

IS THE POO-ULI A HAWAIIAN HONEYCREEPER (DREPANIDINAE)?¹

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Abstract. The Poo-uli (*Melamprosops phaeosoma*), discovered on Maui in 1973, was originally believed to be a Hawaiian honeycreeper (Drepanidinae). Doubts as to the validity of this classification prompted an investigation of the defining characters of the subfamily and the possible position of *M. phaeosoma* within it. The Drepanidinae are monophyletic with a suite of certain and possible synapomorphies that cluster the group, but *Melamprosops* lacks all of these characters. Hawaiian honeycreepers have a distinctive odor which the Poo-uli lacks. Its tongue has prominent rearward projections whereas drepanidine tongues lack "lingual wings." Most drepanidines lack the usual passerine predator-response behaviors but *M. phaeosoma* exhibits them. Vocalizations of the Poo-uli do not resemble those of any of the three vocal groupings of Hawaiian honeycreepers. The color pattern of *M. phaeosoma* is unique among native Hawaiian birds. Phenotypic characters thus provide no basis for inclusion of *Melamprosops* in the Drepanidinae; its relationships are unknown.

Key words: Poo-uli; Maui; Drepanidinae; drepanidine odor; avian tongues; Hawaiian honeycreepers; *Melamprosops phaeosoma*.

INTRODUCTION

The Poo-uli (*Melamprosops phaeosoma*) is a recently discovered Hawaiian native bird (Casey and Jacobi 1974) with a restricted range in the rainforests of the northeastern slope of Haleakala, Maui (Scott et al. 1986). The bird is a small passerine (length ca. 14 cm) with a short, thick, and vaguely finchlike bill that superficially resembles that of *Ciridops anna* (Casey and Jacobi 1974), a Hawaiian honeycreeper, and those of some small tanagers (pers. observ.). Two study skins with tongues are preserved (Casey and Jacobi 1974). They are dark brown above, buffy below, with rufous-tinged flanks and a broad black mask (see illustration in Pratt et al. 1987). Both skins are now believed to be in immature or subadult plumage. Breeding adults observed in 1986 were plain gray above, white below, with a sharply defined and prominent black mask and lacked most of the rufous and brown tones (A. Engilis, P. Ching, pers. comm.). The Poo-uli has been considered endangered since its discovery (Casey and Jacobi 1974), but its population has now declined to critically low numbers that inhabit a tiny remnant of a range that was already restricted at discovery (Mountainspring et al. 1990). Thus, additional anatomical material is

unlikely to become available and any assessment of the systematic position of *Melamprosops* must be based on existing specimens and observations of live birds.

Casey and Jacobi (1974) initially placed this genus and species in the Hawaiian honeycreepers (Drepanidinae), apparently on the basis of supposed overall resemblances and probably also on geographic probabilities. *Melamprosops* was considered an offshoot of Amadon's (1950) genus *Loxops* (Casey and Jacobi 1974), which Pratt (1979) regarded as a polyphyletic assemblage now dispersed among five genera (AOU 1983). Pratt (1979) and Berger (1981) considered the position of *Melamprosops* among the Drepanidinae uncertain but Amadon (1986), without giving any supporting evidence, saw "no good reason to hesitate to place *Melamprosops* in the Drepanidinae." The following discussions present several reasons for such hesitation.

MONOPHYLY OF THE DREPANIDINAE

Any argument as to whether *Melamprosops* is a Hawaiian honeycreeper is compromised unless the group can be shown to be monophyletic. As in Darwin's finches, another oft-cited avian example of adaptive radiation, the case for monophyly of the Drepanidinae is weak (Baptista and Trail 1988). Perkins (1893) was the first to suggest that the Hawaiian native finches and honeycreepers belonged to a single taxon. His hy-

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pothesis was widely (and rather uncritically) accepted, although Bryan and Greenway (1944) considered the group possibly diphyletic. Amadon (1950) stated that monophyly was "evident, chiefly as a result of Perkins' field work" but ignored the primary character of drepanidine odor, upon which Perkins' (1893, 1903) hypothesis was based. Anatomical studies by Beecher (1953), Bock (1960), James et al. (1989), Raikow (1976, 1977a, 1977b, 1978), Richards and Bock (1973), and Zusi (1978) demonstrated a remarkable uniformity underlying the spectacular adaptive radiation of externally visible characters among Hawaiian honeycreepers. This uniformity is consistent with monophyly (Raikow 1977b), but none of these studies identified any character that clusters the Hawaiian honeycreepers alone, and none included *Melamprosops*. Bock (1978) described several features of the tongue skeleton shared by *M. phaeosoma* with drepanidines, cardueline finches, and some other passerines. The tongue musculature also has several "drepanidine features," most of which are "shared with cardueline finches and some with other nine-primaried oscines" (Bock 1978). Bock claimed that these "features not only support the inclusion of *Melamprosops phaeosoma* in the Drepanididae, but provide further support for the monophyly of the family." The similarities he cites, however, must be regarded as primitive characters that carry no phylogenetic information. Zusi (in Amadon 1986, pers. comm.) found the interorbital septum of *M. phaeosoma* to be of the general type found in cardueline finches and Hawaiian honeycreepers (Zusi 1978), but did not demonstrate that this type represents a synapomorphy.

These anatomical studies plus behavioral and ecological (Pratt 1979; van Riper 1980, 1987) and biochemical research (Sibley and Ahlquist 1982, Bledsoe 1988) produced a consensus that the Carduelinae are the honeycreepers' closest relatives. A recent genetic study (which did not include *Melamprosops*) based on proteins provided support for monophyly of the Hawaiian honeycreepers, but not for the cardueline/drepanidine relationship (Johnson et al. 1989). Nevertheless, I herein consider that relationship to be well established and show that most Hawaiian honeycreepers possess two certain, and other possible, synapomorphies, but that *Melamprosops* and the enigmatic genus *Paroreomyza* do not share them.

CHARACTER REVIEW

Drepanidine odor. Perkins' (1893) suggestion of monophyly of the Hawaiian honeycreepers was based almost entirely on a character that has been denigrated or ignored by recent workers. He noted that the native Hawaiian finches possess the same distinctive and peculiar odor characteristic of the drepanidine nectar-feeders and insectivores. Virtually all collectors of Hawaiian birds noticed the scent, rather like that of old canvas tents, and their reports are remarkably concordant. By sniffing randomly arranged series of specimens of various passerine birds placed in an opaque cloth bag, A. Engilis and I tested each other's ability to detect the odor and found that we could consistently identify drepanidine specimens on that basis alone. Because the scent is easily picked up on the fingers and transferred to specimens that might not originally have possessed it, investigations based on old specimens are potentially misleading. However, abandoned nests retain the odor indefinitely (Perkins 1903, Bryan 1908, pers. observ.) and thus can be used to investigate the distribution of the odor among species. Odor intensity varies within species (Perkins 1903, pers. observ.) and perhaps seasonally (Henshaw 1902). It may be totally lacking in some individuals, especially in species that inhabit dry habitats (Fisher 1906). I have found the odor to be most noticeable in specimens from very wet areas. For example, specimens of *Hemignathus virens* that I collected on the dry leeward slope of Mauna Kea on the island of Hawaii had only a faint scent, whereas those of the same species taken in the rainy Volcano area on the same island had a pronounced odor. These observations are consistent with the probability that the odor is contained in the uropygial secretions used in preening. In wet areas and during rainy seasons, birds would require more frequent application of water-repellent oils.

Variations notwithstanding, the odor has been reported in nearly all drepanidine species but not in any other native or introduced birds living in the same habitats. Perkins (1893, 1901, 1903) reported "drepanidine odor" in *Chloridops kona*, *Rhodacanthis palmeri*, *Loxioides bailleui*, *Psittirostra psittacea*, *Pseudonestor xanthophrys*, *Loxops coccineus*, *Hemignathus virens*, *H. parvus*, *H. sagittirostris*, *H. obscurus*, *H. munroi*, *Palmeria dolei*, and *Drepanis funerea* (taxonomy updated). From my own experience I can add

Vestiaria coccinea, *Himatione sanguinea*, and *Oreomystis bairdi*. A. Engilis (pers. comm.) detected the odor in *O. mana*. The only supposedly drepanidine genus whose members definitely lack the odor is *Paroreomyza* (Perkins 1903, pers. observ.), although it is very weak or lacking in most specimens of *Telespiza* (Fisher 1906, pers. observ.).

I searched carefully for a similar odor among specimens of all other families of nine-primaried oscines housed at the Louisiana State University Museum of Natural Science, where they would not have had contact with drepanidine specimens. Although a few other taxa have odd scents, no other passerines that I have examined smell like Hawaiian honeycreepers. Importantly, I can find no similar odor among the Carduelinae. Because this trait is novel in the cardueline/drepanidine clade as compared to an outgroup of all other passerines, is unique to the Drepanidinae within the group, and is present in nearly all, if not all species, it can be considered a synapomorphy ("canvas odor" as opposed to "no canvas odor") of the Hawaiian honeycreepers. Despite reluctance among many contemporary ornithologists to accept odors as taxonomic characters, drepanidine odor is useful, particularly because osteological and myological studies have thus far failed to demonstrate unequivocal monophyly of the Drepanidinae. Some have suggested that a chemical analysis would be necessary before such a character could be used. However, if we can say that a bird is "red" without a spectrographic analysis, then we can say that it smells like an old tent without subjecting it to gas chromatography (the challenge of doing so in this case has so far proved insurmountable). Non-quantitative characters are not necessarily invalid, and this one is particularly important because it is the historic foundation of the hypothesis of drepanidine monophyly.

Melamprosops phaeosoma apparently lacks drepanidine odor. A. Engilis and I independently examined both the type and the paratype and agree that they have no such scent. Of course, the presence of drepanidine odor in these specimens would not be very meaningful because of the possibility of postmortem acquisition of the scent from researchers' fingers. However, its absence is telling. The lack of odor is unlikely to be only the result of small sample size or rainfall-related variation because the entire range of the Poo-uli lies in an extremely wet area (Scott et al.

1986), where the odor would probably be pronounced. Nor can its absence be attributed to the immaturity of the two specimens (although the ontogeny of drepanidine odor has not been investigated) because young birds would likely have picked up the scent from the adults during brooding or from the nest. Engilis and I found no trace of drepanidine odor in the two Poo-uli nests now in the Bernice P. Bishop Museum collection. This is significant because some very old specimens of drepanidine nests, especially those collected in wet localities, retain the characteristic scent.

Tongue morphology. Another synapomorphy clustering the same drepanidine genera as their odor can be seen at the proximal end of the corneous tongue. In his classic survey, in which tongues of 118 passerines representing a broad sample of families are illustrated, Gardner (1925) described the "generalized passerine tongue" as ending posteriorly "in a free edge which is deeply concave, with the concavity looking caudad and armed with many sharp conical spines which are firm in texture but bend readily." The sides of the concavity are elongated into a pair of caudal projections now called "lingual wings" (fide D. Homberger, pers. comm.). Lingual wings are present in all passerine tongues illustrated by Gardner (1925) except those of a sunbird (Nectariniidae) and two Hawaiian honeycreepers (*Hemignathus procerus* and *Psittirostra psittacea*). A third drepanidine, *Telespiza cantans*, appears from Gardner's (1925) illustration to have lingual wings, but Raikow (1977b) found that the drawing may have been based on a desiccated specimen and that *T. cantans* also lacks them. Subsequent studies have shown lingual wings present in all passerine taxa except Nectariniidae (Scharnke 1932) and Drepanidinae (Raikow 1977b), although the projections may be very short in some of the Meliphagidae (Scharnke 1931, Dorst 1952). Distally, drepanidine tongues reflect the well-known adaptive radiation in bill morphology in the group, but all variations found in unequivocal Hawaiian honeycreepers lack lingual wings (Fig. 1). Genera not shown in Figure 1 possess tongues resembling one or another of those illustrated. The rolled tubular type (Gadow 1899) is present in nearly identical form in *Vestiaria* (Raikow 1977b), *Drepanis* (Rothschild 1893–1900), and *Palmeria* (Wilson and Evans 1890–1899, Henshaw 1902). Nontubular tongues that resemble those shown for *Telespiza* and *Loxioides* have been described for the other finch-

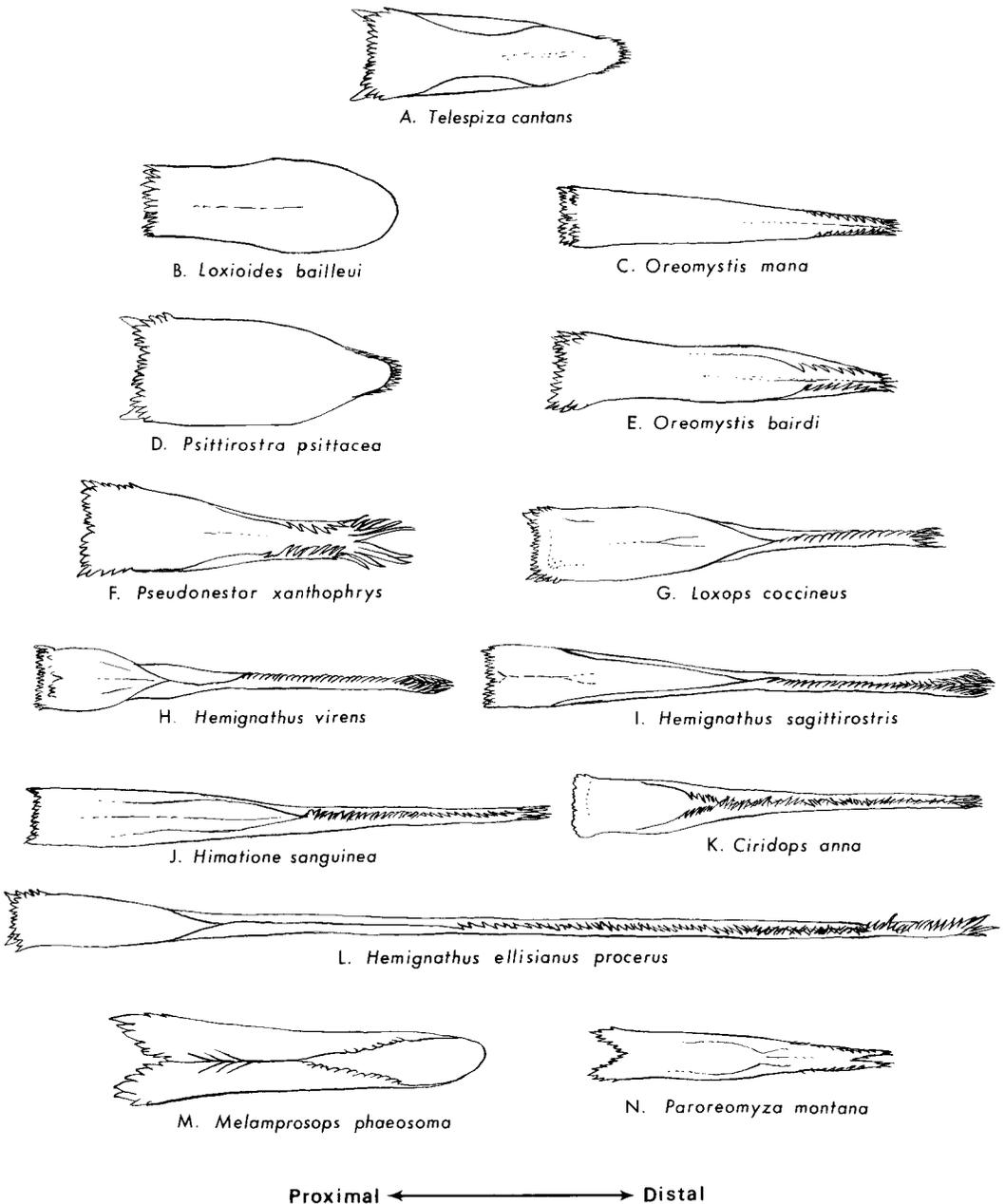


FIGURE 1. Representative tongues of birds classified as Hawaiian honeycreepers: A based on Gardner (1925) with alterations from Raikow (1977b); B, E, and J after Gadow (1899); C, G, H, I, and N after Richards and Bock (1973); D and L after Gardner (1925); F after Frohawk (in Rothschild 1893-1900); K after Bock (1972); M after Bock (1978).

billed genera *Rhodacanthis* (Gadow 1899) and *Chloridops* (Amadon 1950). Thus, the tongue is one of the few anatomical features of Hawaiian honeycreepers for which we have data from all

genera. Raikow (1977b) compared the tongues of drepanidine finches with those of both cardueline and emberizine finches and showed that the drepanidines differed only in lacking lingual

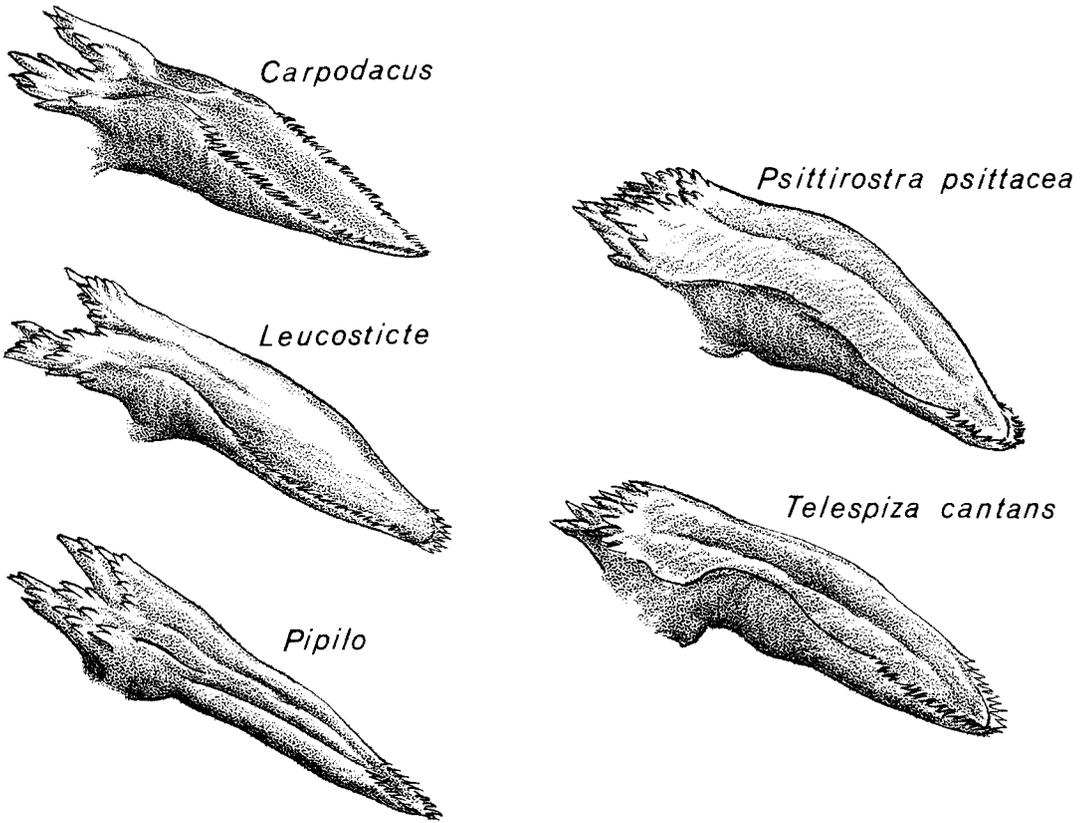


FIGURE 2. Comparison of representative tongues of drepanidine finches (right) and other finch-billed taxa (left), after Raikow (1977b).

wings (Fig. 2). Because this character is restricted to the Drepanidinae within the cardueline/drepanidine clade and is not present in the outgroup of other nine-primaried oscines, it can be regarded as a synapomorphy. The presence of a comparable condition in the ten-primaried Nectariniidae probably is the result of convergence.

The tongue of *Melamprosops phaeosoma* is unlike that of any other passerine yet described (Bock 1978). It is thick and fleshy, with a shallow groove on the dorsal surface that expands distally to form a spoonlike depression, the sides of which have a few blunt serrations. Bock (1978) regarded these serrations as vestiges of the laciniae that form the tube of the rolled tubular drepanidine tongue, implying that it evolved from that type of tongue. The tip of the tongue is rounded and smooth, lacking any trace of the fringed tip or bifurcation characteristic of most passerine tongues (Gardner 1925, Bock 1978). The tip bears little resemblance to the "seed-cup" tongues of

cardueline and some drepanidine finches and is apparently adapted to a diet of terrestrial mollusks (Baldwin and Casey 1983). Such a specialization is unique among Hawaiian passerines. Posteriorly, the tongue exhibits a prominent pair of caudal projections armed with large tubercles and thus differs from the tongues of Hawaiian honeycreepers in the one respect that sets them apart from those of other nine-primaried oscines. It is notable that *Paroreomyza montana*, which, like *M. phaeosoma*, lacks drepanidine odor, represents the only other supposedly drepanidine genus to possess lingual wings (Richards and Bock 1973).

Behavior. Observers accustomed to continental avifaunas have long noted that Hawaiian honeycreepers are seldom attracted by "squeaking," the auditory lures widely used to attract birds (Homel 1991, pers. observ.). Many species, including *Loxioides bailleui*, *Hemignathus munroi*, *Pseudonestor xanthophrys*, *Loxops coccineus*, *L.*

caeruleirostris, *Oreomystis mana*, and *O. bairdi*, virtually never "squeak up." In my own experience and that of A. Engilis (pers. comm.), only the nectar-feeding species such as *Himatione sanguinea*, *Vestiaria coccinea*, and *Palmeria dolei* do so with any regularity. Perkins (1903) reported possibly comparable behavior in both now-extinct species of *Drepanis*. The amakihi *Hemignathus virens*, *H. kauaiensis*, and *H. parvus*, which occasionally feed on nectar, sometimes respond to spishing but usually do not. In contrast such other Hawaiian passerines as *Corvus hawaiiensis* (Perkins 1903), *Chasiempis sandwichensis* (pers. observ.), and *Myadestes obscurus* (pers. observ.) readily squeak up.

Response to squeak lures is believed to be related to predator mobbing (Emlen 1969). True mobbing (Curio 1978) has never been reported in any drepanidine genus other than the enigmatic *Paroreomyza* (Perkins in Wilson and Evans 1890–1899, Bryan 1908, Pratt 1979). Some of the same nectar-feeding honeycreepers that respond to squeak lures also engage in "approach-and-follow" behavior directed at humans. Such behavior has been noted in *Palmeria dolei*, *Drepanis funerea*, and *Vestiaria coccinea* (Perkins 1903, pers. observ.), all nectar feeders, but has not been reported in the finchlike or primarily insectivorous species. Although few avian predators are now present, the existence of drepanidine bones in fossil owl pellets (Olson and James 1982) shows that predation was probably an important selective force in the evolution of Hawaiian honeycreepers. Thus, the apparent absence of mobbing behavior in most species is puzzling, particularly when such behavior has been documented in many cardueline finches and is believed to be innate (Hinde 1954, Altmann 1956). Whether the lack of response to squeak lures and the absence of predator mobbing are synapomorphies of the Drepanidinae cannot yet be determined because insufficient data are available on the occurrence of such traits in passerines generally. Altmann (1956) found no taxonomic correlation with the presence of mobbing behavior. Nevertheless, any species that differ strikingly from most drepanidines in these behaviors should not be uncritically classified with them.

The Poo-uli appears to be such a species. Engilis (1990) reported both response to auditory lures and approach-and-follow behavior, but actual predator mobbing by the Poo-uli has not been observed. Although the nectar-feeding hon-

eycreepers (currently Tribe Drepanidini) exhibit similar behaviors, *Melamprosops phaeosoma* has none of the other characters of that group (Pratt 1979).

Vocalizations. Avian vocalizations can provide meaningful inferences about relationships at lower taxonomic levels. Mundinger (1979) showed that despite the influence of learning, some calls of cardueline finches are useful taxonomic characters at the family level. Isler and Isler (1987) stated that tanager genera could be identified in the field by vocalizations alone. Pratt (1979) found that Hawaiian honeycreepers can be clustered on the basis of vocalizations into groups (the tribes of the 1983 AOU Check-list) that coincide with those based on other characters. Most drepanidine species fall into three large vocal groupings: the finchlike species (Psittirostrini), the red-and-black nectar feeders (Drepanidini), and the thin-billed insectivores (Hemignathini). If *Melamprosops phaeosoma* could be shown to vocally resemble any of these groups, the case for including it among the Drepanidinae would be strengthened.

The songs of drepanidine finches have often been likened to those of various carduelines. The song of *Telespiza cantans* is "loud, melodious, and canarylike, even to the inclusion of trills," and its call notes are also "melodious, some resembling those of the canary" (Berger 1981:112), a cardueline. Fisher (1906) said the calls were "linnetlike," another cardueline comparison. *Telespiza ultima* also has a "canarylike" song, as do (or did) *Loxioides bailleui* (Pratt et al. 1987), *Chloridops kona* (Munro 1960), and *Psittirostra psittacea* (Perkins 1903, Pratt et al. 1987). The exact meaning of "canarylike" is usually unstated. Berger (1981:116) was more specific in stating that the song of *Telespiza ultima* has a "distinct canarylike quality, containing trills, whistles, and warbles." Each of the canarylike songs is distinct and recognizable in its own right, but all are long, complex, unsteretyped, and include varied, frequency-modulated, sustained notes.

The Drepanidini whose vocalizations have been described (*Himatione*, *Palmeria*, *Vestiaria*, and *Drepanis*) have long been recognized as a vocally distinct species-group despite wide divergence *inter se* (Perkins 1903). They resemble the canarylike songs in complexity and lack of stereotypy (Ward 1964), but as a group are characterized by peculiar bell-like or metallic qualities to the notes and often include squeaky or

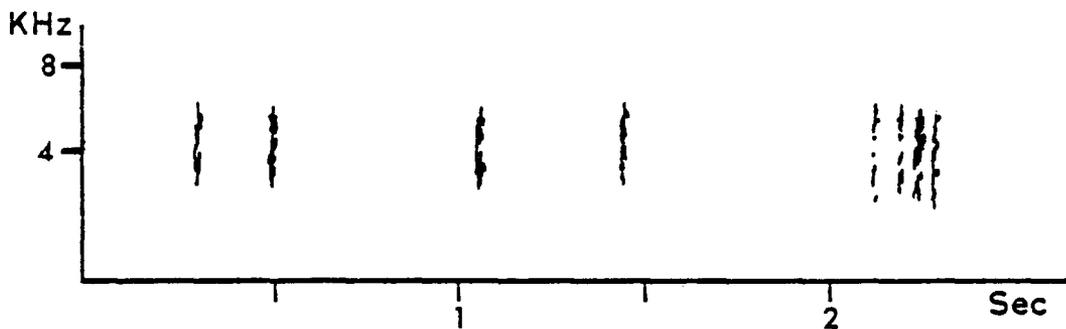


FIGURE 3. Sonagram (Library of Natural Sounds, Cornell Laboratory of Ornithology, No. 5125) of call notes and a short song segment uttered by an immature Poo-uli. Recorded by the author 27 July 1975 in Upper Hanawi watershed, Koolau Forest Reserve, Maui.

mechanical-sounding phrases (Perkins 1903, Pratt et al. 1987). This group also lacks a clear-cut distinction between calls and songs. Calls of the Drepanidini usually represent notes that also are elements of the more complex songs, and some species, such as *Vestiaria coccinea*, exhibit a virtual continuum between single-note calls and complex songs (pers. observ.).

In the Hemignathini, canary-like vocalizations are present only as subsongs (Pratt 1979). The primary songs of all species are simple, rather stereotyped warbles or trills. The notes lack any bell-like or metallic qualities and sound much the same as the trills and warbles that form parts of the more complex songs of the Psittirostrini (Pratt 1979, Pratt et al. 1987). Call notes of the Hemignathini are obviously different from primary songs both in function and complexity and are not incorporated into the longer vocalizations. This vocal grouping includes *Hemignathus*, *Loxops*, *Oreomystis*, and *Pseudonestor*. *Pseudonestor* was placed in the Psittirostrini in the 1983 AOU Check-list, but Pratt (1979) considered it to belong to the Hemignathini, partly on the basis of vocal similarities. Sonagrams of some hemignathine songs are given by Scott et al. (1979).

Melamprosops phaeosoma does not fit into any of the three vocal groupings of Hawaiian honeycreepers even though its call notes resemble those of several other Maui forest birds (Pratt et al. 1987, Mountainspring et al. 1990). The song comprises short, sharp, chips identical to the single-note calls but faster paced with some variation in pitch and rhythm (Engilis 1990). Before nesting birds were observed in 1986, such vocalizations were not even recognized as the pri-

mary song. Mountainspring et al. (1990) stated that a "developed song similar to that of other Hawaiian honeycreepers has never been observed," and Pratt et al. (1987) also considered the song unknown, but both describe vocalizations that in retrospect are probably fragmentary songs. Figure 3 shows such a short song uttered by a juvenile. The full adult song, which comprises a more extensive series of similar notes (Engilis 1990), has never been recorded. This song does not remotely resemble that of any Hawaiian honeycreeper. Although these observations do not preclude the possibility that the Poo-uli is a Hawaiian honeycreeper, they provide no support for such a classification. The only other supposed drepanidine whose vocalizations do not "fit in" is the problematical *Paroreomyza montana* (Pratt 1979).

Coloration. Among Hawaiian honeycreepers, plumage color and pattern varies less among species than such features as bill morphology. Among the Hemignathini are many green species (Pratt et al. 1987) that differ in bill shape and little else. Indeed, certain species of *Hemignathus*, *Loxops*, and *Oreomystis* present considerable problems for field observers (Scott et al. 1979, Pratt et al. 1987). The Psittirostrini are nearly all colored in olive green and yellow, whereas the Drepanidini are known as the "red-and-black group" (Perkins 1903).

The colors and pattern of the Poo-uli are unlike that of any previously known Hawaiian honeycreeper (Casey and Jacobi 1974). The coloration of both the juvenile (brown and buff) and adult (gray and white), without any trace of yellow, are distinctive. Casey and Jacobi's (1974) color photograph, taken inside a yellow tent

(T.L.C. Casey, pers. comm.), is misleading in making the bird look green. Thus, plumage color and pattern provide no basis for inclusion of *Melamprosops phaeosoma* among the Drepanidinae.

DISCUSSION AND CONCLUSION

The above review shows that the classification of *Melamprosops phaeosoma* among the Drepanidinae has virtually no phenotypic basis. Indeed, these characters indicate that its relationships probably lie elsewhere. The Poo-uli does not look, smell, act, or sound like a Hawaiian honeycreeper, and its tongue lacks a derived state that clusters all drepanidine genera except *Paroreomyza* (which may also be incorrectly classified, but to which *Melamprosops* is probably not related). If future biochemical studies indicate that *Melamprosops* is drepanidine after all, some hypothesis will be required to explain the near absence of phenotypic expression of the relationship. At present, the only unequivocal statement that can be made about the affinities of the Poo-uli is that it is a nine-primaried oscine of uncertain affinities ("incertae sedis"). Speculation as to its actual relationships would, at present, be baseless. Because it casts doubt upon the most likely possibility, my hypothesis of what it is not is a first step toward determining what it is.

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