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A NEW SPECIES OF HAWAIIAN FINCH (DREPANIDINI: *LOXIOIDES*) FROM MAKAUWAHI CAVE, KAUA`I

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ABSTRACT.—A new species of Hawaiian finch is described from two fossil maxillae recovered from Holocene lacustrine sediments in Makauwahi Cave, island of Kaua`i. The new species is assigned to *Loxioides* on the basis of characters defined in a previous study of drepanidine phylogeny. The maxilla of the new species resembles that of *L. bailleui* (the only other member of the genus) in its distinctly foreshortened shape, but differs in size and several qualitative characters. The species was sympatric with *Loxioides* cf. *bailleui* during the Holocene on Kaua`i. Like *L. bailleui*, it may have been a resource specialist feeding mainly on leguminous pods. The radiocarbon chronology of the Makauwahi site indicates that the species became extinct in the late Holocene and, more tentatively, that it may have survived well beyond the time when humans first discovered and colonized Kaua`i. *Received 1 October 2004, accepted 22 June 2005.*

Key words: extinction, fossil birds, island biogeography, systematics.

Una Nueva Especie de Pinzón de Hawaii (Drepanidini: *Loxioides*) de la Cueva Makauwahi, Kaua`i

RESUMEN.—Se describe una nueva especie de pinzón de Hawai a partir de dos fósiles de maxilas extraídos de sedimentos lacustres del Holoceno en la cueva Makauwahi, en la isla de Kaua`i. La nueva especie es asignada a *Loxioides* con base en caracteres definidos en un estudio previo sobre la filogenia de los Drepanidini. La maxila de la nueva especie es similar a la de *L. bailleui* (el único otro miembro del género) en su forma marcadamente achatada, pero difiere en tamaño y en varios caracteres cualitativos. La especie fue simpátrica con *Loxioides* cf. *bailleui* durante el Holoceno en Kaua`i. Como *L. bailleui*, puede haber sido un especialista que se alimentaba principalmente de vainas de leguminosas. La cronología de radiocarbono del sitio Makauwahi indica que la especie se extinguió durante el Holoceno tardío y de modo más tentativo, que podría haber sobrevivido más allá del tiempo en que los humanos descubrieron y colonizaron por primera vez Kaua`i.

FOSSIL BIRDS WERE first found on the Hawaiian island of Kaua`i in 1976, weathering out of unconsolidated eolian dunes along the southeast coast (the Makawehi Dune sites; Olson and James 1982). Three new genera and six new species of birds were described from those sites (James and Olson 1991, Olson and James 1991). Subsequent collecting has produced additional fossil birds from Kaua`i, principally from excavations of

Holocene wetland and lake sediments in the central sinkhole of Makauwahi Cave, a karstic cavern located not far from the original dune sites (Fig. 1; Burney et al. 2001). At least 40 species of indigenous seabirds, shorebirds, waterfowl, raptors, and passerines are represented in the diverse faunal assemblage of Makauwahi Cave (Burney et al. 2001). Among the passerines are seven species with finch-like bills: a small finch (*Telespiza persecutrix*) similar to the Laysan and Nihoa finches, a Kona-type finch (*Chloridops wahi*), a new species of koa-finch (*Rhodacanthis forfex*; James and

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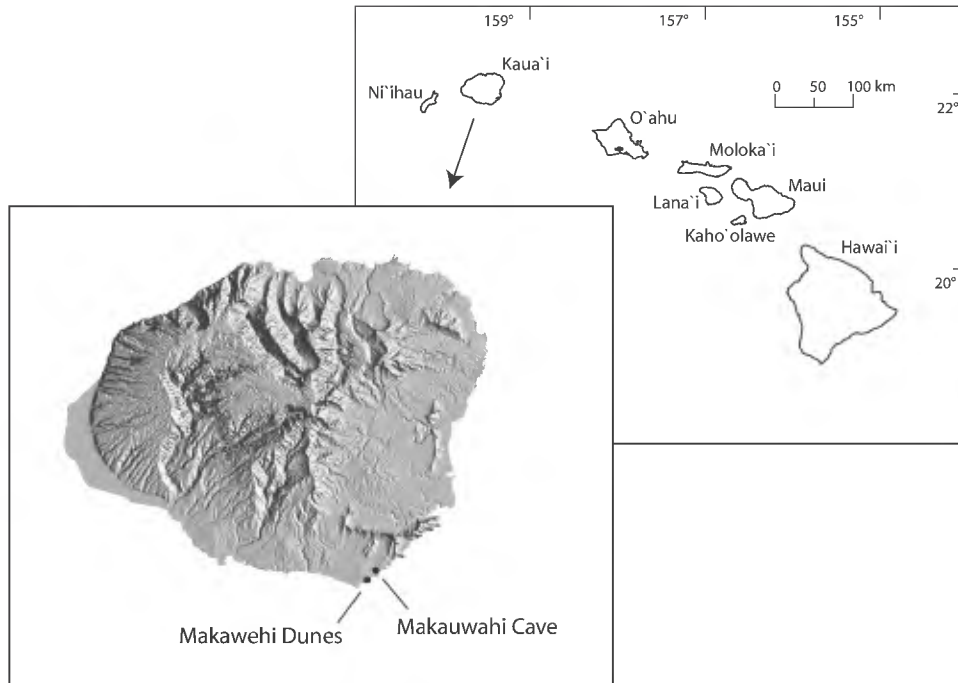


FIG. 1. Map of Kaua'i showing principal collecting localities for fossils of the Drepanidini. The sites with abundant drepanidine fossils date to the Holocene Epoch (Hearty et al. 2000, Burney et al. 2001).

Olson 2005), a species with a cone-shaped bill (*Xestospiza conica*), the O'u (*Psittirostra psittacea*), the Palila (*Loxioides bailleui*; or a sibling species of *L. bailleui* with very similar cranial osteology), and an undescribed species known only by two nearly identical maxillae. Here, we describe the last as a new species of Hawaiian finch.

Because the new species is a member of the adaptive radiation of Drepanidini (the Hawaiian finches or honeycreepers, a tribe of the Fringillidae), the most important taxa with which to compare it are the species of drepanidines with finch-like bills, currently classified in the genera *Telespiza*, *Loxioides*, *Rhodacanthis*, *Chloridops*, *Xestospiza*, and *Orthospiza* (Sibley and Monroe 1990, James and Olson 1991, American Ornithologists' Union 1998). We note that there is some doubt that *Orthospiza*, a monotypic genus restricted in distribution to the island of Maui, is a member of the radiation (James 2004).

METHODS

The two maxillae were included in a previous study of osteological character variation in the

Drepanidini (James 2004). We made use of the characters defined in that study, and made additional comparisons with similar and related species, to diagnose the new species. To assess the relatedness of the new species to other taxa of Fringillidae, we performed phylogenetic analyses using the data matrix from James (2004) and PAUP*, version 4.0B10 (Swofford 2002). Character-state changes were mapped using MACCLADE (Maddison and Maddison 1992). Bone measurements were taken to the nearest 0.1 mm with digital calipers. Terminology of the maxillary structure follows James (2004).

Comparative material examined.—Comparisons were previously made with 87 taxa of Fringillidae: 58 taxa from the Hawaiian Islands (the presumed Drepanidini, of which 23 were represented only by fossils), and 29 from beyond the archipelago, including 20 species of cardueline finches (Carduelini), 8 species selected to survey the Emberizini, and 1 species (*Fringilla coelebs*) to represent the Fringillini (see James 2004). For the present work, we examined the following maxillae of species that are either similar in bill form or closely related to the

new finch according to parsimony analysis (for museum acronyms, see Acknowledgments). Drepanidini: *L. bailleui*: USNM 560602 (female), 91098 (sex unknown), BBM-X 156555 (sex unknown); *T. cantans*: USNM 560948 (sex unknown), 561510 (male), 289283 (male); *T. ultima*: USNM 289277 (female), 289278 (male); *Rhodacanthis palmeri*: AMNH 453623 (male); *R. flaviceps*: AMNH 453644 (female); *C. kona*: AMNH 453677 (male); *C. wahi*: USNM 523453, 523454, 523455 (fossils); *C. regiskongi*: BPBM 158742 (holotype, fossil), 158814 (paratype, fossil). Carduelini: *Pyrrhula pyrrhula*: USNM 321130 (female); *P. erythraca*: USNM 319386 (male). Fringillidae, *incertae sedis*: *Orthospiza howarthii*: USNM 370557 (paratype, fossil), 445797 (paratype, fossil).

SYSTEMATICS

In James's (2004) study of comparative osteology and evolutionary relationships in the Drepanidini, the new species was placed in a clade with *L. bailleui*, the only other member of

the genus *Loxioides* (see fig. 17 in James 2004). However, the parsimony analyses reported in James (2004) do not specifically address whether the new species is properly classified in the Drepanidini as opposed to some other tribe of Fringillidae. We consequently analyzed a partition of James's (2004) data matrix that included the new finch, the 29 extra-Hawaiian taxa (28 species of Fringillidae and *Passer domesticus*), and 30 terminal taxa of drepanidines. The taxa included were those in James's matrix A (appendix 2 in James 2004), with the addition of the new finch. A heuristic search using the parsimony criterion, 100 replicates of random-addition sequences, and TBR (tree bisection and reconnection) branch-swapping placed the new finch within the Drepanidini, once again as sister to *L. bailleui* (Fig. 2).

Of the non-drepanidine taxa of Fringillidae, the Palearctic genus of bullfinches (*Pyrrhula*) is closest to *Loxioides* in general bill shape. *Pyrrhula* differs from *L. bailleui* and the new species in that (1) the maxilla is not as deep in proportion to length, (2) the supranasal bar is much

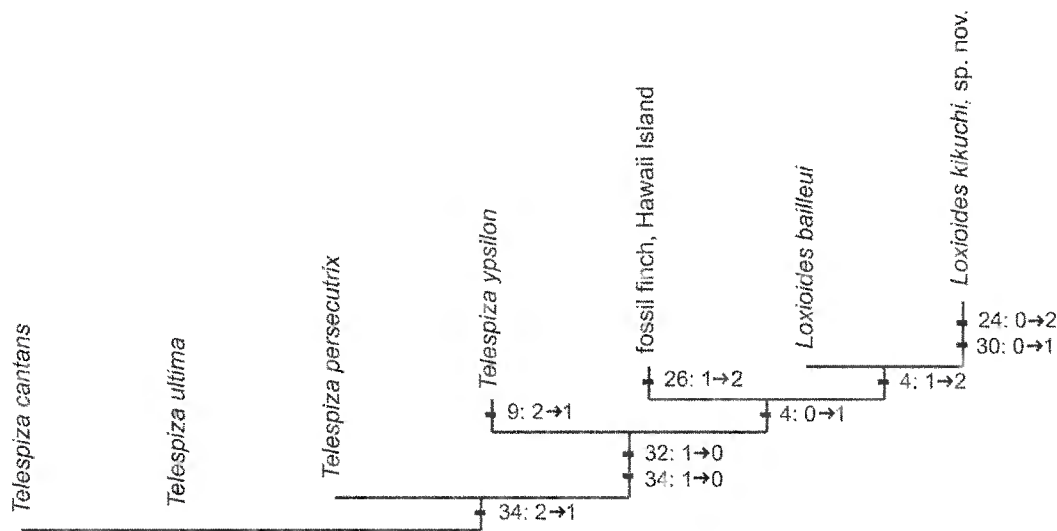


FIG. 2. Unrooted phylogram showing unambiguous osteological character-state changes in *Telespiza* and *Loxioides*. Characters and their states are from James (2004), as follows. Character 4: foreshortening of the conical bill: absent (0), intermediate (1), present (2). Character 9: maxilla: supranasal bar: broad anteriorly (1), very broad anteriorly (2). Character 24: maxilla: nutrient foramen (or multiple tiny foramina) in the anterior wall of the nasal cavity: absent (0), present (1). Character 26: maxilla: median neurovascular sulcus on the ventral surface: moderately developed (2), deep (3). Character 30: maxilla: median crest on the ventral surface: absent (0), present (1). Character 32: mandible: posterior margin of the mandibular rostrum: curved or angular (0), straight (1). Character 34: mandible: sides of the mandibular rostrum: not very thick (0), intermediate thickness (1).

narrower and strut-like rather than expanding anteriorly, (3) the opening of the nasal cavity is larger, (4) the median fossa on the ventral surface is shallower, and (5) the ventral crests are less pronounced. *Pyrrhula* is distinguished from all other fringillid genera in having the median fossa of the ventral maxilla incised by a series of grooves that extend antero-laterad from the median neurovascular sulcus toward the ventral crests (James 2004). These accessory neurovascular grooves are lacking in *L. bailleui* and the new species.

Placement of the new species in the Drepanidini is further affirmed by the logarithmic ratios of the breadth of the supranasal bar to the lateral nasal bar in the two fossil maxillae (ratio in holotype = 0.35; ratio in paratype = 0.40). Among the finch-billed taxa of Fringillidae in James's (2004) study, ratios greater than 0.30 were observed only in the Drepanidini.

Class Aves
Family Fringillidae
Tribe Drepanidini
Genus *Loxioides*

A heuristic parsimony analysis of osteological characters placed *Loxioides* and the new species in a clade with *Telespiza* (the Laysan Finch and relatives). In comparison with other drepanidine finches, the following combination of traits will diagnose the new species as belonging to the *Telespiza* + *Loxioides* clade: dorsal profile of the maxilla strongly arched (nearly straight in *Xestospiza*), supranasal bar very broad anteriorly and tapering posteriorly to a much narrower breadth (narrower and more strut-like in *Orthospiza* and *Chloridops kona*), median fossa of the ventral maxilla moderately excavated (deeper in *Rhodacanthis*, unexcavated in *Orthospiza*), ventral crests of the maxilla extending nearly to the bill tip (not extending as far in *Rhodacanthis*, *Chloridops*, or *Xestospiza*) and forming a distinct ridge (blunt in *Chloridops*).

A supplemental phylogenetic analysis of James's (2004) data for the taxa in the *Telespiza* + *Loxioides* clade, using a branch-and-bound algorithm, confirmed that the new finch is most parsimoniously classified as sister to *L. bailleui* on the basis of osteological characters (Fig. 2). Attributes that place the new species in *Loxioides* rather than *Telespiza* include its short, wide maxilla and the relatively large opening of the nasal cavity.

***Loxioides kikuchi*, sp. nov.**

Figures 3A, 3B, 4A, 4B, 5A, 5B

"Fringillidae: genus undetermined, finch"

(Burney et al. 2001:628)

"Maha`ulepu finch" (see fig. 17 and appendix 2 in James 2004)

Holotype.—USNM 523450 (Figs. 3B, 4B, 5B): maxilla lacking part of the left lateral nasal bar; collected 16 August 1998 by D. A. Burney and members of the Kaua`i Paleocology Expedition. In the excavation described by Burney et al. (2001), the bone was found in pit BAC-EP0, grid II 45, unit V, 3.3 m below datum.

Measurements of holotype.—See Table 1.

Paratype.—USNM 523449 (Figs. 3A, 4A, 5A): maxilla lacking part of the left lateral nasal bar; collected 28 December 1997 by D. A. Burney and members of the Kaua`i Paleocology Expedition. In the excavation described by Burney et al. (2001), the bone was found in pit BAC-EP+, grid ~LL49, unit VI, 2.4 m below datum.

Measurements of paratype.—See Table 1.

Type locality.—Hawaiian Islands: island of Kaua`i: Koloa Quadrangle: Makauwahi Cave (21°53'30"N, 159°25'17"W). Near sea level. State Archaeological Site number 50-30-10-3097. Alternate names for the site are the Grove Farm Caves (W. R. Halliday pers. comm.) and the Maha`ulepu sinkhole and cave complex (Burney et al. 2001), but Makauwahi Cave appears to have precedence (Burney and Kikuchi 2005).

Distribution.—Island of Kaua`i. Known only from the type locality.

Chronology.—Mid- to late Holocene, based on 34 radiocarbon determinations on bones, seeds, fruit, and sediments from the site (Burney et al. 2001). Five ages of sediment and bird bones from unit V (the provenience of the holotype) have a range of 4,380–2,157 cal BP (NZA 10056, 10057; Beta 67395, 110275, 128626), whereas one bone of *Rattus exulans* from the unit had an age range of 961–759 cal BP (NZA 10058). Four ages of seeds and the rind of a gourd from unit VI (the provenience of the paratype) had a range of 575–340 cal BP (Beta 110272, 110273, 115789, 116189). The ranges given are extremes of the 95% probability ranges of the individual radiocarbon determinations, corrected for isotopic fractionation and converted to calendar years using the calibration program CALIB and INTCAL98 (Stuiver et al. 1998).

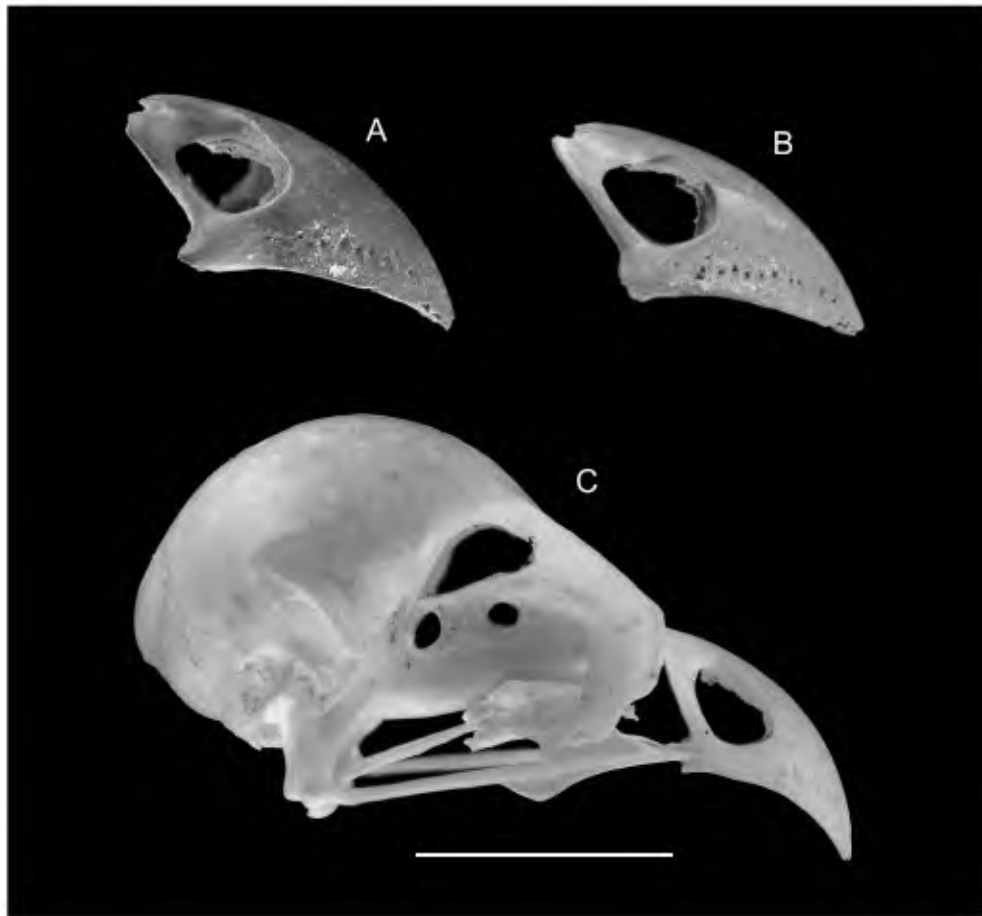


FIG. 3. Maxillae of *L. kikuchi*, compared with the skull of *L. bailleui*, in lateral view. (A) *L. kikuchi*, USNM 523449, paratype. (B) *L. kikuchi*, USNM 523450, holotype. (C) *L. bailleui*, BBM-X 156555. Scale bar = 1 cm.

Diagnosis.—A species of drepanidine finch with the maxilla short in relation to its breadth in comparison with most other finches, and highly arched dorsally. Maxilla similar in general shape to that of *L. bailleui*, from which it differs in larger size and in having the supranasal bar relatively narrow at its narrowest point (Fig. 4) and the posterior margin of the ventral maxilla less recessed medially (Fig. 5). The curvature of the tomial crest of the maxilla increases near the bill tip in *L. bailleui*, creating the effect of a hook, a feature lacking in *L. kikuchi* (Fig. 3). The dorsal surface of the maxilla develops a slight median crest in *L. kikuchi* that is lacking in *L. bailleui* (Fig. 4).

In *L. kikuchi*, a median crest is present on the ventral maxilla, where most drepanidines have a distinct median sulcus (Fig. 5), and the

surface of the median fossa is unusually rugose (Fig 5).

Etymology.—Dedicated to the Kikuchi family of Kauaʻi, especially William (Pila) and Delores (Dolly), who worked closely with us in the excavation of the deposits at the type locality and greatly facilitated our research and exploration on the island. In giving the name, we honor Pila's many years of archaeological research and teaching on Kauaʻi, as well as the hospitality of the entire family: grandparents, parents, and daughters. The name is to be taken as a noun in the nominative case, not the genitive, following the example of Salvadori (1865), who used the name *Uria* (= *Endomychura*) *craveri* to honor the brothers Craveri (Olson 1996). We suggest that an appropriate common name for the new finch is Pila's Palila.

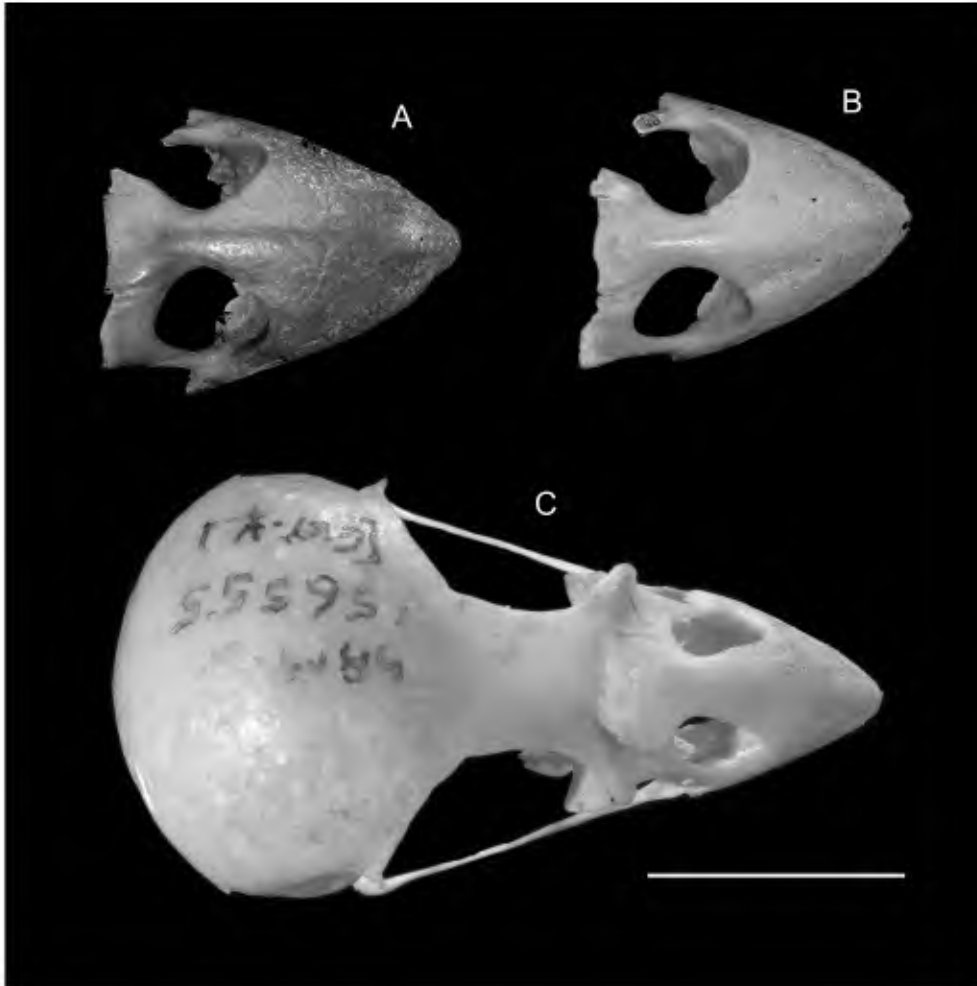


FIG. 4. Maxillae of *L. kikuchi*, new species, compared with the skull of *L. bailleui*, in dorsal view. (A) *L. kikuchi*, USNM 523449, paratype. (B) *L. kikuchi*, USNM 523450, holotype. (C) *L. bailleui*, BBM-X 156555. Scale bar = 1 cm.

Remarks.—See the cover art for an artist's representation of how the new species may have appeared in life.

A median crest in place of the usual median sulcus on the ventral maxilla has not been observed elsewhere in the Drepanidini, yet the condition in *L. kikuchi* is not markedly different from that in *L. bailleui*. The median sulcus in the latter species is extremely shallow, and its sides are slightly elevated above the median fossa, whereas the sulcus is deeper and not elevated in most other drepanidine species. The sulcus tends to be deepest in drepanidines that take nectar or probe in crevices with the bill for

arthropod prey, and shallowest in birds with finch-like bills. James (2004) observed a median crest on the ventral maxilla in several species of Emberizini and in *P. domesticus*.

The maxillae of *L. kikuchi* are larger than the observed range for *L. bailleui* in nearly all dimensions (Table 1). The only measurements taken of *L. kikuchi* that fall within the range for *L. bailleui* are the width of the supranasal bar, which is relatively narrow in *L. kikuchi*, and the length of the narial opening and height through the lateral nasal bar in the parotypical specimen. The maxillae of both specimens of *L. kikuchi* also fall above the 99% confidence limits for *L. bailleui* in

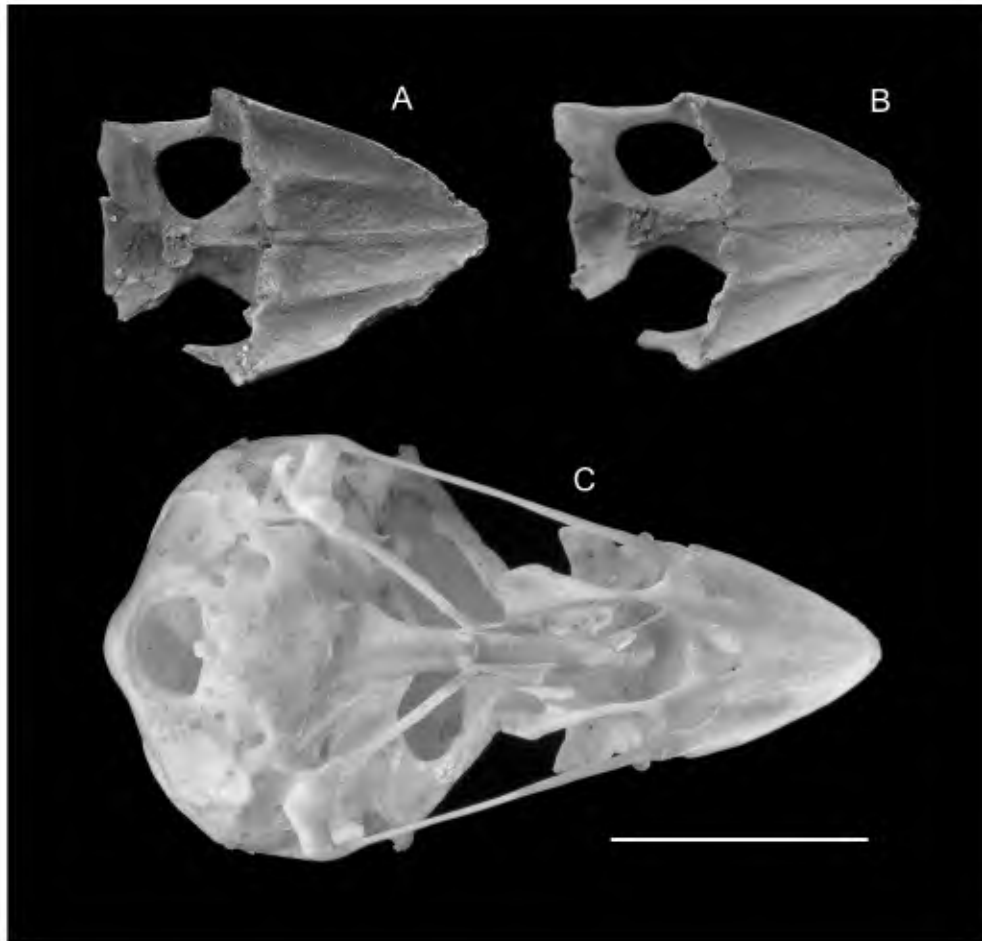


Fig 5. Maxillae of *L. kikuchi*, compared with the skull of *L. bailleui*, in ventral view. (A) *L. kikuchi*, USNM 523449, paratype. (B) *L. kikuchi*, USNM 523450, holotype. (C) *L. bailleui*, BBM-X 156555. Scale bar = 1 cm.

all measurements taken except those mentioned above. The confidence intervals for *L. bailleui* were calculated on the basis of a pooled sample of three males, three probable females, and one individual of unknown sex. Pooling the sample of skeletons is reasonable, considering that field measurements of the exposed culmen of *L. bailleui* reveal only minor sexual size-dimorphism (1.6% difference between means for males and females in samples of 421 male and 240 female after-second-year birds; Banko et al. 2002b).

DISCUSSION

For clues to the former ecological role of the new species, *L. bailleui* is probably the

most appropriate modern ecological analogue. *Loxioides bailleui* is currently restricted to high-elevation open woodland habitat on Mauna Kea, island of Hawai'i (Banko et al. 2002b), though fossils that appear to be the same species occur near sea level at the Makauwahi site and in the 'Ewa Plain sinkholes on O'ahu (Olson and James 1982, Burney et al. 2001). The surviving population is tightly linked ecologically with a native leguminous tree or shrub, the mamane (*Sophora chrysophylla*). The birds are adept at extracting the nutritious but potentially toxic seed embryos from mamane pods (Banko et al. 2002a, b). Breeding is timed to coincide with the peak of pod production, and although the birds rely on alternative foods such as fruit of the naio

TABLE 1. Measurements (mm) of the maxilla in *Loxioides*. The measurements of *L. bailleui* are taken from James and Olson (1991: table 2). The method of taking the measurements is diagrammed in James and Olson (1991: fig 1).

Measurement	<i>L. bailleui</i>			<i>L. kikuchi</i>	<i>L. kikuchi</i>
	Mean \pm SD	Range	<i>n</i>	USNM 523450 Holotype	USNM 523449 Paratype
Dorsal length	12.9 \pm 0.2	12.6–13.2	7	13.8	14.9
Ventral length	6.2 \pm 0.3	5.8–6.6	7	8.2	8.9
Length from lateral corner of naso-frontal hinge	12.8 \pm 0.2	12.5–13.2	7	14.9	15.4
Length from jugal articulation	8.8 \pm 0.3	8.2–9.1	7	11.1	12.3
Length from anterior narial opening	6.3 \pm 0.1	6.1–6.5	7	8.1	9.3
Maximum width	8.1 \pm 0.2	7.9–8.4	6	10.6	11.3
Length of narial opening	3.9 \pm 0.2	3.6–4.2	6	4.5	4.2
Height of narial opening	3.5 \pm 0.2	3.1–3.7	6	4.4	4.3
Height through lateral nasal bar	6.7 \pm 0.3	6.5–7.1	6	7.2	6.8
Minimum width of supranasal bar	2.3 \pm 0.2	2.0–2.6	7	2.0	2.2

tree (*Myoporum sandwicense*) when mamane pods are less available, they do not disperse out of their current *Sophora*–*Myoporum* woodland habitat even in times of scarcity (Banko et al. 2002b).

Might *L. kikuchi* likewise have been a resource specialist whose distribution and ecology were linked with a particular leguminous tree or shrub? We know a good deal about the Holocene vegetation near the type locality from pollen, spores, seeds, and other plant macrofossils preserved in the fossil site (Burney et al. 2001). The natural vegetation surrounding the cave in the mid- to late Holocene consisted of two major components: (1) a diverse lowland forest and scrub association composed of species that now occur in both dry and mesic habitats (i.e. *Dodonaea*, *Pritchardia*, and *Zanthoxylum*) and (2) strand vegetation, represented by grasses and such typical strand species as *Scaevola tacada* and *Jacquemontia ovalifolia*.

The lowland forest and scrub association was much more diverse than the *Sophora*–*Myoporum* woodland inhabited by *L. bailleui* on Mauna Kea. Neither *Sophora* nor *Myoporum* has been recorded from the site, though their presence cannot be ruled out (D. A. Burney pers. comm.) The legumes that have been identified include *Kanaloa* sp., *Acacia koa*, *Erythrina* sp., and *Sesbania tomentosa*. The most abundant legume in the pollen record is *Kanaloa* sp., but

this shrub makes up only ~2% of the pollen and spores counted in the sedimentary levels where it is most common, a much lower abundance for *Kanaloa* pollen than has been observed in Holocene sediment profiles from drier lowland sites on O'ahu (Athens 1997). Although legumes were apparently rare, other potential foods for finches, such as fruit of *Dodonaea* and *Scaevola* and seeds of *Zanthoxylum* and *Santalum*, were abundant. We conclude that, although its apparent sister relationship to *L. bailleui* suggests that *L. kikuchi* was a resource specialist that fed mainly on leguminous pods, it is equally possible that the species visited the locality to feed on other types of plant resources among the bounty offered by the mixed lowland habitat.

The paratype of *L. kikuchi* was found in a stratigraphic unit that dates to only three to six centuries ago. There is a chance that the paratype is an older fossil that was displaced upward from a lower stratigraphic unit, because tsunami waves appear to have dropped exogenous rocks and sediment into the sinkhole ~400 years ago, disturbing the stratigraphic associations somewhat for the period between roughly 2,000 and 400 years ago (Burney et al. 2001). It is more likely that the paratype was found in its original stratigraphic context, which would indicate that the species survived for many centuries after

human arrival on Kaua'i; human settlement of the island having been accomplished by Polynesian voyagers at least 11 centuries ago (Burney and Burney 2003). The species may even have survived into the historical period on Kaua'i. Its presence could easily have been overlooked by Captains Cook and King, who made first European contact with the islanders in 1778 and 1779 but had little chance to observe birds on Kaua'i (Medway 1981), and perhaps by Townsend and Nuttall, who made several inland treks to collect birds and plants in 1835 (Townsend 1999).

In that same year, western-style plantation agriculture was initiated in the islands with the incorporation of Koloa Plantation on southern Kaua'i, not far from Makauwahi Cave (Beechert 1985). Considerably later, the first fairly systematic ornithological collecting on Kaua'i was conducted by the resident Knudsen family, from 1866 to 1893 (Olson and James 1994), a period when plantation agriculture was rapidly expanding. The Knudsens (and Townsend as well) focused their collecting on the southern region of the island that encompasses Makauwahi Cave. Because it seems unlikely that *L. kikuchi* was still extant during the Knudsens' ornithological survey, we infer that its extinction took place sometime between 2,000 and 111 years ago. Ecological changes that accompanied human settlement, either in the prehistoric or historical settlement periods or perhaps during both, are most likely to blame.

The fossils identified as *Loxioides* cf. *bailleui* from Makauwahi Cave consist of an associated individual preserving the maxilla, basicranium, partial palatines, and the frontal with interorbital septum; and a mandible found separately. These skeletal elements are highly diagnostic of the species, leaving no doubt that *L. bailleui*, or conceivably a sibling species that was nearly identical in cranial osteology, once occurred in sympatry with *L. kikuchi* on Kaua'i. The surviving population of *L. bailleui* is thus the remnant of a formerly widespread species group that was ecologically and biogeographically more complex than has been assumed.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- ATHENS, J. S. 1997. Hawaiian native lowland vegetation in prehistory. Pages 248–270 in *Historical Ecology in the Pacific Islands* (P. V. Kirch and T. L. Hunt, Eds.). Yale University Press, New Haven, Connecticut.
- BANKO, P. C., M. L. CIPOLLINI, G. W. BRETON, E. PAULK, M. WINK, AND I. IZHAKI. 2002a. Seed chemistry of *Sophora chrysophylla* (mamane) in relation to diet of specialist avian seed predator *Loxioides bailleui* (palila) in Hawaii. *Journal of Chemical Ecology* 28:1393–1410.
- BANKO, P. C., L. JOHNSON, G. D. LINDSEY, S. G. FANCY, T. K. PRATT, J. D. JACOBI, AND W. E. BANKO. 2002b. Palila (*Loxioides bailleui*). In *The Birds of North America*, no. 679 (A. Poole and F. B. Gill, Eds.). Birds of North America, Philadelphia.
- BEECHERT, E. D. 1985. *Working in Hawaii: A Labor History*. University of Hawaii Press, Honolulu.
- BURNEY, D. A., H. F. JAMES, L. P. BURNEY, S. L. OLSON, W. KIKUCHI, W. L. WAGNER, M. BURNEY, D. McCLOSKEY, D. KIKUCHI, F. V. GRADY, AND OTHERS. 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs* 71:615–641.
- BURNEY, D. A., AND W. K. P. KIKUCHI. 2006. A millennium of human activity at Makauwahi Cave, Mahaulepu, Kauai. *Human Ecology* 34: in press.

- BURNEY, L. P., AND D. A. BURNEY. 2003. Charcoal stratigraphies for Kaua'i and the timing of human arrival. *Pacific Science* 57:211–226.
- HEARTY, P. J., D. S. KAUFMAN, S. L. OLSON, AND H. F. JAMES. 2000. Stratigraphy and whole-rock amino acid geochronology of key Holocene and last interglacial carbonate deposits in the Hawaiian Islands. *Pacific Science* 54:423–442.
- JAMES, H. F. 2004. The osteology and phylogeny of the Hawaiian finch radiation (Fringillidae: Drepanidini), including extinct taxa. *Zoological Journal of the Linnean Society* 141:207–255.
- JAMES, H. F., AND S. L. OLSON. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands, Part 2: Passeriformes. *Ornithological Monographs*, no. 46.
- JAMES, H. F., AND S. L. OLSON. 2005. The diversity and biogeography of koa-finches (Drepanidini: *Rhodacanthis*), with descriptions of two new species. *Zoological Journal of the Linnean Society* 144:527–541.
- MADDISON, W. P., AND D. R. MADDISON. 1992. *MacClade: Analysis of phylogeny and character evolution*, version 3.0. Sinauer Associates, Sunderland, Massachusetts.
- MEDWAY, D. G. 1981. The contribution of Cook's third voyage to the ornithology of the Hawaiian Islands. *Pacific Science* 35:105–173.
- OLSON, S. L. 1996. The name of the Craveri brothers' murrelet. *Western Birds* 27:167–168.
- OLSON, S. L., AND H. F. JAMES. 1982. *Prodromus* of the fossil avifauna of the Hawaiian islands. *Smithsonian Contributions to Zoology* 365:1–59.
- OLSON, S. L., AND H. F. JAMES. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands, Part 1: Non-Passeriformes. *Ornithological Monographs*, no. 45.
- OLSON, S. L., AND H. F. JAMES. 1994. A chronology of ornithological exploration in the Hawaiian Islands, from Cook to Perkins. Pages 91–102 in *A Century of Avifaunal Change in Western North America* (J. R. Jehl, Jr., and N. K. Johnson, Eds.). *Studies in Avian Biology*, no. 15.
- SALVADORI, T. 1865. Descrizione di altre nuove specie di uccelli esistenti nel museo di Torino nota seconda. *Atti Società Italiana di Scienze Naturali* 8:370–389.
- SIBLEY, C. G., AND B. L. MONROE. 1990. *Distribution and Taxonomy of Birds of the World*. Yale University Press, New Haven, Connecticut.
- STUIVER, M., P. J. REIMER, E. BARD, J. W. BECK, G. S. BURR, K. A. HUGHEN, B. KROMER, G. MCCORMAC, J. VAN DER PLICHT, AND M. SPURK. 1998. INTCAL98 radiocarbon age calibration, 24,000–0 cal BP. *Radiocarbon* 40:1041–1083.
- SWOFFORD, D. L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods)*. Sinauer Associates, Sunderland, Massachusetts.
- TOWNSEND, J. K. 1999. *Narrative of a Journey across the Rocky Mountains, to the Columbia River, and a Visit to the Sandwich Islands, Chili, &c., with a Scientific Appendix*. [Reprinted, with an introduction and annotation by George A. Jobanek.] Oregon State University Press, Corvallis.

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