



FRONTISPIECE. The three known plumages of Ula-ai-hawane (*Ciridops anna*) based on the three best-preserved specimens. Top row: adult male (MCZ 10995) in lateral, dorsal, and ventral views. Middle row: subadult male (AMNH 459008). Bottom row: adult female (AMNH 230275). Paintings by Julian P. Hume.



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HISTORY, STRUCTURE, EVOLUTION, BEHAVIOR, DISTRIBUTION, AND ECOLOGY OF THE EXTINCT HAWAIIAN GENUS *CIRIDOPS* (FRINGILLIDAE, CARDUELINI, DREPANIDINI)

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ABSTRACT.—The extinct drepanidine genus *Ciridops* is known from five historically taken specimens of *Ciridops anna* from the island of Hawaii, the last in 1892, and from fossil populations on Molokai, Oahu, and Kauai. The origins of the historical specimens and the taxonomic history of the genus are reviewed. The plumages of *C. anna* are interpreted as highly sexually dimorphic (red males vs. greenish females); the juvenile plumage of males included brownish feathers that appear to have been retained and mixed with the incoming definitive plumage. The thigh musculature and pelvic and hindlimb osteology show that the strong legs and feet of *Ciridops* were probably used to move plant debris in search of insects. The closest living analog may be the Yellowhead (*Mohoua ochrocephala*) of New Zealand. Analysis of stomach contents of the single fluid-preserved specimen of *C. anna* disclosed remains of insects that are widely distributed in Hawaiian forest ecosystems. The traditionally claimed association of *Ciridops anna* with palms of the genus *Pritchardia* suggests that *Ciridops* may have fed in the accumulated debris in the axils of palm leaves. The patchy distribution of fossils of *Ciridops* may result from the birds being associated with nearly pure stands of *Pritchardia* that were in turn patchily distributed. Vulnerability of *Pritchardia* to introduced seed predators, including rats and humans, and to destruction of lowland habitats by cutting and burning, may have caused the prehistoric extinction of *Ciridops* on all islands except Hawaii. Received 2 March 2012. Accepted 25 May 2012.

Among the most beautiful (Frontispiece, Fig. 1) and enigmatic of the exuberant adaptive radiation of Hawaiian cardueline finches of the tribe Drepanidini, is the extinct Ula-ai-hawane (*Ciridops anna*). This is among the rarest of birds, being known historically only from five study skins and remnants of a single skinned body preserved in alcohol. Although *Ciridops* was known historically only from the island of Hawaii, fossils show that it also occurred at least on Molokai, Oahu, and Kauai. Many new insights

into the structure and probable habits of the species of *Ciridops* have been gained through study of the fossil material and from new dissections of the one fluid specimen. Additional new information on the history and habits of *C. anna* comes from archival sources. This paper presents the new data and attempts to gather all previous knowledge regarding the genus *Ciridops*, reserving species-level revision of the fossil material for future studies.

HISTORY AND DISPOSITION OF HISTORIC SPECIMENS OF *CIRIDOPS ANNA*

The first published indication of the existence of the bird that became *Ciridops anna* was in a

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FIG. 1. The two additional existing specimens of Ula-ai-hawane (*Ciridops anna*). Left column: lateral, ventral, and dorsal views of subadult male (BMNH 1939.12.9.58) in which the reds have faded in alcohol to an orangish hue. Right column (top 2 figures) lateral and ventrolateral views of adult male holotype of *Ciridops anna* (BPBM 19). Right column, bottom figure: Iiwi (*Vestiaria coccinea*) (BMNH 95.7.20.172) in dorsal view to contrast wing pattern with *Ciridops anna*. Note the light colored patch in the inner secondaries is on the outer webs in *Ciridops* and on the inner webs in *Vestiaria*. Paintings by Julian P. Hume.

two-page catalog drawn up by Sanford Ballard Dole, a Honolulu lawyer and amateur ornithologist, later to become the first territorial governor of Hawaii and then a Federal judge (Damon 1957, Allen 1988). This list (Dole 1876) was drawn up to accompany a collection of mounted birds that formed part of a display of Hawaiiana for the centennial exhibition in Philadelphia in 1876, the birds having been collected and mounted by James Dawkins Mills, an ardent amateur naturalist and taxidermist who resided in Hilo, Hawaii, from 1851 until his death in 1887. He and his bird-catcher Hawelu are believed to have collected mainly in the Oloa area of Puna on the island of Hawaii (Olson 1999b) with his greatest activity probably having been around 1859–1860 (Manning 1978, 1979, 1981). Under the family Fringillidae, in which was also included the drepanidine *Psittirostra psittacea*, Dole (1876: 2) wrote the following:

“Ulaaihawane. Not previously described. 5½ in.[ches] long. Bill short, straight. Toes 3 front, 1 back. Wing coverts and breast red; throat, primaries and tail, black; secondaries white; head grey; merging into white on the upper part of the neck, and grey again on the back. Habitat Hawaii. Probably belongs to the genus *Fringilla*.”

It is uncertain which of Mills' specimens were actually on exhibit in Philadelphia; some in Dole's catalog were possibly omitted, whereas others that were not listed may have been included (Manning 1978, 1979). After the birds from the Philadelphia exhibition were returned to Mills, the naming of the new '*Fringilla*' fell to Dole (1878: 49–50), who called it *Fringilla anna*, the account being otherwise a verbatim repetition from the 1876 list, to which was added: “This is a bird of remarkable beauty, its peculiar combination of colors producing a most harmonious and elegant effect.” The type locality ‘Hawaii’ refers to the island of Hawaii rather than to the archipelago. Nowhere in Dole's (1878) list of Hawaiian birds does he mention the number of specimens examined for the species listed.

Mills retained his collection probably up until his death in 1887, after which portions were sold at auction (Manning 1978), although the bulk of it was later acquired by Charles Reed Bishop at some time between 1884 and 1888, after which it became the nucleus of the bird collections of the Bishop Museum (Manning 1978). The first indication that there were at least two specimens

of *Ciridops* in the Mills collection was supplied by Wilson, who stated that “I procured a specimen from Hon. C. R. Bishop, which had been obtained by the late Mr. Mills of Hilo. Mr. Bishop has a very much finer example remaining, with more grey about the head and neck taken by the same gentleman.... The present specimen [is] now in the collection of the Hon Walter Rothschild” (Wilson and Evans 1893: 23).

Bishop's ‘much finer specimen’ is the one now in the Bishop Museum (BPBM 19). The second one Wilson obtained from Bishop in 1888, along with several other rare birds obtained by Mills (Manning 1978), in exchange for species Wilson had collected that Bishop did not possess. Wilson's specimen of *Ciridops* eventually passed to Rothschild (Rothschild 1900:183), doubtless through purchase, as Wilson sold a number of his specimens to other museums, such as the Rijksmuseum in Leiden (Olson and James 1986) and museums in Paris and Liverpool (Olson 1999a). That specimen of *Ciridops* ultimately went to the American Museum of Natural History (AMNH 459008) in New York when Rothschild's bird collection was sold in 1931 (Murphy 1932). It is not in definitive plumage, the secondaries being brown rather than white and part of the belly dark brown rather than red. It has been regarded as a syntype or cotype of the species by numerous authors (e.g., Henshaw 1902, Munro 1944, Amadon 1950, Banko 1979), but it does not agree with Dole's (1878) original description and has no status as a type. The Bishop Museum specimen is thus the holotype (Olson 1994), as also stated by Rothschild (1907a: 41).

Two additional specimens, one in the definitive red plumage (MCZ 10995) and the other in a distinctive greenish plumage (MCZ 10987 exchanged to New York where it is now AMNH 230275), appeared rather mysteriously with a few other Hawaiian birds among the old collections of the Museum of Comparative Zoology at Harvard (Bangs 1910). I proposed that this small collection had its origin in the expedition of William T. Brigham and Horace Mann Jr. to the Hawaiian Islands in 1864–1865 (Olson 1992). I also built an entirely circumstantial case for the specimens' possibly having been taken on Molokai, owing to some comments inserted by Brigham into Dole's (1869) first list of Hawaiian birds. I no longer consider this to be a plausible geographical origin. Newly examined correspondence in the Smithsonian Institution Archives (RU 182, volume 186, page 355,

box 40, folder 16) reveals that Brigham “tried hard to purchase those birds [Mills’ collection] eleven years ago [1865] when I saw them in Mr. Mills’ collection in Hilo, Hawaii, but his price was beyond my means.” (W. T. Brigham from Boston 13 Nov 1876 to S. F. Baird at the Smithsonian). This is the first certain indication that the Mills collection was in existence as early as 1865. Thus, it now seems much more likely that Brigham negotiated some sort of purchase or exchange with Mills or one of his collectors that resulted in his obtaining the small collection that included the two ‘Harvard’ specimens of *Ciridops*. It is therefore possible that four of the five historically known specimens of *Ciridops anna* have the same general source—James Mills from the area above Hilo.

The last specimen of *Ciridops anna* was obtained on 2 February 1892 near the headwaters of the Awini River in the Kohala Mountains of northwestern Hawaii by native Hawaiian hunters for Rothschild’s collector, Henry Palmer. This was preserved whole in spirits of wine, from which Rothschild, in what must be viewed with hindsight as an irreparable loss of anatomical information, had it prepared as a study skin sometime before 1900, at which time he wrote that “the beautiful red has faded away” (Rothschild 1900: 183). Fortunately, the skinned trunk, along with the hyoid apparatus, was retained in spirits, both this and the skin (BMNH 1939.12.9.58) having gone to the British Museum (Natural History) with the Rothschild bequest in 1939. The details of the circumstances surrounding the capture of this last specimen of *Ciridops* are recorded in the journals of Palmer (Rothschild 1893: Diary 7) and his assistant George C. Munro (1892).

Capture of Ciridops.—The five existing specimens of *Ciridops anna* are all in remarkably good condition with plumage that shows little or no signs of wear, although what this may mean in terms of timing of molt cycle is uncertain because, except for the last specimen obtained by Palmer, it is not known at what time of year any of them were collected. None of them shows any evidence of shot damage and it is likely that all may have been trapped alive by birdcatchers using traditional means such as birdlime, snares, and other means (Emerson 1894). The one obtained for Palmer and preserved in spirits must have been killed soon after capture for the stomach contents to have remained undigested and in good condition. The label indicates it was ‘shot by a native’ and Munro (1892) reports that the natives “shot it while feeding” but I have not noticed any

shot damage in either the skin or the remaining body in fluid.

SYSTEMATIC HISTORY

Dole (1878) reflected the opinion, long voiced subsequently, that the bill of the Ula-ai-hawane was finch-like by placing it in the genus *Fringilla*, probably intending that usage in a more or less Linnaean sense rather than suggesting any close relationship with the few species now restricted to the genus *Fringilla*. Subsequent to Dole’s (1878) description, which was reprinted by Sclater (1880), there was no further mention of the species, apart from a query in a footnote by Sharpe (1888), who wondered what *Fringilla anna* might be. Newton (1892:469) placed it in the new genus *Ciridops* and considered that “it probably belongs to the fauna which I have above called ‘Columbian’ (for want of a better name); but I cannot suppose it to have been so early a settler as the Drepanididae, since it has changed so little.” In this he may have meant that it had changed so little from other finch-like Hawaiian passerines, which at that time were not recognized as being part of the drepanidine radiation. In the final arrangement of pages of Wilson and Evans (1890–1899), *Ciridops* was placed at the beginning of the drepanidines, followed by the species of the red-and-black group. Gadow (1899: 243) considered there was nothing to be gained by excluding *Ciridops* from the Drepanididae, citing hearsay reports of its frayed or tubular tongue. That information came from the specimen received in spirits by Rothschild (1900: 181) who remarked that the “tongue seems to prove that this genus belongs to the Drepanidae and not to the Fringillidae, the only two families which would have any chance of claiming it.” Perkins (1901, 1903) was the first to advocate that all the Hawaiian birds then included in the Drepanididae, plus the finch-billed species previously considered ‘fringilline,’ constituted a monophyletic radiation regardless of the family in which they were placed. Perkins divided the expanded Drepanididae into two ‘divisions’ and included *Ciridops* in his Division 1 (the ‘red and black’ group later often called a subfamily Drepanidinae). Its position he regarded as “quite certain” (Perkins 1901: 585), specifically mentioning similarities shared between *Ciridops* and *Vestiaria* (scarlet plumage, black wings and tail, white in wings) and also *Palmeria* (blackish-gray [lanceolate] throat feathers). Bryan (1901) placed *Ciridops* in the Drepanididae at the end of the red group after *Himatione* and preceding

Chlorodrepanis. Henshaw (1902: 57) placed this “finch-like bird” at the end of the red-and-black species. Amadon (1950: 174) considered the bill of *Ciridops* to be “finch-like” but that it was otherwise “nearest *Palmeria* but without a crest and with lanceolate feathers on the crown throat, and cheeks only.” Amadon (1950: 231) believed the drepanidines had evolved from nectar-feeding coerebid-like birds and, that within the red-and-black group, *Ciridops*, with its supposedly “most tanager-like” bill, was considered to be the most derived member. Bock (1970, 1979) and Richards and Bock (1973) acknowledged the drepanidines to have been derived from the Carduelinae, and considered *Ciridops* to be basal to the entire radiation, having given rise both to the ‘red and black’ group and to *Loxops* and the remainder of the radiation, including all the taxa that are much more finch-like than *Ciridops*. Bock (1979: 65) later placed *Ciridops* at the base of the red-and-black group “which may be representative of the founding stock of the Hawaiian honeycreepers.” Raikow (1977: 115) argued that *Ciridops* must have branched off among the slender-billed non-finch-like forms in the drepanidine radiation but that the “finch-like or tanager-like bill... is difficult to explain in conjunction with the fully tubular tongue, especially since little is known of its feeding habits” so that “perhaps the bill shape... is only secondarily finch-like.” The bill shape of the then newly discovered Poo-uli (*Melamprosops phaeosoma*) was considered to be “closest to that of the extinct ‘*ula-‘ai-hawane* (*Ciridops anna*)” (Casey and Jacobi 1974: 220). An osteological analysis consistently grouped *Ciridops* with the red-and-black clade (*Drepanis*, *Vestiaria*, *Himatione*, and *Palmeria*), usually in a basal position but in a strict consensus tree in the most derived position (James 2004). There are no reliable generic-level characters to separate the highly curved-billed genera *Drepanis* and *Vestiaria* (Pratt 1979a, 2005), and only size and plumage characters appear to separate *Palmeria* from *Himatione*. The argument for merging all four of these genera in *Drepanis* (Fleischer in Pratt 2005: 77) has received strong recent support from discovery of a natural hybrid between *Vestiaria coccinea* and *Himatione sanguinea* (Knowlton et al. in press). *Drepanis sensu lato* and *Ciridops* would thus represent a simple dichotomy so that which one would be ‘basal’ becomes moot. The hindlimb morphology of *Ciridops* is certainly derived relative to that of *Drepanis* (s.l.) and if its

short bill evolved from a longer-billed ancestor, then *Ciridops* would certainly appear to be the more specialized genus compared with *Drepanis*.

Genus *Ciridops* Newton 1892: 469.

Type Species.—*Fringilla anna* Dole (1878), by monotypy; gender, common, probably intended as feminine by analogy with *Loxops*, although all genera ending in *-ops* are now to be treated as masculine by decree of International Commission on Zoological Nomenclature (Pratt 1979b).

Authorship of the Generic Name.—Newton (1892: 469) introduced a note of ambiguity concerning the authorship of *Ciridops*: “... there is one very puzzling species, of which only a few specimens seem to have been preserved, that needs particular attention. This was described by Judge Dole under the name of ‘*Fringilla anna*,’ but, of course, is no true *Fringilla*. Mr. Wilson brought home but a single specimen.... and, I believe will establish for it a new genus, *Ciridops*.” Despite this, the name was clearly established at that moment by Newton, who, I believe (Olson 2003), was also the chief author of most of what was written in Wilson and Evans (1890–1899), where the reference was cited (1893: 23) as “‘*Ciridops* ----, Wilson’, Nature, xlv. page 469 (17 Mar 1892)”. Rothschild (1900, 1907b), W. A. Bryan (1901), Perkins (1903), and E. H. Bryan (1958), for example, attributed the genus to Wilson, but Richmond (1902: 673) more precisely lists the author as “‘Wilson’ Newton.” Later authors (e.g., Bryan and Greenway 1944, Amadon 1950, Greenway 1968, AOU 1998) correctly give sole authorship of the generic name *Ciridops* to Newton.

Etymology.—Pratt (2005: 273) evidently did not consult the original description of the genus and appears to have contrived an etymology, stating that *Ciridops* is “most often translated as ‘shining face’,” or that “the name probably was intended to mean ‘looking like Scylla’s ciris’.” *Ciridops* had not previously, to my knowledge, been translated as ‘shining face’ except by Pratt (2002a), the Greek word for ‘shining’ being *lampros*. Newton (1892: 469), however, explicitly declared that *Ciridops* was “so named because its bright coloration recalls the well-known *Emberiza ciris* of Linnaeus, the Painted Bunting of authors, or ‘Nonpareil’ of bird dealers.”

Included Species.—*Ciridops anna*, *Ciridops tenax* James and Olson 1991, *Ciridops* sp. (Oahu) James and Olson 1991.

Ciridops anna (Dole 1878)

Synonymy.—Ulaaihawane Dole 1876: 2; *Fringilla anna* Dole 1878: 49 [type-locality, Hawaii]; '*Fringilla anna*.—Newton 1892:468; *Ciridops [anna]*.—Newton 1892:469; *Ciridops anna*.—Wilson and Evans 1893:23, and all subsequent authors; *Ciridops anna*.—Rothschild 1907a: 215 (lapsus).

Holotype.—BPBM 19, in the presumed definitive adult male plumage. AMNH 459008, in presumed subadult male plumage, is not a syntype or cotype.

Etymology.—The specific name *anna* has been widely and understandably assumed (Amadon 1944; Jobling 1991; Mearns and Mearns 1992; Pratt 2002a, 2005) to have been a tribute to Anna Prentice Cate (b. 16 Jul 1842, Castine, Maine; d. 29 Aug 1918, Honolulu), who married Sanford Ballard Dole on 19 May 1873, although Dole did not publish any explanation for the name. Thus, there remains a distinct possibility that *anna* could have been meant to honor Dole's cousin Anna Ward. Dole traveled from New England to California in 1868 with Anna and her daughter Maybelle with both of whom he continued to maintain close ties (Allen 1988). Dole named *Fringilla anna* at a time when his wife was in New England, their relations were strained, and Dole was in the process of a Hawaiian '*hanai*' adoption of 14 year-old Elizabeth Napoleon, an arrangement that was not entirely satisfactory to either Elizabeth or Mrs. Dole (Allen 1988). When Elizabeth later married Eben Low, she named her first daughter Annabelle Dole Low, supposedly to commemorate Anna Dole and Maybelle Ward, but there was ambiguity as to whether the eponymous Anna was Mrs. Dole or Maybelle's mother (Allen 1988: 168–171). Dole may deliberately have intended that the Anna of *Fringilla anna* could not be pinned down with certainty, which is how it stands.

Vernacular Names.—On the island of Hawaii in the 19th century, *Ciridops anna* was evidently widely and consistently known as 'Ulaaihawane' or 'Ula-ai-hawane,' with various usages of glottal stops and macrons but correctly written in Hawaiian as '*ula-ai-hāwane*. This was first made known by Dole (1876, 1878), who doubtless received his information from James Mills (Manning 1978), who in turn would have been informed by the birdcatcher Hawelu (Manning 1981). Wilson, who also interviewed Hawelu, reported that "I used to hear repeatedly of the 'Ulaaihawane,' by which name it is well known to

the natives, who told me that it feeds on the fruit of the Hawane palm, whence its name—Ula (red), ai (to eat), Hawane (the Hawane palm)" (Wilson and Evans 1893: 23). The Hawaiian name *loulou* is customarily used for the palm itself (*Pritchardia* spp.), but, counter to the impression conveyed by Pratt (2005), *hawane* may be used for the tree also, as well as its more usual application to the fruit ('nuts') alone (Pukui and Elbert 1986). Earlier ornithological writers usually used the term 'hawane palm.' The preceding information probably originated mostly in the Olaa District between Hilo and the volcano of Kilauea. The name Ula-ai-hawane was also used, or at least understood, in the Kohala District in the northwestern part of the island, where Hawaiians collecting for Palmer obtained the last specimen, as is evident from the diaries of both Munro (1892) and Palmer (Rothschild 1893). There does not appear to be any justification for Palmer's emendation of the name to 'Ulaaiwhane' (Rothschild 1900: 184). Other apparent lapses are 'Waiihawane' = (Bryan and Greenway 1944: 133), 'ul-ai-hawane' (Carlquist 1965:85), 'Uha'aihawane' (Banko 1987: title page), and 'ulalhawane' (Allen 1988: 59). Henshaw (1902: 58) called it the 'hawane finch.' Mathews (1930: 808) invented many English names for birds out of flights of fancy and called *Ciridops anna* "White-naped Mano," which was a *lapsus* for 'mamo,' a name that he also applied to *Palmeria dolei* ("Crowned Mamo"), although no Hawaiian had ever referred to either species as a 'mamo.' German vernaculars include "Hawaii Fink" (Duncker 1953: 240) and the ludicrous "Annakleidervogel" of Luther (1972:179), *Kleidervogel* being German for drepanidine birds from the use of their feathers by Hawaiians in making garments (*Kleider*), so that Luther's name might also be taken to mean 'the bird of Anna's clothing.' Pratt's (2005: 273, 275) "red palmcreeper" for *C. anna* and "Kaua'i Palmcreeper" for *C. tenax* are bookish inventions perhaps reflecting a preference for continuing to call the Drepanidini 'honeycreepers' rather than finches.

EXTERNAL MORPHOLOGY AND PLUMAGES OF *CIRIDOPS ANNA*

External Morphology

Appearance and Proportions of Bill, Wings, and Feet.—No aspect of the external morphology is known for any of the fossil populations of *Ciridops* and that of *C. anna* may be taken as

TABLE 1. External measurements (mm) of skin specimens of *Ciridops anna*. Culmen length is from base of feathers to tip. Width of culmen and depth of bill taken at level of anterior margin of nostril.

Museum number and presumed sex and age	Wing chord	Tail length	Tarsus length	Culmen length	Culmen width	Bill depth
BPBM 19, adult male (holotype; Wetmore's measurements in parentheses)	81.5 (83.0)	48.8 (49.0)	19.7 (21.0)	11.8 (11.0)	4.4	
MCZ 10995, adult male	80.4	46.2	21.2	10.6		5.6
AMNH 459008, subadult male	74.8	43.3	19.7	11.4	4.1	5.2
BMNH 1939.12.9.58, subadult male	77.1	42.7	22.3	9.9	3.5	4.6
AMNH 230275 (formerly MCZ 10987), adult female	72.0	45.4	20.9	9.3	3.9	4.4

representative for the genus. The most detailed description available is from notes by Alexander Wetmore when he visited the Bishop Museum as part of the *Tanager Expedition* (Olson 1996). His description was based on the holotype (BPBM 19) and is far more detailed and accurate than Rothschild's (1900: 181), which was presumably based on one or both of the specimens then in his collection (AMNH 459008; BMNH 1939.12.9.58):

Wing 83.0 [mm], tail 49.0, culmen from base 11.0, tarsus 21.0. Nostril set in a slight depression only partly concealed by frontal plumes. Culmen slightly curved downward, sides of bill nearly straight in outline; gently rounded. Outline of maxillary tomium faintly concave, slightly sinuate. Tip of maxilla acute on sides, slightly broadened when viewed from above. Lower mandible with sides rounded. Line of gonys straight. Mandibular rami slightly less than half [the length of the] gonys. Feathers of forehead short and plushlike. Small rictal bristles present. Wing formula 7, 8, 6, 5, 9, 4, 3, 2, 1. [Primaries] 6, 7, 8 nearly equal, 9 only slightly shorter than 5. Wing tip about 20.0 mm. Tenth primary on upper side of wing 8.0 mm long. Tarsus scutellate. Basal joint of 4th toe wholly adherent to middle toe. Basal joint of 2nd toe adherent to middle toe for slightly more than one third length. Second toe with claw reaching beyond base of claw on middle toe. Fourth toe with claw reaching to base of claw on middle toe. Hind toe and claw strong equal to or slightly more than middle toe without claw. Tail very slightly notched, rectrices 12. Feathers of throat and ear coverts lanceolate with long slender tips. (A. Wetmore field notes, 31 Mar 1923, Division of Birds archives, Smithsonian Institution).

Skin Measurements (Table 1).—Additional measurements of the bill of *Ciridops anna* (MCZ 10995) taken prior to the removal of the skull from the skin (Olson et al. 1987) include: culmen length from anterior rim of nostril, 7.9 mm; length of rostrum along tomium, 11.7 mm; mandibular symphysis length, 7.4 mm; basal mandible width, 4.5 mm; basal rostrum width, 6.1 mm. Middle toe with claw 0.76 inches (19 mm), hind toe with claw 0.64 inches (16 mm) (Rothschild 1900: 183, AMNH 459008).

Soft Part Colors.—Wilson reported the color of the irides to be "dark hazel" (Wilson and Evans 1893: 24), but that was either a guess used to instruct his artist or a surmise based on the fact that most drepanidines have brown eyes. He also reported "bill and feet pinkish brown" presumably based on dried skins. Pratt (2002a: 9) gives the bill and leg color as "brown."

Plumages

Presumed Adult Male Plumage.—BPBM 19 and MCZ 10995 (Frontispiece, Fig. 1). J. P. Hume, H. D. Pratt (in litt. 20 Jan 2012), and I consider these two specimens to be identical in plumage and Pratt's illustrations (Raikow 1977; Pratt et al. 1987; Scott et al. 1988; Pratt 2002a, b; Pratt 2005, 2010) may be considered idealizations of both (H. D. Pratt, pers. comm.). Illustrations in Carlquist (1965) and Berger (1972, 1981) may be based on BPBM 19 but are poor at best. Underparts: throat and breast, extending onto upper belly, black, grading to brownish on the flanks; the rest of the belly is scarlet, there is a light patch at the anterior of the vent region that has been described as tawny but in MCZ 10995 is lemon yellow, the rest of the vent and undertail coverts are rich brown. Upperparts: the lores, forecrown, posterior portion of the mantle, wings

(except innermost secondaries), and tail black; feathers of the throat, forehead, and auriculars stiffened and pale grayish along the shafts; the occiput and anterior part of mantle are silvery gray shading into gray-brown posteriorly; the outer webs of the innermost secondaries are white, narrowly fringed with scarlet. The white patch in the wing is similar to but evidently not homologous with that of Iiwi (*Vestiaria coccinea*), in which it is the inner webs that are white. The scarlet portions of the plumage are extremely glossy, although less so in BPBM 19, which had been on exhibit and exposed to light.

Presumed Subadult Male Plumage.—AMNH 459008 (Frontispiece). Original color illustrations are in Wilson and Evans 1893 (copied by many subsequent authors), Rothschild (1907a), and Pratt (2002a, 2005). Described by Rothschild (1900: 183) as: “Lores and forehead velvety black, this colour gradually shading into the ashy grey of the crown, nape, and hind-neck, which colour again shades off into the dark sepia-brown colour of the back. Rump and upper tail-coverts dark glossy red. Tail-feathers uniform black. Primaries and secondaries black, only the outer webs of the last three secondaries earthy brownish buff (nearest to Ridgway’s [1886] ‘clay-colour’ on plate v. fig. 8); scapulars and tips of some of the greater wing-coverts of the same colour. Feathers on the sides of the head and neck, chin, and throat black with silvery-grey shaft-stripes. Breast down to the middle of the uppermost part of the abdomen black. Middle of abdomen, vent, and under tail coverts tawny brown. Sides of abdomen largely glossy red.” Pratt (2002a: 9) found that it “mostly resembles the adult plumage except: black of forehead and lores more extensive with black breast band extending anteriorly through the throat to include the chin; middle of back, shoulder, flank, lower belly, crissum, outer webs of tertials, edges and broad tips of greater upper secondary coverts tawny, remainder black.”

BMNH 1939.12.9.58 (Fig. 1). Skinned from alcohol and said by Rothschild (1900:183) to agree with the preceding specimen “except that the beautiful red has faded away in the spirits and that apparently the head has been darker.” It is apparently this faded specimen that was illustrated by Ren Hathway to accompany the Foreword on extinct birds by Fuller (2002: plate F20). This specimen was regarded as immature by Perkins (1903) and Munro (1944). “The secondaries of [this] specimen were almost certainly brown

(definitely not white), which was restricted to the outer webs. There is a fine border of orange (same colour as the other faded red colouration) on the outer edge of the brown outer webs, which may have also been more reddish in life. Interestingly, the chestnut-brown on the belly is clearly unaffected by alcohol” (J. Hume in litt. 11 Jan 2012). This specimen, despite fading, is clearly in a plumage equivalent to that of the preceding, the most obvious indication being the brown coloration extending from the undertail coverts up the midline of the belly to intersect the black breast (this is scarlet in the adult), and the brown portions of the inner secondaries (white in the adult).

Presumed Adult Female Plumage.—AMNH 230275 (Frontispiece). Color illustrations; Pratt et al. (1987), Pratt (2002a, 2005, 2010). This was regarded as an adult female by Bangs (1910: 68–69) who described it as: “Forehead clothed in stiffened, pointed, semi-erect feathers as in the adult male. Top of head, nape and sides of head cinnamon washed with dull olive-yellow on forehead and with the lores and a narrow frontal band more dusky; cheeks with paler shaft-stripes to the feathers; lower back grayish cinnamon, gradually passing into the purer color of the head; rump and upper tail coverts olive-yellow; tail dusky, fringed with olive-yellow; primaries blackish, narrowly edged with dark olive-yellow; secondaries more broadly edged with the same, the innermost nearly wholly dark olive-yellow; throat dull cinnamon, the feathers with paler shaft stripes, slightly washed with yellow-olive in lower middle; chest and breast dingy-smoke-gray, somewhat washed with olive, gradually passing into dark olive-yellow on belly; under wing coverts, axillars, under tail coverts and a small patch in lower middle belly dilute rufous cinnamon. The general pattern thus resembles that of the adult male, though the colors themselves are very different.” The bill is noticeably smaller and more gracile in this specimen than in the subadult male AMNH 459008, which may be a sexual difference.

Discussion of Plumages of *Ciridops anna*

The specimen in greenish plumage is so different from the other four known specimens that Bangs (1910) considered it to be the adult female; but, because in the rest of the red-and-black drepanidines the adult female is like the male, Amadon (1950: 174) considered the green bird to be immature and stated that the “remaining immature

feathers” in “a specimen not quite adult” (AMNH 459008) “agree with the plumage” of the green specimen, which is not true. The most conspicuous remaining feathers in the transitional specimen are the brown inner secondaries and the brown midline of the belly, of which there is no trace in the green bird, whereas there is no trace of green, nor any gray in the breast, in the supposedly molting bird.

Yet the green plumage continued to be regarded as ‘immature’ (Pratt et al. 1987) or ‘juvenile’ (Pratt 2002a, 2005). Pratt (2002a: 9) recognized “3 distinct plumages ... with one in transition,” but in the same paragraph he stated that the bird in red plumage with brown inner secondaries “cannot be a transitional stage because it includes feathers not present in either” of the other known plumages. This was mooted by the discovery that at least parts of the juvenile plumage of the Hawaii Mamo (*Drepanis pacifica*) were of a decidedly brown color, similar to that retained in the ‘transitional’ plumage of *Ciridops anna* (Olson and Hume 2009). The plumage of the exquisite greenish specimen, which appears to be completely fresh and without wear, shows no evidence of the fluffiness, pointed rectrices, or other signs of a truly juvenile plumage (Olson and Hume 2009), making acceptance of it as being in the adult female plumage the only reasonable conclusion—one that was then accepted by Pratt (2010: 647, figure and legend).

The only possible indication we have of breeding or molt cycles comes from the bird taken 2 February in ‘transitional’ plumage (BMNH 1939.12.9.58). February is a time when neither Apapane (*Himatione sanguinea*) nor Iiwi are undergoing any molt (Fancy and Ralph 1997, 1998). Thus, if *Ciridops* were on a similar cycle, ‘transitional’ male plumage with brown feathers may not have been evanescent and possibly lasted a full molt cycle so that it may have taken 2 years for males to attain the definitive plumage. This gains support from half of known male specimens being in non-definitive plumage. If *Ciridops anna* were a highly territorial species, there would have been a decided evolutionary advantage for fully adult territorial males to be able to distinguish females and non-territorial subadult males from threatening conspecific invaders.

INTERNAL MORPHOLOGY OF *CIRIDOPS*

Tongue Morphology

The tongue of *Ciridops anna* was first illustrated by Rothschild (1900: plate 83, figs. 55,

55a—natural size and enlarged) who made no further comment on it other than that it indicated that *Ciridops* belonged with the “Drepanidae” rather than the Fringillidae (Rothschild 1900: 181). Amadon (1950: 222) reproduced the enlarged view along with the tongues of other drepanidines. Carlquist (1965: 125) constructed a ‘tongue phylogeny’ by superimposing illustrations from Amadon (1950) on Amadon’s tree of drepanidine relationships, but many of the tongues were redrawn in different views from the originals and are probably in part fanciful. Bock (1972: 76) illustrated the tongue in several views in great detail and found the structure of the corneous tongue in *Ciridops* to be similar to that in other drepanidines with tubular tongues but that it “differs from that of ‘coerebids’... in that no coerebid possesses laciniae along the upturned lateral edges of the corneous tongue.” The tongue of *Ciridops* was fringed and tubular as typical of the presumably nectarivorous tongues of its close relatives but was shorter in accordance with the short length of the bill.

Osteology of *Ciridops anna*

The skeletal morphology of *Ciridops* was investigated using fossil material and also the skull and mandible, humerus, tibiotarsus, and tarsometatarsus removed (Olson et al. 1987) from the remaining Harvard study skin of *C. anna* (MCZ 10995), and the pelvis and femur from BMNH 1939.12.9.58.

Cranial Osteology.—The skull and mandible of *Ciridops anna* are decidedly not finchlike “but are shortened versions of the thin weak structures found in the nectarivorous genera *Himatione*, *Palmeria*, *Vestiaria*, and *Drepanis*” (James and Olson 1991: 73). Four characters were identified that confirmed the placement of *Ciridops* with that same ‘red and black’ group of drepanidines (Division 1 of Perkins 1903), from which *Ciridops* was distinguished “by its much shorter bill, constricted dorsal nasal bar, upturned retro-articular process of the mandible, deep mandibular ramus (middle part), and enlarged mandibular foramen” (James and Olson 1991: 73).

The skull and mandible of *Ciridops* are contrasted (Figs. 2, 3) with those of a typical nectarivore, the Apapane, and the Poo-uli, which, although not typical of the truly finch-like drepanidines such as *Telespiza*, is a basal taxon within the radiation (Lerner et al. 2011) and

considerably more finch-like than *Ciridops*. The bill of *Ciridops* is much weaker than in *Melamprosops* and, in many respects, is much more like that of *Himatione* except that it is shortened. The nostril is much larger with an ossified nasal septum, and scarcely differs in size or structure from that of *Himatione*, whereas in *Melamprosops* the nostril is smaller, rounder, and lacks a septum. The dorsal nasal bar in *Ciridops* is even thinner than in *Himatione* and quite unlike the much more reinforced nasal bar of *Melamprosops*. In dorsal view, the mandible of *Ciridops* with its prominent retroarticular processes, scarcely differs from that of *Himatione* except in the shorter, wider symphysis, contrasting with the much wider, heavily reinforced and much more finch-like structure in *Melamprosops*.

Postcranial Osteology.—No peculiarities were noted in the humerus or other bones of the wing and pectoral girdle of *Ciridops*. However, great differences in the pelvis of *Ciridops* from that of its near relatives (Fig. 4), reflect the much greater development of the pelvic musculature described herein. The surface of the antitrochanter in *Ciridops* is unusually large mainly due to greater extension anteriorly. The pelvis of *Ciridops* is decidedly broader and more robust with the anterior iliac shield being much wider and more rounded and the posterior portion of the ilium shorter and much broader. The terminal process of the ilium is short and triangular in *Ciridops*, versus long and pointed in its closest relatives. The great medial expansion of the anterior shields cause the dorsal iliac crests almost to meet at the midline, concealing most of the anterior portion of the synsacrum, whereas in more typical drepanidines the dorsal crests are fairly widely separated with deep V-shaped grooves between them to accommodate the posterior termini of the dorsal vertebral musculature. The wider posterior surfaces of the ilia in *Ciridops* reduce the size of the visible posterior portion of the synsacrum, which appears recessed and has much larger intervertebral foramina. The great differences in the pelvis of *Ciridops* reflect just part of the complex of changes involved in the evolution of the hindlimb for the active moving of objects with the foot.

Fossils of exceptionally stout passerine femora were most puzzling when first encountered on Kauai and Molokai, being quite unlike the femur in any species of Hawaiian passerine known at the time (Fig. 5A, D). A supposition that these might belong to species of *Ciridops* was eventually

confirmed by comparison with the femur of *C. anna* that was revealed after dissection of the fluid-preserved trunk specimen. It also became apparent that equally stout fossil tibiotarsi and tarsometatarsi (Fig. 5B, C) were also referable to *Ciridops* (Olson et al. 1987; James and Olson 1991; fig. 35). The hindlimb elements of *C. tenax* of Kauai are somewhat less specialized than in other taxa of the genus (James and Olson 1991). The robust tarsometatarsus reflects the larger foot observed by many authors from examination of the skin specimens. Similarly robust hindlimb elements occur in the unrelated species that appear to be possible functional analogs of *Ciridops*.

Myology of *Ciridops anna*

The only anatomical specimen in existence of *Ciridops anna* was examined to ascertain if the peculiar stout femora repeatedly encountered as fossils really belonged to species of *Ciridops*, this being the remnants of a trunk preserved in alcohol in the British Museum (Natural History). Originally, the entire bird had been preserved in fluid but it “was skinned out of alcohol many years ago while still in the Rothschild collection and is now a skin Reg. no. 1939.12.9.58” (Cowles in Bock 1972: 61). The value of the resulting skin was greatly compromised because the red pigments rapidly faded in alcohol, but we can be grateful that as much of the internal anatomy was preserved as remained with this fragmentary specimen.

The tongue and related musculature of that specimen was the subject of detailed dissections by Bock (1972) with some modifications to the descriptions being added later (Bock 1978). The results revealed relatively little in the absence of comparisons across a variety of other drepanidines. Some resemblances were noted to species of ‘*Loxops*’ (which included a minimum of three currently recognized genera) and to cardueline finches in general (Bock 1970, Richards and Bock 1973) but without an assessment of how the hyoid musculature of *Ciridops* might differ from that of its presumed closer relatives such as *Vestiaria* or *Himatione*.

Bock (1972: 77) considered that “little additional morphological evidence can be gleaned from the alcoholic remnant of *Ciridops anna*, so that no new anatomical data will be forthcoming unless additional anatomical specimens are found which is extremely unlikely,” which put undue

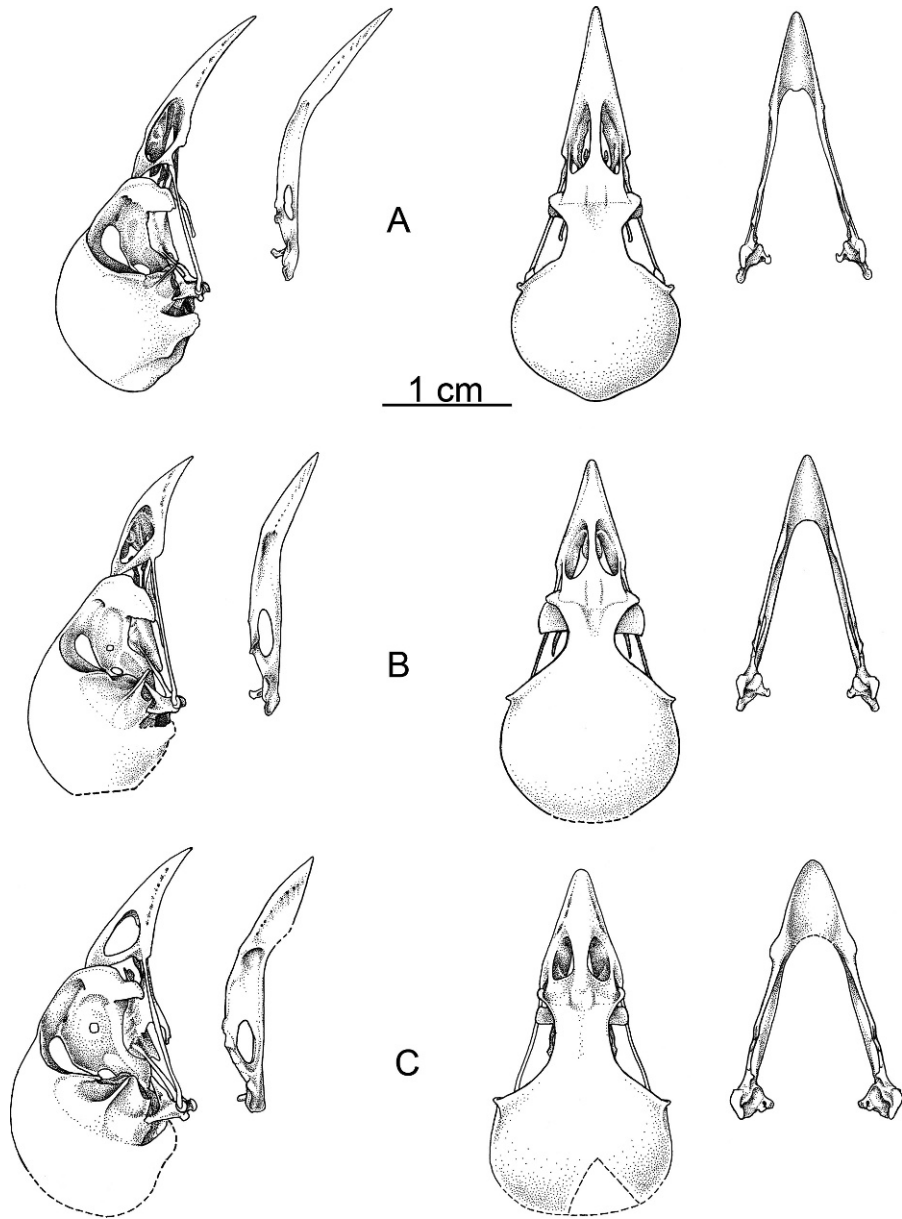


FIG. 2. Skulls and mandibles in lateral (left) and dorsal (right) views. (A) *Himatione sanguinea* (USNM 118858); (B) *Ciridops anna* (MCZ 10995); (C) *Melamprosops phaeosoma* (AMNH 810456).

emphasis on the importance of the tongue. I took a more hopeful approach, and carefully dissected the thigh musculature of this remnant and found that it did yield important and interesting new anatomical data.

When I examined it, the specimen consisted of the pelvis and thighs, a few caudal vertebrae, and a partial presacral vertebral column extending into

the cervical series. The ribs had been cut through and all of the pectoral assemblage was absent. The left thigh had been savaged by persons unknown, the femur being cut through in at least two places and the musculature mangled. Raikow (1976) had previously been able to study the condition of *M. obturatorius lateralis* from the left side. The thigh musculature was relatively intact on the right side,

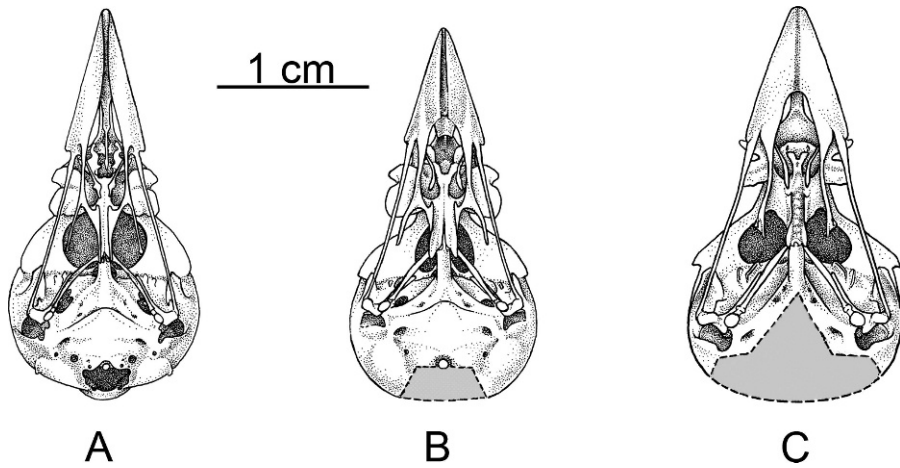


FIG. 3. Skulls in ventral views: (A) *Himatione sanguinea* (USNM 118858); (B) *Ciridops anna* (MCZ 10995); (C) *Melamprosops phaeosoma* (AMNH 810456).

although some of the origins of the more posterior muscles had been cut through, and the cut below the knee had destroyed the insertions of others. Some of the internal organs remained relatively intact, such as the intestines and anus, gizzard, and heart. The liver had been mangled. The gizzard had been sliced through, revealing that it was completely filled with food that miraculously had not been washed out and lost and which I removed and had analyzed. It seems incredible that this step had not been taken earlier, particularly in view of the considerable published speculation on the possible food habits of the species.

Each muscle of the right thigh was compared directly with its counterpart in *Himatione sanguinea* (hereafter HS) and *Vestiaria coccinea* (VC) and with the descriptions in Raikow (1976). Each muscle was removed and preserved with appropriate labeling in individual plastic envelopes. Ultimately, the femur and pelvis were removed and cleaned and these are discussed under osteology.

The descriptions below are strictly comparative, the typical pelvic musculature of drepanidines having been illustrated and discussed adequately by Raikow (1976). The relative sizes of muscles between species were often subjective due to differential preservation. The muscles in the specimen of *Ciridops*, as noted by Bock (1972), were fortunately well-preserved and easily dissected, which was not always the case with some of the comparative material.

M. iliotibialis cranialis (Fig. 6A, B, C).—This muscle in *Ciridops* was markedly wider (5.2 mm at widest point) than in VC (3.4 mm) or HS (3.1 mm). It was also thicker. The relative sizes differ considerably (Fig. 6C). The part of the insertion on the medial part of the patellar tendon was still intact but the remainder had been destroyed in skinning.

M. iliotibialis lateralis (Fig. 6A, B).—*Ciridops* differs from VC and HS in that the posterior 3 mm of the origin was not fleshy but aponeurotic. The origin then became fleshy from a narrow band just above the antitrochanter; these fleshy fibers attached deep to a strong tendinous raphe running ventrally from the

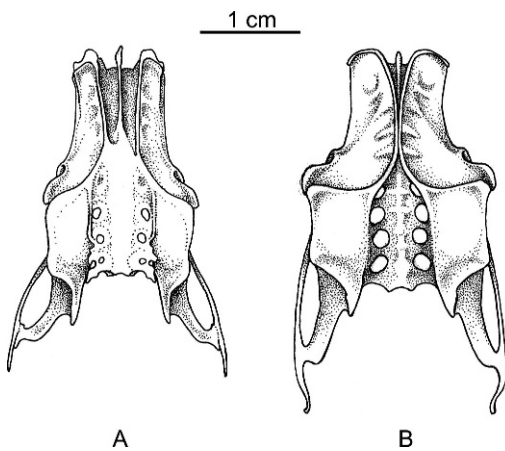


FIG. 4. Pelves in dorsal view. (A) *Vestiaria coccinea* (USNM 553205); (B) *Ciridops anna* (BMNH 1939.12.9.58).



FIG. 5. Hindlimb elements of *Ciridops* (A, B, C) compared with *Vestiaria coccinea* (D, E, F) (USNM 553205). (A) *Ciridops* sp., fossil from Oahu (USNM 255124, image reversed to facilitate comparison); (B, C) *Ciridops anna* (MCZ 10995). Groupings are femora in posterior view, tibiotarsi and tarsometatarsi in anterior view. Note the shorter but much more robust limb bones in *Ciridops*.

iliac crest, to which also were strongly attached fibers from the cranial portion of *M. iliofibularis* (Fig. 6)—unlike either VC or HS. The origin extended as a broad aponeurosis over *Mm. ilioprochanterici* (Fig. 6B). Fleshy fibers did not approach the iliac crest except in the anterior 2.5 mm, where the origin was almost fleshy. The width of this muscle at its origin was 13.0 mm, as in VC.

M. ilioprochantericus caudalis (Fig. 6D).—This muscle was strikingly different in *Ciridops*, being much larger with a distinctly squared posterior margin (Fig. 6D), causing the cranial portion of the iliac shield to assume a conspicuously different shape (Fig. 4) as compared with VC or HS. A portion of this muscle in *Ciridops* extended into the gap between the corner of the iliac crest and the antiprochanter, unlike the other genera compared. With its greater area and thickness, this muscle easily had twice the volume of that in either VC or HS. The tendon of insertion was considerably stronger and extended farther caudally than in those genera, leaving a deeper scar on the femur.

Mm. ilioprochantericus cranialis et medius.—These muscles were essentially similar to those of

VC and HS but were larger and more robust. The origin of *M. ilioprochantericus cranialis* was more extensive posteriorly in *Ciridops*.

Mm. femorotibialis externus et medius.—These fused muscles did not differ greatly from those of VC or HS but some of the fibers of the externus originated farther proximally, about half way up the shaft of the femur, possibly correlated with the shortening of the femur.

M. femorotibialis internus.—Similar to VC and HS but larger and considerably thicker.

M. iliofibularis.—The origin in *Ciridops* appeared proportionately shorter but was more aponeurotic; the belly was larger and thicker than in VC or HS.

M. flexor cruris lateralis.—The posterior portions of both pars pelvina and pars accessoria had been disturbed in skinning. Differences from VC and HS were difficult to detect, but the insertion seemed to extend farther medially and distally.

M. caudiliofemoralis.—The belly had been cut in skinning and the origin was lacking. The muscle was similar in size and position to that in VC or HS but the insertion was more distal (the gap between the tendons of insertion of *M.*

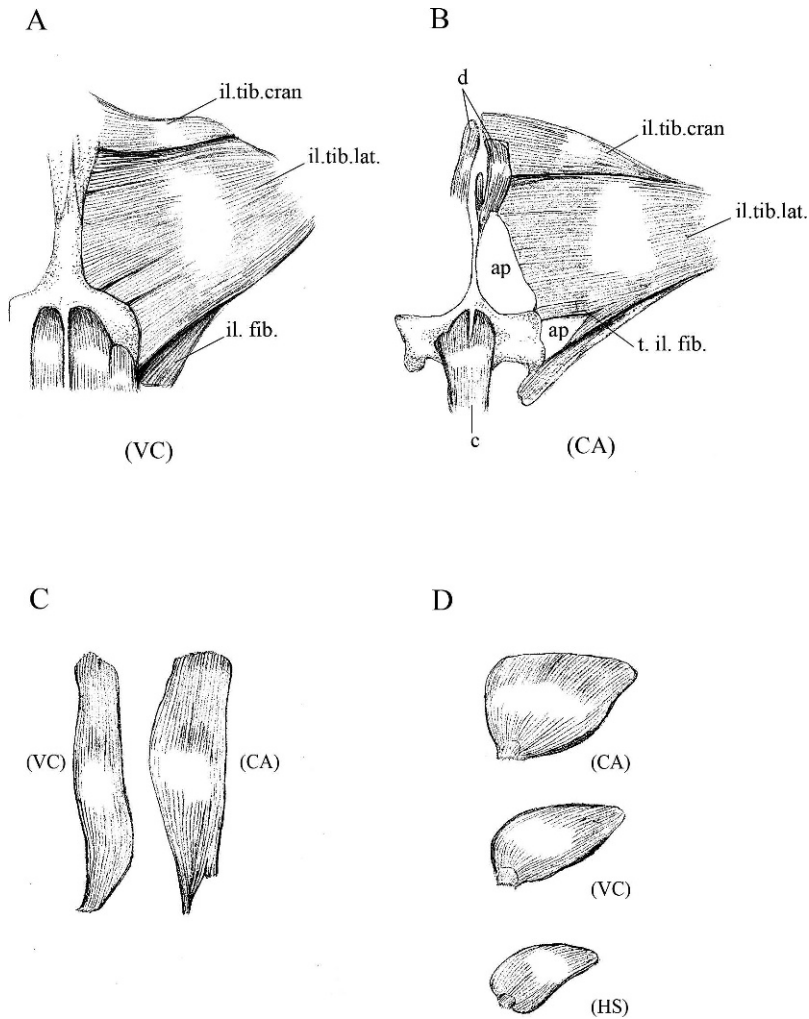


FIG. 6. Schematic diagrams of thigh musculature of *Ciridops anna* (CA) compared with that of *Vestiaria coccinea* (VC) and *Himantopus mexicanus* (HS). (A, B) dorsolateral views of superficial thigh muscles emphasizing the aponeurotic origins of *M. iliotibialis lateralis* in *Ciridops*: c = caudal musculature, d = dermal muscles, il. tib. cran = *M. iliotibialis cranialis*, il. tib. lat. = *M. iliotibialis lateralis*, il. fib. = *M. iliofibularis*, t. il. fib. = a tendon deep to the region indicated that is shared with *M. iliofibularis*; (C) comparative size and shape differences in *M. iliotibialis cranialis*; (D) comparative size and shape of *M. iliotrochantericus caudalis* in lateral view between three genera of drepanidines. Figures are all approximately to scale.

caudiliofemorals and *M. ischiofemorals* was 2.5 mm in *Ciridops*, 1.9 mm in VC and HS).

M. ischiofemorals.—The belly was somewhat larger and deeper, corresponding with the slightly broader and more deeply cupped ischium; tendon of insertion broader and stronger than in VC or HS.

M. flexor cruris medialis.—This had been cut away from the origin in skinning. It was similar to VC but perhaps slightly more robust.

M. pubischiiofemorals.—The pars caudalis was similar to HS, whereas in VC the origin was less

discrete and lay partially under the posterior part of pars cranialis. The pars cranialis was similar to the other species.

M. obturatorius lateralis.—Both pars dorsalis and pars ventralis were present, as noted by Raikow (1976:783). These were larger and better developed than in VC or HS.

M. obturatorius medialis.—This appeared to be slightly larger than in VC.

M. iliofemorals internus.—There were no detectable differences in this small muscle.

M. flexor hallucis longus.—Only the origin of the medial head remained. This appeared to be exceptionally strongly developed, more so than in VC or HS, and the more expanded distal end of the femur would have acted to provide increased area for attachment of this muscle.

Discussion of Myology

Almost all of the thigh muscles of *Ciridops* were markedly better developed than those of its nearest relatives *Vestiaria* and *Himatione*. These muscles are mainly those involved in moving the femur or holding it in position, although one is involved in flexing the hind toe, all of which indicate a much more vigorous use of the hindlimb than in related species.

Functional Interpretation of Hindlimb Anatomy and Morphological Analogs of *Ciridops*

The pelvis and hindlimb structure of *Ciridops* diverge significantly from those of all other Drepanidini, including especially its presumed closest relatives (*Vestiaria* and *Himatione*). All of the hindlimb elements are much more robust but this is most evident in the exceptionally short, stout femur. The pelvis is correspondingly modified to accommodate the much more strongly developed musculature of the thigh. This indicates active use of the hindlimb in some activity other than simply perching or hopping from branch to branch (or along the ground), which are probably the only major uses of the hindlimb in other drepanidines.

Therefore, to hypothesize the activity in which *Ciridops* may have been engaging it is necessary to identify other passerines with similar adaptations of the pelvis and hindlimb, particularly the femur. The most extreme adaptations of this nature are found in the chowchillas (*Orthonyx*), which occur in woodlands of Australia (familial level relationships of *Orthonyx*, as well as *Bowdleria* and *Mohoua*, are still unresolved, although they are not closely related to one another). The femur in *Orthonyx* is extremely short and stout, appearing almost like that of a loon (Gaviidae) and quite unlike that of most other passerines (Olson 1990b, Boles 1993). These birds have a specialized foraging behavior in which one foot is used as a brace and the other for vigorously scratching and removing forest litter in a search for prey (Zusi 1978). Another group with similar, although less extreme morphological and behavioral adaptations are the

New Zealand fernbirds of the genus *Bowdleria* (Olson 1990b), which also use the hindlimb not only to scratch and push away detritus but also to pick up leaves with the feet (Best 1979). Both *Orthonyx* and *Bowdleria* are almost completely terrestrial, however, which is unlikely to have been the case with *Ciridops*.

A much better analog for *Ciridops* are the two more specialized species of the New Zealand genus *Mohoua*, the Whitehead (*M. albicilla*) and Yellowhead (*M. ochrocephala*). These are medium-small arboreal birds with a short bill with a curved culmen that compares quite favorably in overall shape with that of *Ciridops*, and with large, strong feet. The pelvis and hindlimb are specialized along the same lines as those of *Ciridops* with the femur in particular being notably short and stout (Olson 1990a). The Yellowhead feeds in treetops but also roots “through the accumulations of rubbish that fall down and collect” in the forks of trees, at which time they grip with one foot, use the tail as a prop, and “scratch vigorously with the other foot, sending down a shower of debris” (Soper 1976: 50).

The claimed close association between *Ciridops anna* and loulou palms (*Pritchardia*) is perhaps best explained not by the bird eating the fruit or any other part of the palm itself, the fruits usually being much too large for a bird the size of *C. anna* to process, but by the birds finding food among the litter that accumulated in the axils of the palm leaves. This ‘rubbish’ was presumably moved by the bird’s using its large and well-muscled feet and legs to expose invertebrates hidden within the accumulation.

That the crowns of *Pritchardia* palms (Fig. 7) act to accumulate debris has been observed in the field by botanist C. D. Bacon (in litt. 14 Dec 2011):

“First are things that get trapped in the crown—seeds, leaves, and debris from *other* plants, small herbaceous plants and mosses, and invertebrates, anything you can imagine falling from other plants or the sky into a plant. The second contribution is from morphological attributes of the crown itself—the upper sides of the leaf sheath and petiole are often very fibrous and sometimes pubescent with dense, woolly hairs. These fibers and hairs more often than not, split off and break at the margins, and fall into the crown and might also offer easy



FIG. 7. Crown of the palm *Pritchardia martii*, endemic to Oahu, Hawaiian Islands showing the density of the bases of the petioles and inflorescences, and the amount and potential for accumulation of debris in the leaf axils. This is hypothesized to have been the specialized feeding niche of the species of *Ciridops*, which may have used its hypertrophied feet and pelvic musculature to move debris in search of insect prey. Photograph by Christine D. Bacon.

access to nesting materials. Furthermore, some species, like *P. viscosa*, have short, stiff inflorescences that likely drop mature fruits into their own crown. The stem apex where things collect is protected by the crown and the surrounding leaves, and would maintain moisture and shade, and potentially provide a food source for insects and other invertebrates that would also be in the crown.”

Scott et al (1986) suggested that the affinity of *Ciridops* for palm trees recalled the Point-tailed Palmcreeper (*Berlepschia rikeri*, Furnariidae) of South America, which is closely associated with stands of palms of the genus *Mauritia*. I examined several skeletons (USNM) of *Berlepschia* and found that it has none of the hindlimb adaptations of *Ciridops* and probably obtains its food by probing with its long, slender bill.

BEHAVIOR OF *CIRIDOPS ANNA*

General Demeanor.—Little was recorded concerning behavior of *Ciridops anna* in the field. Emerson (1894: 103) in his treatise of ancient Hawaiian bird hunters, who sought plumes for feathered garments and symbols, remarked that there “was, I am told, another red-feathered bird called *ula-ai-hawane*, a beautiful thing in scarlet, wild and shy, a great fighter, a bird rarely taken by the hunter. Its plumage would have been a

welcome addition to the resources of Hawaiian feather-workers had it been obtainable.” I assume Emerson’s information came from native hunters. Perkins (1903: 405) had no personal experience with *Ciridops*, but he heartily endorsed Emerson’s characterization, stating that the “reputed pugnacity of this bird is quite in accord with what one might expect, and is characteristic of the section of the family to which it belongs, which seems generally to consist of stronger birds, well able to drive from their food those of similar habits in the other section [his Division 2]. If, as there is reason to suppose, the *Ula-ai-hawane* obtained its chief food supply from these palms, which are themselves by no means abundant and are known to have been visited by other Drepanididae species, this pugnacity may well have been developed to an unusual degree.” This is highly speculative, but aspects of the plumage and distribution of *Ciridops* can be interpreted in the context of a territorial bird dependent upon a patchy food source.

Vocalizations.—The only hint of any vocalization of *Ciridops anna* comes from Munro (1892: 20 Feb) in which he describes a “sweet low tweet” that turned out to be made by Akepa (*Loxops coccineus*) but that natives had confused with *Ciridops*. Munro (1944) later seemed to write the whole incident off as bungling, but his journal is more ambiguous. He had heard many Akepa in the Kona District prior to his venture to the Kohalas and yet he let himself be misled at the time. Perhaps there was a note of *Ciridops* that resembled a note of the Akepa.

Previous Speculation on Possible Food Habits.—Wilson was told “that it feeds on the fruit of the Hawane palm” (Wilson and Evans 1893: 23). “It seems to have been found only in the neighbourhood of the Loulu palms (*Pritchardia*), the blossoms of which as well as the unripe fruit supplied it with food” (Perkins 1903: 405). The supposedly short, thick bill of *Ciridops* “lends credence to the statement that it had departed from the nectar-feeding habits of its relatives and subsisted on fruit” (Amadon 1950: 205). If *Ciridops* were frugivorous “fruits of the palm *Pritchardia* are claimed to be its food source; if so, one of the smaller-fruited species of *Pritchardia* is to be suspected” (Carlquist 1974: 162). “The short, straight beak of *Ciridops*, now extinct, is believed to have been adapted for a diet of palm fruits” (Carlquist 1982: 9). Fruit of some or all *Pritchardia* is too large “to have been swallowed whole” by *Ciridops* (Pratt 2002a: 5), which has

neither a particularly wide gape nor any adaptations whatever for crushing or manipulating large objects with the bill. Munro (1892) records the last specimen being shot “while feeding on the lo[u]lu berries which abound in that place” he also noted that the fruits in that area were some 20 mm in diameter, which is much too large for a *Ciridops* to eat except for small pieces of exocarp and no such food was found in the stomach of that same bird.

“No justification exists, however, for Amadon’s statement (1950: 223) that ‘.... some drepaniids that rarely or never take nectar, such as... and *Ciridops anna*, still have a tubular tongue’ [italics Bock’s]. So little is known about the feeding habits of *Ciridops*, that no one knows whether or not this bird fed on nectar. In the absence of any contrary factual information, I would conclude from its tongue morphology that *Ciridops* fed on nectar at least during part of the year” (Bock 1972: 75). I concur that it would have been unlikely that *Ciridops* did not take nectar when it was available, considering that many birds with no special adaptations for nectarivory are known to feed opportunistically on nectar (Fisk and Steen 1976, Franklin 1999). Speculation that *Ciridops* actually fed on fruit or nectar of *Pritchardia* palms based solely on the Hawaiian name is not supported by either the gut contents of the single fluid specimen nor by the morphological adaptations of the genus.

Gizzard Contents and Their Interpretation.—The gizzard in the alcoholic trunk specimen (BMNH 1939.12.9.58) had been slashed open by some previous examiner and could be seen to be crammed with food. The contents were carefully removed and later identified by workers skilled in identifying food items from droppings obtained in field studies of Drepanidini. The overall insectivory indicated for *Ciridops* was mentioned briefly by Scott et al. (1986: 156, and cited by Pratt 2005: 275) based on communication from me concerning these findings: 1 adult lepidopteran (wing scales only), 13 adult psyllids (Hemiptera, jumping plant lice), 38 psyllid eggs, three adult psocids (Psocoptera, bark lice), 26 adult ‘*Drosophila*-like’ Diptera, 2 mites (Acari), 1 spider, 6 seeds of unknown fruit, 1 anther? (C. P. Ralph in litt. to Olson 30 Jun 1981).

This collection of arthropods is similar to the food items taken by other drepanidines in forest ecosystems on the island of Hawaii, including Apapane (Fancy and Ralph 1997), Iiwi (Fancy

and Ralph 1998), Amakihi (*Loxops virens*; Lindsey et al. 1998), and Akepa (Lepson and Freed 1997). The first three are specialized nectar feeders and Akepa feed occasionally on nectar as well. Nectar, however, provides no protein so that even the most nectarivorous of birds, such as hummingbirds (Trochilidae), must feed on insects and spiders as well.

The arthropods fed on by *Ciridops* and many other drepanidines are probably dispersed nearly throughout the forest ecosystems on Hawaii. Thus, it may not be so much a matter of specializing on a particular kind of prey as becoming adapted to extract widely available generalized prey from particular niches within the ecosystem. *Ciridops* differed from all of its relatives in having strong feet and leg muscles that I hypothesize evolved for moving vegetable matter that accumulated in the axils of palm fronds. It may have fed on the same kinds of insects and spiders taken by Apapane and Iiwi, but it could gain access to them in places that could not be exploited by species whose hindlimbs were adapted solely for perching.

DISTRIBUTION AND ECOLOGY OF THE GENUS *CIRIDOPS*

Stejneger (1900: 72) wondered why *Ciridops*, along with *Viridonia*, *Loxioides*, *Rhodacanthis*, and *Chloridops*, should be confined to Hawaii and not have representatives on the other islands. Carlquist (1974: 129) considered that “the rarity and early extinction of some of the Hawaiian honeycreepers may have left gaps in our geographical distribution; *Ciridops* might have occurred on islands other than the island of Hawaii, for example.” He could hardly have foreseen how the fossil record would completely upend everything previously thought to be known about the distribution of Hawaiian birds. The only direct evidence of the distribution of *Ciridops* comes from the scant historical record and from fossils (Fig. 8).

Because of repeated hearsay reports of the Ula-i-hawane, Wilson ventured that “I have little doubt that it will be found, perhaps in some numbers, in the upland region of the interior, which I was unable to explore....My friend Mr Francis Spencer, writing to me quite recently [presumably about 1892], says that his natives had seen the bird in the swampy forest-region above Ookala [Keanakolu District according to Banko (1987: 248)] on Hawaii, and his description leaves

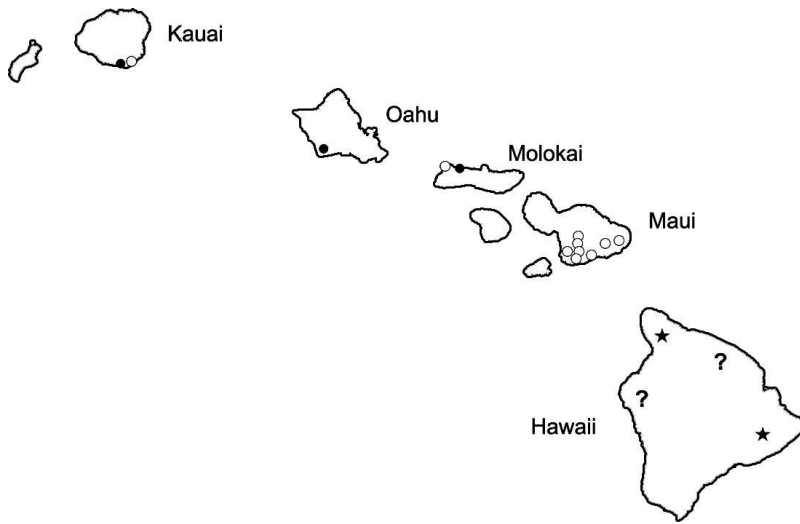


FIG. 8. Outline map of the Hawaiian Islands showing the known distribution of the genus *Ciridops*. Stars indicate the general localities where the historic specimens were taken, whereas question marks represent dubious records—that in the west is the Kona District (Perkins 1903) and that in the east is the Ookala area (Wilson and Evans 1893). Solid circles indicate sites where fossils of *Ciridops* have been recovered (that on Oahu includes several separate but adjacent sites); open circles indicate fossil sites with small passerines but lacking remains of *Ciridops*.

no doubt of its identity” (Wilson and Evans, 1893: 23). It is uncertain why Perkins (1903: 405) regarded *Ciridops* to have been “widely distributed on the island of Hawaii... and to have inhabited both the Kona and Hilo districts as well as the Kohala mountains.” I know of no other information concerning *Ciridops* in the Kona District. Perhaps Perkins was told that by a local source that he failed to mention or surmised a wider range based on the distribution of *Pritchardia*, which he noted had persisted into the late 19th century “in the dense forests above Hilo,” and “in the Kohala mountains and the Kona district.” There is no historic record of *Ciridops* from the Kona District, where several species of birds were last known before becoming extinct (e.g., Olson 1999a). Important fossils of passerines have been discovered in lava tubes on Hawaii (e.g., *Hemignathus vorpalis*, James and Olson 2003), but the fossil record on that island is sporadic and incomplete and many historically known birds have not yet been found as fossils, including *Ciridops*.

The accounts of Munro (1892) and Palmer (Rothschild 1893) describe searching for *Ciridops* in the Kohala Mountains. At the place where the last specimen had been taken shortly before by native hunters, Palmer noted only eight *Pritchardia* palms, and where four of them grew

together was the spot the last *Ciridops* was found (Rothschild 1893: Diary 7). They made an unsuccessful search for the bird at elevations above this point and at 1,200 m and above conditions were described as “almost living in the water” because of heavy rain and the temperatures were so low that they gave up the pursuit (Rothschild 1893: Diary 7). Thus, perhaps, arose the misperception that *Ciridops anna* was an inhabitant of “montane forest” (e.g., AOU 1998: 677). The cold, wet Kohala Mountains were probably submarginal habitat for *Ciridops* at best, much as the last few struggling individuals of *Melamprosops phaeosoma* passed out of their miserable existence in the dank slopes of windward Haleakala on Maui, when the fossil record shows that the species thrived at lower elevations on the drier leeward slope of the mountain.

In contrast with Hawaii, the fossil record on Maui is extensive and reasonably comprehensive as far as it goes; yet no fossils of *Ciridops* are known (James and Olson 1991). This may, however, reflect the fact that no productive fossil sites have yet been found in the lowlands of Maui, the lowest site producing quantities of predator-accumulated passerine fossils being Puu Naio Cave at 305 m elevation (James et al. 1987). If *Ciridops* did occur on Maui, as its

presence on Hawaii and Molokai would make probable, the birds were probably confined to lowland habitats.

Fossils of *Ciridops*, apparently referable to *C. anna* on Molokai, were found in the Moomomi Dunes (Olson and James 1982) where suitable forest habitat was probably adjacent at the time of deposition, whereas no fossils of *Ciridops* were found in the dune deposits at Ilio Point, a particularly isolated locality in a harsh, arid part of the island where probably only beach scrub habitat was able to persist. Given that *Ciridops* was definitely present on Molokai, it seems likely that a representative of the genus would have been on Lanai as well, although on that island the fossil record is scant (Dove and Olson 2011) and as yet includes no passerines.

On Oahu, a species of *Ciridops* is fairly abundantly represented in the sinkhole deposits in the southwestern part of the island at Barbers Point. The bill and hindlimb bones appear to be somewhat shorter than in *C. anna* and it should perhaps be recognized as a separate species but has not yet been named (James and Olson 1991).

The fossil species *Ciridops tenax* James and Olson (1991) was described from the Makawehi dune deposits in southeastern Kauai, where the diversity of species of various passerines indicates the presence of adjacent dry lowland forest. Yet not one bone of *Ciridops tenax* has yet been found in the Quaternary lake deposits excavated at Maha'ulepu, about 2 km to the east of the Makawehi dunes, despite a great abundance of fossil material, including hawks and owls, and the exceptional diversity of species and quality of preservation (Burney et al. 2001). This suggests a rather strong habitat avoidance by *Ciridops tenax*. Although *Pritchardia* palms were present and abundant at Maha'ulepu, the flora was extremely diverse, including several species of trees now restricted to upland localities where they are evidently relicts. The overall impression of the environment at Maha'ulaepu is a diverse, moist, closed-canopy forest. Therefore, the habitat preference of *Ciridops* may have been for drier, more open habitat in which *Pritchardia* grew in monospecific stands.

Ciridops tenax may be the most primitive species of the genus because of its apparently less specialized hindlimb elements. Kauai is the oldest of the islands on which *Ciridops* was known to occur, suggesting that the genus may have originated there and spread eastward with the formation of the younger islands of the main Hawaiian chain.

The available evidence suggests that one form or another of *Ciridops* probably occurred throughout all the main Hawaiian Islands, although confirming its presence on Maui would certainly be desirable. The fossil record also shows that potential avian predators occurred throughout the range of *Ciridops*. The extinct, long-legged, bird-eating owls of the genus *Grallistrix* are known from Kauai, Oahu, Molokai, and Maui, but apparently did not occur on Hawaii (Olson and James 1991). The presence of fossils of *Ciridops* in the deposits on Kauai, Oahu, and Molokai is almost certainly attributable in whole or in part to those owls and bones of *Ciridops* were found in what was clearly an owl pellet on Molokai (Olson and James 1982). The Hawaiian Hawk (*Buteo solitarius*) of the island of Hawaii is known from bones of the same or very similar species from Molokai, Oahu, and Kauai, and small forms of *Circus* adapted for catching birds are known from fossils on Molokai and Oahu (Olson and James 1991). Thus, the species of *Ciridops*, like the other small passerines that shared their habitat, would have had to have as keenly evolved predator-avoidance behavior as any of their mainland ancestors.

Assuming a close, if not totally dependent, relationship between *Ciridops* and loulou palms (*Pritchardia*), we may extrapolate more about the probable inter- and inraisland range and habitat preferences of the birds, albeit with a certain degree of circularity, based on information on *Pritchardia* from Hodel (2007). The apparent diversity of *Pritchardia* is centered on the Hawaiian Islands, although there are scattered outliers in Fiji, Tonga, Cook Islands, and the Tuamotus whose distribution suggests there were probably widespread human-caused prehistoric extinctions elsewhere in Oceania. The nominal 23 species in the Hawaiian Islands consist almost entirely of allopatric populations most of which are severely restricted in range and now often consist of only a few living individuals. Specific characters are extremely variable and are usually only useful for defining species when used in combination. Only three species occur on more than one island and all of those occur on Maui Nui, which included the combined islands of Maui, Molokai, and Lanai during lowered sea levels of glacial periods.

Pritchardia occurs naturally now on all the main Hawaiian Islands except the small, ecologically devastated island of Kahoolawe, and also on the remote island of Nihoa. The plants may occur

in dry to very wet forest but not above 1,400 m and probably constituted a dominant aspect of the vegetation only in lowlands. Evidence of this comes from Holocene fossil pollen on Oahu, and pollen and seeds on Kauai, indicating that *Pritchardia* was one of the most prevalent plants in the diverse lowland floras of those islands (Athens et al. 1992, Athens 1997, Burney et al. 2001). However, *Ciridops* did not necessarily occur in all places where *Pritchardia* grew, as at Maha'ulepu on Kauai, and the birds may have preferred areas in which palms grew practically to the exclusion of other forest cover (Fig. 9). Nearly monocultural stands may have been patchily distributed resulting in patchy distribution of *Ciridops* on Kauai and Molokai and perhaps contributing to our failure as yet to find *Ciridops* anywhere on Maui.

EXTINCTION

Destruction of lowland habitats (Olson and James 1982) by burning and clearing for agriculture and introduction of the seed predator *Rattus exulans* following Polynesian colonization, doubtless gave rise to the obviously relictual distribution and extinction or near extirpation of populations of *Pritchardia*, and probably explains the disappearance of *Ciridops* everywhere but on Hawaii during the prehistoric period. After European colonization, the introduction of grazing and browsing ungulates, additional species of rats and mice as well as carnivores such as dogs and cats, and alien species of birds with their diseases, accelerated the destruction of Hawaiian habitats and biota.

By the late 1800s on Hawaii, *Pritchardia* palms seemed "to have been always of sparse or local distribution, and still exist singly or in scattered clumps in the dense forest above Hilo, where I have often observed them, as well as in the Kohala mountains and the Kona district" (Perkins 1903: 405). Hartlaub (1896a, b) included *Ciridops anna* among recently extinct or threatened species, affirming Newton's (1892) statement that it was 'truly native,' and remarking that the published illustration left a strange impression (Hartlaub 1896b: 26).

Rothschild (1900: 183) considered the species to be "one of the rarest in the world," but only 7 years later listed it under the category "quite extinct" (Rothschild 1907a: 200). Amadon (1944: 12) remarked that "The speedy disappearance of this bird is puzzling. Possibly it was on the verge of



FIG. 9. The isolated and protected islet of Huelo, off the northern coast of Molokai, showing one of the few remaining nearly pure stands of loulu palm (*Pritchardia*). This stand has survived due to the absence of seed predators such as rodents and pigs, and protection from human disturbance such as fire and cultivation. Similar patchy monocultural stands of *Pritchardia* may have been the preferred habitat of the species of *Ciridops* in lowlands of the Hawaiian Islands prior to the arrival of humans. Photograph of *P. hillebrandii* by Donald R. Hodel, copyright 2006.

extinction when discovered." Greenway (1958) regarded it as extinct prior to the 1950s. Possible sight and sound records mentioned from the island of Hawaii about 1937 (Banko 1987: 240) are not credible. The extinction of *Ciridops anna* was considered to have preceded the extinctions caused when avian malaria in the Hawaiian Islands reached epizootic proportions after 1920 (van Riper et al. 1986).

From both Munro's (1892) and Palmer's (Rothschild 1893) journals, it is evident that in 1892 *Ciridops anna* was beyond extremely scarce. That the local hunters Palmer recruited in his quest for this bird were highly motivated is indicated by Palmer's account book (Bishop

Museum Archives), which he kept in minute detail with every indication of scrupulous honesty. The last entry for 13 February 1892 is “Ulaaihawane specimen [\$]50.00.” At that time a payment of fifty dollars for a single specimen of bird would have been a truly extraordinary amount that must have excited attention throughout the island. Palmer used a conversion rate of £1 British sterling = ~\$4.80, but there is probably little use in trying to comprehend the 1892 value of \$50 in Hawaii in current dollars or pounds sterling. More useful is an indication of what that amount would purchase locally then in goods and services. The next entry in Palmer’s account book was “Purchas[e] one horse [\$]60.00,” when a horse was probably the greatest single expense he had in the field. At the same time, he was paying Munro, a New Zealander, \$25.00 per week for physically demanding but diligent and skilled labor. For local laborers, \$50.00 must have represented an astronomical sum and the offer of such remuneration is a near certain indication that no more of the birds could be obtained regardless of the amount of effort expended. As further demonstration of just how much Rothschild must have desired specimens of *Ciridops*, a little over 2 months later Palmer paid half as much (\$25.00 on 20 Apr) for a living specimen of the Hawaii Mamo, which, like *Ciridops anna*, was the last of its kind ever taken. Without that last specimen of *Ciridops*, however, our much-expanded knowledge of the morphology of the genus would have gone unknown. Thus, in hindsight, \$50 for the last *Ciridops anna* may have been one of most fortunate purchases Walter Rothschild ever made.

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