

Prehistoric Birds and Bats from the Atiahara Site, Tubuai, Austral Islands, East Polynesia¹

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Abstract: The Austral Islands in French Polynesia have a depauperate land bird fauna and until recently have been little investigated archaeologically or paleontologically to know whether this is natural. Here we report an avifaunal assemblage and bones of bats of the genus *Pteropus* from the Archaic period (ca. A.D. 1000–1450) cultural site Atiahara, on Tubuai. Fifteen taxa are reported from the island, and a new species of rail in the genus *Gallirallus* is described. The data indicate that several petrel species have been extirpated from the island and that former land bird inhabitants included at least two small pigeons and a flightless rail.

THE AUSTRAL ISLANDS (Figure 1), French Polynesia (Maria Atoll, Rimatarā, Rurutu, Tubuai, Raivavae, Rapa, and the Marotiri rock spires), have the smallest total landmass (144 km²) of any East Polynesian archipelago aside from the Pitcairn group (43 km²). They are high islands but too low to attract orographic rain, although because of their southern position there is abundant rainfall. Tubuai (151° W and 23° S) has a landmass of 45 km² and a maximum elevation of 409 m. It is the largest of the Australs and consists of two main volcanic cores surrounded by a vast coastal plain. Encircling the landmass is a large lagoon with an area almost twice the size of the island itself.

The Austral Islands are, archaeologically, one of the least-studied archipelagoes in East Polynesia, but recent research is beginning to address this shortfall (Bollt 2005a,b, 2007, 2008, Kennett et al. 2006). On Tubuai, the

Atiahara site is the most important found so far. It was first excavated in the 1990s, the preliminary results of which were published in Eddowes (1998). The site is developed in an open, calcareous sand deposit with an Early Eastern Polynesian (EEP) or Archaic period (ca. A.D. 1000–1450) artifact assemblage that is contemporaneous with the Peva dune site on Rurutu (Bollt 2005a,b, 2007, 2008, Steadman and Bollt 2010), as well as with other sites in the southern Cooks (e.g., Allen 1992, Walter 1998). Diagnostic Archaic artifacts excavated from Atiahara include perforated tooth pendants, objects made of pearlshell (pendants, tattooing needles, coconut graters, harpoon tips, and a superb variety of one-piece fishhooks), and a wide array of adze types (e.g., Walter 1996).

The stratigraphy of the Atiahara site varies in complexity, becoming increasingly simpler toward the coast (north). Briefly, as outlined in Figure 2, beneath the topsoil (Layer A) there is a bed of calcareous sand (Layer B), the upper part of which has been turned by modern plowing. In the majority of the excavated area, the plow cuts have not penetrated deeply enough to disturb the Archaic cultural layer. The latest cultural layer (Layer C) exists either singly as a charcoal-stained deposit, or else in two or three sublayers (C1, C2, C3), closely superimposed one on top of the other and separated by thin lenses of windblown sand (Layer D). At the southern end of the excavation, another cultural layer beneath Layer C is evident (Layer E), which is a

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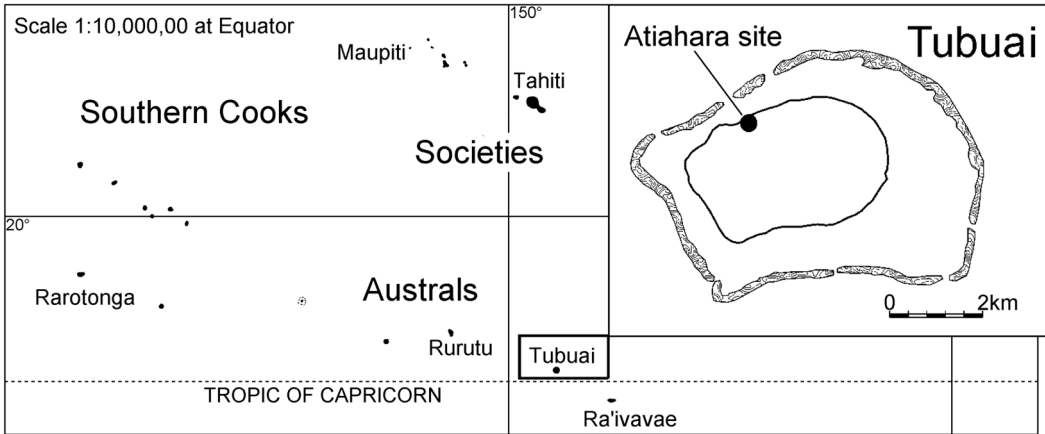


FIGURE 1. Central East Polynesia. *Inset*: Tubuai, showing surrounding barrier reef and location of the Atiahara site.

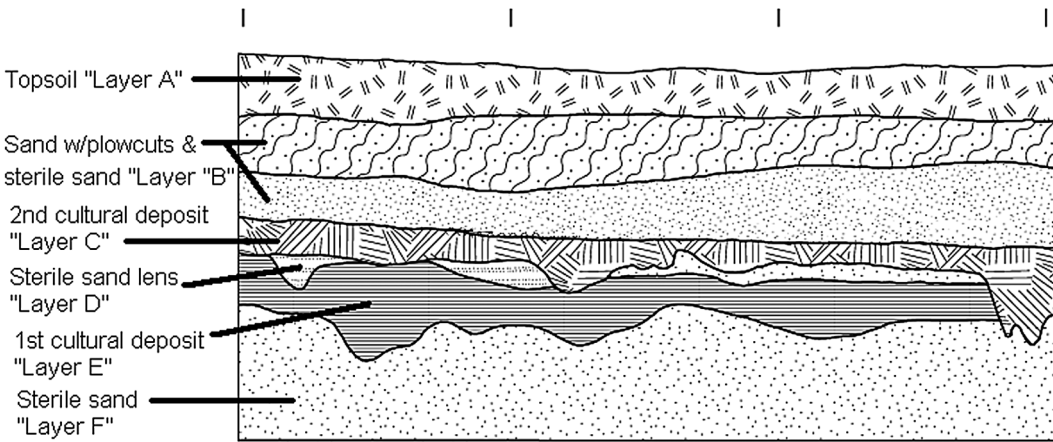


FIGURE 2. Representative wall profile of Atiahara stratigraphy.

denser, brown sand deposit, sometimes with a charcoal-stained sublayer beneath. The faunal assemblages from Layers E and C differ, suggesting two occupation periods. There is approximately four times more fish bone, shellfish, and bird bone in Layer E than in C, but in C there is two to three times the amount of domesticated animal (primarily pig) bone than in Layer E. However, the artifacts from both layers are typologically identical. Beneath the cultural layers, sterile sand (Layer F) continues for a depth of about 1 m until the coral hardpan is reached.

In total, the cultural layers yielded hundreds of Archaic artifacts including adzes and stone tools, fishhooks, and diagnostic ornaments and other tools; many basalt debitage flakes were found as well, in addition to hundreds of pieces of worked pearlshell (R.B., unpubl. data). Numerous hearths, fire pits, and earth ovens provided samples of wood charcoal and marine shell suitable for radiocarbon dating. The site has revealed the largest collection of faunal remains from the archipelago, consisting of thousands of fish bones, much shell, and thousands of whole

and fragmentary bones of pig, dog, chicken, rat, turtle, marine mammal, and flying fox (*Pteropus*). The cultural layers, with many postholes and pits, appear to have been a series of one or more habitation sites, probably occupied over a period of several generations (R.B., unpubl. data). Upon the Atiahara site, activities included food preparation, cooking, adze making, and the manufacturing of pearl-shell fishhooks and other bone and shell tools.

Prehistoric Record of Birds

Before our study, the only prehistoric land birds known from the Austral Islands were from a small excavation at the Atiahara site, Tubuai, by Richard Shutler in 1995 and the Peva site on Rurutu (Steadman and Bollt 2010). The bones from Atiahara are dominated by fish (Steadman 2006: tables 7–11). That bird bones were few (0.2% of the number of individual specimens) and pig bones were nearly as frequent as rat bones suggests that recovery of small bones at Atiahara in 1995 was less complete than at Peva. The 11 bird bones from the Atiahara site provide the only glimpse of Tubuai's prehistoric avifauna (Steadman 2006: tables 7–12, Table 3 herein). These few bones revealed a fruit-dove (*Ptilinopus* undescribed sp.) by a nearly complete tibiotarsus that differs much from those of the geographically nearest congeneric species, *P. rarotongensis* on the Cook Islands and *P. buttoni* to the southeast on Rapa.

The only other prehistoric bird bones known from the Austral Islands are 12 associated bones of a petrel from a small species of *Pterodroma* the size of *P. nigripennis* or *P. cookii* from a noncultural context in Coconut Cave on Rurutu (Steadman 2006).

In the nineteenth century the Australs and the southern Cooks were so famous for their parakeet feathers that Tahitians called them the Paroquet [parakeet] Islands or *Fenua-ʻura* (“Red land”) (Henry 1928:464). The name “Red land” is most likely derived from Kuhl's Lorikeet (*Vini kublii*), also called the Rimatara Lorikeet (Pratt et al. 1987), because it had been regarded as endemic to that island. Species of *Vini* were likely found throughout

the Cooks and Australs in prehistory. In fact, three species of *Vini* are known to have occurred on single islands in the Cooks, Societies, and Marquesas that have respectable records of prehistoric birds (Steadman 2006). In the southern Cook Islands, *V. kublii* is known prehistorically from Atiu and Mangaia, with Mangaia also having the two larger, extinct species *V. vidivici* and *V. sinotoi*, which are known only from bones in Archaic middens or precultural deposits (Steadman 1991, 2006).

The indigenous land bird fauna of the Austral Islands is now depauperate, with only three endemic taxa (Steadman 2006: tables 7–10): the Rapa fruit dove, *Ptilinopus buttoni*; Kuhl's lorikeet, *V. kublii* on Rimatara; and the Rimatara Reed Warbler, *Acrocephalus vaughani*. Four widespread species are also present: three semiaquatic tramp species, a heron, *Egretta sacra*; a duck, *Anas superciliosa*; and a rail, *Porzana tabuensis*; and a winter visitor, the long-tailed cuckoo, *Eudynamis taitensis* (Aitken 1930, Ehrhardt 1980, Steadman 2006). On Tubuai, the avifauna is now even more depauperate (Table 1).

A key question relates to the former presence of the Pacific Flying Fox (*Pteropus tonganus*), now absent from the Australs. During the Archaic period this species was extirpated on neighboring Rurutu (Weisler et al. 2006, Bollt 2007, 2008), as well as on islands in the southern Cooks (Allen 1992, Walter 1998); it still exists on two islands in the latter group (Mangaia and Rarotonga). Finding this species on Rurutu has extended its eastern limit in the Pacific by hundreds of kilometers. There is a strong possibility that humans transported it eastward (Weisler et al. 2006); alternatively, Rurutu and the Australs may have been part of the natural range of *P. tonganus*. If *Pteropus* is lacking from levels before human presence on Tubuai, then the hypothesis of human transport would be corroborated.

Here we extend knowledge of the prehistoric fauna of the Austral Islands by describing a noteworthy avifauna and *Pteropus* bones in the Atiahara assemblage excavated during 3 November to 24 December 2007 by R.B.

TABLE 1

Birds Currently Found in the Tubuai Fauna after Aitken (1930), Ehrhardt (1980), Steadman (2006), and Thibault and Bretagnolle (2007)

Scientific Name	Common Name
Oceanic and coastal species	
<i>Pterodroma ultima</i>	Murphy's Petrel
<i>Puffinus nativitatis</i>	Christmas Shearwater
<i>Puffinus pacificus</i>	Wedge-tailed Shearwater
<i>Gygis alba</i>	White Tern
<i>Anous stolidus</i>	Brown Noddy
<i>Anous minutus</i>	Black Noddy
<i>Fregata minor</i>	Great Frigatebird (nonbreeding)
<i>Fregata ariel</i>	Lesser Frigatebird (nonbreeding)
<i>Sula leucogaster</i>	Brown Booby
<i>Phaethon lepturus</i>	White-tailed Tropicbird
<i>Phaethon rubricauda</i>	Red-tailed Tropicbird
<i>Heteroscelus incanus</i>	Wandering Tattler
<i>Pluvialis fulva</i>	Pacific Golden-Plover
Indigenous taxa	
<i>Anas superciliosa</i>	Pacific Black Duck
<i>Egretta sacra</i>	Pacific Reef-Heron
<i>Porzana tabuensis</i>	Spotless Crake
Migratory species	
<i>Calidris alba</i>	Sanderling
<i>Eudynamis taitensis</i>	Long-tailed Koel
<i>Limosa lapponica</i>	Bar-tailed Godwit
<i>Numenius tabitiensis</i>	Bristle-thighed Curlew
Introduced species	
<i>Acridotheres tristis</i>	Common Myna
<i>Gallus gallus</i>	Red Junglefowl
<i>Lonchura castaneothorax</i>	Chestnut-breasted Mannikin
<i>Zosterops lateralis</i>	Silvereye

MATERIALS AND METHODS

From 3 November to 24 December 2007, R.B. directed a new excavation of the Ati-hara site with a team consisting of 10 student and professional volunteers from Hawai'i, the University of Otago, the University of Auckland, and the Australian National University. In total, they excavated over 130 m² of pristine ground in untouched areas surrounding the original bulldozed trench and previously dug areas. Numerous hearths, fire pits, and earth ovens provided samples of wood charcoal and marine shell suitable for radiocarbon

dating. Sediments were dry-screened using 3.2 mm (1/8 inch) mesh; additional samples were screened for land snails using 1 mm mesh and wet screening. The large collection of faunal remains included over 25,000 fish bones, over 300 kg of shell, and thousands of whole and fragmentary remains of pig, dog, chicken, rat, turtle, marine mammal, and flying fox. Bird remains were sorted from these in the laboratory and sent to T.H.W. They were identified by T.H.W. after comparison with reference skeletons in the South Australian Museum, Adelaide, and Australian Museum, Sydney. The anatomical nomenclature used for specific bone landmarks when describing specimens follows Baumel and Witmer (1993). We follow the taxonomic sequence and nomenclature advocated by Gill et al. (2010).

Important comparative specimens are listed where relevant. Measurements were made with dial calipers (Tesa) to 0.1 mm.

Radiocarbon Dating

Two samples of charred bark were chosen for dating because this medium does not suffer from problems of inbuilt age, as is potentially an issue with wood charcoal, and neither does it have the problems of bone where the collagen fraction weathers away rapidly in tropical environments and exclusion of humic acid and other contaminants is problematical. The radiocarbon analyses were determined at the Australian National University Radiocarbon Laboratory, Canberra, using the Single Stage Accelerator Mass Spectrometer.

Abbreviations: AM, Australian Museum, Sydney; F, female; M, male; MNI, minimum number of individuals; NISP, number of individual specimens. Elements: cmc, carpometacarpus; hum, humerus; fem, femur; juv, juvenile; rad, radius, tib, tibiotarsus; tmt, tarsometatarsus; M, male; F, female; L, left; R, right. L and R preceded by p, s, or d indicate the proximal, shaft, or distal part of the element, respectively. We use the term "magn." (from Latin, magnitudino) to indicate that the taxon is the approximate size of the following listed modern species.

RESULTS

Dating

Two radiocarbon dates were obtained from a C-layer pit fill in the 2007 excavation: (1) Laboratory code SSAMS 7120, submitter's sample identification TVB624, excavation unit K5 Hole, 200–210 cm depth, charred bark, conventional radiocarbon age 930 ± 60 yr B.P., calibrated age 686–921 yr B.P.; (2) SSAMS 7138, TVB633, excavation unit K5 Pit Fall, 175–180 cm depth, charred bark, conventional radiocarbon age 855 ± 30 yr B.P., calibrated age 675–769 yr B.P. (Calibrations from SH curve using Calib 5.0.)

SYSTEMATIC ACCOUNT

Class MAMMALIA
Family PTEROPODIDAE

Pteropus tonganus tonganus, Tongan Fruit Bat
MATERIAL: Right dentary with m2 (Unit

L5, Layer E [Figure 3]); L dentary with m2 (Unit ?, Layer C).

Comparisons were made with: *Pteropus samoensis*, AM M.23231, F; AM M.23238, F, both Vanua Levu, Fiji. *P. tonganus geddiei*, AM M.27167, M, Vanuatu. *P. tonganus tonganus*, AM M.23219, F; AM M.23216, F, both Fiji. *P. vetulus*, AM M.24454, New Caledonia. The size of the Tubuai specimens is similar to that of *P. samoensis* and *P. tonganus tonganus* (Table 2). *Pteropus tonganus geddiei* is significantly larger (Flannery 1995) as exemplified by M.27167 in Table 2. *Pteropus vetulus* is a much smaller fruit bat. The Tubuai specimens are referred to *P. tonganus tonganus* on the basis of the morphology of m2. The fossil has a short and wide m2 with well-rounded cusps buccally and lingually of the shallow central basin of the molar with no distinct posterior buccal cusp. Those of *P. samoensis* are more elongate, have relatively sharp crests buccally and lingually, and have a distinct posterior buccal cusp separated by a notch from the more anterior buccal cusp.

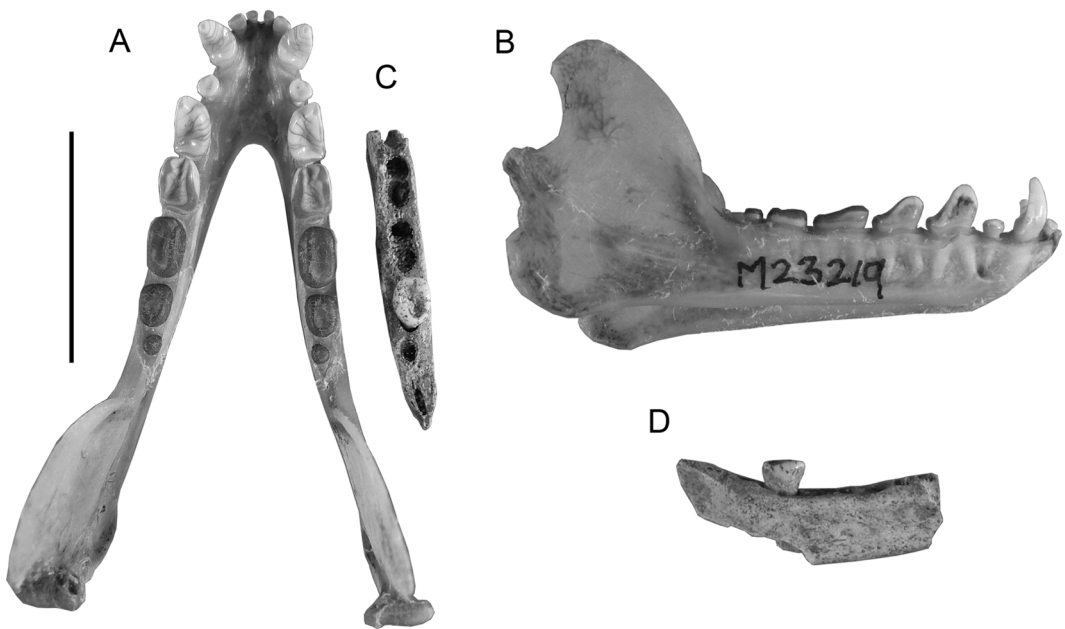


FIGURE 3. Mandible of *Pteropus tonganus tonganus*, AM M.23219, in dorsal view (A) and right lateral view (B) compared with the Tubuai specimen from Unit L5, Layer E (C, D). Scale bar is 20 mm.

TABLE 2
Measurements (mm) of Mandibles of Various *Pteropus* Species Compared with the Tubuai Specimen

Taxon	Cat. No./ID	Depth 1 ^a	Length m2	Width m2
Tubuai specimen	L5/E	6.7	3.6	2.8
<i>P. samoensis</i>	M.23231	6.7	3.3	2.4
<i>P. samoensis</i>	M.23238	6.4	3.5	2.4
<i>P. tonganus geddiei</i>	M.27167	8.8	3.8	3.5
<i>P. tonganus tonganus</i>	M.23219	6.2	3.3	2.5
<i>P. tonganus tonganus</i>	M.23216	6.3	3.2	2.5

Abbreviations: Cat. No., catalog number in the mammal collection, Australian Museum; ID, excavation identification; m2, mandibular molar 2.

^a Depth of mandible below alveolus for molar 1.

BIRDS

In Material lists, the catalog number in the Ornithology collection of the Australian Museum is followed by the unit or excavation square, the layer or origin, and the element for each specimen.

Order GALLIFORMES Family PHASIANIDAE

Gallus gallus, Chicken

MATERIAL: AM O.72463, Unit G3, Layer C1, sL tmt; AM O.72464, H5, Layer C, pL cmc; AM O.72484, H3, Layer F, dL tmt; AM O.72485, Q4, Layer E, pL tmt; AM O.72535, L12, Layer F, pL rad. cf. *Gallus gallus*: AM O.72529, L12, Layer F, juv. dL tmt. Total 5 + ?1 specimens, 2 individuals.

Order PROCELLARIIFORMES Family PROCELLARIIDAE

Pterodroma sp. magn. *P. macroptera*, Gray-faced Petrel

MATERIAL: AM O.72480, G2, Layer E, dR hum.

This specimen lacks the condylus dorsalis and has a shaft width at the proximal side of the processus supracondylar dorsalis of 7.9 mm. It does not differ in any way from a specimen of *P. macroptera*, AM O.58521, and so is tentatively referred to that taxon. *Pterodroma macroptera* ranges to about 130° W between 30° and 50° S (Gill et al. 2010) so may well be expected in waters around the Austral Islands.

Pterodroma sp. magn. *P. neglecta*, Kermadec Petrel

MATERIAL: AM O.72449, K3, Layer C, dL tib, pL tmt of a juvenile/fledgling. Proximal width tmt = 6.7 mm, distal width tib = 5.48 mm.

Pterodroma neglecta has a wide breeding distribution from Lord Howe Island and the Kermadecs to the Juan Fernández Islands far to the east of the Austral Islands. It still breeds on Rapa and Raivavae in the Australs (Thibault and Bretagnolle 2007). Several other tropical Pacific species are similar in size to the Kermadec petrel, and the fossils could potentially belong to any of them: *P. cervicalis*, White-naped Petrel; *P. alba*, Phoenix Petrel; *P. heraldic*, Herald Petrel; and *P. atrata*, Henderson Petrel. Regardless of their identity, these two bones are evidence of a medium-sized *Pterodroma* species formerly breeding on Tubuai.

Pterodroma sp. magn. *P. brevipes*, Collared Petrel

MATERIAL: AM O.72440, L1, Layer C, pL ulna; AM O.72450, T/V1, Layer C, R cmc; AM O.72466, T4, Layer C1/2, dL hum; AM O.72518, F/G, Layer ?, sR hum; AM O.72519, J4, Layer E, sL ulna; AM O.72521, K12, Layer F, dL ulna; AM O.72528, X3, Layer E, RdR ulna, d cmc. Nine specimens; MNI, 2.

Several similar-sized small petrels are found in the tropical Pacific (e.g., Onley and Scofield 2006). Gould's Petrel, *Pterodroma*

leucoptera, with *P. l. leucoptera* breeding on Cabbage Tree Island, Tasman Sea, and *P. l. caledonica* in New Caledonia, migrates to the tropical eastern Pacific (Gill et al. 2010). The Collared Petrel, *Pterodroma brevipes*, sometimes considered a subspecies of *P. leucoptera* and now rare and endangered, breeds in South Vanuatu, Makira (Solomon Islands), Fiji, Western Samoa, Rarotonga (Cook Islands), Raivavae in the Austral Islands (Thibault and Bretagnolle 2007), and was historically known breeding in Tahiti and Samoa (Onley and Scofield 2006). Black-winged Petrel, *Pterodroma nigripennis*, breeds on islands in the Tasman Sea and on islands around New Caledonia and New Zealand, Tonga, Rarotonga, to as far east as Rapa in the southern Austral Islands. It has an expanding distribution (Gill et al. 2010) but has a more southern range than *P. brevipes*. All have wider nonbreeding distributions.

On the basis of the morphology of postcranial elements none of these taxa can be separated, but given that *P. brevipes* is still breeding in the northern part of the Austral group, we think it more likely that the bones listed here belong to that species.

Puffinus sp. magn. *P. pacificus*, Wedge-tailed Shearwater

MATERIAL: AM O.72468, N13, Layer C, sR tib.

This specimen is a fragment of shaft preserving all of the fibular crest. The length of the fibular crest is ca. 18 mm, and shaft width below the fibular crest is 3.9 mm. It is more slender than in *Puffinus tenuirostris* (e.g., AM O.59307, O.57724), which had shaft widths of 4.2 and 4.3 mm. *Puffinus pacificus* is widespread in the tropical western Pacific (Thibault and Bretagnolle 2007) and varies in size, but this specimen matches AM O.58459 (fibular crest 19.5 mm long, shaft width 4.1 mm) though others are smaller (e.g., AM O.65692 [fibular crest 15.2 mm, shaft width 3.5 mm]).

Puffinus sp. magn. *P. lherminieri*, Audubon's Shearwater

The phylogenetic relationships of small tropical shearwaters are currently poorly

understood (Austin et al. 2004). The major checklists recognize only a few species, with *P. lherminieri* being used for most tropical populations and *P. assimilis* for most higher-latitude populations (e.g., Warham 1990, Carboneras 1992). Genetic data from a comprehensive sampling of taxa reveal a much more complex situation in which the widespread form in the tropical Pacific, *P. l. dichrous*, and *P. l. polynesiae* from Ta'u, American Samoa, constitute part of a distinct lineage including Indian Ocean forms that would take the name *P. bailloni* (Tropical Shearwater), with *P. lherminieri* (Audubon's Shearwater) restricted to the Atlantic Ocean and *P. assimilis* to Australasia (Austin et al. 2004). The situation is further complicated by the small shearwater *P. assimilis myrtae* described from Rapa Island, in the southern Austral Islands (Bourne 1986, Thibault and Bretagnolle 2007). Molecular data suggest that this extant population is more closely related to *Puffinus newelli* of Hawai'i, and that it may be of hybrid origin (Austin et al. 2004). It is doubtful that the fragmentary material from Tubuai could be certainly identified, so pending clarification of the taxonomy we refer these specimens to *Puffinus* sp. magn. *P. lherminieri* to indicate the size class to which they belong.

MATERIAL: AM O.72447, O5, Layer C, dR hum; AM O.72448, I5, Layer C, dL hum; AM O.72511, F/G3, Layer F, dR hum; AM O.72514, R2, Layer D/E, pR hum; AM O.72515, F/G2, Layer G, pL hum; AM O.72517, X2, Layer F (150–160 cm), dL hum; AM O.72523, I2, Layer F, pR hum; AM O.72524, T9, Layer E, pL hum; AM O.72532, R3, Layer E/F, sR tib, sL hum; AM O.72525S4, Layer E, dRdL hum, pR ulna; AM O.72512, T4, Layer E, dR ulna; AM O.72513, L13, Layer F, pR ulna, sR tib; AM O.72515, L10, Layer F, dL ulna; AM O.72520, L15, Layer E, sL ulna; AM O.72527, Q3, Layer E, sR hum. Nineteen specimens; MINI, 3 individuals.

Family PHAETHONTIDAE

Phaethon lepturus, White-tailed Tropicbird

MATERIAL: AM O.72534, K12, Layer E, dR ulna; AM O.72533, N15, Layer E, R cor.

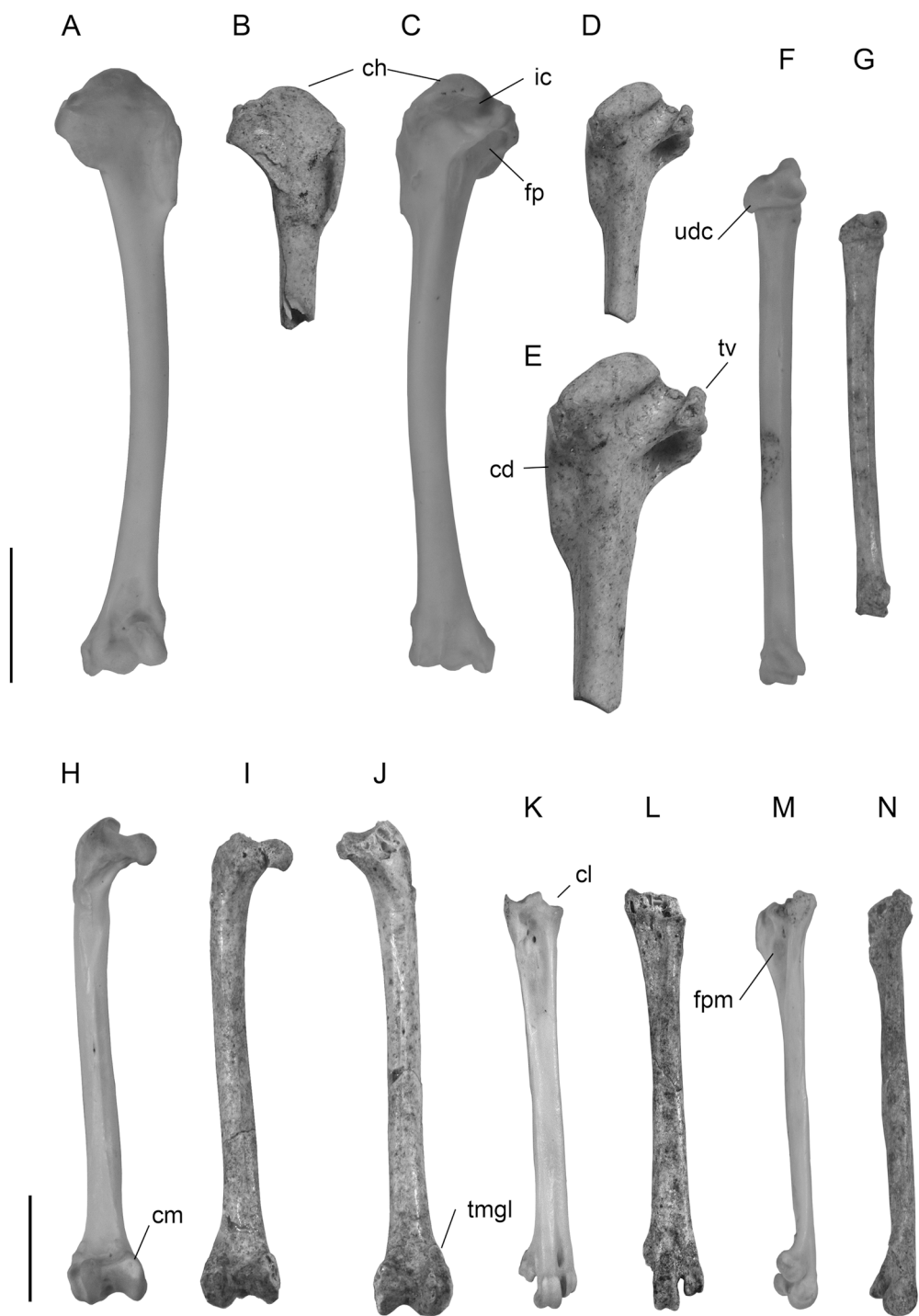


FIGURE 4. Selected elements of *Gallirallus philippensis* (A, C, F, H, K, M) compared with *Gallirallus steadmani* Worthy & Bolt, n. sp. (B, D, E, G, I, J, L, N). Left humeri in cranial (A, B) and caudal aspect (C–E); right ulnae in cranial aspect; femora (left H, I; right J) in ventral aspect; and left tarsometatarsi in dorsal (K, L) and medial (M, N) aspects. Abbreviations: cd, crista deltopectoralis; ch, caput humeralis; cl, cotyla lateralis; cm, condylus medialis; fp, fossa pneumotricipitalis; fpm, fossa parahypotarsalis medialis; ic, incisura capitis; tmgl, tuber. m. gastrocnemialis lateralis; tv, tuberculum ventrale; udc, ulnar cotyla dorsalis. Scale bar is 10 mm except for E, which is 1.5× others in row.

cf. *Phaethon lepturus*: AM O.72465, D2, Layer C, sL hum; AM O.72441, F1, Layer C, pR ulna. Total 2 + ?2 specimens, 1 individual.

Order GRUIFORMES

Family RALLIDAE

Genus *Gallirallus* Lafresnaye, 1841

The fossils listed in this section are referred to *Gallirallus*, sensu Kirchman and Steadman (2006a) and Steadman (2006), rather than to other genera of rails found in the Pacific Ocean region because they have the following combination of characters (modified from Kirchman and Steadman [2006a] and Worthy [2004]). Humerus: fossa pneumotricipitalis deepened ventroproximally with prominent crus ventrale fossae. Ulna: thin in cranial aspect, craniocaudally wider than dorsoventral depth, ventral facies flattened with angular junction with margo cranialis. Femur: distal half of corpus femoris gradually widening distally; condylus medialis in medial aspect not circular, somewhat angular caudally; caudal impressio ansa musculus iliofibularis (sensu Baumel and Witmer 1993: note 260; not as per Livezey and Zusi 2006: char 2050) is distally adjacent to the trochlea fibularis and proximally abuts the larger round tuberculum m. gastrocnemialis lateralis. Tibiotarsus: impressio ligamentum collateralis medialis deep and wide; medial and lateral margins of facies cranialis rounded (not angular); facies cranialis convex rather than flattened in distal half; sulcus extensorius about 1/3 shaft width, narrowly separated from medial margin; depressio epicondylaris lateralis deep; condylus medialis in medial aspect not circular, with caudocranial depth greater than proximodistal depth. Tarsometatarsus: length less than femur length; corpus tarsometatarsi much wider than deep; fossa parahypotarsalis medialis shallow; fossa metatarsi I short and shallow; crista medianoplantaris slopes gradually from hypotarsus to shaft (not abruptly, nor hooked distally); cotyla medialis is rectangular in proximal aspect with flattened dorsal margin; cotyla medialis distinctly proximal to lateral cotyla.

The gallinules (*Gallinula ventralis*, *G. tenebrosa*, and *G. mortierii*) and the swamphens

(*Porphyrio* spp.) all differ markedly from *Gallirallus* in having the tarsometatarsus markedly longer than the femur, in addition to some of the features listed here. Other rails such as *Amaurornis olivacea* and *Poliolimnas cinereus* also differ in having the tarsometatarsi more elongate than the femora. However, the crakes included in *Porzana* found in Oceania (e.g., *P. tabuensis* and *P. pusilla*) have the tarsometatarsus shorter than the femur but are smaller than species of *Gallirallus* and also differ in having the distal portion of the tibiotarsus flattened anteriorly, with the medial and lateral margins angular, the fossa metatarsi I of the tarsometatarsus deeper, and the hypotarsus more elongate.

The following species was flightless, thus precluding dispersal over hundreds of kilometers of ocean, so it is assumed to have evolved on Tubuai from a volant ancestor, as have many rails in Oceania (e.g., Slikas et al. 2002, Steadman 2006, Kirchman and Steadman 2006a). It is thus unlikely to be conspecific with flightless rails elsewhere, so we have limited our comparisons mainly to the widespread volant *G. philippensis*.

Gallirallus steadmani Worthy & Bollt, n. sp.

Figure 4; Table 3

HOLOTYPE: AM O.72500, proximal left humerus, preserving part of the shaft and the entire proximal end, stained a light brown but otherwise undamaged. Preserved length 18.0 mm, maximum proximal width 8.3 mm, craniocaudal depth at tuberculum ventrale 5.1 mm, length of crista deltopectoralis 8.6 mm, and minimum shaft width in caudal view 2.3 mm.

PARATYPES: AM O.72470, pL humerus, K2, Layer F; AM O.72490, R ulna, L11, Layer F; AM O.72504, L tarsometatarsus joined from two halves, H2/H3, Layer F; AM O.72458, R femur joined from two halves, N13, Layer C; AM O.72476, L femur, N14, Layer F.

TYPE LOCALITY: The Atihara archaeological site, square L11, Layer F, Tubuai, Austral Islands. Collected by R. Bollt et al. during 3 November to 24 December 2007.

REFERRED MATERIAL: Layer A/B: AM O.72444, unit L4, dL tib.

Layer C: AM O.72455, C2/C3, L fem (-d); AM O.72454, D3, dL fem; AM O.72442, E1, pR tib; AM O.72443, F4, dL tib; AM O.72456, G1, dLdR tib; AM O.72461, G4, dL tib; AM O.72446, I4, juv R tmt; AM O.72452, I5, pR tib; AM O.72459, J5, pL fem; AM O.72453, K5, dL fem; AM O.72460, L5, dR hum; AM O.72451, N16, dL tib; AM O.72457, O15, dR tib; AM O.72462, ?, pR fem; AM O.72445, X3, sR fem. Seventeen specimens (including paratypes); MNI, 4.

Layer E: AM O.72479, G2, pL tmt; AM O.72495, G3, sL fem; AM O.72492, I3, dR fem; AM O.72497, I4, sL tib; AM O.72499, J4, pR hum; AM O.72502, K4, sR fem; AM O.72478, L13, d + sR tib; AM O.72472, L15, sR tib; AM O.72509, M2, dL fem; AM O.72505, M4, dL tmt; AM O.72522, M4, sR fem; AM O.72491, M14, dR fem; AM O.72496, P1, sR fem; AM O.72486, P3, dL tib; AM O.72526, Q3, sL fem; AM O.72488, S4, sL tib; AM O.72489, T1, pR tmt, pL fem, dL fem; AM O.72493, T10, R fem; AM O.72650, T10, pR tib; AM O.72477, V2, dL tib; AM O.72481, W4, d + sR hum. Twenty-three specimens; MNI, 3.

Layer F: AM O.72469, K12, dL fem; AM O.72471, L11, dR tib; AM O.72473, Y3, p + sR tib; AM O.72474, F5, pR tib; AM O.72475, L13, dL tib; AM O.72482, J3, pR tmt; AM O.72483, H3, sR fem; AM O.72487, O14, sR tib; AM O.72494, F1, sR fem; AM O.72498, O13, pL tib; AM O.72501, L14, dL tib; AM O.72506, N13, dL tmt; AM O.72508, M14, dL tib. Eighteen specimens (including type series); MNI, 3.

Layer G: AM O.72503, F/G2, pR tmt.

Layer unknown: AM O.72507, F2/G2, (C2 Fe G), p + sL fem.

Total number of specimens, 61; combined MNI, 10.

ETYMOLOGY: The species is named after David Steadman, to reflect the huge contribution he has made to Pacific paleornithology and to the understanding that *Gallirallus*-like rails have spawned one of the most spectacular radiations of birds known.

DIAGNOSIS: A flightless species with leg bones of size similar to that of volant *Galli-*

rallus philippensis (Oceania) or *G. striatus* (Asia) but that differs from those species by: humerus and ulna, relative to femur size, much smaller; humerus with relatively thinner shaft, less robust tuberculum ventrale, concave dorsal facies adjacent to crista deltopectoralis, and reduced bicipital crest; femur with more elongate tuberculum m. gastrocnemialis lateralis and relatively broader distal tarsi.

DESCRIPTION AND COMPARISON: Comparisons were made with the following specimens of *Gallirallus philippensis*: AM O.56994, 59296, 64202, 71174, 72331, 72342, and 70869; and comparative data obtained from Steadman (1987), Steadman et al. (2000), Worthy (2004), and Kirchman and Steadman (2005, 2006a,b, 2007).

Humerus. Although the proximal width is similar to that in humeri of *G. philippensis* (e.g., AM O.70869), the shaft is relatively narrower. Dorsally, the surface between the crista deltopectoralis and the shaft is concave, whereas it is convex in *G. philippensis*. The caput humeri narrows in caudocranial depth toward its ventral edge, whereas it is widest near the ventral edge in *G. philippensis*, caused by a distinct bulge overhanging the incisura capitis. In proximal view, the tuberculum ventrale is relatively narrower, and, unlike the fossil, in *G. philippensis* the tuberculum thickens cranially (i.e., as it approaches the base of the incisura capitis). The crista deltopectoralis is relatively thicker distally and has a deeper sulcus on its ventral side. The crista bicipitalis has a straight distal margin, whereas it is rounded in *G. philippensis* by a thin protuberant flange. The fossa brachialis is relatively deeper.

Ulna: The ulna is about 20% shorter than expected given the femur lengths available, the impressio brachialis is relatively more deeply excavated, and the cotyla dorsalis is not hooked distally such that the distocranial margin of the cotyla dorsalis in cranial view is straight. In contrast, in the same aspect, the dorsal side of the cotyla dorsalis in *G. philippensis* is distinctly hooked distally.

Femur: The femur does not differ appreciably from those of modern *G. philippensis* (e.g., AM O.70869), except in the diameter of the tuberculum m. gastrocnemialis lateralis,

TABLE 3

Summary Statistics of Measurements (mm) of Femora, Tibiotarsi, and Tarsometatarsi of *Gallirallus steadmani* Worthy & Bolt, n. sp., and Values for Humeri and an Ulna

Character	L	PW	PD	SW	DW	dLC	dMC	DW Dorsal Condyle
Femora								
Average	45.4	7.3	6.3	3.2	7.7			
SD	1.29	0.37	0.38	0.17	0.12			
Count	3	6	5	12	3			
Minimum	44.0	6.8	5.9	2.9	7.6			
Maximum	46.5	7.8	6.9	3.4	7.8			
Tibiotarsi								
Average		6.2		2.8	6.0	5.9	6.0	
SD		0.36		0.16	0.29	0.26	0.28	
Count		5		9	7	8	6	
Minimum		5.6		2.5	5.6	5.6	5.7	
Maximum		6.5		3.0	6.3	6.3	6.3	
Tarsometatarsus								
Average	40.0	6.2		3.0	6.2			
SD		0.35		0.12				
Minimum		5.9		2.9				
Maximum		6.4		3.1				
Count	1	2		3	1			
Humerus		8.4, 9.0		2.3, 2.6	5.3			
Ulna	31.5 est.	3.6		1.7	3.6			3.4

Abbreviations: SD, standard deviation; L, length; PW, maximum proximal width; PD, proximal depth; SW, shaft width at midshaft for femora and tarsometatarsi, minimum values for tibiotarsi; DW, maximum distal width; dLC, anterior-caudal depth lateral condyle; dMC, anterior-caudal depth medial condyle.

which is as wide as the proximal trochlea fibularis in the fossil but is relatively elongate and narrower than the trochlea in *G. philippensis*. Such a round tuberculum m. gastrocnemialis lateralis is seen in large flightless *Gallirallus* species (for example, *G. australis* [AM O.53856]), but the elongate form is found in other equally large flightless rails (for example, *G. sylvestris* [AM O.56432, 58027, 58028, and 64571]), so it being circular is not related to flightlessness. Available measurements (Table 3) suggest that the Tubuai bird had femora at the small end of the size range for Oceanic *G. philippensis* (Kirchman and Steadman 2007).

Tibiotarsus: The tibiotarsus does not differ appreciably in shape or size from those of *G. philippensis*, and the size of available specimens is at the small end of the range for Oceanic *G. philippensis* (Table 3) (Kirchman and Steadman 2007).

Tarsometatarsus: Compared with tarsometatarsi of *G. philippensis* of similar length

(e.g., AM O.70869), those of *Gallirallus steadmani* have a broader distal end and the fossa parahypotarsalis medialis is shallower proximad of the foramen vasculare proximalia such that it barely forms a notch in the medial facies at the base of the hypotarsus. In *G. australis*, *G. sylvestris*, and in all *G. philippensis* examined, the fossa extends to the proximal end and is bound by a ridge, creating a distinct groove medially. However, in the equally large, flightless *G. lafresnayanus* (AM B.6147) the fossa did not extend to the proximal end.

Compared with other flightless species of *Gallirallus*, *G. steadmani* is larger than *G. wakensis* (Wake Island [Kirchman and Steadman 2006a]), *G. pisonii* (Aguiguan, Marianas [Kirchman and Steadman 2006a]), and *G. modestus* (Chatham Islands, New Zealand [Trewick 1997]).

It is smaller than the volant *G. torquatus* (Philippines–New Guinea [Kirchman and Steadman 2007]) and the following flightless species: *G. owstoni* (Guam, Marianas

[Kirchman and Steadman 2006a]), *G. temptatus* (Rota, Marianas [Kirchman and Steadman 2006a]), *G. pendiculatus* (Tinian, Marianas [Kirchman and Steadman 2006a]), *G. insignis* (New Britain [Kirchman and Steadman 2006a]), *G. ernstmayeri* (New Ireland, Bismarcks [Kirchman and Steadman 2006a]), *G. lafresnayanus* (New Caledonia [AM B.6147]), *G. sylvestris* (Lord Howe Island [AM O.56431]), *G. australis* (New Zealand [Kirchman and Steadman 2006b]), *G. dieffenbachii* (Chatham Islands, New Zealand [Trewick 1997]), *G. rovianna* (New Georgia, Solomon Islands [Kirchman and Steadman 2006a]), *G. woodfordi* (Isabella, Solomon Islands [Kirchman and Steadman 2006a]), *G. poecilopterus* (Viti Levu, Fiji [Worthy 2004]), *G. vekamato* ('Eua, Tonga [Kirchman and Steadman 2005]), *G. storrsolsoni* (Huahine, Society Islands [Kirchman and Steadman 2006b]), and *G. roletti* (Tahuata, Marquesas [Kirchman and Steadman 2007]).

A few flightless species from Oceania have similar size based on leg bones: the poorly known *G. epulare* (Nuku Hiva, Marquesas) has similar-sized tibiotarsi but has a relatively shorter ulna, and *G. gracilitibia* (Ua Huku, Marquesas) has a relatively more reduced humerus (Kirchman and Steadman 2007). Closer to the Austral Islands but still more than 1,000 km distant, *G. huiatua* (Niue) has a similar length of tarsometatarsus but is more gracile, with narrower shaft and proximal widths (Steadman et al. 2000). *Gallirallus ripleyi* (Mangaia, Cook Islands), also with similar distal width of tibiotarsi, has a narrower distal end of the femur, a wider distal end of the tarsometatarsus, and even more greatly reduced wings, with a much shorter ulna and a narrower distal end of the humerus (Steadman 1987, Kirchman and Steadman 2006b).

Gallirallus steadmani is much smaller than the flightless, extremely long-billed *Vitirallus* (Vitilevu), which otherwise differs in numerous features, including a humerus with a much more reduced crista bicipitalis, crista deltopectoralis rolled over the cranial surface, sulcus extensorius separated from medial margin by wider ridge, and cotylae medialis et lateralis near level with each other, rather

than the medial cotyla being appreciably offset proximally from the lateral one (Worthy 2004).

Indeterminate charadriiform 1

MATERIAL: AM O.72530, J9, Layer E, dL fem.

This specimen is the size of *Pluvialis fulva* (Pacific Golden-Plover) but differs from that species. It does not appear to be referable to either *Heteroscelus incana* or *Limosa lapponica*, and its identity remains indeterminate.

Indeterminate charadriiform 2

MATERIAL: AM O.72467, O3, Layer D, L hum.

Length: estimated length 31.5 mm, distal width 5.2 mm.

This specimen is missing the ventral tubercle and head but preserves the characteristic impressio coracobrachialis and most of the larger crista deltopectoralis. The humerus is smaller than the humerus of *Heteroscelus brevipes* (AM O.58080) or *Calidris acuminata* (AM O.71525) but similar to that of *Calidris ferruginea* (AM O.59867). It differs from humeri of *Tringa* and *Calidris* by a more flattened intumescentia humeralis, a broader impressio coracobrachialis, a more proximally located angle on the crista deltopectoralis relative to the junction of the crista bicipitalis and the shaft, and the processus supracondylaris dorsalis is more dorsally directed rather than inclined somewhat cranially. These features and the size appear consistent with *Prosobonia cancellatus*, as evident in an image of a humerus of this species provided by Mike Dickison (University of Canterbury, pers. comm. to T.H.W., 2009). These initial observations suggest that this humerus possibly might be referable to a *Prosobonia* species, which genus has several extinct taxa in the eastern Pacific (Steadman 2006), with the remaining species, *P. cancellata*, endangered. Confirmation of this referral awaits future research.

Order COLUMBIFORMES

Family COLUMBIDAE

Gallicolumba sp. indet., undetermined ground dove

MATERIAL: AM O.72510, I4, Layer E, pL ulna.

This specimen is identified as *Gallicolumba* and distinguished from *Ptilinopus* by the following features: the cranioventral margin of the cotyla ventralis is angular (curved in *Ptilinopus*), the crista intercotylaris is high and prominent (much lower in *Ptilinopus*), the olecranon is low and rounded (higher and pointed in *Ptilinopus*), and the impressio brachialis is more widely separated from the tuberculum ligamentum collateralis ventralis. The proximal width of this specimen is 4.7 mm, which is similar in size to *Gallicolumba jobiensis* (AM O.72023, O.64814). Characterization of the species of *Gallicolumba* from Atiahara will require additional material.

DISCUSSION

The Atiahara site on Tubuai in the Austral Islands, French Polynesia, contains a rich Archaic material cultural assemblage (R.B.,

unpubl. data). The two radiocarbon dates provide calibrated ages of 686–921 yr B.P. and 675–769 yr B.P. for basal layers of the deposit. In addition to these dates, initial habitation, based on the initial appearance of introduced pollen and invertebrates from swamp core samples, dates to between 750 and 850 yr B.P. (M. Prebble and N. Porch, Australian National University, Canberra, pers. comm.). Together, these data indicate that the Atiahara site represents an early phase of habitation on Tubuai dating to the thirteenth–fourteenth centuries A.D., making it contemporaneous with another Archaic-period site in the valley of Peva on the neighboring island of Rurutu (Bollt 2005*a,b*, 2007, 2008).

We report 109 identifiable bird bones representing 23 individuals from the Atiahara site (Table 4), which markedly expands the meager record reported by Steadman (2006). A total of 14 indigenous breeding species of birds, dominated by seabirds, is now known

TABLE 4
Total Avifauna Recorded from the Atiahara Site, Tubuai

Species	Steadman (2006), NISP	2007 NISP	2007 MNI
Phasianidae			
<i>Gallus gallus</i>	3	5 + ?1	2
Procellariidae			
<i>Pterodroma</i> sp. magn. <i>P. macroptera</i>		1	1
<i>Pterodroma</i> sp. magn. <i>P. neglectus</i>		2	1
<i>Pterodroma</i> sp. magn. <i>P. brevipes</i>		9	2
<i>Puffinus</i> sp. magn. <i>P. pacificus</i>		1	1
<i>Puffinus</i> sp. magn. <i>P. lherminieri</i>	1	19	3
<i>Pachyptila</i> sp.	1		
Phaethontidae			
<i>Phaethon lepturus</i>	3	2 + ?2	1
Columbidae			
<i>Gallicolumba</i> sp. indet.		1	1
<i>Ptilinopus</i> n. sp.	1		
Rallidae			
<i>Gallirallus steadmani</i> , n. sp.		61	10
Charadriiformes			
<i>Anous stolidus</i>	1		
<i>Gygis candida</i>	1		
Indeterminate sp. et gen. 1		1	1
Indeterminate sp. et gen. 2		1	1
Totals	11	109	23

Abbreviations: NISP, number of individual specimens; MNI, minimum number of individuals.

from the island. In the fossil assemblage, petrels (Procellariidae) are the most diverse group, and included are at least three species of *Pterodroma* and two species of *Puffinus*. The small *Puffinus* sp. magn. *P. lherminieri* and the small *Pterodroma* sp. magn. *P. brevipes* were relatively abundant in the assemblage, which indicates that these taxa almost certainly had breeding populations on the island. Similarly, the medium-sized petrel *Pterodroma* sp. magn. *P. neglectus* is represented by juvenile bones of an unfledged chick, also indicating breeding. Most of the other petrel taxa are widespread in the Pacific and may have either bred or been visitors to the island, with the exception of a bone of *Pachyptila*, a genus that breeds in southern oceans at latitudes higher than 45°, so that a breeding colony in the Austral Islands is most unlikely, contra Steadman (2006:401). Instead, the specimen more likely represents a vagrant attracted to the island by large populations of other petrels (Worthy 2007). Various species of *Pachyptila* regularly range into the tropical Pacific during their nonbreeding seasons (Gill et al. 2010), so rare bones from such vagrant individuals might be expected in samples from islands with former significant petrel populations.

The terns *Gygis* and *Anous* spp. and the tropicbird *Phaethon lepturus* are widely recorded in Oceania (Steadman 2006), so their presence as reported by Steadman (2006) is not unexpected. What is more surprising is the general lack of diversity of land birds, with only four species, of which *Gallus* is a human-transported taxon, in the deposit (Steadman 2006; data herein [Table 4]).

One of these, however, a small, endemic, flightless species of *Gallirallus*, dominates the fauna in terms of specimens recovered, with 61 bones of 10 individuals, and adds to the diversity of the genus, which has recently been shown to have been rich in endemic species across the Pacific (Steadman 1987, 2006, Steadman et al. 2000, Worthy 2004, Kirchman and Steadman 2005, 2006a,b, 2007).

Evolution of flightless distinct rails has at times been rapid (for example, *Porzana atra* on Henderson Island, which island has only been subaerial for about 380 kyr [Blake

1995], and other examples given by Slikas et al. [2002]). Many of the *Gallirallus*-group species were thought to have been derived from a volant ancestor like *Gallirallus philippensis*, for example (Steadman 2006). Recently, Kirchman (2009) demonstrated that for the more distinctive taxa, the extant *G. philippensis* is not their direct ancestor. However, a few fossil taxa, little different from *G. philippensis* but still flightless, make *G. philippensis* as currently construed appear to be paraphyletic. Reasons for such paraphyly among distinctive taxa can include recent or past hybridization events and incomplete lineage sorting, as reviewed by Joseph and Omland (2009), and were in part invoked by Kirchman (2009) to explain the data. *Gallirallus steadmani*, described herein, is another flightless taxon that is about as distinct from *G. philippensis* as the various Marianas species (Kirchman and Steadman 2006a, Kirchman 2009), so it may conceivably be closely related to the *G. philippensis* radiation, or more likely because of its geographic location it may be a sister species to *G. ripleyi* of Mangaia and *G. huiatua* of Niue and derived from an earlier spreading volant ancestor. It is likely that other islands in the Austral group will have endemic rails when faunas are forthcoming.

The remaining land birds, both very scarce, are small pigeons of the genera *Gallucolumba* and *Ptilinopus*, neither of which occurs on Tubuai today, although *Ptilinopus buttoni* occurs on Rapa (Steadman 2006). Several bones of a species of *Gallucolumba* have been reported from Peva on Rurutu (Steadman and Bolt 2010). It is likely, therefore, that before human arrival in the Austral group, species of *Ptilinopus* and *Gallucolumba* existed on each of the larger islands. That the fossil *Ptilinopus* recorded by Steadman (2006) from Tubuai differs from extant *P. buttoni* of Rapa suggests that perhaps at least each of the larger islands (Rimatara, Rurutu, Tubuai, Raivavae, and Rapa) had endemic taxa of these genera, with the only survivor being *P. buttoni* on Rapa.

The archaeological material is almost certainly an incomplete sample of the fauna before human occupation because bones of the

lorikeet *Vini* and reed warbler *Acrocephalus* were not found, although both genera are known elsewhere in the Australs and almost certainly had populations on Tubuai. Thus, further archaeological material will almost certainly increase the known diversity of the prehistoric avifauna of Tubuai.

In addition to the avifauna, three *Pteropus* bones were recovered from the Atiahara site, one of which could be identified as *Pteropus tonganus tonganus*. This supports the identification by Weisler et al. (2006) of an edentulous dentary from the adjacent island of Rurutu as *P. tonganus*. This is important because the edentulous mandible described by Weisler et al. could possibly have been another similar-sized species such as *P. samoensis*. The recent discovery of two further *Pteropus* species among historically collected material (Helgen et al. 2009), both now presumed extinct, shows that Samoa formerly had four sympatric species. The new species are considerably smaller (*P. coxi*) or considerably larger and more robust (*P. allenorum*) than the Tubuai specimens. The evidence to hand suggests that these far-eastern pteropids were *Pteropus tonganus tonganus*.

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