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SYSTEMATICS OF THE HAWAIIAN "CREEPERS" *OREOMYSTIS* AND *PAROREOMYZA*[1]

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Abstract. A group of small, insectivorous, straight-billed Hawaiian honeycreepers once regarded as forms of a single species *Loxops maculata* are actually five species that comprise two genera that are not closely related to any others in the subfamily or to each other. The two genera differ in color patterns, plumages, presence of nasal setae, wing/tail proportions, foraging behavior, diet, vocalizations, nest construction, odor, predator-response behavior, tongue morphology, and cranial features. In all respects wherein the Drepanidinae differ from other passerines, *Oreomystis* has the characteristics of the subfamily but *Paroreomyza* does not. Its placement among the Hawaiian honeycreepers is uncertain. *Oreomystis* includes two species, the Hawaii Creeper *O. mana* of Hawaii and the Akikiki *O. bairdi* of Kauai. *Paroreomyza* has three species: the Oahu Alauahio *P. maculata*, the Kakawahie *P. flammea* of Molokai, and the Maui Alauahio *P. montana* with subspecies on Lanai (*P. m. montana*) and Maui (*P. m. newtoni*). The English epithet "creeper" should no longer be used for members of *Paroreomyza*.

Key words: Akikiki; alauahio; Drepanidinae; Hawaiian creeper; Kakawahie; Oreomystis; Paroreomyza.

INTRODUCTION

At the time of European discovery, each of the six main Hawaiian Islands harbored a small, straight-billed, simple-tongued, insectivorous bird. These birds varied widely from island to island in plumage color, and most had distinctive native names: *'akikiki* on Kauai; *'alauahio* on Oahu, Lanai, and Maui; and *kakawahie* on Molokai; the Hawaii representative had no known native name. Latin epithets for the six named forms (ignoring generic designations) are: *bairdi* (Kauai), *maculata* (Oahu), *flammea* (Molokai), *montana* (Lanai), *newtoni* (Maui) and *mana* (Hawaii). All have traditionally been considered to belong to the Hawaiian honeycreepers (Drepanidinae). At first, these birds were allocated among several genera (Wilson and Evans 1890–1899, Rothschild 1893–1900), but soon a consensus developed that they were closely related (Henshaw 1902; Perkins 1903). Early 20th century authors classified the forms as five species in the genus *Oreomyza.* Perkins (1903) recognized two subgenera, *Oreomyza* and *Paroreomyza,* and when the former name was found to have been preoccupied, the latter became that of the genus, despite Stejneger's (1903) emendation of his earlier name (Stejneger 1887) to *Oreomystis.* The type of *Oreomystis* (= *Oreomyza* Stejneger 1887) was *bairdi,* and that of *Paroreomyza* was *maculata.*

Perkins' (1903) subgenera were not recognized by subsequent authors, but Bryan and Greenway (1944) divided the genus into two species along the same lines: *P. bairdi* (including *mana*) and *P. maculata* (including *flammea, montana,* and *newtoni*). Amadon (1950) considered all the forms conspecific and made *Paroreomyza* as subgenus of *Loxops* (into which he also placed several species later included in *Hemignathus*). Amadon (1950:166) offered no biological basis for lumping these forms, but considered this taxonomy more "convenient" than the alternative of recognizing five species. Raikow (1977), citing several distinctions, separated *Paroreomyza* from Amadon's *Loxops* but did not question Amadon's single-species concept. Olson and James (1982) recognized four species and distributed them among three genera as *Oreomystis bairdi, Loxops mana, Paroreomyza maculata* (including *newtoni* and *montana*), and *P. flammea.* This classification appears *ex cathedra*: its basis is as yet unpublished. Berger (1981) and the American Ornithologists' Union (AOU 1983) recognized five species in two genera, based on Pratt (1979) as follows: *Oreomystis* is found on Kauai (*O. bairdi*) and Hawaii (*O. mana*); *Paroreomyza* is found on the central Hawaiian Islands of Oahu (*P. maculata*), Molokai (*P. flammea*), Maui (*P. montana newtoni*), and Lanai (*P. montana mon-*

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tana). This paper sets forth the basis for this classification and amplifies the data I presented earlier (Pratt 1979).

English names for these birds present an etymological tangle. The stable and unambiguous names of Hawaiian origin have, unfortunately, fallen into disuse because of taxonomy that lumped the two genera and their five species into a single species. The name "creeper" was first used in this complex when Henshaw (1902) called *Oreomystis mana,* which had no known native name, the Olive Green Creeper. Munro (1944) extended use of the term to the other forms as well. It is now so entrenched in the literature that its use herein as a taxonomically noncommittal collective for members of *Oreomystis* and *Paroreomyza* is almost unavoidable.

Previous classifications that united *Oreomystis* and *Paroreomyza* in a single species were based almost entirely on studies of museum specimens. None of the "creepers" is highly specialized as compared to other Hawaiian birds, and probably their very lack of striking specializations led to their being lumped. Field observers have consistently commented about the behavioral dissimilarities of *Oreomystis* and *Paroreomyza.* Henshaw (1902:49) accepted the classification developed by museum ornithologists and wrote of the "marked difference in habits between species so closely allied" when comparing *O. mana* and *P. montana.* The following analysis of a variety of characters not only shows consistent variation along the lines represented by the two genera, but also reveals that *Paroreomyza* is a maverick in the entire drepanidine context.

METHODS

Field studies of three populations of *Paroreomyza* are now impossible or nearly so. *Paroreomyza m. montana* and *P. flammea* are extinct (Berger 1981, Pratt et al. 1987) and *P. maculata* has been seen only a few times in recent decades (Shallenberger and Pratt 1978, Bremer 1983). However, *P. m. newtoni* remains common in East Maui (Scott et al. 1986, Pratt et al. 1987). Although *Oreomystis mana* is an endangered species (Pratt et al. 1987) and *O. bairdi* has experienced alarming recent declines (Pyle 1992), both were numerous enough in the 1970s to provide meaningful data for this study. I conducted studies at various places and times on Hawaii (Keauhou Ranch/Kilauea Forest Reserve, August 1974, August 1975, and April–May 1977; Kaloko Mauka Subdivision, May 1977 and February 1978; incidental observations at various seasons at these localities and the Kulani Tract and Hakalau Forest National Wildlife Refuge 1974–1991), Maui (Lake Waianapanapa area, August 1974; Polipoli Springs, April 1975; and numerous short visits to Hosmer Grove in Haleakala National Park and the adjacent Waikamoi Preserve, 1978–1991), and Kauai (headwaters of Halehaha Stream in the Alakai Swamp, June–July 1975; Kokee State Park, May 1976, October 1976, March and May–June 1977, and January 1978; and near Kawaikoi Stream, April and November 1989). I have searched unsuccessfully for *P. flammea* on Molokai (Molokai Forest Reserve, July 1975) and *P. maculata* on Oahu (North Halawa Valley, September 1976; Poamoho Trail, April 1990). In the field I noted foraging behavior, postures, and vocalizations. I also made extensive tape recordings of vocalizations, now archived in the Library of Natural Sounds (LNS), Laboratory of Ornithology, Cornell University. On Kauai and Maui I collected a few specimens prepared as study skins and deposited in the collection of the Louisiana State University Museum of Natural Science. Tissues of the Maui specimens were saved for study by Johnson et al. (1989). I examined study skins in the collections of the Bernice P. Bishop Museum, Honolulu; American Museum of Natural History, New York; and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. I took standard measurements (Baldwin et al. 1931) of bill, wing, and tail and analyzed them using Duncan's (1955) Multiple Range Test. Under the guidance of R. L. Zusi, I examined skulls of *Oreomystis bairdi, O. mana, Paroreomyza montana,* and *P. flammea* at the Smithsonian Institution. I also examined specimens of nests of all species of *Paroreomyza* and *Oreomystis* at the Bishop Museum.

CHARACTER ANALYSIS

Coloration and plumages. The most obvious variation among the species of *Paroreomyza* and *Oreomystis* is in coloration (Pratt et al. 1987). Adult male *P. montana* are bright yellow below and on the forehead, with the dorsum olive green. Male *P. maculata* are greener than Maui birds, with a white belly and undertail coverts and a broad dark streak from the bill through the eye onto the upper auriculars (Shallenberger and Pratt 1978, Pratt et al. 1987). In adult *P. flammea*

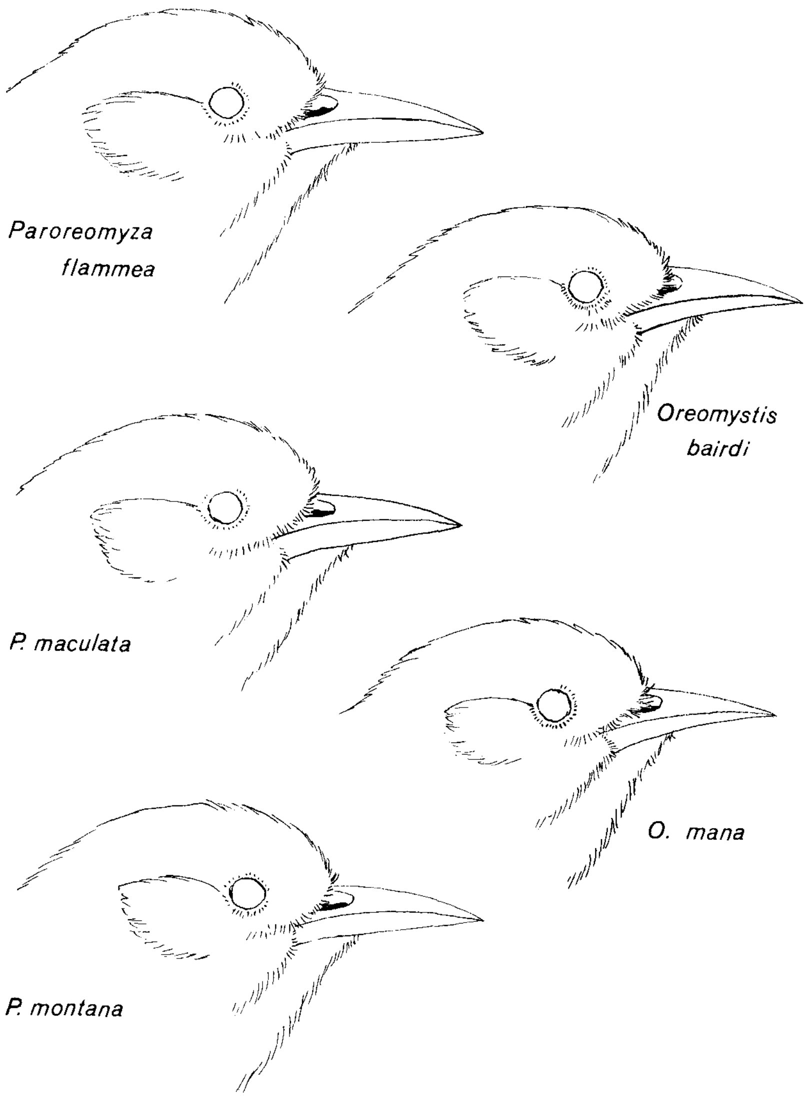

FIGURE 1. Profiles of heads of Hawaiian "creepers."

males, the yellow is replaced by brilliant flame red. The rather bright colors of *Paroreomyza* contrast with the drab ones of both *Oreomystis.* Hawaii Creepers (*O. mana*) are dull gray-green above, dingey white below, and nondescript generally (Scott et al. 1979). Less colorful still is the Kauai species (*O. bairdi*), drab greenish gray above and grayish white below. For color illustrations of all forms and plumages, see Pratt et al. (1987).

Adult females of both *Oreomystis* are identical to the males in color, whereas all *Paroreomyza* are sexually dichromatic. In *P. montana* females are simply less yellow than the males. Female *P. flammea* are reddish brown above and buffy white below, with a variable amount of orange on the throat. Female *P. maculata* differ from males in having pale lores and broad white wing-bars, and in the nearly total loss of yellow pigment. Among other *Paroreomyza,* wing-bars are found only in some immatures. *Oreomystis* never have wing-bars, but their immatures have distinctive plumages. Young *O. mana* have paler sides of the face than adults and a white superciliary, whereas im-

TABLE 1. Measurements of male Hawaiian "creepers" with mean, standard deviation (brackets), range (parentheses), and significance (letters[1]).

Species	*n*	Wing chord	*n*	Tail length	*n*	Bill width	*n*	Culmen	*n*	Bill depth
Oreomystis bairdi	15	52.6 [2.61] (49–59)AB	15	39.3 [2.19] (35–44)E	15	4.92 [0.21] (4.6–5.4)B	15	13.0 [0.66] (12.2–14.6)C	14	5.28 [0.24] (4.9–5.7)A
O. mana	42	51.9 [1.68] (48–55)B	45	40.8 [2.17] (37–47)D	47	4.57 [0.20] (4.1–5.0)C	48	12.6 [0.64] (11.1–14.1)D	39	4.86 [0.33] (4.1–5.5)B
Paroreomyza maculata	20	53.1 [1.74] (50–56)A	22	46.0 [2.65] (40–51)BC	20	5.01 [0.35] (4.3–5.5)B	21	13.8 [0.50] (12.7–14.6)B	20	4.56 [0.26] (4.2–5.0)C
P. flammea	28	50.2 [1.72] (47–54)C	25	51.7 [2.26] (47–56)A	26	5.23 [0.26] (4.8–6.0)A	27	14.3 [0.68] (13.1–15.5)A	24	4.49 [0.31] (3.9–5.0)C
P. montana newtoni	20	49.9 [1.68] (47–54)C	19	45.4 [1.46] (42–48)C	20	4.67 [0.29] (4.2–5.3)C	21	12.2 [0.54] (11.2–13.2)D	19	4.06 [0.25] (3.7–4.6)D
P. m. montana	14	46.4 [1.34] (43–48)D	14	47.2 [0.97] (45–49)B	14	4.41 [0.17] (4.1–4.7)D	15	12.7 [0.60] (11.4–13.7)CD	14	4.00 [0.24] (3.6–4.6)D

[1] Means with the same letter not significantly different ($P < 0.05$).

TABLE 2. Measurements of female Hawaiian "creepers" with mean, standard deviation (brackets), range (parentheses), and significance (letters[1]).

Population	*n*	Wing chord	*n*	Tail length	*n*	Bill width	*n*	Culmen	*n*	Bill depth
Oreomystis bairdi	11	52.0 [1.61] (49–54)A	11	38.8 [1.94] (36–42)D	11	5.05 [0.22] (4.8–5.5)A	9	12.5 [0.37] (12.2–13.0)A	10	5.02 [0.27] (4.6–5.5)A
O. mana	21	50.2 [1.54] (48–53)B	23	40.3 [2.00] (37–45)D	21	4.53 [0.23] (4.0–5.2)D	22	12.2 [0.54] (11.2–13.1)AB	18	4.69 [0.23] (4.4–5.1)B
Paroreomyza maculata	12	49.7 [1.92] (47–54)B	21	42.2 [2.16] (38–46)C	21	4.71 [0.22] (4.2–5.0)BC	21	12.2 [0.54] (11.6–13.7)A	20	4.40 [0.37] (3.8–5.2)C
P. flammea	15	48.0 [1.73] (45–51)CD	15	47.9 [2.50] (44–52)A	11	4.90 [0.29] (4.5–5.4)AB	14	12.5 [0.80] (11.0–14.1)A	10	4.26 [0.25] (3.8–4.6)CD
P. montana newtoni	6	48.7 [1.21] (47–50)BC	6	45.3 [2.07] (42–48)B	6	4.63 [0.43] (4.2–5.2)CD	6	11.5 [0.56] (10.8–12.3)C	6	3.82 [0.09] (3.7–4.0)E
P. m. montana	4	46.3 [1.50] (44–47)D	3	47.7 [2.08] (46–50)AB	3	4.26 [0.15] (4.1–4.4)D	3	11.6 [0.05] (11.5–11.6)BC	3	3.93 [0.05] (3.9–4.0)DE

[1] Means with the same letter not significantly different ($P < 0.05$).

mature *O. bairdi* have distinctive white "spectacles."

The bills of both *Oreomystis* are pale except for a trace of dusky pigment along the culmen. *Oreomystis bairdi* has a pink bill, whereas that of *O. mana* is often nearly white. In contrast, all *Paroreomyza* have the upper mandible dark and the lower one yellow (*P. maculata* and *P. montana*) or red (*P. flammea*).

Bill shape. Most recent observers have noted subjectively different "facial expressions" to the two creeper groups. This difference is attributable to subtle but consistent differences in bill shape (Fig. 1). In *Oreomystis,* the bill is slightly decurved, with an arched culmen and concave gonys. The culmen is also arched in *Paroreomyza,* but the gonys is straight or slightly convex, never concave, and thus the bill looks straight in profile. Richards and Bock (1973) used opposite terms and described the bills of *P. montana* and *P. flammea* as decurved and that of *O. mana* as straight. The seeming disagreement is probably only semantic. These qualitative differences in shape are not revealed by standard linear measurements of bill length, width, and depth (Tables 1, 2).

Nostrils. Both species of *Oreomystis* have nasal setae that are "well developed, so as to be able to shield the whole length of the nasal openings," whereas in *Paroreomyza* these feathers are "entirely absent, or at least very short and little developed" (Perkins 1903:397). A fully developed nasal operculum is present in *Paroreomyza,* but *Oreomystis* has only a partial operculum (Richards and Bock 1973; Raikow 1977, pers. observ.).

Proportions. Relative lengths of wing and tail (Tables 1, 2) vary along the same generic lines as other characters. The wing/tail ratios of *Paroreomyza montana* and *P. flammea* are near unity, whereas those of *Oreomystis bairdi* (1.33) and *O. mana* (1.25) reveal them to be relatively short-tailed (Tables 1, 2). This distinction is not clear-cut, however, because *P. maculata* (1.15 male, 1.18 female) is intermediate in this character.

Foraging behavior. Richards and Bock (1973: 117), who had limited field observations of *Paroreomyza montana,* hypothesized on the basis of its smaller jaw muscles and frail skull as compared to *Oreomystis mana* that the Maui bird could not "probe and pry as vigorously as *mana* and spends more time gleaning its arthropod prey from the surface of leaves and off the bark than probing in crevices." My field observations confirm their prediction. The foraging movements of *P. montana* are distinctly different from those of the two *Oreomystis.* An active, sprightly bird, *P. montana* virtually never clings close to the bark of a tree but rather sits upright, usually with the tarsi clearly exposed. This point is important because considerable confusion has resulted from imprecise use of the term "creeping" in reference to *Paroreomyza.* For example, Henshaw (1902), after describing the creeping behavior of *O. mana,* stated that *P. montana* is "noticeable for the same habit," but then went on primarily to discuss their differences. Richards (in Richards and Bock 1973:22), in reporting his two days of field observations described the Maui Alauahio's feeding "along the small branches . . . and among the twigs and leaves" and further described their foraging with "heads constantly moving, the bills being probed under lichens and among the leaves." Although he stated that "the creeping ability of this race seems as good as that of the Hawaii Creeper," his descriptions all involved feeding methods that could only loosely be called creeping. In my experience, the most frequent foraging site for *P. montana* is among leaves rather than along large branches. In such situations, it gleans its insect prey in a manner similar to that of many wood-warblers (Parulinae). Only about 20% of my observations of *P. montana newtoni* involved birds foraging in any manner that could be called creeping in the broadest sense. They may spiral along a lateral or vertical branch, but usually do so by perching on smaller side branches rather than by clinging to the main axis. By such movements, the birds can give the impression of "creeping," even though they do no true creeping, as exhibited for example by nuthatches (Sittidae) and holarctic creepers (Certhiidae). The foraging behavior of *P. flammea* was apparently similar to that of *P. montana* (Bryan 1908). Recently, two *P. maculata* were observed feeding in leaf axils of *Koa acacia* as well as "creeping up the dead Koa branches probing the bark" (sic) with quick, deliberate movements (Bremer 1986). I believe that the above description is another example of imprecise use of the term "creeping," inasmuch as Engilis (in Bremer 1986) remarked about the long-legged appearance of the birds when they "fed on Koa branches." The legs are probably the least noticeable feature on a bird engaged in creeping as defined herein. Thus *P. maculata* probably forages in much the same way as its congeners.

The foraging of the *Paroreomyza* creepers contrasts strongly with the decidedly nuthatch-like behavior of the two *Oreomystis*. These birds creep slowly over large trunks and branches of trees with the head downward or upward but do not brace with the tail. They are bark-pickers rather than leaf-gleaners, and often perch parallel to the branch on which they are feeding. They crouch low on their legs and seldom perch upright with the tarsi exposed. These characteristic movements are apparently innate and are obvious even in caged birds (Raikow 1974).

Aerial sallies to capture flying insects are very rare among Hawaiian honeycreepers. I have never observed any such behavior in either species of *Oreomystis*. However, the Maui Alauahio (*P. montana*) occasionally feeds in this manner (pers. observ.). Whether the other species of *Paroreomyza* make aerial sallies for insects is not known.

Diet. Both *Oreomystis* and *Paroreomyza* are primarily insectivorous, but *P. montana* also takes nectar (Berger 1981; Carothers 1982, pers. observ.). Comparable data for the other two species of *Paroreomyza* are lacking. I have seen *O. bairdi* visiting ohia-lehua (*Metrosideros collina*) flowers on two occasions, and *O. mana* feeding once in blossoms of naio (*Myoporum sandwicense*), but I have no other evidence of nectarivory in *Oreomystis*. The previously described short nasal setae and full nasal operculum in *Paroreomyza* are probably related to nectar-feeding inasmuch as such features are characteristic of nectarivorous birds generally. Additionally, the horny palate of *P. montana* has a "medial slot with parallel lateral ridges" into which the tongue fits as an adaptation to occasional nectarivory (Richards and Bock 1973:117). Such an arrangement is lacking in *Oreomystis*. Many Hawaiian honeycreepers take nectar, but all others share a distinctive suite of adaptations including a characteristic tubular tongue (Amadon 1950, Raikow 1977) quite unlike the feeding apparatus of *P. montana*. Thus nectar-feeding probably arose independently in *Paroreomyza*.

Vocalizations. The two creeper genera differ strikingly in vocalizations and attendant behavior. *Paroreomyza montana* (Perkins 1903, pers. observ.), *P. maculata* (Bryan 1905), and *P. flammea* (Bryan 1908) all utter a distinctive loud call note variously described as "*chick*" or "*cherk*" (Fig. 2). It is given continuously while the birds forage but is especially noticeable during mobbing. The calls of the two *Oreomystis* (Fig. 2) are "more or less different" (Perkins 1903:414) from those of *Paroreomyza*. Both give an upwardly inflected "*sweet*" that is similar but not identical in the two species. The call varies in intensity but is often very quiet. Hawaii Creepers also have a distinctive fast "*whit-whit, whit-whit-whit*" given by small (family?) groups (Scott et al. 1979, Pratt et al. 1987).

The songs of both *Oreomystis* are short trills (Fig. 2) that resemble somewhat the songs of other Hawaiian honeycreepers such as *Hemignathus virens* and *L. coccineus* (for comparisons, see Scott et al. 1979). *Oreomystis bairdi* also has a complex whisper song like those of several other drepanidines (Pratt 1979), but no whisper song has been reported for *O. mana*. In my experience, both species always sing from a perch. *Oreomystis bairdi* gives both its loud trill and its whisper song while clinging nuthatch-like to large trunks or branches, whereas *O. mana*, although it sometimes sings while creeping, usually perches at right angles to a limb to sing.

The song of *Paroreomyza montana* does not resemble even remotely the trills of the two *Oreomystis*. Henshaw (1902:50) described it as "an ecstatic warbling song . . . quite unlike the voice of any other Hawaiian (sic) bird." The song incorporates the typical call note into a jumble of short modulated whistles and chirps (Fig. 2). The song can be a monotonously repeated stereotypical phrase or a livelier, more continuous warble vaguely reminiscent of some songs of the House Finch (*Carpodacus mexicanus*). The livelier song is heard during aggressive encounters with other Maui Creepers or in association with a display in which the bird, singing continuously, rises into the air and flutters back to its perch (Henshaw 1902, pers. observ.). Unfortunately, the songs of *P. maculata* and *P. flammea* have never been described.

Nests. Hawaiian honeycreepers generally build symmetrical open cup nests rather similar to those of many small passerines (Berger 1981). Usually they are wider than tall, and placed in a crotch or fork that supports the weight of the nest from below. Nests of *Oreomystis bairdi* (Eddinger 1972) and *O. mana* (Sakai and Johanos 1983, Freed et al. 1987) are typical, the latter being, according to Perkins (1903), nearly identical to that of the Common Amakihi (*Hemignathus virens*). *Oreomystis mana* sometimes nests in cavities (Freed et al. 1987). Nests attributed to *Paroreomyza*

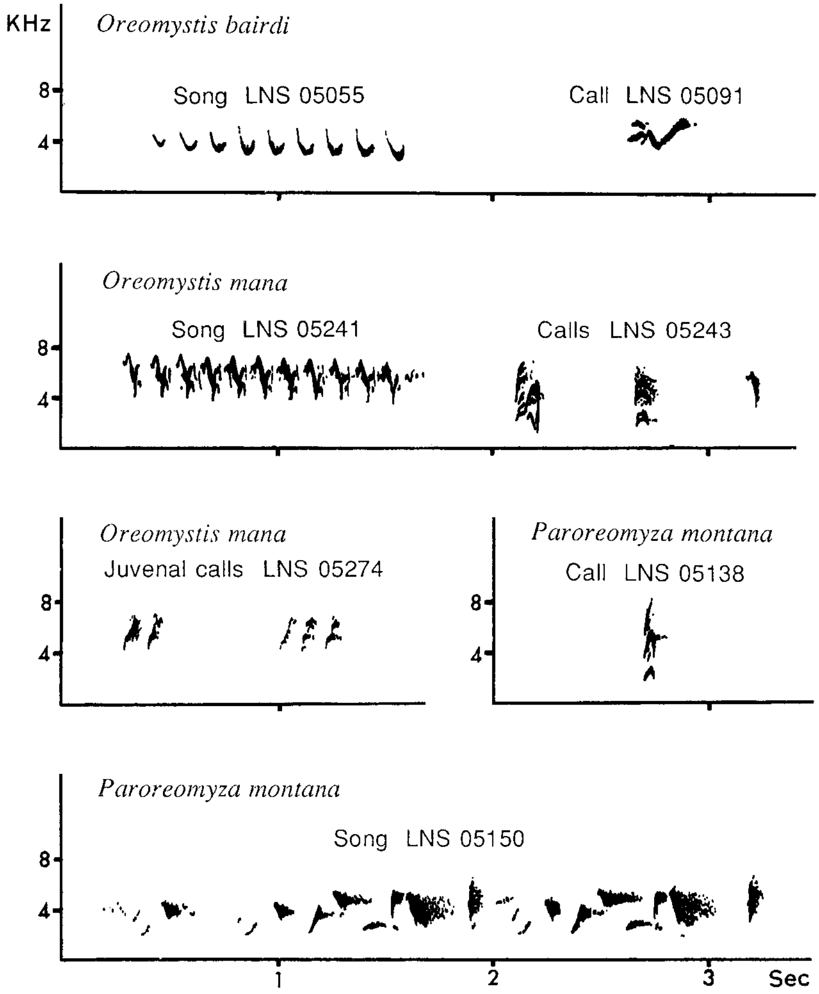

FIGURE 2. Vocalizations of the Hawaiian "creepers" (traced from sonagrams for clarity). Recorded by the author as follows: *Oreomystis bairdi,* Kokee, Kauai, 14 May 1976 (song) and 9 October 1976 (call); *O. mana,* Keauhou Ranch, Hawaii, 1 May 1977 (song), 29 April 1977 (calls), and Kaupulehu Forest Reserve, Hawaii, 3 May 1977 (juvenal call); *Paroreomyza montana,* Polipoli Springs, Maui, 26 April 1977 (call) and 27 April 1977 (song). Catalog numbers from the Library of Natural Sounds, Laboratory of Ornithology, Cornell University.

maculata (Bryan 1905), *P. flammea* (Bryan 1908), and *P. montana* (van Riper 1972, Berger 1981) have been described and are represented in the Bishop Museum collection. They differ from those of *Oreomystis* and other Hawaiian honeycreepers in that they tend to be suspended rather than supported from below. They may have a large vertical support on one side, with secondary support from smaller surrounding branches. Thus they are slightly asymmetrical, often funnel-shaped, and taller than wide. *Paroreomyza* nests are usually built nearer (2.4–6 m) the ground (Bryan 1905, 1908; Berger 1981) than those of *Oreomystis,* whose nests are placed high (6–13 m) in the trees (Eddinger 1972, Berger 1981, Sakai and Johanos 1983).

Odor. Hawaiian honeycreepers possess a characteristic musty scent (Pratt 1992). This "drepanidine odor" has been reported in nearly all genera of Hawaiian honeycreepers, but is notably absent in the probably non-drepanidine *Melamprosops* (Pratt 1992) and in *Paroreomyza* (Perkins, in Wilson and Evans 1890–1899, pers. observ.). Both species of *Oreomystis* have the typical odor, but my freshly collected specimens of *P. montana* lacked it.

Predator-response behavior. Birders have long noted that Hawaiian honeycreepers rarely respond to auditory lures ("spishing" or "squeaking") used to attract birds (Pratt et al. 1987, Homel 1991, Pratt 1992). Further, the related (Emlen 1969) behavior of predator mobbing (Curio 1978) has never been reported in any drepanidine genus other than *Paroreomyza. Paroreomyza montana* readily respond to squeaking and even without such stimuli often gather about an observer and create a noisy commotion. Bryan (1908) reported such behavior also in *P. flammea.* Perkins (in Wilson and Evans 1890–1899) said that *P. montana* mob Short-eared Owls (*Asio flammeus*). I once observed several *P. montana* mobbing a feral cat in the Upper Hanawi rainforest. As the cat crept through the underbrush, the birds followed it and set up a vocal clamor that could be heard from a considerable distance, attracting participants from all directions until perhaps a dozen had gathered. Although such Hawaiian honeycreepers as *Hemignathus virens, Himatione sanguinea, Vestiaria coccinea, Palmeria dolei,* and *Pseudonestor xanthophrys* were nearby, none joined the mobbing flock. On Hawaii, where both the Short-eared Owl and the Hawaiian Hawk (*Buteo solitarius*) sometimes take small birds (Berger 1981) but where no *Paroreomyza* occurs, mobbing behavior has been reported in such non-drepanidine species as the Hawaiian Crow (*Corvus hawaiiensis*) and the Elepaio (*Chasiempis sandwichensis*) (Perkins 1903, Berger 1981), but not in *Oreomystis mana* or any other Hawaiian honeycreeper. Also, neither species of *Oreomystis* "squeaks up," although some nectar-feeding honeycreepers (e.g., *Hemignathus virens, Vestiaria coccinea*) occasionally do so (Pratt 1992).

Tongue morphology. The tongues of both groups of Hawaiian creepers are similar in overall configuration to the tongues of many insectivorous passerines (Gardner 1925). They are narrow and nontubular with the distal end slightly bifid with small lateral and terminal laciniae (Richards and Bock 1973). No other Hawaiian honeycreepers exhibit tongues with this distal configuration, but all others have a snyapomorphic condition of the proximal end of the corneous tongue: they lack the caudal projections ("lingual wings") found in nearly all other passerine tongues (Pratt 1992). The tongues of *Oreomystis bairdi* (Gadow in Wilson and Evans 1890–1899) and *O. mana* (Richards and Bock 1973) share this synapomorphy, but that of *Paroreomyza montana* has prominent lingual wings (Richards and Bock 1973). The only other supposed Hawaiian honeycreeper to possess lingual wings is *Melamprosops phaeosoma* (Bock 1978), which is probably not a drepanidine (Pratt 1992). The presence of lingual wings in *Paroreomyza montana* sets it apart not only from *Oreomystis* but from all other Hawaiian honeycreepers. The similarities of the distal ends of the tongues of *Oreomystis* and *Paroreomyza* are therefore probably the result of convergence.

Cranial features. Richards and Bock (1973) illustrated skulls of *Oreomystis mana* (= *Loxops maculata mana*), *Paroreomyza montana* (= *L. maculata newtoni*), *L. coccineus,* and *Hemignathus virens* (= *L. virens*). My own interpretation of their drawings is that the skull of *O. mana* is much more similar in general appearance and in certain details to the skulls of *L. coccineus* and *H. virens* than it is to that of *P. montana,* which is much frailer and more delicate than the others. The interorbital septum in *O. mana* is, like those of *L. coccineus* and *H. virens,* of the distinctive, nearly complete cardueline/drepanidine type as described by Zusi (1978). In contrast, the septum of *P. montana* is represented only by a narrow band of bone above a very large interorbital fenestrum. My own examination, with the aid of R. L. Zusi, of the skulls of *P. montana* and *P. flammea* revealed that both lack the solid bony palate typical of both the Carduelinae and the Drepanidinae (Sushkin 1929, Amadon 1950). Furthermore, the "lateral flange" of the palatine process of the premaxilla, a presumably derived condition shared by cardueline finches and Hawaiian honeycreepers (Bock 1960), is very small (if really present at all) in the two *Paroreomyza.* Zusi (pers. comm.) considered all of these atypical features "derivable" from the more usual drepanidine conditions, but the possibility that they are not so derived cannot be excluded. In any case, in this suite of characters *Paroreomyza* again stands in contrast not only to *Oreomystis* but to Hawaiian honeycreepers generally.

RELATIONSHIPS

The foregoing review demonstrates that despite the superficial similarities that misled earlier taxonomists, the Hawaiian creepers fall into two well-defined and distinctive groups. Furthermore, far from being conspecific, the two groups may not even be closely related. The two are now regarded as separate genera by most investigators (e.g., Olson and James 1982, American Ornithologists' Union 1983, Johnson et al. 1989, James and Olson 1991). *Oreomystis* possesses all the anatomical features that indicate a close relationship between the Drepanidinae and Carduelinae (Bock 1960, Raikow 1978, Zusi 1978), as well as such characters as drepanidine odor, lack of mobbing behavior, and truncate lingual wings that characterize the Drepanidinae as a taxon (Pratt 1992). In contrast, *Paroreomyza* exhibits none of these characters unequivocally and possesses no phenotypic synapomorphy to ally it with *Oreomystis* or any other drepanidine genus. For these reasons, I earlier (Pratt 1979) suggested that *Paroreomyza* might not truly belong to the Drepanidinae. If it is drepanidine, it would represent an early branch that diverged before the characters that cluster the rest of the honeycreepers evolved. However, *Paroreomyza* must be regarded as highly autapomorphic rather than "primitive" because it would be one of the least cardueline-like drepanidine genera lacking virtually all the characters that support the hypothesis of a cardueline/drepanidine relationship. A biochemical systematic study by Johnson et al. (1989) found *Paroreomyza* to be drepanidine, but not closely related to any other genus. They regarded *Oreomystis* as the sister-group of *Paroreomyza,* but showed a point of divergence as long ago as two million years. These results are consistent with my findings with regard to the distinctiveness of *Paroreomyza,* but not the systematic position of *Oreomystis.*

Oreomystis, unlike *Paroreomyza,* is unquestionably drepanidine, but forms a group separate from the cluster of other thin-billed genera (*Hemignathus, Loxops, Ciridops, Himatione, Palmeria, Vestiaria,* and *Drepanis*), all of which posses the uniquely derived (Raikow 1977) drepanidine tubular tongue. *Oreomystis* probably represents an independent descent from a finchlike drepanidine ancestor. Olson and James (1982) and James and Olson (1991) considered it monotypic, and considered *O. mana* to be closely related to the amakihis (*Hemignathus* in part) and akepas (*Loxops*), all of which they placed in *Loxops.* However, *mana* and *bairdi* are similar in foraging behavior, sexual dimorphism, bill shape, nasal setae, and tongue morphology and differ in these respects from amakihis. Whether any of these resemblances are synapomorphic is problematical. Because their tongues resemble Gardner's (1925) "generalized passerine tongue," at least at the distal end, they could be regarded as symplesiomorphic. However, if their tongues are secondarily derived from the heavier tongue of a finchlike drepanidine ancestor, they might represent a synapomorphy. In either case, the nontubular tongue of *mana* is inconsistent with its placement in any genus (e.g., *Hemignathus* or *Loxops*) whose other members all possess the highly derived drepanidine tubular tongue.

SPECIES LIMITS IN *OREOMYSTIS*

Obviously, two species that are not unequivocally congeneric can hardly be considered conspecific. Because they are isolated at opposite ends of the main Hawaiian Islands, they may represent relicts. Both are nuthatch-like creepers, but they tend to choose somewhat different foraging sites: interior branches of 5–10 cm diameter and large upright trunks for *O. bairdi,* smaller limbs and twigs and occasionally large trunks for *O. mana* (pers. observ.). The interspecific plumage differences in both adults and immatures are greater than those existing between sympatric species pairs of Hawaiian honeycreepers such as *Hemignathus kauaiensis* (= *H. virens stejnegeri* of AOU 1983) and *H. parvus* on Kauai and *H. virens* and *H. sagittirostris* on Hawaii (Pratt et al. 1987). Although the songs of both species are trills, they are readily distinguished by human ears and look rather different in sonagrams (Fig. 2). The Akikiki (*O. bairdi*) rarely sings. I have heard its song, which had not been described previously, only twice despite many hours of observation at various seasons. In contrast, the Hawaii Creeper is quite vocal; I have never observed it for long without hearing the song. Whether the occasional cavity-nesting of the Hawaii Creeper (Freed et al. 1987) represents a significant interspecific difference will not be known until further data are available on the nesting of the Akikiki (Eddinger 1972).

SPECIES LIMITS IN *PAROREOMYZA*

The classification of the various *Paroreomyza* as species or subspecies is somewhat subjective. The conspecificity of the Lanai (*P. m. montana*) and Maui (*P. m. newtoni*) forms is not controversial; their mensural differences (Tables 1, 2) are slight and the only color difference is a subtly but consistently yellower dorsum in the former. *Paroreomyza flammea,* with its striking red males, is very distinctive as compared to the two "yellow" species. This feature alone would justify, in my opinion, the recognition of *flammea* as a full species. Amadon (1950) denigrated the importance of the color difference because, he said, such color shifts are "accomplished readily." This observation does not, however, address the question of whether the color difference is an isolating mechanism. Bill measurements (Tables 1, 2) show significant ($P > 0.05$) differences among the three species with *P. flammea* the largest and *P. montana* the smallest. Noteworthy here is that Molokai, Maui, and Lanai were united as a single island (Maui Nui) during the last glaciation and may have separated as recently as 12,000 years ago (Juvik and Austring 1979, Olson and James 1982). If *P. flammea* and *P. montana* differentiated on the fragments of Maui Nui in such a short time span, we might expect them to resemble each other more closely than either resembles *P. maculata* of Oahu. However, the two Maui Nui forms represent the variational extremes in color and bill size. Bock (1970) considered the bill size difference great enough for the two to coexist on a single island. James and Olson (1991) report *P. montana* fossils from Molokai, where only *P. flammea* survived in historic times. Thus, *P. flammea* and *P. montana* were probably sympatric on Maui Nui, and their differences may represent "character displacement." Because of the likelihood of past sympatry, they must be considered two species.

The status of the Oahu form is more difficult to assess. Adult males of *P. maculata,* although they have noticeable differences, are somewhat similar to those of *P. montana.* However, females and immatures of the Oahu bird, with their pale lores and bold white wing-bars, differ strikingly from their *P. montana* counterparts. Nevertheless, the color differences are not as great as those that differentiate *P. montana* and *P. flammea,* and any ecological or behavioral differences are as yet undocumented. The song of *P. maculata* has never been described; its discovery would help to assess the bird's status. Olson and James (1982) regarded *P. maculata* as conspecific with *P. montana,* but later (James and Olson 1991) split the two. Because the coloration and bill size differences of *P. maculata* seem to be of the same magnitude as those that exist between the sympatric species pairs of Hawaiian honeycreepers previously cited, I also consider it a separate species.

ENGLISH NAMES

The AOU (1983) used the English name "creeper" with various island designations for members of both genera. Pratt et al. (1987) recommended reversion to the name Kakawahie for *P. flammea,* but retained "creeper" in the names of *P. montana* and *P. maculata.* However, reversion to the hawaiian epithet *'alauahio* pronounced *allow-ah-HEE-oh*) for the members of *Paroreomyza* would be more consistent with guidelines for English names established by the American Ornithologists' Union (1983) because the use of "creeper" in *Paroreomyza* implies a closer relationship with *Oreomystis* than probably exists. As a proper name, "creeper" should be restricted to *O. mana* among the Drepanidinae. Because of controversy as to whether the Hawaii Creeper and *O. bairdi* are congeneric, use of the taxonomically noncommittal Hawaiian name Akikiki for the latter is the best course. English names consistent with these suggestions are as follows: Hawaii Creeper (*O. mana*), Akikiki (*O. bairdi*), Oahu Alauahio (*P. maculata*), Maui Alauahio (*P. montana*), and Kakawahie (*P. flammea*).

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