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Two New Species of Rails (Aves: Rallidae) from Mangaia, Southern Cook Islands[1]

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ABSTRACT: Two species of rails, *Porzana rua* n. sp. and *Gallirallus ripleyi* n. sp., are described from bones of late Holocene age found in caves on Mangaia, southern Cook Islands. Their relatively small pectoral elements show that both of these species were flightless. *Porzana rua* resembles most closely the living *P. atra* of Henderson Island and the recently extinct *P. monasa* of Kosrae Island, Carolines. *Gallirallus ripleyi* is most similar to the recently extinct *G. wakensis* of Wake Island. Some combination of predation and habitat alteration by humans and introduced mammals (rats, dogs, and pigs) is probably responsible for the extinction of *P. rua* and *G. ripleyi* within the past 1000 years. Fossils of a third species of rail from the Mangaian caves are referred to the living species *Porzana tabuensis*, although these specimens may represent an undescribed subspecies. *Porzana tabuensis* might survive on Mangaia and elsewhere in the southern Cook Islands, although entire specimens have never been collected. An X ray of the only two specimens (skins) of *Porzana monasa* (Kittlitz) shows that this species from Kosrae (Kusai) Island, Carolines, was flightless or nearly so. It is likely that all islands in the Pacific were inhabited by one or more species of flightless rail before the arrival of humans. In both *Porzana* and *Gallirallus*, at least one early wave of colonization produced flightless species throughout Oceania, followed by a less thorough and much more recent (probably late Holocene) wave of colonization by the volant *P. tabuensis* and *G. philippensis*.

IN 1984 AND 1985, I conducted a survey of the fossil and modern vertebrates of the southern Cook Islands, a scattered group of eastern Polynesian islands that has been largely ignored by vertebrate biologists. During 5 weeks on Mangaia, the second largest and southernmost of the Cook Islands, I collected fossils from six different caves in the limestone "makatea" region of the island. I have briefly reported elsewhere on Mangaia, its caves, and fossils from the 1984 collections (Steadman 1985). Here I decribe the fossils of three species of rails from the Mangaian caves, two of which are new.

METHODOLOGY

All fossils are cataloged in the Vertebrate Paleontology collections of the U.S. National Museum of Natural History, Smithsonian Institution (USNM). Skeletons used in the comparisons are from USNM, except for that of *Porzana atra* from the American Museum of Natural History (AMNH 1220). Osteological nomenclature usually follows Baumel et al. (1979). Measurements were taken with dial calipers with 0.05 mm increments and rounded to the nearest 0.1 mm. All fossils were collected from surface levels. Most of the fossils were encrusted with calcitic deposits that were removed by etching with dilute acetic acid.

SYSTEMATIC PALEONTOLOGY

Class Aves
Order Gruiformes
Family Rallidae
Genus *Porzana* Vieillot 1816

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Porzana differs from the only other genus of small rail in Oceania (*Poliolimnas*) in the following respects: the femur with a relatively stouter shaft; the tibiotarsus with a relatively stouter shaft, especially in the distal end; and the tarsometatarsus with a more prominent ridge on the proximomedial portion of the shaft and a longer crista medialis hypotarsi. These characters corroborate those of Olson (1970) in maintaining *Poliolimnas* as distinct from, although closely related to, *Porzana*.

Porzana rua, n. sp.

HOLOTYPE: Associated complete humerus and two tarsometatarsi (Figure 1), USNM 402876, collected 13 April 1984, by D. W. Steadman and T. Ngatokorua, in Te Rua Rere Cave, Tava'enga District, Mangaia, southern Cook Islands, lying on the cave floor, about 460 m from the entrance.

TOPOTYPICAL PARATYPES: Associated ulna, tibiotarsus, and tarsometatarsus (USNM 402877); four tibiotarsi (USNM 402878–402881); tarsometatarsus (USNM 402882), collected from 3 to 17 April 1984, by D. W. Steadman and T. Ngatokorua. Associated ulna, femur, two tibiotarsi, and tarsometatarsus (USNM 402883), ulna (USNM 402884), associated two tibiotarsi and tarsometatarsus (USNM 402885), tarsometatarsus (USNM 402886), collected 6 June 1985, by D. W. Steadman, T. Ngatokorua, and S. Falcone.

ADDITIONAL PARATYPES: Toruapuru Cave (Ivirua District), collected 6 April 1984, by D. W. Steadman, M. Ora, Ng. Ora, and T. Ngatokorua: humerus (USNM 402887). Tapukeu Cave (Tamarua District), collected 14 April 1984, by D. W. Steadman: tarsometatarsus (USNM 402888). Tuatini Cave (Veitatei District), collected 9 June 1985, by D. W. Steadman and P. Kareroa: femur (USNM 402889).

DIAGNOSIS: A medium-sized species of *Porzana* (Tables 1–5) with pectoral elements of the skeleton relatively more reduced (Table 6) than in any congener except *P. astrictocarpus* Olson 1973a of St. Helena Island, South Atlantic. Overall size larger than in *P. tabuensis*, *P. palmeri*, or *P. astrictocarpus*. Humerus: stouter and straighter than in *P. atra*, *P. tabuensis*, or *P. astrictocarpus*, with crista pectoralis rotated more ventrally, producing a weak proximal portion of the shaft. Ulna: straighter than in *P. atra*, *P. tabuensis*, *P. palmeri*, or *P. astrictocarpus*, with a smaller cotyla dorsalis. Femur: stouter than in *P. atra* or *P. tabuensis*, with a larger facies articularis acetabularis and a better developed impressiones obturatoriae. Tibiotarsus: relatively stouter than in *P. tabuensis*. Tarsometatarsus: shaft more slender in medial aspect than in *P. atra*.

ETYMOLOGY: From the Mangaian and Rarotongan word *rua*, meaning "hole, excavation, grave, abyss, cavity, pit, opening, chasm, etc." (Savage 1980:317). As used here, *rua* refers both to "cave" and "grave," because the limestone caves from which the specimens were collected served as the final resting places for this and many other species of extinct birds, as well as for numerous persons. Te Rua Rere, the cave that is the type locality of *P. rua*, means "flying cave" or "jumping cave." (Thus the English Te Rua Rere "Cave" is redundant but is retained for the sake of English-speaking persons.) As used here, *rua* is a feminine noun in apposition.

Porzana tabuensis (Gmelin) 1789, subspecies uncertain

REFERRED MATERIAL: Toruapuru Cave, Ivirua District, Mangaia: nearly complete associated skeleton (USNM 402890), collected 6 April 1984 by D. W. Steadman, M. Ora, Ng. Ora, and T. Ngatokorua. Te Rua Rere Cave, Tava'enga District: humerus and tarsometatarsus (USNM 402891), collected in 1983 by G. Paulay; humerus (USNM 402892) and tarsometatarsus (USNM 402893), collected 13 and 17 April 1984 by D. W. Steadman and T. Ngatokorua; tibiotarsus (USNM 402894), collected on 6 June 1985 by D. W. Steadman, T. Ngatokorua, and S. Falcone.

Along with the fossils of extinct rails, the Mangaian caves yielded five lots of fossils that I refer to the living *P. tabuensis*. These specimens, particularly the nearly complete, as-

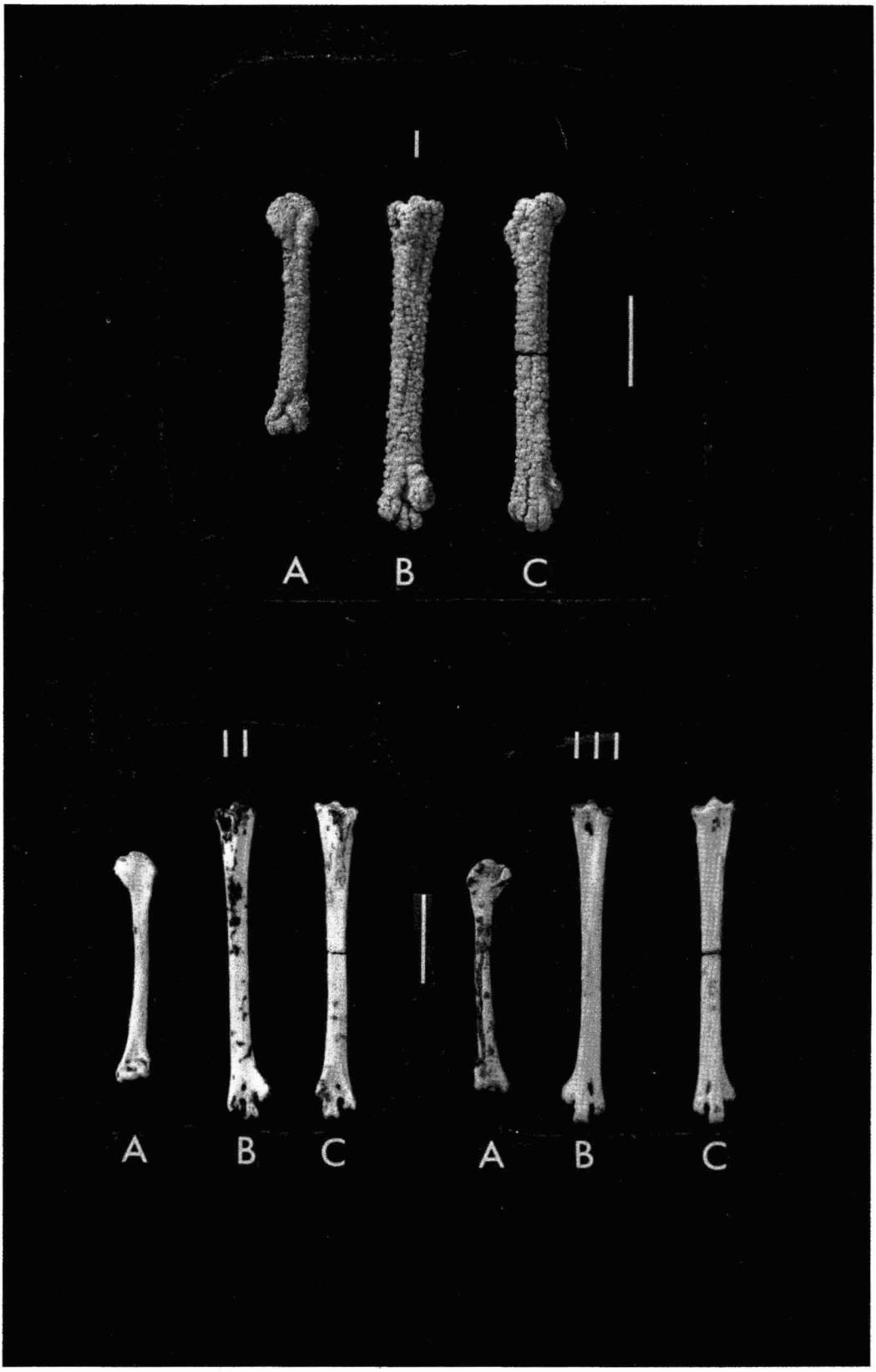

FIGURE 1. Holotype of *Porzana rua*, new species (USNM 402876). Associated humerus (*A*) and two tarsometatarsi (*B*, *C*) before (I) and after (II, III) preparation. Scale bar = 1 cm.

TABLE 1

THE HUMERUS OF *Porzana*

SPECIES, LOCALITY, AND SEX	TOTAL LENGTH (mm)	PROXIMAL WIDTH (mm)	DISTAL WIDTH (mm)
P. rua, n. sp.	25.2	4.9	3.8
Mangaia (USNM 402876)	1	1	1
P. tabuensis	25.8	4.8	3.4
Tonga	1	1	1
P. tabuensis	26.0	5.0	3.8
Mangaia (USNM 402890, 402892)	1	1	3.7–3.8 2
P. atra	28.4	5.6	3.9
Henderson Island	1	1	1
P. palmeri	19.9	4.1	2.9
Laysan Island	19.0–20.7 8	3.9–4.2 8	2.8–3.0 8
P. astrictocarpus	20.2	4.2	3.1
St. Helena Island from Olson (1973*a*)	19.8–20.9 4	4.0–4.3 4	3.0–3.2 4
P. pusilla	28.0	5.5	3.8
China (M)	1	1	1
P. fusca	32.4	6.3	4.4
Thailand (M)	1	1	1
P. porzana	35.3	7.2	4.9
Cyprus (M)	1	1	1
P. carolina	34.1	6.5	4.7
California (M)	1	1	1

NOTE: M = male; F = female. Mean, range, and sample size are given.

TABLE 2

THE ULNA OF *Porzana*

SPECIES, LOCALITY, AND SEX	TOTAL LENGTH (mm)	MINIMUM DEPTH OF SHAFT (mm)
P. rua, n. sp.	19.4	1.1
Mangaia (USNM 402877, 402883, 402884)	19.0–19.7 3	1.0–1.1 3
P. tabuensis	19.8	1.1
Tonga	1	1
P. tabuensis	20.6	1.2
Mangaia (USNM 402890)	1	1
P. atra	21.4	1.2
Henderson Island	1	1
P. palmeri	14.8	0.9
Laysan Island	14.3–15.4 9	0.8–1.0 9
P. astrictocarpus	14.8	—
St. Helena Island from Olson (1973*a*)	1	
P. pusilla	23.0	1.3
China (M)	1	1
P. fusca	27.2	1.3
Thailand (M)	1	1
P. porzana	30.4	1.6
Cyprus (M)	1	1
P. carolina	28.3	1.5
California (M)	1	1

NOTE: M = male; F = female. Mean, range, and sample size are given.

sociated skeleton from Toruapuru Cave (USNM 402890, certain elements of which are depicted in Figure 2), show that *P. tabuensis* from Mangaia is larger with a relatively more reduced wing than in the only available modern skeleton of *P. tabuensis* (USNM 345124), an unsexed bird from an unspecified island in Tonga. The Mangaian form of *P. tabuensis* may represent an undescribed subspecies, although skeletal specimens from elsewhere in eastern Polynesia are needed to pursue this idea. The subspecies of *P. tabuensis* that inhabits the Cook Islands today is unknown because of a lack of modern specimens from anywhere in the group. Holyoak (1980:27) reports this species from Mitiaro and Atiu, presumably on "sight" (sound?) records, noting also that "it may well be present on Mauke and Mangaia and possibly elsewhere." Holyoak and Thibault (1984:66) report that *P. tabuensis* is known to Mangaians according to C. C. Clerk (in litt.). The current status of *P. tabuensis* on Mangaia is discussed below under "Extinction."

Genus *Gallirallus* Lafresnaye 1841

I follow Olson (1973*b*) in recognizing *Gallirallus* (including *Hypotaenidia*) as distinct from *Rallus*. *Gallirallus* differs from other genera of Oceanic rails in its relatively stout tarsometatarsus with the medial trochlea flaring more mediad from the shaft. Likewise, the tibiotarsus and coracoid are relatively stout, and the latter is especially broad across the sternal end. The mandible is long and straight.

TABLE 3

THE FEMUR OF *Porzana*

SPECIES, LOCALITY, AND SEX	TOTAL LENGTH (mm)	PROXIMAL WIDTH (mm)	PROXIMAL DEPTH (mm)	DEPTH OF HEAD (mm)	LEAST WIDTH OF SHAFT (mm)
P. rua, n. sp.	29.8	5.2	4.4	2.4	2.2
Mangaia	1	5.1–5.3	4.3–4.5	2.4–2.5	2.1–2.2
(USNM 402883, 402889)		2	2	2	2
P. tabuensis	27.7	3.9	3.5	1.8	1.8
Tonga	1	1	1	1	1
P. tabuensis	30.1	4.4	3.9	2.1	2.0
Mangaia	1	1	1	1	1
(USNM 402890)					
P. atra	33.9	5.2	4.3	2.2	2.0
Henderson Island	1	1	1	1	1
P. palmeri	25.7	4.3	3.5	2.0	1.9
Laysan Island	1	1	1	1	1
P. astrictocarpus	27.0	—	—	—	1.9
St. Helena Island	25.3–29.0				1.8–2.2
from Olson (1973*a*)	8				10
P. pusilla	29.8	4.3	3.4	2.1	1.9
China (M)	1	1	1	1	1
P. fusca	34.9	5.3	4.0	2.4	2.1
Thailand (M)	1	1	1	1	1
P. porzana	38.8	5.6	5.0	2.5	2.6
Cyprus (M)	1	1	1	1	1
P. carolina	34.7	5.7	4.6	2.4	2.3
California (M)	1	1	1	1	1

NOTE: M = male; F = female. Mean, range, and sample size are given.

Gallirallus ripleyi, n. sp.

HOLOTYPE: Associated distal half of tibiotarsus and complete tarsometatarsus (Figure 3), USNM 402895, collected 13 April 1984, by D. W. Steadman and T. Ngatokorua in Te Rua Rere Cave, Tava'enga District, Mangaia, southern Cook Islands, lying on the cave floor about 300 m from the entrance.

TOPOTYPICAL PARATYPES: Coracoid and mandible (USNM 402896, 402897; Figure 4), collected 3 April 1984, by D. W. Steadman and T. Ngatokorua.

DIAGNOSIS: A small species of *Gallirallus* (Tables 7–10) with pectoral elements of the skeleton reduced more than in other congeners except *G. wakensis* and *G. owstoni*. Overall size of most elements smaller than in any species except *G. wakensis*. Mandible: more slender than in other species but most closely approached by *G. wakensis*. Coracoid: shaft and sternal end mediolaterally expanded but dorsoventrally compressed; in sternal aspect, facies articularis sternalis more curved than in *G. wakensis*; impressio musculo sternocoracoidei deeper than in *G. wakensis*, *G. owstoni*, or *G. philippensis*. Tibiotarsus: distal end broad relative to depth. Tarsometatarsus: stouter in dorsal aspect than in other species except *G. australis*; proximal portion of shaft shallow in medial aspect; medial trochlea more rounded in medial aspect.

ETYMOLOGY: Named after S. Dillon Ripley, in recognition of his long interest in the Rallidae and in the systematics and conservation of birds on tropical islands, including the sponsorship of D. T. Holyoak's fieldwork in the Cook Islands in 1973.

TABLE 4

THE TIBIOTARSUS OF *Porzana*

SPECIES, LOCALITY, AND SEX	LENGTH FROM DISTAL END OF FIBULAR CREST TO PROXIMAL END OF TENDINAL BRIDGE (mm)	LEAST WIDTH OF SHAFT (mm)	LEAST DEPTH OF SHAFT (mm)
P. rua, n. sp.	34.8	2.0	1.8
Mangaia	32.9–36.6	1.9–2.1	1.7–1.8
(USNM 402879, 402880)	2	2	2
P. tabuensis	27.5	1.6	1.3
Tonga	1	1	1
P. tabuensis	31.1	1.6	1.5
Mangaia	1	1	1.5
(USNM 402890, 402894)			2
P. atra	35.9	2.1	1.7
Henderson Island	1	1	1
P. monasa	37.0	—	—
Kusai Island	1		
P. palmeri	25.1	1.6	1.3
Laysan Island	24.2–26.3	1.6–1.7	1.2–1.4
	9	9	9
P. astrictocarpus	—	1.9	—
St. Helena Island		1.7–2.0	
from Olson (1973*a*)		7	
P. pusilla	31.5	1.7	1.4
China (M)	1	1	1
P. fusca	37.8	1.9	1.6
Thailand (M)	1	1	1
P. porzana	37.7	2.2	1.8
Cyprus (M)	1	1	1
P. carolina	34.9	2.0	1.8
California (M)	1	1	1

NOTE: M = male; F = female. Mean, range, and sample size are given.

DISCUSSION

Evolution and Biogeography

Flightlessness occurs in many species of rails on islands throughout the world that lack mammalian predators. Thus it is not surprising that both *Porzana rua* and *Gallirallus ripleyi* evolved a flightless condition on Mangaia, where the only native mammal is the frugivorous "flying fox" *Pteropus tonganus* (Wodzicki and Felten 1981). The evolutionary stages and mechanisms for attainment of flightlessness in rails have been described by Olson (1973a). Insular forms of *Porzana* and *Gallirallus* are both particularly prone to flightlessness, the former being represented by *P. palmeri* of Laysan, *P. sandwichensis* and at least eight undescribed species of *Porzana* from the Hawaiian Islands (Olson and James 1982a, 1982b, 1984, pers. comm.), *P. atra* of Henderson, *P. monasa* of Kosrae (Carolines), *P. astrictocarpus* of St. Helena in the South Atlantic, and several undescribed forms from Bermuda (Olson 1977). Flightless species of *Gallirallus* include *G. wakensis* of Wake (Greenway 1958:82, 216–218), *G. owstoni* of Guam (Baker 1951:118–120; Ripley and Beehler 1985), *G. dieffenbachii* and *G. modestus* of the Chatham Islands (Olson 1975), *G. australis* and possibly *G. insignis* of New Zealand (Olson 1977), *G. pacificus* of Tahiti, known only from a painting done in 1773 or 1774 by Georg Forster during Captain James

TABLE 5

THE TARSOMETATARSUS OF *Porzana*

SPECIES, LOCALITY, AND SEX	TOTAL LENGTH (mm)	PROXIMAL WIDTH (mm)	LEAST WIDTH OF SHAFT (mm)	LEAST DEPTH OF SHAFT (mm)	DISTAL WIDTH (mm)
P. rua, n. sp.	34.7	4.9	2.2	1.5	4.8
Mangaia	34.3–35.1	4.9–5.0	2.1–2.3	1.4–1.6	4.7–4.8
(USNM 402876, 402877, 402882, 402885)	3	3	4	4	2
P. tabuensis	25.8	3.4	1.8	1.3	3.5
Tonga	1	1	1	1	1
P. tabuensis	28.5	3.8	2.0	1.4	3.8
Mangaia	27.9–28.7	3.8	1.8–2.1	1.4	3.7–3.9
(USNM 402890, 402891, 402893)	3	2	4	3	3
P. atra	34.4	4.7	2.2	1.7	4.6
Henderson Island	1	1	1	1	1
P. monasa	35.6	—	—	—	4.8
Kusai Island	34.7–36.6				1
	2				
P. palmeri	23.5	3.6	1.9	1.4	3.7
Laysan Island	22.5–24.7	3.4–3.7	1.8–2.0	1.3–1.4	3.6–3.9
	9	9	9	9	9
P. astrictocarpus	27.0	4.0	2.0	—	4.2
St. Helena Island	26.2–27.9	3.9–4.1	1.9–2.1		4.1–4.4
from Olson (1973*a*)	7	7	5		5
P. pusilla	29.1	3.7	1.8	1.4	3.7
China (M)	1	1	1	1	1
P. fusca	34.8	4.2	1.9	1.6	4.5
Thailand (M)	1	1	1	1	1
P. porzana	34.8	4.4	2.2	1.8	4.5
Cyprus (M)	1	1	1	1	1
P. carolina	35.5	4.2	2.1	1.8	4.4
California (M)	1	1	1	1	1

NOTE: M = male; F = female. Mean, range, and sample size are given.

Cook's second voyage (Lysaght 1953, 1959; Olson 1973*b*), and the recently discovered *G. okinawae* of Okinawa (Ripley and Beehler 1985). The occurrence of *G. ripleyi* on Mangaia lends credence to the validity of *G. pacificus* by providing a specimen-based example of an endemic species of *Gallirallus* from eastern Polynesia.

Porzana rua is similar, both in size (Tables 1–5) and in qualitative features, to *P. atra*, a flightless species that still lives on Henderson Island in the Pitcairn Group of southeastern Polynesia. The main difference between the two species is the more reduced pectoral girdle in *P. rua* than in *P. atra* or any other species of *Porzana* known in the Pacific, although a similar level of pectoral reduction is found in *P. astrictocarpus* Olson 1973a of the South Atlantic. *Porzana rua* differs otherwise from *P. astrictocarpus* as noted in the Diagnosis section. The similarity of *P. rua* to *P. atra*, and perhaps to *P. palmeri*, *P. monasa*, and *P. astrictocarpus* as well, may be due mainly to their having similar or identical ancestors. Based upon size and plumage, Olson (1973*a*) suggested that *P. pusilla*, whose distribution is given in Olson's Fig. 6, was ancestral to *P. palmeri* and *P. astrictocarpus*. *Porzana rua* may also be closely related to *P. pusilla*, although the plumage of the former probably never will be known. *Porzana tabuensis* is the only volant species of *Porzana* in Oceania, yet its relationships to the flightless species of *Porzana* are not clear. I have found no unique features in the postcranial osteology of any species of *Porzana*, including *P. pusilla* or *P.*

TABLE 6

RATIO OF HUMERUS TO TARSOMETATARSUS IN *Porzana*

SPECIES, LOCALITY, AND SEX	RATIO OF LENGTH OF HUMERUS TO LENGTH OF TARSOMETATARSUS	VOLANCY*
P. rua, n. sp.	0.74	NV
Mangaia	1	
(USNM 402876)		
P. tabuensis	1.00	V
Tonga	1	
P. tabuensis	0.90	V?
Mangaia	1	
(USNM 402890)		
P. atra	0.83	NV
Henderson Island	1	
P. palmeri	0.85	NV
Laysan Island	0.81–0.90	
	8	
P. astrictocarpus	0.75	NV
St. Helena Island from Olson (1973*a*); based upon means only	1	
P. pusilla	0.96	V
China (M)	1	
P. fusca	0.93	V
Thailand (M)	1	
P. porzana	1.01	V
Cyprus (M)	1	
P. carolina	1.02	V
California (M)	1	

NOTE: M = male; F = female. Mean, range, and sample size are given.

* V = volant; NV = nonvolant.

tabuensis, that would strongly suggest ancestral relationships to flightless species.

Porzana monasa (Kittlitz) 1858 is known only from two skins collected on Kosrae Island, Carolines, in December 1827 or January 1828 by F. H. von Kittlitz (Baker 1951:121–123; Greenway 1958:238–240). The two specimens of *P. monasa*, housed in the collections of the Zoological Institute, USSR Academy of Sciences, Leningrad, have been X-rayed (Figure 5) to provide the measurements in Tables 4 and 5. Unfortunately, neither the humerus nor the complete ulna is preserved in these specimens, thus precluding direct comparison with the pectoral elements of *P. rua*. Based upon the length of the carpometacarpus in the X ray, *P. monasa* must have been flightless, although the pectoral reduction was relatively less than in *P. astrictocarpus* or *P. rua*. The tibiotarsus and tarsometatarsus of *P. monasa* are roughly the same lengths as those of *P. rua* of Mangaia. Because the latter certainly was flightless and evolved *in situ* on Mangaia, and the same must be true for *P. monasa* on Kosrae, one can assume that these two rails represent different species. Surgical removal of a tarsometatarsus from a skin of *P. monasa* would provide valuable evidence for diagnosing *P. monasa* more thoroughly. What little is known about the habits and extinction of *P. monasa* has been summarized in Greenway (1958:238–240), who makes no reference to the flying ability of this species.

Another poorly known form of *Porzana* deserves mention. Like *Gallirallus pacificus*, *Porzana nigra* is a rail known only from a painting done in Tahiti by Georg Forster on Cook's second voyage in 1773 or 1774. Although Lysaght (1956) and Bruce et al. (1983) have assumed that *P. nigra* must pertain to *P. tabuensis*, the occurrence of two species of *Porzana* on Mangaia shows that this assumption may be invalid. Like *P. rua* of Mangaia, *Porzana nigra* of Tahiti may represent an endemic, flightless species that did not survive long enough to be recorded from life (Olson and Steadman, in press). Rather than assume that *P. nigra* represents a living species, it is just as likely that this is only one of the hundreds or thousands of populations of flightless rails that must have become extinct in the Pacific since human takeover of the islands.

Gallirallus ripleyi is most similar to *G. wakensis* in size and in degree of pectoral modification for flightlessness. Considering the vast distance between Mangaia and Wake, this resemblance might be interpreted as a result of parallel evolution from a similar ancestor. *Gallirallus philippensis* is the only oceanic species of *Gallirallus* that is volant. This widespread, polymorphic species ranges from the Philippines and eastern Indonesia to the western Polynesian islands of Samoa, Tonga, and Niue (Ripley 1977). The nearest that any living species of *Gallirallus* approaches Mangaia is the population of *G. philippensis goodsoni*

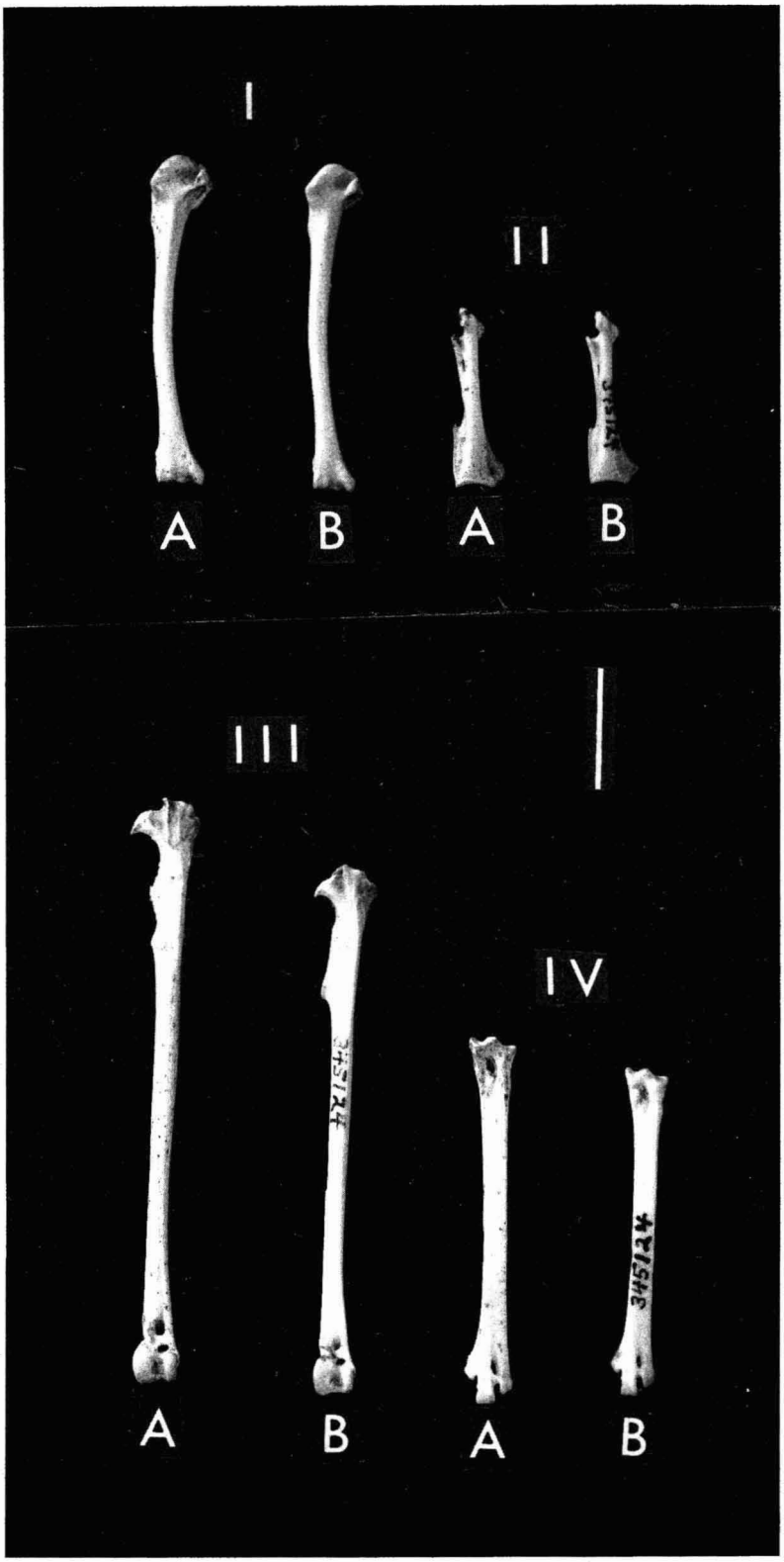

FIGURE 2. *Porzana tabuensis*. Humerus (I), coracoid (II), tibiotarsus (III), and tarsometatarsus (IV). *A*, associated fossil skeleton from Mangaia, USNM 402890. *B*, modern skeleton (sex undetermined) from Tonga, USNM 345124. Scale bar = 1 cm.

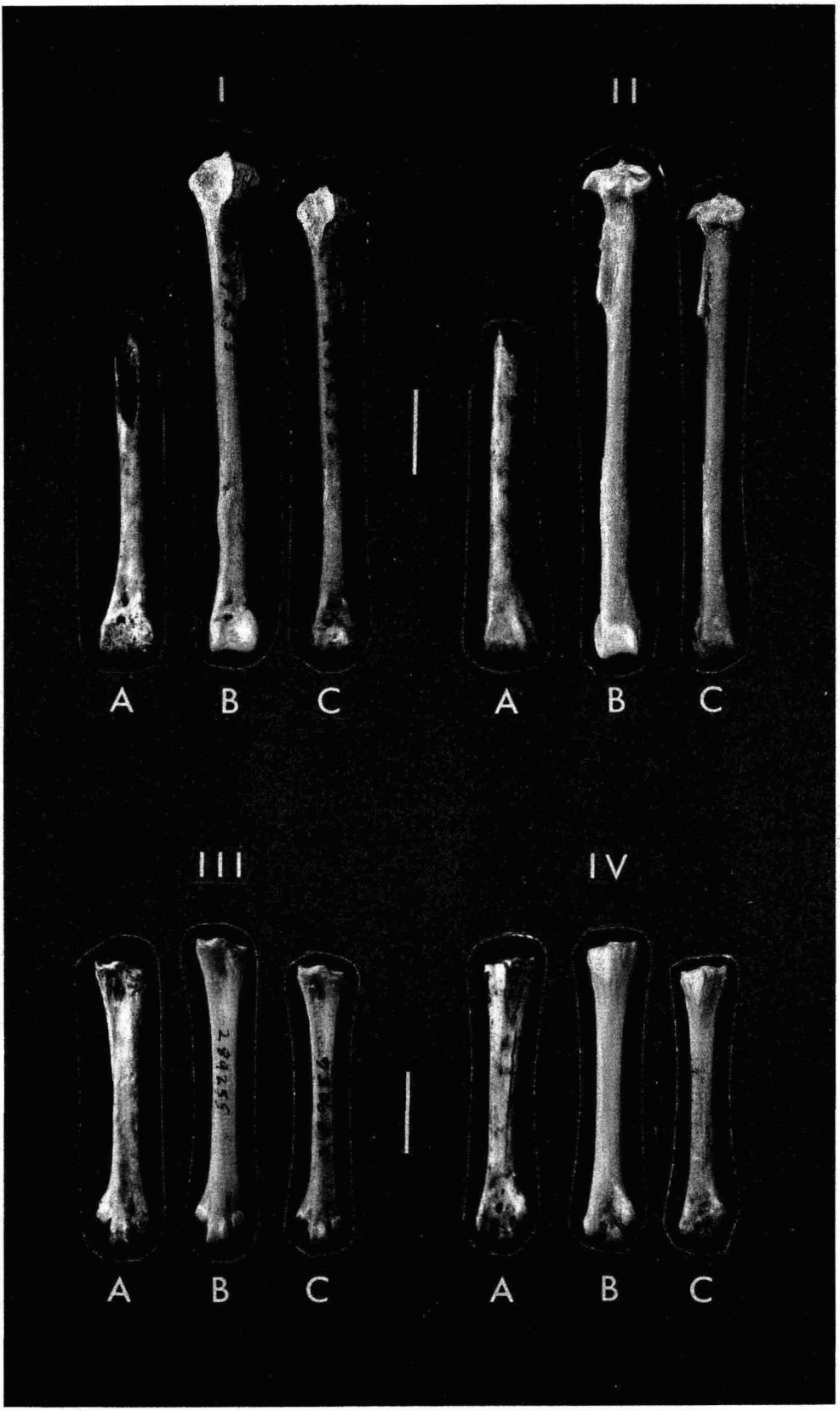

FIGURE 3. *Gallirallus*. Tibiotarsus in cranial (I) and caudal (II) aspects. Tarsometatarsus in dorsal (III) and plantar (IV) aspects. *A*, holotype of *G. ripleyi*, new species, USNM 402895. *B*, *G. wakensis*, male, USNM 289255. *C*, *G. wakensis*, female, USNM 289256. Scale bar = 1 cm.

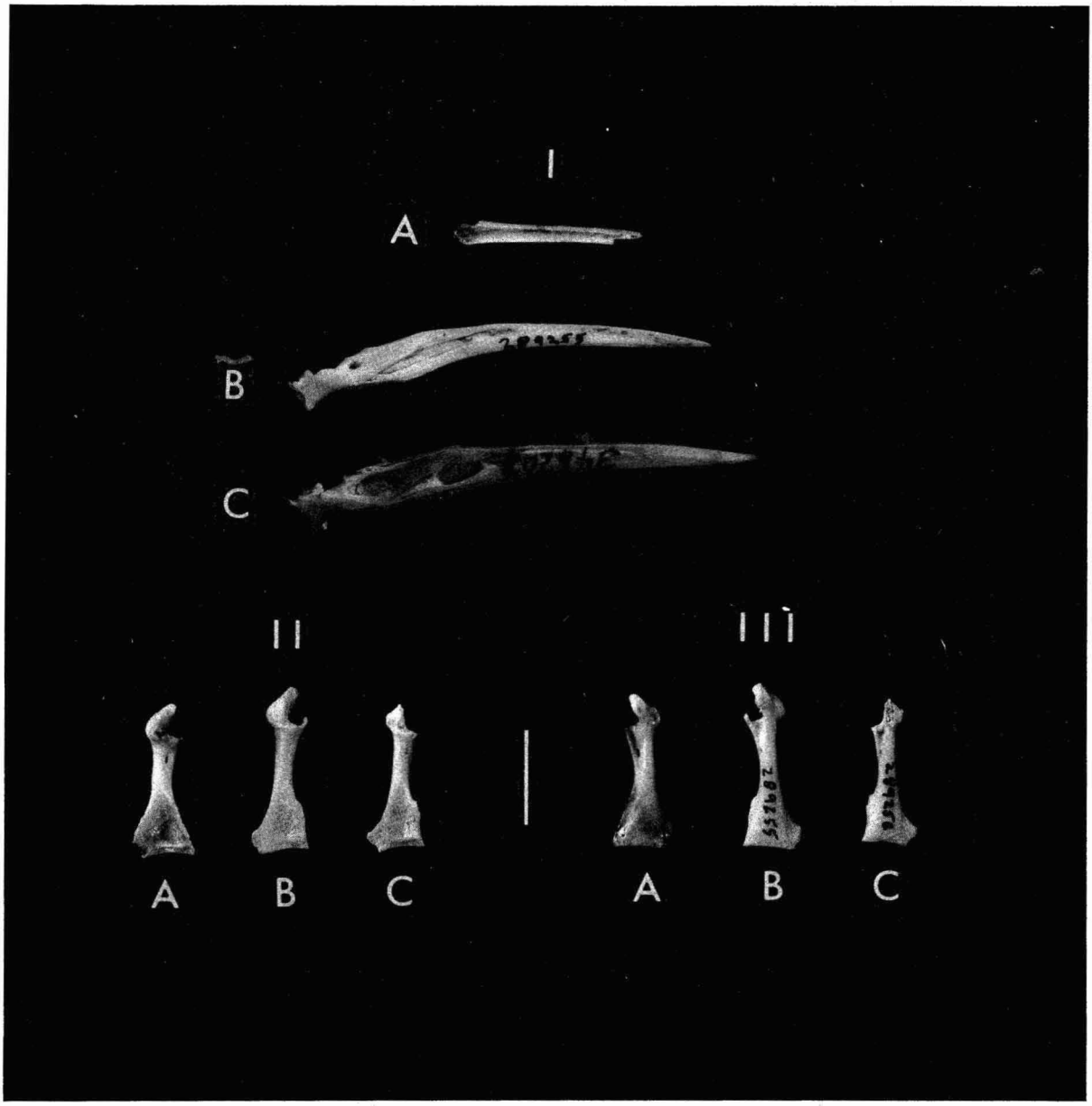

FIGURE 4. *Gallirallus*. Mandibular ramus (I) in right lateral aspect. *A*, paratype of *G. ripleyi*, new species, USNM 402897. *B*, *G. wakensis*, male, USNM 289255. *C*, *G. philippensis*, male, USNM 346207. Coracoid in dorsal (II) and ventral (III) aspect. *A*, paratype of *G. ripleyi*, new species, USNM 402896. *B*, *G. wakensis*, male, USNM 289255. *C*, *G. wakensis*, female, USNM 289256. Scale bar = 1 cm.

TABLE 7

THE CORACOID OF *Gallirallus*

SPECIES, LOCALITY, AND SEX	TOTAL LENGTH (mm)	WIDTH OF STERNAL FACET (mm)	LEAST WIDTH OF SHAFT (mm)	LEAST DEPTH OF SHAFT (mm)	LENGTH OF HUMERAL FACET (mm)
G. ripleyi, n. sp.	15.3	5.4	2.0	1.1	2.8
Mangaia	1	1	1	1	1
(USNM 402896)					
G. wakensis	16.0	5.3	1.8	1.2	2.6
Wake Island	15.4–16.8	5.0–5.7	1.7–1.9	1.1–1.5	2.5–2.8
(8M, 8F)	15	16	16	16	3
G. owstoni	21.2	5.8	2.2	1.5	3.4
Guam	20.6–21.6	5.5–6.0	1.9–2.6	1.1–1.7	3.3–3.6
(6M, 1F)	7	7	7	7	7
G. philippensis	22.2	6.4	2.8	2.0	3.5
New Zealand, Tonga,	22.0–22.5	5.9–6.8	2.6–3.2	1.8–2.1	3.4–3.6
captive (1M, 3?)	4	4	4	4	4
G. striatus	23.0	5.3	2.2	1.6	3.4
China? (M)	1	1	1	1	1
G. torquatus	26.5	7.3	2.7	1.8	4.0
Philippines (M)	1	1	1	1	1
G. australis	33.4	9.9	4.7	2.9	5.6
New Zealand,	32.4–34.5	9.4–10.7	4.6–4.8	2.8–2.9	5.5–5.6
captive (3M)	3	3	3	3	3

NOTE: M = male; F = female. Mean, range, and sample size are given.

from Niue (Kinsky and Yaldwyn 1981), 1300 km west-northwest of Mangaia. Based solely upon modern distributions, *G. philippensis* would be a likely choice as the ancestor or nearest relative of most or all of the flightless, insular species of *Gallirallus*. Nevertheless, this connection has not been demonstrated and is not evident from examination of skeletal specimens. *Gallirallus torquatus* and *G. striatus* of the Indo-Malaysian region resemble *G. ripleyi* to some extent in their concave dorsal surface of the sternal half of the coracoid, although these species lack other features that would suggest a close relationship to *G. ripleyi*.

The invasion of the Pacific by *Gallirallus* may have resembled that of *Porzana* in having a first wave of colonization that produced flightless species, such as *G. australis*, *G. dieffenbachii*, *G. wakensis*, *G. owstoni*, *G. ripleyi*, and *G. pacificus*, followed by another wave of colonization by the living and volant *G. philippensis*, which thus far has penetrated eastward no farther than Niue and Samoa. The first wave of *Gallirallus* was more thorough and widespread, for recently I have discovered two other undescribed, flightless species of *Gallirallus* among bones from archaeological sites on Huahine, in the Society Group, and on Ua Huka and Tahuata, Marquesas, at the northeastern edge of Polynesia. The idea that at least two waves of colonization occurred in Oceania for *Porzana* and *Gallirallus* is mentioned by Olson and Steadman (in press) with regard to eastern Polynesia, although strong supportive evidence exists for New Zealand as well, where Millener (1981:258, 579–580, 588–592) has shown that the extant species of volant rails, including *Porzana tabuensis* and *Gallirallus philippensis*, are very rare or nonexistent as Holocene fossils, suggesting that these species may have colonized New Zealand since the arrival of Polynesians. The endemic, flightless species of rails in New Zealand, nearly all of which became extinct since the arrival of Polynesians, generally occur commonly in the Holocene fossil record, including Polynesian-derived midden deposits.

As additional flightless species of *Porzana*

TABLE 8

THE TIBIOTARSUS OF *Gallirallus*

SPECIES, LOCALITY, AND SEX	DISTAL WIDTH (mm)	DEPTH OF MEDIAL CONDYLE (mm)	DEPTH OF LATERAL CONDYLE (mm)
G. ripleyi, n. sp.	6.3	5.9	5.5
Mangaia	1	1	1
(USNM 402895)			
G. wakensis	5.4	5.5	5.3
Wake Island	5.1–5.7	5.0–5.7	4.9–5.6
(2M, 1F)	3	3	3
G. owstoni	6.6	6.9	6.8
Guam	6.5–6.7	6.7–7.2	6.5–7.0
(6M, 1F)	7	7	7
G. philippensis	5.7	6.0	5.6
Captive	5.5–5.9	5.9–6.0	5.5–5.6
(1M, 1?)	2	2	2
G. striatus	5.2	5.5	5.4
China? (M)	1	1	1
G. torquatus	6.7	7.3	7.1
Philippines (M)	1	1	1
G. dieffenbachii	7.3	7.3	7.0
Chatham Islands	1	1	1
G. australis	12.0	12.3	11.7
New Zealand,	11.4–12.4	11.6–12.8	11.3–12.2
captive (3M)	3	3	3

NOTE: M = male; F = female. Mean, range, and sample size are given.

and *Gallirallus* become known through paleontological and archaeological studies, it may become increasingly difficult to find characters to distinguish the various forms, even though the attainment of flightlessness prohibits genetic interchange between islands. In *Porzana rua* as well as in *Gallirallus ripleyi*, the key to diagnosing these new species adequately is having associated lots of fossils that include elements of both the pectoral and pelvic limbs. Without such associated material, isolated fossils would be more difficult to assign to species.

Extinction

One or more species of flightless rails probably lived on nearly every Pacific island before the time of human influence (Steadman and Olson 1985). The survival into historic times of endemic species of flightless rails on small, low, rather uniform islands such as Laysan and Wake is evidence that the area, elevation, and habitat diversity of an island need not be great in order to support endemic rails. Human activities, however, are not compatible with the survival of flightless rails. The extreme vulnerability of flightless, ground-nesting birds on islands has been documented for many different taxa on many different island groups (Greenway 1958) and need not be repeated here. The colonization of Mangaia by Polynesians some 1000 years ago (Bellwood 1979:348), accompanied by rats, dogs, pigs, and chickens, signaled the end for *Porzana rua*, *Gallirallus ripleyi*, and other species of birds. (See the list of extinct species in Steadman 1985.) Within the past millennium, the precise time of extinction for these birds is unknown. No ornithological collecting was conducted on Mangaia until Holyoak visited the island in 1973 (Holyoak 1974, 1980), so it is difficult to determine which of Mangaia's birds became extinct in prehistoric versus historic times.

Only one of the three species of rails known from Mangaia survives there today, and this very likely is *Porzana tabuensis*, although no modern specimens exist to document its occurrence. According to the Mangaians, a small, black rail exists on their island. This elusive bird is known as the "mo'o mo'o." Many Mangaians told me of seeing or hearing the "mo'o mo'o" on rare occasions in the taro swamps on the inner side of the makatea. These persons generally said that the bird has become rarer during their own lifetimes. As noted in Steadman (1985), the capture of a modern specimen of "mo'o mo'o" is a goal of future fieldwork on Mangaia. It would seem at first that the "mo'o mo'o" will prove to be *P. tabuensis*, particularly because some Mangaians claim that it can fly, although weakly and not for long distances, and because one would presume that a volant or barely volant species would persist longer than a flightless species such as *Porzana rua*. Nevertheless, when confronted with Plate 9 of duPont (1976), in which both *P. tabuensis* and *P. atra* are illustrated in color, the Mangaians invariably pointed to *P. atra* as being their "mo'o mo'o," noting the totally black body and the bright red iris and tarsus. Until a specimen is pro-

TABLE 9

THE TARSOMETATARSUS OF *Gallirallus*

SPECIES, LOCALITY, AND SEX	TOTAL LENGTH (mm)	PROXIMAL WIDTH (mm)	DISTAL WIDTH (mm)	LEAST WIDTH OF SHAFT (mm)	LEAST DEPTH OF SHAFT (mm)	RATIO OF LEAST WIDTH TO TOTAL LENGTH
G. ripleyi, n. sp.	32.9	5.6+	6.2	3.0	2.0	0.091
Mangaia	1	1	1	1	1	1
(USNM 402895)						
G. wakensis	35.0	5.9	6.0	2.7	2.0	0.078
Wake Island	33.2–36.0	5.6–6.1	5.8–6.2	2.4–2.9	1.8–2.1	0.072–0.081
(2M, IF)	3	3	3	3	3	3
G. owstoni	49.1	6.8	7.1	3.3	2.4	0.068
Guam	47.4–50.6	6.5–7.0	6.7–7.5	3.2–3.5	2.3–2.5	0.063–0.072
(6M, 1F)	7	7	7	7	7	7
G. philippensis	39.7	6.3	5.6	2.9	2.2	0.072
captive	38.9–40.5	6.1–6.5	5.0–6.3	1	2.1–2.2	1
(1M, 1?)	2	2	2		2	
G. striatus	40.4	5.4	5.5	2.9	2.0	0.072
China? (M)	1	1	1	1	1	1
G. torquatus	54.1	7.1	7.6	3.4	2.6	0.063
Philippines (M)	1	1	1	1	1	1
G. dieffenbachii	47.0	7.7	8.8	3.7	2.4	0.079
Chatham						
Islands	1	1	1	1	1	1
G. australis	68.0	12.3	14.1	6.2	4.5	0.091
New Zealand,	65.2–69.9	11.6–13.0	13.7–14.6	5.6–6.6	4.3–4.6	0.086–0.094
captive (3M)	3	3	3	3	3	3

NOTE: M = male; F = female. Mean, range, and sample size are given.

TABLE 10

THE HUMERUS AND THE RATIOS OF HUMERUS AND CORACOID TO TARSOMETATARSUS IN *Gallirallus*

SPECIES, LOCALITY, AND SEX	LENGTH OF HUMERUS (mm)	RATIO OF LENGTHS: HUMERUS TO TARSOMETATARSUS	RATIO OF LENGTHS: CORACOID TO TARSOMETATARSUS	FLYING ABILITY*
G. ripleyi, n. sp.	—	—	0.46	NV
Mangaia			1	
(USNM 402895, 402896)				
G. wakensis	32.6	0.93	0.46	NV
Wake Island	30.7–33.9	0.92–0.94	0.46–0.47	
(2M, IF)	3	3	2	
G. owstoni	42.7	0.87	0.43	NV
Guam	41.4–44.7	0.83–0.92	0.42–0.45	
(6M, 1F)	7	7	7	
G. philippensis	45.8	1.16	0.56	V
Captive	44.0–47.5	1.09–1.22	0.56	
(1M, 1F)	2	2	2	
G. striatus	44.7	1.11	0.57	V
China? (M)	1	1	1	
G. torquatus	49.7	0.92	0.49	V?
Philippines (M)	1	1	1	
G. dieffenbachii	44.1	0.94	—	NV
Chatham Islands	1	1		
G. australis	60.1	0.89	0.49	NV
New Zealand,	57.8–62.5	0.88–0.89	0.49–0.50	
captive (3M)	3	3	3	

NOTE: M = male; F = female. Mean, range, and sample size are given.
*V = volant; NV = nonvolant.

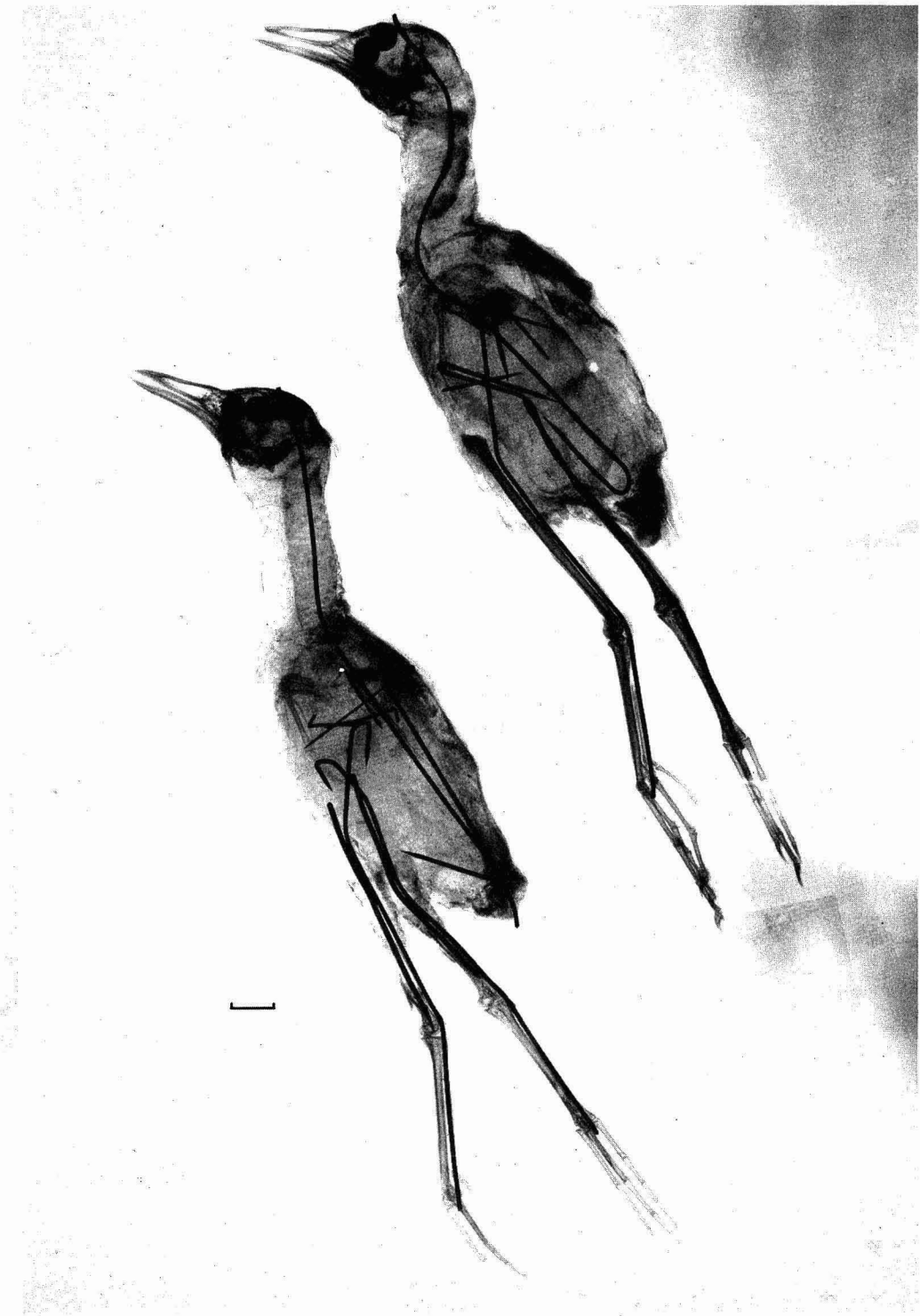

FIGURE 5. X ray of holotype specimens of *Porzana monasa*. Zoological Institute, USSR Academy of Sciences, Leningrad. Scale bar = 1 cm.

cured, it is uncertain whether Mangaia's rare but surviving "mo'o mo'o" might be *P. rua* rather than *P. tabuensis*.

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