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INTRODUCTION

The Hawaiian honeycreepers are a monophyletic group of the Carduelinae (Aves: Fringillidae) endemic to the Hawaiian Islands. They were traditionally classified as a family of their own (Drepanididae), but more recently as a subfamily (AOU 1983, 1998) of Carduelinae, and now a branch embedded within the Carduelinae (Zuccon et al. 2012, Chesser et al. 2013). Along with Darwin's finches of the Galapagos, they are the "textbook example" of insular adaptive radiation. With species that span and even expand the full range of passerine variation (Ziegler 2002, H. D. Pratt 2005, 2010b; T. K. Pratt et al. 2009), their classification holds interest well beyond their geographic distribution and beyond interest in other cardueline taxonomy. Unfortunately, the alpha taxonomy (Table 1) of the Hawaiian honeycreepers has been rather confusing. In fact, the only names for Hawaiian carduelines that have remained unchanged and unambiguous over time are the English ones derived as loan words from Hawaiian, making familiarity with those names a prerequisite for understanding the technical literature or making sense of taxonomic turbulence.

HISTORICAL PERSPECTIVES

James (2004) reviewed the systematic history of the Hawaiian honeycreepers (often nicknamed “dreps”) up to the most recent decade. Since Amadon’s (1950) classic specimen-based monograph, the first to apply the modern biological species concept (Mayr 1942) to the group, three main schools of thought have offered revisions. Pratt’s (1979) earliest effort, first published with a few changes in Berger (1981), was the first since Perkins (1903 [2012]) to incorporate behavioral and vocal data, including the first sound recordings (Pratt 2009a) of many species (archived in the Macaulay Library, Cornell Laboratory of Ornithology), as well as studies of breeding biology and ecology (Eddinger 1970, 1972a, b; van Riper 1975, 1978, 1980, 1987). The AOU (1983) adopted this taxonomy for the 6th edition of its checklist, although some species splits (Pratt 1989b; 1992b; Pratt et al. 1987) were only accepted later (AOU 1998).

Almost simultaneously, Olson and James (1982) introduced a different classification, later refined (Olson and James 1991, 1995; James and Olson 1991), based on their work with newly discovered Holocene Hawaiian bird remains. They also developed pioneering techniques for extracting anatomical data from study skins (Olson et al. 1987), which led to James’s (2004) landmark monograph that featured a comprehensive survey of drepanidine osteology and a phylogeny that places “fossil” taxa into the context of historically known species with which they were contemporaneous (Olson and James 1984, Burney et al. 2001).

Following the discovery of PCR in the late 1980s, molecular data became increasingly important in honeycreeper systematics, but in the early stages produced some enigmatic results that challenged conventional beliefs. Limited taxon sampling and inconsistencies among early studies (compare, for example, Johnson et al. 1989; Tarr and Fleischer 1995; Feldman, in Freed 1999; and Fleischer et al. 1998) led to skepticism of results that challenged well-supported hypotheses based on traditional methods (Pratt 2001). More robust and inclusive molecular studies (Reding et al. 2008, Lerner et al. 2011) have solved many of these problems, but at the time, controversies raged that sometimes became acrimonious (see James 2001). However, both James (2004) and Pratt (2005) stated the belief that consensus would come when molecular studies included all or nearly all taxa and achieved consistent results.

TABLE 1. Comparison of this study with three historically influential taxonomies of Hawaiian honeycreepers. Note: Generic initial abbreviations read vertically in columns.

English name	**Perkins 1903**	**Amadon 1950**	**AOU 1998**	**This study**
Poo-uli	N/A	N/A	*Melamprosops phaeosoma*	*Melamprosops phaeosoma*
Oahu Alauahio	*Oreomyza maculata*	*Loxops m. maculata*	*Paroreomyza maculata*	*Paroreomyza maculata*
Kakawahie	*O. flammea*	*L. maculata flammea*	*P. flammea*	*P. flammea*
Maui Alauahio	*O. montana*	*L. maculata montana*	*P. montana*	*P. montana*
Akikiki	*O. bairdi*	*L. maculata bairdi*	*Oreomystis bairdi*	*Oreomystis bairdi*
Laysan Finch	*Telespyza cantans*	*Telespyza c. cantans*	*Telespiza cantans*	*Telespiza cantans*
Nihoa Finch	N/A	*T. cantans ultima*	*T. ultima*	*T. ultima*
Greater Koa Finch	*Rhodacanthis palmeri*	*P. palmeri*	*Rhodacanthis palmeri*	*Rhodacanthis palmeri*
Lesser Koa Finch	*R. flaviceps*	*P. flaviceps*	*R. flaviceps*	*R. flaviceps*
Kona Grosbeak	*Chloridops kona*	*Chloridops kona*	*Chloridops kona*	*Chloridops kona*
Palila	*Loxioides bailleui*	*Psittirostra bailleui*	*Loxioides bailleui*	*Loxioides bailleui*
Ou	*Psittacirostra psittacea*	*Psittirostra psittacea*	*Psittirostra psittacea*	*Psittirostra psittacea*
Lanai Hookbill	N/A	N/A	*Dysmorodrepanis munroi*	*Dysmorodrepanis munroi*
Kauai Akialoa	*Hemignathus procerus*	*Hemignathus procerus*	*Hemignathus ellisianus*	*Akialoa procerus*
Oahu Akialoa	*H. lichtensteini*	*H. obscurus ellisianus*	*H. ellisianus*	*A. ellisiana*
Maui-nui Akialoa	*H. lanaiensis*	*H. o. lanaiensis*	*H. ellisianus*	*A. lanaiensis*
Lesser Akialoa	*H. obscurus*	*H. o. obscurus*	*H. obscurus*	*A. obscurus*
Kauai Nukupuu	*Heterorhynchus hanapepe*	*H. lucidus hanapepe*	*H. lucidus*	*Hemignathus hanapepe*
Oahu Nukupuu	*Heterorhynchus. lucidus*	*H. l. lucidus*	*H. lucidus*	*H. lucidus*
Maui Nukupuu	*Heterorhynchus. affinis*	*H. l. affinis*	*H. lucidus*	*H. affinis*

TABLE 1. Continued…

English name	**Perkins 1903**	**Amadon 1950**	**AOU 1998**	**This study**
Akiaploaau	*Heterorhynchus wilsoni*	*H. wilsoni*	*H. munroi*	*H. wilsoni*
Maui Parrotbill	*Pseudonestor xanthophrys*	*Pseudonestor xanthophrys*	*Pseudonestor xanthophrys*	*Pseudonestor xanthophrys*
Greater Amakihi	*Viridonia sagittirostris*	*Loxops sagittirostris*	*Hemignathus sagittirostris*	*Viridonia sagittirostris*
Anianiau	*Chlorodrepanis parva*	*L. parva*	*Magumma parva*	*Magumma parva*
Hawaii Creeper	*Oreomyza mana*	*L. maculata mana*	*Oreomystis mana*	*Manucerthia mana*
Akekee	*Loxops caeruleirostris*	*L. coccineus caeruleirostris*	*Loxops caeruleirostris*	*Loxops caeruleirostris*
Oahu Akepa	*L. rufa*	*L. coccineus rufa*	*L. coccineus*	*L. wolstenholmei*
Maui Akepa	*L. ochraceus*	*L. coccineus ochraceus*	*L. coccineus*	*L. ochraceus*
Hawaii Akepa	*L. coccineus*	*L. c. coccineus*	*L. coccineus*	*L. coccineus*
Kauai Amakihi	*Chlorodrepanis stejnegeri*	*L. virens stejnegeri*	*Hemignathus kauaiensis*	*Chlorodrepanis stejnegeri*
Oahu Amakihi	*C. virens chloris*	*L. virens chloris*	*H. flavus*	*C. flavus*
Hawaii Amakihi	*C. virens virens*	*L. virens virens*	*H. virens*	*C. virens*
Black Mamo	*Drepanorhamphus funerea*	*Drepanis funerea*	*Drepanis funerea*	*Drepanis funerea*
Hawaii Mamo	*Drepanis pacifica*	*Drepanis pacifica*	*Drepanis pacifica*	*Drepanis pacifica*
Iiwi	*Vestiaria coccinea*	*Vestiaria coccinea*	*Vestiaria coccinea*	*D. coccinea*
Apapane	*Himatione sanguinea*	*Himatione sanguinea*	*Himatione sanguinea*	*Himatione sanguinea*
Laysan Honeycreeper	*H. freethi*	*H. s. freethii*	*H. sanguinea*	*H. fraithii*
Akohekohe	*Palmeria dolei*	*Palmeria dolei*	*Palmeria dolei*	*Palmeria dolei*
Ula-ai-hawane	*Ciridops anna*	*Ciridops anna*	*Ciridops anna*	*Ciridops anna*

RESOLVING POINTS OF DISPUTE

Monophyly of the group. —Two synapomorphies, a squared-off tongue base without backward projections, and what has come to be called "drepanidine odor", define the core clade of Hawaiian honeycreepers (Pratt 1979, 2005). However, two taxa, *Melamprosops* (Poo-uli) and *Paroreomyza* (alauahios and Kakawahie), lack both, and on that basis Pratt (1992a, b) suggested that they might not be part of the honeycreeper radiation. Tarr and Fleischer (1995) found some equivocal molecular evidence that suggested that *Paroreomyza* might, indeed, represent an independent colonization of Hawaii. Later, Fleischer et al. (2001), using mtDNA sequence data and osteological characters, found that both *Melamprosops* and *Paroreomyza* were members of the honeycreeper clade, but their position within it was unclear. Analysis of 39 phenotypic characters (Pratt 2001) also upheld the monophyly of the group, and James's (2004) finding that certain cranial features united the whole clade settled the matter (Pratt 2005). Pratt (2001, 2005) considered both *Paroreomyza* and *Melamprosops* to be basal offshoots that diverged from the rest of the clade before the defining synapomorphies evolved, and recent molecular studies have upheld that finding (Reding et al. 2008, Lerner et al. 2011).

Relationship of *Oreomystis* and *Paroreomyza*. —Although *Paroreomyza* lacks the features that define the core honeycreeper clade (Tarr and Fleischer 1995, Pratt 2001, 2005; James 2004), *Oreomystis* has them both, which would suggest that these two genera belong to different clades, with *Paroreomyza* outside the main radiation of the group and *Oreomystis* within it. Nevertheless, Johnson et al. (1989), Feldman (in Freed 1999), and Fleischer et al. (1998) found a sister relationship between *Oreomystis* and *Paroreomyza*, and Fleischer et al. (2001) added osteological support for that hypothesis. Pratt (2001) considered these genera to be independent sequential basal offshoots in the honeycreeper radiation, as corroborated by Reding et al. (2008) in a robust molecular study that included both mtDNA and nuclear genes. Enigmatically, the same lab (Lerner at al. 2011) subsequently produced a topology in which *Oreomystis* and *Paroreomyza* are again sister genera, a topology that would require seemingly impossible reversals or duplications of the two complex synapomorphies that unite the core honeycreeper clade. Perhaps this is a case in which a cladistic analysis of phenotypic data can help to resolve enigmatic molecular results. Interestingly, the two lineages of Galapagos warbler finches (*Certhidea)*, which also are a basal thin-billed branch in a finchlike radiation, present a similar situation, with phenotypic data informing interpretations of conflicting or unexpected molecular topologies (Grant & Grant 2008: Fig. 10.3).

Systematic position of the Hawaii Creeper. — The Akikiki (*O. bairdi*) and the Hawaii Creeper share a large suite of seemingly synapomorphic characters of coloration, plumages, bill shape, tongue structure, vocalizations, social behavior, and ecology (Pratt 1992b, 2001; Foster et al. 2000, Lepson and Woodworth 2002), and therefore have long been regarded as congeners (Pratt 1979, 1992b; AOU 1998). However, osteology suggests that the creeper, but not the Akikiki, is instead related to the amakihis (James and Olson 1991, James 2004). Early mtDNA sequence studies (Fleischer et al. 1998, 2001) suggested a relationship between the akepas and the Hawaii Creeper, again with no close relationship to the Akikiki. Addition of nucDNA to the dataset finally brought representatives of all three “schools” together (Reding et al. 2008) and convincingly supported the hypothesis that the striking similarities of the Hawaii Creeper and the Akikiki are, after all, “one of the most remarkable and noteworthy examples of convergence ever demonstrated” (Pratt 2001:96). The grouping of the Hawaii Creeper with the akepas has now been upheld by further anatomical (Olson 2009) and genetic (Lerner et al. 2011) data, and the AOU (Chesser et al. 2013) moved it from *Oreomystis* to *Loxops*. Lerner et al. (2011) showed the Hawaii Creeper as a basal branch of its clade, which is sister to the amakihis. Reding et al. (2008) stated that further research would be necessary to determine whether the creeper deserved a monotypic genus, but Pratt (2009b), on the basis of its different morphotype as compared to the cross-billed akepas, named the new genus *Manucerthia* for it. Lerner et al. (2011) estimated the creeper/akepa divergence time as 1.9 Ma, earlier than the divergences of several other currently recognized honeycreeper genera. (As discussed below, very rapid speciation among island birds may justify recognition of genera younger than continental ones.) Interestingly, the Hawaii Creeper, whose tongue is virtually identical to that of *O. bairdi* and unlike any other drep tongue, is the only member of the core clade of honeycreepers to entirely lack their distinctive tubular tongue, a remarkable evolutionary reversal, and further reason for separating it generically from the akepas and amakihis, both of which have typical tubular tongues (Pratt 2005).

Generic limits among drepanidine finches. — Because so many of them are extinct and poorly known (James and Olson 2005, 2006; Olson 1999, 2014), the finch-billed dreps are the least resolved group within the radiation. Pratt (2001) included all except *Psittirostra* in a single clade and suggested the possible merger of *Loxioides* (palilas) and *Chloridops* (Hawaiian grosbeaks). James (2004), in contrast, recognized two finch clades: *Telespyza*/*Loxioides* and *Chloridops*/*Rhodacanthis* (koa finches). Until the relationships of these genera are better resolved, perhaps by ancient DNA (the majority of new species described from subfossil bones have been finches), maintaining all of the nominal genera, as recommended by James and Olson (1992) and James (2004), seems prudent. The unique autapomorphic genera *Psittirostra* (Ou) and *Dysmorodrepanis* (Lanai Hookbill; James et al. 1989) are likely allied with the drep finches, but exact relationships are unclear. James (2004) placed them in a separate clade with the Maui Parrotbill, but, as discussed next, the parrotbill is probably not a drepanidine finch.

Systematic position of the Maui Parrotbill. — Both molecular (Fleischer et al. 1998, 2001) and phenotypic characters suggest that the Maui Parrotbill *Pseudonestor xanthophrys*, which has long been grouped with the drepanidine finches because of its heavy bill (Amadon 1950, Berger 1981, AOU 1983, James 2004), is instead, as Pratt (1979) first suggested, allied with the Akiapolaau, with which it shares a unique jaw muscle (Zusi 1989), similar foods and feeding movements (Simon et al. 1997), plumage color and sequence (Berlin et al. 2001), breeding ecology (Simon et al. 2000), and apparently synapomorphic juvenile “beacon” calls (T. K. Pratt et al. 2001; Pratt 2005). Its finch-like characters appear to be superficial, a secondary result of thickening of the bill, and another example of convergence within the honeycreeper radiation. Bock (1970) showed how a parrot-like bill could be derived directly from a “heterobill”. Although James (2004) allied *Pseudonestor* with *Psittirostra*, she could not refute the hypothesis that it was related to the heterobills. Pratt (2001) even suggested that it could be placed in *Hemignathus*, but later pointed out (Pratt 2009b) that doing so would violate the genus/morphotype equivalency among Hawaiian honeycreepers. As with the Hawaii Creeper, the parrotbill's tongue is not of the drepanidine tubular type. However, it resembles a developmental stage of the drep tongue (Pratt 2005) in which the lateral laciniae have not yet interlaced dorsally to form the tube (Bryan and Seale 1900), so it can easily be seen as a derivative, perhaps by neoteny (Pratt 2005), and is not as striking an evolutionary character reversal as the tongue of *Manucerthia*.

Composition of *Hemignathus*. —All original members of "greater *Hemignathus*" were birds with down-curved bills, "amakihi plumage" (Pratt 2001, 2005), short primary songs, and complex whisper songs (Pratt 1979). Although Amadon (1986) and Olson and James (1988, 1995) raised strong objections to it, the AOU (1998:673) considered the enlarged *Hemignathus* a natural group, subject to future genetic analyses, and James's (2004) osteological study included all of its components (plus, enigmatically, the "red-and-black" honeycreepers) in a single clade. "Greater" *Hemignathus* comprises four easily distinguished subgroups, Pratt's (2005) subgenera, based on bill morphology: *Hemignathus* sensu stricto (heterobills); *Akialoa* (the long-billed akialoas); *Chlorodrepanis* (the short-billed amakihis); and *Viridonia* (the arrow-billed Greater Amakihi). Pratt (2009b, 2010b) elevated these to full genera.

The first step in what turned out to be the dismemberment of the enlarged *Hemignathus* was the separation of *Magumma* (Anianiau), which was long associated with the amakihis, early naturalists even calling it the "Lesser Amakihi". Pratt (1979) kept it with the amakihis largely by default, but re-evaluation of its characters (Conant et al. 1998, Pratt 2001), as well as molecular data (Tarr and Fleischer 1993, Fleischer et al. 1998, 2001) showed it to be quite distinctive, as Banks et al. (2008) acknowledged. Note, however, that James (2004) still imbedded the Anianiau within the amakihis.

A similar re-evaluation of the Greater Amakihi (Pratt 2001, 2005) suggested that the monotypic *Viridonia* had also been mischaracterized by the few naturalists who studied it in life (Henshaw 1902, Perkins 1903). Its icterid-like bill barely meets the curved-bill criterion, and its feeding apparatus, with strong retroarticular processes used for gaping, is rather different from those of amakihis (Richards and Bock 1973). James (2004) associated *Viridonia* with the fossil genus *Aidemedia* (with which it might eventually be merged), in a clade that is sister to the akepas, which also are gapers. No genetic data on *Viridonia* have yet been published. If future research reveals *Viridonia* not to be a sister group to the amakihis, then a change of English name would be appropriate. Pratt (2005) suggested "Arrowbill" (a translation of the specific epithet *sagittirostris*) as an appropriate alternative.

Groupings of the remaining heterobills, akialoas, and typical amakihis are not controversial, but the relationships among these groups are unresolved. Because the akialoas look much like giant long-billed amakihis (Pratt and Pratt 2001), Pratt (1979) regarded the two as sister groups. From osteological data, James and Olson (1995) and James (2004) classified akialoas in their own genus, *Akialoa*, as a sister group to *Hemignathus* (sensu stricto), and the *Chlorodrepanis* amakihis (including Anianiau) as sister to the "red-and-black" honeycreepers, a relationship supported otherwise only by Raikow (1977). Lerner et al. (2011) showed amakihis as a sister group to the akepas and

Hawaii Creeper, and nowhere near the "red-and-black" group. Pratt's (1979) "greater *Hemignathus*" is clearly not a monophyletic group, and here *Hemignathus* includes only the heterobills. With the amakihis placed in *Chlorodrepanis*, the specific epithet for the Akiapolaau can revert to the original *wilsoni*.

Composition of *Loxops*. —Amadon (1950) combined all of the short-billed insectivorous dreps into a massive and completely undiagnosable "greater *Loxops*". It included the akepas (*Loxops* sensu stricto), the amakihis, the Anianiau, and "the Creeper". Both the eclectic school (Pratt 1979) and the osteologists (Olson and James 1982, James and Olson 1991) removed "the Creeper" (*L. maculata* of Amadon) from it, and Pratt (1979) divided that conglomerate "species" into *Oreomystis* and *Paroreomyza*, with two and three species respectively, following Bryan and Greenway (1944). Osteology produced a similar result, except that James and Olson (1991) presciently retained one "subspecies" (Hawaii Creeper) in a still-large *Loxops*, which James (2004) eventually showed to be paraphyletic. The remaining components of "greater *Loxops"* (Greater Amakihi and Anianiau) were discussed under *Hemignathus*. Reding et al. (2008) and Lerner et al. (2011) provided genetic evidence that at least three remnants of Amadon's greater *Loxops* (amakihis, akepas, and Hawaii Creeper) do form a monophyletic group, so a future "not-so-much-greater *Loxops*" is conceivable.

Generic limits in the red-and-black clade. — The divergence of *Manucerthia* ca. 1.9 Ma occurred well before the ca. 1.6 Ma split between the curve-billed and straight-billed members of the nectarivorous red-and-black clade (age estimates from Lerner et al. 2011). Therefore, if *Manucerthia* is placed in *Loxops*, then *Vestiaria*, *Himatione*, and *Palmeria* must be combined for the taxonomy to have temporal symmetry (unfortunately we lack genetic data for the extinct and critically positioned *Drepanis* and *Ciridops*). Although the merger of all the red-and-black genera may eventually be justified, as R. L. Fleischer (pers. comm.) has suggested, it would upset the morphotype/genus equivalency, which has heuristic value, and would be premature given current knowledge.

On the other hand, keeping *Vestiaria* separate from *Drepanis* violates the morphotype/genus principle. Pratt (1979) first proposed the merger of these two sickle-billed genera, which can be diagnosed solely on what appear to be species-level color differences. Even so, Berger (1982) and AOU (1983) did not accept the merger, and even some subsequent authors who otherwise followed Pratt's (2005, 2010b) classification, maintained *Vestiaria* as separate (e. g. Gill & Donsker 2014). Interestingly, the color differences between the cardueline Red Siskin *Carduelis cucullata* and Black Siskin *C. atrata* parallel those of the Iiwi and Hawaii Mamo, yet no one would suggest putting them in separate genera on that basis. Note also that James (2004) found the mamos and Iiwi to be very similar osteologically. Amadon (1986) suggested that if *Vestiaria* and *Drepanis* were merged, then *Palmeria* and *Himatione* should be also, and Pratt (2001) found some support for that concept. The merger of *Palmeria* and *Himatione* would not strongly challenge the morphotype principle advocated here because their bills and feeding habits are similar, but their plumage differences are far more striking, involving structure and pattern as well as pigmentation, than those between the Iiwi and the mamos. Lerner et al. (2011) did not include *Drepanis* in their matrix, but James's (2004) results suggest that the split between

Drepanis and *Vestiaria* would likely be even more recent than the ca. 1.4 Ma divergence of *Palmeria* and *Himatione*. Generic limits are not based on age of divergence, but such criteria do provide a useful way to compare proposed genera among the Hawaiian honeycreepers.

SPECIES LIMITS

Following the custom established by the "modern synthesis" (Mayr 1942), Amadon (1950) combined many nominal honeycreeper species into large polytypic species. In fact, his "Creeper", which is now accepted as five species placed in three genera, may be the most egregious example ever of abuse of the polytypic species concept. Restoration to species rank of many taxa treated as subspecies by Amadon (1950) has now been widely accepted (AOU 1998, Pyle and Pyle 2009, Pratt 2010b, Gill and Donsker 2014) including the Laysan and Nihoa finches (Banks and Laybourne 1977, James and Olson 1991, Fleischer et al. 1998); Kauai Amakihi (Pratt 1979, 1989a; Pratt et al. 1987; Johnson et al. 1989; Olson and James 1991; Conant et al. 1998; Tarr and Fleischer 1994, AOU 1995); Oahu Amakihi (Tarr and Fleischer 1994, AOU 1995); Akekee (Pratt 1989b, AOU 1991, Lepson and Pratt 1997); alauahios and Kakawahie (Pratt 1979, 1992b; James and Olson 1991); Akikiki (Pratt 1992b, Foster et al. 2000), and the Hawaii Creeper (Pratt 1992b, Lepson and Woodworth 2002). All of these splits comply with Pratt's (2010a) criteria for biological species limits among allopatric island birds. However, discussed below are several suggested splits involving extinct, or near-extinct, forms that have not yet been accepted by any world checklist.

The nukupuus (*Hemignathus*) are known historically from Kauai (*hanapepe*), Oahu (*lucidus*), and Maui (*affinis*). The congeneric Akiapolaau was long thought to be the island of Hawaii's representative of the complex, but the recently discovered Giant Nukupuu (*H. vorpalis*) was sympatric with it into human times on that island (James and Olson 2003). Note that a study skin of a nukupuu reported from the same island (Olson and James 1994) may actually have come from Oahu (James and Olson 2003). All nukupuu taxa known from study skins have long been considered subspecies of *H. lucidus*, but Pratt and Pratt (2001) and T. K. Pratt et al. (2001) noted what they regarded as species-level color differences among them, and they suggested these taxa might be better regarded as separate species. R. C. Fleischer (pers. comm. in Pratt 2005) reported as yet unpublished large genetic distances among them. Pratt and Pyle (2000) believed that conflation of plumage characters of the three forms in field guides, which resulted from considering them conspecific, contributed to many false sight reports. Pratt (2005, 2010b) was the first modern author to recognize three species of nukupuu. The discovery of the Giant Nukupuu (James and Olson 2003) now suggests that the currently recognized single species might be paraphyletic, and given interisland plumage differences greater than those among the three species of amakihi (T. K. Pratt et al. 2009), recognition of three nukupuu species may be the most reasonable classification for now.

The akialoas have a tangled history at the species level. Bryan and Greenway (1944) combined them all as a single species. Current AOU (1998) taxonomy recognizes two, as did Amadon (1950), but the line between them shifted, based on comments by Pratt et al. (1987), from between Oahu and Kauai (AOU 1983) to between Maui and Hawaii (AOU 1998). The Kauai form survived into the 1960s, but the others were extinct before the 20th century, and none of their songs were ever recorded (Lepson and Johnston 2000; Pratt 2005). The few specimens from Lanai and Oahu are scattered among the world's museums, so that even accurate depiction of plumages has been problematic (Pratt 2005). Paleontological discoveries have complicated the picture. Olson and James (1995) described the Hoopoe-billed Akialoa *A. upupirostris* from bones found on Kauai and Oahu, where it was sympatric with historically known forms, and an as yet unidentified or undescribed large akialoa was sympatric with the Lesser Akialoa on Hawaii (James and Olson 2003). Given the uncertainty of relationships among them, Olson and James (1995) recommended the recognition of all four historically known forms (*stejnegeri* on Kauai, *ellisianus* on Oahu, *lanaiensis* on Maui-nui, and *obscurus* on Hawaii) as species, and Pratt (2005, 2010b) concurred. As with the nukupuus, such a taxonomy seems the most prudent for the time being because we simply do no know enough to form the hypothesis that any of the named taxa are conspecific.

The split of the Akekee from the Akepa, based on a convincing suite of potential isolating mechanisms (Pratt 1989b, AOU 1991), is not controversial, but whether the remaining three forms (*wolstenholmei* on Oahu; *ochraceus* on Maui; and *coccineus* on Hawaii) should be treated as subspecies of the Akepa or as three species is difficult to determine given the limited data available for two of them (Pratt and Pratt 2001, Pratt 2005). The Oahu bird is long extinct and known from few specimens, and the Maui birds were known in the 20th century from only a few sightings (Lepson and Freed 1997) and are also likely extinct (Pratt 2010b). Limited evidence suggests that the Maui Akepa and the Hawaii Akepa differed in nest placement, a key factor in splitting the Akekee from the Akepa (Pratt 1989b). Maui males resembled Hawaii birds in being brilliant orange, except that roughly half of adults had a distinctive mustard yellow color morph (Pratt 2005). Oahu males were a much darker brick red instead of orange. Females differed less than males among the three islands. These differences are certainly as large as those observed among several other species groups of honeycreepers. According to R. L. Fleischer (pers. comm. in Pratt 2005), preliminary unpublished molecular data indicate fairly large genetic distances among the forms, and Pratt (2010b) treated them as three species.

The Laysan Honeycreeper *Himatione fraithii* (see Pyle 2011 for spelling of the epithet) was endemic to Laysan Atoll in the Northwestern Hawaiian Islands, and was considered a species until Bryan and Greenway (1944) and Amadon (1950) classified it as a subspecies of Apapane. Such a classification overlooks several potential isolating mechanisms (Pratt and Pratt 2001, Pratt 2005, Pyle and Pyle 2009) and species-level anatomical differences (James and Olson 1991, Olson and Ziegler 1995). Pratt (2005, 2010b) and Pyle and Pyle (2009) restored it to species status. The Laysan Honeycreeper appears to be a full biological species by almost any standard.

PHYLOGENIES

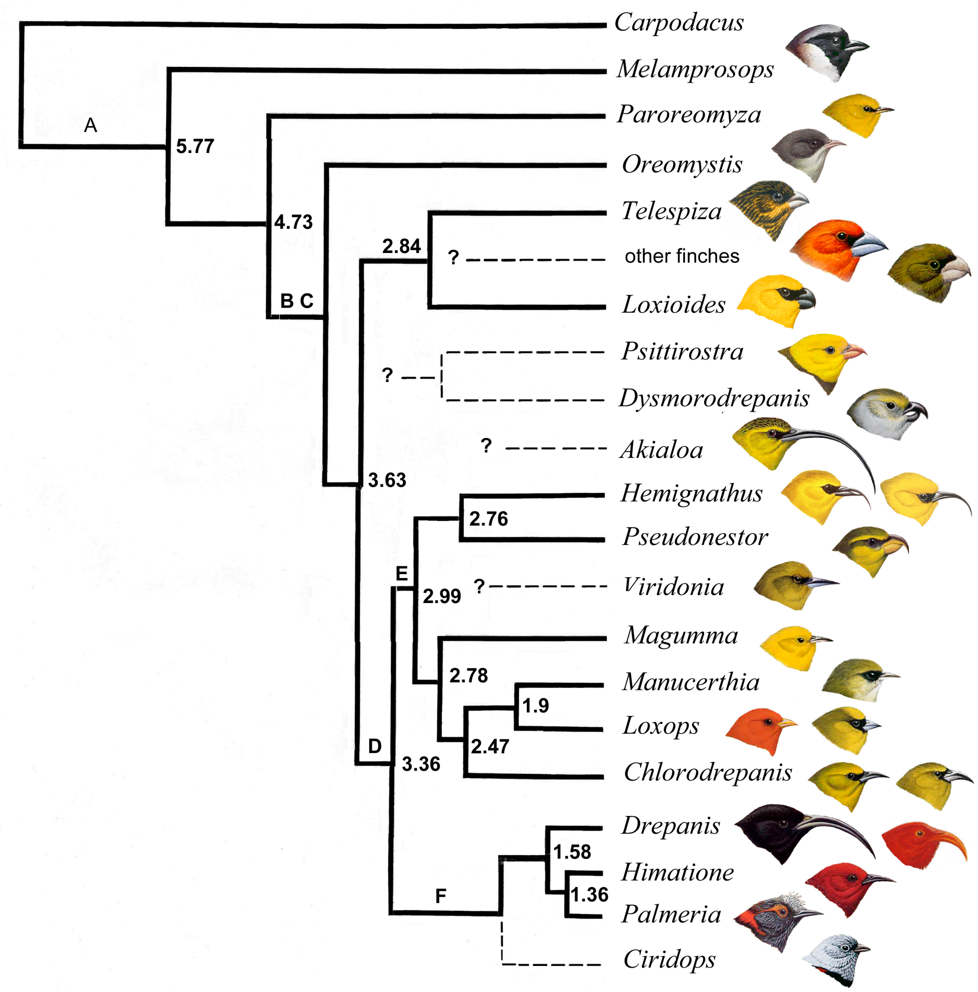
This proposal is for a taxonomy, not a specific phylogeny. However, the molecular phylogeny generated by Lerner et al. (2011) is fully compatible with these generic limits, and its terminal taxa can be labeled using them without any splits or repeats despite the fact that seven extinct but historically known genera are not included. Also, their topology corresponds reasonably well with Pratt's (2005, 2010b) sequence of genera except for the placement of *Chlorodrepanis*, *Manucerthia*, and *Oreomystis*, so it seems a consensus taxonomy, at least at the generic level, may now be possible.

Figure 1 depicts a possible branching sequence based on phylogenies of Reding et al. (2008) and Lerner et al. (2011). The basic framework (solid lines) is that of Lerner except that the topology involving *Paroreomyza* and *Oreomystis* is taken from Reding et al. (2008), which provides a more believable pattern relative to basic synapomorphies; and the node between the red-and-black clade and that of the "green" group of thin-billed dreps is rotated on its axis 180° so that the most recently diverged genera are at the end of the sequence, by convention. The column of generic names at the right may be read top to bottom as the recommended sequence of genera, but note that no phylogenetic pattern could be derived just from the sequence.

TAXONOMIC CONSENSUS AND THE FUTURE

Pratt (2009b) expressed the philosophy that genera are inherently artificial and designed for convenience; that they should at least be monophyletic; and they should be diagnosable morphologically. For the rapidly radiating Hawaiian honeycreepers, some classifications have favored large genera comprising multiple morphotypes (i.e. Amadon 1950, "greater *Psittirostra*"; Amadon (1950) and James (2004) "greater *Loxops*"; and Pratt 1979 and AOU 1983 "greater *Hemignathus*"). Others feature narrower genera that represent distinct and diagnosable morphologies (i.e. James and Olson 1991, James 2004 except for *Loxops*; Pratt 2005, 2010b). Pratt (2009b) came to believe that a classification for the Hawaiian honeycreepers that had more and smaller genera, keyed to morphotypes, would facilitate discussion of this rapid adaptive radiation, which, as stated earlier, has produced examples that span the entire range of passerine variation and would be phenotypically comparable to what mainland genera typically represent. The divergence times found by Lerner et al. (2011) for these genera would be much more recent than are typical for mainland passerine genera, indeed being comparable to divergence times for species (Tarr and Fleischer 1995). But just as with species, some genera are young and some are old, and recency of divergence, especially in archipelagic situations where evolutionary processes are clearly accelerated (Grant and Grant 2008, 2014; Andersen 2014), should not be used as a criterion for setting generic limits. In the well-known radiation of Darwin's finches of the Galapagos Islands, ca. 15 species classified in five genera, each representing a distinct morphotype, have evolved in less than 3 million years (Grant and Grant 2008). By the classification proposed here, the Hawaiian honeycreepers evolved more than 62 species in 26 genera (4 known only as subfossils) in less than 5 million years (Lerner et al. 2011), which seems roughly comparable, considering the richer ecological range available in Hawaii (Pratt 2005), the exponential nature of speciation, and the fact that no comparable paleontological record exists for Darwin's finches. In both radiations, the rapidity of speciation has been problematic in determining phylogeny (Tarr and Fleischer 1995, Zink 2002), and in both cases striking morphological variation has resulted from surprisingly little genetic differentiation (Tarr and Fleischer 1995, 1998; Grant and Grant 2008).

Figure 1: A diagrammatic representation of Hawaiian honeycreeper evolution. Solid lines are based on the phylogenetic topology of Lerner et al. (2011), with the branches leading to *Oreomystis* and *Paroreomyza* changed (see text) to agree with the branching sequence of Reding et al. (2008). Dashed lines indicate possible positions of historically extinct taxa for which molecular data are as yet unavailable. Numbers adjacent to nodes indicate time (Ma) of divergence given by Lerner et al. (2011). Capital letters indicate where key synapomorphies first appeared: A) flat cranial floor and associated anatomical features (James 2004); B) loss of backward-projecting "lingual wings" (Pratt 1979, 1992a, b); C) "drepanidine odor" (Perkins 1903; Pratt 1992a, b); D) drepanidine tubular tongue (Raikow 1977; Pratt 1979, James 2004); E) simple short primary songs, complex whisper songs (Pratt 2005); F) complex but not canary-like primary songs with metallic, reedy, and dissonant notes (Pratt 2005).



This consensus taxonomy was first published in *Handbook of the Birds of the World* (Pratt 2010b), but not in an accessible checklist format because historically extinct species were treated separately. It follows Pratt's (2005) monograph as modified (Pratt 2009b) in the light of subsequent genetic data (Reding et al. 2008), and produces a completely symmetrical taxonomy across the clade, with each genus representing a distinct morphotype. Interestingly, for the most recent comprehensive Hawaii checklist, Pyle & Pyle (2009) independently derived nearly identical generic limits (P. Pyle, pers. comm.). Various other checklists, including the IOC World Bird List (Gill & Donsker 2014) and the upcoming revised edition of the Howard & Moore world checklist (Dickinson 2003; E. C. Dickinson, pers. comm.) use similar classifications. This taxonomy differs substantially from that of the AOU (1998) as amended (Banks et al. 2008) in that it breaks up greater *Hemignathus* into four genera, recognizes the genus *Manucerthia*, and merges *Vestiaria* with *Drepanis*.

One advantage of this taxonomy is that it has the potential for long-term stability. Ongoing research on DNA extracted from museum specimens of extinct taxa is currently suspended because of factors external to the research itself (R. Fleischer, pers. comm.), and when we will have those results cannot be predicted. But whatever those findings, these basic generic limits would be unlikely to change significantly, although new phylogenies may suggest a rearrangement of the sequence. In other words, while the cards in the deck remain the same, they might be reshuffled. We may eventually want to fine tune a bit by combining some or all of the finch genera and merging *Palmeria* with *Himatione*, but that would only reduce the total genera by four at the most.

Could we designate fewer genera? Given current knowledge, we would have to maintain *Melamprosops*, *Paroreomyza*, and *Oreomystis* no matter what. We could then place all the drep finches in *Loxioides*, keeping *Psittirostra* (and probably *Dysmorodrepanis* because we don't know what else to do with it) separate. The rest of the radiation then falls into three clades, which we could designate as genera: *Hemignathus*, *Loxops*, and *Drepanis* (where the extinct *Akialoa*, *Viridonia*, and *Ciridops* might fall among these is largely irrelevant in this assessment). Or we could just call them all *Drepanis*! But what would we gain? Except in the case of the finches, such a reduction in number of genera would do away with the concept of genus/morphotype equivalency in the Hawaiian honeycreepers and thus destroy the heuristic value of such a classification. It would make comparisons with Darwin's finches, whose genera are tied to morphotypes, more strained, and would obscure the much broader adaptive radiation of the Hawaiian group.

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