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NEW SPECIES AND RECORDS OF BIRDS FROM PREHISTORIC SITES ON NIUE, SOUTHWEST PACIFIC

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ABSTRACT.—We report the first prehistoric bird bones from the isolated limestone island of Niue, South Pacific. Discovered in a cave known as Anakuli, the bones are Holocene in age but lack cultural association. They represent three extinct species: a night-heron (*Nycticorax kalavikai*), a new species known thus far only from Niue but closely related to an extinct undescribed species from Tonga; the “Niuafu’ou” Megapode (*Megapodius pritchardii*), known historically only from Niuafu’ou (Tonga) but recorded from prehistoric sites elsewhere in Tonga; and *Gallirallus huiatua*, a new species of flightless rail presumably endemic to Niue and distinct from extinct, flightless congeneric species from island groups immediately east (Cook Islands) and west (Tonga) of Niue. The first two species are in accord with the overall biogeographic affinity of the extant avifauna of Niue, which is West Polynesian rather than East Polynesian. Received 15 Sept. 1999, accepted 15 Feb. 2000.

The limestone island of Niue is isolated between the Cook Islands (800 km to the east), Samoa (560 km to the north-northwest), and Tonga (480 km to the west; Fig. 1). A large island by Polynesian standards (259 km²), Niue attains a maximum elevation of 68 m in the perimeter ring of coralline limestone that surrounds a gently depressed (min elev. 34 m) central basin (Dept. Lands Survey New Zealand 1977). The geology of Niue, an uplifted Pliocene atoll, has been well described by Aharon and coworkers (1987), Wheeler and Aharon (1991), and Paulay and Spencer (1992).

The affinities of the indigenous terrestrial

flora and fauna of Niue are West Polynesian (especially Tongan) rather than East Polynesian (Sykes 1970, Wodzicki 1971, Steadman 1997). The modern Niuean landbird fauna comprises 10 species (Townsend and Wetmore 1919, Wodzicki 1971, Kinsky and Yaldwyn 1981, Hay and Powlesland 1998, Powlesland and Hay 1998): three rails (*Porzana tabuensis samoensis*, *Gallirallus philippensis goodsoni*, *Porphyrio porphyrio* cf. *samoensis*), two columbids (*Ducula pacifica pacifica*, *Ptilinopus porphyraceus whitmeei**), a lorikeet (*Vini australis*), a barn-owl (*Tyto alba lulu*), a swiftlet (*Collocalia spodiopygia spodiopygia*), a triller (*Lalage maculosa whitmeei**), and a starling (*Aplonis tabuensis brunnescens**). The three subspecies endemic to Niue are marked with an asterisk (*). All 10 species are widespread in West Polynesia. Only *Porzana tabuensis* and *Ducula pacifica* occur on islands east of Niue.

Herein we document the former presence on Niue of three species of ground-dwelling birds, two of which are described as new herein.

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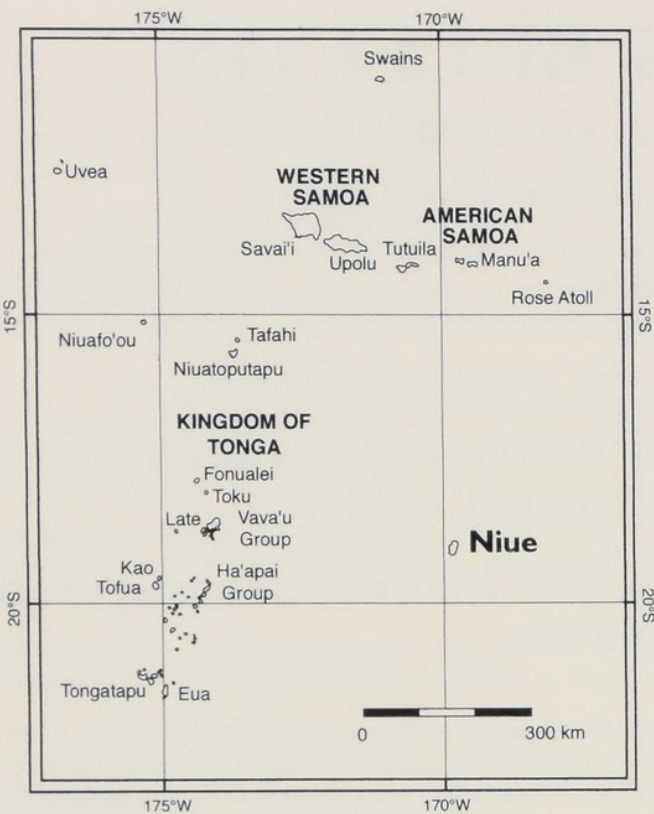


FIG. 1. The West Polynesian region.

METHODS

The Anakuli site.—As part of the Niue Archaeological Project (Walter and Anderson 1995), T.H.W. investigated 22 cave and rockshelter sites on Niue during 10 June–1 July 1994, January 1995, and 5 January–1 February 1996. The single site with appreciable prehistoric bird bones was Anakuli, a cave located behind Tuatea School at Hakupu Village (19° 07' S, 169° 50' W). The fauna from the other sites has been described elsewhere (Worthy et al. 1998). No vertebrate paleontological field research had taken place before on Niue, where a previous archaeological survey disclosed 59 unexcavated cave sites (Trotter 1979).

Anakuli has a round entrance about 2 m across that opens from a flat ground surface to a shaft about 4 m deep. The landing is the top of a talus cone in a cham-

ber about 4 m across that slopes down on one side for about 6 m. The floor is covered by large coral boulders, derived from clearing the land above, as well as copious amounts of domestic rubbish. Because the site appeared to have potential as a pitfall trap for accumulating fossils of birds, an excavation was made at the lowest point of the chamber where the talus abutted the natural wall of the cave.

The overlying human refuse was cleared to reveal the original sediment surface of the cave. The upper layer (I) consisted of consolidated, water-rolled fragments of coral rubble 5–10 cm deep. Beneath this was Layer II, a loose deposit of fine reddish brown, soil-derived sediment containing coral rubble and bones in the upper 20 cm. Below this the sediment (Layer III) was clean coral rubble without soil or bones. Finally, flowstone deposits covered the floor of the cave. Bones of the Pacific rat (*Rattus exulans*) were found in Layer I but were absent from Layers II and III, suggesting a pre-Polynesian age for the bones of extinct birds, which were confined to Layer II. No prehistoric cultural materials were present in any of the layers.

An area of about 2.5 m² was excavated. The bone deposit was limited to an arc about 1 m long and 0.5 m wide along the cave's wall. Flowstone mounds on the floor confined the lateral extent of the deposit. Thus, the bones had accumulated in a hollow where water collected at the base of the talus slope.

Sixty-five bones representing five species of birds were recovered from Anakuli. Two of these species still live on Niue and will not be discussed further: *Porzana tabuensis*, represented by the distal end of a tarsometatarsus and the distal end of a tibiotarsus; and the distal end of a carpometacarpus of a columbid similar to that of *Ducula pacifica*. Most of the specimens from Anakuli belong to three species of birds that no longer occur on Niue and are the subject of this paper.

Radiocarbon dating.—A shaft of tibiotarsus and a shaft of tarsometatarsus of the new species of *Nycticorax* described below were submitted to the Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand, for Accelerator-Mass Spectrometer (AMS) radiocarbon (¹⁴C) dating. The interior and exterior of each bone were scraped, brushed, and rinsed with distilled water.

TABLE 1. Radiocarbon dating results (68% confidence intervals) from *Nycticorax* bones from Anakuli, Niue. Weight is the collagen yield after acid demineralization and the percent of collagen weight compared to the original bone weight. Radiocarbon age is uncalibrated and uncorrected for d¹³C and given as years before present (yr BP). Calibrated age is corrected for d¹³C, calibrated for atmospheric variation in ¹⁴C, and presented in calendar years before present (CAL BP). NZA = Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand.

Lab No.	Skeletal element	Weight (mg)	Radiocarbon age (yr BP)	d ¹³ C	Calibrated age (CAL BP)
NZA5884	tibiotarsus	6 (1.4%)	4523 ± 92	–20‰	5277–4992
NZA5885	tarsometatarsus	34 (4%)	3447 ± 75	–20.3‰	3801–3795, 3723–3543, 3510–3495

The remaining bone was ground in a percussion mortar, sieved to 212 μm , and placed in acid (HCl) until effervescence ceased. The amount of collagen left in each sample (<50 mg) was insufficient to do a gelatin extraction, so the collagenous material was dated after this acid demineralization stage. This left the possibility of humic contamination in the dated samples, because humics are removed effectively only by gelatinization (Redvers-Newton and Coote 1994). Humic contamination may be minimal because the soils above the site are shallow, with little organic litter and no moss cover. Humates might contaminate the sample with older or, more likely, younger organic carbon, whereas possible carbonate contamination, although likely to be minor, would tend to make the apparent age older. Because neither of these samples meets the highest standards for AMS ^{14}C dating of bone (see Stafford et al. 1988, 1991), we regard the radiometric chronology of the bone deposit at Anakuli to be tentative.

The two bones of *Nycticorax* new sp. from Anakuli yielded mid-Holocene ^{14}C dates in the neighborhood of 5300 and 3600 years old (Table 1). These age determinations are reasonable given that the dated bones were recovered below the bones of *Rattus exulans*, an introduced species that first arrived in nearby Tonga about 2800 years ago (D.W.S. and D. V. Burley, pers. obs.) and is unlikely to have lived on Niue any earlier.

Techniques.—The prehistoric bones are catalogued in the collections of the National Museum of New Zealand Te Papa Tongarewa (MNZ). Skeletons used in our comparisons are from MNZ, Florida Museum of Natural History (UF), U.S. National Museum of Natural History (USNM), University of Michigan Museum of Zoology (UMMZ), and University of Washington Burke Museum (UWBM). The following skeletons were used for intergeneric comparisons of ardeids: *Ardea sumatrana* USNM 488342; *A. alba* USNM 610600; *A. pacifica* USNM 613003; *A. novaehollandiae* MNZ 12684, USNM 613003; *Egretta sacra* UF 39393, USNM 560712, UWBM 42724, 42783; *Butorides striatus* USNM 559813; *Botaurus poeciloptilus* USNM 502126; *B. stellaris* USNM 502140; *Ixobrychus sinensis* UF 38131, 39923; *I. flavicollis* UF 39524; *Nycticorax caledonicus* USNM 558301; *Nycticorax nycticorax* MNZ 19310, UF 35841; and *N. (Nyctanassa) violacea* UF 22905. Specimens measured in Tables 3–5 are as follows: *Nycticorax* new species MNZ 537651, 37692; *N.* undescribed species ('Eua) UF 52971; *N. caledonicus* USNM 556979, 558301, 561542, 612629, UMMZ 224713; *N. nycticorax hoactli* USNM 289884, 431388, 431964, 432698, 488680, 489903, 499390, 501635, 501991, 610608, 610609, UF 22900, 22901, 35841; *N. n. nycticorax* USNM 292037, 319467, 430526, 430527, UF 11440, 11453, 2897, 22899; *N. violacea* USNM 18028, 18501, 318841, 491403, 502477, 558045, 611552, UF 11447; *N. leuconotus* UMMZ 201761; *Megapodius pritchardii* MNZ 37701, 37702, 37706, 37707, USNM 319633, 319634; *M. freycinet* USNM 556998, 557007,

557015, 557018; *M. eremita* UF 40180; *M. alimentum* UF 51879, 57791, 57792, 57795, 57796, 57916, BPBM 165670; *Gallirallus* new species MNZ S37708, 37709, 37710, 37711; *G. ripleyi* UF 51320, 51499, 53933, 53936, 53939, 53997, 54287, 54352, 54529, USNM 402895; *G.* undescribed sp. 'Eua UF 51729, 51734, 51735, 51991, 52058, 52137, 52354, 52518; *G. philippensis* MNZ 25267, UWBM 42863, 42865, 42866, UF 39854, 39855.

Prehistoric bones of *Nycticorax*, *Megapodius*, and *Gallirallus* from Tonga and the Cook Islands are primarily from UF, with smaller collections from USNM. Osteological nomenclature usually follows Baumel and coworkers (1993). Measurements were taken with digital calipers with 0.01 mm increments, rounded to the nearest 0.1 mm.

SYSTEMATIC PALEONTOLOGY

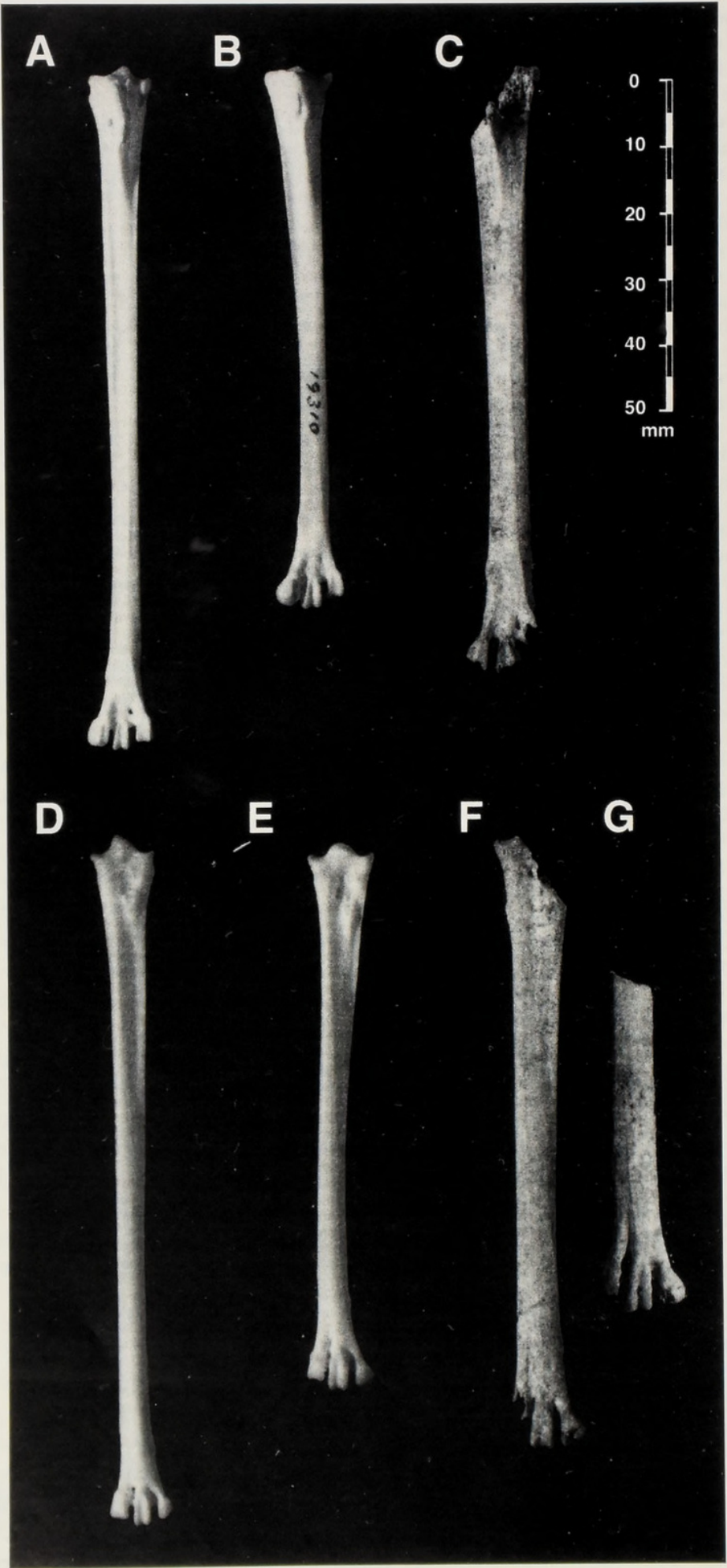
Order Incertae sedis (Olson 1985)

Family Ardeidae

Genus *Nycticorax* Rafinesque

The holotypical tarsometatarsus of the new species is referred to *Nycticorax* (including *Nyctanassa* but excluding *Caltherodius* and *Gorsachius*; for various opinions on generic classification of night-herons see Payne and Risley 1976, Sheldon et al. 1995) rather than other genera of Ardeidae because of the following combination of characters: trochlea metatarsi IV slightly grooved distally; more proximal placement of distal foramen relative to proximal end of trochlea metatarsi III; parallel orientation of trochlea metatarsi III with shaft; gradual protruding of trochlea metatarsi II from corpus tarsometatarsi; distal foramen small; medial side compressed, especially proximally, to a narrow flange; anteriorly, distal to the tuberositas musculo tibialis cranialis, the bone is flat and slopes medially (not markedly concave as in *Ardea*); posteriorly, the shaft is convex with a weak intermuscular line laterally placed (in *Ardea* the shaft is concave and the intermuscular line is prominent and laterally placed and in *Botaurus* the shaft is concave with a prominent intermuscular line centrally placed).

All other elements of the new species also have characters of *Nycticorax* rather than of other ardeid genera. Notable among these characters are: mandible with medial groove bridged by an oblique ridge; coracoid with relatively slender shaft, dorsal surface of sternal end deeply concave, and the ridge between the facies articularis humeralis and processus acrocoracoideus very steep in dorsal view; scap-



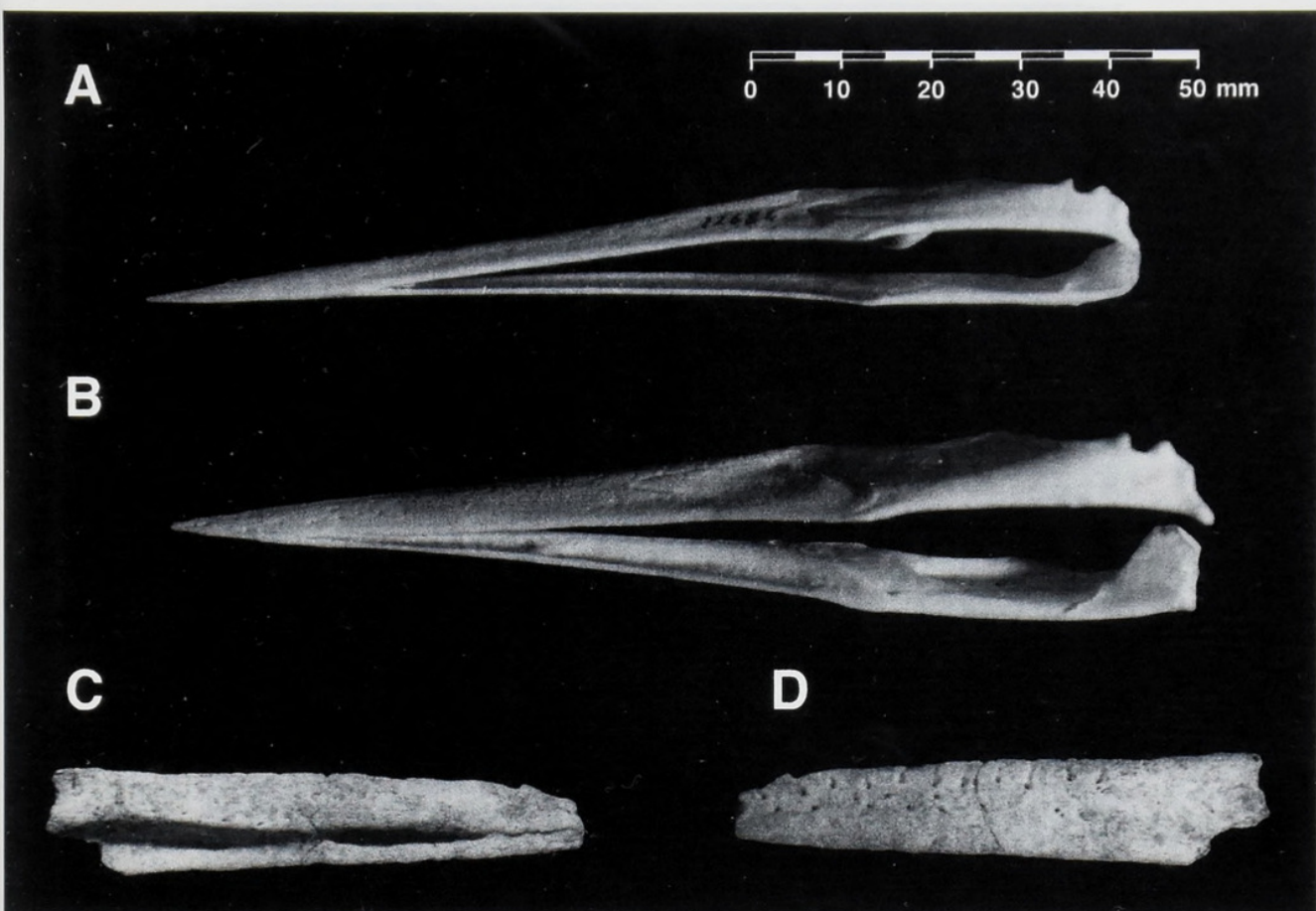


FIG. 3. The mandible of herons in lateral (A, B, D) and medial (C) aspects. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C, D. *Nycticorax kalavikai*, new species, MNZ S37653.

ula with the facies articularis clavicularis rising dorsally from the plane of the shaft (dorsal margin straight in *Ardea* and *Egretta*) and rounded proximo-dorsally (pointed in *Ardea* and *Egretta*); carpometacarpus with processus extensorius directed more medially (more proximally in *Ardea* and *Egretta*), and the os metacarpi alulare with a marked fossa; tibiotarsus with smooth posterior edge to area interarticularis (notched in *Ardea*, *Egretta*, and *Botaurus*).

***Nycticorax kalavikai*, new species**

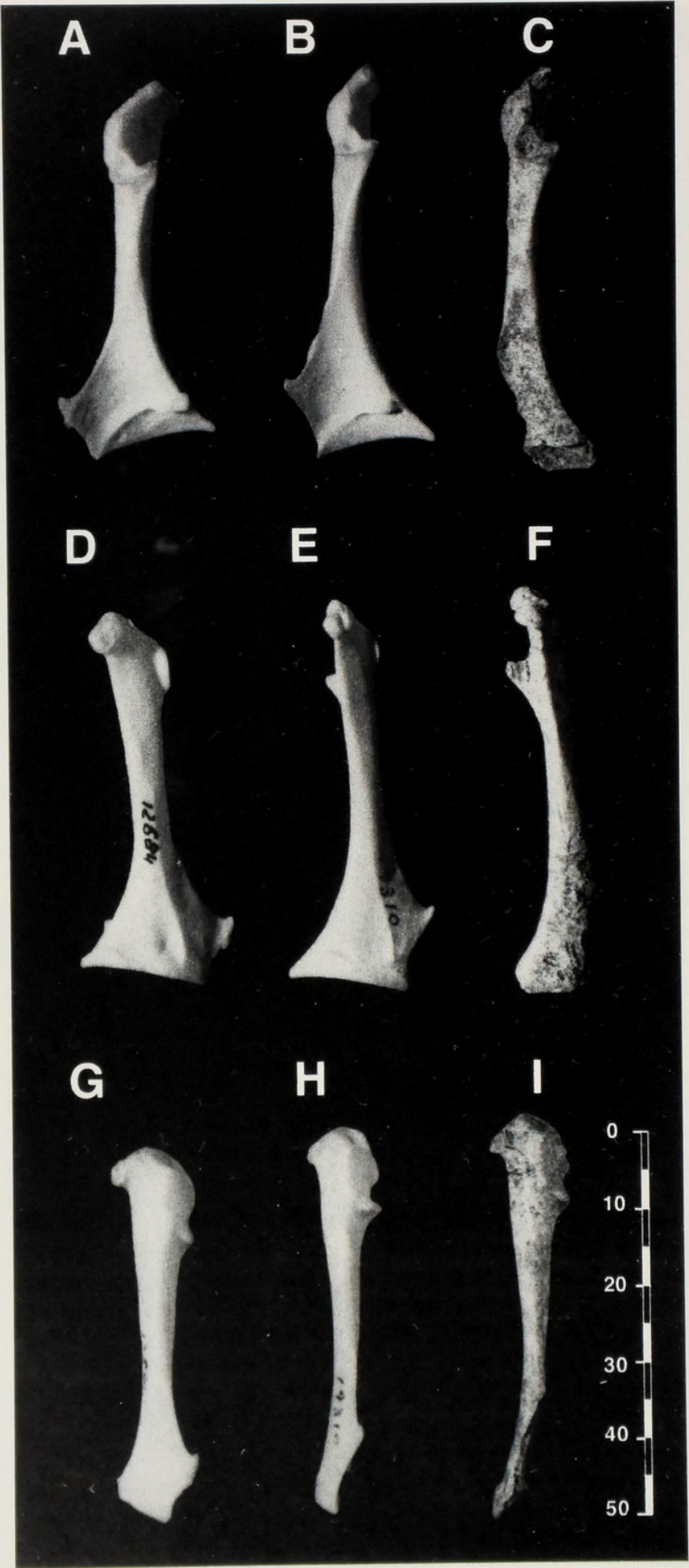
Holotype.—MNZ S37651, tarsometatarsus (Fig. 2, Table 3), collected by T. H. Worthy on 7–12 January 1995 at Anakuli, Niue.

Topotypical paratypes.—MNZ S37652–S37700, occipital fragment of cranium, pter-

ygoïd, 4 incomplete mandibles (Fig. 3), coracoid (Fig. 4), 2 scapulae (Fig. 5), anterior portion of sternum, 4 cervical vertebrae (numbers 6, 10, 11, 12), thoracic vertebra (number 17), distal humerus, 2 distal and 1 complete ulnae (Fig. 6), 1 distal and 2 proximal radii, 4 proximal and 3 shafts of carpometacarpi (Fig. 7), pelvis, 3 femoral shafts, 3 distal and 1 proximal tibiotarsi (Fig. 8), 8 tarsometatarsi, pedal digit I (phalanx 1), pedal digit III (phalanx 2), pedal digit IV (phalanx 1). Minimum of four individuals. Selected measurements of paratypes are as follows: coracoid: length 52.7 mm; radius: distal width 7.8 mm; ulna: total length: 123 mm, proximal width 10.6 mm, width of shaft 5.3 mm, depth of shaft 4.9 mm, distal width 7.6, 7.8, 8.4 mm; carpometacar-

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FIG. 2. The tarsometatarsus of herons in plantar (A–C) and a acrotarsial (D–G) aspects. A, D. *Ardea novaehollandiae* MNZ 12684. B, E. *Nycticorax caledonicus* MNZ 19310. C, F. *Nycticorax kalavikai*, new species, MNZ S37651, holotype. G. *Nycticorax kalavikai*, new species, MNZ S37652.



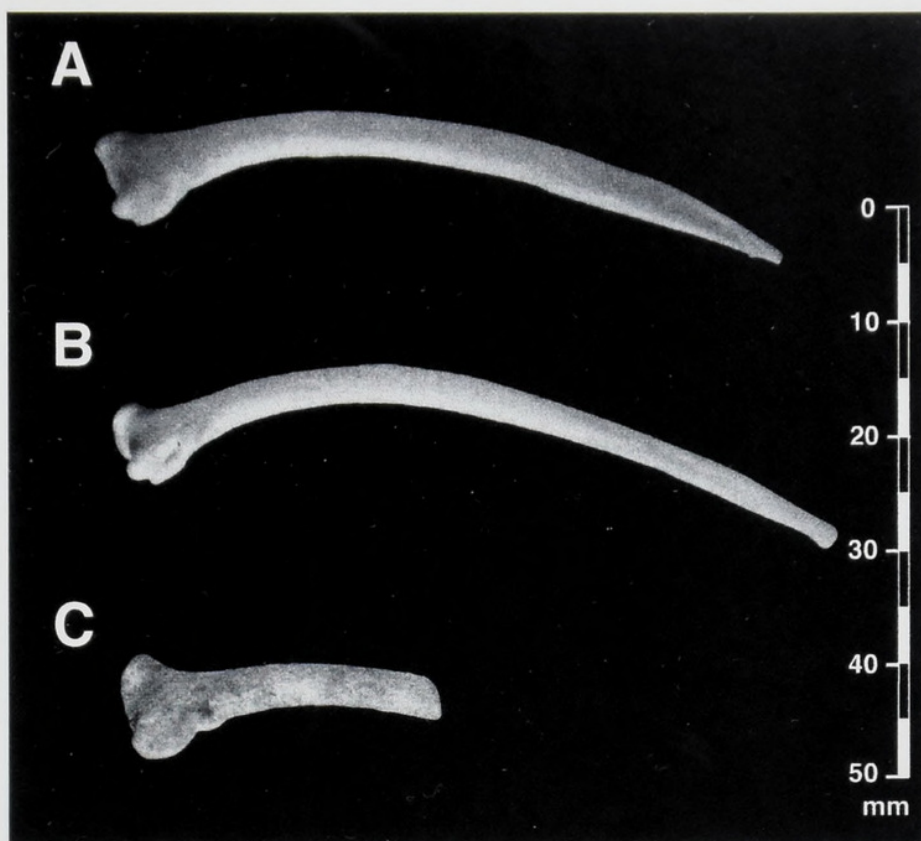


FIG. 5. The scapula of herons in dorso-medial aspect. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C. *Nycticorax kalavikai*, new species, MNZ S37658.

pus: proximal width 12.4 mm; femur: width of shaft 6.3, 6.3, 6.4 mm, depth of shaft 6.4, 6.6, 6.6 mm; tibiotarsus: proximal width 11.8 mm, proximal depth 13.8 mm, minimum width of shaft 6.1, 5.8, 6.1, 5.3 mm, distal width 12.4, 11.4 mm.

Diagnosis.—A large species of *Nycticorax* that differs from living congeneric species in these major features (see Table 2 for comparative details and additional characters in all extant species of *Nycticorax*): rostrum narrower and straighter; dentary thicker and deeper overall with deep median groove; sternum with double foramen pneumaticum; coracoid with more rounded ventro-humeral and latero-humeral portions of shaft, more deeply excavated in the triosseal canal dorso-medial of the facies articularis humeralis than in *N. caledonicus*, and facies articularis clavicularis

larger, overlapping the shaft more; scapula with more rounded facies articularis humeralis; ulna shorter (relative to leg elements) than in *N. caledonicus*, with less prominent papillae remigiales caudales, more dorso-ventrally expanded shaft, larger tuberculum carpalae that encloses a marked fossa between it and the condylus ventralis ulnaris, and a longer condylus dorsalis ulnaris; carpometacarpus with deeper fossa supratrochlearis, shorter overall; femur, tibiotarsus, and tarsometatarsus stouter; tarsometatarsus with fossa infracoty-laris dorsalis relatively shallower.

Etymology.—From the Niuean words *kalavi* (land crab) and *kai* (food; see McEwen 1970). The name *kalavikai* alludes to our speculation that land crabs, typically abundant on raised limestone islands in Oceania, may have been an important food for this extinct night-heron.

FIG. 4. The coracoid of herons in dorsal (A–C), ventral (D–F), and lateral (G–I) aspects. A, D, G. *Ardea novaehollandiae* MNZ 12684. B, E, H. *Nycticorax caledonicus* MNZ 19310. C, F, I. *Nycticorax kalavikai*, new species, MNZ S37657.

TABLE 2. Osteological character summary for species of *Nycticorax*.

Skeletal element Character	<i>N. kalavikai</i>	<i>N. caledonicus</i>	<i>N. nycticorax</i>	<i>N. violacea</i>	<i>N. leuconotus</i>
PTERYGOID					
Stoutness				slender	slender
Dorsal surface	medium barely concave	stout very concave	stout very concave	very concave	barely concave
ROSTRUM					
Shape in dorsal aspect	narrow	narrow curved, tapers gradually	broad curved, tapers gradually	narrow curved, tapers gradually	narrow curved, tapers gradually
Shape in lateral aspect	straight, tapers less gradually				
DENTARY					
Overall depth	deep	shallow	shallow	shallow	shallow
Medial groove	deep	deep	shallow	deep	deep
Angle of cutting surface	acute	more obtuse	acute	more obtuse	more obtuse
Lateral surface	± flat	± flat	flat-convex	concave	± flat
STERNUM					
Dorso-ventral compression of sulcus articularis coracoideus	more	less	less	less	less
Foramen pneumaticum	double	double	single	single	single
CORACOID					
Ventro-humeral & latero-humeral portion of shaft	rounded	rounded	sharper	sharper	rounded
Sulcus musculo supracoracoideus	deep	deep	shallow	deep	deep
SCAPULA					
Facies articularis humeralis	rounded	intermediate	oblong	oblong	oblong

TABLE 2. CONTINUED.

Skeletal element Character	<i>N. kalavikai</i>	<i>N. caledonicus</i>	<i>N. nycitorax</i>	<i>N. violacea</i>	<i>N. leuconotus</i>
ULNA					
Papillae remigiales caudales	weak	weak	strong	strong	weak
Dorso-ventral expansion of shaft	more	more	less	less	less
Tuberculum carpale	large	small	small	small	small
Condylus dorsalis ulnaris	long	short	short	short	long
CARPOMETACARPUS					
Fossa supratrochlearis	deep	intermediate	shallow	shallow	shallow
Processus pisiformis in proximal aspect	large	small	small	small	small
Length relative to ulna	short	long	long	long	long
FEMUR					
Overall shape	stout	intermediate	slender	slender	slender
TIBIOTARSUS					
Overall	stout	stout	slender	slender	slender
Incisura intercondylaris between distal margin of condyles	more concave	less concave	less concave	less concave	less concave
TARSOMETATARSUS					
Overall shape	stout	stout	slender	stout	slender
Dorso-ventral compression of proximo-medial margin of shaft	intermediate	compressed	thickened	compressed	compressed

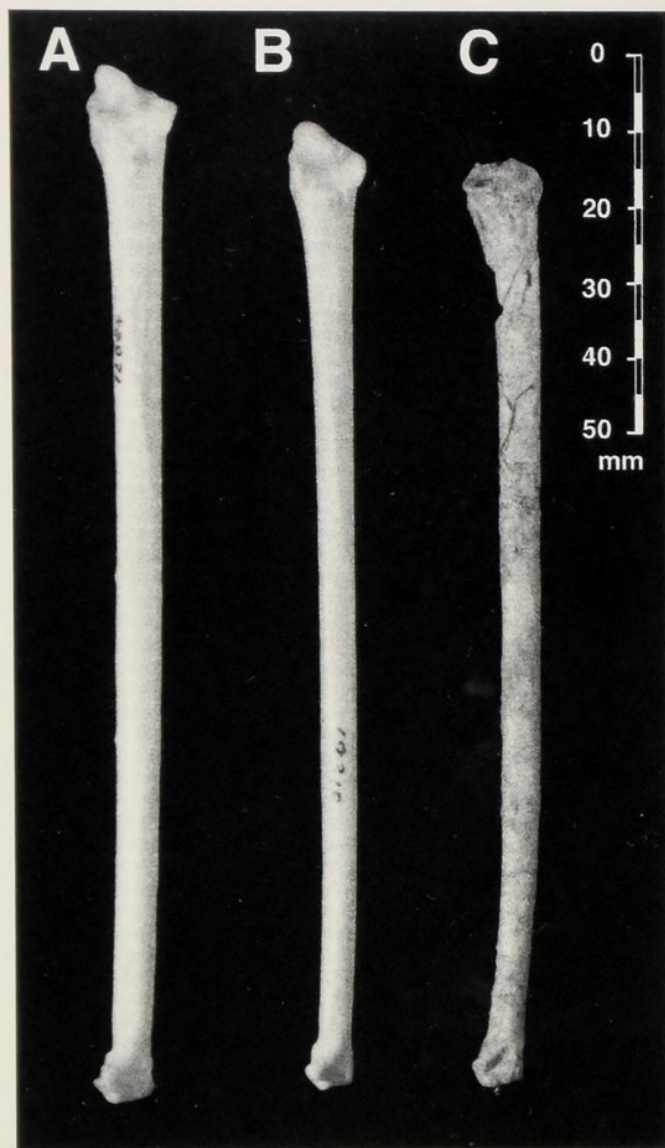


FIG. 6. The ulna of herons in medial aspect. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C. *Nycticorax kalavikai*, new species, MNZ S37667.

Crustaceans are a regular part of the diet in living species of *Nycticorax* (Martínez-Vilalta and Motis 1992).

Remarks.—Although males average slightly larger than females in most linear skeletal measurements in *Nycticorax nycticorax* and *N. violacea*, the overlap is considerable (Adams 1955) and we do not consider sexual dimorphism to be an important factor in evaluating the measurements of fossil night-herons. We agree with Payne and Risley (1976) that *N. nycticorax* and *N. caledonicus* are similar osteologically, and are more similar to *N. kalavikai* in having a narrower bill than in *N. violacea*. Because it shares more characters with *N. kalavikai* than with other species, *N.*

caledonicus is probably the closest living relative of *N. kalavikai*, as might be suspected on geographical grounds.

Nycticorax kalavikai is known thus far only from Niue. It is the first extinct species of *Nycticorax* to be described from Polynesia. From a cave on the Tongan island of 'Eua, however, D.W.S. has recovered three bones (rostrum, tarsometatarsus, pedal phalanx) of another extinct, late Quaternary species of *Nycticorax*. The undescribed species from 'Eua is included in faunal lists by Steadman (1993a, 1995) and measurements given in Table 3; it will be described by D.W.S. in a separate paper. In the Mascarene Islands (Indian Ocean), three endemic, allopatric species of *Nycticorax* became extinct since human arrival about 500 years ago (Mourer-Chauviré et al. 1999). Unlike the Polynesian forms, two of the three Mascarene species had relatively small wings and may have been flightless. An undescribed, extinct form of *Nycticorax* is known as well from Ascension Island in the Atlantic Ocean (S. L. Olson 1977, pers. comm.).

Order Galliformes

Family Megapodiidae

Genus *Megapodius* Quoy and Gaimard

Megapodius pritchardii Gray

Material.—MNZ S37701–S37707, proximal carpometacarpus, 2 femora (Fig. 9), 1 proximal and 2 distal tarsometatarsi (Fig. 10), pedal phalanx, collected at Anakuli, Niue by T. H. Worthy on 7–12 January 1995. Minimum of two individuals.

Remarks.—This material resembles modern skeletons of *Megapodius pritchardii* (from Niuafo'ou, Tonga) in all qualitative features. The Niuean bones average slightly larger than in two modern specimens of *M. pritchardii* (Table 4) but are distinctly smaller than in the living *M. freycinet* sensu lato (Moluccas through Vanuatu) and the extinct *M. alimentum* of Tonga (Steadman 1989). The fossil femur from Niue resembles that of *M. pritchardii* and differs from that of *M. freycinet* in that the distal medial condyle is markedly longer than deep in medial aspect, rather than being about as deep as long.

The only other record of a megapode from as far east as Niue is from an archaeological site on Ofu, American Samoa (Steadman

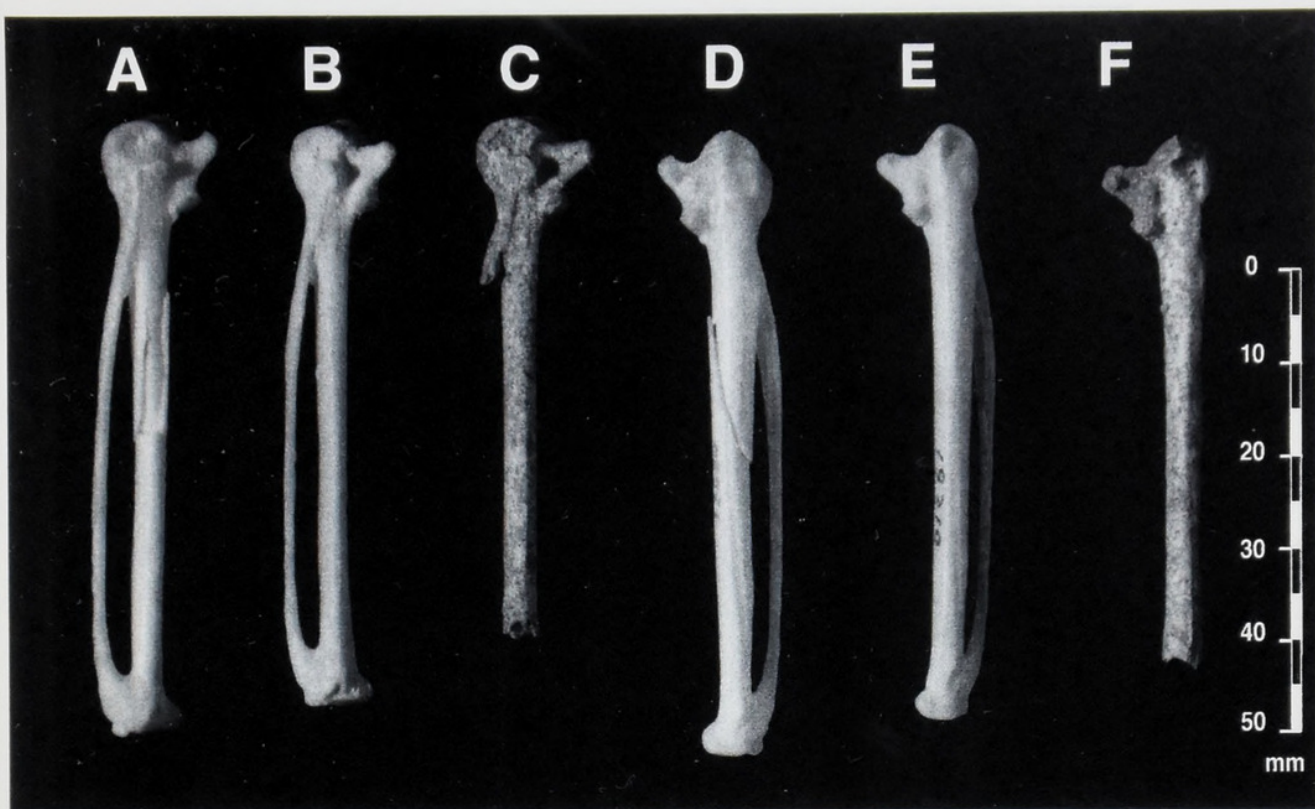


FIG. 7. The carpometacarpus of herons in ventral (A–C) and dorsal (D–F) aspects. A, D. *Ardea novaehollandiae* MNZ 12684. B, E. *Nycticorax caledonicus* MNZ 19310. C, F. *Nycticorax kalavikai*, new species, MNZ S37673.

1993b). The limited material from Ofu (fragmentary ulna and femur) is in the small size range of *M. freycinet* sensu lato, and is larger than in *M. pritchardii*. Until more material is available, however, we cannot be certain whether these two easternmost records of megapodes represent the same or different species.

Order Ralliformes (Gruiformes)
Family Rallidae
Genus *Gallirallus* Lafresnaye

***Gallirallus huiatua*, new species**

Holotype.—MNZ S37708, tarsometatarsus (Fig. 11), collected at Anakuli, Niue by T. H. Worthy on 7–12 January 1995.

Topotypical paratypes.—MNZ S37709–S37711, proximal ulna, shaft of femur, distal tibiotarsus (Fig. 12). Minimum of one individual.

Diagnosis.—A medium-sized (Table 5) species of *Gallirallus* that differs from congeners as follows. Ulna more dorso-ventrally compressed than in *G. philippensis*. In cranial aspect, femur with mid-shaft relatively

straight as in *G. philippensis* (constricted in *G. ripleyi* and *G. undescribed* sp. from 'Eua) and distal half of shaft of intermediate stoutness as in *G. ripleyi* (thickened in *G. undescribed* sp. from 'Eua, narrow in *G. philippensis*). Tibiotarsus with deep incisura intercondylaris as in *G. undescribed* sp. from 'Eua (shallow in *G. ripleyi*, intermediate to deep in *G. philippensis*) and flat disto-dorsal portion of shaft as in *G. ripleyi* (concave in *G. undescribed* sp. from 'Eua and *G. philippensis*). Tarsometatarsus slender overall as in *G. philippensis* (stout in *G. ripleyi* and *G. undescribed* sp. from 'Eua), with shallow shaft (deep in the others), and flat disto-dorsal surface of shaft (concave in *G. undescribed* sp. from 'Eua and *G. philippensis*, intermediate to concave in *G. ripleyi*).

Etymology.—From the Niuean compound word *hui-atua*, which means “the bones [*hui*] of the dead [*atua*]” (Smith 1902:207).

Remarks.—The morphology of *Gallirallus huiatua* does not argue for a closer relationship to any one species than another, including the two geographically nearest congener-

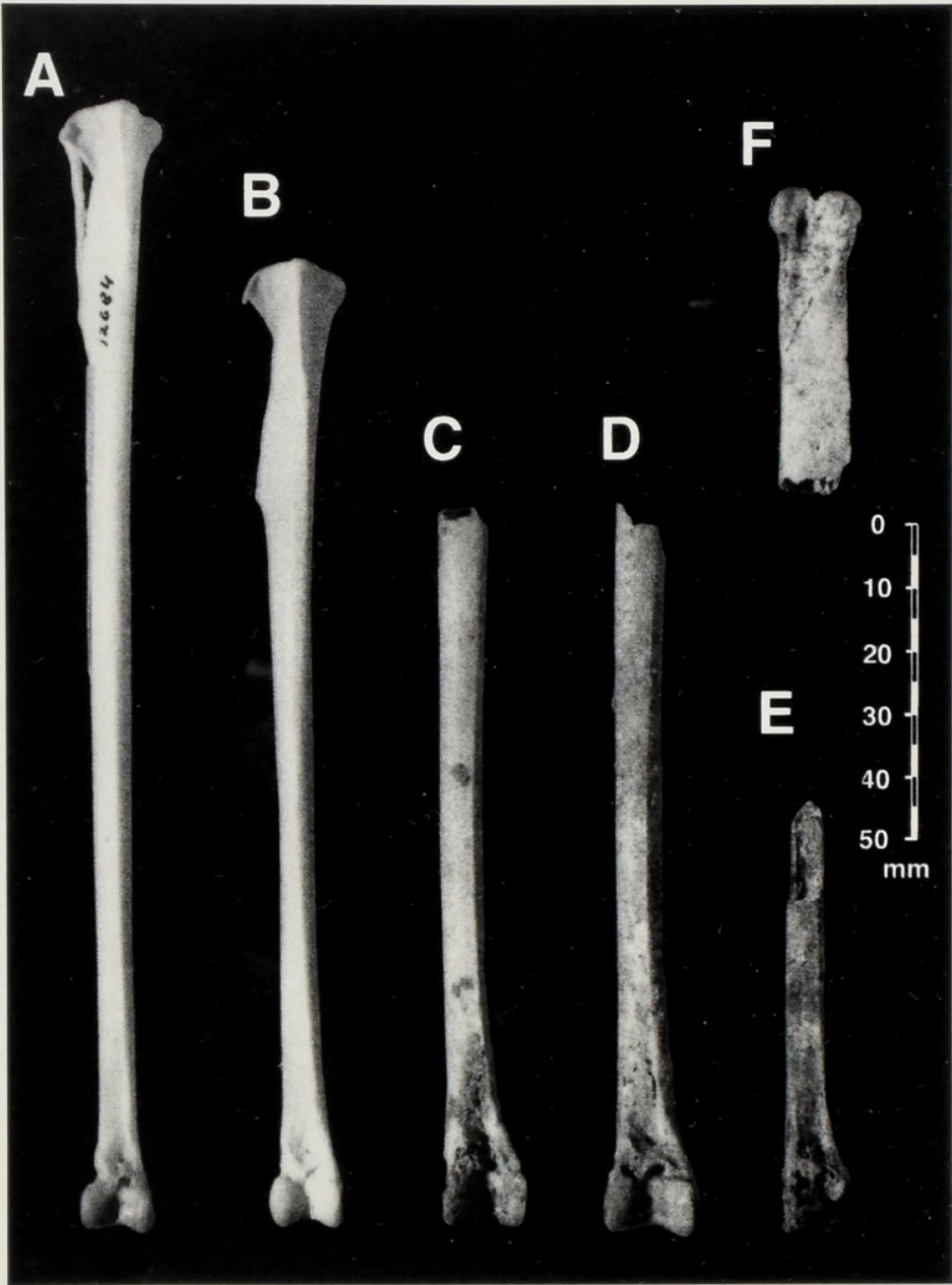


FIG. 8. The tibiotarsus of herons in dorsal aspect. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C–F. *Nycticorax kalavikai*, new species, MNZ S37683–S37686.

ic flightless species, *G. ripleyi* of Mangaia (Steadman 1987) and *G.* undescribed species of ‘Eua (Steadman 1993a). Selected intra-elemental ratios (C/A of ulna; B/A, C/A, D/A of femur) and inter-elemental ratios [C(ulna)/C(femur)] in Table 5 suggest that *G. huiatua* was flightless. The widespread, volant *G. philippensis* occurs on Niue today. Unlike its flightless congeners, *G. philippensis* is unknown on remote islands of Oceania before the arrival of people (Steadman 1993a, 1995).

DISCUSSION

The West Polynesian (Fiji, Tonga, Samoa) rather than East Polynesian affinities of the Niuean avifauna are strengthened by the addition of *Nycticorax kalavikai* and *Megapodius pritchardii*. Neither genus is known on islands east of Niue. The nearest localities with resident species of *Nycticorax* are New Caledonia (*N. c. caledonicus*), the Solomon Islands (*N. c. mandibularis*), Palau (*N. c. pelawensis*; Peters 1930, Martínez-Vilalta and Motis 1992), and prehistorically in Tonga

TABLE 3. Measurements (in mm) of the tarsometatarsus in *Nycticorax*, with mean, range, and sample size. SU, sex unknown. The measurements of *N. caledonicus* include the subspecies *N. c. hilli* and *N. c. caledonicus*.

	<i>N. kalavikai</i> , new sp. (SU) Niue	<i>N.</i> undescribed sp. (SU) 'Eua, Tonga	<i>N. caledonicus</i> (2M, 3F) Halmahera, Australia, New Caledonia	<i>N. nycticorax</i> <i>hoaculi</i> (8M, 6F) North America, Bolivia	<i>N. n. nycticorax</i> (4M, 3F, SU) France, Zaire, Zimbabwe, China, Japan	<i>N. violacea</i> (M, F, SU) Florida, Haiti, Barbuda, Swan Is., Panama, Galápagos	<i>N. leuconotus</i> (F) Zambia
TARSOMETATARSUS							
Distal width	12.6	13.1	10.8 10.0–11.7 5	11.1 10.5–12.0 14	9.5 9.1–10.3 8	10.3 9.5–10.9 8	8.3
Width of middle trochlea	3.9 3.9 2	3.9 1	3.3 3.0–3.6 5	3.4 3.1–3.7 14	2.9 2.7–3.1 8	3.1 2.7–3.4 8	2.5 1
Depth of middle trochlea	—	7.6	6.2 6.0–6.3	6.3 6.0–6.7	5.6 5.4–6.1	5.6 5.3–6.1	4.9
Width of shaft at distal foramen	9.0 8.8–9.0 2	9.3 1	6.9 6.5–7.2 5	7.4 6.8–8.0 14	6.2 5.9–6.6 8	7.2 6.8–7.7 8	5.8 1
Depth of shaft at distal foramen	4.0 3.9–4.1 2	4.5 1	3.2 3.1–3.6 5	3.2 2.9–3.5 14	2.9 2.8–3.1 8	2.8 2.7–3.0 8	2.5 1

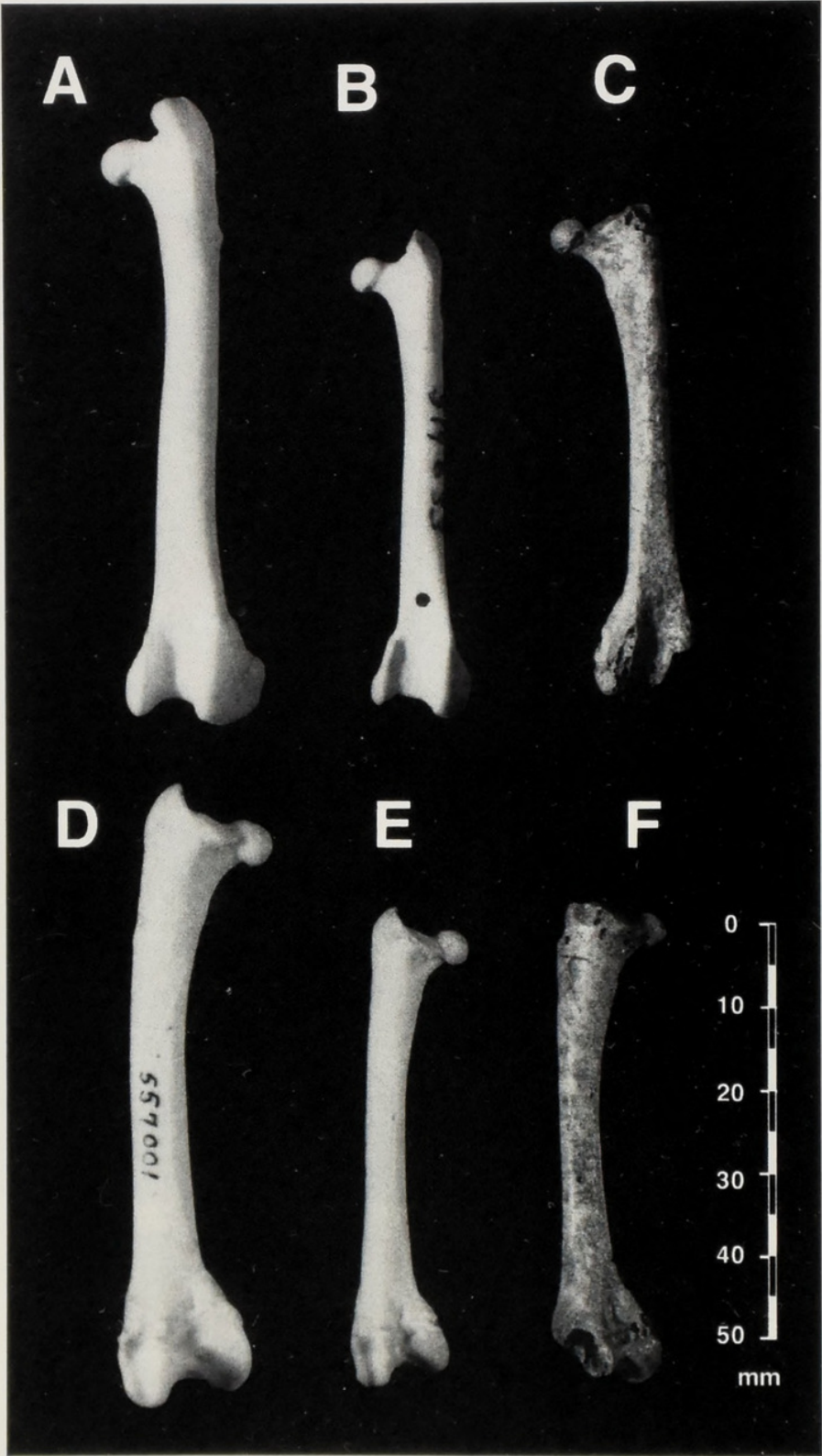


FIG. 9. The femur of *Megapodius* in dorsal (A–C) and ventral (D–F) aspects. A, D. *M. freycinet*, USNM 557001. B, E. *M. pritchardi*, USNM 319633. C, F. *M. pritchardii*, MNZ S37702.

(Steadman 1993a). The nearest localities for *Megapodius* are Tonga (*M. pritchardii* and three extinct species) and American Samoa (*Megapodius* sp., near *M. freycinet* s.l.; Steadman 1999). *Gallirallus huiatua* is not similar

to any of the flightless species of *Gallirallus* known thus far. Morphological and phylogenetic details of the radiation of flightless species of *Gallirallus* across the tropical Pacific remain poorly understood.

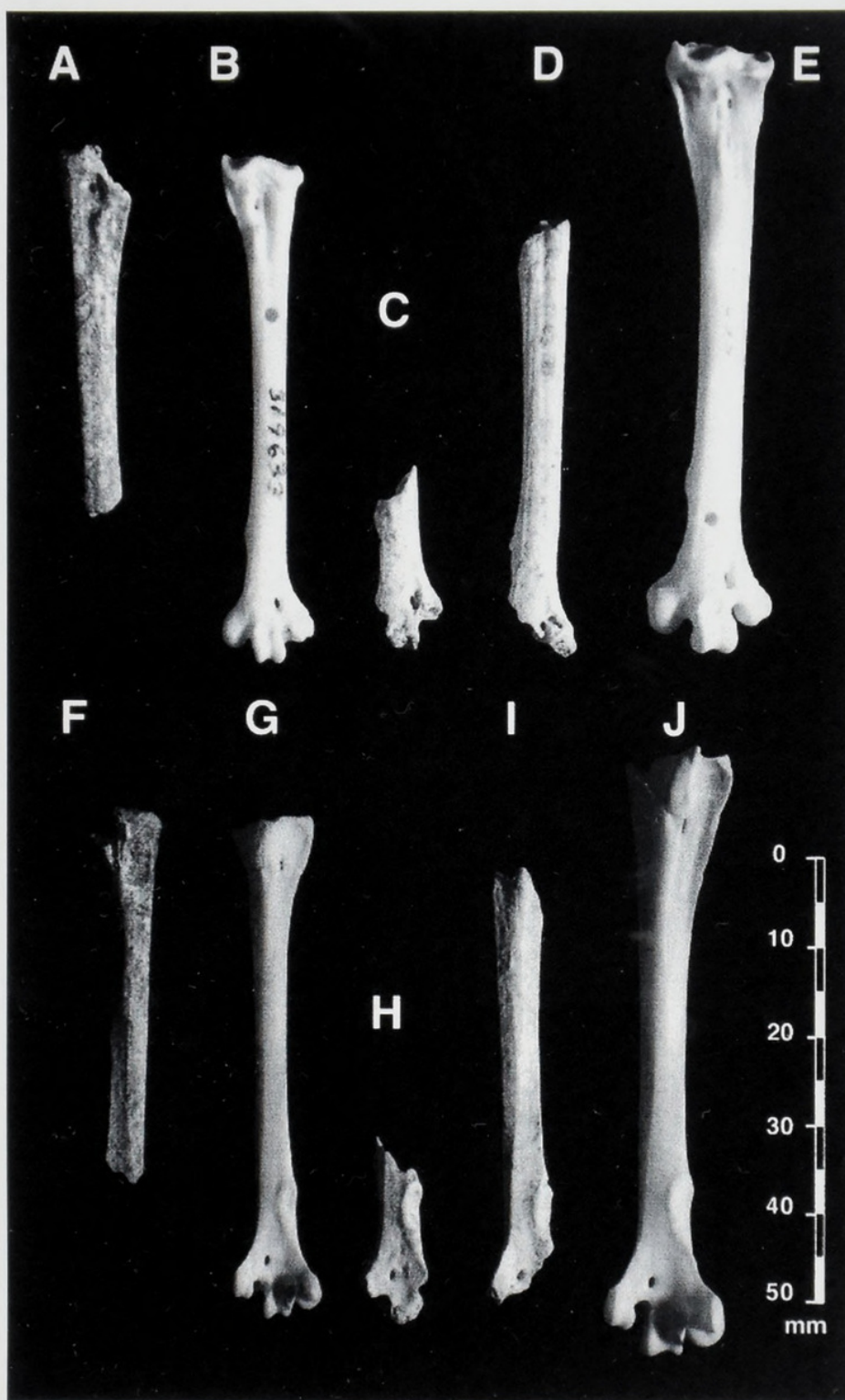


FIG. 10. The tarsometatarsus of *Megapodius* in acrotarsial (A–E) and plantar (F–J) aspects. A, C, D, F, H, I. *M. pritchardii*, MNZ S37704–S37706. B, G. *M. pritchardii*, USNM 319633. E, J. *M. freycinet* USNM 557001.

Hunting (see Loeb 1926) and habitat loss may have been involved in the loss of night-herons, megapodes, and flightless rails on Niue (as is believed to be the case on other oceanic islands; Steadman 1995), although the bones from Anakuli provide no direct evi-

dence of this. The absence of rat bones in Layer II of Anakuli suggests that the bones analyzed herein were deposited before people arrived on Niue, which is supported by the two radiocarbon dates obtained on bones of *Nycticorax kalavikai*. The likely calendar age

TABLE 4. Measurements (in mm) of the carpometacarpus, femur, tarsometatarsus, and pedal digit III, phalanx I of *Megapodius*, with mean, range, and sample size.

	<i>M. pritchardii</i> Niue (SU)	<i>M. pritchardii</i> Niufo'ou, Tonga (SU)	<i>M. freycheti</i> Halmahera, Indonesia (2M, 2F)	<i>M. eremita</i> Isabel, Simbo, Solomon Islands (3F, SU)	<i>M. alimentum</i> Ha'apai, Tonga (SU)	<i>M. alimentum</i> 'Eua (SU)
CARPOMETACARPUS						
Least width of shaft	2.7	2.5 2.4–2.6	3.1 2.9–3.2	3.0 2.7–3.2	—	—
	1	2	4	4		
Least depth of shaft	3.3	3.0	4.0	3.9	—	—
		3.0	3.8–4.2	3.7–4.3		
	1	2	4	4		
FEMUR						
Total length	53.1	49.4 49.0–49.9	64.9 62.5–67.7	66.8 64.1–68.7	70.2+ 70.0+ 70.5+	—
	1	2	4	4	3	
Least width of shaft	4.5	4.4 4.2–4.5	6.4 6.0–6.7	5.9 5.7–6.1	6.5 6.2–7.0	—
	1	2	4	4	3	
Least depth of shaft	4.7	4.5 4.3–4.7	6.1 5.6–6.6	5.3 4.6–5.5	6.3 5.9–6.5	—
			4	4	3	
	1	2				
TARSOMETATARSUS						
Least width of shaft	4.5 4.3–4.7	3.9 3.9	5.6 5.1–6.2	5.3 5.1–5.4	5.8 5.5–6.2	—
	2	2	4	3	3	
Least depth of shaft	2.7	2.5	3.4	3.4	3.5	—
	2.7	2.4–2.6	3.1–3.6	3.3–3.4	3.3–3.7	
	2	2	4	3	3	

TABLE 4. CONTINUED.

	<i>M. pritchardii</i> Niue (SU)	<i>M. pritchardii</i> Niuafu'ou, Tonga (SU)	<i>M. freycinet</i> Halmahera, Indonesia (2M, 2F)	<i>M. eremita</i> Isabel, Simbo, Solomon Islands (3F, SU)	<i>M. alimentum</i> Ha'apai, Tonga (SU)	<i>M. alimentum</i> Eua (SU)
PEDAL DIGIT III, PHALANX I						
Total length	14.3	13.8 13.7-13.8	17.4 17.1-17.7	15.6 14.6-16.9	—	20.0
Proximal width	1 4.6	2 4.2 4.2	4 5.7 5.4-6.0	3 5.5 5.4-5.6	—	1 7.8
Proximal depth	1 4.3	1 3.6 3.6-3.7	4 5.4 5.2-5.7	3 4.9 4.6-5.2	—	1 6.7
Least width of shaft	1 2.8	2 2.4 2.4-2.5	4 3.4 3.2-3.6	3 3.2 3.2-3.3	—	1 4.4
Least depth of shaft	1 2.1	2 1.8 1.8-1.9	4 2.8 2.4-3.0	3 2.6 2.5-2.6	—	1 3.4
Distal width	1 3.3	2 2.9 2.8-3.0	4 4.1 3.7-4.3	3 3.7 3.7-3.8	—	1 5.3
Distal depth	1 3.5	2 2.8 2.8	4 4.2 4.0-4.3	3 3.8 3.7-3.9	—	1 5.2
	1	2 2	4	3	—	1

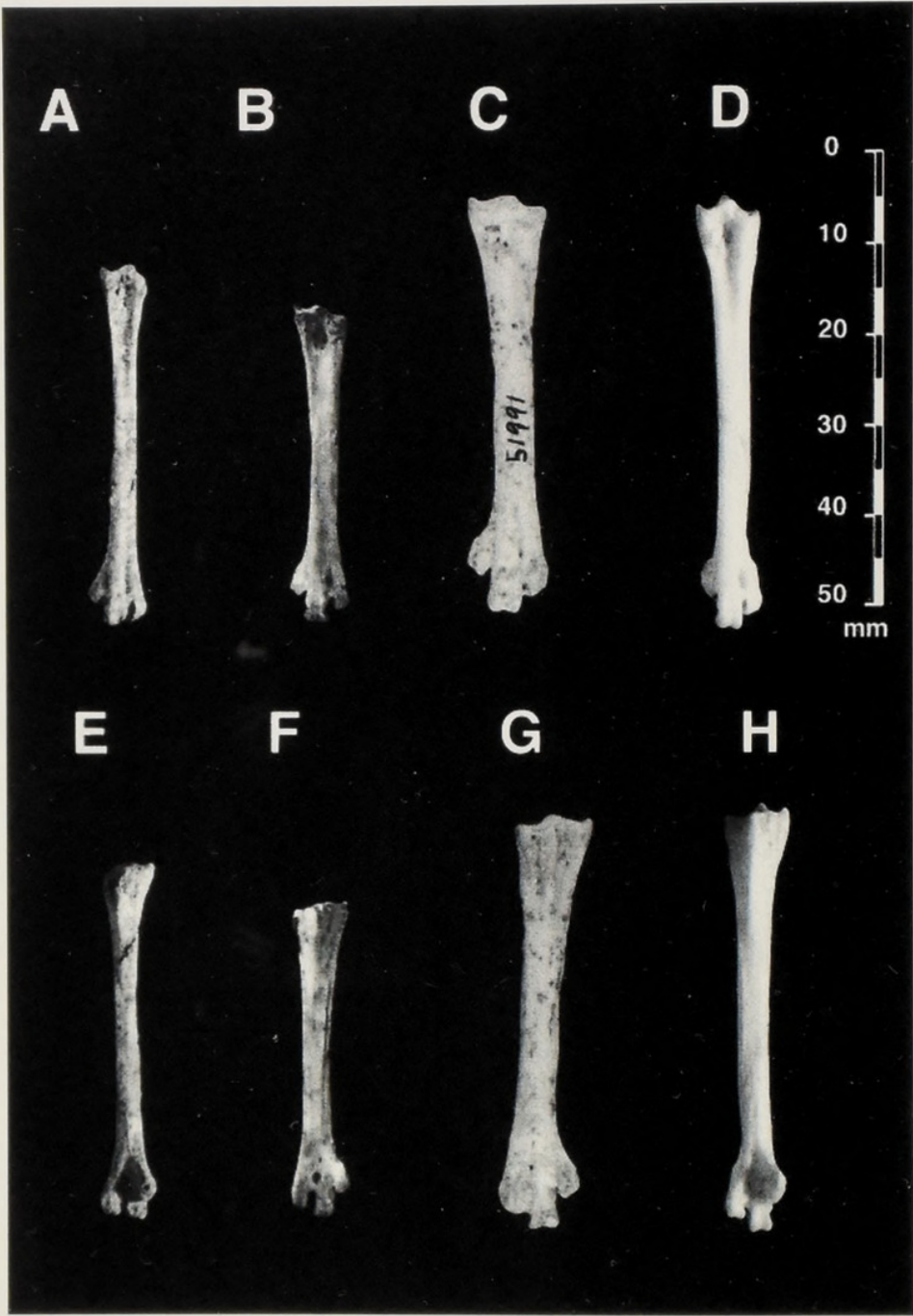


FIG. 11. The tarsometatarsus in acrotarsial (A–D) and plantar (E–H) aspects of *Gallirallus*. A, E. *G. huiatua*, MNZ S37708, holotype. B, F. *G. ripleyi*, USNM 402895. C, G. *G. new sp.*, UF 51991 (*Eua, Tonga). D, H. *G. philippensis*, MNZ 25267.

range of about 5300 to 3600 years ago is about 1500 years older than the oldest archaeological remains on Niue (Walter and Anderson 1995).

Our sampling of the pre-human avifauna of Niue is very incomplete. The pitfall nature of Anakuli probably explains why the site collected mainly ground-dwelling species such as herons, megapodes, and rails. Arboreal species, such as pigeons, doves, parrots, and passerines, must also have been part of the pre-

human avifauna of Niue but are poorly represented in the bone deposit. As many as 20 other extirpated species of birds, still unrecorded, are likely to have been present on Niue before human arrival, if the much more extensive pre-cultural fossil records from adjacent island groups (Tonga, Cook Islands) are any indication (Steadman 1993a, 1995). A more complete picture of the avifauna that greeted the first people on Niue awaits the discovery of other bone deposits.

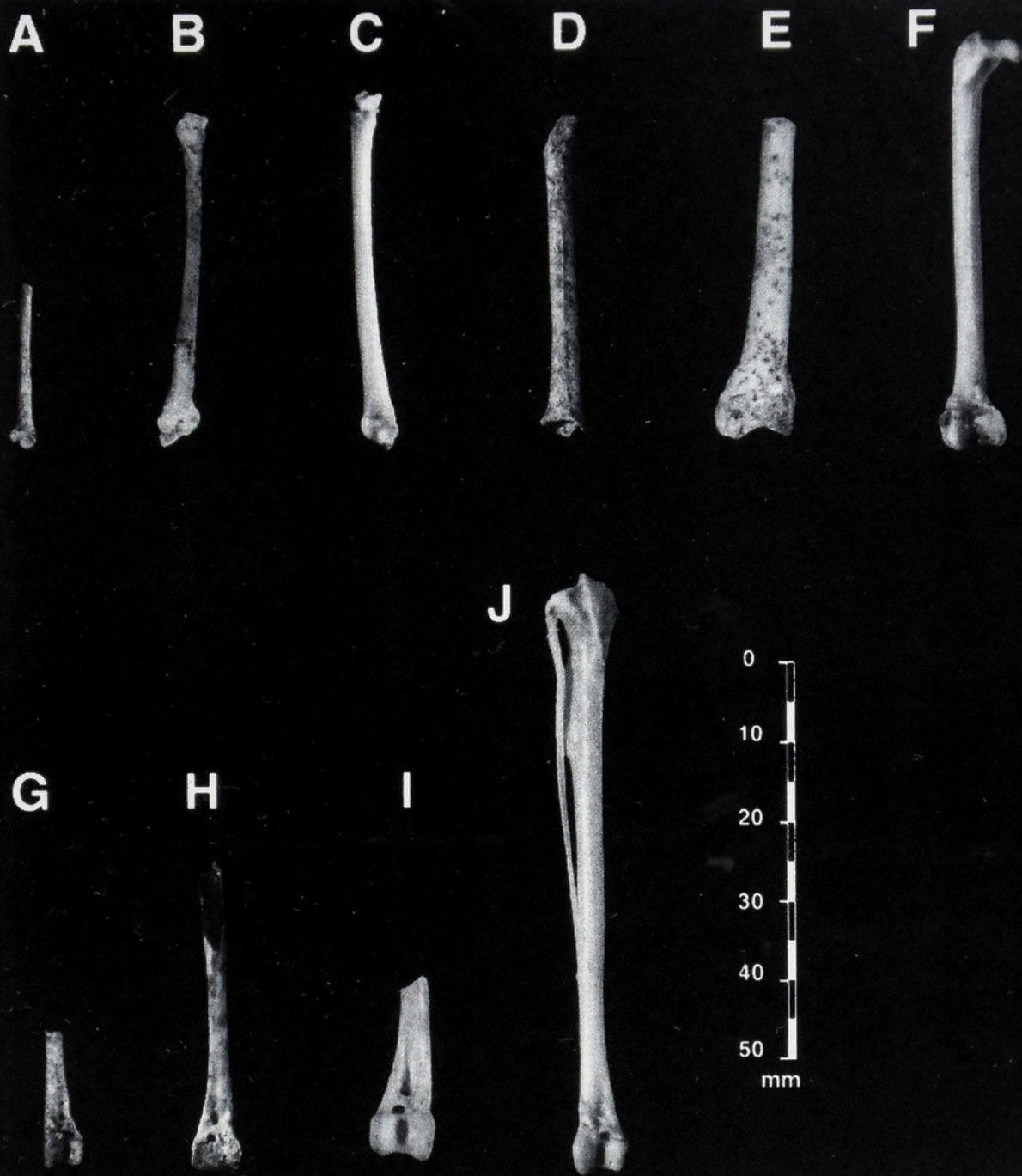


FIG. 12. The ulna in ventral aspect (A–C), femur in ventral aspect (D–F), and tibiotarsus in dorsal aspect (G–J) of *Gallirallus*. A, D, G. *G. huiatua*, MNZ S37709–S37711. H. *G. ripleyi*, USNM 402895. B, E, I. *G.* undescribed sp., UF 51734, 52518, 51729 ('Eua, Tonga). C, F, J. *G. philippensis*, MNZ 25267.

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TABLE 5. Measurements (in mm) of the ulna, femur, tibiotarsus, and tarsometatarsus of *Gallirallus*, with mean, range, and sample size.

	<i>G. huiatua</i> Niue (SU)	<i>G. ripleyi</i> Mangaia (SU)	<i>G. undescribed</i> sp. 'Eua (SU)	<i>G. philippensis</i> Tonga, Samoa (3M, 2F)
ULNA				
A. Proximal depth	3.7	—	5.5	4.7
	1		1	4.1–5.1 5
B. Width of midshaft	1.9	1.8	3.2	2.8
	1	1	3.1–3.3 2	2.4–3.1 5
C. Depth of midshaft	1.5	1.3	2.4	2.3
	1	1	2.4 2	2.0–2.5 5
C/A	0.41	—	0.44	0.50
				0.48–0.52 5
C (ulna)/C (femur)	0.41	0.39	0.54	0.63
				0.61–0.67 5
FEMUR				
A. Length of shaft	29.6	25.5	38.5	34.4
	1	1	1	29.6–38.2 5
B. Width of midshaft	3.5	2.9	4.4	3.7
	1	1	4.2–4.5 3	3.1–4.1 5
C. Depth of midshaft	3.7	3.3	4.4	3.7
	1	1	4.1–4.7 3	3.3–4.1 5
D. Least depth of distal shaft	3.4	3.4	4.5	3.6
	1	1	4.2–4.8 3	3.2–4.0 5
B/A	0.12	0.11	0.12	0.11
				0.10–0.11 5
C/A	0.12	0.13	0.12	0.11
				0.10–0.11 5
D/A	0.11	0.13	0.12	0.11
				0.10–0.11 5
TIBIOTARSUS				
Least width of shaft	2.5	2.7	3.8	3.3
	1	2.3–2.9 5	1	2.9–3.6 5
Least depth of shaft	2.4	2.5	3.2	2.9
	1	2.4–2.7 5	1	2.6–3.2 5
Distal width	5.5	6.3	8.0	6.4
	1	1	1	5.5–7.2 5

TABLE 5. CONTINUED.

	<i>G. huiatua</i> Niue (SU)	<i>G. ripleyi</i> Mangaia (SU)	<i>G. undescribed</i> sp. Eua (SU)	<i>G. philippensis</i> Tonga, Samoa (3M, 2F)
Depth of inner condyle	5.8 est	6.0	7.8	6.8
	1	1	1	6.2–7.2 5
Depth of outer condyle	5.7 est	5.9	7.3	6.5
	1	5.6–6.2 2	1	6.0–7.0 5
TARSOMETATARSUS				
Total length	39.5 est	32.9	45.1	45.0
	1	1	1	40.0–49.9 4
Length of shaft	30.9	25.0	33.6	37.3
	1	1	1	30.9–39.6 5
Proximal width	5.6 est	5.7	8.7	6.7
	1	1	1	5.8–7.4 5
Proximal depth	6.4	5.8	8.8	7.0
	1	1	1	6.5–7.4 5
Least width of shaft	2.5	3.1	4.5	3.1
	1	3.1 2	1	2.7–3.4 5
Least depth of shaft	2.2	2.1	2.9	2.6
	1	2.0–2.2 3	2.7–3.1 2	2.3–2.8 4
Distal width	6.3	6.2	8.3	6.7
	1	6.1–6.3 3	7.8–8.8 2	6.2–7.2 4

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