

# The diversity and biogeography of koa-finches (Drepanidini: *Rhodacanthis*), with descriptions of two new species

HELEN F. JAMES\* and STORRS L. OLSON

Division of Birds, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA

Received May 2004; accepted for publication March 2005

All known populations of koa-finches, genus *Rhodacanthis*, became extinct in the Holocene epoch. Two new species are described here from Quaternary fossil sites in the Hawaiian Islands. One new species, from Kauai and Maui, is roughly the size of the historically known greater koa-finch (*R. palmeri*) but differs in having a more robust skull and in bill morphology. The second new species, from Oahu and Maui, is similar in size to the lesser koa-finch (*R. flaviceps*) but closer to *R. palmeri* in qualitative osteological traits. The two species of koa-finches known historically from the island of Hawaii are distinct in osteology from the fossil koa-finches on the older Hawaiian islands, indicating that at least two of the four known speciation events in the genus took place within approximately the past 500 kyr. However, the similarity of maxillae from Pleistocene and Holocene sites on Oahu suggests that the Oahu population maintained morphological stasis through the climate changes of the late Quaternary. The evidence that speciation occurred on the youngest island in the archipelago suggests that the process of community assembly on newly emergent Hawaiian landscapes was a stimulus to evolutionary diversification in *Rhodacanthis*. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 144, 527–541.

ADDITIONAL KEYWORDS: *Acacia koa* – character displacement – extinction – evolutionary rates – fossils – Hawaiian honeycreepers – Hawaiian Islands – island biogeography – Quaternary – speciation.

## INTRODUCTION

At least 11 species in the adaptive radiation of Hawaiian finches (honeycreepers auct., tribe Drepanidini) have become extinct in historical times. Among them were two species of koa-finches, genus *Rhodacanthis*, that disappeared from the island of Hawaii in the 1890s. Since then, discoveries of fossil koa-finches have extended the range of the genus to Kauai, Oahu and Maui (Olson & James, 1982; James *et al.*, 1987; James, 1987; James & Olson, 1991; Olson, 1999). The fossil record of koa-finches consists of relatively few identified specimens originating in sites that are widely dispersed in space and time, which has made it difficult to work out the systematic relationships among populations. The fossil sample consists of only eight individuals, and to compound the problem, no

skeletal specimens were originally preserved of the two historical species (greater koa-finch, *R. palmeri*; lesser koa-finch, *R. flaviceps*) before they became extinct.

In order to obtain comparative osteological material of rare and extinct species of drepanidines, a cosmetically acceptable method was developed to remove skulls and a few limb bones from specimens of study skins (Olson *et al.*, 1987). A single, partial skeleton was removed from a skin for each of the two historical species, making it possible to attribute certain fossil specimens to *Rhodacanthis*. However, these fossils were not identified to species level (James & Olson, 1991). The osteological sample of *Rhodacanthis* has recently increased by two fossil specimens from the excavations at Maha'ulepu Cave on Kauai (Burney *et al.*, 2001) and an additional skull of *R. palmeri* removed from an unlabelled head of a former study skin. After studying the expanded sample, we conclude that the fossils represent two new species.

\*Corresponding author. E-mail: jamesh@si.edu

## METHODS

The fossil series of *Rhodacanthis* was identified in previous papers (James & Olson, 1991; James, 2004) and consists entirely of cranial material because isolated postcranial bones in fossil sites could not be confidently determined. Species limits within *Rhodacanthis* were assessed based on qualitative osteological comparisons and osteometric data. Qualitative comparisons made use of the characters defined in James (2004), with the addition of more detailed comparisons within *Rhodacanthis*. Our assessment of species limits drew upon existing knowledge about intra- and interspecific morphological variation in the historically known species of *Rhodacanthis* (Olson, 1999), and in other better-sampled fossil and recent species of drepanidines. Bone measurements were taken with digital calipers to the nearest 0.1 mm.

## COMPARATIVE MATERIAL EXAMINED

Bones removed from skins: *Rhodacanthis palmeri*, AMNH 453623 adult male, skull lacking the ventral and anterior walls of the braincase, mandible, both humeri (one damaged), right tibiotarsus lacking proximal end, right tarsometatarsus; UMCZ 27/Dre/5/e/18 adult male (by plumage), skull lacking the posterior and ventral parts. *Rhodacanthis flaviceps*, AMNH 453644 adult female, skull lacking the base of the braincase and part of its anterior wall, both humeri lacking heads, right tibiotarsus and tarsometatarsus. Museum acronyms are identified in the acknowledgements.

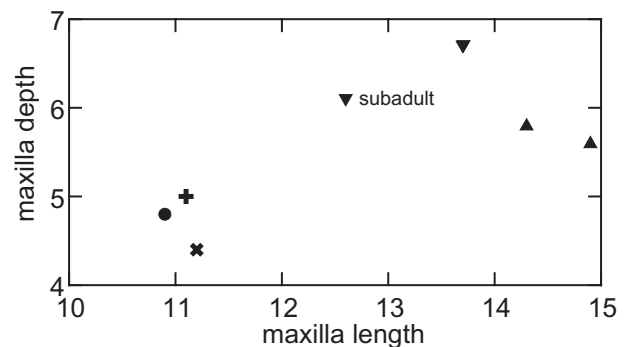
## SYSTEMATICS

We can form some preliminary expectations about the fossil populations by taking the two historical species as 'modern' analogues. For example, the historical species occurred together on the island of Hawaii and were close enough in size that the original collectors and several subsequent authors interpreted the specimens of *R. flaviceps* as small individuals of *R. palmeri* (Munro, 1944; Pratt, 1979). Later, skulls removed from skins helped clarify that *R. flaviceps* is a distinct species which differs in qualitative traits of bill morphology (James & Olson, 1991). In evaluating the fossil sample, we should therefore be alert, on the one hand, to the possibility that more than one species of *Rhodacanthis*, overlapping in size in at least some measurements, may occur on the same island. On the other hand, by analogy with *R. palmeri*, sexual size dimorphism is not likely to be pronounced. Olson (1999) detected little to no dimorphism (less than 1% difference between the averages for males vs. females)

in traditional measurements of museum study skins of that species.

James and Olson (1991) divided the fossil sample available in 1991 into two size classes comparable to the sizes of the two historical species. Cranial measurements of all available osteological specimens of the genus are given in Tables 1 and 2. Four of the fossils are identified as subadults because they exhibit small pores and striations on part of the bone surface, but all four are fully formed and appear to have reached or nearly reached adult size. Although the usefulness of the mensural data is compromised both by missing data and the circumstance that half of the fossils are subadults, the data are at least consistent with the notion of a smaller and a larger size class of koa-finches, as illustrated by a graph of the length vs. depth of the maxilla (Fig. 1).

In the larger size class, the sample encompasses two individuals from Kauai, one from Maui and two skulls removed from museum specimens of *R. palmeri*. All five specimens preserve the maxilla, and three of the specimens preserve the cranium. The fossil maxillae share a distinctive dorsal crest as well as other traits not observed in *R. palmeri* or *R. flaviceps*; hence we ascribe them to a single new species. This leaves us with the smaller fossils to evaluate. We previously commented that those fossils differ from *R. flaviceps* and tend to resemble *R. palmeri* in qualitative traits (James & Olson, 1991). The magnitude of the size difference between the smaller fossils and the osteological specimens of *R. palmeri* is too great to be



*Rhodacanthis* population:  
 ● *R. flaviceps*, Hawaii Island  
 × *R. litotes*, sp. nov., Maui  
 + *R. litotes*, sp. nov., Oahu  
 ▲ *R. palmeri*, Hawaii Island  
 ▼ *R. forfex*, sp. nov., Kauai

**Figure 1.** Graph of the length vs. depth of the maxilla in fossil and historical specimens of *Rhodacanthis*. Length taken along the ventral midline; depth taken at the anterior margin of the nasal cavity. Measurements are in millimetres.

**Table 1.** Cranial measurements (mm) of *Rhodacanthhis* (hol., holotype; par., paratype). Some of these data were taken from James & Olson (1991: table 7)

	<i>R. palmeri</i> AMNH 453623 Hawaii	<i>R. palmeri</i> UMZC 27/Dre/5/e/18 Hawaii	<b>R. forfex</b> <b>sp. nov.</b> hol., USNM 524870 Kauai	<b>R. forfex</b> <b>sp. nov.</b> par., USNM 524871 Kauai	<b>R. forfex</b> <b>sp. nov.</b> par., USNM 445792 Maui	<i>R. flaviceps</i> AMNH 453644 Hawaii	<i>R. aff. flaviceps</i> USNM 445795 Oahu: Ulupau Head	<i>R. aff. flaviceps</i> BPBM 158861 Oahu: Barber's Point	<i>R. aff. flaviceps</i> USNM 445794 Maui
<i>Skull:</i>									
1. Maximum width across zygomatic processes (dorsal edge)	18.1*	-	19.6	-	-	17.3	-	-	-
2. Minimum width caudal of the postorbital processes	16.7*	-	16.4	-	-	15.5	-	-	-
3. Minimum supraorbital width (across frontal)	8.7	8.1	9.6	-	-	7.8	-	-	-
4. Width across nasofrontal hinge	12.2	12.5	13.4	-	-	11.0	-	-	-
5. Depth, from caudal end of basiphenaoid rostrum to roof of braincase	-	-	15.4	-	-	-	-	-	-
<i>Maxilla:</i>									
6. Dorsal length along midline	20.4	21.3	22.5†	-	-	17.7	-	17.3	-
7. Ventral length along midline	14.3	14.9	13.7‡	12.6	-	10.9	-	11.1	11.2 <sup>d</sup>
8. Length from lateral corner of nasofrontal hinge	20.4	21.5	21.3	-	-	17.7	-	17.8	-
9. Length from jugal articulation	15.5	17.0	16.1	14.2	15.7	13.4	-	13.1	13.5§

Table 1. Continued

	<i>R. palmeri</i> AMNH 453623 Hawaii	<i>R. palmeri</i> UMZC 27/Dre/5/e/18 Hawaii	<i>R. forfex</i> sp. nov. hol., USNM 524870 Kauai	<i>R. forfex</i> sp. nov. par., USNM 524871 Kauai	<i>R. forfex</i> sp. nov. par., USNM 445792 Maui	<i>R. flaviceps</i> AMNH 453644 Hawaii	<i>R. aff. flaviceps</i> USNM 445795 Oahu: Ulupau Head	<i>R. aff. flaviceps</i> BPBM 158861 Oahu: Barber's Point	<i>R. aff. flaviceps</i> USNM 445794 Maui
10. Length from anterior rim of nasal cavity	12.3	13.0	13.2	11.5	-	9.8	-	9.7	9.6§
11. Width across jugal articulations	12.1	12.0	12.9	11.4	-	10.2	10.6	10.7	11.3
12. Width of nasofrontal hinge	11.7	11.9	12.8	-	-	10.6	-	11.5	-
13. Depth through lateral nasal bar	8.6	9.0	9.8	-	-	8.3	-	8.0	-
14. Depth at anterior rim of nasal cavity	5.8	5.6	6.7	6.1	-	4.8	4.4	5.0	4.4
15. Length of nasal cavity opening	4.5	5.1	4.4	-	-	4.5	4.4	4.5	5.1
16. Depth of nasal cavity opening	4.6	4.4	4.7	-	-	3.5	3.8	4.0	4.1
17. Minimum width of dorsal nasal bar	2.0	1.9	2.5	1.5	-	1.7	1.7	1.9	1.6

\*Damage to the braincase may have caused this skull to contract somewhat in these dimensions. †Measured while holding the maxilla and skull in articulation.

‡Measurement does not include the broken maxillary processes of the palatines. §Approximately 1.2 mm should be added to these measurements to compensate for the broken tip of the maxilla. USNM 524871 and 445794 are subadult.

**Table 2.** Measurements (mm) of the mandible of *Rhodacanthis* (par., paratype). Most of these data are repeated from James & Olson (1991: table 8). USNM 445793 and 445796 are subadult

	<i>R. palmeri</i> AMNH 453623 Hawaii	<i>R. palmeri</i> UMZC 27/Dre/5/e/18 Hawaii	<i>R. flaviceps</i> AMNH 453644 Hawaii	<i>R. litotes</i> <b>sp. nov.</b> par. USNM 445793	<i>R. litotes</i> <b>sp. nov.</b> par. USNM 445796
1. Total length	30.0	29.4	26.1	26.3	–
2. Length of tomial crest	16.5	15.6	12.9	13.7	13.0
3. Symphysis length	10.3	9.9	8.7	7.9	7.4
4. Greatest width of symphyseal part	12.4	11.9	11.4	11.6	11.4
5. Greatest width of mandible	20.1	19.6	18.8	–	–
6. Depth of symphyseal part	6.0	5.3	5.7	4.6	4.8
7. Width of articular end with medial process	6.0	–	–	5.4	–
8. Depth at lateral cotyla	2.8	3.0	3.1	2.8	–
9. Depth at angle of mandible	6.2	6.6	6.2	5.8	–
10. Ramus length (intermediate part)	12.5	11.8	11.0	11.1	–

attributed to intraspecific variation, considering the negligible sexual size dimorphism observed in the latter species. We conclude that the smaller fossils cannot be ascribed to *R. palmeri* and assign them instead to a second new species.

SUBFAMILY CARDUELINAE  
TRIBE DREPANIDINI

A cladistic analysis of osteological characters placed the historical and fossil taxa of *Rhodacanthis* in the tribe Drepanidini (James, 2004). The fossil cranium of the larger new species may also be assigned to the Drepanidini by the following combination of characters:

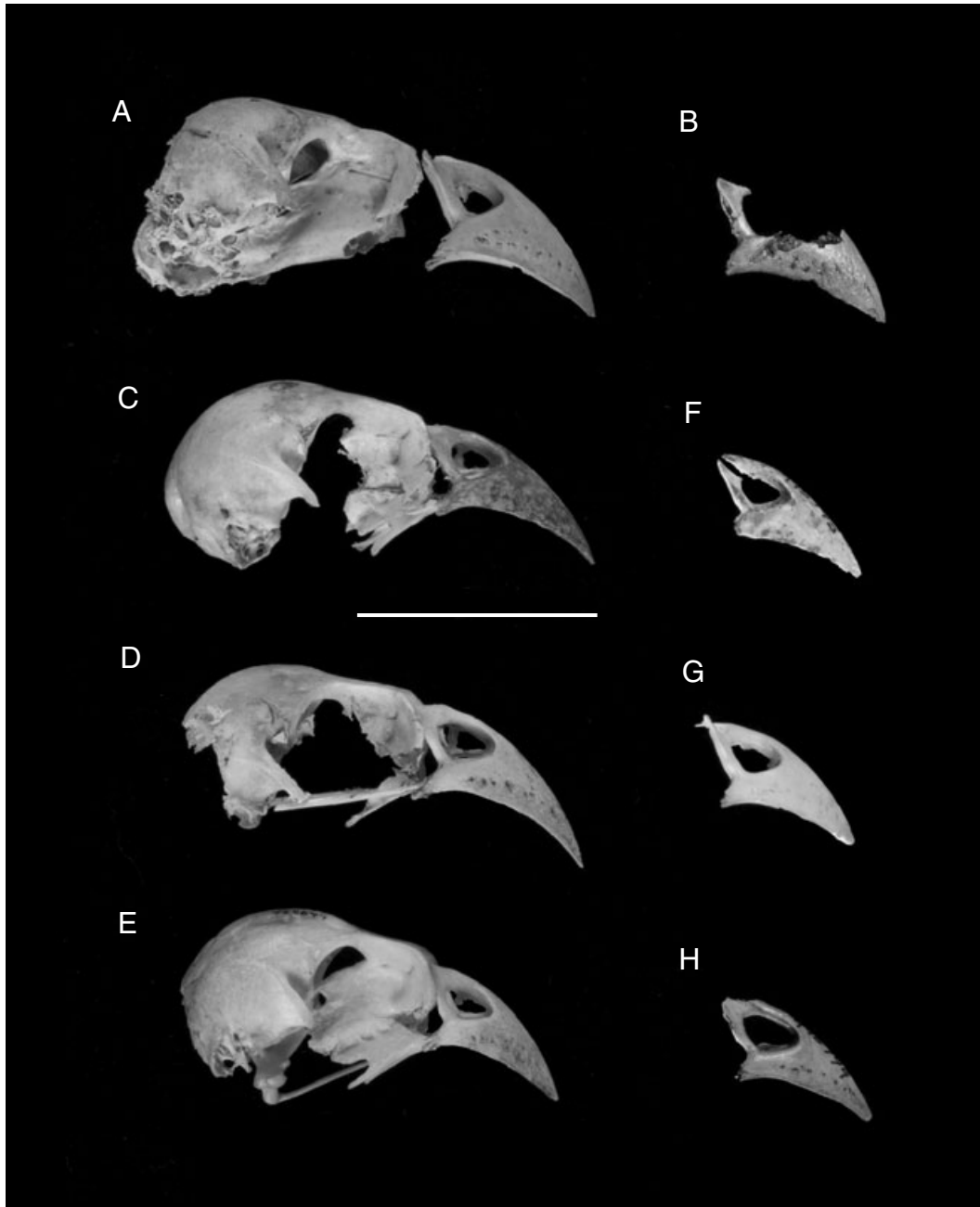
1. The olfactory nerve travels through the interorbital septum, a trait that is universally present in the Drepanidini and in a few species of Carduelini but not known to occur in any other Passeriformes (James, 2004: character 63).
2. The interorbital septum is fully ossified, thick and entirely double-walled, as expected for a cardueline or drepanidine finch with a deep, finch-like bill (Fig. 2; Zusi, 1978; James, 2004: character 52).
3. In agreement with most species of the Drepanidini but different from other nine-primaried oscines, it has a very distinct scar for the attachment of musculus (M) protractor pterygoidei *sensu stricto* on the

interorbital septum, with a raised border anteriorly and dorsally (James, 2004: character 50).

GENUS *RHODACANTHIS* ROTHSCHILD, 1892

*Included species:* *R. palmeri* Rothschild, 1892; *R. flaviceps* Rothschild, 1892; *R. forfex* **sp. nov.**; *R. litotes* **sp. nov.**

Within the Drepanidini, both new species were placed by cladistic analysis in a clade composed of the genera *Rhodacanthis* and *Chloridops* and the species *Xestospiza conica* (James, 2004: fig. 17). In common with other members of that clade, the new species have sturdy, finch-like bills with pronounced ventral crests of the maxilla that extend about 2/3 of the way to the bill tip (James, 2004: character 20). The new species resemble *Rhodacanthis* and *Chloridops* rather than *Xestospiza* in having a strongly arched rather than an almost straight dorsal profile of the maxilla, and in lacking a planar dorsal surface of the maxilla (James, 2004: character 6). They are referable to *Rhodacanthis* as opposed to *Chloridops* in having the ventral crests of the maxilla sharp rather than blunt (James, 2004: character 18), the median fossa of the ventral maxilla relatively wide (James, 2004: character 17), and in lacking a ventral bulge on the tomial crest of the maxilla (lateral view; James, 2004: char-



**Figure 2.** Crania and maxillae of *Rhodacanthis* in lateral view. A, *R. forfex* sp. nov., USNM 524870 holotype. B, *R. forfex* sp. nov., USNM 445792 paratype. C, *R. palmeri*, AMNH 453623. D, *R. palmeri*, UMZC 27/Dre/5/e/18. E, *R. flaviceps*, AMNH 453644. F, *R. litotes* sp. nov., USNM 445795 paratype. G, *R. litotes* sp. nov., BPBM 158861 holotype. H, *R. litotes* sp. nov., USNM 445794 paratype. Scale bar = 2 cm.

acter 14). They differ further from *Chloridops kona* or *C. wahi* in having the median fossa of the maxilla deeply excavated (James, 2004; character 16). The mandible of *R. litotes* (unknown for *R. forfex*) differs from that of *C. kona* or *C. wahi* by the absence of a median fossa along the dorsal symphysis.

The sharp median crest of the posterior portion of the parasphenoidal rostrum in *R. forfex* (discussed below) is assumed to be characteristic of *Rhodacanthis* as a whole, although this skull region is not preserved in any other available specimen of the genus.



**RHODACANTHIS FORFEX SP. NOV.**

(FIGS 2A–B, 3A–B, 4A–B)

*P[sittirostra]* (*Rhodacanthis*) aff. *palmeri* James *et al.*, 1987: 2353.*Rhodacanthis* aff. *palmeri* James & Olson, 1991: 44. James, 2004: 249, fig. 17.*Rhodacanthis*, undescribed species Olson, 1999: 6.*Rhodacanthis* sp. Burney *et al.*, 2001: table 2.

**Holotype:** Nearly complete cranium with disarticulated maxilla, USNM 524870 (Figs 2A, 3A, 4A), collected 07.i.1998 by David Burney and other members of the Kauai Palaeoecology Expedition (Burney *et al.*, 2001). The maxilla lacks a small piece of the nasals adjacent to the nasofrontal hinge, and the basicranium is badly abraded. The specimen includes a detached piece of the occipital region of the skull about 13 mm in diameter.

**Type locality:** Island of Kauai: Koloa Quadrangle: Makauwahi Cave (21°53'30"N, 159°25'17"W, near sea level). State Archaeological Site #50-30-10-3097; alternately known as the Mahaulepu cave and sinkhole complex. In the excavation described by Burney *et al.* (2001), the holotype was collected from Unit IV of the east pit.

**Distribution:** Kauai: Makauwahi Cave. Maui: Makena Quadrangle: Puu Naio Cave (20°37'N, 156°24'E, 393 m a.s.l.).

**Etymology:** from Latin, *forfex*, a scissors, in reference to the specialized feeding behaviour of members of the genus. Adults of the two species of *Rhodacanthis* that were observed in life by ornithologists used their sharp maxillary and mandibular tomia (and presumably the crests on the lingual surface of the maxilla) to cut up the green pods of the koa tree (*Acacia koa*), a native legume, in order to consume the pods and seeds (Perkins, 1893; Munro, 1944).

**Measurements of holotype:** See Table 1.

**Paratypes:** Kauai, Makauwahi Cave: Maxilla lacking the fused nasals near the nasofrontal hinge and the left lateral nasal bar, USNM 524871. Collected from Unit V of the east pit, 04.ii.1998, by David Burney and other members of the Kauai Palaeoecology Expedition. Maui, Puu Naio Cave: Maxilla lacking the dorsal surface except near the bill tip, and also missing the posterior half of the bone from the right side only, USNM 445792, collected 13.ii.1984 by S. L. Olson, H. F. James, D. W. Steadman and C. Walseth (Figs 2B, 3B, 4B). The excavation at Puu Naio Cave in 1984 is described by James *et al.* (1987).

**Measurements of paratypes:** See Table 1.

**Age of referred specimens:** Holocene, based on a series of radiocarbon dates on bone collagen, plant material

and coprolites recovered from the cave excavations that produced fossils of the species (James *et al.*, 1987; James & Burney, 1997; Burney *et al.*, 2001).

**Description:** The maxilla differs from that of all other species of *Rhodacanthis* in having a distinct median crest on the dorsal surface (Fig. 3), and a slightly concave rather than convex profile of the tomial crest (ventral view). The cranium is more robust than other available crania of the genus, with larger zygomatic and postorbital processes, and the scars for attachment of the temporal musculature more sharply delineated and more extensive, rising further onto the dorsal surface of the skull (Fig. 3). Differs further from *R. flaviceps* in having a larger skull and maxilla, a deeper median fossa on the ventral surface of the maxilla, and virtually parallel rather than slightly divergent lateral crests of the maxilla. Differs further from *R. palmeri* in having the maxilla anterior of the nasal cavities deeper (Figs 1, 2). The maxilla of *R. forfex* differs from that of *R. litotes*, the other new species, in the ways mentioned for *R. palmeri*, and also in being distinctly larger.

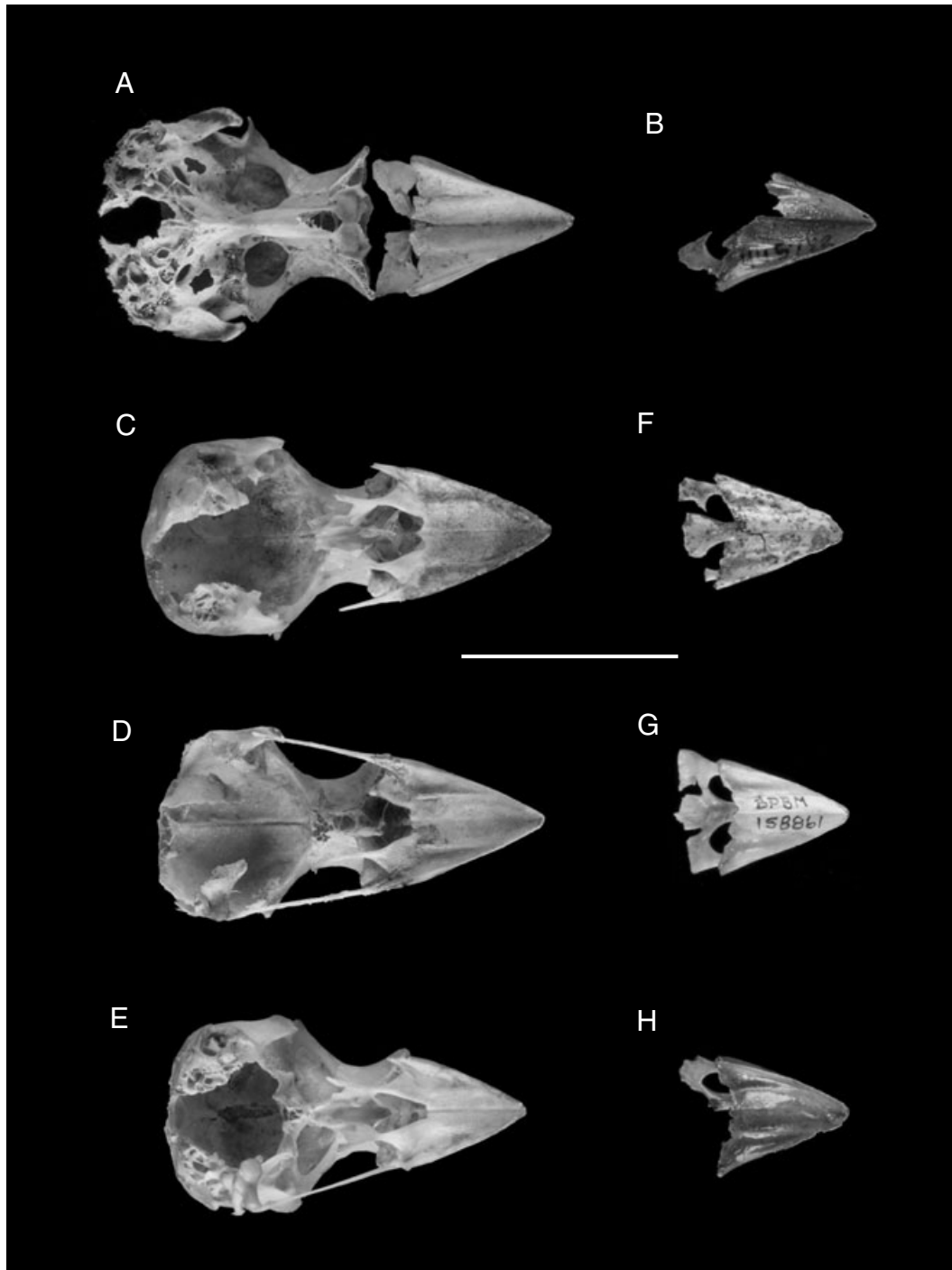
**Remarks:** Because of damage to the modern specimens caused during the skinning process, the holotype of *R. forfex* is the only osteological specimen of *Rhodacanthis* in which the posterior portion of the parasphenoidal rostrum is preserved (Fig. 4), revealing its distinctive sharp-edged median crest. Such a crest does not occur in related drepanidine genera with finch-like bills (*Telespiza*, *Loxioides*, *Chloridops* and *Xestospiza*; see James, 2004), but is found in the cardueline genus *Coccothraustes* (hawfinches and relatives *sensu* Howell *et al.*, 1968; James, 2004: character 57, fig. 4) and in an even more extreme state of development in the Maui Parrotbill (*Pseudonestor xanthophrys*) (Zusi, 1989), a drepanidine with a parrot-like bill and jaw mechanism. In *Pseudonestor* and *Coccothraustes*, the crest is correlated functionally with an expanded origin of M. pterygoideus retractor along the parasphenoidal rostrum and onto the interorbital septum (Zusi, 1989). The parasphenoidal crest also occurs in parrots, which have a specialized jaw musculature with extensive origin of the pterygoideus muscle on the interorbital septum (Burton, 1974).

Assuming that the parasphenoidal crest observed in *R. forfex* also indicates a strengthened and expanded M. pterygoideus retractor, we can speculate that it developed as part of an adaptive complex in the skeletonomuscular system of the entire genus *Rhodacanthis* for feeding on leguminous pods. M. pterygoideus retractor is the only muscle that can depress the maxilla without exerting simultaneous pressure to raise the mandible (Zusi, 1989). Its expansion in *Rhodacanthis* might have allowed greater biting force by the maxillary rostrum and greater independence of action



**Figure 3.** Crania and maxillae of *Rhodacanthis* in dorsal view. A, *R. forfex* sp. nov., USNM 524870 holotype. B, *R. forfex* sp. nov., USNM 445792 paratype. C, *R. palmeri*, AMNH 453623. D, *R. palmeri*, UMZC 27/Dre/5/e/18. E, *R. flaviceps*, AMNH 453644. F, *R. litotes* sp. nov., USNM 445795 paratype. G, *R. litotes* sp. nov., BPBM 158861 holotype. H, *R. litotes* sp. nov., USNM 445794 paratype. Scale bar = 2 cm.





**Figure 4.** Crania and maxillae of *Rhodacanthis* in ventral view. A, *R. forfex* sp. nov., USNM 524870 holotype. B, *R. forfex* sp. nov., USNM 445792 paratype. C, *R. palmeri*, AMNH 453623. D, *R. palmeri*, UMZC 27/Dre/5/e/18. E, *R. flaviceps*, AMNH 453644. F, *R. litotes* sp. nov., USNM 445795 paratype. G, *R. litotes* sp. nov., BPBM 158861 holotype. H, *R. litotes* sp. nov., USNM 445794 paratype. Scale bar = 2 cm.

by the maxillary vs. mandibular rostra, helping the birds to slice up fibrous pods.

The fossil of an 'additional Kauai finch' mentioned by Olson & James (1982: 40), from the Makawehi

Dunes of southern Kauai, cannot be referred to *R. forfex*. That fossil consists only of the caudal part of a mandibular ramus, and its lateral cotyla differs in shape from the distinctive cotyla of *Rhodacanthis*.

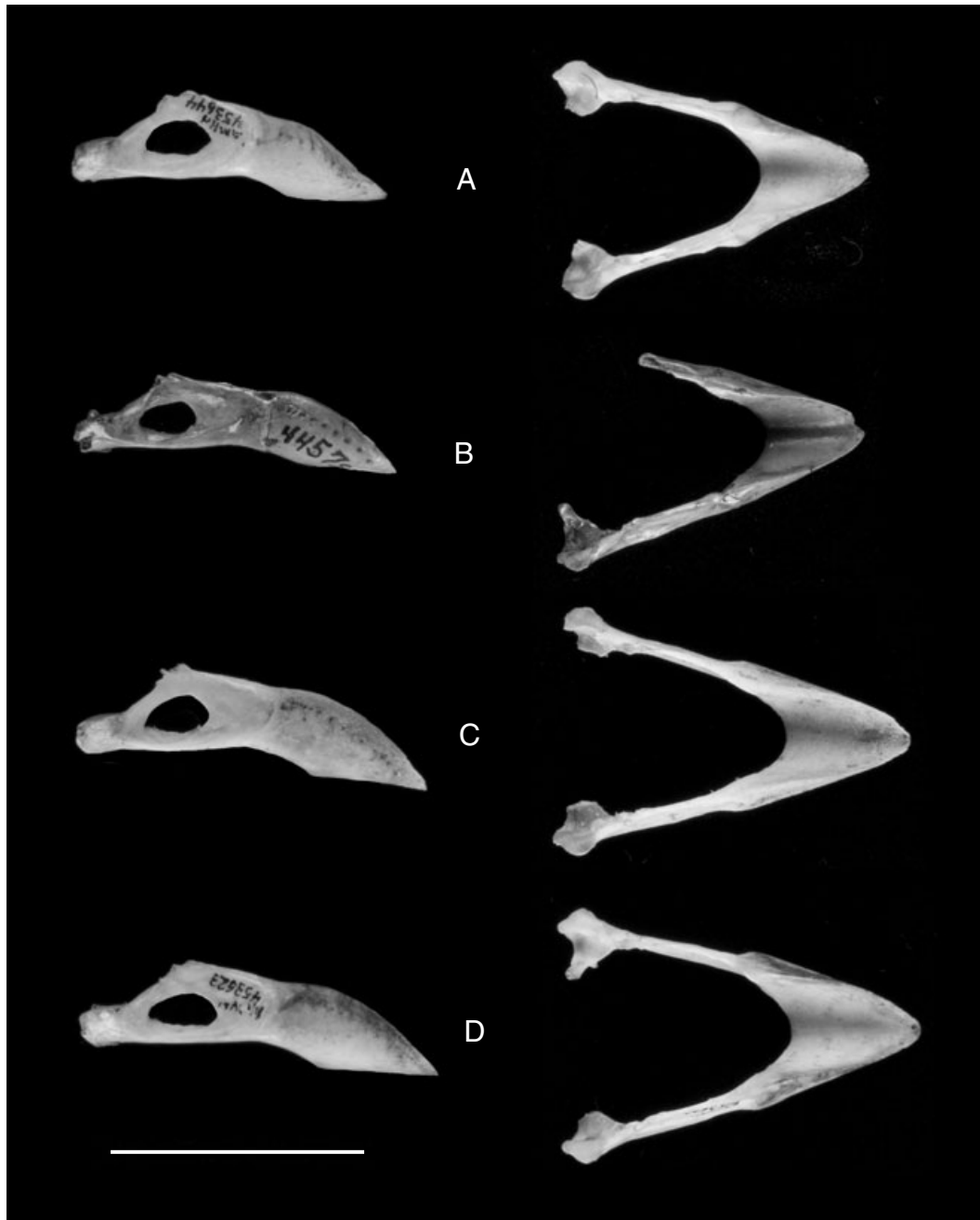
**RHODACANTHIS LITOTES SP. NOV.**

(FIGS 2F–H, 3F–H, 4F–H, 5B)

*Psittirostra* (*Rhodacanthis*) *flaviceps* Olson & James, 1982: 39, 45.*Psittirostra* (*Rhodacanthis*) sp. James, 1987: 225, 228.*P[sittirostra]* (*Rhodacanthis*) aff. *flaviceps* James *et al.*, 1987: 2353.*Rhodacanthis* aff. *flaviceps* James, 2004: 249, fig. 17.**Holotype:** Complete maxilla, BPBM 158861, collected 23.vii.1981 by Aki Sinoto, Patrick C. McCoy *et al.* (Figs 2G, 3G 4G).**Type locality:** Island of Oahu, Ewa Quadrangle: large sinkhole c. 3.6 km N of Barber's Point (21°18'N, 158°6'E, c. 15 m a.s.l.); Bishop Museum archaeological site 50-Oa-B6-22 (Olson & James, 1982: 27).**Distribution:** Oahu: Ulupau Head and Ewa Plain. Maui: all specimens were collected at Puu Naio Cave (James *et al.*, 1987).**Etymology:** From Greek, *litotes*, a figure of speech in which an idea is affirmed by denying the contrary, an understatement. Once referred to *R. flaviceps*, the fossils are now recognized as a distinct species because they lack several characters that make *R. flaviceps* appear to be the more specialized and distinctive of the two.**Measurements of holotype:** See Table 1.**Paratypes:** Oahu: Maxilla lacking the major parts of the left lateral nasal bar and the fused nasals anterior to the nasofrontal hinge, USNM 445795, collected at Ulupau Head, Oahu (James, 1987), 26.iii.1986, by S. Olson and H. James (Figs 2F, 3F, 4F). Maui: Maxilla lacking the left lateral nasal bar and part of the cofused nasals anterior of the nasofrontal hinge, USNM 445794, collected ii.1984 by S. L. Olson, H. F. James *et al.* (Figs 2H, 3H, 4H). Mandible lacking the posterior part of the left ramus, USNM 445793, collected 11.ii.1984 by S. L. Olson, H. F. James *et al.* (Fig. 5B). The symphyseal part of a mandible with portions of the intermediate parts of the ramus attached, USNM 445796, collected 28.iii.1988 by H. F. James.**Measurements of paratypes:** See Tables 1 and 2.**Age of referred specimens:** Quaternary. The paratype from wetland sediments at Ulupau Head is > 300–400 kyr old (James, 1987; Hearty *et al.*, 2005). All other specimens are Holocene in age, based on radiocarbon dates on purified collagen from the bones of extinct birds excavated from the same sedimentary deposits as the *Rhodacanthis* bones (James *et al.*, 1987; James & Burney, 1997), and from other similar sedimentary deposits on the same local landscape (Athens *et al.*, 2002).**Description:** A species of finch, known from fossils of the maxilla and mandible and similar in most respects to *R. palmeri*. Smaller than *R. palmeri* or *R. forfex* but similar in size to *R. flaviceps* (Fig. 1). The maxilla differs from that of *R. flaviceps* but resembles *R. palmeri* and *R. forfex* in having the lateral crests nearly parallel rather than slightly divergent and the median fossa deeper (Fig. 4). The mandible differs from *R. flaviceps* but resembles *R. palmeri* and *R. forfex* in the slightly recurved rather than nearly straight ventral profile of the mandibular symphysis (lateral view), and in the lateral profile of the tomial crest, which describes a smooth rather than a broken curve (Fig. 5). In addition to its smaller size, *R. litotes* differs from *R. forfex* in the absence of a dorsal median crest on the maxilla and the nearly straight to convex rather than slightly concave lateral profile of the tomial crest of the maxilla (ventral view).**Remarks:** As further evidence that the fossil sample from Maui contains two species, the paratypical mandibles occlude very smoothly with the holotypical maxilla of *R. litotes*, whereas they do not conform at all to the shape of the larger maxilla from Maui referred to *R. forfex*.Even though the two fossil maxillae from Oahu are very different in age, they resemble each other closely in morphology and differ from the maxilla of *R. litotes* from Maui in having a noticeably smaller aperture of the nasal cavity (Fig. 2F–H).

## DISCUSSION

There is a recent trend in alpha systematics of Hawaiian birds towards recognizing island populations as distinct species rather than subspecies (Pratt & Pratt, 2001). In most cases the change has been supported by data showing the genetic separation of populations that are only slightly differentiated in morphology (e.g. Tarr & Fleischer, 1993; Browne *et al.*, 1997; Rhymer, 2001). Our finding of unrecognized species among the island populations of *Rhodacanthis* is consistent with the trend. The four named species of *Rhodacanthis* are more differentiated in osteology than are some of the extant island populations of drepanidines that are now recognized as distinct species, such as the Oahu vs. Maui populations of creepers, *Paroreomyza maculata* and *P. montana*, or the Oahu vs. Molokai through Hawaii populations of amakihis, *Hemignathus* [*Loxops* auct.] *flavus* and *Hemignathus* [*Loxops* auct.] *virans* (Table 3; American Ornithologists' Union, 1998). Viewed from this perspective, the fossil record of *Rhodacanthis* may contain at least one additional cryptic species. The difference in aperture of the nasal cavity in the Oahu vs. Maui fossils of *R. litotes* suggests that those two



**Figure 5.** Mandibles of *Rhodacanthis* in lateral and dorsal views. A, *R. flaviceps*, AMNH 453644. B, *R. litotes* sp. nov., USNM 445793 paratype. C, *R. palmeri*, UMZC 27/Dre/5/e/18. D, *R. palmeri*, AMNH 453623. Scale bar = 2 cm.

populations might be recognized as distinct species if more fossils or genetic data were available for them.

*Rhodacanthis* was able to disperse to both ends of the main chain of Hawaiian islands and to colonize at least two of the islands twice (Fig. 6). Considering the small number of fossils collected, there is every reason to suspect that additional island populations remain to be discovered. In particular, the disjunct distribu-

tions of both new species suggest that *R. forfex* was once distributed on each of the main islands except Hawaii, and that *R. litotes* was formerly present on each of the islands except Hawaii and perhaps Kauai.

*Rhodacanthis litotes* was present on Oahu in the Pleistocene, in a deposit that is constrained to be 300–400 kyr old. The fossil maxillae from the Pleistocene and Holocene of Oahu are remarkably alike in mor-

**Table 3.** Summary of osteological character differences among koa-finches, *Rhodacanthis*

	<i>R. litotes</i> sp. nov.	<i>R. flaviceps</i>	<i>R. palmeri</i>	<i>R. forfex</i> sp. nov.
1. Size class: small (0), large (1)	0	0	1	1
2. Cranium; temporal musculature: less extensive (0), more extensive (1)	?	0	0	1
3. Cranium: less robust (0), more robust (1)	?	0	0	1
4. Maxilla, dorsal crest: slight or absent (0), pronounced (1)	0	0	0	1
5. Maxilla anterior of nasal opening: shallower (0), intermediate (1), deeper (2)	1	1	0	2
6. Maxilla, median fossa: deep (0), shallower (1)	0	1	0	0
7. Maxilla, nasal cavity aperture: smaller (0), larger (1)*	0/1	0	0	0
8. Maxilla, ventral crests: parallel (0), slightly divergent (1)	0	1	0	0
9. Mandible, tomial crest: describes a smooth (0) vs. broken curve (1)	0	1	0	?
10. Mandible, ventral symphysis: nearly straight (0), curved dorsad (1)	0	1	0	?

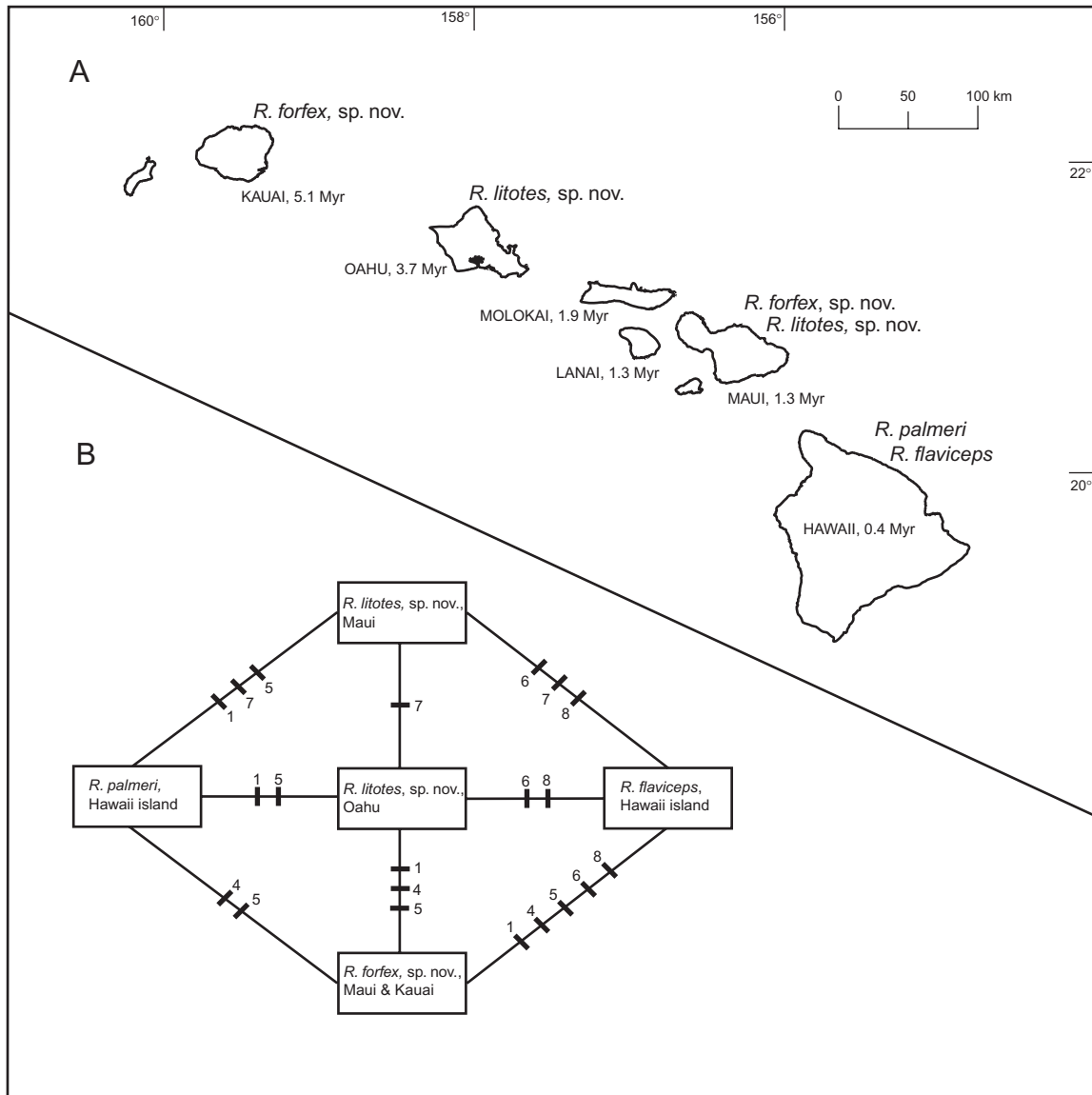
\*The nasal cavity aperture is larger in the maxilla of *R. litotes* from Maui only.

phology, yet they differ from those found on other islands. This suggests that the Oahu population was isolated and maintained morphological stasis in bill morphology through at least two cycles of global glaciation and deglaciation. Global climate changes of the Quaternary are known to have altered the distribution of dry and wet vegetation communities in the islands. Sedimentary pollen cores taken at middle to high elevations on the islands of Oahu and Maui indicate cooler drier conditions from the last glacial maximum to the early Holocene, wetter conditions in the mid-Holocene, and a climatically variable late Holocene (Burney *et al.*, 1995; Hotchkiss & Juvik, 1999). Apparently, shifts of this nature did not produce any permanent change in the bill morphology of *R. litotes* on Oahu.

The evidence of stasis on the older island of Oahu contrasts with evidence of morphological change and speciation on Hawaii, the youngest island in the chain. The two historical species of koa-finches from that island differ in morphology from those on neighbouring Maui and the older islands to the north-west. The most common dispersal pattern that has been recognized among endemic lineages of Hawaiian plants and animals is for colonization to take place from older to younger islands down the chain (Funk & Wagner, 1995). If we assume that koa-finches dispersed from older Maui to younger Hawaii, then they have made at least two successful colonizations of the new land-

scape since the island emerged about 500 kya. In both cases the colonizing population apparently underwent morphological change and speciation. It is also possible that, rather than dispersing to Hawaii, the genus evolved on Hawaii and dispersed to the older islands, with one back-colonization of Hawaii. The latter scenario would compress the history of the genus into roughly half a million years and require even more rapid dispersal, morphological evolution and speciation, again with two speciation events on the island of Hawaii.

The classic model to explain speciation and diversification in the Drepanidini invokes an allopatric phase when two populations of a species diverge genetically on separate islands, followed by a sympatric phase when ecological competition between the two populations causes character displacement and the reinforcement of reproductive isolating mechanisms (Bock, 1970). The distribution of *Rhodacanthis* is consistent with the character displacement model, in the sense that at least two islands hosted two species of the genus that were differentiated from each other in size and finer points of bill morphology. However, we should also consider the evidence of recent speciation on a youthful island, vs. morphological stasis in a population on an older island. This suggests that speciation and morphological change occurred during the early stages of community assembly on new landscapes. In such immature communities, other forces



**Figure 6.** A, distribution of species of *Rhodacanthis*. Potassium-argon dates (from Clague, 1996) show the progression of older to younger islands towards the south-east. B, diagram of osteological character differences among island populations of koa-finches. The characters are identified by number in Table 3. Characters with missing data were omitted from the diagram.

besides character displacement might underlie morphological changes. For example, early colonists may have encountered ecological release rather than intensified competitive interactions, if their competitors had not yet colonized from the older islands. Also, an avian population that became established before one or more of its food resource species had dispersed from older landscapes could have been forced to adapt to alternative foods. The temporal perspective from fossils and geological history thus suggests alternatives to the character displacement model for koa-finch diversification, but does not enable us to choose among explanations.

At least six island populations comprising four species of koa-finches have become extinct during the Holocene Epoch. The precise causes of extinction of koa-finches are unknown, but in general, Holocene extinctions of Hawaiian forest birds are associated with human settlement of the archipelago (e.g. Olson & James, 1984; James *et al.*, 1987; James, 1995; Burney *et al.*, 2001).

ACKNOWLEDGEMENTS

We are grateful to M. de L. Brooke and R. J. Symonds of the University Museum of Zoology, Cambridge



(UMZC) for permission to study the skull from a head of *Rhodacanthis palmeri*, and to F. V. Grady, J. P. Angle and R. L. Zusi of the National Museum of Natural History (USNM) for helping to prepare the specimen. For lending specimens in their care, we thank C. H. Kishinami and the late A. C. Ziegler of the Bishop Museum (BPBM) in Honolulu, and G. Barrowclough of the American Museum of Natural History in New York (AMNH). Thanks also to those who collected fossils with us, most recently at Makauwahi Cave on Kauai (see Burney *et al.*, 2001). David Burney provided comments on a draft of the manuscript. Research support was provided by Scholarly Studies, Radiocarbon, and Wetmore funds of the Smithsonian Institution, Department of Defense Legacy grant, and NSF grant DEB 9707260 to D. A. Burney. We dedicate this paper to the memory of our late colleagues and close friends William Kikuchi and Alan Ziegler.

## REFERENCES

- American Ornithologists' Union.** 1998. *Check-list of North American birds*, 7th edn. Lawrence, KS: Allen Press/ American Ornithologists' Union.
- Athens JS, Tuggle HD, Ward JV, Welch DJ.** 2002. Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i. *Archaeology in Oceania* **37**: 57–78.
- Bock WJ.** 1970. Microevolutionary sequences as a fundamental concept in macroevolutionary processes. *Evolution* **24**: 704–722.
- Browne RA, Anderson DJ, Houser JN, Cruz F, Galsgow KJ, Hodges CN, Massey G.** 1997. Genetic diversity and divergence of endangered Galápagos and Hawaiian petrel populations. *Condor* **99**: 812–815.
- Burney DA, DeCandido RV, Burney LP, Kostel-Hughes FN, Stafford TW Jr, James HF.** 1995. A Holocene record of climate change, fire ecology and human activity from montane Flat Top Bog, Maui. *Journal of Paleolimnology* **13**: 209–217.
- Burney DA, James HF, Burney LP, Olson SL, Kikuchi W, Wagner W, Burney M, McCloskey D, Kikuchi D, Grady FV, Gage R, Nishek R.** 2001. Fossil evidence for a diverse biota from Kauai and its transformation since human arrival. *Ecological Monographs* **71**(4): 615–641.
- Burton PJK.** 1974. Jaw and tongue features of the Psittaciformes and other orders with special reference to the anatomy of the tooth-billed pigeon (*Didunculus strigirostris*). *Journal of Zoology* **174**: 255–276.
- Clague DA.** 1996. The growth and subsidence of the Hawaiian-Emperor volcanic chain. In: Keast A, Miller SE, eds. *The origin and evolution of Pacific Island biotas, New Guinea to Eastern Polynesia: patterns and processes*. Amsterdam: SPB Publishing, 35–50.
- Funk VA, Wagner WL.** 1995. Biogeographic patterns in the Hawaiian Islands. In: Wagner W L, Funk V A, eds. *Hawaiian biogeography: evolution on a hotspot archipelago*. Washington, DC: Smithsonian Institution Press, 379–419.
- Hearty PJ, James HF, Olson SL.** 2005. The geological context of middle Pleistocene crater lake deposits and fossil birds at Ulupau Head, Oahu, Hawaiian Islands. In: Alcove JA, Bover P, eds. *Proceedings of the International Symposium 'Insular Vertebrate Evolution: the Palaeontological Approach.'* *Monografies de la Societat d'Història Natural de les Balears* **12**: 113–128.
- Hotchkiss S, Juvik JO.** 1999. A late-Quaternary pollen record from Ka'au Crater, O'ahu, Hawai'i. *Quaternary Research* **52**: 115–128.
- Howell TR, Paynter RA, Rand AL Jr.** 1968. Subfamily Carduelinae, serins, goldfinches, linnets, rose finches, grosbeaks, and allies. In: Paynter RA, ed. *Check-list of birds of the world*, vol. XIV. Worcester, MA: The Hefferman Press Inc./ Museum of Comparative Zoology, 207–305.
- James HF.** 1987. A late Pleistocene avifauna from the island of Oahu, Hawaiian Islands. *Documents de la Laboratoire de Géologie de Lyon* **99**: 221–230.
- James HF.** 1995. Prehistoric extinctions and ecological changes on oceanic islands. *Ecological Studies* **115**: 88–102.
- James HF.** 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 HF, Burney DA.** 1997. The diet and ecology of Hawaii's extinct flightless waterfowl: evidence from coprolites. *Biological Journal of the Linnean Society* **62**: 279–297.
- James HF, Olson SL.** 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. Part II. Passeriformes. *Ornithological Monographs* **46**: 1–88.
- James HF, Stafford TW Jr, Olson SL, Steadman DW, Martin PS, McCoy P.** 1987. Radiocarbon dates on bones of extinct birds from Hawaii. *Proceedings of the National Academy of Sciences, USA* **84**: 2350–2354.
- Munro GC.** 1944. *Birds of Hawaii*. Honolulu: Tongg.
- Olson SL.** 1999. Kona Grosbeak (*Chloridops kona*), Greater Koa-finch (*Rhodacanthis palmeri*), and Lesser Koa-finch (*Rhodacanthis flaviceps*). In: Poole A, Gill F, eds. *The birds of North America* 424. Philadelphia, PA: The Birds of North America, Inc, 1–20.
- Olson SL, James HF.** 1982. *Prodromus of the fossil avifauna of the Hawaiian Islands*. Smithsonian Contributions to Zoology 365. Washington, DC: Smithsonian Institution, vi + 59pp.
- Olson SL, James HF.** 1984. The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. In: Martin PS, Klein RG, eds. *Quaternary extinctions: a Prehistoric revolution*. Tucson, AZ: University of Arizona Press, 768–780.
- Olson SL, Angle JP, Grady FV, James HF.** 1987. A technique for salvaging anatomical material from study skins of rare or extinct birds. *Auk* **104**(3): 510–512.
- Perkins RCL.** 1893. Notes on collecting in Kona, Hawaii. *Ibis (Series 6)* **5**(1): 101–112.
- Pratt HD.** 1979. A systematic analysis of the endemic avifauna of the Hawaiian Islands. PhD dissertation, Louisiana State University, Baton Rouge, LA. UMI Microfilms 79–28440.

- Pratt HD, Pratt TK. 2001.** The interplay of species concepts, taxonomy, and conservation: lessons from the Hawaiian avifauna. *Studies in Avian Biology* **22**: 68–80.
- Rhymer JM. 2001.** Evolutionary relationships and conservation of the Hawaiian anatids. *Studies in Avian Biology* **22**: 61–67.
- Tarr CL, Fleischer RC. 1993.** Mitochondrial-DNA variation and evolutionary relationships in the amakihi complex. *Auk* **110**(4): 825–831.
- Zusi RL. 1978.** The interorbital septum in cardueline finches. *Bulletin of the British Ornithologists Club* **98**(1): 5–10.
- Zusi RL. 1989.** A modified jaw muscle in the Maui Parrotbill (*Pseudonestor*: Drepanididae). *Condor* **91**: 716–720.