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THE PREHISTORY OF TERRESTRIAL REPTILES AND BIRDS IN THE CENTRAL LAU GROUP, FIJI

Gregory K. Pregill[1] and David W. Steadman[2]

ABSTRACT

We identified nearly 1000 bones of reptiles and birds from 20 prehistoric sites in caves and rockshelters on four islands (Lakeba, Nayau, Aiwa Levu, and Aiwa Lailai) in the Lau Group of Fiji. The bones are Late Holocene in age (ca. 2800 to 200 years old) and are contemporaneous with prehistoric human habitation of the islands. They represent 32 species (7 reptiles, 25 non-passerine landbirds). Six of the seven taxa of squamate reptiles recovered from the prehistoric sites are indigenous to the Lau Group, including an undescribed and presumably extinct species of gekkonid lizard. While the Lau islands have never been surveyed comprehensively for modern squamate reptiles, six other species of lizards known to occur in Lau today are not represented with certainty in any of the bone deposits (the geckos *Hemidactylus frenatus* and *Lepidodactylus lugubris*, and skinks *Emoia cyanura*, *E. impar*, *Cryptoblepharus eximius*, and *Lipinia noctua*). Except for *C. eximius*, these synthropic and not necessarily native species are widespread on Pacific islands, with much or all of their dispersal being due to human agency. For landbirds, the prehistoric bones increase the species richness values from 21 to 29 species on Lakeba, from 17 to 19 species on Nayau, from 18 to 26 on Aiwa Levu, and from 16 to 17 on Aiwa Lailai. The extinct species of birds consist of two megapodes (*Megapodius alimentum*, *M. amissus*), two flightless rails (*Gallirallus* undescribed sp., *Porzana* undescribed sp.), and a pigeon (*Ducula lakeba*). Three living species of birds recorded prehistorically, but that no longer occur on these islands, are characteristic of freshwater habitats: the heron *Butorides striatus* and two volant rails, *Porzana tabuensis* and *Poliolimnas cinereus*. Three other extant species recorded from bones on Lakeba, but that no longer inhabit that island or any others in Lau, are the pigeon *Didunculus* cf. *strigirostris*, parrot *Prosopeia* sp., and lorikeet ?*Charmosyna amabilis*. Much of the inter-island differences in total species richness of birds (modern + prehistoric) is probably due to uneven sampling of prehistoric bones, which are both older (on average) and more abundant on Lakeba and Aiwa Levu than on the other two islands. Reconstructing the composition of the reptile and bird communities as they existed at first human contact demonstrates the unappreciated species richness of very small islands, a concept of interest to biogeographers and conservation biologists.

Key words: archaeological sites; Aves; Squamata; Fiji; Lau Group; late Holocene; extinction.

[1]Department of Biology, University of San Diego, 5998 Alcalá Park, San Diego, California, 92110 USA; <pregill@sandiego.edu>
[2]Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA 32611-7800; <dws@flmnh.ufl.edu>

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INTRODUCTION

In spite of the worldwide interest in biodiversity in recent decades, many Pacific islands remain poorly surveyed (if at all) even for relatively conspicuous groups of animals such as reptiles and birds (Crombie and Pregill, 1999; Steadman, 2006b). The Lau Group in Eastern Fiji is a good example of this phenomenon. Its reptile fauna has never been thoroughly surveyed in the field; all that is known about the distribution of reptiles in Lau is from the indispensable monograph by George Zug (1991) on the lizards of Fiji, which lists museum records of Lauan species. Most of these records are based on specimens at the American Museum of Natural History (AMNH) collected by the Whitney South Sea Expedition, which briefly visited some islands in Lau in the 1920s (Burt and Burt, 1932). Other specimen records are in the collections of The Natural History Museum, London (NHM), Bernice P. Bishop Museum (BPBM), Museum of Comparative Zoology, Harvard University (MCZ), and National Museum of Natural History, Smithsonian Institution (USNM). The prehistoric squamate specimens that we describe here are from islands for which modern species lists vary from reasonably complete (Aiwa Levu) to inadequate (Lakeba) to nearly non-existent (Nayau, Aiwa Lailai). Although most of our field work in Lau focused on survey and excavation of paleontological (non-cultural) and archaeological (cultural) sites, we were able to add species to the modern lizard faunas, and to gather new information on other species recorded previously.

Birds of the Lau Group also are among the most poorly known in West Polynesia. Mentioned in a very general way in review works such as Watling (1982, 1985, 2001), Clunie (1984), and Pratt et al. (1987), nothing had been reported about their relative abundance or habitat relationships until Janet Franklin and DWS began point-count surveys on Lakeba in May 1999 (Steadman and Franklin, 2000). During February and March 2000, and October 2001, we did more point-count surveys on Lakeba as well as on Nayau and Aiwa Levu (Franklin and Steadman, 2010). We also visited Aiwa Lailai briefly, but were unable to conduct point-counts there. The islands of Lau lack most of the species of landbirds found on the six largest, western Fijian islands (Watling, 1982, 2001; Steadman, 2006b). Considering both modern and

prehistoric records, only two (*Mayrornis lessoni*, *Myzomela jugularis*) of the 27 species of landbirds that still exist in Lau are endemic to Fiji. These values compare with 14 of 47 modern species on Viti Levu, which is the largest island in Fiji.

Beginning in 2001, Sean Connaughton, Sharyn Jones, Sepeti Matararaba, Patrick O'Day, GKP, and DWS excavated a number of prehistoric sites on four islands in Lau. The resulting archaeological information, including the stratigraphy, chronology, and cultural materials recovered from the sites, was reported by Jones O'Day et al. (2004), Jones et al. (2007), and Jones and Quinn (2009). We present here the results of our studies of the reptile and bird bones from these same sites.

STUDY AREA AND METHODS

Fiji is the largest archipelago in West Polynesia (Fig. 1), with a land area of 18,272 km^2 and ca. 106 islands >1 km^2 (Steadman, 2006b). Fiji is also the region's oldest and most geologically complex island group (Hathway and Colley, 1994; Rodda, 1994). The Lau Group of eastern Fiji consists of 54 named islands (35 of them >1 km^2) totaling 376 km^2 (Steadman, 2006b). Composed of raised coralline limestone, volcanic rocks, or combinations thereof, the islands of Lau are late Miocene to Pleistocene in age; ≤10 million years old). We did research on four islands in Lau: Lakeba, Aiwa Levu, Aiwa Lailai, and Nayau.

Our field work in Lauan prehistory began when GKP, DWS, and Sepeti Matararaba conducted test excavations on Lakeba and Aiwa Levu in February-March 2000. Sharyn Jones and Patrick M. O'Day subsequently surveyed Aiwa Levu and Aiwa Lailai in September 2001 and May 2002 (Jones et al. 2007). Field work on Nayau took place at various times in 2001 and 2002 (Jones O'Day et al., 2004). Archaeological structures and pottery scatters were mapped, described, photographed, and plotted on air photos and a geological map (issued by the Mineral Resources Department of Fiji). Surveys were done by walking multiple linear transects down the long axes of each island.

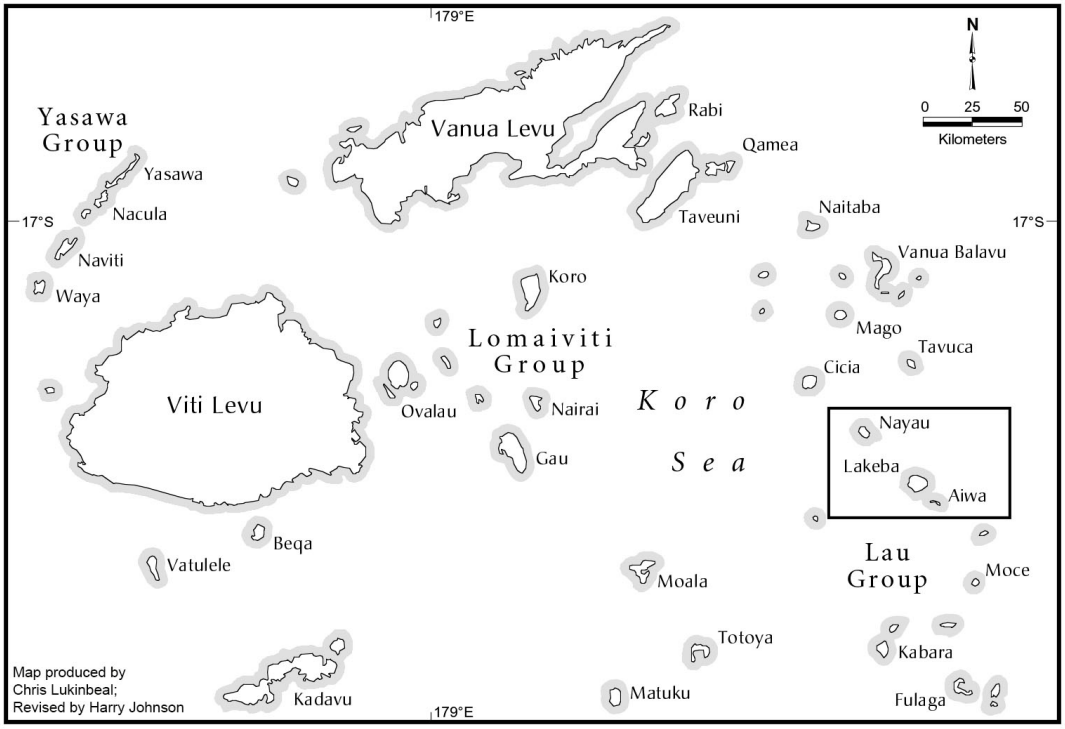

Figure 1. Map of Fiji Islands, with location of Central Lau Group highlighted.

Particular attention was paid to any karst features that might accumulate sediment, such as caves, rockshelters, and sinkholes. Our test excavations were done typically in 5-10 cm levels, following the natural stratigraphy whenever possible. All excavated sediment was passed through nested sieves of 1/2, 1/4, 1/8, and 1/16 inch mesh. All cultural material was collected from the sieves, including shell, bone, pottery, lithics, non-local rock, and any other artifacts. Standardized field forms were used to record our excavations. Full archaeological details are described in Jones O'Day et al. (2004), Jones et al. (2007), Jones (2009), and Jones and Quinn (2009).

Of more than 30 sites examined, 20 yielded bones of reptiles and birds, which are the topic of this paper. Most of these 20 sites are younger than 500 Cal BP (calendrically calibrated years before present), which equals AD 1450. Seven of the sites are associated with radiocarbon (^{14}C) dates (Table 1), whereas the other sites have age estimates based on similarities of their artifact assemblages with those from ^{14}C-dated sites.

We did not work at the major Lapita archaeological site of Qara ni Puqa, discovered on Lakeba in the 1970s by Simon Best (Best, 1984, 2002) and with an important set of prehistoric non-human bones recently summarized by Worthy and Clark (2009). The prehistoric bones that we collected are deposited in the Florida Museum of Natural History, University of Florida (UF). The reptile bones, stored in the UF Vertebrate Paleontology Collection (see Appendix 1), were identified by GKP with the aid of comparative skeletons at hand (GKP series) or borrowed from museum collections (National Museum of Natural History, Smithsonian Institution, USNM; San Diego Natural History Museum, SDSNH). The bird bones, housed in the UF Ornithology Collection (see Appendix 2), were identified by DWS with the aid of comparative skeletons at UF or borrowed from museum collections (USNM; American Museum of Natural History, AMNH; Delaware Museum of Natural History, DMNH; University of Washington Burke Museum, UWBM). Because skeletons of living Fijian passerine birds (Order Passeriformes) are not well represented in museum collections, DWS has not been able to identify the prehistoric passerine bones from Lau.

Taxonomic and nomenclatural details for reptiles are found in Zug (1991, 2013). Estimated snout-vent lengths (SVL) of fossil individuals were extrapolated from comparative skeletons of known size (Pregill and Worthy, 2003).

RESULTS

Squamate Reptiles

Table 2 compiles the number of identifiable specimens (NISP) for each reptilian taxon by island and locality. Catalog numbers are listed in Appendix 1. The status of each reptilian taxon on the four Lauan islands is summarized in Table 3.

Aiwa Levu, Aiwa Lailai, and Lakeba Islands

Brachylophus fasciatus (Lau Banded Iguana).—Osteological characters for *Brachylophus* are given in de Queiroz (1987) and Pregill and Worthy (2003). The bones recovered from Aiwa Levu and Aiwa Lailai represent juveniles (est. SVL 80–90 mm) to adults (est. SVL 150–185 mm). Both islands presently support populations of *B. fasciatus* (AMNH 29016, 29033–35, BPBM 1499). Usually concealed in the forest canopy, the iguanas occasionally descend to more visible places on tree trunks. On Aiwa Levu, our Lakeban field assistants shook loose an adult male from canopy vines on 23 February 2000. After dropping to the ground, the iguana ran a short distance to a nearby tree and climbed about 2 m high. We released it after taking measurements (SVL 160 mm, tail 515 mm) and noting that it was missing most of the 1st and 2nd digits of the left manus. Literature records exist for *B. fasciatus* on Lakeba (Cahill, 1970; Gibbons and Watkins, 1982), but no Lakebans with whom we spoke were aware of iguanas still living on their island. If iguanas do survive on Lakeba, we suspect that it would be in the rugged and largely isolated limestone forest southwest of Nasaqalau, described by Franklin and Steadman (2010). Other Lau records for *B. fasciatus* include Oneata, Vatu Vara, Fulaga, and Yacata (Zug, 1991).

Keogh et al. (2008) have shown that iguanas

Table 1. Radiocarbon (^{14}C) dates from prehistoric sites on three islands (Nayau, Aiwa Levu, Aiwa Lailai) in the Lau Group, Fiji. Unless designated otherwise, each determination (by Beta Analytic Inc., Miami, Florida) is on a single bone or single piece of wood charcoal. The conventional ^{14}C age is adjusted for $^{13}C/^{12}C$ ratios. Calibrated for atmospheric variation in ^{14}C follows OxCal version v3.10 (Bronk Ramsey, 1995, 2001), with multiple intercepts often required to account for 0.95 probability. These ^{14}C dates are compiled from O'Day et al. (2004), Jones (2007), and Jones et al. (2007).

Beta-number	Material dated	Island/site: unit	Layer/ Level	$^{13}C/^{12}C$(‰)	Conventional ^{14}C age (yr BP)	OxCal cal BP (2 sigma)
164249	coracoid *Gallus gallus*	**Nayau** WaiTE	I/1	-19.5	560 ± 40	650–580 (.50) 570–510 (.45)
164248	tarsometatarsus *Ptilinopus*	**Nayau** WaiTE	II/2	-21.1	550 ± 40	650–580 (.43) 570–510 (.52)
164247	radius *Pteropus samoensis*	**Nayau** WaiTE	II-III/3	-19.9	690 ± 40	690–620 (.58) 610–550 (.38)
164259	adult tibia *Homo sapiens*	**Nayau** Qara L	I/2	-15.7	700 ± 40	710–620 (.58) 610–550 (.30)
165468	radius *Pteropus tonganus*	**Nayau** NukuT 2	II-III/3	-19.2	50 ± 60	280–180 (.28) <150 (.68)
173059	metatarsal *Homo sapiens*	**Nayau** NukuT 2	IV/1	-16.6	420 ± 40	540–420 (.80) 380–320 (.16)
164251	juvenile radius *Pteropus tonganus*	**Aiwa Levu** AR1: 2	I/1	-19.2	280 ±40	470–280 (.91) 170–150 (.04)
164258	mandible *Pteropus samoensis*	**Aiwa Levu** AR1: 4	II/3	-19	360 ± 40	510–310 (.95)
164260	wood charcoal	**Aiwa Levu** AR1: 2	II/5 (oven)	-25.7	200 ± 70	430–360 (.06) 330–10 (.89)
164261	wood charcoal	**Aiwa Levu** AR1: 2	III/10 (oven)	-25.6	570 ± 40	650–510 (.95)
164252	adult humerus *Homo sapiens*	**Aiwa Levu** AR1: 2	III/13	-11.8	2310 ± 40	2440–2410 (.01) 2370–2290 (.68) 2270–2150 (.33)
165466	radius *Pteropus samoensis*	**Aiwa Levu** AC2: 2	I/1	-18.9	960 ± 40	960–760 (.95)
165467	radius *Pteropus samoensis*	**Aiwa Levu** AC2: 3	II/2	-19.1	1630 ± 40	1690–1670 (.02) 1610–1410 (.94)
165465	tarsometatarsus *Gallus gallus*	**Aiwa Levu** AC2: 1	II/2	-12.5	2380 ± 40	2710–2630 (.16) 2620–2590 (.01)v 2500–2330 (.78)
165469	humerus *Ducula pacifica*	**Aiwa Levu** GR: 1	II/5	-20.3	450 ± 40	550–430 (.92)v 360–330 (.03)
172192	wing phalanx *Pteropus tonganus*	**Aiwa Lailai** DAU: 1	IIIb/4	-10.5	1510 ± 40	1520–1310 (.95)
172191	Tarsometatarsus *Gallus gallus*	**Aiwa Lailai** DAU: 2	IV/5	-19.1	2300 ± 50	2460–2150 (.95)

Table 2. Prehistoric records of reptiles from the Lau Group, Fiji. Site abbreviations: **Lakeba:** 197OR, site 197 Owl Roost; OSRS, Osonabukete Rockshelter. **Nayau:** WaiTW, Waiturutu West; WaiTE, Waiturutu East; UluNK, Ulunikoro; DKT, Daku ni Tuba; KnG, Koro ni Gasau; NMM, NaMasiMasi. **Aiwa Levu:** ALC2, Aiwa Levu Cave 2; ALR1, Aiwa Levu Rockshelter 1; CsRS, Campsite Rockshelter. **Aiwa Lailai:** DRS, Dau Rockshelter. MNI, minimum number of individuals; NISP, number of identified specimens.

	Lakeba		Nayau						Aiwa Levu			Aiwa Lailai	Totals	
	197OR	OSRS	WaiTE	WaiTW	UluNK	DKT	KnG	NMM	ALC2	ALR1	CsRS	DRS	NISP	MNI
Brachylophus fasciatus	—	—	—	—	—	—	3	—	28	23	8	16	78	5
Iguanidae large sp.	—	—	—	—	—	—	—	—	—	2	—	—	2	1
Gehyra oceanica	10	—	3	158	1	—	—	4	7	129	—	—	312	17
Nactus pelagicus	—	—	1	—	—	—	2	—	1	5	—	—	9	4
Gekkonidae, gen. & sp. unknown	—	—	—	—	—	—	—	—	2	5	2	—	9	6
Emoia cf. *E. trossula*	—	—	—	—	—	—	—	—	—	21	—	3	24	5
cf. *Emoia trossula* or *concolor*	3	4	1	—	5	—	—	2	—	—	—	—	15	5
Emoia sp.	—	—	—	—	—	—	2	4	—	—	—	—	6	2
Candoia bibroni	1	—	3	—	—	1	—	—	—	3	1	—	9	5
Total NISP	14	4	8	158	6	1	7	10	38	188	11	19	464	50
Total species	3	1	4	1	2	1	3	3	4	7	3	2	9	—

on the main islands of Fiji (Viti Levu, Vanua Levu, Ovalau, Kadavu) are distinct from the Lau populations in several morphological and genetic characters. The former have been assigned to a new species, *Brachylophus bulabula*, with the vernacular name Fiji Banded Iguana. *Brachylophus fasciatus* (Lau Banded Iguana) is thus restricted to the Lau species and the extant Tongan populations that were introduced there prehistorically (Pregill and Steadman, 2004).

Iguanidae large sp. (Large extinct iguana).—Two metapodials of a large iguanid from the Aiwa 1 site on Aiwa Levu lie well outside the size range of *Brachylophus fasciatus*, coming from an individual(s) of ca. 375–400 mm SVL. The extinct, giant iguana *Lapitiguana impensa* (est. SVL 500 mm) is known only from fossils on Viti Levu (Pregill and Worthy, 2003). The smaller but still quite large *B. gibbonsi* (est. SVL 350 mm), also extinct, is known only from archaeological sites in the Ha'apai Group, Tonga (Pregill and Dye, 1989; Pregill and Steadman, 2004). The prehistoric bones reported here could belong to either of these or to some other extinct, giant species of iguana. More material is needed to improve the taxonomic resolution.

Brachylophus gibbonsi was a desirable item in the diet of the early human colonists of Ha'apai, who consumed it to extinction (Steadman et al., 2002; Pregill and Steadman, 2004). It is tempting to speculate that *B. gibbonsi* may have been brought to Aiwa Levu by Tongans, as archeological and ethnological evidence indicate substantial contact with the people of Lau (Best, 1984, 2002). However, *B. gibbonsi* became extinct in Ha'apai within a century of first human contact (ca. 2850 Cal BP), whereas the metapodials from Aiwa 1 (Unit 2, IV/13) are from a stratigraphic horizon dated at ca. 2300 Cal BP, which is roughly 500 years after the presumed extinction of large iguanas in Tonga.

Gehyra oceanica (Oceania Gecko).—The bones are easily referred to *G. oceanica* on the basis of size and their osteological details (Pregill, 1993): the dentary tapers toward the symphysis; little if any of the lingual side of the bone is visible below the splenial; labial overlap of the coronoid just reaches the level of the most posterior tooth; and about one-third of each tooth is exposed above the parapet of the jaw. The frontal in *Gehyra* [*oceanica*, *mutilata*, *vorax*] is distinguished by its broad proportions and rolled, convex supraorbital borders (Fig 2A). The bones reported here represent adult individuals ranging in estimated SVL from 65 to 80 mm.

Gehyra oceanica is common on both Aiwas today (AMNH 29023-26), and throughout Fiji and many other Pacific Islands. On Aiwa Levu, we found adults, juveniles, and hatchlings concealed behind the exfoliating bark of decaying tree trunks. On Aiwa Lailai, several were located inside rotting, upright tree trunks, and a communal clutch of 15 eggs was found in a decaying stump. On Lakeba, where *G. oceanica* has not been reported in literature, we observed a subadult feeding on moths around a light outside our guesthouse in Tubou. Additional Lauan records include Fulaga, Komo, Namuka-i-lau, Nayabo, Moce, Ogea Levu, Ogea Driki, and Vatoa (Zug, 1991).

Nactus pelagicus (Pacific Slender-toed Gecko).—The dentary of *N. pelagicus* is distinguished by a long surangular process that in a fully articulated mandible extends posteriorly past the level of the posterior border of the coronoid. The teeth are small and peglike, and >25% of the crown is exposed above the parapet of the jaw. The frontal is long and narrow, being nearly five times longer than the intraorbital width. The parietal border curves slightly inward toward the snout. The frontal is moderately concave dorsally and the supraorbital margins are flat (Fig. 2B). In isolated frontals, the facets for the prefrontal are visible dorsally, unlike those of the postfrontal.

This gecko is common today on Aiwa Levu. At night we frequently encountered it in the vicinity of our camp perched on small branches and limestone crags. Adults measured up to 68 mm SVL, which is slightly greater than the maximum reported for *N. pelagicus* elsewhere in Fiji (65 mm; Zug, 1991). Other than Aiwa (AMNH 29097), the only other Lauan records for *N. pelagicus* are from Ono-i-Lau (USNM 229981) and the bones reported here from Nayau (see below). It is otherwise fairly

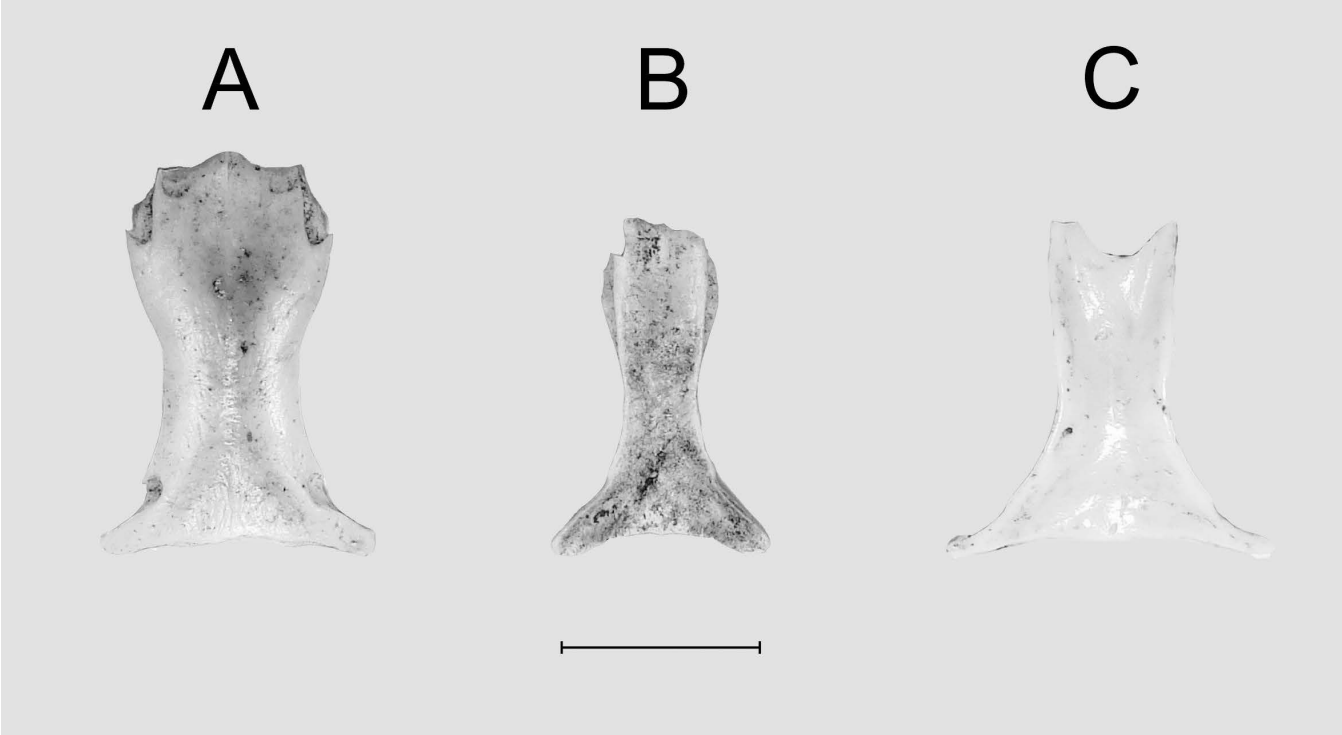

Figure 2. Frontal bones (in dorsal aspect) of three geckos from bone deposits on Aiwa Levu, Lau Group, Fiji. **A**. *Gehyra oceanica.* **B**. *Nactus pelagicus*. **C**. Extinct gekkonid, gen and sp. unknown. Scale equals 5 mm..

broadly distributed in Fiji (Zug, 1991).

Gekkonidae gen. and sp. unknown (unknown gecko).—The frontal bone is a distinctive element among genera of Pacific island gekkonids (Pregill, 1993, 1998). The prehistoric bones from Aiwa Levu (Table 2) are unlike those in any genus of gecko known in Fiji or any other island group in Polynesia or Micronesia. Our comparisons included species of *Gehyra*, *Nactus*, *Perochirus*, *Gekko*, and *Lepidodactylus*. Confined to deeper strata, the fossils presumably represent an extinct species. One complete frontal (Fig. 2C) is as wide across the parietal border as it is in midsagittal length (8.2 mm). From the anterior end, the supraorbital margins are parallel (2.8 mm width) for about 60% of the frontal's length, and then they diverge to the lateral tips of the parietal border. The smooth dorsal surface is concave from the upward sweep of the supraorbital margins. All of the referred frontals are essentially the same size and represent individuals with estimated SVL's of 70–80 mm. The only Fijian gecko with a remotely similar frontal is *Nactus pelagicus*, but in *Nactus* the frontal is smaller, proportionately longer and narrower, and the parietal border has rounded rather than pointed lateral processes (Fig. 2B).

The concave prehistoric frontals are somewhat similar to those in *Cyrtodactylus*, a primarily Asian/Indo-Malaysian genus with ca. 130 recognized living species (e.g., Grismer et al., 2012). Three species of *Cyrtodactylus* occur in Melanesia (New Guinea, Solomon Islands) but no farther east in Oceania (McCoy, 1980). Other diplodactylid genera (Kluge, 1987; Bauer, 1990) are possible, but our osteological information on them is limited. New Caledonia hosts three endemic diplodactylid genera (*Bavayia, Eurydactylodes, Rhacodactylus*) comprising about 20 species (Bauer and Sadlier, 2000). The endemic gecko fauna of Fiji (excluding Rotuma) is limited to *Gehyra vorax* on the larger islands, and *Lepidodactylus manni* (max. SVL 48 mm), which is presently known from Viti Levu,

Ovalau, and Kadavu (Zug, 1991). Whatever the prehistoric gecko eventually is determined to be, it is almost certainly an extinct species.

The other prehistoric bones referred to this indeterminate taxon are from a similarly-sized gecko. As with the frontal, they differ consistently in detail from the same elements of *Gehyra oceanica*. For example, the maxilla has a broader subdental shelf, the pterygoid has a straighter quadrate process, and the head of the femur is less deflected.

Emoia trossula (Fiji Barred Treeskink) .—Skink bones are easily distinguished from those of geckos (Pregill, 1993, 1998), and the prehistoric bones are referred to this large (max. SVL 104–107 mm) species of *Emoia* by numerous cranial details. *Emoia trossula* was first described as a Fiji/Rotuma endemic (Brown and Gibbons, 1986), but subsequent populations of *trossula*-like skinks were reported from ‘Eua, Tonga (Zug, 1991; Pregill, 1993) and Rarotonga, Cook Islands (Crombie and Steadman, 1987). Although Brown (1991) referred these outliers to *E. trossula*, recent analysis of more material demonstrates that this is not the case. The Cook Island skinks are a distinct lineage, *E. tuitarere* (Hamilton et al., 2010), as are the Tongan lizards, *E. mokolahi* (Zug et al., 2012). As now understood, *Emoia trossula* is a Fiji endemic. It is the only large skink present on Aiwa Levu and Aiwa Lailai today. The similarly-sized *E. nigra* ranges from the Solomons and Vanuatu to Fiji, then east to Tonga and Samoa. Its known distribution in Fiji, however, is limited to Rotuma, Nukubasaga, Koro, Ovalau, and formerly the largest islands of Viti Levu and Vanua Levu; there are no records of *E. nigra* from the Lau Group.

Emoia trossula also may be extinct on Viti Levu and Vanua Levu, but it otherwise occurs on many of the smaller islands in the Lau Group, including Aiwa Levu, Cicia, Kanacea, Lakeba, Ono-i-lau, Tuvuca, and Vatu Vara (Zug, 1991). We recorded two of these skinks over seven days on Aiwa Levu, and three in just over 2 hours on Aiwa Lailai. This result might be due simply to chance, but possibly could reflect different population densities. Both sightings on Aiwa Levu involved a single individual foraging on the ground below fairly open understory late in the morning. When they detected our approach, each of these skinks ascended 2–3 m up the nearest large tree. Of the three individuals seen on Aiwa Lailai, two were on tree trunks about 2 m off the ground, whereas the other was about 6 m up in the canopy.

On Lakeba, the only other skink approaching the size of *Emoia trossula* is the Fijian Green Treeskink, *E. concolor.* The largest males of this species reach about 95 mm SVL (Zug, 1991, 2013); some of the seven referred bones (Table 2) could belong to *E. concolor*. *Emoia trossula* is known from Lakeba by a single specimen (MCZ 16965). We did not find it alive on that island. By contrast, no museum records of *E. concolor* exist for Lakeba, even though we found it regularly on trees in and near Tubou village. Three individuals occupied a mango tree (*Mangifera indica*) and the trunks of coconut palms (*Cocos nucifera*) around our guest house. Other Lauan records for *E. concolor* include Kanacea, Vanua Balavu, Mago, Cicia, Moce, and Vatoa (Zug, 1991).

Candoia bibroni (Pacific Tree Boa).—Based on museum data, this snake was fairly widespread in Fiji historically, with Lauan records from Lakeba, Vanua Belavu, Ogea Levu, and Fulaga (McDowell, 1979; Zug, 1991). The bones reported here are the only evidence of its presence on Aiwa. We never saw it there, nor have our Fijian guides. Likewise, we have little information on its current status on Lakeba, where local residents knew of this snake but never had seen it. They added that when encountered (by others) it is usually killed. Our only evidence for its persistence on Lakeba was a shed skin that we found on the floor of a small cave at Seliseli Point.

Nayau

Bones of squamate reptiles were recovered from six of 14 archaeological sites excavated on Nayau (Jones O’Day et al., 2004). None of the material is older than ca. 710 Cal BP. No species was represented by more than five bones at any site (Table 3) except for a large sample (ca. 155 bones) of *Gehyra oceanica* from one unit. The bones

represent one snake (*Candoia bibroni*), and four or five species of lizards: the iguana *Brachylophus fasciatus*, the gekkonids *Gehyra oceanica* and *Nactus pelagicus*, and one or two skinks of the genus *Emoia*. Identification of the geckos is confidently based on cranial elements. The larger bones of *Emoia* are referred to *E. trossula* based on their large size (est. SVL 100–110 mm), and agreement in structural details with comparative material. The smaller bones (est. SVL 55–70 mm) probably represent a second species of *Emoia* rather than subadult *E. trossula*. In the latter, tooth crowns are not as blunt as in the prehistoric bones.

Our interpretation of the Nayau squamate material is constrained by the fact that the contemporary lizard and snake fauna of Nayau is almost unknown. There are no literature records for the island (Zug, 1991). Our only direct field observations were by DWS on 23-24 October 2001, when he noted the following. *Emoia cyanura* was common and widespread across much of the island. *Cryptoblepharus eximius* was common and widespread along the coast (always within 15 m of the shoreline). In limestone forest just inland from Naracivo village, a very large (est. SVL 130 mm), stocky, uniformly dark skink was seen running on the ground. Its size, proportions, and coloration suggested *E. trossula*. At this same locality, a fairly large (est. SVL 65 mm) but more slender and colorful (yellow, green, brown) skink, suggestive of *E. concolor*, was observed 1–3 m high on a tree. People on Nayau told DWS that *Brachylophus* does not live there, although *Candoia bibroni* does. DWS also saw a sea snake, *Laticauda* cf. *L. laticauda* (est. SVL 40 cm) swimming inside the fringing reef in about 1 m of water at low tide south

Table 3. Summary of squamate reptiles recorded from four islands in the Lau Group, Fiji. +, present, museum specimen(s) exist; Nr, new modern record (photo voucher), this study; P, prehistoric record, this study.

Taxon	Lakeba	Nayau	Aiwa Levu	Aiwa Lailai
Brachylophus fasciatus	+	P	+, P	+, P
Iguanidae large sp.	—	—	P	—
Gehyra oceanica	Nr, P	P	+, P	Nr
Hemidactylus frenatus	Nr	—	—	—
Gekkonidae gen. et sp. indet.	—	—	P	—
Lepidodactylus lugubris	Nr	—	+	—
Nactus pelagicus	Nr	P	+, P	—
Cryptoblepharus eximius	Nr	—	+	—
Emoia cyanura	Nr	—	Nr	—
Emoia concolor	Nr, P?	P?	—	—
Emoia impar	Nr	—	Nr	—
Emoia trossula	+, P?	P?	+, P	Nr, P
Lipinia noctua	+	—	—	—
Candoia bibroni	+, P	P	P	—

of Salia.

The presence of *Candoia* and the four lizards is not unexpected in a late prehistoric context on Nayau, given their current distribution in the Lau Group and their prehistoric occurrence on Aiwa and Lakeba. Undoubtedly Nayau hosts additional lizard species that were not represented by bones (Table 3).

Birds

The prehistoric non-passerine bird bones that we identified from 20 sites on the four islands represent 21 indigenous species, which are summarized in Table 4 and listed by element in Appendix 2. Our compilation does not include seabirds or migratory shorebirds, which have fundamentally different habitat requirements and dispersal mechanisms than resident landbirds. Because the fossils of songbirds (Passeriformes) were not identified, the estimated prehistoric species richness values of landbirds are minimum values for each island. The extent of the underestimates could be considerable, given that our use of fine-meshed sieves recovered 205 prehistoric passerine bones from 15 sites on the four islands in Lau. In nearby Tonga, where passerine bones have been analyzed because better modern comparative skeletons are available, seven of the 13 identified species of songbirds no longer occur in the island group (Steadman, 2006b:table 6-10).

Lakeba

One site (Qara ni Puqa, or site 197) has yielded bird bones associated with Lapita pottery dated to ca. 2800 Cal BP, including two extinct species (the megapode *Megapodius alimentum*, and pigeon *Ducula lakeba*; Steadman, 1989a, 1999, 2006b; Worthy, 2000, 2001; Best, 2002). An up-to-date summary of the bird bones from Qara ni Puqa is found in Worthy and Clark (2009). *Megapodius alimentum* has been recorded as well in the Ha'apai Group, 'Eua, and Tongatapu in Tonga (Steadman, 1989b, 1999, 2006b), whereas *D. lakeba* is known only from the Lau Group and Viti Levu, and may have been endemic to Fiji.

Three extant species have been recorded from Lakeba as prehistoric bones, but no longer occur on the island; they are the heron *Butorides striatus* and two volant species of rails, *Porzana tabuensis* and *Poliolimnas cinereus*. These aquatic to semi-aquatic species are widespread in Oceania. Their extirpation from Lakeba took place within the past millennium. Three other extant species recorded from bones, but that no longer inhabit Lakeba, are forest-dwellers; they are the pigeon *Didunculus* cf. *strigirostris*, parrot *Prosopeia* sp., and lorikeet ?*Charmosyna amabilis*. *Didunculus* is otherwise known from Samoa (the living *D. strigirostris*) and Tonga (the extinct *D. placopedetes*; Steadman, 2006a). *Prosopeia* and *Charmosyna* exist on large islands of western Fiji (the living *P. personta*, *P. tabuensis*, and *C. amabilis*), but nowhere in the Lau Group. Altogether, prehistoric bones increase the landbird fauna on Lakeba from 21 to at least 29 species (Table 5).

Nayau

Most if not all of the bird bones recovered on Nayau are <1000 cal BP (Jones O'Day et al., 2004). From post-Lapita cultural and non-cultural (barn-owl roost) contexts, 80 bird bones represent nine extant, native species of non-passerine landbirds (Table 4). Two of the species are extirpated (the widespread, volant, aquatic rail *Porzana tabuensis* and the locally distributed, forest-obligate ground-dove *Gallicolumba stairi)*, which increases Nayau's landbird fauna from 17 to at least 19 species (Table 5). *Gallicolumba stairi* was once widespread in Western Polynesia, but many populations have been reduced or eliminated since human arrival (Steadman, 2006b).

If modern comparative specimens become available, identifying the 75 prehistoric passerine bones from Nayau would be especially intriguing because only four species of passerines are known to exist on Nayau today (Franklin and Steadman, 2010), compared to seven (Lakeba) or six (Aiwa Levu, Aiwa Lailai) on the other islands.

Aiwa Levu

The 74 non-passerine landbird bones from pre-Lapita through post-Lapita contexts on Aiwa Levu represent 16 species (Table 4). Five of these species are extinct (the megapodes *Megapodius*

Table 4. Prehistoric records of non-passerine landbirds from the Lau Group, Fiji. i, introduced species (not included in totals). Taxa in brackets [ ] do not necessarily represent a taxon other than those identified more specifically. Site abbreviations: **Lakeba:** QNP, Qara ni Pusi; GYR, Gyrocarpus Rockshelter; QSE, Qara Selesele; QNQ, Qara ni Puqa Rockshelter (site 197); 197OR, site 197 Owl Roost; OSC, Osonabukete Cave; OSRS, Osonabukete Rockshelter; WAI, Wainiabia Cave; VAR, Vagadra Rockshelter; LVR, Lost

	Lakeba									
	QNP	GYR	QSE	QNQ	197OR	OSC	OSRS	WAI	VAR	LVR
Egretta sacra	—	—	6	—	—	—	—	—	—	—
Butorides striatus	—	—	—	1	—	—	—	—	—	—
Anas superciliosa	—	—	—	2	—	—	—	—	—	—
†*Megapodius alimentum*	—	—	—	49	—	—	—	—	—	—
†*Megapodius amissus/ molistructor*	—	—	—	—	—	—	—	—	—	—
Gallus gallus (i)	1	3	1	4	—	—	1	—	—	—
Gallirallus philippensis	2	—	—	9	2	—	—	—	—	—
†*Gallirallus* undesc. sp.	—	—	—	—	—	—	—	—	—	—
Porzana tabuensis	—	—	—	1	—	—	1	1	1	—
† *Porzana* undesc. sp.	—	—	—	—	—	—	—	—	—	—
Poliolimnas cinereus	—	—	—	—	1	—	—	—	—	—
Porphyrio porphyrio	—	—	—	41	—	—	—	—	—	—
Columba vitiensis	1	—	—	8	—	—	—	—	—	—
Gallicolumba stairii	—	—	—	8	—	—	—	—	1	—
Didunculus cf. *strigirostris*	—	—	—	8	—	—	—	—	—	—
Ptilinopus perousii	—	—	1	—	—	—	—	—	—	—
Ptilinopus porphyraceus	—	—	—	13	8	—	—	—	—	—
[*Ptilinopus* sp.]	—	—	—	1	—	—	—	—	—	2
Ducula pacifica	—	—	—	6	—	—	—	—	—	—
Ducula latrans	—	—	—	—	—	—	—	—	—	—
†*Ducula lakeba*	—	—	—	92	—	—	—	—	—	—
[*Ducula* sp.]	—	—	—	—	—	—	—	—	—	—
[Columbidae sp.]	—	—	—	20	—	—	—	—	—	—
Prosopeia sp.	—	—	—	3	—	—	—	—	—	—
Vini solitarius	—	—	—	8	—	—	—	—	—	—
?Charmosyna amabilis	—	—	—	1	—	—	—	—	—	—
Tyto alba	—	—	1	4	1	5	—	—	—	—
Collocalia spodiopygia	—	—	—	—	—	—	—	—	—	—
Halcyon chloris	1	—	4	2	—	—	—	—	—	—
Passeriformes	21	—	5	1	5	—	5	3	11	13
Total (excluding *Gallus gallus* and Passeriformes)										
NISP	4	—	12	277	12	5	1	1	2	2
Species	3	—	4	19	4	1	1	1	2	1

Village Rockshelter. **Nayau:** WaiTW, Waiturutu West; WaiTE, Waiturutu East; UluNK, Ulunikoro; Waiturutu West; WaiTE, Waiturutu East; UluNK, Ulunikoro; DKT, Daku ni Tuba; NMM, NaMasiMasi. **Aiwa Levu:** ALC1, Aiwa Levu Cave 1; ALC2, Aiwa Levu Cave 2; ALR1, Aiwa Levu Rockshelter 1; GRS, Goat Rockshelter. **Aiwa Lailai:** DRS, Dau Rockshelter. Data from QNQ are from Worthy (2000, 2001) and especially Worthy and Clark (2009); all other data are updated from Steadman (2006b:table 6-8).

Nayau					Aiwa Levu				Aiwa Lailai	Totals		
WaiTE	WaiTW	UluNK	DKT	NMM	ALC1	ALC2	ALR1	GRS	DRS	Bones	Sites	Islands
—	—	—	—	—	—	—	—	—	—	6	1	1
—	—	—	—	—	—	—	—	—	—	1	1	1
—	—	—	—	—	—	—	1	—	—	3	2	2
—	—	—	—	—	—	—	3	—	—	52	2	2
—	—	—	—	—	—	—	1	—	—	1	1	1
—	—	—	2	8	—	7	8	—	6	41	10	4
—	1	—	1	2	10	1	7	2	—	37	10	3
—	—	—	—	—	—	—	3	—	—	3	1	1
—	—	2	—	—	—	—	—	—	—	6	5	2
—	—	—	—	—	—	—	1	—	—	1	1	1
—	—	—	—	—	—	—	—	—	—	1	1	1
—	—	—	—	—	1	3	1	—	—	46	4	2
—	—	3	—	—	—	2	5	—	—	19	5	3
—	3	—	—	—	3	—	3	—	3	21	6	4
—	—	—	—	—	—	—	—	—	—	8	1	1
4	30	2	—	—	—	—	1	—	1	39	6	4
1	—	2	—	—	—	—	—	—	—	24	4	2
—	—	—	—	—	—	—	—	—	—	3	2	1
—	—	—	—	—	—	—	8	—	26	40	3	2
—	—	—	—	—	—	—	4	—	2	6	2	2
—	—	—	—	—	—	1	—	—	—	93	2	2
—	—	—	—	2	—	—	1	—	2	5	3	2
—	—	—	—	—	—	—	3	—	—	23	2	2
—	—	—	—	—	—	—	—	—	—	3	1	1
—	—	—	—	—	—	—	—	—	—	8	1	1
—	—	—	—	—	—	—	—	—	—	1	1	1
—	—	2	—	—	—	1	—	—	—	14	6	3
—	8	—	—	—	—	4	1	—	—	13	3	2
3	16	4	—	—	2	—	3	—	—	35	8	3
5	53	15	—	2	5	2	58	—	1	205	16	4
8	58	15	1	4	16	12	46	2	34	482	—	—
3	5	6	1	2	4	6	16	1	5	25	—	—

alimentum, *M. amissus*/*molistructor*, the rails *Gallirallus* undescribed sp., *Porzana* undescribed sp., and the pigeon *Ducula lakeba*). *Megapodius alimentum* and the much larger *M. molistructor* (Fig. 3) also occur commonly in Lapita archaeological sites in Tonga (Steadman et al., 2002), whereas *M. amissus* (slightly smaller than *M. molistructor*) is known with certainty only from Viti Levu, Fiji (Worthy, 2000). The single specimen of a large megapode from Aiwa Levu is not an adequate basis to distinguish *M. molistructor* from *M. amissus*. The two extinct forms of rails are not represented by enough material to warrant the description of species at this time; *Porzana* undescribed sp. is known only from a tibiotarsus, and *Gallirallus* undescribed sp. is known only from an ulna, tibiotarsus, and pedal phalanx. *Ducula lakeba*, described from Qara ni Puka Rockshelter (Worthy, 2001), is known thus far only from Lakeba and Aiwa Levu.

Three species are extant but no longer occur on Aiwa Levu (the duck *Anas superciliosa*, rail *Porphyrio porphyrio*, and pigeon *Ducula latrans*). The most important site on this small island is the well stratified Aiwa Levu Rockshelter 1, which is ^{14}C dated from 470–280 Cal BP in upper strata to 2370–2150 Cal BP in lower strata, with some bird bones probably even older. The bones from Aiwa Levu Cave 2 are from sediments dated from 960–760 Cal BP (stratum I) to 2710–2330 Cal BP (stratum II). Because Aiwa Levu, Aiwa Lailai, and Lakeba were joined as one large island (ca. 1000 km^2) in the late Pleistocene, both flightless rails presumably once were endemic to that entire land mass. Whether they survived on all three islands through the Holocene until the time of human arrival is unknown.

The prehistoric bird bones increase Aiwa Levu's landbird fauna from 18 to at least 26 species, which is nearly as many as have been recorded from the much larger island of Lakeba. Along with the Tongan island of Ha'afeva (1.8 km^2), Aiwa Levu played a key role in demonstrating that, before human arrival, very small West Polynesian islands were able to support substantially larger sets of species than exist in modern bird communities (Steadman, 2006b; Franklin and Steadman, 2008).

Aiwa Lailai

Aiwa Lailai has yielded one bone deposit, a cultural site called Dau Rockshelter, dated from 1520–1310 cal BP (Layer IIIB) to 2460–2150 cal BP (Layer IV; Jones et al., 2007). The 18 non-passerine landbird bones from this site represent four species of columbids, among which only the extant pigeon *Ducula latrans* does not still exist on Aiwa Lailai. Much of the difference in the modern/prehistoric species-richness values between Aiwa Levu and nearby Aiwa Lailai (18/26 vs. 16/17; Table 5) is undoubtedly due to the much less complete sampling of both modern and prehistoric birds on the latter.

DISCUSSION

Reptiles

Six of the seven squamate taxa recovered from Aiwa Levu (Tables 2–3) are indigenous members of the Fiji/Lau herpetofauna. Presumably the seventh taxon (Gekkonidae gen. and sp. indet.) is also native. All of these taxa except *Nactus pelagicus* occur in prehistoric strata (>200 Cal BP). The absence of *N. pelagicus* from deeper (older) levels may be a sampling bias. Indeed, natural sampling biases affect the presence/absence and relative abundance of any particular lizard species in a prehistoric insular fauna (Pregill, 1998). Those with cryptic life styles, low population density, and particularly species with small body size are likely to be represented poorly, if at all, as prehistoric bones, regardless of whether the accumulation is of cultural or non-cultural origin. The most abundant species in the prehistoric sites on Aiwa Levu is *Gehyra oceanica*, represented by a minimum of 11 individuals. All other species are represented by six or fewer individuals. Hence, the low number of *N. pelagicus* bones is not unexpected, nor is the total absence of small species of skinks (*Emoia impar*, *E. cyanura*, *Cryptoblepharus eximius*) and geckos (*Lepidodactylus lugubris*).

Except for the occasional consumption of an iguana (*Brachylophus fasciatus*), none of the fossil squamates seems to have been important in the diet

Figure 3. Humeri in anconal (A, B) and palmar (C, D) aspects, and pedal phalanges (digit IV, phalanx 1) in acrotarsial (E, F) and plantar (G, H) aspects of extinct species of *Megapodius*. A, C. *M. alimentum*, UF 62852, Aiwa Levu Rockshelter 1, Aiwa Levu, Fiji. B, D. *M. alimentum*, UF 57785, Tongoleleka site, Lifuka, Tonga (type locality). E, G. *M. molistructor*/*amissus*, UF 61225, site Aiwa Levu Rockshelter 1, Aiwa Levu, Fiji. F, H. *M. alimentum*, UF 57905, Tongoleleka site, Lifuka, Tonga (type locality).

Table 5. Modern and prehistoric landbirds from the four islands with prehistoric data in the Central Lau Group, Fiji. [e], endemic to Fiji; M, modern record; P, prehistoric record; †, extinct species. Passerine bones are unstudied. Updated from Steadman (2006b:table 6-9).

	Lakeba	Nayau	Aiwa Levu	Aiwa Lailai	Total M / P
ARDEIDAE					
Egretta sacra – Pacific Reef-heron	M, P	M	M	M	4 / 1
Butorides striatus – Striated Heron	P	–	–	–	– / 1
ANATIDAE					
Anas superciliosa – Pacific Gray Duck	M, P	M	P	–	2 / 1
ACCIPITRIDAE					
Circus approximans – Swamp Harrier	M	M	M	M	4 / –
FALCONIDAE					
Falco peregrinus – Peregrine Falcon	–	–	M	M	2 / –
MEGAPODIIDAE					
†*Megapodius alimentum* – Consumed Megapode	P	–	P	–	– / 2
†*Megapodius amissus/molistructor* – Extinct Megapode	–	–	P	–	– / 1
RALLIDAE					
Porzana tabuensis – Sooty Crake	P	P	–	–	– / 2
[e]†*Porzana* undesc. sp. – Aiwa Flightless Crake	–	–	P	–	– / 1
Poliolimnas cinereus – White-browed Crake	P	–	–	–	– / 1
Gallirallus philippensis – Banded Rail	M, P	M, P	M, P	–	3 / 3
[e]†*Gallirallus* undesc. sp. – Aiwa Flightless Rail	–	–	P	–	– / 1
Porphyrio porphyrio – Purple Swamphen	M, P	M	P	–	2 / 2
COLUMBIDAE					
Columba vitiensis – White-throated Pigeon	M, P	M, P	M, P	M	4 / 3
Gallicolumba stairii – Shy Ground-dove	M, P	P	M, P	M, P	3 / 4
Didunculus cf. *strigirostris* – Tooth-billed Pigeon	P	–	–	–	–
Ptilinopus perousii – Many-colored Fruit-dove	M, P	M, P	M, P	M, P	4 / 4
Ptilinopus porphyraceus – Purple-capped Fruit-dove	M, P	M, P	M	M	4 / 2
Ducula pacifica - Pacific Pigeon	M, P	M	M, P	M, P	4 / 2
Ducula latrans – Peale's Pigeon	–	M	P	P	1 / 2
[e]†*Ducula lakeba* – Lakeba Pigeon	P	–	P	–	– / 2
PSITTACIDAE					
Prosopeia sp. – Shining parrot	P	–	–	–	–
[e]?*Charmosyna amabilis* – Red-throated Lorikeet	P	–	–	–	–
Vini solitarius – Collared Lory	M, P	–	–	–	1 / –
TYTONIDAE					
Tyto alba – Common Barn-owl	M, P	M, P	M, P	–	3 / 3
APODIAE					
Collocalia spodiopygia – White-rumped Swiftlet	M	M, P	M, P	M	4 / 2
ALCEDINIDAE					
Halcyon chloris – Collared Kingfisher	M, P	M, P	M, P	M	4 / 3
HIRUNDINIDAE					
Hirundo tahitica – Pacific Swallow	M	M	–	–	2 / –

Table 5. Continued.

	Lakeba	Nayau	Aiwa Levu	Aiwa Lailai	Total M / P
STURNIDAE					
Aplonis tabuensis – Polynesian Starling	M	M	M	M	4 / –
CAMPEPHAGIDAE					
Lalage maculosa – Polynesian Triller	M	–	M	M	3 / –
MONARCHIDAE					
[e]*Mayrornis lessoni* – Slaty Flycatcher	M	–	M	M	3 / –
Clytorhynchus vitiensis – Fiji Shrikebill	–	–	M	M	2 / –
Myiagra vanikorensis – Vanikoro Flycatcher	M	–	M	M	3 / –
MELIPHAGIDAE					
[e]*Myzomela jugularis* – Orange-breasted Honeyeater	M	M	–	–	2 / –
Foulehaio carunculata – Wattled Honeyeater	M	M	M	M	4 / –
TOTAL					
M	21	17	18	16	–
M+P	29	19	26	17	–
Island area (km^2)	55.94	18.44	1.21	~1.0	–
Inhabited	+	+	–	–	–
Total person-days of survey (M)	46	15	22	2	–
Total non-passerine landbird bones (P)	186	80	74	18	–

of Aiwa Levu's prehistoric people. Fishes account for 81% of the overall bones from the island's archaeological contexts, and marine invertebrates (mainly mollusks) also contributed substantially to the diet of prehistoric Fijians (Jones et al., 2007). Nevertheless, humans and their commensals (rats, cats, dogs) are likely responsible for the near (or complete?) extirpation of the Pacific Tree Boa (*Candoia bibbroni*) from Lakeba. This snake's apparent absence now from uninhabited Aiwa Leva and Aiwa Lailai, which lack cats and dogs, is less clear.

Six species of lizards not represented with certainty in any of the bone deposits are nonetheless present on Aiwa Levu and/or Lakeba today (Table 3). These include *Hemidactylus frentatus* (House Gecko), *Lepidodactylus lugubris* (Mourning Gecko), the sibling species *Emoia cyanura* and *E. impar* (White-bellied Copper-striped Skink, Dark-bellied Copper-striped skink), *Cryptoblepharus eximius* (Fiji Snake-eyed Skink), and *Lipinia noctua* (Moth Skink). The two species of Copper-striped skinks have not been recorded previously on Aiwa Levu, whereas, oddly, none except *L. noctua* has been reported for Lakeba, which was visited by the Whitney South Sea Expedition in the 1920s (Burt and Burt, 1932) and by other naturalists since. Except for *C. eximius*, most of these lizards are widely dispersed throughout the Pacific. The nearly trans-oceanic Mourning Gecko, *L. lugubris*, has been recorded from other Lau islands including Aiwa Levu (Zug, 1991). On Lakeba it occupied our guesthouse in Tubou, and on Aiwa Lailai we found it syntopically with *Gehyra oceanica* in a rotting tree stump.

The House gecko, *Hemidactylus frenatus*,

also has a wide, albeit spotty, distribution in the Pacific as a human commensal. It is a recent adventive in Fiji, first recorded from the Nadi/Lautoka area of Viti Levu in 1980 (Zug, 1991). Of the three geckos that we recorded in or near the guesthouse in Tubou, Lakeba (*H. frenatus, Gehyra oceanica, Lepidodactylus lugubris*), the first was the most common. We found no evidence of it on uninhabited Aiwa Levu.

Both species of Copper-striped skinks, *Emoia cyanura* and *E. impar,* are widespread and sympatric in much of Oceania, although *E. impar* was not recognized as a distinct species until two decades ago, thus compromising earlier records of *E. cyanura* (Ineich, 1987; Ineich and Zug, 1991; Brown, 1991). Both skinks occur on Aiwa Levu and Aiwa Lailai. They are common diurnal lizards but we made no attempt to estimate their relative abundance. They occur in all manner of terrestrial habitat, especially areas with patchy sunlight (Steadman et al., 1999), and also are not averse to scampering up into trees. On Lakeba, we saw these skinks in several areas around the periphery of the island, and at least *E. cyanura* on the cross-island road between Tubou and Yadrana.

Zug (1991) recognized *Cryptoblepharus eximius* as a Fiji endemic distinct from other Oceanic populations of *C. poecilopleurus*. This typically coastal species is common on islands in the Lau Group such as Aiwa Levu, Cicia, Kanacea, Karoni, Namula-i-lau, Navutu-i-ra, Nayabo, Ono-i-lau, and Wailagalala. On Aiwa Levu, we found it to be abundant on the rocky slope above the east-end cove. They became active shortly after sunrise, darting over and under limestone rubble and fallen pandanus leaves, syntopically with *Emoia cyanura* and *E. impar*. On Lakeba we found several climbing in a timber pile at the end of the Tubou jetty.

Birds

Only on Lakeba and Aiwa Levu are any of the bird bones that we studied old enough to be associated with Lapita pottery (ca. 2850–2700 Cal BP) and thus more likely to be from extinct or extirpated species (Steadman et al., 2002; Worthy and Clark, 2009). Many of the bird bones from Lakeba and Aiwa Levu, most or all from Aiwa Lailai, and all from Nayau are much younger, typically <2000 Cal BP and often <1000 Cal BP (Jones O'Day et al., 2004; Steadman, 2006b; Jones et al., 2007). This young age probably explains why we did not find extinct species of megapodes, rails, and pigeons on Nayau or Aiwa Lailai.

Lau's modern birdlife is part of the West Polynesian avifaunal region, defined by the current or past presence of these living species (* = endemic to the region): the rails *Gallirallus philippensis, Porzana tabuensis*, and *Porphyrio porphyrio*, columbids **Gallicolumba stairi,* **Ptilinopus perousii*, *P. porphyraceus, Ducula pacifica*, and **D. latrans,* parrots **Vini solitarius* and **V. australis*, barn-owl *Tyto alba,* swift *Collocalia spodiopygia*, kingfisher *Halcyon chloris*, triller **Lalage maculosa*, shrikebill **Clytorhynchus vitiensis*, honeyeater **Foulehaio carunculata*, and starling *Aplonis tabuensis* (Steadman, 2006b). The last four of these species are passerines, prehistoric bones of which we did not study. Nevertheless, we recorded 16 of these 17 species in Lau, either still alive, from prehistoric bones, or both. The single missing species was *Vini australis*.

The relative abundance and species richness of landbirds on Lakeba today are greatest in submature/mature limestone forest, the terrestrial habitat least affected by people (Steadman, 2006b:table 6-6; Franklin and Steadman, 2010). This is due primarily to increases in columbids (*Gallicolumba stairi*, *Ptilinopus perousii*, *P. porphyraceus*, *Ducula pacifica*) and passerine insectivores (*Mayrornis lessoni*, *Myiagra vanikorensis*). Based on our point-counts and other observations from all four islands, it is clear that habitat quality is more important than island area in structuring the landbird communities of the Lau Group. Lakeba is mostly deforested and has 2500 people as well as eight species of non-native vertebrates (chickens *Gallus gallus*, Pacific rats *Rattus exulans*, black rats *R. rattus*, cats *Felis catus*, dogs *Canis domesticus*, horses *Equus caballus*, pigs *Sus scrofa*, and cows *Bos taurus*). Aiwa Levu is uninhabited, 100% forested, and lacks non-native mammals except Pacific rats and goats (*Capra hircus*). Columbids are much more

abundant on Aiwa Levu than on nearby Lakeba. Two other species found on Aiwa Levu (*Falco peregrinus*, *Clytorhynchus vitiensis*) seem to be extirpated on Lakeba, whereas the nectarivore *Myzomela jugularis* is the only species found today on Lakeba but not Aiwa Levu.

Nayau is mostly deforested and has ca. 430 people as well as chickens, rats (both spp.?), cats, dogs, horses, pigs, and cows. From our brief visit in October 2001, the most distinctive aspects of Nayau's current landbird fauna are the common presence of the pigeon *Ducula latrans* in forested areas (this species is absent today on the other three islands; Table 5), and the absence or extreme rarity (island-wide) of the passerines *Lalage maculosa*, *Mayrornis lessoni*, *Clytorhynchus vitiensis*, and *Myiagra vanikorensis*.

Most species of landbirds in Lau also occur elsewhere in in Tonga and/or Samoa, where birds have been surveyed much more extensively (Steadman, 1998, 2006b; Steadman and Freifeld, 1998; Friefeld, 1999; Steadman et al., 1999). Considering all available survey data from Lau, Tonga, and Samoa, we can make these generalizations about the current status of these six species characteristic of West Polynesia. The pigeon *Ducula pacifica* is generally absent on islands that lack secondary or mid-/late-successional native forest; it tends to increase in abundance with greater maturity of the forest. The fruit-dove *Ptilinopus porphyraceus*, which occurs on more islands in this region than any other columbid, also increases in abundance as forests mature, although it is more tolerant of secondary forest in abandoned plantations. The ground-dove *Gallicolumba stairi* is a forest obligate that is absent or very rare on inhabited islands. On the other hand, the very widespread barn-owl *Tyto alba*, swift *Collocalia spodiopygia*, and kingfisher *Halcyon chloris* show no clear inter- or intra-island trends in habitat preference or relative abundance. These three species of landbirds seem to be the most tolerant of human impacts.

Of the eight species of birds known on Lakeba only from prehistoric bones, we presume that the two extinct species, namely the megapode *Megapodius alimentum* (Fig. 3) and the pigeon *Ducula lakeba*, and three of the extant species that are extirpated on Lakeba (*Didunculus* cf. *strigirostris*, *Prosopeia* sp., ?*Charmosyna amabilis*) were forest obligates. Three species extirpated on Lakeba but extant elsewhere (the heron *Butorides striatus*, and rails *Porzana tabuensis* and *Poliolimnas cinereus*) prefer freshwater wetlands, which may have been more extensive on Lakeba's coastal plain at first human contact. A possible mechanism for the loss of freshwater wetlands on Lakeba would be siltation from erosion caused by land clearing and gardening. The species known to have been lost on Nayau, Aiwa Levu, or Aiwa Lailai also were either likely forest obligates (megapodes, flightless rails, pigeons) or wetland species (duck, swamphen).

CONCLUSIONS

Our estimate of the composition of reptile and bird communities at human contact identified 29 species (7 reptiles, 22 non-passerine landbirds) from prehistoric bones on four islands (Lakeba, Nayau, Aiwa Levu, and Aiwa Lailai) in the Lau Group of Fiji. The bones range in age from ca. 2800 to 400 Cal BP, and represent six taxa of squamate reptiles that are indigenous to the Lau Group, including an undescribed and presumably extinct gekkonid lizard. The Lau islands never have been comprehensively surveyed for modern squamate reptiles, yet five of the six species of lizards that occur in Lau today are not represented with certainty by prehistoric bones (two geckos and three skinks), suggesting considerable turnover after human arrival. These synthropic species may not be indigenous to Lau.

Although the prehistoric loss of indigenous lizard species may have been offset by human introductions, the avifauna lost rather than gained species with the arrival of people. Prehistoric bones increase the species richness of landbirds from 21 to 29 species on Lakeba, from 17 to 19 species on Nayau, from 18 to 26 on Aiwa Levu, and from 16 to 17 on Aiwa Lailai. Studies of prehistoric vertebrates always are limited by the quality and quantity of sites and bones that are available; the inter-island differences in species richness of birds

are probably due, therefore, to the uneven sampling of prehistory (Franklin and Steadman, 2008), with bone assemblages from Lakeba and Aiwa Levu that are both older and more abundant than those from Nayau or Aiwa Lailai. In spite of these inherent imperfections in the availability of prehistoric data, our study demonstrates the dominant role of humans on faunal changes in the Lau islands.

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Appendix 1. Catalog numbers (Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida; UF) for prehistoric reptile bones from four islands in the Lau Group, Fiji. Except for Koro Ni Gasau Rockshelter 1 and Campsite Rockshelter, the site abbreviations are defined in Table 4. LAKEBA—**197OR**, UF 300301–300314; **OSRS**, UF 300315–300318. NAYAU—**WaiTW**, UF 300338–300348; **WaiTE**, UF 300363–300367; **UluNK**, UF 300349–300354; **DKT**, UF 300355–300356; **NMM**, UF 300357–300362, 300375–300384; Koro Ni Gasau Rockshelter 1, UF 300368–300374. AIWA LEVU—**ALC2**, UF 300473–300490; **ALR1**, UF 300385–300472, 300491–300498; **Campsite Rockshelter**, UF 300499–300511. AIWA LAILAI—**DAUR**, UF 300319–300337.

Appendix 2. Identified skeletal elements of prehistoric birds (Ornithology Collection , Florida Museum of Natural History, University of Florida; UF) from four islands in the Lau Group, Fiji. Site abbreviations are defined in Table 4.

LAKEBA—**QNP:** *Gallus gallus*, pedal phalanx UF 60634; *Gallirallus philippensis*, 2 tibiotarsi UF 60637, 60654; *Columba vitiensis*, femur UF 60629; *Halcyon chloris*, coracoid UF 60633. **GYR:** *Gallus gallus*, femur UF 60630, tibiotarsus UF 60631, fibula UF 60632. **QSE:** *Egretta sacra*, humerus UF 60674, femur UF 60669, 2 tibiotarsi UF 60672, 60673, tarsometatarsus UF 60667, pedal phalanx UF 606681; *Gallus gallus*, tibiotarsus UF 60671; *Ptilinopus perousii*, scapula UF 60698; *Tyto alba*, tibiotarsus UF 60668; *Halcyon chloris*, scapula UF 60701, humerus UF 60692, ulna UF 60694, radius UF 60700; Passeriformes, cranium UF 60697, mandible UF 60699, scapula UF 60702, humerus UF 60693, tibiotarsus UF 60695. **QNQ**: non-UF specimens; details in Worthy and Clark (2009). **197OR:** *Gallirallus philippensis*, vertebra UF 60719, tibiotarsus UF 60711; *Poliolimnas cinereus*, pedal phalanx UF 60705; *Ptilinopus porphyraceus*, 2 ulnae UF 60703, 60715, femur UF 60710, tibiotarsus UF 60712, fibula UF 60721, tarsometatarsus UF 60718, hallux UF 60722, pedal phalanx UF 60720; *Tyto alba*, humerus UF 60709; Passeriformes, ulna UF 60716, carpometacarpus UF 60617, 2 tibiotarsi UF 60613, 60614, tarsometatarsus UF 60704. **OSOC:** *Tyto alba*, radius UF 59259, carpometacarpus UF 59258, manus phalanx UF 59262, rib UF 59261, pedal phalanx UF 59260. **OSOR:** *Gallus gallus*, pedal phalanx UF 60728; *Porzana tabuensis*, femur UF 59263; Passeriformes, humerus UF 60723, 3 tibiotarsi UF 60724–60726, scapula UF 60727. **WAI:** *Porzana tabuensis*, humerus UF 59293; Passeriformes, rostrum UF 59298, 2 tibiotarsi UF 59294, 59295. **VAR:** *Porzana tabuensis*, femur UF 59271; *Gallicolumba stairi*, femur UF 59270; Passeriformes, cranium UF 59277, 2 mandibles UF 59275, 59276, humerus UF 59265, 2 ulnae UF 59272, 59273, carpometacarpus UF 59274, 4 tibiotarsi UF 59266–59269. **LVR:** *Ptilinopus* sp., rostrum + mandible UF 59288; Passeriformes, 2 mandibles UF 59285, 59286, 4 humeri UF 59278–59281, 3 ulnae UF 59290–59292, carpometacarpus UF 59289, femur UF 59284, tibiotarsus UF 59282, tarsometatarsus UF 59283.

NAYAU—**WaiTE:** *Ptilinopus perousii*, coracoid UF 63016, 2 femora UF 61297, 63021, tibiotarsus UF 63022; *Ptilinopus porphyraceus*, tibiotarsus UF 63018; *Halcyon chloris*, radius UF 63023, 2 femora UF 61296, 63019; Passeriformes, 3 humeri UF 63024, 63025, 63028. **WaiTW:** *Gallirallus philippensis*, humerus UF 61376; *Gallicolumba stairi*, ulna UF 61409, 2 tibiotarsi UF 61362, 61397; *Ptilinopus perousii*, mandible UF 61311, sternum UF 61314, 2 coracoids UF 61336, 61338, scapula UF 61382, 4 humeri UF 61299, 61377, 61388, 61405, 3 ulnae UF 61341, 61391, 61410, 2 radii UF 61353, 61395, carpometacarpus UF 61344, 5 femora UF 61331–61334, 61373, 5 tibiotarsi UF 61321–61323, 61330, 61369, 3 tarsometatarsi UF 61348, 61350, 61448, hallux UF 61425; *Eudynamys taitensis*, humerus UF 61298; *Collocalia spodiopygia*, sternum UF 61319, 3 coracoids UF 61429, 61430, 61445, scapula UF 61444, ulna UF 61431, synsacrum UF 61427, tibiotarsus UF 61426; *Halcyon chloris*, sternum UF 61316, 3 coracoids UF 61337, 61339, 61340, humerus UF 61300, ulna UF 61412, 3 radii UF 61352, 61354, 61365, 3 femora UF 61335, 61384,

61398; Passeriformes, skull UF 61304, 2 mandibles UF 61310, 61402, 4 sterna UF 61313, 61315, 61317, 61318, 2 coracoids UF 61403, 61440, scapula UF 61446, 12 humeri UF 61301–61303, 61363, 61378, 61379, 61389, 61390, 61400, 61406–61408, 9 ulnae UF 61342, 61343, 61371, 61380, 61392–61394, 61411, 61442, 3 carpometacarpi UF 61345, 61404, 61447, synsacrum UF 61306, 3 femora UF 61383, 61401, 61447, 7 tibiotarsi UF 61324–61329, 61385, 8 tarsometatarsi UF 61347, 61349, 61351, 61396, 61416–61419. **UluNK:** *Porzana tabuensis*, humerus UF 63029, tarsometatarsus UF 63030; *Columba vitiensis*, sternum UF 63057, scapula UF 63031, radius UF 63058; *Ptilinopus perousii*, radius UF 63034, carpometacarpus UF 63035; *Ptilinopus porphyraceus*, ulna UF 63036, tibiotarsus UF 63037; *Tyto alba*, coracoid UF 63033, femur UF 63032; *Halcyon chloris*, humerus UF 63053, 2 radii UF 63054, 63055, tarsometatarsus UF 63056; Passeriformes, coracoid UF 63045, 4 humeri UF 63038–63041, 2 ulnae UF 63043, 63044, 4 femora UF 63042, 63047–63049, 3 tibiotarsi UF 63050–63052, tarsometatarsus UF 63046. **DKT:** *Gallus gallus*, 2 pedal phalanges UF 63059, 63060; *Gallirallus philippensis*, tibiotarsus UF 63061. **NMM:** *Gallus gallus*, rostrum UF 63335, coracoid UF 63325, ulna UF 63327, 3 tibiotarsi UF 63330, 63331, 63333, tarsometatarsus UF 63340, 2 pedal phalanges UF 63324, 63334; *Gallirallus philippensis*, vertebra UF 63328, scapula UF 63322; *Ducula* sp., radius UF 63332, tibiotarsus UF 63323; *Aplonis tabuensis*, mandible UF 63337, scapula UF 63338.

AIWA LEVU—**ALC1:** *Gallirallus philippensis*, 2 ulnae UF 60745, 60750, radius UF 60751, 3 femora UF 60740, 60747, 60748, tibiotarsus UF 60734, 3 tarsometatarsi UF 60733, 60739, 60947; *Porphyrio porphyrio*, tibiotarsus UF 60729; *Gallicolumba stairi*, 2 tibiotarsi UF 60730, 60731, synsacrum UF 60735; *Halcyon chloris*, humerus UF 60736, ulna UF 60746; Passeriformes, 2 humeri UF 60737, 60738, 2 ulnae UF 60742, 60743, tibiotarsus UF 60732. **ALC2:** *Gallus gallus*, rib UF 60729, 2 carpometacarpi UF 60788, 60800, tarsometatarsus UF 60793, 3 pedal phalanges UF 60794, 60798, 60799; *Gallirallus philippensis*, scapula UF 60801; *Porphyrio porphyrio*, scapula UF 60789, radius UF 60786, femur UF 60784; *Columba vitiensis*, coracoid UF 60787, humerus UF 60785; *Ducula lakeba*, tarsometatarsus UF 60809; *Tyto alba*, humerus UF 60807; *Collocalia spodiopygia*, 2 carpometacarpi UF 60791, 60796, 2 tibiotarsi UF 60792, 63247; Passeriformes, 2 coracoids UF 60804, 60805. **ALR1:** *Anas superciliosa*, ulna UF 60762/60763 (2 fitted fragments); *Megapodius alimentum*, rib UF 61262, humerus UF 62852, notarium UF 61260; *Megapodius amissus/molistructor*, pedal phalanx UF 61225; *Gallus gallus*, mandible UF 62839, 2 radii UF 62833, 62842, carpometacarpus UF 62832, notarium UF 62841, 2 tarsometatarsi UF 60758, 60760; *Gallirallus philippensis*, humerus UF 61263, 2 femora UF 60752, 61280, 3 tarsometatarsi UF 61268, 61274, 62856, pedal phalanx UF 61216; *Gallirallus* undescribed sp., ulna UF 61224, tibotarsus UF 60775, pedal phalanx UF 60776; *Porzana* undescribed sp., tibiotarsus UF 60769; *Porphyrio porphyrio*, pedal phalanx UF 62828; *Columba vitiensis*, 2 ulnae UF 62836, 62837, 2 radii UF 62834, 62835, carpometacarpus UF 60759; *Gallicolumba stairi*, humerus UF 61231, femur UF 61245, tibiotarsus UF 62857; *Ptilinopus perousii*, coracoid UF 61213; *Ducula pacifica*, 2 sterna UF 62846, 62850, 2 coracoids UF 62827, 62843, 2 scapulae UF 62849, 62859, carpometacarpus UF 60753, tibiotarsus UF 62853, fibula UF 62845; *Ducula latrans*, 2 sterna UF 60754, 60761, 2 radii UF 60766, 60772, pedal phalanx UF 62838; *Ducula* sp., scapula UF 62831; Columbidae sp., manus phalanx UF 62861, pedal phalanx UF 60770, ungual phalanx UF 61217; *Collocalia spodiopygia*, ulna UF 61252; *Halcyon chloris*, dentary UF 61281, scapula UF 61291, humerus UF 62858; Passeriformes, 3 mandibles UF 60783, 61244, 62830, sternum UF 61251, 3 coracoids UF 60778, 61223, 61267, 10 humeri UF 60771, 60774, 60780, 61210, 61232–61236, 62829, 12 ulnae UF 60755, 61209, 61230, 61237–61239, 61259, 61264–61266, 62823, 62824, radius UF 61254, manus phalanx UF 61287, 3 synsacra UF 61257, 61282, 61283, femur UF 61246, 11 tibiotarsi UF 60757, 60781, 61240–61243, 61255, 61271–61273, 62825, 11 tarsometatarsi UF 60756,

60782, 61249, 61250, 61269, 61270, 61275, 61276, 61278, 61279, 62826. **GRS:** *Gallirallus philippensis*, cranium UF 61293, tibiotarsus UF 61294. **CRS:** *Ducula* sp., mandible UF 60810, carpometacarpus UF 60811.

AIWA LAILAI—**DAUR:** *Gallus gallus*, mandible UF 62787/62791 (2 fitted fragments), humerus UF 63344, pelvis UF 62804, 2 tibiotarsi UF 63351, 63355, pedal phalanx UF 62802; *Gallicolumba stairi*, sternum UF 63345, tibiotarsus UF 62813, tarsometatarsus UF 62786; *Ptilinopus perousii*, carpometacarpus UF 62810; *Ducula pacifica*, 4 dentaries UF 62788–62790, 62808, sternum UF 62792/62794–62796/62799 (5 fitted fragments), 4 coracoids UF 62806, 62807, 62817, 62818, 2 scapulae UF 62822, 63880, humerus UF 63343, 2 ulnae UF 62815, 62819, 3 radii UF 62783, 62820, 63354, 2 carpometacarpi UF 62793, 63356, 2 femora UF 62811, 63350, 3 tibiotarsi UF 62784, 62785, 62816, 2 tarsometatarsi UF 62812, 63353, pedal phalanx UF 62809; *Ducula latrans*, sternum UF 63346, scapula UF 62800; *Ducula* sp., rib UF 63347, ulna UF 63349.

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Send communications about this publication to:

Editor of the Bulletin
Florida Museum of Natural History
University of Florida
P.O. Box 117800
Gainesville, FL 32611-7800 USA

FAX: 352-846-0287
Email: bulletin@flmnh.ufl.edu
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