

WHY THE HAWAI‘I CREEPER IS AN *OREOMYSTIS*: WHAT PHENOTYPIC CHARACTERS REVEAL ABOUT THE PHYLOGENY OF HAWAIIAN HONEYCREEPERS

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Abstract. A Phylogenetic Analysis Using Parsimony (PAUP) of 39 phenotypic characters of myology, osteology, tongue morphology, bill morphology, plumage and coloration, behavior, and ecology produced a tree that strongly supports, with a few exceptions, current American Ornithologists' Union classification of Hawaiian honeycreepers (Drepanidinae). These results are compared with those from three different biochemical and genetics laboratories and those of a cranial osteology study. The honeycreepers, including the aberrant genera *Melamprosops* and *Paroreomyza*, are shown to be monophyletic and a subgroup of the Fringillidae. The Maui Parrotbill *Pseudonestor xanthophrys* is related to thin-billed taxa rather than to the drepanidine finches. The genus *Hemignathus*, the present limits of which have been widely challenged, is shown to be strongly supported by a large suite of characters, except that the parrotbill may belong in it and the 'Anianiau (*H. parvus*) should be removed from it and placed in its own genus *Magumma*. *Hemignathus* can be divided into four or five subgenera. The generic pairs *Chloridops/Loxioides*, *Himatione/Palmeria*, and *Vestiaria/Drepanis* can justifiably be lumped as *Loxioides*, *Himatione*, and *Drepanis* respectively. The genera *Paroreomyza* and *Oreomystis* are not closely related, and the latter includes the Hawai'i Creeper (*O. mana*). Synapomorphies of the two species of *Oreomystis* include: lack of adult sexual dimorphism; lack of wing-bars; distinctive juvenal plumages; bill shape and coloration; foraging behavior; flocking behavior; juvenal begging calls; and a simple, narrow, nontubular tongue unique among honeycreepers. Hypothesized relationships of the Hawai'i Creeper with 'akepas (*Loxops*) based on mtDNA studies, or to 'amakihis (*H. virens* and relatives) based on osteology, are incompatible with hypotheses based on a wide range of other characters.

Key Words: Drepanidinae; Hawai'i Creeper; Hawaiian honeycreepers; *Hemignathus*; *Magumma*; *Oreomystis*; *Pseudonestor*.

The classification of the Hawaiian honeycreepers (Drepanidinae) has been controversial since the American Ornithologists' Union (AOU 1983) abandoned the longstanding classification of Amadon (1950) in favor of a new one based on Berger's (1981) use of my revision (Pratt 1979). This classification has been followed in most general references since, including Scott et al. (1986), Pratt et al. (1987), Sibley and Monroe (1990), and the AOU (1983, 1991, 1998), but its use has not been without criticism. Amadon (1986) felt that "the genera of the Hawaiian honeycreepers have been bandied about in rather cavalier fashion," and Olson and James (1995) bemoaned the wide acceptance of my classification "among non-taxonomists without any consideration having been given to its merits." Olson and James (1982) introduced a different classification, based largely on osteological studies, that has evolved in subsequent works (James and Olson 1991; Olson and James 1991, 1988, 1995), but has not as yet been widely adopted. The two schools have come to agreement on several points, and the remaining differences involve primarily the limits of the genera *Loxops* and *Hemignathus* and the placement of the Hawai'i Creeper (*Oreomystis mana* of AOU 1998 or *Loxops mana* of James and Olson 1991) and 'Akikiki or Kaua'i Creeper (*O. bairdi*). James

(1998) conducted a phylogenetic analysis of cranial osteology, the first study to include all taxa, both historical and subfossil. Her phylogeny (for historically known taxa only) is presented by Fleischer et al. (*this volume*). Recently, various allozyme (Johnson et al. 1989, Fleischer et al. 1998) and mtDNA studies (Tarr and Fleischer 1993, 1995; Feldman 1997; Fleischer et al. 1998; Fleischer et al. *this volume*) have suggested patterns of relationship that challenge both AOU (1998) and James and Olson's (1991) taxonomy. Because genetic technologies are still advancing, hypotheses of relationships based on them must be considered tentative. Each succeeding study seems to change the picture, the various methods show little concordance in their results, and the various laboratories do not agree even when performing essentially the same analyses. To their credit, the authors of these studies have been very conservative in recommending taxonomic changes. Molecular studies virtually never mention phenotypic characters, the traditional tools of systematists, because they consider such "adaptive" characters too subject to the vagaries of natural selection to be evolutionarily informative (R. Fleischer, pers. comm.). Also, no genetic study of Hawaiian honeycreepers has addressed the possibility that past hybridization could have a profound effect on per-

ceived patterns of divergence, although hybridization has been shown to have played a major role in the adaptive radiation of the similar-aged Darwin's finches (Grant 1994). Although DNA studies may ultimately answer all phylogenetic questions, I agree with Raikow (1986) that concordance testing with more traditional methods is still the only reasonable way to evaluate their hypotheses. In this volume, Fleischer et al. do exactly that by using data from mtDNA along with phenotypic osteological characters to assess the phylogenetic placement of the Po'ouli (*Melamprosops phaeosoma*). In the two decades since my first effort (Pratt 1979), many new possible phenotypic synapomorphies have been discovered and others re-evaluated. Clearly now is the time to provide a cladistic analysis of this eclectic mix of traditional phenotypic characters, so that meaningful comparisons with genetic studies can be made.

METHODS

Scientific names used herein are those of the AOU (1998) unless otherwise noted. I conducted phylogenetic analyses of 39 characters (Table 1) derived from studies of myology, osteology, tongue morphology, bill morphology, plumage and coloration, behavior, and ecology using PAUP* (Swofford 1999) and MacClade 3.01 (Maddison and Maddison 1992). Table 2 shows the data matrix. The first 3 characters were segregated to simplify some manipulations done with them. The 26 taxa include the chaffinches (Fringillinae) and cardueline finches (Carduelinae) as outgroups. Groups are coded as possessing a character if any included species does so. Question marks indicate gaps in the data. I have liberally used vernacular names for three reasons: 1) to be as taxonomically noncommittal as possible in entering the data; 2) to make my trees directly comparable to others presented in this volume that also use Hawaiian names; and, most importantly, 3) because these are the only available names that have remained unambiguous for two centuries.

Phenotypic data are admittedly subject to some manipulation by the investigator because characters can be described in various ways. Thus the coding of several characters requires explanation. In Character 21, for example, long sickle-shaped bills are found among 'akialoas (*Hemignathus* spp.) and in the 'I'iwi (*Vestiaria coccinea*) and mamos (*Drepanis* spp.), but they differ between the two groups in the nature of the bony support (Baldwin 1953). By combining two features, Character 21 codes this character without introducing known homoplasy. Tongue shape (Character 15) and bill shapes (Characters 19–22) could have been approached several different ways, but I found that qualitative descriptions worked better than quantitative ones. I also did not order these characters because whether they represent transformational series is uncertain. Character 26 ('amakihi coloration) represents a suite of possibly synapomorphic characters that appear to have evolved in tandem. 'Amakihi coloration includes: 1) plumage olive green dorsally; 2) under-

parts yellow to olive green, paler than dorsum; 3) lores narrowly dark gray or black; 4) bill dark gray to black, usually with bluish base to mandible; 5) females and juvenals like males but less yellow; and 6) juvenals with at least faint wingbars. These characters must be grouped because they are not independent of one another.

I applied similar techniques and the same data set (plus other characters) in a different analysis that will be explained under the discussion of the Hawai'i Creeper below.

RESULTS

With all characters at the same weight, I conducted a heuristic search that yielded a total of 390 equally parsimonious trees. From those, a 50% majority rule consensus tree (Fig. 1a) was computed that had a length (L) of 130 steps, a consistency index (CI) of 0.546, and a retention index (RI) of 0.720. The numbers on the lines indicate the percentage of trees that possess the branch shown. The result produced some apparent anomalies. Although the two 'alauahios (*Paroreomyza montana* and *P. maculata*) and the Kākāwahie (*P. flammea*) stand apart as I predicted (Pratt 1992b), the Po'ouli remains imbedded in the largest clade even though it also lacks the "defining characters" (Pratt 1992a), Characters 1–3 in Table 1, that presumably cause *Paroreomyza* to segregate in the tree. The difference for the Po'ouli is that it possesses an interorbital septum (Characters 11–12) like those of other Hawaiian honeycreepers (Zusi 1978; James and Olson 1991; Fleischer et al., *this volume*). Such a topology requires that the "defining" characters be secondarily lost in *Melamprosops*. This hypothesis lacks credibility because: 1) only these three among the 46 characters are virtually exclusive to Hawaiian honeycreepers as compared with all other passerines; 2) they probably represent gene complexes rather than single loci; and 3) they were favored by natural selection in the Hawaiian environment and retained in most of the drepanidine taxa, so it is difficult to discern how a reversal would be advantageous. If, as hypothesized by Pratt (1992a), drepanidine odor is a defense against predation, then for a lineage to lose it and have to compensate for the loss by the redevelopment of energy-taxing predator mobbing behavior (which dreps with the odor also lack), is certainly counterintuitive if not unpar-simonious. Similarly, the loss of lingual wings (or conversely the development of a squared-off base to the tongue) seems unlikely to have occurred more than once among the honeycreepers because it has happened only one other time (among sunbirds) in the entire passerine order. A strict consensus tree of the same data set (Fig. 1b; L = 125, CI = 0.576, RI = 0.715) collapsed

many of the nodes and revealed a lack of resolution among most taxa (but note that the *Hemignathus/Pseudonestor* clade, discussed below, survives, as do pairings of mamos and 'I'iwi, Palila and Kona Grosbeak, and the two creepers).

Consequently, I conducted a second analysis giving Characters 1–3 a weight of 2, with all others remaining weighted at 1. This run produced 150 equally parsimonious trees. The majority-rule consensus tree (Fig. 1c; L = 136, CI = 0.551, RI = 0.723) has a much more intuitively satisfying topology and is also more consistent with the findings of Fleischer et al. (*this volume*) and Pratt (1992a) with regard to *Melamprosops*. Furthermore, its topology is so robust that most of it survives in a strict consensus tree (Fig. 1d; L = 125, CI = 0.576, RI = 0.715).

These consensus trees support a number of hypotheses, some of which have taxonomic implications: 1) the Hawaiian honeycreepers, including *Melamprosops* and *Paroreomyza*, are monophyletic; 2) *Melamprosops* and *Paroreomyza* independently diverged from the “main line” of drepanidine evolution very early, before the “defining characters” of Pratt (1992a, b) evolved; 3) the drepanidine finches form a clade that does not include the 'Ō'ū (*Psittirostra psittacea*), Lāna'i Hookbill (*Dysmorodrepanis munroi*), or the Maui Parrotbill; 4) the genera *Chloridops* and *Loxioides* are sister taxa, as suggested by James and Olson (1991); 5) the 'amakihis, 'akialoas, and “heterobills” form a clade that corresponds to the currently recognized genus *Hemignathus* (AOU 1998) except that 6) the 'Anianiau (*H. parvus*) is not included in it, as suggested by Conant et al. (1998); 7) *Pseudonestor* may be a *Hemignathus*; it is more closely related to the thin-billed taxa than to the drepanidine finches as suggested very early by Perkins (1903) and later by Bock (1970) and Pratt (1979) but not accepted by the AOU (1983); 8) the remaining honeycreepers may divide into two clades along the traditional “red” vs. “green” lines; 9) several of the “red” genera are closely related and possibly warrant merger; 10) *Paroreomyza* is not closely related to *Orcomystis*; which 11) includes the Hawai'i Creeper. Several of these require further comment.

DISCUSSION

DREPANIDINE FINCHES

Amadon (1950) placed all the drepanidine finches (except the hookbill, which he regarded as an aberrant specimen) in the genus *Psittirostra* rather than recognizing the five genera previously named, most of which at the time would have been monotypic. This arrangement also re-

flected his hypothesis that these birds' finchlike characters were secondarily derived from a thin-billed ancestor. Greenway (1968) split the genus into *Psittirostra* for the 'Ō'ū and *Loxioides* for the rest, and Banks and Laybourne (1977) advocated re-establishment of the original five genera, primarily on the basis that Amadon's *Psittirostra* was morphologically too broad, and breaking it up reflected degrees of phenotypic divergence comparable to those among various mainland finch genera. With a cardueline ancestry fairly well established, Amadon's large *Psittirostra* also appeared to represent a paraphyletic assemblage based on plesiomorphies (Pratt 1979). Olson and James (1982b) maintained Amadon's *Psittirostra* but recognized five subgenera. Later (James and Olson 1991), they recognized all five genera, several of which by then had gained new members described from prehistoric remains, and added several new finchlike genera. Although my phylogeny would support Greenway's (1968) classification, I would caution against making any sweeping taxonomic changes at this time. This study included relatively few characters that could differentiate the finch genera, so the apparent monophyly of the group could easily be an artifact. Any changes, with the possible exception of the merger of *Chloridops* and *Loxioides* suggested by both this study and James and Olson (1991), should await publication of James's (1998) dissertation, new fossil discoveries, and ongoing studies based on ancient DNA extracted and amplified from prehistoric remains (R. L. Fleischer, pers. comm.).

MAUI PARROTBILL

Not only does the parrotbill cluster with the thin-billed taxa *contra* previous classifications (Raikow 1977, AOU 1983), but it may belong in the genus *Hemignathus*. Once the conflation of its huge but fundamentally different bill with the large bill of the 'Ō'ū (Raikow 1977) is eliminated, the similarities of the parrotbill to the hemignathines, especially the 'Akiapōlā'au (*H. munroi*), are overwhelming. Synapomorphies are as varied as a modified jaw muscle (Zusi 1989) and juvenile call notes (pers. obs.). Interestingly, the mtDNA phylogeny of Fleischer et al. (1998, *this volume*) also supports a close 'Akiapōlā'au/parrotbill relationship, although not necessarily the current composition of *Hemignathus* (see below). The parrotbill's tongue (Character 16) is unique among the honeycreepers, elongated with lateral and terminal projections. It looks very much like a drepanidine tubular tongue that has simply been unrolled, and can easily be seen as derived from a tubular ancestor. However, osteological studies (James 1998, Fleischer et al. *this volume*) group the par-

TABLE 1. CHARACTER STATES FOR PAUP* ANALYSES OF HAWAIIAN HONEYCREEPERS

<i>Characters used in Figure 1</i>	
Defining characters of Hawaiian honeycreepers (Pratt 1992a):	
1.	Drepanidine odor
0.	Absent
1.	Present
2.	Proximal end of tongue
0.	With prominent "lingual wings."
1.	Squared off, with no large backward projections.
3.	Mobbing behavior
0.	Present
1.	Absent
Anatomy:	
4.	Pattern of insertion of the 3 branches of <i>M. flexor digitorum longus</i> (Raikow 1978)
0.	ABB
1.	ABA
5.	Condition of <i>M. peroneus brevis</i> tibial head (from Raikow 1978)
0.	Absent
1.	Present
6.	Condition of <i>M. pterygoideus retractor</i> (Zusi 1989)
0.	Not enlarged
1.	Highly enlarged
7.	Tibial head of the shank muscle <i>M. peroneus brevis</i> (Raikow 1977, 1978)
0.	Absent
1.	Present
8.	Coracoidal head of the upper forelimb muscle <i>M. deltoideus minor</i> (Raikow 1977)
0.	Absent
1.	Present
*9.	Condition of <i>M. plantaris</i> (Raikow 1977)
0.	Present
1.	Absent
2.	Variable within taxon.
10.	Solid bony palate (Sushkin 1929, Amadon 1950)
0.	Absent
1.	Present
11.	Interorbital septum thickness (Zusi 1978)
0.	Thin, single-walled
1.	Thick, double-walled
2.	Thick, double-walled but with thin area in center
12.	Fenestration of interorbital septum (Richards & Bock 1973, Zusi 1978)
0.	Large fenestrae
1.	Solid
2.	Small fenestrae or none (variable)
13.	Floor of cranial fenestra in profile (Zusi 1978)
0.	With hump or upward protrusion
1.	Flat
14.	Palatine process of the premaxilla (Bock 1960, Richards & Bock 1973)
0.	Present
1.	Absent (= fused) with lateral flange at anterior end
2.	Absent (= fused) with reduced lateral flange
Tongue adaptations:	
*15.	Overall shape
0.	"Nontubular, fleshy above, corneous below and caudolaterally" with "a rounded tip edged with small papillae" (James et al. 1989).
1.	As above but "far less fleshy, more slender" (Gadow 1899).
2.	Straight and shallowly troughlike (Richards and Bock 1973).
3.	Thin, tubular for half or more of length.
4.	Fleshy but narrow, with spoonlike tip (Bock 1978).

TABLE 1. CONTINUED

<i>Characters used in Figure 1</i>	
*16. Tongue margins	0. Smooth, not raised dorsad (Gadow 1899, Gardner 1925, Clark 1912, Amadon 1950, Raikow 1977, James et al. 1989).
	1. Slightly raised, with short lateral and terminal laciniae at distal end (Gadow 1899, Richards and Bock 1973).
	2. Slightly raised, with long lateral and terminal laciniae (Rothschild 1893–1900).
	3. Strongly raised and curved inwards progressively toward tip, lateral laciniae interlaced distally (Gadow 1899, Raikow 1977).
*17. Seed-cup modifications	0. Mixed within taxon.
	1. No specialization for seeds
	2. Seed-cup tip (Gadow 1899, Amadon 1950)
Bill morphology (mostly pers. obs.):	
18. Nasal Operculum (Raikow 1977, James et al. 1989)	0. Not expanded downward
	1. Partially developed
	2. Expanded downward to nearly cover nostril
19. Finchlike bill shape	0. Finchlike
	1. Finchlike but elongated (i.e. tanager-like)
	2. Not finchlike
*20. Unique morphologies	0. Bill shape represented elsewhere among passerines
	1. Heavy, hooked maxilla
	2. Heavy, parrotlike bill
	3. Slightly crossed bill tips
	4. "Heterobill" morphology
*21. Sickle-shaped bills	0. Not sickle-shaped
	1. Sickle-shaped, thin
	2. Sickle-shaped, thick
22. Inflation of bill	0. Bill not inflated
	1. Bill highly inflated, subglobose
*23. Profile of gonys	0. Strongly convex
	1. Slightly convex
	2. Straight to slightly concave
	3. Strongly concave
Plumage and Coloration (pers. obs.)	
24. Sparrow-like streaking	0. Present at least in juveniles
	1. Never present
*25. Juvenal plumage	0. No age-related plumage variation
	1. Juvenile distinct but patterned like adult female
	2. Juvenile patterned differently from either adult
26. Presence of "amakihī coloration" (see text for details):	0. Not present
	1. Present
	2. Present with secondary modifications
	3. Present with loss of distinctive female and juvenile plumages
27. Purring or cooing wing note in flight	0. No
	1. Yes

TABLE 1. CONTINUED

<i>Characters used in Figure 1</i>	
28.	Primaries with truncate tips
	0. No
	1. Yes
29.	Plumage texture
	0. Soft, non-shiny
	1. Shiny or hardened
*30.	Predominant plumage colors
	0. Yellow-green, yellow, or red
	1. Black, red, and/or yellow
	2. Brown and black
	3. Dull green or gray
	4. Variable in group
Behavior and ecology	
*31.	Song quality
	0. Canarylike (Perkins 1903, Pratt 1996a)
	1. Dissonant whistles, bell-like and mechanical sounds (Perkins 1903, Bryan 1908, Pratt 1996a)
	2. Lively, quiet chittering (Engilis 1990, Kepler et al. 1996)
	3. Lively whistles interspersed with call-like notes (Pratt 1992b, Pratt 1996a)
	4. Song of simple trills or warbles (Perkins 1903, Henshaw 1902, Pratt 1996a)
*32.	Song complexity (Newton 1973; Pratt 1979, 1996)
	0. Complex
	1. Mixed complex and simple
	2. Simple
*33.	Distinct juvenal call beyond fledging
	0. Absent or unrecognized
	1. Rapid juvenal begging calls in flocks (Scott et al. 1979; Fig. 2)
	2. Evenly spaced "sound beacon" from solitary chick (BNA; pers. obs.)
34.	Whisper songs (Pratt 1979, 1996a, b)
	0. No whisper song
	1. Whisper songs similar to primary songs.
	2. Whisper songs distinct from primary songs.
35.	Nest sanitation
	0. Absent at some point in nesting cycle (Newton 1973; van Riper 1980a; Pletschet and Kelly 1990; Morin 1992a, b; BNA)
	1. Throughout nesting cycle.
*36.	Primary adult diet (Perkins 1903, Berger 1981, BNA)
	0. Seeds
	1. Soft fruits
	2. Nectar
	3. Mixed
	4. Invertebrates
37.	Nest construction roles (Newton 1976, Morin 1992b, BNA)
	0. Construction by female only.
	1. Construction mainly by female with limited help from male.
	2. Construction by both sexes.
38.	Size of territory (Newton 1976, BNA)
	0. Large territories.
	1. Small territories in immediate area of nest.
*39.	Display flights over breeding area (Newton 1976, Morin 1992a, BNA)
	0. Absent
	1. Present

TABLE 1. CONTINUED

<i>Characters used in Figure 1</i>	
*40.	Presence of red in plumage
	0. Yes
	1. No
*41.	Bill color
	0. Pale throughout (may have darker tip)
	1. Pale with dark culmen
	2. Brown or gray with pale base
	3. Black with bluish base to mandible
	4. All black
*42.	Attenuation of bill
	0. None
	1. Slight
	2. Moderate
	3. Pronounced
	4. Extreme
*43.	Presence of yellow in plumage (adult male)
	0. Yellow head only
	1. No yellow (or very little)
	2. Yellow underlying entire plumage, nowhere bright
	3. Yellow throughout plumage, with bright areas
	4. Nearly all yellow.
*44.	Black or gray feathering in face
	0. None
	1. Broad, not confined to lores
	2. Confined to lores
*45.	Presence of wing bars
	0. Never present
	1. Faint in juveniles, absent in adults
	2. Present in juveniles only
	3. Present in some adults
*46.	Color pattern of crown and supraloral area
	0. Uniformly colored
	1. Indistinct pale eyebrow
	2. Bold, distinct eye stripe
	3. Contrasting crown and forehead
	4. Pale supraloral fleck

Notes: All characters ordered except those with asterisks. Citations for every data point not given. Summaries are cited where useful. The abbreviation BNA refers to the Birds of North America series of the American Ornithologists' Union (Baird 1994; Fancy and Ralph 1997, 1998; Lepson 1997, Lepson and Freed 1997, Lepson and Pratt 1997, Pratt et al. 1997, Simon et al. 1997, Lindsey et al. 1998; Olson 1998a,b,c; Snetsinger 1998; Baker and Baker 2000a,b; Sykes et al. in press).

rotbill with two other taxa that have strongly hooked bills ('Ō'ū and hookbill), but different tongues. This grouping could easily be viewed as the result of homoplasy or just superficial resemblances. It is reminiscent of Raikow's (1977: 113) clustering of the parrotbill with the 'Ō'ū on the basis of their vaguely similar bill shape and the fact that such placement was "not refuted by other characteristics." That placement is now refuted by many other characters, and the parrotbill, despite its large bill, clearly belongs among the thin-billed taxa. However, I do not suggest merger of *Pseudonestor* and *Hemignathus* until the relationships are better understood, even though my findings seem to show that, with

Pseudonestor excluded, *Hemignathus* is paraphyletic.

HEMIGNATHUS AND LOXOPS

Except for the *Pseudonestor* problem, the above results clearly support current AOU (1998) taxonomy that restricts *Loxops* to the 'ākepas and groups the 'amakihis, 'akialoas, and heterobills in *Hemignathus*. However, the current inclusion of the 'Anianiau in the latter genus is not justified. For a detailed discussion of the reasoning behind these conclusions, see Co-nant et al. (1998). DNA studies also support recognition of a monotypic *Magumma* for the 'Anianiau. Tarr and Fleischer's (1995) restriction-

TABLE 2. DATA MATRIX FOR PAUP* ANALYSIS OF HAWAIIAN HONEYCREEPERS USING CHARACTER STATES FROM TABLE 1

Taxon	Character state															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Chaffinches	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cardueline finches	0	0	0	0	1	0	0	1	0	1	1	1	1	1	0	0
<i>Telespiza</i> finches	1	1	1	1	?	0	0	1	0	1	1	1	1	1	0	0
Palila	1	1	1	?	?	?	?	?	?	?	1	1	1	?	0	0
koa finches	1	1	?	?	?	?	?	?	?	?	1	1	1	?	0	0
Kona Grosbeak	1	1	?	?	?	?	?	?	?	?	1	1	1	?	0	0
'Ō'ū	1	1	1	0	1	0	0	1	0	?	1	1	1	?	0	0
Lāna'i Hookbill	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	0
Po'ouli	0	0	0	?	?	?	?	?	?	?	2	2	1	?	4	0
Kākāwahie/'alauahios	0	0	0	?	?	?	?	?	?	0	0	0	1	2	2	1
Maui Parrotbill	1	1	1	?	?	1	?	?	?	?	2	2	1	?	1	2
Hawai'i Creeper	1	1	1	?	?	?	?	?	1	?	2	2	1	1	2	1
'Akikiki	1	1	1	0	1	?	0	1	0	?	2	2	1	?	2	1
'ākepas/'Akeke'e	1	1	1	?	?	?	?	?	?	1	2	2	1	1	3	3
'Anianiau	1	1	1	?	?	?	?	?	?	?	2	2	1	?	3	3
Greater 'Amakihi	1	1	?	?	?	?	?	?	?	?	2	2	1	?	3	3
'amakihis	1	1	1	0	1	0	1	1	1	?	2	2	1	2	3	3
'akialoas	1	1	?	0	1	0	1	1	0	1	2	2	1	1	3	3
nukupu'us	1	1	?	0	1	?	?	?	?	?	2	2	1	?	3	3
'Akiapōlā'au	1	1	1	0	1	1	0	1	0	?	2	2	1	?	3	3
'Ula-'ai-hawane	1	1	?	?	?	?	?	?	?	?	2	2	1	?	3	3
'Apapane	1	1	1	0	1	0	1	1	1	1	2	2	1	1	3	3
'Ākohekohe	1	1	1	1	1	0	1	1	1	?	2	2	1	?	3	3
'I'iwi	1	1	1	0	1	0	0	1	1	1	2	2	1	2	3	3
Black Mamo	1	1	?	?	?	?	?	?	?	?	?	?	1	?	3	3
Hawai'i Mamo	1	1	?	?	?	?	?	?	?	?	?	?	1	?	3	3

fragment mtDNA study of a limited number of taxa found the 'Anianiau widely separated from the 'amakihis in a clade of its own. Fleischer et al.'s (1998, *this volume*) mtDNA sequencing study included additional taxa and grouped the 'Anianiau with the heterobilled 'Akiapōlā'au (*H. munroi*) and the parrotbill. James's (in Fleischer et al., *this volume*) osteological phylogeny, however, maintains the grouping of the 'Anianiau with the 'amakihis, which may reflect the superficial resemblance that led to the former name "Lesser 'Amakihi" and my own (Pratt 1979) uncritical placement of this species in *Hemignathus* before closer scrutiny (Conant et al. 1998).

James and Olson (1991: Table 14) restricted *Hemignathus* to 'akialoas and the heterobills, and later (Olson and James 1995) subdivided it and placed the former in a new genus *Akialoa*. They grouped the 'amakihis with the 'ākepas, 'Anianiau, and Hawai'i Creeper in *Loxops*. Thus constituted, *Loxops* would be close to Amadon's (1950) characterization (Pratt 1979, Conant et al. 1998). James's (1998) newly analyzed osteological data (Fleischer et al., *this volume*) provide no support for such an arrangement. In fact, her phylogeny not only supports restriction of *Loxops* to 'ākepas, but can be interpreted as sup-

porting a large *Hemignathus* as currently recognized. The 'amakihis, heterobills, and akialoas are members of a single clade even on osteological grounds, but the picture is complicated by the inclusion of the "red" honeycreepers in the same clade. This result reveals one of the weaknesses of single-character or single-complex analyses. With only one suite of characters, the computer program has no way of distinguishing homoplasy or parallelism from synapomorphy. The bill morphologies among the "red" birds (i. e., short down-curved bills, long sickle-bills, etc.) parallel those found in *Hemignathus*, but other characters (i. e., behavior, plumage type, sequence of plumages, and vocalizations) show that these resemblances are not synapomorphic with similar morphologies among the "green" birds (Perkins 1903, Amadon 1950). I suspect that a combination of the osteological data with my own would resolve this discrepancy and bring James's (1998) phylogeny and mine into substantial agreement. With the red birds removed, James's uppermost clade fairly closely approximates *Hemignathus* as currently delimited (AOU 1998).

Fleischer et al.'s (1998) mtDNA sequence phylogeny supports neither an enlarged *Hemignathus* nor an enlarged *Loxops*. In it, the heter-

TABLE 2. EXTENDED.

																	Character state											
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39						
0	0	0	0	0	0	1	0	1	0	0	0	0	4	?	2	0	0	1	0	0	0	0						
0	0	0	0	0	0	1	0	1	0	0	0	0	4	0	0	0	1	0	0	0	1	1						
1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0						
2	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1						
2	0	0	0	0	0	1	1	1	0	0	0	0	0	?	?	?	?	?	0	?	?	?						
2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	?	1	?	0	?	?	1						
1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	?	1	?	?	1						
1	1	2	1	0	0	0	1	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?						
1	?	1	0	0	0	0	1	1	0	0	0	0	2	2	0	0	0	1	4	2	?	0						
1	1	2	0	0	0	1	1	1	0	0	0	0	3	1	0	2	1	3	?	?	?	1						
1	0	2	2	0	0	0	1	1	2	0	0	0	0	4	2	2	0	4	1	0	0	0						
1	1	2	0	0	0	2	1	2	0	0	0	0	3	4	2	1	0	1	4	1	1	0						
1	1	2	0	0	0	2	1	2	0	0	0	0	3	4	2	1	2	1	4	?	?	?						
1	2	2	3	0	0	2	1	1	0	0	0	0	4	2	0	2	0	4	0	1	1	1						
1	2	2	0	0	0	2	1	1	0	0	0	0	4	2	0	2	1	3	1	1	0	0						
1	2	2	0	0	0	2	1	0	3	0	0	0	4	2	?	?	?	4	?	?	?	?						
1	2	2	0	1	0	3	1	1	1	0	0	0	4	2	0	2	0	3	1	0	1	1						
1	2	2	0	1	0	3	1	1	1	0	0	0	4	2	?	?	?	?	3	?	?	?						
1	2	2	4	1	0	3	1	1	1	0	0	0	4	2	?	?	?	?	4	?	?	?						
1	2	2	4	1	0	1	1	1	1	0	0	0	4	2	2	2	1	4	0	?	?	0						
1	2	1	0	0	0	1	1	2	0	?	0	1	1	?	?	?	?	?	?	?	?	?						
1	2	2	0	0	0	2	1	2	0	1	1	1	1	0	0	0	1	2	2	1	1	1						
1	2	2	0	0	0	2	1	2	0	1	0	1	1	1	0	0	2	1	2	0	1	1						
1	2	2	0	2	0	3	1	2	0	1	1	1	1	0	0	0	1	2	1	1	0	0						
1	2	2	0	2	0	3	1	0	0	1	0	0	1	1	?	?	?	?	2	?	?	?						
1	2	2	0	2	0	3	1	0	0	1	0	1	1	?	?	?	?	?	2	?	?	?						

obills group with the parrotbill and 'Anianiau, the 'amakihi is sister-group to the red birds, and the Hawaii Creeper is sister-group to the 'akepas. The analysis does not include the Greater 'Amakihi or the 'akialoas. According to R. Fleischer (pers. comm.) the branching sequence among the thin-billed honeycreepers is not well defined by the techniques used in their study, so I believe we should await further developments before tinkering with a taxonomy so well supported by phenotypic characters.

Although the phenotypic data support a large *Hemignathus*, they also support the recognition of four (or five if *Pseudonestor* is included) subgenera within it: *Hemignathus* for the heterobills; *Akialoa* for the 'akialoas; *Chlorodrepanis* for the "typical" 'amakihi; and *Viridonia* for the Greater 'Amakihi. The latter two cannot be combined as has been done in the past (Greenway 1968) because such a construct would be paraphyletic. In fact, future studies should consider the possibility that the Greater 'Amakihi, like the 'Anianiau, warrants a genus of its own.

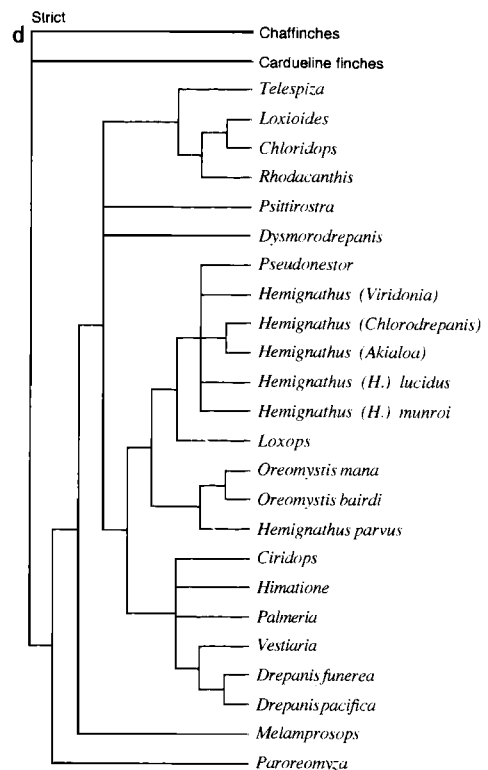
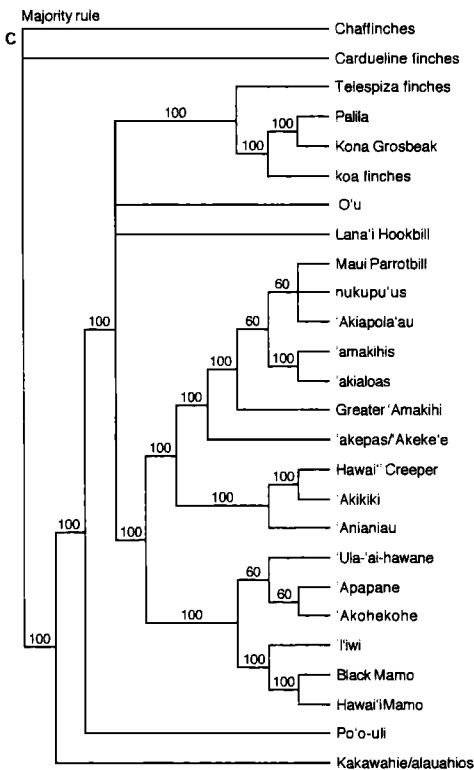
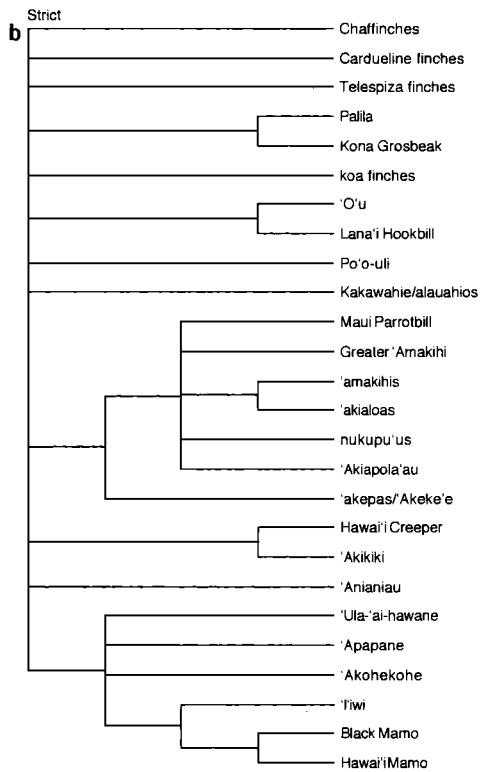
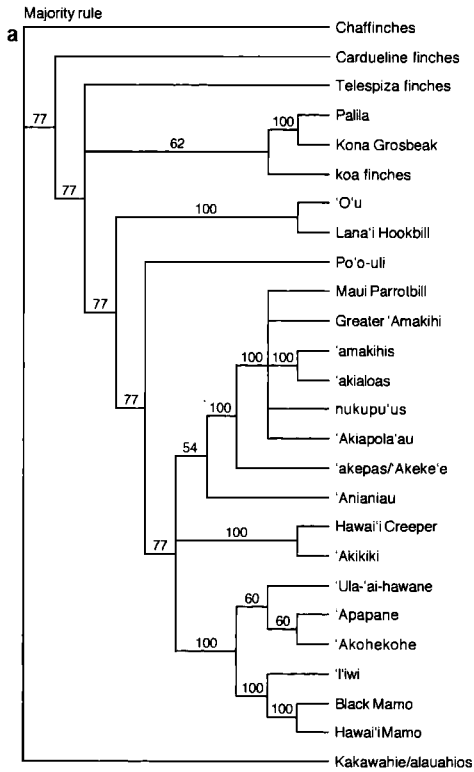
THE "RED-AND-BLACK" GENERA

Every study reviewed herein shows that the members of this subgroup, recognized from the

time of Perkins (1903), do indeed form a well-defined clade. R. C. Fleischer (pers. comm.), on the basis of the small degree of genetic difference between them, believes all of the "red" genera could justifiably be merged. On phenotypic grounds, the genera *Vestiaria* and *Drepanis* differ solely on a relatively minor red-to-yellow color shift, hardly a generic-level distinction by modern standards, but my earlier suggestion (Pratt 1979) that they should be merged was not accepted by Berger (1981). Also, the 'Apapane and 'Akohekohe (*Palmeria dolei*) are close structurally and behaviorally, although the latter's unique plumage features make it look superficially rather different. The lumping of *Himatione* and *Palmeria* is not as strongly supported by my phylogeny as the *Vestiaria/Drepanis* merger.

HAWAI'I CREEPER

So now we come to the one species whose taxonomic position is the subject of the widest disagreement among competing evolutionary hypotheses and hence the namesake of this paper. The Hawai'i Creeper is a small, drab Hawaiian honeycreeper endemic to the island of Hawai'i (Scott et al. 1979). Its dull gray-green



coloration and generally inconspicuous behavior may have contributed to the fact that the Hawaiians did not distinguish it from the Hawai'i 'Amakihi (*Hemignathus virens*; Perkins 1903). It was first described (Wilson 1891) as *Himatione mana*, but Amadon (1950) included it in his large genus *Loxops* as one of the subspecies of the "Creeper," a "species" subsequently shown to be a grouping of five species in either 2 (Pratt 1979, 1992b) or 3 (Olson and James 1982b, James and Olson 1991) genera. The O'ahu, Moloka'i, and Maui/Lāna'i components of Amadon's "Creeper" are now placed in the enigmatic genus *Paroreomyza*, which now appears to represent a very early divergence in the evolution of the honeycreepers (Tarr and Fleischer 1995, Fleischer et al. 1998, this study). The genus *Oreomystis* comprises the remaining two species, the 'Akikiki or Kaua'i Creeper, *O. bairdi*, and the Hawai'i Creeper, *O. mana*. Johnson et al. (1989), Feldman (1997; phylogeny reproduced in Freed 1999) and Fleischer et al. (1998, *this volume*) present strong allozyme, mtDNA, and osteological evidence that *O. bairdi* is the sister-group of *Paroreomyza*, although the placement of that clade varies among the studies. For this relationship to hold, the honeycreepers' squared-off tongue base (Character 2) would have to have evolved twice independently, an unlikely prospect as discussed earlier. This study achieved very different results (Fig. 1) in which *Paroreomyza* and *Oreomystis bairdi* are as far apart as any other two drepanidine genera. Tarr and Fleischer's (1995) restriction-site study supports this finding, but is out of step with their later mtDNA sequence analyses.

On osteological grounds, Olson and James (1982) and James and Olson (1991) place the Hawai'i Creeper in their large *Loxops* and considered it closely related to the 'amakihis (Olson and James 1995). However, James's (1998) phylogeny (see Fleischer et al., *this volume*) shows it only as a sister group to most of the other thin-billed honeycreepers, a position rather close to where it appears in my study (except that the 'Akikiki is paired with it). Thus the osteological phylogeny and mine actually differ more strikingly on the placement of *O. bairdi* than on that of the Hawai'i Creeper. The osteological phylogeny, if correct, would require either the creation of a new monotypic genus for the creeper or the recognition of a huge genus *Drepanis* that

would include everything from the creeper to heterobills to mammos. If the red birds were removed from this assemblage as suggested above, the creeper could be in *Hemignathus*. Interestingly, Feldman's (1994) independent mtDNA study showed the Hawai'i Creeper as sister group to the red honeycreepers which clade in turn formed an unresolved trichotomy with the 'amakihis and 'ākepas. Although distinctive, this hypothesis is closer to those derived from osteology and this study than to the other mtDNA results. Fleischer et al. (1998, *this volume*) hypothesize on the basis of mtDNA sequencing that the Hawai'i Creeper forms a clade with the 'ākepas which in turn is sister to an odd assemblage that includes the heterobills, parrotbill, and 'Anianiau. So is this enigmatic little bird an odd offshoot of its own, sister to the 'Apapane (*Himatione sanguinea*) and 'I'iwi, a non-crossbilled 'ākepa, or an *Oreomystis*?

The question of whether *Oreomystis* is related to *Paroreomyza* is independent of whether the Hawai'i Creeper and the 'Akikiki are congeners. So numerous are the phenotypic similarities of the Hawai'i Creeper to the 'Akikiki that manuscript reviewers of Pratt (1992b) questioned even considering them separate species, let alone members of different genera. The Hawai'i Creeper is vaguely similar in overall coloration to female and juvenile 'amakihis, female 'Akepa (*Loxops coccineus*), and both sexes of 'Akeke'e (*L. caeruleirostris*; Scott et al. 1979, Pratt et al. 1987), but differs in important details. Unlike 'amakihis and 'ākepas, adults are not sexually dichromatic. They have a broad gray mask, shaped more like the black mask of *L. caeruleirostris* than the narrow black lores of 'amakihis. Unlike 'amakihis but resembling 'ākepas, neither adults nor juveniles ever have wing-bars. And unlike both 'amakihis and 'ākepas, juveniles have a distinctive plumage with pale feathering in the lores and over the eye. In plumage features, the Hawai'i Creeper closely resembles *Oreomystis bairdi*, which also lacks sexual dichromatism as an adult, has a distinctive pale-faced juvenile plumage, and lacks wing-bars.

The creeper's bill is nearly straight with a concave gonys (Pratt 1992b), pale except for a dusky tinge, variable in extent, along the culmen. In overall shape it is somewhat intermediate between that of an 'amakihi and that of an 'ākepa (without crossed tips) and resembles that

←

FIGURE 1. Phylogenetic trees of Hawaiian honeycreepers: a) unweighted tree, 50% majority-rule consensus; b) unweighted strict consensus tree; c) majority rule tree with Characters 1–3 weighted 2; d) strict consensus of weighted trees, with AOU (1998) scientific name equivalents and *Hemignathus* divided into four subgenera. See Tables 1 and 2 for data and coding. See text for analysis details.

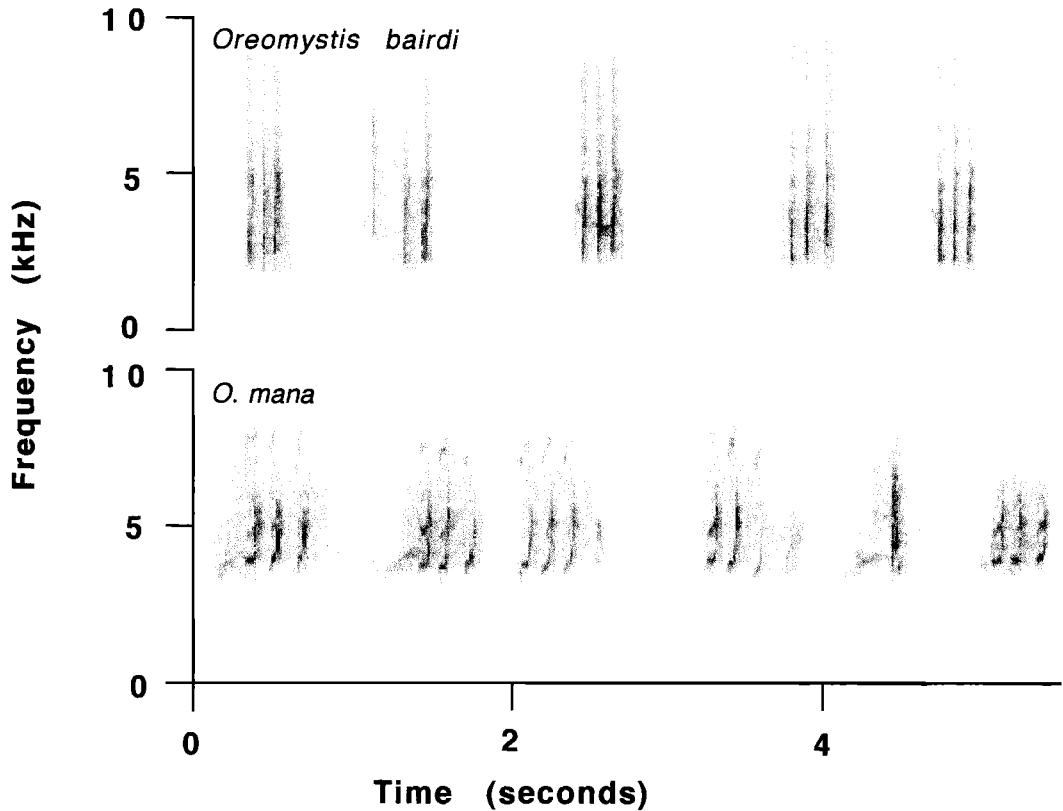


FIGURE 2. Juvenile begging calls of the 2 species of *Oreomystis*. *O. bairdi* recorded 6 August 1997 by David Kuhn near the Mohihi Trail above Koa'ie Stream, Alaka'i Wilderness Preserve, Kaua'i (not archived). *O. mana* recorded by the author 4 May 1977 at Keauhou Ranch, Ka'u District, Hawai'i (Cornell Laboratory of Ornithology, Library of Natural Sounds No. 05274). Audiospectrograms prepared on a Macintosh computer using Canary© software program.

of *Oreomystis bairdi* in nearly every detail except that it is somewhat thinner, light gray rather than pale pink, and has somewhat more dark pigment above (Pratt et al. 1987). Because their bills are nearly identical in shape, the most parsimonious hypothesis would seem to be that the two creepers share a common ancestry, but bill shape does not argue strongly against an 'ākepa relationship for them both.

The nuthatch-like foraging of the Hawai'i Creeper differs from that of *Oreomystis bairdi* only in that the chosen substrates average larger for the latter (Pratt 1992b). Of all the 'amakihi species, the Kauai 'Amakihi (*H. kauaiensis*) is the most frequent bark-picker, but it would never be characterized as nuthatch-like (Conant et al. 1998). Nor does the Hawai'i Creeper forage in any way resembling the feeding of either species of *Loxops* (Lepson and Pratt 1997, Lepson and Freed 1997). Following fledging, tightly structured family groups of both Hawai'i Creeper (Scott et al. 1979, Pratt et al. 1987) and 'Akikiki

(Pratt 1992b, Conant et al. 1998) forage together with frequent begging notes from the juveniles. Both may eventually join larger mixed-species flocks with 'amakihis, 'ākepas, and other species (Pratt et al. 1976, Lepson and Freed 1997, pers. obs.). Similar tightly structured family foraging groups with distinctive calls have not been reported in 'amakihis or 'ākepas (Lepson and Pratt 1997, Lepson and Freed 1997), although they both join looser flocks. Because the hypothesized ancestor of the drepanidines was a seed-eating cardueline finch, the nuthatch-like foraging of the two creepers can be viewed as a synapomorphy.

The song of the Hawai'i Creeper is a short trill similar to that of *O. bairdi*, but many other drepanidine species also sing short trills, so adult songs reveal little about relationships (Scott et al. 1979, Pratt et al. 1987, Pratt 1992b, Pratt 1996). One noteworthy difference is that songs of both *Oreomystis* are highly stereotyped, whereas those of such potential relatives as

'amakihi and 'akepas are highly variable even when uttered by the same individual (Pratt 1979, 1996; Pratt et al. 1987). The begging notes of Hawai'i Creeper juveniles flocking with their parents after fledging are very similar to those of juvenile 'Akikiki (Fig. 2) in similar context, which were first recorded in 1997 and are thus not included in recently published tapes (Pratt 1996). The individual notes of 'Akikiki juveniles are slightly shorter and cover a somewhat wider frequency range than those of the Hawai'i Creeper, but they have a similar syncopated rhythm, with notes grouped in short bursts (Fig. 2). Although a few other Hawaiian honeycreepers (e. g. *Pseudonestor xanthophrys*, *Hemignathus munroi*) have distinctive juvenile begging notes that persist long after fledging, none have the same sound or rhythmic pattern of the two creepers. No long-persisting juvenile begging notes have been reported among either 'amakihi or 'akepas, nor among cardueline finches, and thus the juvenile calls appear to be another synapomorphy linking the two *Oreomystis*.

But it is the tongues that present the most enigmatic observations. The Hawai'i Creeper's tongue is narrow and nontubular, with a notched, slightly frayed tip (Richards and Bock 1973) and resembles the tongue of *O. bairdi* in virtually every detail (Pratt 1992a). Such a tongue tip differs strikingly from that of the hypothetical ancestral Hawaiian honeycreeper (Raikow 1977), is found only in the Hawai'i Creeper and the 'Akikiki, and, unlike that of the parrotbill, is difficult to envision as a derivative of the highly derived drepanidine tubular type. The most likely explanation for two taxa sharing in detail such a complex derived morphology is that they both inherited it from a common ancestor. The simple, notched tongue certainly appears to be a defining synapomorphy in *Oreomystis*.

If Raikow (1977, 1985, 1986) is correct that the tubular drepanidine tongue defines a major clade of the Drepanidinae that includes both the "green" and "red" groups, *Oreomystis* cannot belong to it unless its distal tongue morphology is secondarily derived from the tubular form. Of course, such derivation is clearly possible. Both the DNA and osteology trees of Fleischer et al. (*this volume*) require this secondary derivation for the Hawai'i Creeper but not the 'Akikiki. My unweighted tree (Fig. 1a) shows the two-member *Oreomystis* as one branch of an unresolved trichotomy with the "red" clade on the one hand and the "green" clade on the other, but my weighted tree (Fig. 1c) places it, like both of those of Fleischer et al. (*this volume*), in a position that requires secondary derivation of the *Oreomystis* tongue from a tubular ancestor.

This result prompted me to conduct an addi-

tional analysis that focused on the "green" birds, including all species-level taxa and additional characters (40–46 in Table 1) that, for reasons mentioned earlier, could not be used with the broader sample of taxa. I included the three *Paroreomyza* species and the monotypic *Psittirostra* for comparative purposes and so that the relationships of *Pseudonestor* would also be re-examined. All characters were unweighted in this analysis, and Character 35 (nest sanitation) was ordered rather than unordered as previously. Table 3 is the data matrix for this analysis. A heuristic search of the 46 characters produced 180 trees, from which majority-rule and strict consensus trees (Fig. 3; L = 109, CI = 0.661, RI = 0.732) were derived. This time, the two *Oreomystis* sorted out as the sister group to the entire clade defined by the tubular tongue (but including *Pseudonestor*), which I believe is a reasonable placement for it. Note that the earlier pairing of *Oreomystis* with 'Anianiau did not hold up in this more detailed analysis, and I regard it as an artifact.

Problems of possible homoplasy complicate analysis of another anatomical feature that has figured prominently in the taxonomic history of the creepers. Raikow (1976) found that some Hawaiian honeycreepers, like many other passerines, have lost the plantaris, a minor muscle of the shank. Of the taxa he studied, only the 'amakihi and the "red" genera *Himatione*, *Palmeria*, and *Himatione* lacked the plantaris. Unfortunately, he included neither an 'akepa nor any of the "creepers" (which were all then considered conspecific) other than *Oreomystis bairdi*. Nevertheless, Raikow (1977) separated "the Creeper" generically from the 'amakihi based on the loss of the plantaris in the latter. If the loss of the plantaris is a uniquely derived character state within the honeycreeper taxon, then the logical conclusion is that the taxa that share this condition form a clade ('amakihi plus the red-and-black birds), a grouping that appears in Fleischer et al.'s (1998) mtDNA tree. Subsequent dissections (S. L. Olson, pers. comm.) revealed that the Hawai'i Creeper lacks the plantaris, a result that might also seem to support a relationship to 'amakihi. How useful is loss of the plantaris as a key to phylogeny? Clearly, it cannot be considered a synapomorphy in any broad sense, because it has occurred several times among passerines generally, and at least twice among the Carduelinae (Raikow 1976, 1977, 1978). Furthermore, avian muscles have been shown to be subject to evolutionary reversals (i. e., to become re-established in a lineage after loss; Raikow et al. 1979) as well as sufficiently variable individually to present problems for phylogenetic studies based on few specimens

TABLE 3. DATA MATRIX FOR PAUP* ANALYSIS OF "HEMIGNATHINE" SPECIES OF HAWAIIAN HONEYCREEPERS USING CHARACTER STATES FROM TABLE 1

Taxon	Character state																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>Psittirostra</i>	1	1	1	1	1	0	0	1	0	?	1	1	1	?	0	0	1	1	1	1	0
<i>Paroreomyza maculata</i>	0	0	0	?	?	?	?	?	?	0	0	0	1	2	2	1	1	1	2	0	0
<i>Paroreomyza montana</i>	0	0	0	?	?	?	?	?	?	0	0	0	1	2	2	1	1	1	2	0	0
<i>Paroreomyza flammea</i>	0	0	0	?	?	?	?	?	?	0	0	0	1	2	2	1	1	1	2	0	0
<i>Pseudonestor</i>	1	1	1	?	?	1	?	?	?	?	2	2	1	?	1	2	1	0	2	2	0
<i>Oreomystis mana</i>	1	1	1	?	?	?	?	?	1	?	2	2	1	1	2	1	1	1	2	0	0
<i>Oreomystis bairdi</i>	1	1	1	0	1	?	0	1	0	?	2	2	1	?	2	1	1	1	2	0	0
<i>Loxops coccyneus</i>	1	1	1	?	?	?	?	?	?	1	2	2	1	1	3	3	1	2	2	3	0
<i>Loxops caeruleirostris</i>	1	1	1	?	?	?	?	?	?	?	2	2	1	?	3	3	1	2	2	3	0
<i>Hemignathus sagittirostris</i>	1	1	?	?	?	?	?	?	?	?	2	2	1	?	3	3	1	2	2	0	0
<i>Hemignathus virens</i>	1	1	1	0	1	0	1	1	1	?	2	2	1	2	3	3	1	2	2	0	1
<i>Hemignathus flava</i>	1	1	1	0	1	0	?	1	1	?	2	2	1	2	3	3	1	2	2	0	1
<i>Hemignathus kauaiensis</i>	1	1	1	0	1	0	?	1	1	?	2	2	1	2	3	3	1	2	2	0	1
<i>Hemignathus parvus</i>	1	1	1	?	?	?	?	?	?	?	2	2	1	?	3	3	1	2	2	0	0
<i>Hemignathus ellisianus</i>	1	1	?	0	1	0	1	1	0	1	2	2	1	1	3	3	1	2	2	0	1
<i>Hemignathus obscurus</i>	1	1	?	?	?	?	?	1	0	1	2	2	1	1	3	3	1	2	2	0	1
<i>Hemignathus lucidus hanapepe</i>	1	1	?	?	?	?	?	?	?	?	2	2	1	?	3	3	1	2	2	4	1
<i>Hemignathus lucidus lucidus</i>	1	1	?	?	?	?	?	?	?	?	2	2	1	?	3	3	1	2	2	4	1
<i>Hemignathus lucidus affinis</i>	1	1	?	?	?	?	?	?	?	?	2	2	1	?	3	3	1	2	2	4	1
<i>Hemignathus munroi</i>	1	1	1	0	1	1	1	1	0	?	2	2	1	?	3	3	1	2	2	4	1

(Raikow et al. 1990). Further complicating matters is the lack of information on the plantaris condition of 'ākepas, the Greater 'Amakihi, and the 'Anianiau. Thus the hypothesis that the plantaris has been lost more than once in drepanidine evolution is by no means far-fetched, and the usefulness of this character in reconstructing phylogeny is severely compromised. Nevertheless I included it (Character 9) in my analyses as an unordered character.

The case for inclusion of the Hawai'i Creeper in *Oreomystis* based on "traditional" taxonomic data is straightforward, unequivocal, and supported by every tree topology in this study, al-

though the placement of that genus among the others remains controversial. The phenotypic evidence in this case, which includes certain and probable synapomorphies of plumage sequence, coloration, bill and tongue morphology, vocalizations, social behavior, and ecology are too numerous and varied to be dismissed out of hand, as has been done in recent molecular studies, none of which have even mentioned this striking conflict of genetic and phenotypic data. Nor in my opinion can so many similarities be credibly attributed to convergence or homoplasy.

R. L. Fleischer (pers. comm.) has suggested that a past hybridization event could produce the re-

TABLE 3. EXTENDED.

Character state																									
22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	
0	0	1	1	0	0	0	0	0	0	0	0	0	?	1	?	1	?	1	0	1	0	0	1	0	
0	1	1	1	0	0	0	0	0	3	1	0	2	1	3	?	?	?	1	1	0	3	1	3	2	
0	1	1	1	0	0	0	0	0	3	1	0	2	1	3	?	1	1	1	1	0	3	2	1	0	
0	1	1	1	0	0	0	0	0	3	1	0	2	1	3	?	?	?	0	1	0	1	0	0	0	
0	0	1	1	2	0	0	0	0	4	2	2	2	0	4	1	0	0	1	1	2	3	2	1	2	
0	2	1	2	0	0	0	0	3	4	2	1	0	1	4	1	0	0	1	1	0	2	1	0	0	
0	2	1	2	0	0	0	0	3	4	2	1	2	1	4	?	?	?	1	1	0	1	0	0	0	
0	2	1	1	0	0	0	0	0	4	2	0	2	0	4	0	1	1	0	0	0	1	0	0	0	
0	2	1	1	0	0	0	0	0	4	2	0	2	1	4	2	?	0	1	0	0	3	1	0	3	
0	2	1	0	2	0	0	0	0	4	2	?	?	?	4	?	?	?	1	3	3	2	2	0	1	
0	3	1	1	1	0	0	0	0	4	2	0	2	0	3	0	1	1	1	3	2	3	2	2	1	
0	3	1	1	1	0	0	0	0	4	2	0	2	?	3	1	?	?	1	3	2	3	2	3	4	
0	3	1	1	1	0	0	0	0	4	2	0	2	1	3	1	0	0	1	2	3	3	2	2	1	
0	2	1	1	0	0	0	0	0	4	2	0	2	1	3	1	1	0	1	1	1	4	0	0	0	
0	3	1	1	1	0	0	0	0	4	2	?	?	?	3	?	?	?	1	2	4	3	2	1	1	
0	3	1	1	1	0	0	0	0	4	2	?	?	?	3	?	?	?	1	2	4	2	2	2	1	
0	3	1	1	1	0	0	0	0	4	2	?	?	?	4	?	?	?	1	4	4	3	2	1	0	
0	3	1	1	1	0	0	0	0	4	2	?	?	?	4	?	?	?	1	3	4	3	2	1	0	
0	3	1	1	1	0	0	0	0	4	2	?	?	?	4	?	?	?	1	4	4	3	2	1	2	
0	1	1	1	1	0	0	0	0	4	2	2	2	1	4	1	?	0	1	4	4	3	2	1	0	

sults seen here, but considers convergence more likely. The name *Oreomyza* (= *Oreomystis*) *perkinsi* was based on a possible hybrid specimen of which one parent was a Hawai'i Creeper (Amadon 1950:176–177), so hybridization is neither unprecedented nor unreasonable. Furthermore, if Tarr and Fleischer (1995) and Fleischer et al. (1998) are correct that the drepanidine radiation resulted from a recent rapid burst of speciation, then hybridization need not indicate “next-of-kin” relationship, especially because intergeneric hybrids are fairly frequent in birds (Bledsoe 1988a). In the similarly rapidly evolving Darwin's finches, hybridization

has clearly played a role (Grant 1986, 1994), and as Freeland and Boag (1999:584) pointed out, “it is extremely difficult with existing data to differentiate between the effects of lineage sorting and hybridization.” Recently, P. R. Grant (pers. comm. *vide* Thane Pratt) reported a pattern of hybridization and subsequent backcrossing among the Geospizinae that, if it occurred among Hawaiian honeycreepers, could explain the apparent conflict of phenotypic and genotypic data for the Hawaii Creeper. In such a scenario, hybrids would involve primarily, or only, male *Oreomystis* mating with female ‘ākepas or ‘amakihis. Given the song vari-

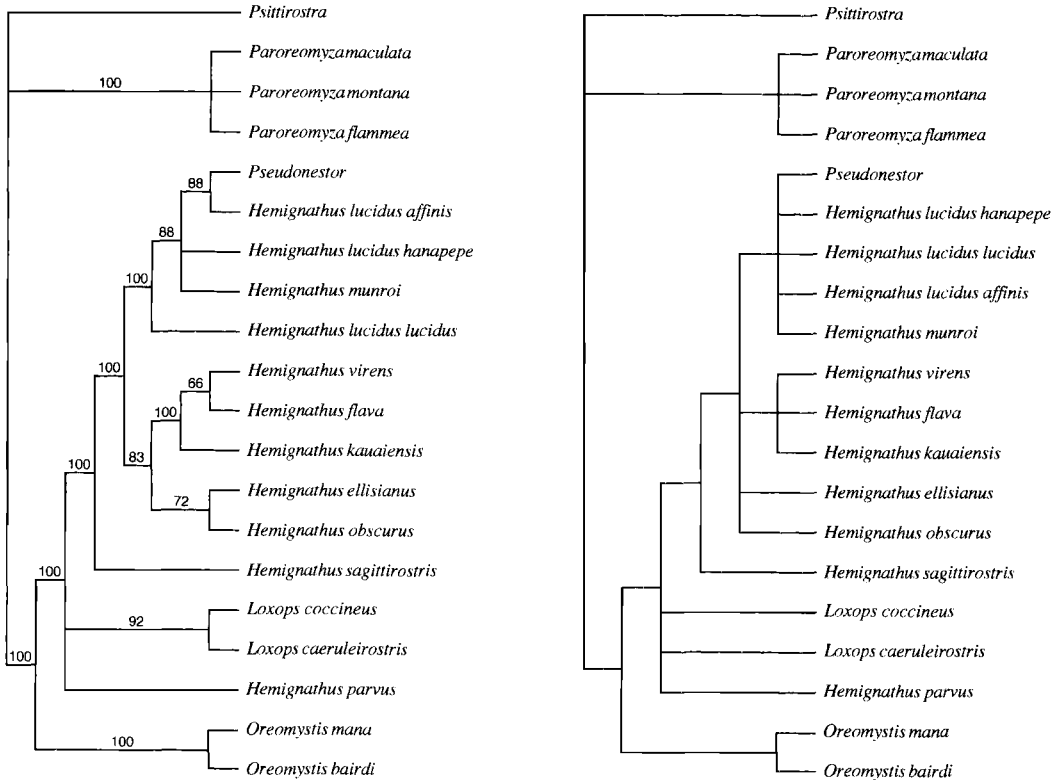


FIGURE 3. Species-level phylogeny of "hemignathine" Hawaiian honeycreepers plus *Paroreomyza* and *Psittirostra*. Left, 50% majority-rule consensus tree; right, strict consensus tree. Taxonomy follows AOU (1998).

ation of the latter two groups and the relative uniformity of *Oreomystis* songs, non-*Oreomystis* females might be more likely to mate with a male *Oreomystis* than *Oreomystis* females to mate with a non-*Oreomystis* male. Offspring of such matings would then mate preferentially with *Oreomystis* or hybrids because males would sing the songs of their fathers and females would respond to songs of their fathers. If the birds with mixed ancestry became the ancestors of the Hawai'i Creeper, then they could retain all of the phenotypic synapomorphies of *Oreomystis* but possess mtDNA, which represents solely the female line of descent, "stolen" from another species. Ongoing studies of nuclear DNA (R. Fleischer, pers. comm.) may help to solve this problem. Of course, the past hybridization event might not have involved the Hawai'i Creeper at all; it could instead be the reason why the 'Akikiki turns up in the "wrong" place in some phylogenies. Indeed, the molecular and osteological phylogenies reviewed here are more similar in their placement of the Hawai'i Creeper than the 'Akikiki.

Removal of the Hawai'i Creeper from the genus *Oreomystis* at this stage would clearly be prema-

ture, especially because we would have no unequivocal alternative. At present, the DNA laboratories offer us three different hypotheses. This analysis of phenotypic characters shows very strong support for the current taxonomy, which is somewhat weakly corroborated by osteological studies and one mtDNA analysis. Furthermore, plausible hypotheses can be offered to explain the observed lack of genetic and phenotypic congruence. Until nuclear DNA studies are completed and possible hybridization is addressed, the prudent course is to avoid taxonomic changes based solely on molecular data. If future studies prove that the evolution of the Hawai'i Creeper was entirely independent of *Oreomystis bairdi*, then the large number and varied character of apparent synapomorphies of these two species will represent one of the most remarkable and noteworthy examples of convergence ever demonstrated. That finding would be exciting, but the burden of proof clearly lies with those who would remove the Hawai'i Creeper from *Oreomystis*. Why is the Hawai'i Creeper an *Oreomystis*? Because that is what the most consistent available evidence shows it to be.

SUMMARY

This study shows that the alpha taxonomy of the Hawaiian honeycreepers currently in use (AOU 1998) has a solid foundation in phenotypic characters. None of the taxa, with the possible exception of *Hemignathus*, are paraphyletic, and generic limits, with a few minor exceptions, are reasonable. Hypothesized relationships at variance with current usage and based on genetic studies must be considered preliminary and tentative until consistent results are achieved. Taxonomic and sequence changes suggested by these results include: 1) the merger of *Chloridops* and *Loxioides*, or at least adjacent placement in the taxonomic order; 2) removal of the 'Anianiau from *Hemignathus* and classification as *Magumma parva*; 3) recognition of four subgenera of *Hemignathus* (*Hemignathus*, *Akialoa*, *Chlorodrepanis*, and *Viridonia*); 4) the placement of *Pseudonestor* adjacent to *Hemignathus*

in taxonomic sequence, or even merger of the two genera; 5) lumping of *Vestiaria* into *Drepanis* and probably also *Palmeria* into *Himatione*; and 6) movement of *Melamprosops* and *Paroreomyza* to the beginning of the sequence, preceding *Telespiza*.

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