp defining ridge to the sulcus medially.

In *V. watlingi*, the *cotyla scapularis* is deep, the *facies articularis humeralis* is directed laterally but its surface is convex in a humeral-sternal alignment. The *processus procoracoideus* has a small foramen. In *N. woodfordi* and *G. sylvestris* the humeral facet is directed laterally but in *G. australis* it is directed dorsally.

No specimen of *V. watlingi* preserves the lateral process so its form is unknown.

Sternum

The sternum is represented by a single fragmentary specimen for which maximum width is estimated to be 18.8 mm. The keel is very reduced with a height above the basin of only 7.4 mm.

Femur (Fig. 3B,C, Table 10)

The femora referred to *Vitirallus watlingi* are very similar to those of other large *Gallirallus*-like rails, but the following features are significant. They are shorter than those of *N. woodfordi* but are of similar slender form (Table 3). The femur shafts of *V. watlingi* have parallel sides over the mid-60% of length as have those of *N. woodfordi*, but femora of *Nesoclopeus poicilopterus* MNZ S38264 and *Gallirallus australis* have more robust shafts that progressively widen from mid length distally. Mid shaft width is less than mid shaft depth in *V. watlingi*, as in *Nesoclopeus woodfordi*, *N. poicilopterus* MNZ S38264, *G. australis*, and *G. sylvestris*.

The *crista supracondylaris medialis* originates at the *condylus medialis* as a very robust ridge, more so in larger individuals, that bounds a shallow *fossa poplitea* medially, resulting in a medial profile of the condyle-ridge area being >90°. This results in the distal end not being "hooked" ventrally when seen in medial view. In *G. australis* and *G. sylvestris*, the ridge

Table 8 Summary statistics (mm) of *Vitirallus watlingi* measurements: ulnae, data from MNZ S37137, 37544, 37139, 37138; carpometacarpi, data from MNZ S 37139, 37546, 37138, 37572. For abbreviations, see Methods.

	Ulna TL	Ulna PW	Ulna SW	Ulna DW	Cmc TL	Cmc PW
Mean	42.98	5.35	2.57	4.69	25.02	6.65
Standard error	0.864	0.092	0.036	0.118	0.307	0.319
Standard deviation	1.932	0.292	0.095	0.313	0.969	0.902
Minimum	39.6	4.8	2.5	4.2	23.5	6.0
Maximum	44.4	5.7	2.7	5.1	26.8	8.8
Count	5	10	7	7	10	8

adjacent to the popliteal fossa is relatively small so that the medial profile of the condyle-ridge area is about 90°. However, the ridge is strongly developed in *Nesoclopeus woodfordi* and *N. poicilopterus* (MNZ S38264). The *crista supracondylaris medialis* continues up the shaft above the popliteal fossa as a well-defined ridge in both *Vitirallus* and *Nesoclopeus*, but not in *Gallirallus australis* and *G. sylvestris*.

Tibiotarsus (Fig. 3E,F, Table 11)

The tibiotarsus of *Vitirallus watlingi* is similar to other *Gallirallus*-like rails in general shape, but there are several distinguishing features. It has a very shallow *fossa retropatellaris medialis*, whereas in *Nesoclopeus poicilopterus* MNZ S38264 and *N. woodfordi* this fossa is much deeper. The condition in *Gallirallus australis* is like that of *V. watlingi*. The *crista fibularis* abruptly rises from the shaft proximally so that in anterior view its top is clearly defined, but in *Nesoclopeus* the top of the fibula crest is continuous with a ridge leading to the proximal end. In *V. watlingi*, the *fossa flexoria* undercuts the *facies articularis lateralis* to a greater extent than does the *impressio ligamentum collateralis medialis* to the *facies articularis medialis*, and there is usually a sharp ridge separating the fossae on the shaft.

In *V. watlingi*, the sulcus for the tendon of *musculus fibularis brevis* on the lateral side of the anterior face is wide and forms a marked notch where it passes caudad of the *condylus lateralis*. In *N. woodfordi, N. poicilopterus* MNZ S38264, *G. australis*, and *G. sylvestris*, this sulcus is narrower.

The *sulcus extensorius* in *Vitirallus* is narrow, about a third of adjacent shaft width, but it is bound medially by a relatively robust ridge immediately above the *pons supratendineus*. This medial bounding ridge is narrower in *Nesoclopeus* and *Gallirallus*.

Table 9 Measurements (mm) of *Vitirallus watlingi* coracoids. For abbreviations, see Methods. Catalogue number (Cat. no.) prefixed by MNZ S.

Cat. no.	Part	Medial length	Length scapular facet to acrocoracoid
37545	R	27.7	6.8
37545	pR		6.4
37545	pL		7
37572	pL		6.7

Table 10 Summary statistics (mm) of *Vitirallus watlingi* femora measurements. For abbreviations, see Methods. Data from MNZ S37135, 37137, 37136, 37138, 37540, 37553, 37566, 37572.

	TL	PW	SW	DW
Mean	66.40	12.29	4.93	11.76
Standard error	1.473	0.154	0.127	0.225
Standard deviation	3.897	0.486	0.492	0.841
Minimum	60.7	11.6	4.2	10.5
Maximum	71.4	13.1	6	13.3
Count	7	10	15	14

Tarsometatarsus (Fig. 3G,H, Table 12)

The tarsometatarsus of *Vitirallus watlingi* is shorter than to that of *Nesoclopeus* spp. and *Tricholimnas lafresnayanus*, but has stouter proportions, although not to the extent of *Gallirallus australis*. The *cotyla medialis* is only slightly proximal to the *cotyla lateralis* whereas it is more offset in *Nesoclopeus woodfordi*, *N. poicilopterus* MNZ S38264, *Gallirallus australis*, and *Tricholimnas lafresnayanus* (MNZ unreg., Pindai Cave).

The *sulcus extensorius* is as deeply excavated mesial of the *tuberositas musculus tibialis cranialis* as laterad of it, so that the tuberosity is centred in a wide flat groove. In contrast, in *N. woodfordi*, *N. poicilopterus* MNZ S38264, *Gallirallus australis*, and *G. sylvestris*, the area mesial of the tuberosity is narrow and elevated compared with the base of the extensor sulcus on the lateral side of the tuberosity. In *Tricholimnas lafresnayanus* (MNZ unreg., Pindai Cave) the extensor sulcus is more deeply excavated than in *Nesoclopeus* or *G. australis* so that the medial bounding ridge is narrow and the sulcus passes mesial of the tuberosity, with a depth similar to that seen in *V. watlingi*.

The *cristae plantare medialis* and *lateralis* are obvious and widely separated at mid-length by a flat area, and mid-shaft width is greater than depth. In *N. woodfordi*, *N. poicilopterus* MNZ S38264, and *Tricholimnas lafresnayanus* (MNZ unreg., Pindai Cave), these cristae converge towards mid-length where their separation is less than half shaft width. The cristae are parallel and separated by a flat area of about half shaft width in *G. australis*.

There is a deep and broad sulcus between the *crista plantare medialis* and the hypotarsus in *V. watlingi*. In *Nesoclopeus woodfordi* and *N. poicilopterus* MNZ S38264, the sulcus has similar depth but is narrower. In *Tricholimnas lafresnayanus* (MNZ unreg., Pindai Cave) and *Gallirallus australis*, the sulcus is much shallower.

Table 11 Summary statistics (mm) of *Vitirallus watlingi* tibiotarsi measurements. For abbreviations, see Methods; D mc, depth medial condyle; D lc, depth lateral condyle. Data from MNZ S37132, 37020, 37137, 37024, 37139, 37138, 37539, 37572.

	TL	AL	PW	SW	DW	D mc	D lc
Mean	100.53	98.04	10.46	5.41	9.61	9.71	9.11
Standard error	1.326	1.070	0.385	0.166	0.079	0.081	0.081
Standard deviation	2.653	2.393	0.862	0.524	0.379	0.354	0.345
Minimum	97.4	95.2	9.5	4.8	9.1	9.1	8.6
Maximum	103.8	101.3	11.6	6.3	10.4	10.4	9.7
Count	4	5	5	10	23	19	18

Table 12 Summary statistics (mm) of *Vitirallus watlingi* tarsometatarsi measurements. For abbreviations, see Methods. Data from MNZ S37135, 37137, 37136, 37139, 37541, 37138, 37566.

	TL	PW	SW	SD	DW	D T3
Mean	61.99	10.05	4.92	4.22	10.09	5.39
Standard error	1.460	0.150	0.071	0.089	0.128	0.058
Standard deviation	3.576	0.619	0.225	0.282	0.404	0.192
Minimum	56.7	9.4	4.6	3.9	9.4	5.0
Maximum	65.4	11.2	5.3	4.7	10.7	5.6
Count	6	17	10	10	10	11

In *V. watlingi*, the *fossa metatarsi I* is deeper than it is in *N. poicilopterus* MNZ S38264.

The notch across the base of *trochlea metatarsi III* on the dorsal surface is more pronounced than in *Nesoclopeus woodfordi*, *N. poicilopterus* MNZ S38264, and *G. australis* (character unknown for *Tricholimnas lafresnayanus*).

Indeterminate species of rail

Three bones that are inadequate for describing a species, are indicative of another species of rail having lived on Viti Levu. MNZ S38257 pL tmt and S37479 d+sL tt from Udit Cave, and S37314 R tt, from Wainibuku Cave, both sites in Wainibuku, Viti Levu, represent a smaller and more slender rail than *Nesoclopeus poicilopterus*. The tarsometatarsus features an elongate and deep hypotarsus (proximal width = 8.2 mm) and the tibiotarsi are elongate and slender (MNZ S37314 is 85 mm from the top of the fibular crest to the distal end, shaft width 4.35 mm, distal width c. 7.0 mm). They have similar proportions and size to *Gallinula ventralis* Gould, 1837 MNZ22101 (male), but differ with a more flattened anterior facies to the tibiotarsus and a deeper hypotarsus on the tarsometatarsus. That they may be referable to a species of gallinule is likely, as historically, *Gallinula pacifica* (Hartlaub & Finsch 1871) is known from Samoa and *Gallinula silvestris* (Mayr, 1933) from San Cristobel in the Solomon Islands (Taylor & van Perlo 1998).

DISCUSSION

The addition of *Vitirallus watlingi* n. sp. and of the undescribed possible gallinule from the fossil fauna, means that Viti Levu once had at least seven sympatric rails: *Porphyrio melanotus*, *Poliolimnas cinereus*, *Porzana tabuensis*, ?*Gallinula* sp., *Gallirallus philippensis*, *Nesoclopeus poicilopterus*, and *Vitirallus watlingi*. This then is the most diverse rallid fauna known from a single island in the Pacific after New Zealand's main islands which had eight species (Worthy & Holdaway 2002).

Viti Levu has a marked rainfall gradient resulting in a dry western zone and a wet eastern zone supporting dense rainforests. The western zone now supports extensive grasslands and fernlands which is assumed to have been established and is now maintained by anthropogenic burning (Dickinson et al. 1998). The Voli Voli sites lie near the Sigatoka River mouth in the dry zone, and that *Vitirallus* was common and *Nesoclopeus* apparently absent in the prehuman environment there suggests that populations of these genera may have been largely separated by environmental preferences. In support of this contention, *Nesoclopeus* was historically recorded from swamps and wetter eastern districts (Watling 1982), and was found in the Wainibuku and Wailotua caves in the eastern region.

As is usual in insular systems, it is the flightless taxa that are now extinct. On Viti Levu these extinctions are assumed to have taken place after the arrival of humans and their commensal mammals about 3200 years ago. The most derived and highly modified species went extinct first. In the headwaters of the Sigatoka River anthropogenic deforestation began about 2000 years ago (Dickinson et al. 1998) and the resultant habitat changes probably contributed to the extinction of *Vitirallus*. However, a major factor in its extinction was doubtless predation by both people and by rodents—*Rattus exulans* (Peale, 1848) and *R. praetor* (Thomas, 1888) were both introduced by Lapita folk (White et al. 2000; Worthy et al. unpubl. data). *Vitirallus* was likely highly vulnerable to both predators given the susceptibility of analogous taxa (Holdaway 1999; Worthy & Holdaway 2002). The advent of European colonisation in the 19th century resulted in the addition of *Rattus rattus*, *R. norvegicus*, and the mongoose *Herpestes auropunctatus* by the 1880s and these species soon resulted in the complete loss of *Nesoclopeus* and *Dendrocygna*. To these may be added a megapode known as the "sasa" which was never collected, but which was described by Wood & Wetmore (1926), and may well be that recently described from fossils as *Megapodius amissus* (Worthy 2000). Fortunately, the mongoose has a restricted distribution because in its presence other species have been extirpated, for example, Wood & Wetmore (1926) reported the loss of *Gallirallus philippensis* from Viti Levu, and the purple swamphen is now absent from this island as well. Thus, the rail fauna of Viti Levu is now restricted to infrequent occurrences of two crakes.

The 47 land birds known historically for Viti Levu (Watling 1982) are now augmented by several species extinct in prehistoric times: a giant megapode *Megavitiornis altirostris*, a typical megapode *Megapodius amissus*, a giant flightless pigeon *Natunaornis gigoura*, a large *Ducula*, a snipe *Coenocorypha miratropica* (Worthy 2000, 2001a, 2003), and now two rails. Thus, a total of nine birds (19% of land birds) are now known to be extinct out of the original prehuman complement of Viti Levu. However, as well as the locally extirpated rails (*Gallirallus philippensis*, *Porphyrio melanotus*), several species of petrels are known or can be presumed to be extirpated from Viti Levu (Worthy et al. unpubl. data) and other birds, e.g., the pink-billed parrotfinch *Erythrura kleinschmidti* and the long-legged warbler *Trichocichla rufa*, are very rare and endangered (Watling 1982). Thus, Viti Levu has suffered substantial avifaunal loss since human arrival and is alike in this respect with most islands of the Pacific.

ACKNOWLEDGMENTS

Staff at the Fiji Museum were instrumental in facilitating fieldwork that led to the discovery of the specimens. In particular, I thank K. Vusoniwailala (Director), T. Sorovi-Vunidilo (Archaeologist), S. Matararaba (Mata) (Field Officer), J. Naucabalavu, W. Copeland, and K. Nanda (Museum Education Officer). D. Watling and P. Nunn gave generously of their time and knowledge of Fiji. Fieldwork was greatly aided by G. Udy of New Zealand, S. Matararaba (Fiji Museum), and A. J. Anderson, Australian National University, Canberra, Australia.

I am particularly grateful to the Roko Tui Nadroga/Navosa, I. Kedralevu and the Provincial Officers—U. Kunaturaga, S. Moceacagi, and M. Nagata for helping with access to sites. Thanks are due the following landowners who gave me access to their lands and caves. Voli Voli—L. Tubou (owner), N. Tubou, and S. Batimala (Turanga-ni-koro); Wainibuku Area—D. Singh, K. Vukeiono; Wailotua—Ratu Asaeli Roseru, and E. Cavu.

J. Cooper very generously provided X-ray photographs of the BMNH skeletons of *Nesoclopeus*. Robert Faucett and Chris Filardi, at UWBM, generously facilitated the loan of the *Nesoclopeus* specimens and Storrs Olson, at USNM, the loan of the *Amaurornis olivacea* specimens. Access to the MNZ collections was generously facilitated by Alan Tennyson and Sandy Bartle. I thank Michael Hall of the photography department MNZ for the images. The comments and suggestions of David Steadman and another referee improved the manuscript.

This study was made possible by financial assistance of the Wenner-Gren Foundation, the Royal Society of New Zealand and the Australian Research Council to A. J. Anderson who directed the multi-disciplinary project on the colonisation of Fiji and its effects, of which this research was part.

REFERENCES

Anderson, A. J.; Clark, G. R. 1999: The age of Lapita settlement in Fiji. *Archaeology in Oceania 34*: 31–39.

Anderson, A.; Ayliffe, L.; Questiaux, D.; Sorovi-Vunidilo, T.; Worthy, T. 2001: The terminal age of the Fijian megafauna. *In*: Anderson A.; Lilley, I.; O'Connor, S. *ed*. Histories of old ages: essays in honour of Rhys Jones. Canberra, ACT, Australia, Research School of Pacific and Asian Studies, The Australian National University, Pandanus Books. Pp. 251–264.

Andrews, C. W. 1896: On the extinct birds of the Chatham Islands. Part 2. The osteology of *Palaeolimnas chathamensis* and *Nesolimnas* (gen. nov.) *dieffenbachii*. *Novitates zoologicae 3*: 260–271.

Balouet, J. C.; Olson, S. L. 1987: An extinct species of giant pigeon (Columbidae: *Ducula*) from archaeological deposits on Wallis (Uvea) Island, South Pacific. *Proceedings of the Biological Society of Washington 100*: 769–775.

Balouet, J. C.; Olson, S. L. 1989: Fossil birds from late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology 469*: 1–38.

Baumel, J. J.; Witmer, L. M. 1993: Osteologia. *In*: Baumel, J. J.; King, A. S.; Breazile, J. E.; Evans, H. E.; Vanden Berge, J. C. *ed*. Handbook of avian anatomy: Nomina Anatomica Avium, 2nd ed. Cambridge, Massachusetts, USA. 799 p. *Publications of the Nuttall Ornithological Club 23*: 45–132, fig. 4.1–4.18.
Chase, C. G. 1971: Tectonic history of the Fiji Plateau. *Geological Society of America Bulletin 82*: 3087–3110.
Dickinson, W. R.; Burley, D. V.; Nunn, P. D.; Anderson, A. J.; Hope, G.; De Biren, A.; Burke, C.; Matararaba, S. 1998: Geomorphic and archaeological landscapes of the Sigatoka dune site, Viti Levu, Fiji: interdisciplinary investigations. *Asian Perspectives 37*: 1–31.
Flannery, T. F. 1995: Mammals of the south-west Pacific & Moluccan Islands. Chatswood NSW, Australia, Reed Books, in association with the Australian Museum.
Gibbons, J. R. H. 1985: A brief environmental history of Fiji. *Domodomo 3*: 110–123.
Gilbert, T. 1984: Limestone and volcanic caves of the Fiji Islands. *Transactions of the British Cave Research Association 11*: 105–118.
Holdaway, R. N. 1999: Introduced predators and avian extinction in New Zealand. *In*: MacPhee, R. D. E. *ed*. Extinctions in near time: causes, contexts, and consequences. Advances in paleobiology. New York, Plenum Press. Pp. 189–238.
James, H. F.; Olson, S. L. 1991: Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part 2. Passeriformes. *Ornithological Monographs 46*: 1–88.
Livezey, B. C. 1998: A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Philosophical Transactions*: *Biological Sciences (B) 353(1378)*: 2077–2151.
Mayr, E. 1945: Birds of the southwest Pacific. New York, The Macmillan Company. 316 p.
Molnar, R. E.; Worthy, T. H.; Willis, P. M. A. 2002: An extinct Pleistocene endemic mekosuchine crocodylian from Fiji. *Journal of Vertebrate Paleontology 22*: 612–628.
Olson, S. L. 1973: A classification of the Rallidae. *The Wilson Bulletin 85*: 381–416.
Olson, S. L. 1975: A review of the extinct rails of the New Zealand region (Aves: Rallidae). *National Museum of New Zealand Records 1*: 63–79.
Olson, S. L. 1977: A synopsis of the fossil Rallidae. Chapter 5. *In*: Ripley, S. D. *ed*. Rails of the world, a monograph of the family Rallidae. Toronto, Feheley. Pp. 339–373.
Olson, S. L.; James, H. F. 1991: Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part 1. Non-Passeriformes. *Ornithological Monographs 45*: 1–88.
Pernetta, J. C.; Watling, D. 1979: The introduced and native terrestrial vertebrates of Fiji. *Pacific Science 32*: 223–244.
Pregill, G. K.; Worthy, T. H. 2003: A new iguanid lizard (Squamata, Iguanidae) from the late Quaternary of Fiji, southwest Pacific. *Herpetologica 59*: 57–67.
Rodda, P. 1994: Geology of Fiji. *In*: Stevenson, A. J.; Herzer, R. H.; Ballance, P. F. *ed*. Geology and submarine resources of the Tonga-Lau-Fiji region. SOPAC Technical Bulletin 8. Pp. 131–151.
Sangster, G. 1998: Purple swamphen is a complex of species. *Dutch Birding 20*: 13–22.
Sangster, G.; Hazevoet, C. J.; van den Berg, A. B.; Roselaar, C. S.; Sluys, R. 1999: Dutch avifaunal list: species concepts, taxonomic instability, and taxonomic changes in 1977–1998. *Ardea 87*: 139–165.
Schodde, R.; de Naurois, R. 1982: Patterns of variation and dispersal in the buff-banded rail (*Gallirallus philippensis*) in the south-west Pacific, with a description of a new subspecies. *Notornis 29*: 131–142.
Slikas, B.; Olson, S. L.; Fleischer, R. C. 2002: Rapid, independent evolution of flightlessness in four species of Pacific Island rails (Rallidae): an analysis based on mitochondrial sequence data. *Journal of Avian Biology 33*: 5–14.
Steadman, D. W. 1987: Two new species of rails (Aves: Rallidae) from Mangaia, Southern Cook Islands. *Pacific Science 40*: 27–43.
Steadman, D. W. 1988: A new species of *Porphyrio* (Aves: Rallidae) from archaeological site in the Marquesas islands. *Proceedings of the Biological Society of Washington 101*: 162–170.
Steadman, D. W. 1989a: Extinction of birds in Eastern Polynesia: a review of the record, and comparisons with other Pacific Island groups. *Journal of Archaeological Science 16*: 177–205.
Steadman, D. W. 1989b: New species and records of birds (Aves: Megapodiidae, Columbidae) from an archaeological site on Lifuka, Tonga. *Proceedings of the Biological Society of Washington 102*: 537–552.
Steadman, D. W. 1992: New species of *Gallicolumba* and *Macropygia* (Aves: Columbidae). *Los Angeles County Museum of Natural History, Science Series 36*: 329–348.

Steadman, D. W. 1993: Biogeography of Tongan birds before and after human impact. *Proceedings of the National Academy of Sciences USA 90*: 818–822.
Steadman, D. W. 1994: Bird bones from the To'aga site, Ofu, American Samoa: prehistoric loss of seabirds and megapodes. *University of California Archaeological Research Facility, Contributions 51*: 217–228.
Steadman, D. W. 1995: Prehistoric extinctions of Pacific Island birds: Biodiversity meets zooarchaeology. *Science 267*: 1123–1131.
Steadman, D. W.; Intoh, M. 1994: Biogeography and prehistoric exploitation of birds from Fais Island, Yap State, Federated States of Micronesia. *Pacific Science 48*: 116–135.
Steadman, D. W.; Rolett, B. 1996: A chronostratigraphic analysis of landbird extinction on Tahuata, Marquesas Islands. *Journal of Archaeological Science 23*: 81–94.
Steadman, D. W.; Worthy, T. H.; Anderson, A. J.; Water, R. 2000: New species and records of birds from prehistoric sites on Niue, Southwest Pacific. *Wilson Bulletin 112*: 165–186.
Steadman, D. W.; Zarriello, M. C. 1987: Two new species of parrots (Aves: Psittacidae) from archaeological sites in the Marquesas Islands. *Proceedings of the Biological Society of Washington 100*: 518–528.
Taylor, B.; van Perlo, B. 1998: Rails. A guide to the rails, crakes, gallinules and coots of the world. Pica Press. 600 p.
Trewick, S. A. 1997a: Sympatric flightless rails *Gallirallus dieffenbachii* and *G. modestus* on the Chatham Islands, New Zealand; morphometrics and alternative evolutionary scenarios. *Journal of the Royal Society of New Zealand 27*: 451–464.
Trewick, S. A. 1997b: Flightlessness and phylogeny among endemic rails (Aves: Rallidae) of the New Zealand region. *Philosophical Transactions of the Royal Society of London, Series B, 352*: 429–446.
Turbott, E. G. (Convener) 1990: Checklist of the birds of New Zealand and the Ross Dependency, Antarctica. 3rd ed. Ornithological Society of New Zealand Inc., Random Century.
Watling, D. 1982: Birds of Fiji, Tonga and Samoa. Wellington, New Zealand, Millwood Press.
Watling, D.; Zug, G. 1998: Annotated list and conservation status of Fijian terrestrial reptiles and amphibians (Draft). Fiji biodiversity strategy and action plan. Technical Group 2—Terrestrial vertebrates and invertebrates.
White, J. P.; Clark, G.; Bedford, S. 2000: Distribution, present and past, of *Rattus praetor* in the Pacific and its implications. *Pacific Science 54*: 105–117.
Wood, C. A.; Wetmore, A. 1926: A collection of birds from the Fijian islands. *Ibis 1926*: 91–136.
Worthy, T. H. 1999: What was on the menu—avian extinction in New Zealand. *New Zealand Journal of Archaeology 19*: 125–160.
Worthy, T. H. 2000: The fossil megapodes (Aves: Megapodiidae) of Fiji with descriptions of a new genus and two new species. *Journal of the Royal Society of New Zealand 30*: 337–364.
Worthy, T. H. 2001a: A giant flightless pigeon gen. et sp. nov. and a new species of *Ducula* (Aves: Columbidae), from Quaternary deposits in Fiji. *Journal of the Royal Society of New Zealand 31*: 763–794.
Worthy, T. H. 2001b: A new species of *Platymantis* (Anura: Ranidae) from Quaternary deposits on Viti Levu, Fiji. *Paleontology 44*: 665–680.
Worthy, T. H. 2003: A new extinct species of snipe *Coenocorypha* from Viti Levu, Fiji. *Bulletin of the British Ornithologists Club 123*: 90–103.
Worthy, T. H.; Anderson, A. J. 1999: Research on the caves of Viti Levu, Fiji, June 1997–October 1998, and their significance for palaeontology and archaeology. Report to the Fiji Museum, ANH, RSPAS, ANU, Canberra, ACT 0200, Australia. 30 p.
Worthy, T. H.; Anderson, A. J.; Molnar, R. E. 1999: Megafaunal expression in a land without mammals—the first fossil faunas from terrestrial deposits in Fiji (Vertebrata: Amphibia, Reptilia, Aves). *Senckenbergiana Biologica 79*: 237–242.
Worthy, T. H.; Holdaway, R. N. 2002: The lost world of the moa: prehistoric life of New Zealand. Indiana, Indiana University Press. xxxiii + 718 p.
Wragg, G. M.; Weisler, M. I. 1994: Extinctions and new records of birds from Henderson Island, Pitcairn Group, South Pacific Ocean. *Notornis 41*: 61–70.