New Species of Extinct Rails (Aves: Rallidae) from Archaeological Sites in the Marquesas Islands, French Polynesia[1]

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Abstract: We examined 53 bones of rails (Rallidae), previously referred to *Gallirallus* n. spp., from archaeological sites on four islands in the Marquesas Islands, French Polynesia. We describe three new, extinct, flightless species of *Gallirallus: G. roletti* (Tahuata), *G. gracilitibia* (Ua Huka), and *G. epulare* (Nuku Hiva). Two bones from Hiva Oa, although probably representing another extinct species of *Gallirallus*, are regarded as an inadequate basis for describing a species. At first human contact, the genus *Gallirallus* probably included many scores if not hundreds of flightless species on islands from the far western Pacific (Okinawa, Philippines, Halmahera) eastward across most of Oceania. As currently understood, the Marquesas Islands represent the eastern range limit of *Gallirallus*.

Bird bones from Pacific islands (Figure 1) have revealed extensive Late Holocene extinctions of land birds following prehistoric human arrival (James and Olson 1991, Olson and James 1991, Steadman 1995, 2006, Worthy and Holdaway 2002). Radiocarbon chronologies of stratified zooarchaeological assemblages indicate that, in the earliest stages of occupation, people consumed a relatively large number of indigenous birds (Steadman and Rolett 1996, Steadman et al. 2002). In East Polynesia, from 50 to 100% of the species of land birds were extirpated from most islands. Especially prevalent among the extinct species are rails (Order Gruiformes, Family Rallidae), most of which were flightless species endemic to single islands. These ground-nesting birds were especially vulnerable to predation by people and their introduced rats, pigs, and dogs.

Nearly all of the known extinct (†) species of flightless rails have been placed in widespread, extant genera, including 7–10 species of *Porzana* from the Hawaiian Islands alone (Olson and James 1991); one to several species each of *Gallirallus*, *Gallinula*, *Porphyrio*, and *Fulica* from New Zealand (Worthy and Holdaway 2002); and many species of *Porzana*, *Gallirallus*, and *Porphyrio* from the rest of Oceania (Steadman 1995, 2006, Kirchman and Steadman 2005, 2006). Thus flightlessness, which became terminally maladaptive only after Polynesians and their commensals colonized the Pacific, evolved independently in insular rails numerous times, even within archipelagos. Of the crudely estimated hundreds (Pimm et al. 1994, Livezey 2003) to 500 to 1,600 (Steadman 2006) to nearly 2,000 (Steadman 1995) species of flightless rails that once existed across the Pacific, fewer than 20 have been described (Worthy 2004). Here we describe the prehistoric bones of rails from archaeological sites on four islands in the Marquesas Islands.

Marquesan Archaeological Sites

Centered at ca. 9° S and 140° W, the Marquesas Islands lie ca. 500 km northwest of the Tuamotu Archipelago and 1,400 km north-

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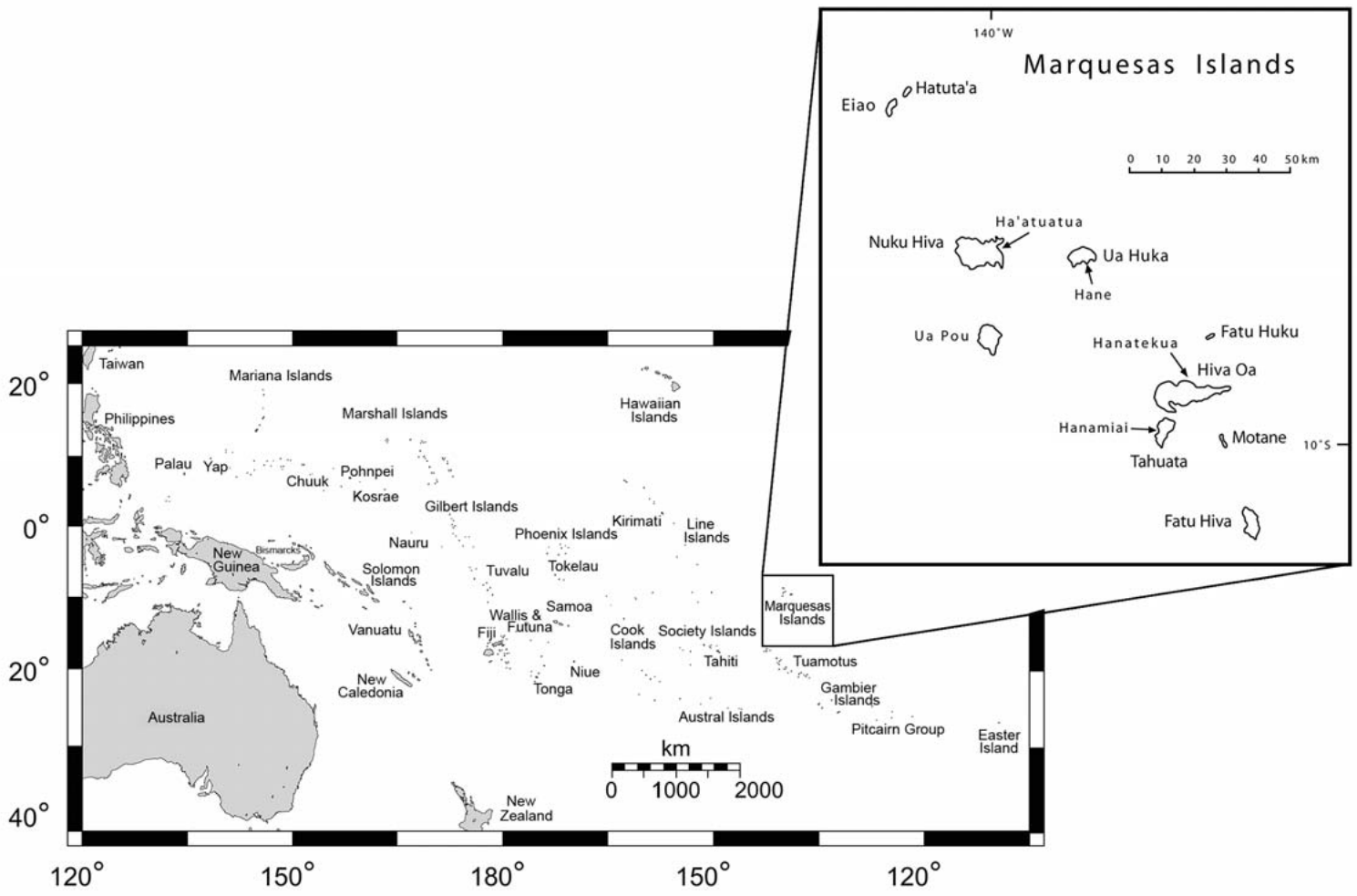

FIGURE 1. Oceania, showing location of the Marquesas Islands and location of the four archaeological sites discussed in this paper.

east of the Society Islands, which are the nearest high islands (Figure 1). The Marquesas consist of 10 major eroded volcanic islands with surface areas that range from <2 to 330 km^2 and maximum elevations from 420 to 1,252 m. Minimum interisland distances among these 10 islands range from 3 to 21 km. Hiva Oa and nearby Tahuata probably were connected to each other during the last Pleistocene glacial interval, whereas Nuku Hiva and Ua Huka remained as separate islands even when the sea level was 120–130 m lower than at present.

The archaeological specimens reported here are 53 bones that were previously referred to "*Gallirallus* new spp." or "*Gallirallus* undescribed spp." by Steadman and Rolett (1996) and Steadman (1989, 2006). The sites represent early human occupations developed in coastal calcareous sands on four islands. The Hanamiai site on Tahuata was excavated by B. V. Rolett in 1984–1985 (Rolett 1998). The sediment excavated at Hanamiai was screen-washed through 1/8-inch (3.2-mm) mesh, producing 716 identifiable bird bones, among which are 70 land bird bones from 10 species (Steadman and Rolett 1996). The Hanatekua Rockshelter on Hiva Oa was excavated in 1967–1968 by Y. H. Sinoto and P. Bellwood (Bellwood 1972), yielding 146 land bird bones from seven species (Steadman 2006). The Hane Dune site (often called merely the Hane site) on Ua Huka, excavated by Y. H. Sinoto in the 1960s (Sinoto 1966, 1970, 1979), is the richest Marquesan site in terms of faunal remains, having yielded more than 12,000 identifiable bird bones, including 2,187 land bird bones from 17 species (Steadman 2006). The Ha'atuatua Dune site (often called merely the Ha'atuatua site) on Nuku Hiva was excavated initially by R. Suggs in 1956 and 1958 (Suggs 1961) and in 1992–1994 by B. V. Rolett and E. Conte (Rolett 1998). The combined excavations at Ha'atuatua Dune yielded 27 bones of land birds belonging to nine species (Steadman 2006).

Based on radiocarbon (^{14}C) dates from reliable stratigraphic levels, the initial human occupation for Tahuata, Hiva Oa, and Nuku Hiva was ca. 1,000 yr B.P. (years before present) and ca. 1,350 yr B.P. for Ua Huka (Rolett 1998). Hane Dune (Ua Huka) is the earliest well-dated site in the Marquesas. Estimates that people arrived in the Marquesas as early as 2,000 yr B.P. (e.g., Sinoto 1979) are from single ^{14}C samples from poorly established stratigraphic contexts or are based on ^{14}C dates with suspected laboratory errors (Rolett 1998).

MATERIALS AND METHODS

Skeletons used for comparison with fossils are from the American Museum of Natural History (AMNH); Bernice P. Bishop Museum (BPBM); Florida Museum of Natural History, University of Florida (UF); National Museum of Natural History, Smithsonian Institution (USNM); National Museum of New Zealand (NMNZ); Département de Archéologie, Centre Polynésien des Sciences Humaines, Tahiti (DAPT); University of Michigan Museum of Zoology (UMMZ); Thomas Burke Memorial Museum, University of Washington (UWBM); and Yale Peabody Museum (YPM). We examined these modern specimens: *Porzana tabuensis*, UWBM 42501, 42528; *Rallus longirostris*, UF 40956, 24200; *Gallirallus striatus*, USNM 85892, 343214, 559919, YPM 107205; *G. torquatus*, UMMZ 228275, 228279, 228280, AMNH 17715–17717, USNM 290445; *G. owstoni*, UF 39918–39921, 39256, 42968, UMMZ 215472, USNM 561968, 611816, 612616, 613738–614744, 614233–614235, 614771, 614772; *G. australis*, UF 24326, 24327, YPM 102249, 110760, 110789, 110790, 110844; *G. philippensis*, UF 39854, 39855, 42902, 42935, 42934, 42933, 43224, UWBM 42865, 42866, 42863, USNM 560651, 560791, 620196; *G.* ["*Nesoclopeus*"] *woodfordi*, UF 39399, 39406, 39409, 39547, 39556, 39574; *Amaurornis olivaceus*, UF 40216; *A. phoenicurus*, UF 24387; *Porphyrio porphyrio*, UF 39388, 39407; *P. martinicus*, UF 39927, 42418, 42419; *Gallinula chloropus*, UF 39927. We also examined these fossil specimens: †*Gallirallus huiatua* tarsometatarsus, NMNZ S37708 (holotype), ulna, NMNZ S37709 (paratype), femur, NMNZ S37710 (paratype), tibiotarsus, NMNZ S37711 (paratype); †*G. ripleyi* rostrum, UF 55596, coracoid, UF 54711, USNM 402896 (paratype), humeri, UF 51402, 55752, ulnae, UF 55215, 54901, femur, UF

51320, tibiotarsi, UF 55283, 59574, USNM 402895 (holotype), tarsometatarsi, UF 55223, USNM 402895 (holotype); †*G. storrsolsoni* rostra, BPBM 166036 (holotype), DAPT 21, humerus, BPBM 166022, ulnae, BPBM 166033, femur, DAPT 27/105, tibiotarsi, BPBM 166023, DAPT 119, tarsometatarsi, BPBM 166034, DAPT 7; †*G. vekamatolu* rostrum, UF 52292, mandibles, UF 51836, 52525, coracoids, UF 52204, 52966, scapulae, UF 52179, 52318, humeri, UF 52333, 52707, ulna, UF 51734, femora, UF 52058, 52518, tibiotarsi, UF 51729, 52211, tarsometatarsi, UF 52002, 52137; †*Porphyrio paepae* femora, BPBM 165649, 166434, tibiotarsus, BPBM 165651; and †*P. mcnabi* femora, BPBM 166031 (holotype), DAPT 39, DAPT 53 (paratypes).

Measurements were taken with electronic digital calipers and rounded to the nearest 0.1 mm. Osteological terminology follows Baumel and Witmer (1993).

COMPARATIVE OSTEOLOGY AND SYSTEMATICS

Family Rallidae

The phylogeny of genera in the Rallidae is not well resolved. As a starting point for genus-level classification, we regard all "typical long-billed rails" (as opposed to swamphens, moorhens, coots, and crakes) from Oceania as species of *Gallirallus* sensu lato. We agree with Worthy (2004) that the recently discovered fossil rail †*Vitirallus watlingi* from Fiji belongs in a separate genus despite having a long (though decurved) bill and sharing other osteological similarities with *Gallirallus*. Our classification agrees with that of Olson (1973) by including in *Gallirallus* the species *australis*, *philippensis*, *owstoni*, *okinawae*, †*wakensis*, *torquatus*, *insignis*, *sylvestris*, †*dieffenbachii*, †*modestus*, *striatus*, and *pectoralis*. Among these species, only *G. philippensis*, *G. torquatus*, *G. striatus*, and *G. pectoralis* are volant. Olson (1973) provisionally retained *G. woodfordi* and †*G. poecilopterus* in *Nesoclopeus* but highlighted their close affinity with *Gallirallus*, within which we classify these two species. This treatment differs from that of Livezey (1998, 2003), who acknowledged the difficulty of establishing relationships in this group solely on the basis of osteology but who divided the 14 species mentioned here among *Gallirallus*, *Nesoclopeus*, *Tricholimnas*, *Cabalus*, and *Habropteryx*.

As defined herein, *Gallirallus* includes at least 17 named flightless species endemic to single islands or islands connected during periods of lowered sea level. This total includes eight extant species (*G. australis* of New Zealand; *G. sylvestris* of Lord Howe Island; *G. owstoni* of Guam; *G. okinawae* of Okinawa; *G. insignis* of New Britain; *G. woodfordi* s.l. of the Solomon Islands [minimally Bougainville, Santa Isabel, and Guadalcanal]; *G. rovianae* of New Georgia, Solomon Islands; and *G. calayanensis* of Calayan, Philippines), five historically extinct species (†*G. wakensis* of Wake Island; †*G. lafresnayanus* of New Caledonia; †G. *modestus* of the Chatham Islands, New Zealand; †G. *poecilopterus* of Viti Levu, Fiji; and †*G. pacificus* of Tahiti, Society Islands), and four previously named prehistoric species (†*G. huiatua* from noncultural Holocene cave deposits on Niue [Steadman et al. 2000]; †*G. ripleyi* from cultural and noncultural late Holocene sites on Mangaia, Cook Islands [Steadman 1987]; †*G. vekamatolu* from precultural strata on 'Eua, Kingdom of Tonga [Kirchman and Steadman 2005]; and †*G. storrsolsoni* from cultural deposits on Huahine, Society Islands [Kirchman and Steadman 2006]).

Genus *Gallirallus* Lafresnaye, 1841

We refer the 53 fossils from the Marquesas Islands to *Gallirallus* rather than to other genera of oceanic rails on the basis of the following characters. Rostrum: long, narrow, and shallow with elongate nares. Mandible: cotyla lateralis narrow and concave, fossa for condylus medialis quadratum (the main articulation surface in the os articulare) shallow and wide. Coracoid: acrocoracoid extends medially over the sulcus musculo supracoracoidei such that the foramen triosseum is less open cranially. Scapula: facies articularis clavicularis relatively small and oriented at a more obtuse angle from corpus scapulae. Humerus: fossa pneumotricipitalis deep and wide with prominent crus ventrale fossae. Ulna: thin in

cranial aspect with rectangular (rather than rounded) margo cranialis. Pelvis: ala preacetabularis ilii broadly continuous with crista dorsalis of synsacrum. Femur: distal end of corpus femoris becomes gradually wider; condylus medialis subcircular in medial aspect; impresso ansae musculo iliofibularis abuts suclus fibularis; rotolar groove broad. Tibiotarsus: craniolateral and craniomedial margins of corpus tibiotarsi rounded rather than sharp; impresso ligamentum collateralis medialis deep and wide; facies articularis femoris large; depressio epicondylaris lateralis deep; condylus medialis subcircular in medial aspect. Tarsometatarsus: corpus tarsometatarsi much wider than deep; medial sulcus hypotarsi not enclosed; fossa parahypotarsalis medialis shallow in proximal aspect; fossa metatarsi I short and shallow; crista plantaris mediana slopes gradually (not steeply) to hypotarsus; distal end of trochlea metatarsi tertii sloped toward medial trochlea; cotyla medialis is rectangular in proximal aspect with flat (not rounded) dorsal margin.

†*Gallirallus roletti* Kirchman & Steadman, n. sp.
Figures 2*A*, 3*A*, 4*A*, 5*A*, 6*A*

HOLOTYPE. Associated complete right femur, BPBM 166447; right tibiotarsus, BPBM 166446; right tarsometatarsus, BPBM 166448; and pedal phalages, BPBM 166449, 166450 (Figure 2*A*). From the Hanamiai archaeological site, Tahuata, Marquesas Islands. Collected by B. V. Rolett and colleagues in 1984–1985.

PARATYPES. Distal rostrum, BPBM 166456 (Figure 3*A*); left articular, BPBM 166458; right articular, BPBM 166542; distal dentaries, BPBM 166436, 166439, 166457; left coracoid (humeral end), BPBM 166455; left proximal femur, BPBM 166435; right femur shaft, BPBM 166445; left distal tibiotarsus, BPBM 166444; left tibiotarsi shafts, BPBM 166437, 166452; right distal tibiotarsus, BPBM 166438; left distal tarsometatarsus, BPBM 166451; nearly complete right tarsometatarsus, BPBM 166440; right proximal tarsometatarsus, BPBM 166454; right tarsometatarus shaft, BPBM 166441. All are from the same locality as the holotype.

DIAGNOSIS. A medium-sized, flightless species of *Gallirallus* (Table 1) distinguished from all examined congeners (except where similarities are noted) as follows. Rostrum (Figure 3*A*): more robust and deep with height to width ratio (at anterior margin of nares) of 1.24 (≤1.03 in all other species of *Gallirallus*); in ventral aspect, trough in os premaxilare deep and wide, crista tomialis thin and sharp. Mandible: in caudal aspect, fossa caudalis with straight lateral and medioventral sides and a deep, narrow groove on top (ventral) side; pars symphysialis long, with rami sloped steeply to form a V-shaped (rather than U-shaped) trough in cranial aspect. Femur (Figures 2*A*, 4*A*): mediodistal margin of neck deeply excavated below facies articularis acetabularis, forming a sulcus in anterior aspect; in ventral aspect, trochanter femoris forms a prominent right angle with facies articularis antitrochanterica; the most proximal impressiones obturatoriae deep and long, forming a groove parallel to the crista trochanteris; in medial aspect, corpus femorus stout and straight, especially on leading edge (facies cranialis). Tibiotarsus (Figures 2*A*, 5*A*): fossa retropatellaris narrow but deep; impresso ligamentum collateralis medialis shallow; fossa flexoria shallow; crista fibularis short but broad, projecting farther from corpus tibiotarsis at distal end than in all except *G. owstoni;* tuberculum retinaculi musculo fibularis prominent (as in †*G. storrsolsoni* and *G. torquatus*) but not forming a tube (as in *G. woodfordi*); condylus medialis and condylus lateralis large relative to width and depth of corpus tibiotarsus. Tarsometatarsus (Figures 2*A*, 6*A*): proportionately stout, although not so much as in †*G. vekamatolu* or †*G. ripleyi;* sulcus extensorius deeply concave; corpus tarsometatarsi shallow relative to its breadth; facies medialis thin in medial aspect, especially proximally (approaching the condition in *Amaurornis olivaceus* or *Porphyrio* spp.); sulcus proximal to the foramen vasculare distale short and shallow; distal trochleae large and widely splayed.

ETYMOLOGY. Named in honor of Barry V. Rolett, whose outstanding research in the Marquesas Islands has been of great importance to both biologists and archaeologists.

FIGURE 2. *A*, †*Gallirallus roletti* holotype consisting of associated femur (BPBM 166447), tibiotarsus (BPBM 166446), tarsometatarsus (BPBM 166448), and two pedal phalanges (BPBM 166449, 166450), *top to bottom*, respectively, Tahuata, Marquesas Islands. Shown with the same elements from *B*, *G. philippensis* (UF 39855, Tutuila, Samoa), and *C*, *G. owstoni* (UF 39921, Guam, Mariana Islands). Scale bar = 5 cm.

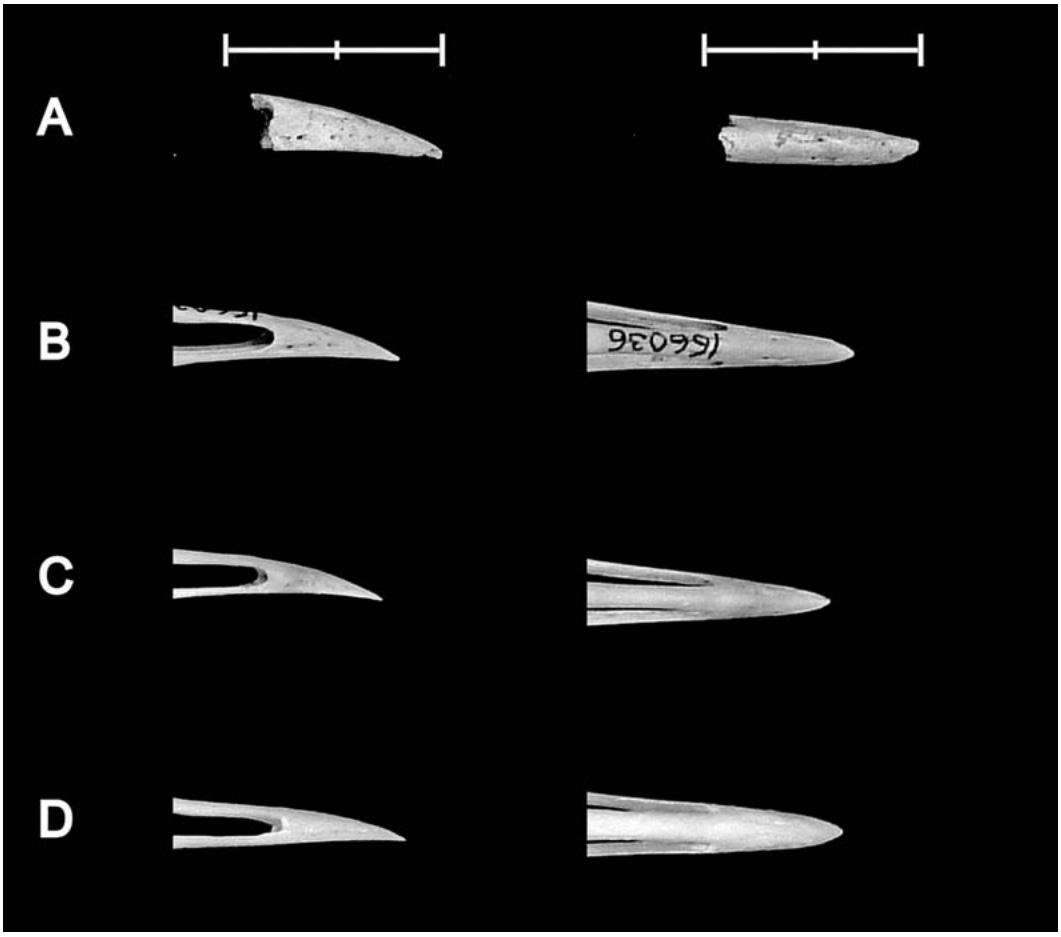

FIGURE 3. Rostra of *A*, †*Gallirallus roletti* (BPBM 166456, Tahuata, Marquesas Islands); *B*, †*G. storrsolsoni* (holotype, BPBM 166036, Huahine, Society Islands); *C*, *G. philippensis* (UF 39855, Tutuila, Samoa); and *D*, *G. owstoni* (UF 39921, Guam, Mariana Islands) in lateral (*left*) and dorsal (*right*) aspects. Scale bars = 2 cm.

In particular, his careful excavations at the Hanamiai site yielded the most extensive and useful series of *Gallirallus* bones from the Marquesas Islands.

REMARKS. In overall size, †*Gallirallus roletti* resembles *G. owstoni*, *G. philippensis*, *G. striatus*, and *G. torquatus*. It is larger than †*G. ripleyi* and †*G. wakensis*, and smaller than *G. australis*, †*G. vekamatolu*, and *G. woodfordi*. The material from Hanamiai represents four individuals, minimally. Lacking the sternum, scapula, and elements of the forelimb, our only evidence that †*G. roletti* was flightless comes from the relatively small size of the coracoid (BPBM 166455) and the larger, more open shape and more medial position of the cotyla scapularis on the dorsal surface of the coracoid, which more closely resembles the condition in flightless rather than volant species of *Gallirallus*. This specimen is pitted over much of its surface, indicating that it may represent a juvenile bird. Comparing this coracoid among those of known juveniles and adults in *G. philippensis* (volant) and *G. owstoni* (flightless) suggests that BPBM 166455 is from a bird 3 to 4 months old and that the cora-

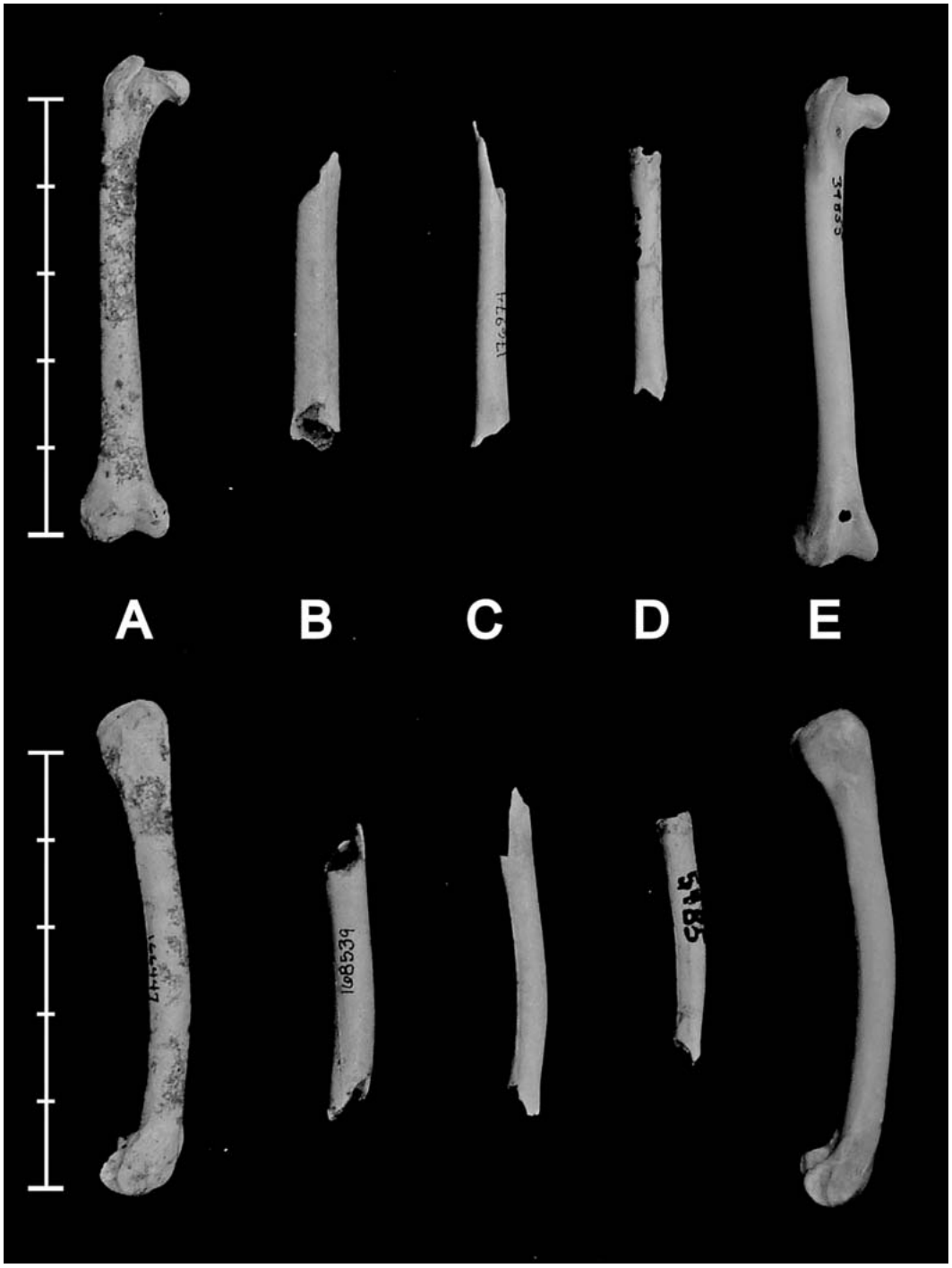

FIGURE 4. Femora of *A*, †*Gallirallus roletti* (holotype, BPBM 166447, Tahuata, Marquesas Islands); *B*, cf. †*Gallirallus* sp. (BPBM 168539, Hiva Oa, Marquesas Islands); *C*, †*G. gracilitibia* (BPBM 176974, Ua Huka, Marquesas Islands); *D*, †G. *epulare* (BPBM 181659, Nuku Hiva, Marquesas Islands); and *E*, *G. philippensis* (UF 39855, Tutuila, Samoa) in dorsal (*top*) and ventral (*bottom*) aspects. Scale bars = 5 cm.

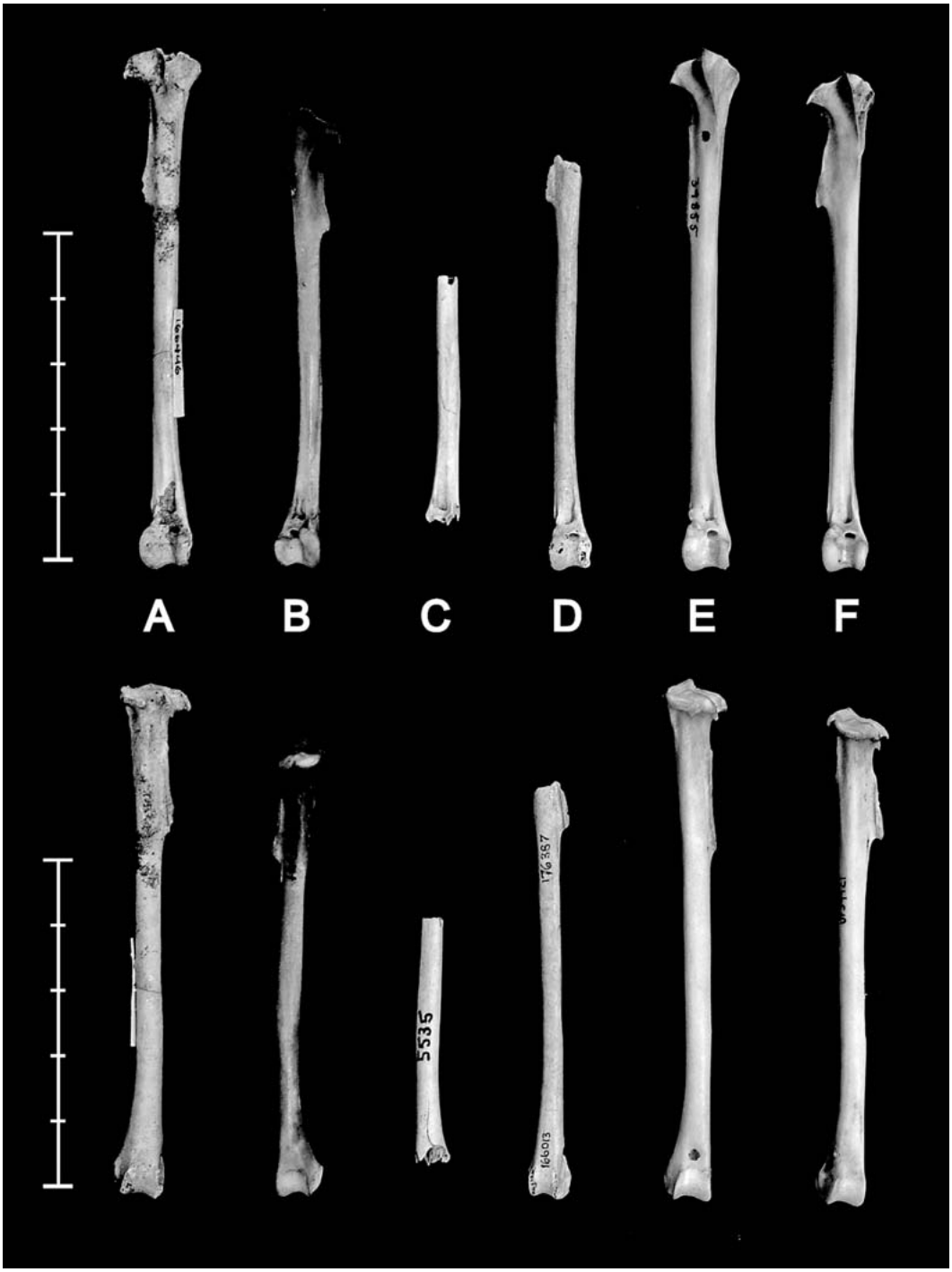

FIGURE 5. Tibiotarsi of *A*, †*Gallirallus roletti* (holotype, BPBM 166446, Tahuata, Marquesas Islands); *B*, †*G. storrsolsoni* (BPBM 166023, Huahine, Society Islands); *C*, †*G. epulare* (BPBM 181661, Nuku Hiva, Marquesas Islands); *D*, †*G. gracilitibia* (holotype, BPBM 166013/176387, Ua Huka, Marquesas Islands); *E*, *G. philippensis* (UF 39855, Tutuila, Samoa); and *F*, *G. owstoni* (UF 39921, Guam, Mariana Islands) in dorsal (*top*) and ventral (*bottom*) aspects. Scale bars = 5 cm.

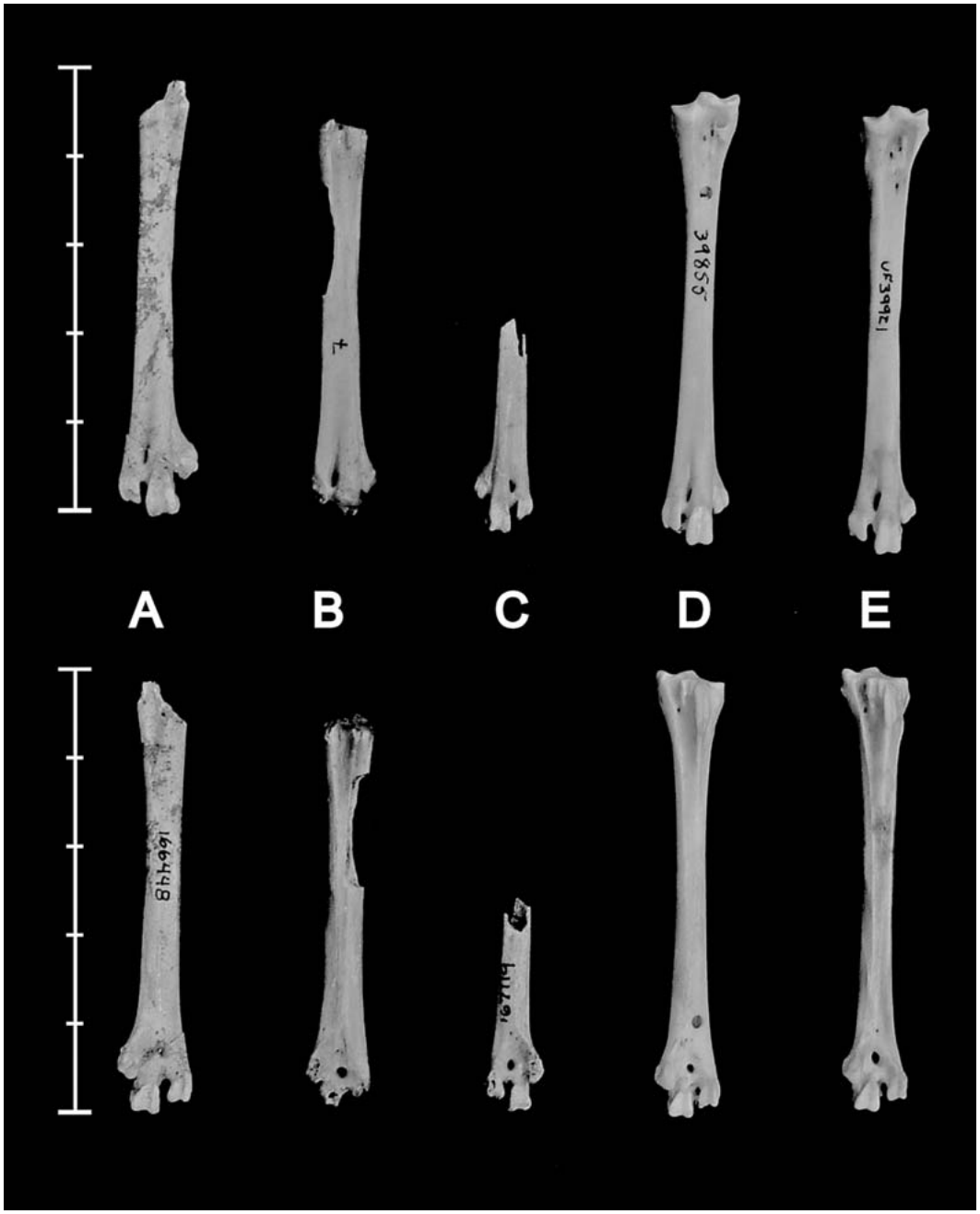

FIGURE 6. Tarsometatarsi of *A*, †*Gallirallus roletti* (holotype, BPBM 166448, Tahuata, Marquesas Islands); *B*, †*G. storrsolsoni* (DAPT 7, Huahine, Society Islands); *C*, †*G. epulare* (BPBM 167119, Nuku Hiva, Marquesas Islands); *D*, *G. philippensis* (UF 39855, Tutuila, Samoa); and *E*, *G. owstoni* (UF 39921, Guam, Mariana Islands) in acrotarsial (*top*) and plantar (*bottom*) aspects. Scale bars = 5 cm.

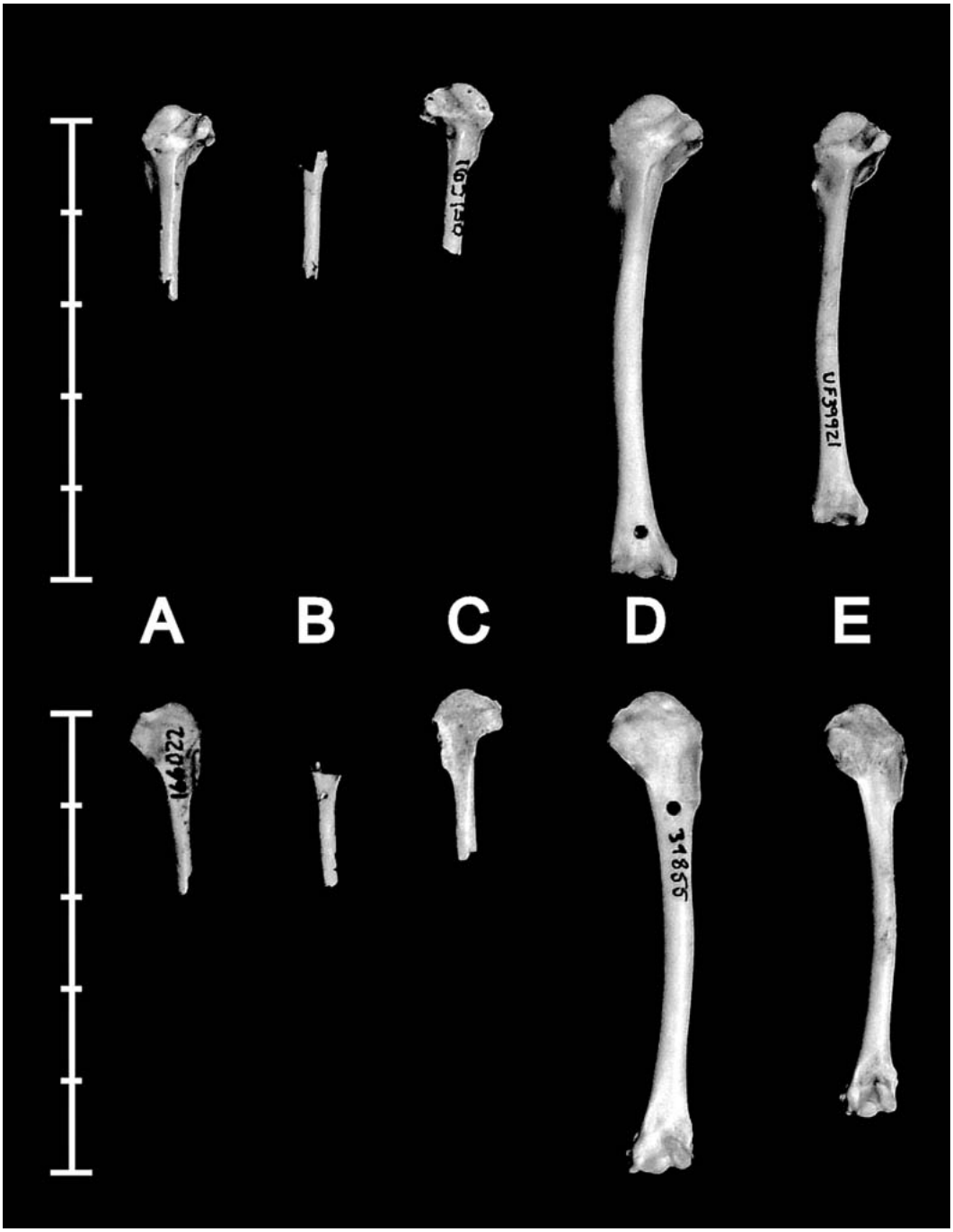

FIGURE 7. Humeri of *A*, †*Gallirallus storrsolsoni* (BPBM 166022, Huahine, Society Islands); *B*, †*G. epulare* (BPBM 181657, Nuku Hiva, Marquesas Islands); *C*, †*G. gracilitibia* (BPBM 163130, Ua Huka, Marquesas Islands); *D*, *G. philippensis* (UF 39855, Tutuila, Samoa); and *E*, *G. owstoni* (UF 39921, Guam, Mariana Islands) in ventral (*top*) and dorsal (*bottom*) aspects. Scale bars = 5 cm.

TABLE 1

Skeletal Measurements (in mm) in †*Gallirallus roletti* and Select Congeners, with Mean, Range, and Sample Size

Parameter	†*G. roletti* U	†*G. storrsolsoni* U	*G. owstoni* M	*G. owstoni* F	*G. australis* M	*G. australis* F	†*G. ripleyi* U	†*G. vekamatolu* U
Rostrum: height at anterior margin of nares	5.2 1	3.7 3.5–3.9 2	3.4 3.2–3.8 5	3.3 3.1–3.5 4	5.3 5.1–5.4 3	4.7 4.4–5.0 4	2.9 1	4.8 1
Rostrum: width at anterior margin of nares	4.2 1	4.1 4.0–4.2 2	4.4 4.0–4.7 5	4.2 3.8–4.5 4	5.5 5.1–5.7 3	5.0 4.5–5.5 4	2.8 1	5.9 1
Femur: length	54.5 1	49.4 1	56.0 54.0–59.2 7	52.4 49.2–54.6 11	80.6 78.7–82.3 3	69.9 66.1–73.4 4	39.8 1	—
Femur: distal width	9.8 1	9.2 1	9.5 8.9–9.9 7	8.7 8.4–9.0 11	16.5 15.9–17.6 3	14.3 13.2–15.0 4	6.7 1	10.9 10.7–11.0 2
Femur: minimum shaft width	4.0 4.0 2	3.9 1	3.8 3.3–4.0 7	3.6 3.4–3.9 11	6.7 6.5–6.9 3	5.6 5.1–5.9 4	3.0 1	—
Tibiotarsus: length	79.5 1	68.6 1	79.9 76.1–84.6 7	75.5 72.9–79.8 11	117.4 116.6–118.7 3	100.0 93.4–105.0 4	—	—
Tibiotarsus: distal width	7.8 7.7–7.9 2	6.9 1	7.4 6.8–7.9 7	6.8 6.5–7.1 11	12.5 12.1–13.1 3	10.8 10.4–11.2 4	6.0 5.6–6.3 3	8.0 7.9–8.0 2
Tarsometatarsus: proximal width	7.9 1	7.4 1	7.6 7.0–8.2 7	7.0 6.7–7.3 11	12.6 12.2–13.4 3	11.0 10.7–11.7 4	5.7 1	8.3 7.8–8.7 2
Tarsometatarsus: distal width	8.7 1	—	8.0 7.2–8.5 7	7.4 7.2–7.8 11	14.0 13.6–14.3 3	12.1 11.2–13.0 4	6.4 6.3–6.5 3	8.5 8.0–9.0 2
Tarsometatarsus: shaft width	3.5–3.9 3.7 2	4.1 1	3.8 3.5–4.0 7	3.4 3.2–3.8 11	6.1 5.6–6.4 3	5.4 5.2–5.6 4	3.0 2.8–3.1 2	4.3 4.0–4.6 2
Tarsometatarsus: shaft depth	2.7 2.5–2.8 2	2.8 1	2.8 2.5–3.0 7	2.5 2.4–2.8 11	4.8 4.5–5.0 3	4.1 3.8–4.6 4	2.2 2.1–2.3 2	3.2 3.0–3.3 2

Note: Specimens of all available subspecies of *G. australis* and *G. philippensis* are combined, given that subspecific differences in size are much smaller than those between males and females. F, female; M, male; U, sex unknown; —, cannot be evaluated.

coid's small size (relative to leg elements) is due to flightlessness rather than to the age of the bird.

Steadman and Rolett (1996) referred 24 specimens to "*Gallirallus* new sp. (Tahuata Rail)," which is named herein as *G. roletti*, based on 22 specimens. The discrepancy is accounted for by an ungual phalanx of †*Porphyrio paepae* (BPBM 166442) being mistakenly listed among the specimens of "*Gallirallus* new sp." in Steadman and Rolett (1996) and by another pedal phalanx (BPBM 166453) whose identity cannot now be determined.

†*Gallirallus gracilitibia* Kirchman & Steadman, n. sp.
Figures 4*C*, 5*D*, 7*C*

HOLOTYPE. Right tibiotarsus lacking proximal end, BPBM 166013, 176387 (Figure 5*D;* two pieces with different catalog numbers

TABLE 1
(continued)

G. philippensis M	*G. philippensis* F	*G. striatus* M	*G. torquatus* M	*G. torquatus* F	*G. woodfordi* M	*G. woodfordi* F
3.1	2.8	2.8	3.2	—	4.3	4.2
2.8–3.4	2.6–2.9	1	3.1–3.3		4.2–4.6	3.9–4.4
5	5		2		3	3
3.7	3.2	3.1	3.4	—	4.7	4.6
3.4–4.2	3.1–3.4	1	3.4–3.4		4.6–4.9	4.5–4.8
5	5		2		3	3
53.8	47.3	45.1	55.5	50.6	72.1	69.6
51.3–54.9	45.0–49.7	42.2–46.9	53.3–57.5	1	72.0–72.3	69.0–70.3
6	6	4	5		3	3
8.7	7.4	45.1	9.3	8.5	13.3	12.7
8.4–9.1	7.0–7.9	42.2–46.9	8.6–9.9	1	13.2–13.4	12.5–12.9
6	6	4	5		3	3
4.0	3.3	2.9	3.9	3.2	5.3	4.8
3.7–4.2	3.1–3.5	2.8–3.1	3.5–4.1	1	5.2–5.3	4.6–5.1
6	6	4	5		3	3
76.9	66.7	62.1	84.2	74.6	105.0	102.8
71.7–80.3	63.0–70.6	58.2–64.3	80.9–87.5	1	100.6–108.8	99.0–105.8
6	6	4	5		3	3
6.9	6.1	5.3	7.2	6.6	10.0	9.5
6.5–7.2	5.6–6.7	5.1–5.6	6.7–7.6	1	9.9–10.1	9.4–9.6
6	6	4	5		3	3
7.0	6.1	5.4	7.4	6.6	10.5	10.0
6.7–7.2	5.8–6.6	5.3–5.5	7.0–7.9	1	10.2–10.7	9.9–10.1
6	6	4	5		3	3
7.1	6.3	5.6	7.8	7.0	10.8	10.6
6.7–7.5	6.0–6.9	5.4–5.7	7.3–8.4	1	10.7–11.0	10.5–10.6
6	6	4	5		3	3
3.5	3.0	2.7	3.6	3.3	4.9	4.6
3.1–3.6	2.8–3.3	2.5–2.9	3.3–3.8	1	4.8–5.0	4.4–4.7
6	6	4	5		3	3
2.8	2.5	2.1	2.7	2.6	4.0	3.8
2.6–3.0	2.3–2.8	2.0–2.2	2.2–2.9	1	3.9–4.2	3.7–4.0
6	6	4	5		3	3

glued together). From the Hane Dune archaeological site, Ua Huka, Marquesas Islands. Collected by Y. H. Sinoto and colleagues on 11 October 1965.

PARATYPES. Right coracoid (humeral end), BPBM 166015; left proximal humerus, BPBM 163130 (Figure 7*C*); right humerus shaft, BPBM 166014; right femur shaft, BPBM 176974 (Figure 4*C*); left distal tibiotarsi, BPBM 163240, 166016, 169146, 170909; left tibiotarsus shaft, BPBM 175384; right distal tibiotarsi, BPBM 166008, 166012, 169145, 175145; right tibiotarsi shafts, BPBM 171294, 175322, 175395, 176725, 176746, 176971, 176972. All are from the same locality as the holotype. A minimum of eight individuals is represented.

DIAGNOSIS. A small to medium-sized (Table 2), flightless species of *Gallirallus* that differs from congeneric species as follows. Coracoid: sulcus musculo supracoracoidei relatively shallower and wider than in volant

TABLE 2

Skeletal Measurements (in mm) of †*Gallirallus gracilitibia* and Selected Congeners with Mean, Range, and Sample Size

Parameter	†*G. gracilitibia* U	†*G. storrsolsoni* U	*G. philippensis* M	*G. philippensis* F	*G. owstoni* M	*G. owstoni* F	*G. torquatus* M	*G. torquatus* F
Humerus: shaft width	2.2 2.1–2.3 2	2.2 1	3.3 3.2–3.4 5	2.9 2.7–3.3 6	2.8 2.6–3.1 7	2.7 2.6–3.0 11	3.2 3.0–3.4 5	2.9 1
Tibiotarsus: shaft width	3.0 2.9–3.3 8	3.4 3.2–3.7 3	3.6 3.3–4.0 6	3.1 2.9–3.3 6	4.1 3.8–4.5 7	3.8 3.4–4.1 11	3.8 3.4–4.0 5	3.3 1
Tibiotarsus: length to fibular crest[a]	54.5 1	50.2 50.2–50.2 2	52.8 51.9–55.3 5	47.1 43.3–51.6 6	57.8 55.2–61.2 7	54.4 52.9–55.9 11	 59.3–61.5 2	59.0 1
Tibiotarsus: distal width	6.4 6.3–6.5 4	6.9 1	6.9 6.5–7.2 6	6.1 5.6–6.7 6	7.4 6.8–7.9 7	6.8 6.5–7.1 11	7.2 6.7–7.6 5	6.6 1

Note: F, female; M, male; U, sex unknown.
[a] Distal end of bone to distal edge of fibular crest.

species. Humerus (Figure 7*C*): crista bicipitalis small; corpus humeri thin and curved; distal junction of crista pectoralis and corpus humeri abrupt, rather than gradually sloping; sulcus ligamentum transversus deep. Femur (Figure 4*C*): corpus femoris gracile. Tibiotarsus (Figure 5*D*): corpus tibiotarsus slender relative to its length; depressio epicondylaris medialis deep.

ETYMOLOGY. From the Latin words *gracilis* (slender, slim, thin) and *tibia* (the shinbone, tibia); see Brown (1956:469, 791). The name *gracilitibia* is a feminine noun in apposition to *Gallirallus*. It refers to the distinctively slender tibiotarsus in this species, especially compared with that of †*G. roletti*.

REMARKS. †*Gallirallus gracilitibia* is a small to medium-sized species (Table 2), exceeded in stoutness of skeletal elements by all congeners but resembling the medium-sized *G. owstoni*, *G. philippensis*, and *G. torquatus* in measurements along the long axes of leg elements. Based on length-to-width ratios of tibiotarsi, †*G. gracilitibia* has the thinnest shaft relative to length of any species of *Gallirallus*, whether flightless or volant (Table 2). Described features of the coracoid and humerus of †*G. gracilitibia*, as well as their size relative to hind limb elements (see Livezey 2003, Kirchman and Steadman 2005, 2006), indicate that this species was flightless.

†*Gallirallus epulare* Kirchman & Steadman, n. sp.
Figures 4*D*, 5*C*, 6*C*, 7*B*, 8*B*

HOLOTYPE. Nearly complete left ulna, BPBM 181658 (Figure 8*B*). From the Ha'atuatua archaeological site, Nuku Hiva, Marquesas Islands. Collected by B. V. Rolett, E. Conte, and colleagues in 1994–1995.

PARATYPES. Left humerus shaft, BPBM 181657 (Figure 7*B*); left femur shaft, BPBM 181659 (Figure 4*D*); left tibiotarsi shafts, BPBM 181660, 181661 (Figure 5*C*), 181662; right tibiotarsus shaft, BPBM 167191; left distal tarsometatarsus, BPBM 167119 (Figure 6*C*). All are from the same locality as the holotype.

DIAGNOSIS. A small species of *Gallirallus* distinguished from congeneric species as follows. Humerus and ulna very small and slender relative to leg elements, especially compared with those of †*G. gracilitibia* from nearby Ua Huka. Ulna: straighter than in volant species. Tarsometatarsus: facies dorsalis of corpus tarsometatarsi highly convex proximal to trochlea metatarsi III; foramen vasculare distale relatively large and round.

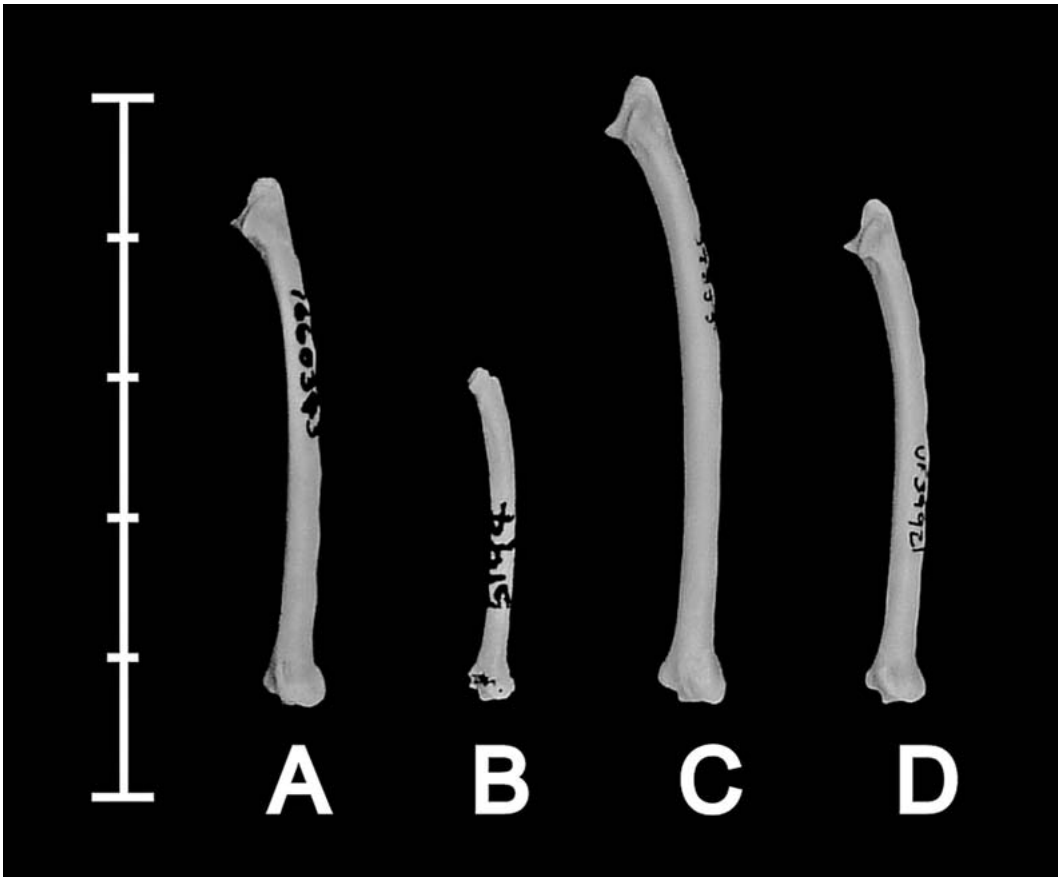

FIGURE 8. Ulnae of *A*, †*Gallirallus storrsolsoni* (BPBM 166033, Huahine, Society Islands); *B*, †*G. epulare* (holotype, BPBM 181658, Nuku Hiva, Marquesas Islands); *C*, *G. philippensis* (UF 39855, Tutuila, Samoa); and *D*, *G. owstoni* (UF 39921, Guam, Mariana Islands) in dorsal aspect. Scale bar = 5 cm.

ETYMOLOGY. From the Latin *epularis* (pertaining to a banquet, belonging to a banquet [Brown 1956:292]). The name *epulare* is an adjective that modifies the masculine *Gallirallus*. It refers to the archaeological context in which the specimens of †*G. epulare* were found, namely that of a kitchen midden dominated by the bony and shelly remains of foods eaten by prehistoric Polynesians.

REMARKS. The humerus, femur, and tibiotarsi lack both the proximal and distal ends and therefore also lack diagnostic features. The most striking feature of †*Gallirallus epulare* is its tiny wing elements relative to its leg elements; the leg elements closely resemble those from a small female *G. owstoni*, but the humerus and ulna are much smaller than those of *G. owstoni* and indeed more closely resemble those of †*G. ripleyi* and †*G. wakensis*.

cf. †*Gallirallus* sp.
Figures 4*B*, 9*A*

MATERIAL. Complete left scapula, BPBM 165655 (Figure 9*A*); shaft of right femur, BPBM 168539 (Figure 4*B*). From the Hanatekua Rockshelter archaeological site, Hiva Oa, Marquesas Islands. Collected by Y. H. Sinoto and colleagues in 1965–1966.

REMARKS. These two bones represent a large, probably flightless species of *Gallirallus*.

TABLE 3

Skeletal Measurements (in mm) of †*Gallirallus epulare* and Selected Congeners with Mean, Range, and Sample Size

Parameter	†*G. epulare* U	†*G. storrsolsoni* U	*G. philippensis* M	*G. philippensis* F	*G. owstoni* M	*G. owstoni* F	*G. torquatus* M	*G. torquatus* F
Ulna: length	25.5*	37.5	43.9	39.2	39.1	36.6	44.0	40.0
	1	1	41.4–44.8	35.2–43.6	36.8–41.5	34.8–38.7	43.0–45.3	1
			6	6	7	11	5	
Ulna: shaft width	2.0	2.7	3.0	2.7	3.0	2.7	3.0	2.8
	1	1	2.8–3.1	2.6–2.8	2.8–3.2	2.6–3.0	2.8–3.1	1
			6	6	7	11	5	
Tibiotarsus: shaft	3.4	3.4	3.6	3.1	4.1	3.8	3.8	3.3
width	1	3.2–3.7	3.3–4.0	2.9–3.3	3.8–4.5	3.4–4.1	3.4–4.0	1
		3	6	6	7	11	5	
Tarsometatarsus:	3.5	4.1	3.5	3.0	3.8	3.4	3.6	3.3
shaft width	1	1	3.1–3.6	2.8–3.3	3.5–4.0	3.2–3.8	3.3–3.8	1
			6	6	7	11	5	
Tarsometatarsus:	2.4	2.8	2.8	2.5	2.8	2.5	2.7	2.6
shaft depth	1	1	2.6–3.0	2.3–2.8	2.5–3.0	2.4–2.8	2.2–2.9	1
			6	6	7	11	5	
Tarsometatarsus:	6.5	—	7.1	6.3	8.0	7.4	7.8	7.0
distal width	1		6.7–7.5	6.0–6.9	7.2–8.5	7.2–7.6	7.3–8.4	1
			6	6	7	11	5	

Note: F, female; M, male; U, sex unknown; —, cannot be evaluated.
* Estimated.

We regard these bones as an inadequate basis for describing a new species but note that the scapula differs from that in all congeneric species in having a relatively thick area between the facies articularis humeralis and facies articularis clavicularis, in proximal aspect, and in having a distinctive flange on ventral surface of corpus scapulae near extremitas caudalis. The femur lacks both the proximal and distal ends but is remarkable in having a relatively wide divergence of the two linea intermuscularis caudalis.

The scapulae of the three named Marquesan species of *Gallirallus* and of †*Porphyrio paepae* (formerly of Tahuata and Hiva Oa) are unknown, thus precluding direct comparison with BPBM 165655. The femoral shaft from Hiva Oa (BPBM 168539 [Figure 4*B*]) is too large to belong to †*P. paepae* and also is larger than that of †*G. roletti*, suggesting that the *Gallirallus* species from Hiva Oa was quite large and that *Gallirallus* from the southern islands were larger than those of the two northern islands.

DISCUSSION

The rail bones from archaeological sites on three Marquesan islands (Tahuata, Nuku Hiva, and Ua Huka) represent three new flightless species of *Gallirallus*, one endemic to each island. A probable fourth species, from Hiva Oa, requires more material before a description is possible. No species of *Gallirallus* exist anywhere today in East Polynesia, where all known species are flightless and extinct. They are †*G. ripleyi* from Mangaia, Cook Islands; †*G. storrsolsoni* from Huahine, Society Islands (both known only from bones from archaeological sites [Steadman 1987, Kirchman and Steadman 2006]); and †*G. pacificus* from Tahiti, Society Islands, which survived to the eighteenth century (Ripley 1977, Taylor 1998).

The species from the Marquesas Islands represent the northwestern limit of *Gallirallus*. The very rich prehistoric record of birds (15,000+ bones from 12 archaeological sites) from Henderson Island (Pitcairn Group) has

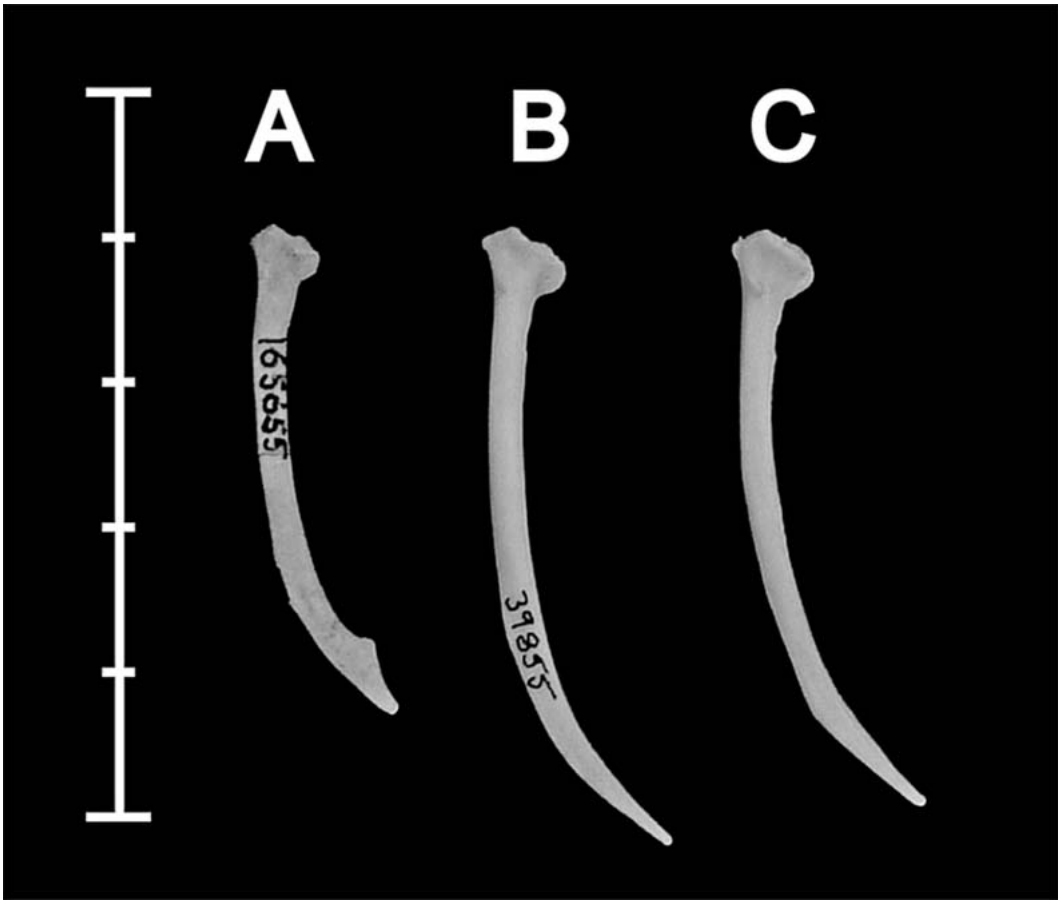

FIGURE 9. Scapulae of *A*, cf. †*Gallirallus* sp. (BPBM 165655, Hiva Oa, Marquesas Islands); *B*, *G. philippensis* (UF 39855, Tutuila, Samoa); and *C*, *G. owstoni* (UF 39921, Guam, Mariana Islands) in dorsal aspect. Scale bar = 5 cm.

not yielded evidence of *Gallirallus* (Steadman and Olson 1985, Wragg 1995). Between the Cook Islands (where †*G. ripleyi* lived) and Henderson Island lie the Austral (Tubuai) Islands, where the single prehistoric land bird bone known represents an undescribed, extinct species of *Ptilinopus* (Columbidae) (Steadman 2006). Likewise, the well-studied fossils from dunes, lava tubes, and lakes in the Hawaiian Islands, which have yielded 7–10 flightless species of *Porzana* rails, lack evidence of *Gallirallus* (Olson and James 1991).

Aside from the species of *Gallirallus*, extinct species of Marquesan land birds known only from prehistoric bones are the swamphen †*Porphyrio paepae*, an undescribed species of sandpiper (*Prosobonia*), two doves (†*Gallicolumba nui* and †*Macropygia heana*), and two species of parrots (†*Vini vidivici* and †*V. sinotoi*) (Steadman and Zarriello 1987, Steadman 1988, 1992, 2006). The extinction of flightless rails in the Marquesas probably took place in prehistoric times. On Tahuata, all but 1 of the 22 specimens of †*Gallirallus roletti* were excavated from Levels G, GH, or H (Phases I and II) at Hanamiai, which represent the early occupation of the site at ca. 1,000–700 yr B.P. (Rolett 1998). A single bone of †*G. roletti* is from Phase III (Level

F), which dates to 700–550 yr B.P. This may be the approximate time of extinction for †*G. roletti*, bones of which were not recovered in the younger Levels A–D (Phases IV, V). Similarly on Ua Huka, all of the bones of †*G. gracilitibia* were from strata dated to >800 yr B.P. (Steadman 1991).

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