

THE HAWAIIAN HONEYCREEPERS (AVES, DREPANIIDAE)

DEAN AMADON

BULLETIN
OF THE

AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 95: ARTICLE 4 NEW YORK: 1950

THE HAWAIIAN HONEYCREEPERS (AVES, DREPANIIDAE)

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 95, article 4, pages 151-262, text figures 1-23,
plates 9-15, tables 1-15

Issued December 11, 1950

Price: \$1.75 a copy

THE HAWAIIAN HONEYCREEPERS
(AVES, DREPANIIDAE)

DEAN AMADON

*Associate Curator
Department of Birds*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 95 : ARTICLE 4
NEW YORK : 1950

CONTENTS

INTRODUCTION	157
THE HAWAIIAN ENVIRONMENT	160
SYSTEMATICS AND DISTRIBUTION	163
ANALYSIS OF MEASUREMENTS	178
MOLTS AND PLUMAGES	193
COLOR AND COLOR PATTERN	197
FEEDING HABITS	199
SONG, NESTING, AND LOCOMOTION	206
PARASITES, DISEASE, AND EXTINCTION	209
COMPARATIVE ANATOMY	213
Skeleton	213
Soft Parts.	221
PHYLOGENY OF THE GENERA AND OF THE FAMILY	231
SPECIATION	234
MACRO-EVOLUTION.	241
SUMMARY	251
APPENDIX 1. NATIVE LAND AND FRESH-WATER BIRDS (EXCEPT DREPANI- IDAE) OF THE HAWAIIAN ISLANDS	254
APPENDIX 2. EXPLANATION OF LOGARITHMIC RATIO DIAGRAMS	258
LITERATURE CITED	260

Page 156 is blank.

INTRODUCTION

KNOWLEDGE OF THE DREPANIIDAE¹ began with the discovery of the Hawaiian Islands by Captain Cook in 1778. His expedition obtained a number of Hawaiian birds later described by Latham, Gmelin, and other ornithologists. Another early expedition that visited the Hawaiian Islands was the United States Exploring Expedition of 1838-1842 led by Wilkes with T. R. Peale as naturalist. These and other explorers secured some Hawaiian birds that quickly became extinct and are scarcely known otherwise.

In the closing decades of the nineteenth century the eminent ornithologist Alfred Newton became interested in the Hawaiian avifauna (Newton, 1892). Scott B. Wilson, through arrangements made by Newton, spent several months in the islands and discovered a number of new birds. After Wilson's return to England he published, with the aid of A. H. Evans, a monograph, "Aves Hawaiiensis" (1890-1899), illustrated with colored plates by F. W. Frowhawk. Hans Gadow contributed valuable supplements to this work on the anatomy and relationships of Hawaiian birds.

One of Newton's pupils, Walter Rothschild, sent his collector, H. C. Palmer, to the Hawaiian Islands where he worked for a number of years. Palmer discovered many new birds and secured a specimen or two of several species then almost extinct. His collection became the basis of Rothschild's "Avifauna of Laysan and the Hawaiian possessions" (1893-1900), a monograph illustrated with colored plates by J. G. Keulemans and figures of the tongues of *Ciridops*

anna and other extinct species. Rothschild included a bibliography of Hawaiian ornithology. Recently H. I. Fisher (1947) published a bibliography covering the period from 1890 to 1946.

Although Rothschild traded or sold part of the great collection of Hawaiian birds amassed by Palmer, most of it came to the American Museum of Natural History where it formed the principal basis for the present study.

In 1892 Newton, as chairman of a committee representing several English scientific societies working in cooperation with the Bishop Museum in Honolulu, was instrumental in sending Dr. R. C. L. Perkins to the Hawaiian Islands to gather material for monographs on the Hawaiian land fauna. Perkins devoted himself to this task with great zeal for more than a decade. To the "Fauna Hawaiiensis" Perkins contributed, in addition to monographs of several orders of insects, the section on birds (1903) and the valuable general introduction and review of the Hawaiian fauna (1913). Perkins was a trained biologist, greatly interested in speciation and other phases of evolution. His conclusions on the origin, relationships, and evolution of the Hawaiian fauna were by far the most important contribution to this subject made up to that time as will be evident from numerous references to them in the following pages.

Recently Elwood C. Zimmerman (1948), entomologist for the Bishop Museum and the Hawaiian Sugar Planters' Association, published the first five volumes of a monograph of the insects of Hawaii. The introductory volume of this work is a copiously illustrated discussion of the geography, geology, and ecology of the Hawaiian Islands and of the evolution of the Hawaiian fauna and flora, with particular reference to insects. Much of the information in the following section is condensed from this valuable work.

Palmer's assistant in the Hawaiian Islands when he was collecting for Rothschild was a young New Zealander, George C. Munro, who settled in Hawaii. Many years later (1944) Munro published a handbook, "Birds

¹ The family name has usually been spelled Drepanidae. Sushkin used Drepanidae, and Mayr (1943, p. 46) favors Drepaniidae. The last-named form has been used here, but I only recently learned of a family of fishes, Drepanidae (genus *Drepane*), and of a family of moths, Drepanidae (genus *Drepana*). To lessen confusion, it will probably be best to retain the spelling Drepaniidae for the avian family and consider it to be based on the genitive of the Greek word *drepanis*, meaning "a bird with sickle-like wings," from *drepane*, a sickle. The derived Latin word does not, it is true, add the syllable *id* in the genitive. It may be necessary for the International Committee to fix arbitrarily names for these three families.

of Hawaii," that is one of the best sources of information on the habits of the honeycreepers.

The American naturalist H. W. Henshaw, later chief of the United States Biological Survey, lived in the Hawaiian Islands for a number of years. He published (Henshaw, 1902) a little volume on Hawaiian birds that ranks with the works of Perkins and Munro as a source of information on their life histories. Henshaw's specimens were better prepared and more fully labeled than those of any other large Hawaiian collection. Some of his specimens were widely dispersed, but most of them were bought for the Bishop Museum by the late Miss A. Alexander.

Which members of the Drepaniidae were described by each of the authorities mentioned above may be determined from the original citations of scientific names to follow. The number of new forms diminished very rapidly with time, so that Perkins found only one new species (*Drepanis funerea*, described by Newton) while Henshaw found none at all. Although Rothschild described the largest number of new drepaniids, these were, as mentioned above, all secured by his collectors, Palmer and Munro. Scott B. Wilson was the only naturalist to describe several new drepaniids that he had collected himself. The last valid member of the Drepaniidae to be described was *Telespyza [Psittirostra] ultima* from Nihoa Island, named by Bryan in 1917. The above historical résumé mentions only a few of the salient facts. Several authors from the time of Newton (1892) to Bryan and Greenway (1944) have given rather complete accounts of the discovery of the Hawaiian avifauna.

Less comprehensive, though important, publications on Hawaiian birds have appeared from time to time. They are mentioned in the following pages and appear in the list of references.

My special interest in the Drepaniidae began when I arranged and combined the specimens of this family in the Rothschild Collection with those already in the American Museum of Natural History. This was done under the supervision of Dr. Ernst Mayr, and together we compared the various forms and sought for a natural sequence of the genera and species. I was impressed, as is everyone

who examines these birds, by the great diversity in their bills (and correlated with this, as we know, in structure of the tongue and in feeding habits). This diversity is so great that the various species were at first divided among several different families. Later, when it became evident, chiefly as a result of Perkins' field work, that they are all closely related members of an endemic Hawaiian group, the Drepaniidae proved to be a striking example of adaptive radiation. In this connection they are often cited in general works on evolution and adaptation.

In the 60 years that have passed since the great monographs of Hawaiian birds were published the study of systematics, genetics, and evolution has made great strides. The Bird Department of the American Museum of Natural History, especially through its Whitney South Sea Expedition, has contributed to this advance. Mayr's volume "Systematics and the origin of species" (1942) and a series of technical reports now numbering well over 50 are concrete evidence of this. The Hawaiian Islands were not visited by the Whitney expedition because of the existence of large collections from there and the precarious status of many of these birds.

Lack's (1945, 1947) extensive studies of the Galápagos finches are also important contributions to our knowledge of the birds of the Pacific islands. These diversified finches are notable for the part they played in Darwin's early studies on the mutability and evolution of species.

These recent studies of Pacific birds made it all the more desirable that the Hawaiian honeycreepers, in many ways the most remarkable of them all, should receive comparable attention. The field experience that should precede such a study was realized unexpectedly when I was stationed in the Hawaiian Islands from April, 1944, until August, 1945, while a member of the United States Army. Most of this time was spent on the Island of Oahu. It was usually possible to spend one day a week during this period studying in the bird room of the Bishop Museum and to make occasional field trips into the mountain forests where two species of Drepaniidae are still common. For over two months I was stationed on Hawaii, the largest of the islands. Here several other

species of Drepaniidae were observed, largely under the capable guidance of Dr. Paul Baldwin, then with the Hawaii National Park.

The present study has profited greatly by advice from many quarters. David Lack, Ernst Mayr, and Elwood C. Zimmerman read the entire manuscript critically. Sir Peter H. Buck, Director of the Bishop Museum, and the members of his staff gave me all possible help. This paper was presented to the faculty of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The members of my committee at Cornell, Professors Arthur A. Allen, William J. Hamilton, Jr., A. H. Wright, and

Perry W. Gilbert, aided me in many ways, as have the members of the Bird Department of the American Museum of Natural History. The first draft of this paper was written while I was in the Army and before the appearance of Lack's studies of the Geospizinae. On many questions we reached similar conclusions independently; on others my opinions have been influenced by perusal of his publications.

Since Paul H. Baldwin is continuing his extensive studies of the life histories of members of the Drepaniidae, such material has been included here only in so far as it bears upon evolution.

THE HAWAIIAN ENVIRONMENT

THE HAWAIIAN ISLANDS lie approximately 2000 miles west of California. To the west and south the nearest volcanic islands are the Marquesas group, some 2000 miles away. Samoa is about 2300 miles distant and Fiji 2800 miles. The nearest continental islands off Asia (Japan) are well over 3000 miles away. Few other islands of any size are so isolated.

Eight islands of the Hawaiian group are inhabited by members of the family Drepaniidae. Their areas and maximum elevations are given in table 1 and their relative positions shown in the map (fig. 1). The Hawaiian Islands consist of a group of main islands in the southeast and a chain of leeward islands, all of very small size, stretching out several hundred miles to the northwest. Of the latter, only Laysan and Nihoa are inhabited by drepaniids or other land birds. Niihau and Kahoolawe in the main islands doubtless once had land birds, but the forests and birds disappeared before the latter were made known to science. The distances between the main islands in land miles range from 73 (Kauai to Oahu) to 9 (Lanai, Maui, Molokai). Hawaii is 29 miles from Maui, while Molokai is 26 miles from Oahu. Nihoa

islands combined. The elevations of Mauna Kea and Mauna Loa, its two highest mountains, are approached by the great volcanic cone of Haleakala on Maui, whose crater is the largest in the world. Nihoa is merely the peak of a mountainous island once higher and larger. Laysan is a coral atoll. The volcanic peak on which it presumably rests nowhere reaches the surface at the present time (table 1).

According to Stearns (1946): "The Hawaiian Archipelago is a group of islands, reefs and shoals strung out from southeast to northwest for 1,600 miles. . . . Seemingly the larger high volcanic islands were built above sea level in Tertiary times, possibly as late as the end of the Pliocene" (pp. 2, 85). The volcanoes then became extinct and erosion began. "This erosion period was long, for deep canyons and high cliffs are found on all the islands, the lateritic soil 5 to 100 feet thick was formed. Then followed a period of great submergence, amounting probably to more than 2,500 feet, accompanied by a new epoch of volcanism when secondary outbreaks continuing into Recent time occurred on all the major islands except Lanai. The islands have undergone a complex series of emergences and submergences. . . . Volcanoes on adjacent islands may have a more closely related history than those on the same islands, because the number of volcanoes incorporated in any particular island depends on the present level of the ocean and is, therefore, entirely fortuitous. . . . Maui, Molokai, and Lanai would be joined if the sea fell 250 feet" (pp. 1, 14, 95, 96).

The channel between Hawaii and Maui is about 6000 feet deep, that between Molokai and Oahu about 2000 feet, and that between Oahu and Kauai over 10,000 feet. Although Maui, Lanai, and Molokai were probably joined at times into a single land mass, the other islands were always separated by channels of considerable depth. Most of the islands are made up of a number of volcanoes and hence may represent the fusion of several small islands.

The shorter estimates of the age of the Hawaiian Islands, such as the estimate of

TABLE 1

AREAS (IN SQUARE MILES) AND ELEVATIONS
(IN FEET) OF THE HAWAIIAN ISLANDS

Island	Area	Maximum Elevation
Hawaii	4030	13,784
Maui	728	10,025
Lanai	141	3,370
Molokai	260	4,970
Oahu	604	4,025
Kauai	555	5,170
Nihoa	0.2	895
Laysan	2	50

is about 175 miles northwest of Kauai and Laysan another 650 miles beyond Nihoa.

It will be noted that all the main islands are of relatively great elevation for their size. The area of Hawaii much exceeds that of the other

Stearns, were based on surface studies of the rate and volume of lava flows and similar evidence. More fundamental approaches to the problem of the age of the Pacific islands, such as the deep borings and the seismic-refraction survey recently made on Bikini Atoll (1949, Dobrin *et al.*, and included references), indicate that the Pacific basin has been sinking with relative rapidity throughout most or all of the Tertiary period. This subsidence may have been as great as 5000 feet or more. Borings to 2556 feet on Bikini

may be correct in his belief that the great complexity and endemism of the Hawaiian biota indicate that some of its components became established as early as the Eocene.

Intermittent volcanic activity probably had an adverse effect on the evolution of the Hawaiian fauna. It is known, however, that lichens appear on lava flows not many centuries old and after a few thousand years the tree *Metrosideros*, a pioneering species, becomes established. Further evidence of the potential rapidity of such processes is the col-

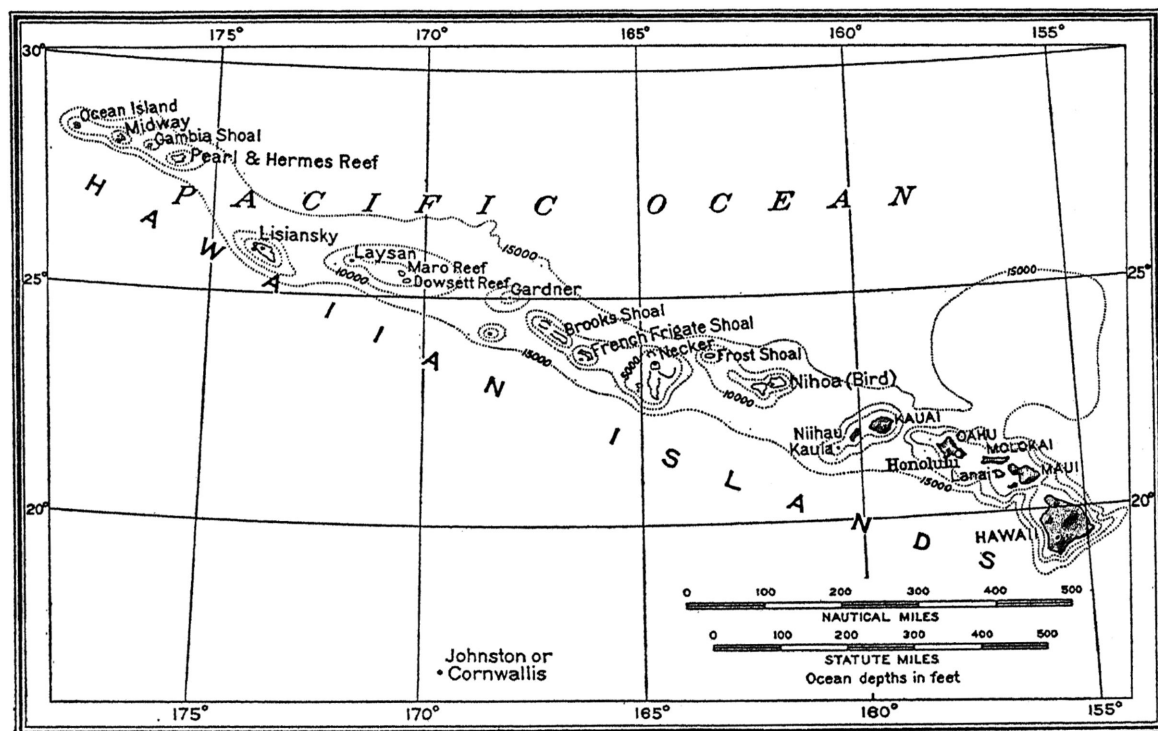


FIG. 1. Map of the Hawaiian Islands.

had already reached a lower Miocene fauna and there were still an estimated 5000 to 10,000 feet more of untapped calcareous deposits resting on the igneous substratum of the island. It is thus evident that the present status of many mid-Pacific islands can tell us little of their former size or their age. The Hawaiian Islands may be as old as the Eocene or even Cretaceous. Insignificant rocks or atolls, e.g., the Hawaiian leeward chain or the Marshall Islands, may have been large islands during much of the Tertiary. Perkins (1913)

onization of the island of Krakatau by hundreds of species of animals and plants during the interval since it was deeply covered with hot volcanic ash by the explosion of 1883 (Dammerman, 1948). Krakatau is, to be sure, rather close to Java and Sumatra.

In historic times Hawaii is the only island of the group that has active volcanoes. Mt. Haleakala on Maui, according to legend, erupted about 1750. The other islands have been quiescent for a longer period. Although much of Maui and Hawaii is composed of

later lava flows than the other islands, some areas on the former are probably as old as Oahu or Kauai. The Kohala section of Hawaii, for example, has extremely deep canyons that indicate considerable age.

That the Hawaiian Islands are of oceanic origin is now rarely questioned. The absence of many families and orders of birds, insects, plants, and other organisms widespread in America or in Polynesia is sufficient evidence that the islands were never connected by land with these areas. While it is somewhat puzzling to visualize how certain mollusks and other invertebrates reached the Hawaiian Islands, changes in sea level in the past may, as Zimmerman (1948) emphasizes, have provided additional stepping stones from Polynesia. The islets in the Hawaiian leeward chain are surrounded by large, shoal-water areas within the 100-fathom line and probably were much larger during the Tertiary.

CLIMATE

The Hawaiian Islands are just within the tropics. Northeast trade winds prevail throughout the year and cool waters drift down from Bering Sea, keeping average

temperatures 10° F. cooler than in most localities of the same latitude. Frost is unknown, except on the higher mountains, and the vegetation is tropical. Mauna Kea and Mauna Loa on Hawaii are snow covered during the winter; Mt. Haleakala on Maui has occasional snow. During the Pleistocene the climate was cooler. According to Stearns (*op. cit.*, p. 32) a glacier about 250 feet thick then capped Mauna Kea. The annual temperature at lower levels on the islands averages 70° to 75° F. Winters average only slightly cooler than summers.

Moisture-laden trade winds are cooled as they encounter the Hawaiian mountains and heavy precipitation results. "On Mount Waialeale on Kauai (elevation 5,080 feet) the average rainfall is the greatest recorded over a period of years of any place on earth . . . the 12 years between 1930 and 1942 show an average of 537.5 inches per year. In the year ending July 24, 1942, 618.75 inches (51.56 feet!) of rain were recorded. . . . On the island of Maui a station at 5,000 feet recorded 562 inches of rain one year, and a lowland station only 8.5 miles away recorded as little as 2.5 inches for one year" (Zimmerman, 1948, p. 25).

SYSTEMATICS AND DISTRIBUTION

AS MENTIONED ABOVE, the species now assigned to the Drepaniidae were once scattered among several families, including the Fringillidae (finches), Dicaeidae (flowerpeckers), and Australian honeyeaters (Meliphagidae). As early as 1871 P. L. Sclater suggested that the finch-like Hawaiian genus *Psittirostra* was really related to the honey-sucking genera, such as *Drepanis* proper. Perkins' insistence that all the species are similar in life and the discovery of intermediate genera such as *Pseudonestor* later led to the recognition of the family Drepaniidae as presently understood.

The relationships of the Hawaiian honeycreepers and the phylogeny of the genera are considered in a later section. The great morphological diversity existing among closely related species in this family makes it advisable to define genera somewhat more broadly than in conservative families. Although this has been attempted, five of the nine genera here recognized are monotypic, and a sixth, *Drepanis*, is composed of a single superspecies. Nevertheless, the number of genera employed is only about half that used by previous revisers.

A few subgenera have been used. While there is some difference of opinion as to the value of this category, it would seem that in formal taxonomic revisions subgenera can be of help in indicating relationships, even though they cannot conveniently be listed in non-taxonomic publications.

Species limits are difficult to define in groups with strongly differentiated insular representatives. One can only guess as to whether or not the individuals of some such populations would interbreed were their ranges to overlap. When such doubt exists, the geographically representative populations can be treated as species and grouped in superspecies. For example, the superspecies *Hemignathus lucidus* occurs on Kauai, Oahu, Maui, and Hawaii. The first three island populations differ chiefly in details of coloration. There is no hesitation in considering them subspecies of *lucidus* (type locality, Oahu). The Hawaii form (*wilsoni*) has a very different bill, among other pronounced char-

acters, and it seems doubtful if it could hybridize successfully with any of the three races of *lucidus*. Accordingly, *wilsoni* is considered a species, forming with *lucidus* a superspecies. The specific components of a superspecies are called semispecies. In this case the semispecies *lucidus* has three subspecies; the semispecies *wilsoni* is monotypic.

For certain comparisons, especially of the number of species of given regions or archipelagos, subspecies and semispecies are of little significance. We can then exclude them and count only superspecies plus other species that are not components of superspecies. The two categories combined are sometimes called "zoogeographic species."

Descriptions of the plumage of the Drepaniidae have been published so often that it was not thought necessary to give more than a brief indication of the coloration. The common name, usually in the Hawaiian language, is given for each species, but not the additional names or variations that exist for some of them. A more condensed list of the forms of Drepaniidae and their distribution is embodied in table 2. The distributions of the species or superspecies of the family are mapped in figures 3 to 6. Photographs of all the species are given in plates 9 to 15.

ORDER PASSERIFORMES PERCHING BIRDS

SUBORDER PASSERES SONG BIRDS

FAMILY DREPANIDAE HAWAIIAN HONEYCREEPERS

DESCRIPTION: Small- or medium-sized song birds apparently related to the assemblage of closely related, chiefly American families that includes the Coerebidae, Parulidae, Thraupidae, Fringillidae, and others. Tenth primary vestigial. Bill variable but without serrations or notches. Tongue usually tubular and with a brush-like tip. Legs, feet, and claws stout, legs rather short. General proportions those usual in small arboreal song birds. Tail square or slightly emarginate or forked. Rictal and nasal bristles sparse, sometimes absent. Color

pattern relatively simple; plumage variously gray, brown, olive, green, yellow, or red. Plumage not metallic or glossy. Nostrils more or less covered by dorsal and ventral opercula. Males somewhat larger than females. Plumage or skin with a peculiar musky odor that is retained for decades by specimens.

Nest an open cup of simple construction placed among twigs, shrubs, or grass. Eggs two or three, spotted. The family is restricted to Hawaii.

REMARKS: More than half of the known species of birds belong to the Passeriformes. The division of this order, especially the Suborder Passeres, into families and subfamilies has never been satisfactorily accomplished. The existence of monophyletic subgroups such as the Drepaniidae which do not seem to differ significantly from related groups in morphology poses a dilemma. It is impossible to frame a satisfactory diagnosis of the Drepaniidae at present. The following is only a tentative statement which should be considered in connection with the later discussion of the anatomy and relationships of the family.

DIAGNOSIS: Nine-primaried passerines with tubular tongues (except in the genus *Psittirostra*) that differ somewhat from those of other nectar-sucking birds. Palato-maxillary bones absent; transpalatine processes long and pointed (except in *Psittirostra*); palatines often meeting beneath the rostrum. These features of the skull in combination will usually separate drepaniids from related forms like the Thraupidae or Icteridae, but, as with the tongue, the acquisition of finch-like characters in *Psittirostra* makes it an exception. Exclusively Hawaiian in distribution.

SUBFAMILY PSITTIROSTRINAE

DIAGNOSIS: Plumage dense and fluffy, without lanceolate or stiffened feathers. No black in plumage except on lores (the young of *Psittirostra cantans* are streaked with blackish). Primaries not truncate or angular at tips. Usually with much green or grayish green in the plumage, at least in the females and young. Females and young usually dull colored; males usually yellow, orange, or red, but sometimes dull like females.

REMARKS: Perkins (1903, p. 383) was the

first to point out that the Drepaniidae are divisible into two distinct groups. He called the present subfamily the "chlorodrepanine" or "green" section.

The above diagnosis mentions only characters in which the Psittirostrinae differ from the other subfamily, the Drepaniinae. The diagnoses of the two subfamilies should be considered together. The two groups also differ in voice and to some extent in habits. The Psittirostrinae are generally less dependent on nectar for food.

GENUS LOXOPS CABANIS

Loxops CABANIS, 1847, Arch. Naturgesch., 13th year, vol. 1, p. 330. Type, by original designation, *Fringilla coccinea* Gmelin.

Oreomyza STEJNEGER, 1887, Proc. U. S. Natl. Mus., vol. 10, p. 99. Type, by original designation, *Oreomyza bairdi* Stejneger. (Not *Oreomyza* Pokorny, 1887.)

Chrysomitridops WILSON, 1889, Proc. Zool. Soc. London, p. 445. Type, by monotypy, *C. caeruleirostris* Wilson.

Viridonia ROTHSCILD, 1892, Ann. Mag. Nat. Hist., ser. 6, vol. 10, p. 112. Type, by monotypy, *V. sagittirostris* Rothschild.

Chlorodrepanis PERKINS, 1899, in Wilson and Evans, Aves Hawaiienses, p. xxi. Type, by subsequent designation of Richmond (1902, Proc. U. S. Natl. Mus., vol. 24, p. 673), *Himatione stejnegeri* Wilson.

Rothschildia "PERKINS," 1899, in Wilson and Evans, Aves Hawaiienses, p. xxi. Type, by original designation, *Himatione parva* Stejneger, 1887. (Not *Rothschildia* Grote, 1896.)

Paroreomyza PERKINS, 1901, Ibis, p. 583. Type, by original designation, *Himatione maculata* Cabanis.

Oreomystis STEJNEGER, 1903, Proc. Biol. Soc. Washington, vol. 16, p. 11. New name for *Oreomyza* Stejneger, 1887.

Magnuma MATHEWS, 1925, Bull. Brit. Ornith. Club, vol. 45, p. 93. New name for *Rothschildia* Wilson and Evans.

Bill pointed (its tips slightly crossed sideways in one species), moderately decurved or almost straight, little if any longer than head, and neither attenuated and greatly decurved nor heavy and grosbeak- or parrot-like. Color ranging from grayish to scarlet, often olive green. Color pattern simple.

SUBGENUS VIRIDONIA ROTHSCILD

Tongue completely tubular; tips of bill not

crossed. Three species; one widespread, two restricted to single islands.

Loxops virens

AMAKIHI

A small, greenish or yellowish (males) species. The bill is rather stout and noticeably decurved. The lores are black. It occurs on all the main islands.

***Loxops virens virens* (Gmelin)**

Certhia virens GMELIN, 1788, *Systema naturae*, vol. 1, pt. 1, p. 479 ("in insulis Sandwich," restricted type locality, Hawaii).

In this race the yellow of the under parts in the males is more strongly washed with olive green than in the other races.

RANGE: Hawaii.

***Loxops virens wilsoni* (Rothschild)**

Himatione wilsoni ROTHSCHILD, 1893, *Bull. Brit. Ornith. Club*, vol. 1, p. 43 (Maui).

Himatione kalaana WILSON AND EVANS, 1896, *Aves Hawaienses*, p. 28 (Molokai).

Himatione chloridoides WILSON AND EVANS, *loc. cit.* (Lanai).

This race averages a little less olive, more yellowish than *v. virens*, but the two can scarcely be separated. Comparison of fresh material is needed. The bill of *wilsoni* may average a trifle heavier than that of *virens*. It is quite out of the question to separate the birds of Lanai, Maui, and Molokai, and few have followed Wilson and Evans in this regard. The race *wilsoni* is intermediate between *virens* and the distinctly yellower *chloris* of Oahu, but much nearer the former.

***Loxops virens chloris* (Cabanis)**

Himatione chloris CABANIS, 1850, *Museum Heineanum*, vol. 1, p. 99 (Oahu).

This subspecies has the under parts deep yellow. It is restricted to Oahu.

***Loxops virens stejnegeri* (Wilson)**

Himatione stejnegeri WILSON, 1889 (1890), *Proc. Zool. Soc. London*, p. 446 (Kauai).

The bill of this race is much stouter than that of the others. In coloration it is like *H. v. chloris* but perhaps averages duller.

RANGE: Kauai.

***Loxops parva* (Stejneger)**

ANIANIAU

Himatione parva STEJNEGER, 1887, *Proc. U. S. Natl. Mus.*, vol. 10, p. 94 (Kauai).

This is the smallest species of the family. It is otherwise like *virens*, but the sexes are both greenish yellow and the bill is less curved. This led Rothschild to associate *parva* with *Loxops maculata*, but Perkins correctly pointed out that its tubular tongue and feeding habits ally it with *virens*. It seems to represent an earlier colonization which became specifically distinct before a second wave of *virens* reached Kauai to give rise to the present *L. virens stejnegeri*.

***Loxops sagittirostris* (Rothschild)**

GREEN SOLITAIRE, GREATER AMAKIHI

Viridonia sagittirostris ROTHSCHILD, 1892, *Ann. Mag. Nat. Hist.*, ser. 6, vol. 10, p. 112 (lower slopes of Mauna Kea, Hawaii).

This is a more robust species than its congeners, with a heavier, almost straight bill. The coloration is very similar to that of *L. v. virens*, to which it may have the same relationship on Hawaii as does *L. parva* on Kauai. Palmer recognized the similarity of *sagittirostris* to *virens* by calling the former the "greater amakihi." This species is known only from a small area of very wet rain forest along the Wailuku River at elevations of 1200 to 4000 feet. This forest gave way to sugar cane, and *sagittirostris* is extinct.

SUBGENUS PAROREOMYZA PERKINS

Similar to the subgenus *Viridonia* but with the tongue only partially tubular. The one species of this subgenus creeps over the trunks and branches of trees in search of insects and rarely or never (in some of the six races) takes nectar. Presumably this is correlated with the less perfect tubular modification of the tongue in *maculata* as compared with other species of *Loxops*.

Perkins placed the Kauai and Hawaii forms of this group in a separate subgenus because of greater development of the nasal bristles and absence of sexual dimorphism. Examination beneath the microscope of the nostrils of examples of all the populations shows the nostrils to be more or less covered by feathers in the two forms mentioned; the

tips of these feathers are broken up into black, bristle-like fibers. In the other four races the nostrils are more exposed, though the Maui race is intermediate in this respect, and some specimens of it have the nostrils as much covered with feathers as the Hawaii and Lanai races. In view of the minor nature of this variation and the state of intermediacy shown by the Maui form, it seems not unreasonable to consider it subspecific in nature. The same is true of the variation in color and in sexual dimorphism found in this group. It is highly unlikely, moreover, that the Kauai and Hawaii forms, at the geographical extremes of the Hawaiian Islands, are really more closely related to each other than to the forms of the adjacent islands. One thus has the choice of dividing this group into five species (only the populations of Lanai and Maui are so similar and so adjacent in range as to be subspecies by almost any standard) or "lumping" them into one species. The latter course seems as likely to be correct as the first and is more convenient. It also gives us a species comparable with the other polytypic species of this genus.

Males of the Molokai race are bright scarlet (gray or yellow in the others) and females reddish brown. In drepaniids, as in birds in general, variation from yellow to red is obviously accomplished readily and need not be considered as necessarily indicating specific difference.

***Loxops maculata mana* (Wilson)**

Himatione mana WILSON, 1891, Ann. Mag. Nat. Hist., ser. 6, vol. 7, p. 460 (Hawaii).

The Hawaii race is a uniform olive green in both sexes and very similar in all details of coloration to *Loxops v. virens* of the same island. The latter may be distinguished by the more curved bill and deeper tone of the coloration.

***Loxops maculata montana* (Wilson)**

Himatione montana WILSON, 1889 (1890), Proc. Zool. Soc. London, p. 446 (Lanai).

The male is yellow ventrally; yellow washed with greenish olive above; dusker on the wings and tail. The female is somewhat duller.

RANGE: Lanai.

***Loxops maculata newtoni* (Rothschild)**

Himatione newtoni ROTHSCCHILD, 1893, Bull. Brit. Ornith. Club, vol. 1, p. 42 (Maui).

This race is very similar to *montana* of Lanai, but the under parts of the male are a shade lighter, more lemon or greenish yellow. RANGE: Maui.

***Loxops maculata flammea* Wilson**

Loxops flammea WILSON, 1889 (1890), Proc. Zool. Soc. London, p. 445 (Kalae, Molokai).

The male is bright scarlet; wing and tail are mostly brown. Even the bill and legs are pinkish. The female is dull brownish gray, becoming almost white below and sparingly washed with pinkish buff. Young males resemble the female, but the bright adult plumage soon appears, and specimens in partially scarlet plumage are common.

RANGE: Molokai.

***Loxops maculata maculata* (Cabanis)**

Himatione maculata CABANIS, 1850, Museum Heineanum, vol. 1, p. 100 (Oahu).

The Oahu creeper resembles the race *montana* but is duller throughout. The adult

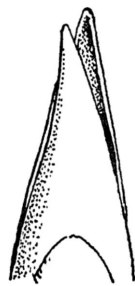


FIG. 2. Ventral view of bill of *Loxops coccinea caeruleirostris*.

female retains white wing bars. In the other subspecies such bars are present in the juvenal but lacking in the adult plumages.

***Loxops maculata bairdi* (Stejneger)**

Oreomyza bairdi STEJNEGER, 1887, Proc. U. S. Natl. Mus., vol. 10, p. 99 (Kauai).

This is the most dully colored of the races. The sexes are alike, whitish below washed

with gray and pale buff and brownish gray dorsally.

RANGE: Kauai.

SUBGENUS *LOXOPS* CABANIS

The bill in this subgenus is rather stout and conical, only very slightly decurved. Its tips are slightly twisted sidewise in opposite directions, thus crossing (fig. 2). This feature is scarcely, if at all, indicated in some immature specimens. The name *Loxops* ("twisted face") refers to the bill (cf. *Loxia*, the true crossbills [Fringillidae], in which the crossing of the

thousand feet, in the mountains of Hawaii, Maui, Oahu, and Kauai. Wilson placed the Kauai form in a separate genus because the male is dull colored like the female, but it is only a well-differentiated representative of the others.

Loxops coccinea

AKEPA

Loxops coccinea coccinea (Gmelin)

Fringilla coccinea GMELIN, 1789, Systema naturae, vol. 1, pt. 2, p. 921 ("in insulis Sandwich" = Hawaii).

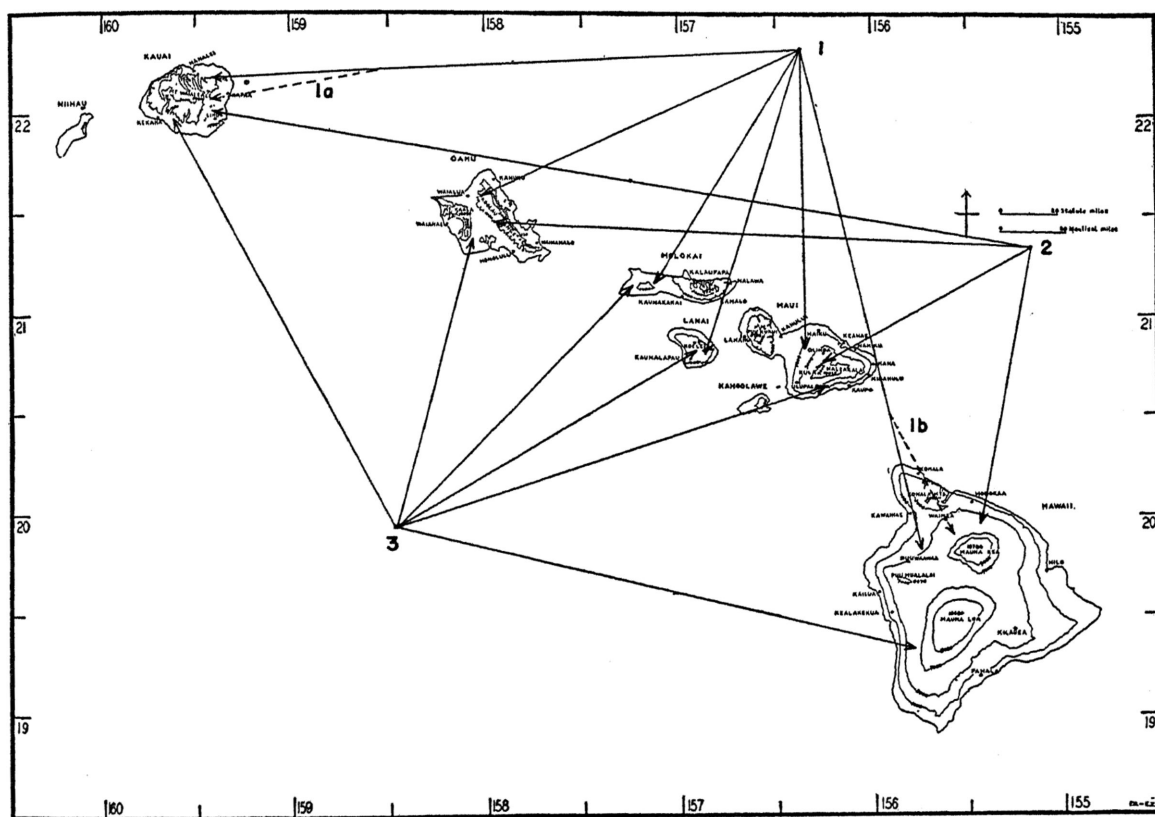


FIG. 3. Distribution of the species of *Loxops*. 1. *Virens*. 1a. *Parva*. 1b. *Sagittirostris*. 2. *Coccinea*. 3. *Maculata*.

mandibles is very much more pronounced). The tail is relatively longer in this subgenus than in the others. The tongue is completely tubular. Nectar is taken occasionally, but the usual diet is insects. This subgenus contains four geographically representative forms that occur, usually at elevations of several

Males are a bright uniform reddish orange, somewhat duller dorsally, with dusky wings and tail. The lores are not black. The female is greenish yellow below, olive or yellowish green above, and very similar in general coloration to *Loxops virens*. The lores are blackish in some of the females and imma-

tures. The bill is yellowish in this race, bluish gray in the others.

RANGE: Hawaii.

Loxops coccinea ochracea Rothschild

Loxops ochracea ROTHSCHILD, 1893, Ibis, p. 112 (Maui).

Some males of the Maui subspecies are dull brownish orange or ochraceous; others are dull yellow, washed with olive above so that two phases seem to exist, as Perkins believed. Since some individuals are intermediate, it is perhaps more nearly correct to say that a wide range of individual variation occurs. Both color types occur in adult males in breeding condition. Females are much like those of *L. c. coccinea* but duller, less yellowish.

Loxops coccinea rufa (Bloxam)

Fringilla rufa BLOXAM, 1826, in Byron, Voyage of H.M.S. Blonde to the Sandwich Islands, app., p. 250 (Oahu).

Male reddish orange, somewhat washed with brownish, especially on the back. Duller throughout than *L. c. coccinea*, which it most nearly resembles. Female quite similar to that of *ochracea*.

Palmer secured one example of the Oahu race; otherwise it is known only from a few very old specimens.

Loxops coccinea caeruleirostris (Wilson)

Chrysomitridops caeruleirostris WILSON, 1889 (1890), Proc. Zool. Soc. London, p. 445 (Kauai).

Yellowish green below, olive green above; yellowish on the crown and rump; lores blackish. Females average slightly duller. Both sexes of *L. coccinea caeruleirostris* are quite similar to the females of *L. c. rufa* and other races of the species, so it is by no means improbable that they all would interbreed freely were their ranges to overlap.

RANGE: Kauai.

GENUS *HEMIGNATHUS* LICHTENSTEIN

Hemignathus LICHTENSTEIN, 1838, Abhandl. K. Akad. Wiss. Berlin, p. 449. Type, by original designation, *Certhia obscura* Gmelin.

Heterorhynchus LAFRESNAYE, 1839, Mag. de Zool., pl. 10 and text. Type, by monotypy, *Heterorhynchus olivaceus* Lafresnaye = *Hemignathus lucidus* Lichtenstein.

Similar to *Loxops* but larger and with the upper mandible much longer than the head, thin and decurved. Lower mandible usually similar but somewhat shorter, and in one species it is straight. Tail relatively short. This genus contains two superspecies. Molokai is the only one of the six main islands on which neither is known to have been represented. The genus affords the most marked example in the family of great variation in the bills of closely allied forms.

SUBGENUS *HEMIGNATHUS* LICHTENSTEIN

Lower mandible thin and decurved like the upper one and at least four-fifths as long. Nasal and rectal bristles virtually absent. Top of head of almost or quite the same shade of color as the back. A more or less pronounced yellowish or whitish supra-ocular stripe present. Tongue long, completely tubular.

Hemignathus obscurus

AKIALOA

Hemignathus obscurus obscurus (Gmelin)

Certhia obscura GMELIN, 1788, Systemae naturae, vol. 1, pt. 1, p. 470 ("Sandwich Islands" = Hawaii).

The coloration of this race is very similar to that of *Loxops v. virens*.

RANGE: Hawaii.

Hemignathus obscurus lanaiensis Rothschild

Hemignathus lanaiensis ROTHSCHILD, 1893, Bull. Brit. Ornith. Club, vol. 1, p. 24 (Lanai).

The Lanai race is larger and somewhat yellower (in the male) than *H. o. obscurus*. It has a more pronounced yellow superciliary stripe.

It is puzzling why this species was present on Lanai but absent on Molokai and Maui. Possibly some races became extinct before they came to the attention of naturalists. This was nearly true of *lanaiensis*. It is known from three or four specimens only.

Hemignathus obscurus ellisianus (Gray)

Drepanis (Hemignathus) ellisiana GRAY, 1860, Catalogue of the birds of the tropical islands of the Pacific Ocean, p. 9 (Oahu).

This long-extinct race is known only from a few skins taken by Deppe and early visitors to Oahu. It resembles *lanaiensis* but accord-

ing to Rothschild is somewhat larger, with a more pronounced yellow superciliary stripe.

Hemignathus procerus Cabanis

KAUAI AKIALOA

Hemignathus procerus CABANIS, 1899, Jour. f. Ornith., p. 331 (Kauai).

While obviously a member of the *obscurus* group, *procerus* has such a strikingly larger bill that it is best treated as a species, forming with *obscurus* a superspecies.

RANGE: Kauai.

SUBGENUS **HETERORHYNCHUS** LAFRESNAYE

Lower mandible heavier than the upper and only about half as long. Nostrils covered with rather long, sparse bristles. Head yellow and more or less sharply demarked from the back. Tongue slightly less tubular than in the subgenus *Hemignathus*.

Hemignathus lucidus

NUKUPUU

In this species the lower mandible, though only about one-half as long as the upper, and heavier, is similarly decurved.

Hemignathus lucidus affinis Rothschild

Hemignathus affinis ROTHSCHILD, 1893, Ibis, p. 112 (Maui).

Under parts and head bright yellow; back olive green. Females and young are duller below, have the crown olive like the back, but their throat is yellow and there are yellow supraocular stripes. This race was found in forests of about 4000 feet elevation on Mt. Haleakala on Maui.

Hemignathus lucidus lucidus Lichtenstein

Hemignathus lucidus LICHTENSTEIN, 1839, Abhandl. K. Akad. Wiss., Berlin, p. 451, pl. 5, figs. 2, 3 (Oahu).

I have seen only one (immature male) specimen of this long-extinct Oahu race. According to Rothschild, the head is less yellow in this race than in the others, and there is a more pronounced yellow supraocular stripe.

Hemignathus lucidus hanapepe Wilson

Hemignathus hanapepe WILSON, 1889, Ann. Mag. Nat. Hist., ser. 6, vol. 4, p. 401 (Kauai).

This Kauai race resembles *affinis*, but the

back is yellower, almost as yellow as the crown.

Hemignathus wilsoni (Rothschild)

AKIAPOLAAU

Heterorhynchus wilsoni ROTHSCHILD, 1893, The avifauna of Laysan, pt. 2, p. 97 (Hawaii).

Lower mandible straight, stout, much like that of a woodpecker. *Wilsoni* is a representative of *lucidus*, but its bill is sufficiently different to indicate specific distinctness. They form a superspecies. *Wilsoni* is larger and more robust than any of the three subspecies of *lucidus*.

The male of *wilsoni* has the under parts bright yellow, the top of the head greenish yellow, more or less demarked from the olive back. The female is duller colored.

RANGE: Hawaii.

GENUS **PSEUDONESTOR** ROTHSCHILD

Pseudonestor ROTHSCHILD, 1893, Bull. Brit. Ornith. Club, vol. 1, p. 35. Type, by monotypy, *Pseudonestor xanthophrys* Rothschild.

Similar to *Hemignathus* in proportions and coloration but smaller. Upper mandible very deep, arched, and compressed, greatly overhanging the lower one which is straight and heavy. Male much larger than female. Tongue only partially tubular.

Pseudonestor xanthophrys Rothschild

PSEUDONESTOR

Pseudonestor xanthophrys ROTHSCHILD, 1893, Bull. Brit. Ornith. Club, vol. 1, p. 36 (Maui).

This remarkable species, which forms such an excellent link (with *Hemignathus*) between the thin-billed and heavy-billed drepaniids, was found in koa forests usually at elevations of 5000 feet or more on Mt. Haleakala, Maui. The bill reminded Rothschild of that of the Kea (*Nestor*).

GENUS **PSITTIROSTRA** TEMMINCK

Psittirostra TEMMINCK, 1820, Manuel d'ornithologie, vol. 1, p. 70. Type, by monotypy, *Loxia psittacea* Gmelin.

Loxioides OUSTALET, 1877, Bull. Soc. Philom. Paris, ser. 7, vol. 1, p. 99. Type, by monotypy, *Loxioides bailleui* Oustalet.

Chloridops WILSON, 1888, Proc. Zool. Soc.

London, p. 218. Type, by monotypy, *Chloridops kona* Wilson.

Telespyza WILSON, 1890, Ibis, p. 341. Type, by monotypy, *Telespyza cantans* Wilson.

Rhodacanthis ROTHSCHILD, 1892, Ann. Mag. Nat. Hist., ser. 6, vol. 10, p. 110. Type, by subsequent designation of Bryan and Greenway (1944, Bull. Mus. Comp. Zool., vol. 94, p. 135) *Rhodacanthis palmeri* Rothschild.

Bill moderately to very heavy, grosbeak-

rate only because *Loxioides* would also have to be merged if they were united. The affinity of all six of these species is evident in their coloration, proportions, and other details. The variation in the tongue, so far as known, parallels that in the bill.

One species occurs throughout the main islands, another is restricted to Nihoa and Laysan, while no fewer than four species are found only on Hawaii.

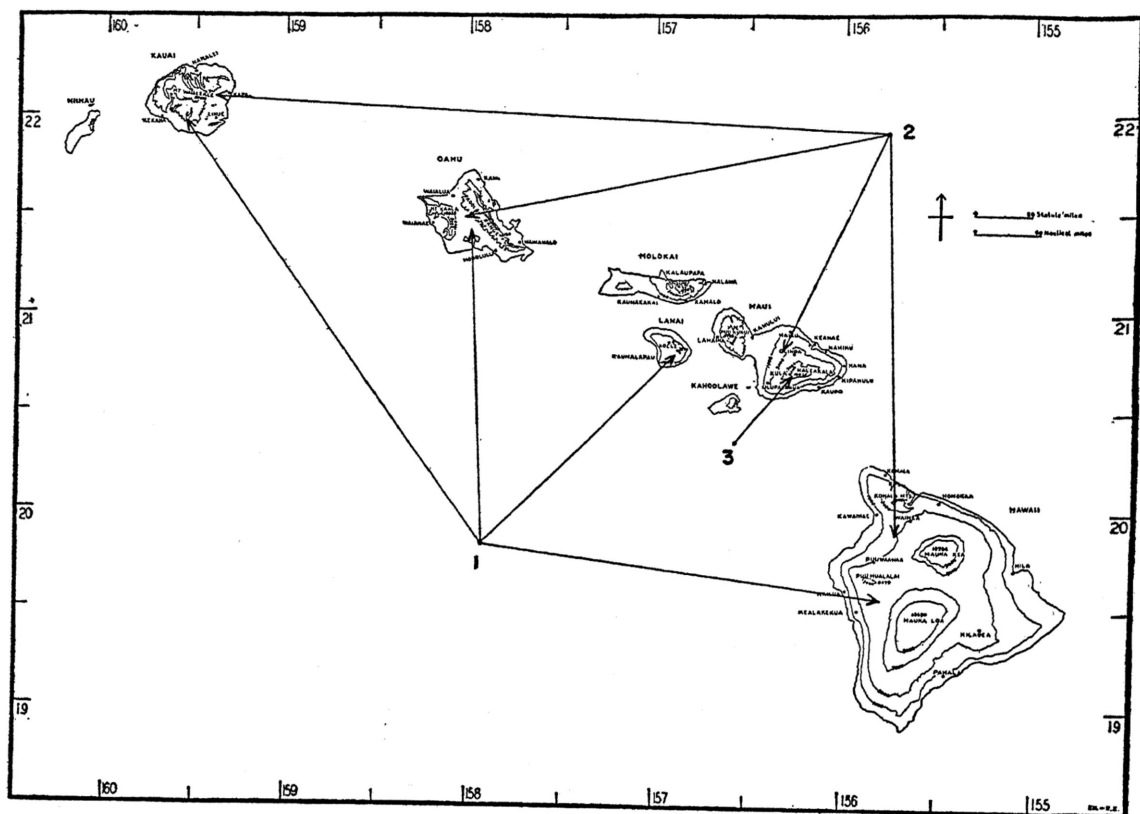


FIG. 4. Distribution of the superspecies of *Hemignathus* and of *Pseudonestor*. 1. *H. obscurus*. 2. *H. lucidus*. 3. *P. xanthophrys*.

or parrot-like. Tongue only slightly or not at all tubular. Tail relatively longer than in *Hemignathus* or *Pseudonestor*.

The six species of *Psittirostra* usually have been kept in five genera, but the differences in their bills are chiefly a gradual and progressive increase in heaviness. Rothschild (1893-1900, p. 201) stated that he described *Rhodacanthis* before having seen *Telespyza* and admitted that he later kept them sepa-

The name has often been emended to *Psittirostra*.

Psittirostra psittacea (Gmelin)

OU

Loxia psittacea GMELIN, 1789, Systema naturae, vol. 1, pt. 2, p. 844 ("in insulis Sandwich" = Hawaii).

Psittirostra psittacea deppei ROTHSCHILD, 1905, Bull. Brit. Ornith. Club, vol. 15, p. 45 (Oahu).

Psittacirostra psittacea oppidana BANGS, 1911, Proc. Biol. Soc. Washington, vol. 24, p. 30 (Molokai).

Dysmorodrepanis munroi PERKINS, 1919, Ann. Mag. Nat. Hist., ser. 9, vol. 3, p. 251 (Kaiholena Valley, Lanai).

Bill more slender and parrot-like than in the congeneric species. In the adult male the head is bright yellow, sharply demarked from the olive green body. The female is uniformly

have had the oil removed. Quite possibly these specimens were originally preserved in alcohol. The areas beneath the wings are much darker than the exposed under parts, suggesting that exposure to bright light may have contributed to their faded, pale appearance. The alleged smaller size of *deppei* may also be a result of poor condition of the specimens. Since the birds of Kauai, west of Oahu, are the same as those of the islands

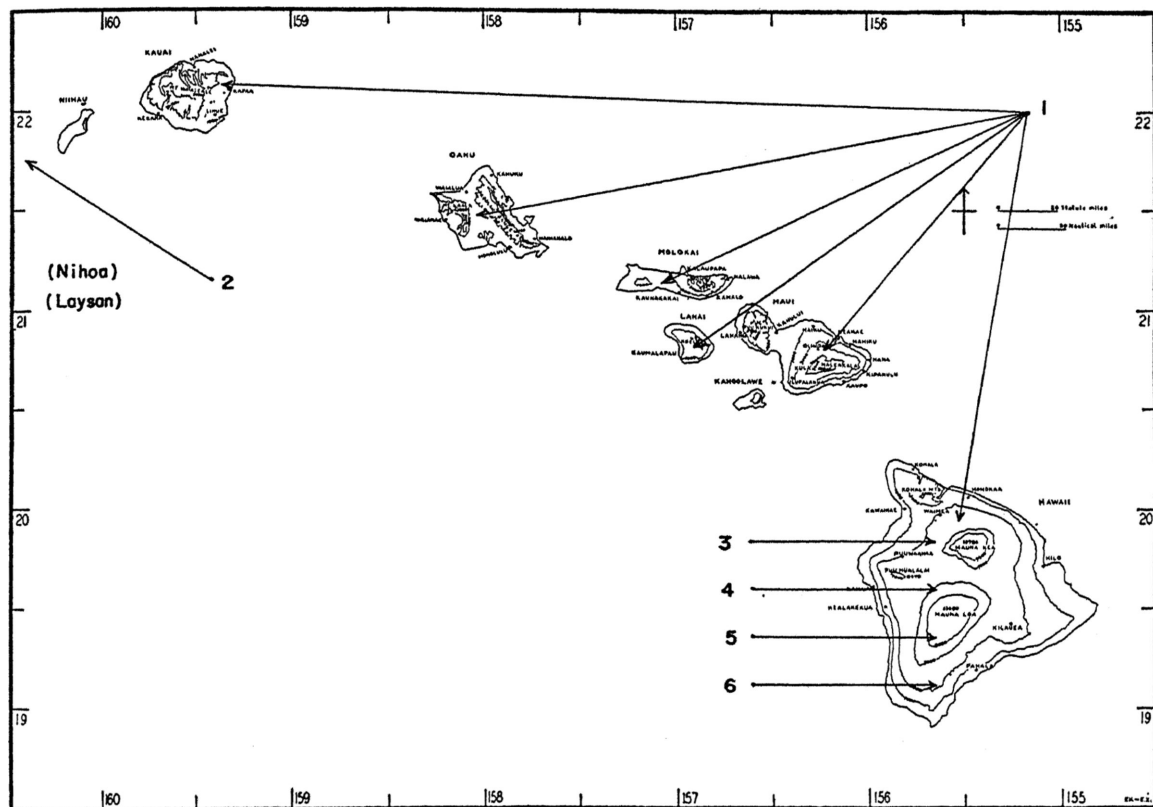


FIG. 5. Distribution of the species of *Psittirostra*. 1. *Psittacea*. 2. *Cantans*. 3. *Bailleui*. 4. *Palmeri*. 5. *Flaviceps*. 6. *Kona*.

olive green above, becoming more or less grayish white ventrally.

This species became extinct at an early date on Oahu. The four birds from that island in the Rothschild Collection, including the type of *deppei*, were collected in 1846. *Deppei* was supposed to be paler, more whitish below (in the male) than *psittacea* proper, but I believe the differences are due to fading and foxing in the old Oahu specimens. They all have whitish bills and feet that appear to

east of Oahu, it would be remarkable if the latter island had a distinct race.

Bangs based his race *oppidana* on three Molokai skins. I am unable to see that six Molokai skins (three males and three females) differ from specimens taken on the other islands. Bryan and Greenway (1944, p. 134), who examined considerable Molokai material, presumably including the type of *oppidana*, reached the same conclusion.

Examination of the unique type of *Dysmo-*

rodrepanis munroi in the Bishop Museum supports Greenway's (1939) conclusion that it is probably an aberrant immature *Psittirostra psittacea* with a deformed bill. Perhaps because of the abnormal bill and consequent inability to feed properly, its plumage is abraded, with evidence of retarded molt.

Psittirostra cantans

LAYSAN FINCH

In this species the bill is considerably heavier than in *P. psittacea*, and the upper mandible does not overlap the lower so much. The appearance of the bill is thus that of a finch rather than a parrot. Head and breast of male lemon yellow, becoming dull white on the abdomen. In fully adult males the upper parts are brownish, strongly washed with yellow. In females the under parts are similar to those of the male, but the flanks are brownish, more or less streaked with black, while the yellow of the throat and breast is usually duller. The upper parts are brownish, washed with yellow on the head. Except on the rump and lower back, the feathers have blackish streaks or blotches. Immatures have an even more streaked appearance. Although the bill of this species is most like that of *P. bailleui*, of *P. flaviceps*, and of *P. palmeri*, all species endemic to Hawaii, this may be misleading. Geographical premises point to *P. psittacea*, which reaches Kauai, as the likeliest ancestor of *cantans*. On the other hand, some of the other species mentioned may once have had a wider distribution.

***Psittirostra cantans ultima* (W. A. Bryan)**

Telespiza ultima W. A. BRYAN, 1917, Auk, vol. 34, p. 71 (Nihoa).

This race differs from the following one chiefly by its much smaller size, though the difference is not too great to preclude treating them as races.

RANGE: Nihoa.

***Psittirostra cantans cantans* (Wilson)**

Telespiza cantans WILSON, 1890, Ibis, p. 341 ("Midway Island"—error=Laysan Island).

RANGE: Laysan; introduced on Midway, where it is now extirpated.

***Psittirostra bailleui* (Oustalet)**

PALILA

Loxioides bailleui OUSTALET, 1877, Bull. Soc. Philom. Paris, ser. 7, vol. 1, p. 100 (Hawaii).

This attractive species is quite similar in coloration to *Psittirostra cantans*, but it is never streaked with black. The head and breast of the male are bright golden yellow, rather sharply set off from the grayish white abdomen and gray back. In the female the throat and breast are duller, while the crown is only slightly yellowish.

This species is restricted to upper forest zones between 4000 and 7000 feet on Hawaii.

***Psittirostra palmeri* (Rothschild)**

GREATER KOA FINCH

Rhodacanthis palmeri ROTHSCCHILD, 1892, Ann. Mag. Nat. Hist., ser. 6, vol. 10, p. 111 (Kona, Hawaii).

This is the largest species of the family. In the adult male the head and breast are bright reddish orange, becoming duller and somewhat yellowish on the abdomen. The back is greenish olive, washed with orange on the rump. Some apparently adult males have less orange on the head than others. The adult female is greenish olive above, paler below, and washed with yellow on the forehead. Immatures are similar to the female but blotched with dark brownish gray on the breast. This species occurred in the koa forests of Hawaii, usually at elevations of about 4000 feet.

***Psittirostra flaviceps* (Rothschild)**

LESSER KOA FINCH

Rhodacanthis flaviceps ROTHSCCHILD, 1892, Ann. Mag. Nat. Hist., ser. 6, vol. 10, p. 111 (Kona, Hawaii).

Similar to *P. palmeri*, the bill identical in shape, but a much smaller bird (wing averaging about 10 to 12 mm. less). The adult male is known only from the type specimen, a very worn October bird that is like a *palmeri* with the orange of the head replaced by yellow.¹

¹ I have recently examined a second adult male of *flaviceps* and another adult female, in the collection of the British Museum (Natural History). The male agrees with the type in color and size and removes whatever doubt may still have existed as regards the specific validity of *flaviceps*.

The adult female (two worn specimens) and immature (three specimens) are similar to females and immatures of *P. palmeri*.

This species is known only from the above six specimens collected by Palmer and Munro between October 1 and 19, 1891 (unless Rothschild disposed of some specimens). In view of the great similarity of the bill of *flaviceps* to that of *P. palmeri* and the fact that *flaviceps* was found in the center of the range of *palmeri*, naturally there has always been a question about its status. Munro (1944, p. 127) wrote that Palmer and he were surprised to find that the koa finches they collected were separated by Rothschild into two species. They had noted the variation in size and color but thought that intermediates occurred. After *flaviceps* had been described, Perkins (1903, p. 437) made a special visit to the area where the type series was secured and examined "some hundreds" of *P. palmeri* without finding any with yellow heads or hearing any notes not attributed to *P. palmeri* or the other species present.

In view of the above, I expected that *P. flaviceps* might be based upon immature or abnormal specimens of *P. palmeri*, but study of the few known examples convinces me that it is a perfectly distinct species. If a hybrid, the parents would presumably be *Psittirostra palmeri* and *P. psittacea*. *P. flaviceps*, however, is not intermediate in size but is a little smaller even than *psittacea*. The bills of these two species are so different that one would certainly not expect a hybrid to have a bill precisely like that of *P. palmeri*. To postulate any other species, such as *Psittirostra bailleui* or *P. kona*, or members of another genus, as parents of hybrids involves still more difficulties.

Of these six specimens three are adults in very worn plumage, while three are immatures in nearly fresh plumage. Their state of plumage corresponds with that of a series of old and young *P. palmeri* taken at the same time. But even if all the six specimens of *flaviceps* were young of the year, they are still too small to be immatures of *palmeri*; the fact that three of them are adults rules out this possibility altogether.

When we consider how quickly some Hawaiian birds became extinct, it is not impossible or even unlikely that *P. flaviceps*

was always rare and soon disappeared. This happened a little later to *P. palmeri* itself, and Henshaw, who visited the same areas in which Palmer, Munro, and Perkins had found it to be common 10 years before, was unable to find a single one; the species has not been seen since.

To summarize, the strikingly smaller size and the distinct coloration of the adult male of *flaviceps*, together with the presence of both adults and immatures among the known specimens, indicate that it is a good species.

RANGE: Hawaii.

Psittirostra kona (Wilson)

GROSBEAK FINCH

Chloridops kona WILSON, 1888, Proc. Zool. Soc. London, p. 218 (Kona, Hawaii).

Bill extremely heavy. In this respect specialized, but the color pattern is the simplest found in the genus. This probably is secondary. Adults and immatures of both sexes are a uniform yellowish green. Young and females are perhaps a little duller and lighter.

Psittirostra kona seemed a rare species even at the time it was discovered and was confined to an area of a few square miles in the Kona district of Hawaii at elevations of about 4000 feet.

SUBFAMILY DREPANIINAE

DIAGNOSIS: Plumage not so soft and fluffy as in the *Psittirostrinae*. Some of the feathers, especially of the head, often more or less lanceolate and stiffened. Tips of primaries sometimes obliquely truncate, producing a whirring sound in flight (especially in *Himatione* and *Vestiaria*). Immature plumage washed or spotted with black; adults brightly colored (except *Drepanis funerea*); sexes alike (? *Ciridops*). Perkins wrote of this subfamily (1903, p. 383), "The skin, moreover, is comparatively thick, and sometimes extremely tough and thick, as cannot fail to be noticed by the collector when using very small charges of powder and shot."

GENUS *HIMATIONE* CABANIS

Himatione CABANIS, 1850, Museum Heineanum, vol. 1, p. 99. Type, by monotypy, *Himatione sanguinea* (Gmelin).

Bill about as long as the head, slightly decurved; feathers of top of head narrow and

slightly lengthened; no crest. Primaries truncate, producing a whirring sound in flight.

Himatione sanguinea

APAPANE

***Himatione sanguinea sanguinea* (Gmelin)**

Certhia sanguinea GMELIN, 1788, *Systema naturae*, vol. 1, pt. 1, p. 479 (Sandwich Islands).

Wings and tail black; abdomen and under tail coverts white; elsewhere bright crimson. Immatures are dusky grayish brown above, more or less washed with buff; lighter, more buffy ventrally.

This subspecies occurs on the six main islands without perceptible geographic variation.

***Himatione sanguinea freethii* Rothschild**

Himatione fraithii (sic) ROTHSCHILD, 1892, *Ann. Mag. Nat. Hist.*, ser. 6, vol. 10, p. 109 (Laysan).

Rothschild named this bird after Captain Freeth, sometime "governor" of Laysan. The original spelling *fraithii* may be considered a *lapsus calami*, especially since Rothschild himself later corrected it to *freethii*.

The Laysan race is similar to *H. s. sanguinea* but a rosier, lighter red. This is in part the result of the fading and bleaching evident in all the land birds of this exposed atoll. The bill is shorter than in the nominate race.

GENUS **PALMERIA** ROTHSCHILD

Palmeria ROTHSCHILD, 1893, *Ibis*, p. 113. Type, by monotypy, *Palmeria mirabilis* Rothschild = *Himatione dolei* Wilson.

Most like *Himatione* but feathers of forehead elongated, stiffened, and recurved to form a curly frontal crest. Tips of primaries somewhat angular but not definitely truncate as in *Himatione*. Feathers of head and body somewhat lanceolate. Bill, feet, and proportions much like those of *Himatione*, but a larger bird; color pattern with resemblances to that of *Ciridops*.

***Palmeria dolei* (Wilson)**

CRESTED HONEYCREEPER

Himatione dolei WILSON, 1891, *Proc. Zool. Soc. London*, p. 166 (Maui).

Plumage black, tipped with gray on the throat and breast, with white on the ends of the wing and tail quills. Body feathers tipped

with bright orange; across the nape and sides of the neck the orange tips are longer, forming a collar. The crest is grayish white. Immatures are dull brownish black, washed with buff, hence like those of *Himatione*. The immatures have a partial crest. Wilson had only one specimen, an immature, when he described this species in the genus *Himatione*.

Palmeria occurs without geographical variation on Maui and Molokai.

GENUS **CIRIDOPS** NEWTON

Ciridops NEWTON, 1892, *Nature*, vol. 45, p. 469. Type, by monotypy, *Fringilla anna* Dole.

Bill rather heavy, short, and finch-like; culmen arched but lower mandible upturned. Nearest *Palmeria* but without a crest and with lanceolate feathers on the crown, throat, and cheeks only. Primaries evidently not truncate (material inadequate).

***Ciridops anna* (Dole)**

ULA-AI-HAWANE

Fringilla anna DOLE, 1879, in Thrum, *Hawaiian almanac*, p. 49 (Hawaii).

Tail, flight feathers, breast, and scapulars black; feathers of crown black tipped with gray of the same shade as the crest of *Palmeria* and becoming buffy posteriorly, forming a buffy band across the nape. Wing coverts, back, rump, and mid abdomen bright red; lower abdomen and under tail coverts brownish buff. Bangs (1910, p. 68) described an unsexed specimen, now in the American Museum of Natural History, which he assumed to be an adult female. It is grayish cinnamon above, brighter on the head, and strongly washed with yellow on the rump. The throat is cinnamon gray, the breast dingy gray, becoming olive-yellow on the abdomen; the wing and tail are brownish. Since in other species of the subfamily the adult female is like the male, it seems probable this specimen is an immature, not an adult female. I compared it with a specimen in not quite adult plumage. The remaining immature feathers of the latter agree with the plumage just described.

This is the least known species of the Drepaniidae. The collection of J. Mills, a taxidermist of Hilo, Hawaii, contained two specimens. These became the cotypes of *Fringilla*

anna, as described by Judge Dole (Amadon, 1944). The better of these two specimens is in the Bishop Museum. The other, in subadult plumage, was taken to England by Scott Wilson and later purchased by Rothschild; it is now in the American Museum. Palmer never saw this species, but native collectors secured one specimen for him. Preserved in the flesh, it permitted Rothschild to figure the tongue of this species; this specimen is now in the British Museum. The Museum of Comparative Zoölogy at Harvard acquired two skins of *Ciridops* (one the "female" described above) in a small lot of Hawaiian material, without known collector or precise data of any kind (Bangs, 1910). These five specimens are the only ones known. *Ciridops* was endemic to Hawaii.

GENUS VESTIARIA FLEMING¹

Vestiaria FLEMING, 1822, Philosophy of zoology, vol. 2, p. 246. Type, by original designation, *Certhia vestiaria* Forster.

Most like *Himatione*, but bill longer than head and strongly decurved; feathers of throat lanceolate and stiffened; those of crown normal; primaries obliquely truncate, producing a whirring sound in flight. Larger than *Himatione*.

Vestiaria coccinea

IIWI

Certhia coccinea FORSTER, 1780, Goettingisches Mag. Wiss., vol. 1, p. 347 (Hawaii).

Vestiaria coccinea suavis BANGS, 1911, Proc. Biol. Soc. Washington, vol. 24, p. 29 (Molokai).

Wings and tail black; inner vanes of inner secondaries white; remainder of plumage brilliant orange red. Bill and feet pinkish red. Immatures are buffy, washed with yellowish and greenish, and spotted with blackish; much brighter, less dingy than immatures of *Himatione* and *Palmeria*.

Found on all of the six main islands and maintaining its numbers fairly well; still present locally even on Oahu.

Bangs described *suavis* as larger than the nominate race, with orange vermilion rather than scarlet vermilion plumage. The one available adult from Molokai does not differ

in color from birds taken on the other islands. As is well known, the color tones of red birds vary with wear and (sometimes) individual variation. While this specimen is at the maximum of size for the species (see table 2), some examples from other islands are almost, if not quite, as large. There is no reason to believe that Molokai birds are enough (if at all) larger than others to justify racial separation. Bryan and Greenway (1944, p. 127) reached the same conclusion, presumably after examining Bangs' material. It would be surprising to find racial variation on Molokai but not on the islands east or west of it, especially in this strong-flying species.

GENUS DREPANIS TEMMINCK

Drepanis TEMMINCK, 1820, Manuel d'ornithologie, ed. 2, vol. 1, p. 86. Type, by subsequent designation of Gray (1840), *Certhia pacifica* Gmelin.

Drepanorhamphus ROTHSCHILD, 1900, The avifauna of Laysan, pt. 3, p. 163. Type, by monotypy, *Drepanis funerea* Newton.

Most like *Vestiaria* but feathers of throat not lanceolate; tips of primaries not sharply truncate; much of body plumage black; size larger; bill relatively longer.

Although the two species of *Drepanis* have minor structural differences, they are closely related. It is unnecessary to recognize *Drepanorhamphus*, and few authors have done so.

Drepanis is known only from Hawaii and Molokai. Quite probably there was once a representative of the genus on Maui, if not on other islands.

Drepanis pacifica (Gmelin)

MAMO

Certhia pacifica GMELIN, 1788, Systema naturae, vol. 1, pt. 1, p. 470 ("in insulis amicis" = Friendly or Tonga Islands, error for Hawaii).

Rump, lower back, under tail coverts, flanks, and bend of wing golden yellow; greater wing coverts whitish; remainder of plumage black. Under tail coverts somewhat elongated and loose webbed or diffuse in structure.

Rothschild gives a figure of the sternum of this species.

RANGE: Hawaii.

¹ Mathews attributes this genus to Jarocki in Zoologia (1821, p. 75).

Drepanis funerea Newton

BLACK OR PERKINS' MAMO; HOA

Drepanis funerea NEWTON, 1893, Proc. Zool. Soc. London, p. 690 (Molokai).

Bill longer and more decurved than in *D. pacifica*; nasal aperture and operculum somewhat elongated; under tail coverts not lengthened. This remarkable species marks the culmination of the tendency in this sub-

W. A. Bryan secured three more in 1907. It has not been seen since.

RANGE: Molokai.

DOUBTFUL SPECIES

Dysmorodrepanis munroi PERKINS

This name is listed above in the synonymy of *Psittirostra psittacea* since it was based on what is believed to be an aberrant individual of that species from Lanai.

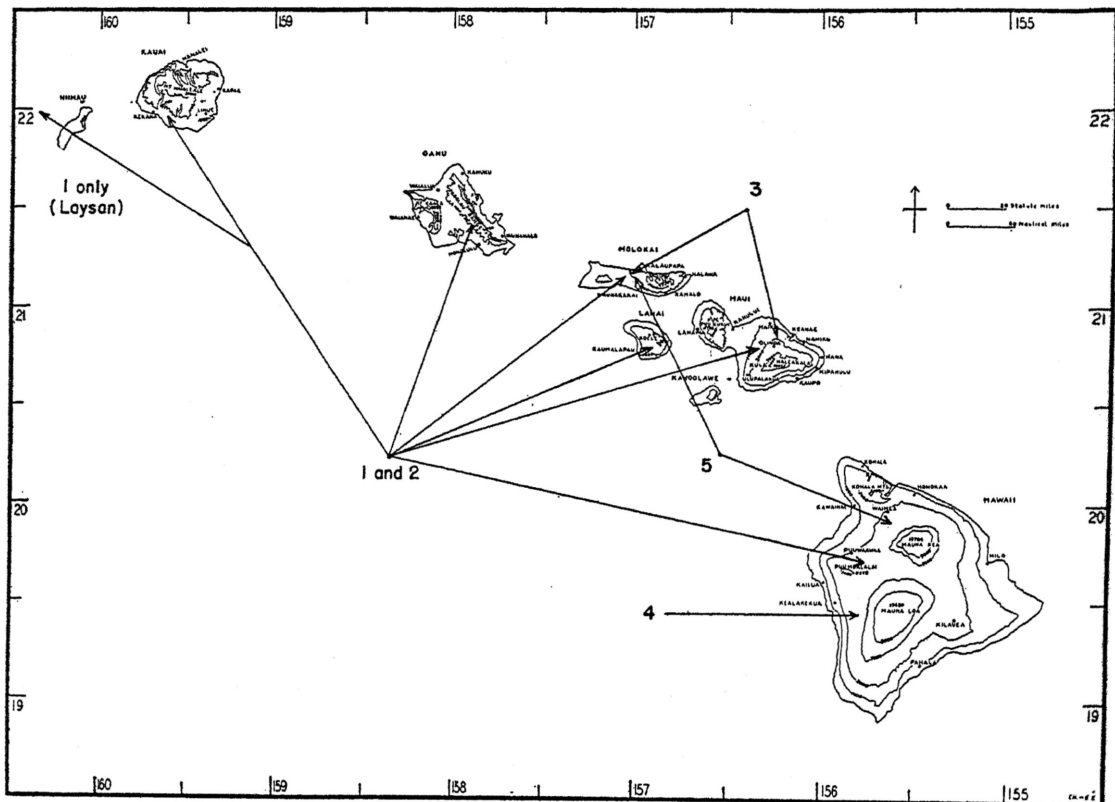


FIG. 6. Distribution of the species or superspecies of the Drepaniinae. 1. *Himatione sanguinea*. 2. *Vestiaria coccinea*. 3. *Palmeria dolei*. 4. *Ciridops anna*. 5. *Drepanis pacifica*.

family towards increasing black in the body plumage. *Funerea* is entirely black except for the whitish outer webs of the outer primaries. Its bill is black, yellowish at the base and around the nostrils. Whether *funerea* and *pacifica* form a superspecies or not is debatable. Perkins discovered this species and took a few specimens. The Meyers family, Perkins' hosts on Molokai, collected a few others.

Oreomyza perkinsi ROTHSCILD

Oreomyza perkinsi ROTHSCILD, 1900, The avifauna of Laysan, pt. 3, p. 129 (Hawaii).

This name was based on one specimen, an adult male collected by Palmer in the Kona district of Hawaii. As Rothschild admitted, it may be a hybrid of *Loxops maculata mana* and *Loxops virens virens*. Others have thought it an aberrant individual of one or the other

of these two. In coloration the type of *perkinsi* is very similar to adult males of *L. v. virens*, but with certain slight divergencies that may be considered in the direction of *L. maculata mana* as follows: the tone of color is slightly paler, especially on the abdomen; the lores are less blackish and the narrow black line of feathers usually found above the base of the upper mandible in *virens* is absent. The bill is nearly straight, more like that of *L. maculata* than of *L. virens*. The lower mandible is typical for *L. maculata mana*, but the upper is longer, with its tip thin and slightly hooked, apparently as a result of lack of the usual wear. The bill was evidently abnormal

so that the mandibles did not meet properly. All this suggests that *perkinsi* is a hybrid of *Loxops maculata mana* and *L. v. virens* rather than an atypical specimen of one or the other.

Sassius simplex ROTHSCHILD AND HARTERT

Sassius simplex ROTHSCHILD AND HARTERT, 1926, Bull. Brit. Ornith. Club. vol. 46, p. 51.

This supposed new genus and species is based on an old, unlabeled specimen in the Vienna Museum. This, it now appears, is an artifact made of patches of skin of Old World sunbirds glued on a carved wooden body (Meise, 1934, p. 123).

ANALYSIS OF MEASUREMENTS

MOST OF THE SPECIMENS measured were collected 50 or more years ago and are now somewhat the worse for wear (see plates). The difficulties of preparing and transporting bird skins in the Hawaiian rain forests added to the initial problem of making good specimens. The entire available series of some forms was collected at seasons when the plumage is badly worn. Few or (in one instance) no specimens were available of some of the rare or extinct drepaniids. In general, therefore, only size variation that is rather pronounced could be analyzed, since more subtle differences were often masked by extraneous variation of one sort or another.

A certain number of wrongly sexed specimens may also affect some of the results, especially as regards range of variation (they are presumably not frequent enough to affect significantly the mean). In a number of species or subspecies adult males are unmistakable, and this source of error is absent.

Measurements were taken to the nearest millimeter or, for some bill lengths, nearest half millimeter. The method of taking the measurements was as follows:

WING LENGTH: Distance from the bend of the wing to the tip of the longest primary, with the primaries pressed flat against the rule.

TAIL LENGTH: Distance from the tips of the longest rectrices to their insertion in the skin. As with wing length, molting or badly worn specimens were not measured.

TARSUS: The length of the tarso-metatarsus is a difficult measurement to obtain accurately in small birds, more particularly from the present skins which often have the legs more or less jammed into the feathers of the abdomen. Because of the high intrinsic error involved in this measurement, the mean tarsal lengths given are only approximate and the range of variation and coefficient of variation are not given.

BILL: Usually the chord of the culmen measured from the edge of the feathering on the forehead or from the nostril to the bill tip is taken. So many drepaniids have sharply curved bills that variations in bill length are seriously minimized in any measurement of

the chord. By bending a flexible celluloid rule along the culmen the real length of the bill was taken from the edge of the frontal feathers to the tip of the bill. In species like *Hemignathus lucidus* with the lower mandible shorter than the upper, the length of the former was also taken as the rule was held along the curvature of the upper mandible.

Even if dividers are used, it is rather difficult to locate precisely the base of the culmen on the forehead; this is why the bill is often measured from the nostril. To hold a rule at the base of the culmen makes accurate measurement even more difficult than with dividers, but the comparatively low range of variation found in the present results indicates that this was achieved with reasonable success. In short-billed species, where slight errors in measurement affect the results more seriously, the standard deviation is not given for this reason. Actually, the chord of the culmen would have been satisfactory for some of these species with short, almost straight bills, but, to make the results comparable, the length of the culmen along its curvature was used throughout.

The horny sheath of a bird's bill continually grows and is worn away. In drepaniids, at least, such wear is much more pronounced in some specimens than in others. In the short-billed species it was found that variation in bill length resulting from such wear is often greater than that resulting from other causes, including the intrinsic (genetic) variation that we seek to measure. This is another reason why the bill measurements secured for such short-billed species are too inaccurate to warrant calculation of the standard deviation. Evidence of the effect of wear on the shape and length of the bill is given by Clancey (1948). He found that in the Old World Tree Sparrow, *Passer montanus*, the bill is longer in spring and early summer than in winter, because this bird eats more soft insects and fewer seeds in the summer than in the winter.

Other dimensions of the bill, such as its depth, are difficult to measure accurately and are less obviously correlated with habits except as a reflection of general strengthening

TABLE 2
MEASUREMENTS OF THE DREPANIIDAE

	Males				Females			
	No.	Range	M	V	No.	Range	M	V
<i>Loxops virens virens</i>								
Hawaii								
Wing	16	62-68	65.2	2.82	2	61-67	64.2	3.03
Tail	19	39-47	44.4	4.35	9	42-47	44.1	3.11
Tarsus			21.5				21.9	
Culmen	18	12.5-15.5	13.9		15	11-14	12.7	
<i>Loxops virens wilsoni</i>								
Lanai								
Wing	5	64-67	64.6		2	60, 60		
Tail	5	43-45	44.6		2	42, 44	43.0	
Tarsus			22.8				20.0	
Culmen	7	13.5-15.5	14.9		2	13.5, 13.5		
<i>Loxops virens wilsoni</i>								
Maui								
Wing	5	65-68	66.8		10	62-67	63.6	2.45
Tail	5	45-47	46.4		8	41-45	43.2	3.47
Tarsus			20.7				21.1	
Culmen	5	15.5-17	16.3		10	13-16.5	14.3	
<i>Loxops virens wilsoni</i>								
Molokai								
Wing	6	64-68	65.5		3	60-64	62.0	
Tail	8	43-47	44.7	3.11	2	41, 41		
Tarsus			21.2				22.0	
Culmen	10	14.5-16.5	15.5		1	13		
<i>Loxops virens chloris</i>								
Oahu								
Wing	16	63-68	65.6	2.01	11	60-63	61.0	1.85
Tail	15	42-47	44.7	2.89	7	38-43	40.6	4.13
Tarsus			20.7				21.4	
Culmen	16	14-16.5	14.9		9	12-14	12.9	
<i>Loxops virens stejnegeri</i>								
Kauai								
Wing	5	66-70	68.2		9	63-67	65.8	2.96
Tail	6	40-42	41.2		6	41-43	42.7	
Tarsus			21.0				21.3	
Culmen	7	17.5-20.5	19.2		9	17-20	17.8	
<i>Loxops parva</i>								
Kauai								
Wing	14	58-62	60.1	1.83	8	57-60	58.7	2.04
Tail	12	40-44	42.1	2.83	6	41-43	42.0	
Tarsus			20.4				20.6	
Culmen	13	12-13.5	12.7		8	11-12	11.7	
<i>Loxops sagittirostris</i>								
Hawaii								
Wing	5	80-83	80.8		6	71-76	73.8	
Tail	5	50-54	52.2		5	45-51	47.8	
Tarsus			24.6				22.0	
Culmen	5	19-22.5	20.7		6	17.5-20.5	19.5	

TABLE 2—Continued

	Males				Females			
	No.	Range	M	V	No.	Range	M	V
<i>Loxops coccinea coccinea</i>								
Hawaii								
Wing	27	61-69	63.8	2.74	12	59-63	61.2	2.09
Tail	26	47-52	49.6	2.64	16	44-49	47.1	2.87
Tarsus			21.0				21.3	
Culmen	25	9.5-11.5	10.4		12	9-11	9.9	
<i>Loxops coccinea ochracea</i>								
Maui								
Wing	17	60-65	63.3	2.59	9	57-63	59.8	2.71
Tail	18	44-52	48.8	4.45	10	45-50	46.8	3.50
Tarsus			20.6				20.3	
Culmen	15	9.5-12	10.8		9	10-10.5	10.2	
<i>Loxops coccinea rufa</i>								
Oahu								
Wing	2	57?, 60			1	55		
Tail	2	43?, 48			1	41		
Tarsus			19.0					
Culmen	1	9.5			1	9		
<i>Loxops coccinea caeruleirostris</i>								
Kauai								
Wing	8	63-67	65.1	2.09	9	59-64	61.8	2.51
Tail	9	51-57	54.6	3.57	8	51-55	52.1	2.44
Tarsus			20.9				20.3	
Culmen	10	10-11.5	10.6		9	10-11	10.5	
<i>Loxops maculata mana</i>								
Hawaii								
Wing	20	65-72	67.5	2.50	16	61-71	65.7	3.82
Tail	18	43-49	45.2	3.14	17	40-49	44.6	5.11
Tarsus			21.2				21.6	
Culmen	17	11-12.5	11.8		12	11-12.5	11.9	
<i>Loxops maculata montana</i>								
Lanai								
Wing	10	57-63	60.9	2.59	4	55-59	57.0	
Tail	10	49-52	50.8	2.30	4	45-50	47.5	
Tarsus			21.8				20.8	
Culmen	10	11.5-13	12.4		4	11-12	11.6	
<i>Loxops maculata newtoni</i>								
Maui								
Wing	6	63-68	65.2		3	60-62	61.0	
Tail	5	50-54	51.4		2	46, 47		
Tarsus			22.2				22.0	
Culmen	8	10.5-12.5	11.7		4	11.5-12.5	11.7	
<i>Loxops maculata flammea</i>								
Molokai								
Wing	15	64-69	66.1	2.03	10	59-64	61.3	2.74
Wing (imm.)	7	62-66	64.3	1.99				
Tail	13	51-56	53.7	2.67	6	50-52	50.5	
Tail (imm.)	7	51-54	52.7	1.95				
Tarsus			22.7				22.0	
Culmen	11	13-16	14.7		6	12.5-14	13.2	
Culmen (imm.)	11	12.5-15	13.9					

TABLE 2—Continued

	Males				Females			
	No.	Range	M	V	No.	Range	M	V
<i>Loxops maculata maculata</i>								
Oahu								
Wing	8	66-71	69.5	2.79	9	59-71	63.1	5.23
Tail	7	48-53	50.3	3.32	8	43-47	44.5	2.76
Tarsus			22.3				20.6	
Culmen	7	13-14	13.4		8	11.5-13.5	12.2	
<i>Loxops maculata bairdi</i>								
Kauai								
Wing	13	66-70	67.5	1.71	8	63-71	66.0	3.11
Tail	9	41-44	42.6	0.70	10	41-45	43.3	3.12
Tarsus			20.7				20.4	
Culmen	10	12-13.5	12.5		9	11-13	11.7	
<i>Loxops "perkinsi"</i>								
Hawaii								
Wing	1	67						
Tail	1	45						
Tarsus	1	24						
Culmen	1	15						
<i>Hemignathus obscurus obscurus</i>								
Hawaii								
Wing	9	76-81	77.8	1.99	5	69-75	73.2	
Tail	9	42-48	44.3	4.38	5	39-43	41.4	
Tarsus			23.7				22.0	
Culmen	8	41-47	43.2	3.97	5	34-44	38.2	
<i>Hemignathus obscurus lanaiensis</i>								
Lanai								
Wing	2	80, 84						
Tail	2	48, 50						
Tarsus			26					
Culmen	2	53, 53						
<i>Hemignathus obscurus ellisianus</i>								
Oahu								
(None examined)								
<i>Hemignathus procerus</i>								
Kauai								
Wing	13	88-94	90.4	2.08	9	85-88	86.1	1.39
Tail	12	52-56	53.5	2.11	10	50-54	51.5	2.78
Tarsus			27.9				25.5	
Culmen	11	65-72	68.1	3.16	8	51-56	52.9	3.33
<i>Hemignathus lucidus hanaepepe</i>								
Kauai								
Wing	2	81, 81			2	78, 78		
Tail	3	47-52	49.7		2	47, 49		
Tarsus			23.7				23.0	
Culmen	3	30-33	31.7		3	27-29	28.3	
<i>Hemignathus lucidus lucidus</i>								
Oahu								
Wing (imm.)	1	77						
Tail (imm.)	1	50?						
Tarsus (imm.)	1	22						
Culmen (imm.)	1	24						

TABLE 2—Continued

	Males				Females			
	No.	Range	M	V	No.	Range	M	V
<i>Hemignathus lucidus affinis</i>								
Maui								
Wing	8	72-79	75.9	3.12	3	69-71	69.7	
Tail	9	47-50	48.3	2.17	3	44-47	46.0	
Tarsus			22.5				21.3	
Culmen	9	28-31	29.1	3.78	2	22, 22		
<i>Hemignathus wilsoni</i>								
Hawaii								
Wing	13	79-87	84.3	2.30	12	76-82	79.2	2.56
Tail	15	48-51	49.6	0.56	13	43-50	46.5	4.43
Tarsus			25.2				24.1	
Culmen	13	25-29	26.9	5.15	7	21-24	22.0	4.86
<i>Pseudonestor xanthophrys</i>								
Maui								
Wing	4	75-78	76.0		4	68-71	69.0	
Tail	4	46-50	48.0		3	40-44	42.7	
Tarsus			24.2				21.0	
Culmen	5	24-27	25.3		4	19-20	19.6	
<i>Psittirostra psittacea</i>								
Hawaii								
Wing	9	95-99	97.1	1.24	10	88-95	91.8	2.17
Tail	10	58-63	60.0	2.68	10	53-59	55.4	3.54
Tarsus			24.7				25.2	
Culmen	10	15.5-18	16.7		7	16-16.5	16.2	
<i>Psittirostra psittacea</i>								
Lanai								
Wing	1	98			4	92-95	92.7	
Tail	1	59			5	55-56	55.4	
Tarsus	1	26					24.0	
Culmen	1	16.5			3	16-16.5	16.2	
<i>Psittirostra psittacea</i>								
Maui								
Wing	4	89-98	94.5					
Tail	5	58-60	59.0					
Tarsus			23.0					
Culmen	3	17-18	17.7					
<i>Psittirostra psittacea</i>								
Molokai								
Wing	3	94-99	96.7		3	91-94	92.3	
Tail	3	56-62	59.7		3	56-59	57.3	
Tarsus			24.5				24.0	
Culmen	3	16-17.5	16.7		3	15-17	15.5	
<i>Psittirostra psittacea</i>								
Oahu								
Wing	2	90?, 95			2	93, 95		
Tail	2	59, 62			2	60, 65		
Tarsus			23.5				23.0	
Culmen	1	17						
<i>Psittirostra psittacea</i>								
Kauai								
Wing	8	95-101	97.7	2.16	4	92-97	95.2	
Tail	8	59-66	62.4	3.67	4	57-63	60.5	
Tarsus			25.3				25.0	
Culmen	6	16-19.5	17.6		4	14.5-16.5	15.4	

TABLE 2—Continued

	Males				Females			
	No.	Range	<i>M</i>	<i>V</i>	No.	Range	<i>M</i>	<i>V</i>
<i>Psittirostra cantans ultima</i>								
Nihoa								
Wing	1	78						
Tail	1	59						
Tarsus								
Culmen	1	14.5						
<i>Psittirostra cantans cantans</i>								
Laysan								
Wing	7	81–87	84.6	2.52	5	80–86	82.2	
Tail	8	60–65	63.3	2.20	4	59–62	60.5	
Tarsus			25.0				25.5	
Culmen	12	17–19	18.1		12	16–18.5	17.2	
<i>Psittirostra bairdii</i>								
Hawaii								
Wing	6	91–94	92.3		7	85–92	88.6	2.33
Tail	8	67–70	68.6	1.78	8	63–67	65.1	1.80
Tarsus			25.6				25.0	
Culmen	10	12–13	12.7		8	10–13.5	11.4	
<i>Psittirostra flaviceps</i>								
Hawaii								
Wing	1	98			3	95–96	95.7	
Wing (imm.)	1	97			1	92		
Tail	1	64			3	60–63	61.7	
Tail (imm.)	1	64			1	62		
Tarsus	1	23.5					22.9	
Tarsus (imm.)	1	24						
Culmen	1	18.5			1	19		
Culmen (imm.)	1	17			1	18		
<i>Psittirostra palmeri</i>								
Hawaii								
Wing	9	107–110	108.8	0.27	3	105–107	105.7	
Wing (imm.)	6	105–110	106.0		1	102		
Tail	10	70–76	73.0	2.21	3	70–73	71.7	
Tail (imm.)	5	70–75	71.8		1	69		
Tarsus			26.7				26.0	
Tarsus (imm.)			25.2				25.0	
Culmen	11	20.5–22	21.3		2	19–21	20.0	
<i>Psittirostra kona</i>								
Hawaii								
Wing	8	87–90	88.4	1.38	8	80–88	84.4	2.90
Tail	9	58–60	59.0	0.36	8	54–58	56.5	2.34
Tarsus			23.0				22.0	
Culmen	9	19.5–21.5	20.0		4	19–22	20.1	
<i>Himatione sanguinea sanguinea</i>								
Hawaii								
Wing	8	73–78	75.1	2.61	5	68–79	73.8	
Tail	7	50–57	54.9	4.06	4	50–58	53.5	
Tarsus			24.3				22.6	
Culmen	9	15.5–17.5	16.7		4	15–17	16.0	
<i>Himatione sanguinea sanguinea</i>								
Maui								
Wing	1	76						
Tail	1	57						
Tarsus	1	24						
Culmen	1	17.5						

TABLE 2—Continued

	Males				Females			
	No.	Range	M	V	No.	Range	M	V
<i>Himatione sanguinea sanguinea</i> Molokai								
Wing	1	73						
Tail	1	50?						
Tarsus	1	24						
<i>Himatione sanguinea sanguinea</i> Oahu								
Wing	3	72-74	73.0		2	68, 73		
Tail	3	50-53	51.7		2	50, 52		
Tarsus			24.5				23.6	
Culmen	2	17, 17.5			6	15-16.5	15.8	
<i>Himatione sanguinea sanguinea</i> Kauai								
Wing	6	72-76	74.3		3	66-69	68.0	
Tail	6	50-55	53.7		3	48-52	49.7	
Tarsus			23.5				23.0	
Culmen	5	16-17	16.4		3	14.5-16	15.3	
<i>Himatione sanguinea freethii</i> Laysan								
Wing	8	66-68	67.2	0.39	6	57-66	61.5	
Tail	6	58-61	58.8		5	55-57	56.0	
Tarsus			22.8				22.8	
Culmen	8	13-15	14.0		4	13-14	13.6	
<i>Palmeria dolei</i> Maui								
Wing	5	91?-97	94.4		1	93		
Tail	4	70-76	74.0		2	67, 75		
Tarsus			31.7				31.0	
Culmen	7	18-20	18.9		3	18-20	18.8	
<i>Palmeria dolei</i> Molokai								
Wing	2	92, 97			2	89, 89		
Tail	3	71-74	72.3		2	67, 70		
Tarsus			32.5				29.0	
Culmen	2	19.5, 20			3	18-18.5	18.2	
<i>Ciridops anna</i> Hawaii								
Wing	1	75 (sex?)			1	73 (ad.?, ♀?)		
Tail	1	45 (sex?)			1	47.5 (ad.?, ♀?)		
Tarsus	1	20.5 (sex?)			1	20 (ad.?, ♀?)		
Culmen	1	10.5 (sex?)			1	9 (ad.?, ♀?)		
<i>Vestiaria coccinea</i> Hawaii								
Wing	9	82-85	83.2	1.24	6	68-78	75.0	
Tail	9	56-59	57.7	0.45	6	50-55	53.2	
Tarsus			26.2				23.9	
Culmen	8	29-32	30.4	5.80	4	24.5-27	25.7	

TABLE 2—Continued

	Males				Females			
	No.	Range	<i>M</i>	<i>V</i>	No.	Range	<i>M</i>	<i>V</i>
<i>Vestiaria coccinea</i>								
Maui								
Wing	1	82			1	75		
Tail	1	57						
Tarsus	1	26			1	23		
Culmen	1	30			1	27.5		
<i>Vestiaria coccinea</i>								
Molokai								
Wing	1	85						
Tail	1	60						
Tarsus	1	27						
<i>Vestiaria coccinea</i>								
Oahu								
Wing	4	78-83	81.2		1	76		
Tail	4	54-58	56.7		1	52		
Tarsus			25					
Culmen	3	28-31	29.7					
<i>Vestiaria coccinea</i>								
Kauai								
Wing	4	80-84	82.0		7	73-79	75.9	2.77
Tail	3	57-59	57.7		9	50-56	53.1	4.19
Tarsus			24.7				23.2	
Culmen	4	29-30	29.5		6	24.5-28	26.0	
<i>Drepanis pacifica</i>								
Hawaii								
Wing	1	107 (sex?)			1	97? (sex?)		
Tail	1	77 (sex?)			1	71? (sex?)		
Tarsus	1	34 (sex?)			1	29 (sex?)		
Culmen	1	45 (sex?)			1	42.5 (sex?)		
<i>Drepanis funerea</i>								
Molokai								
Wing	1	102?			1	104? (sex?)		
Tail	1	78						
Tarsus	1	33			1	30		
Culmen	1	60			1	56		

of the bill in genera like *Pseudonestor*. The illustrations of the bill given elsewhere in this paper are sufficient to show such variation.

The measurements taken as outlined above are summarized in table 2. The coefficient of variation (*V*) is given rather than the stand-

ard deviation (σ) because the latter, though of fundamental importance in deriving other statistics of normal distribution, is not a good index of comparative variation since it is correlated with the absolute size of a particular measurement. This shortcoming is

obviated by using the ratio of (100 times) the standard deviation to the mean, i.e., the coefficient of variation. Anyone wishing the standard deviation can readily derive it from the formula $V=100\sigma/M$.

Some statisticians (e.g., R. A. Fisher) have questioned the assumption that variability is proportionate to absolute size. While the exact degree of such correlation may be debatable, it obviously exists to a sufficient extent to make V more satisfactory than σ for such comparisons.

For the wing and tail lengths, σ and V were calculated for all series of seven or more measurements. It must be kept in mind that even in measurements having a comparatively low variability, such as wing length in

found to obtain quite generally in other birds (table 4).

Miller (1941, p. 366) published a graphic comparison of values of V for 21 species or subspecies of *Junco*. His average values are very similar to those found for the Drepaniidae. For further comparison, coefficients of variability for certain races and age classes of the white-crowned sparrow, *Zonotrichia leucophrys* (from Blanchard, 1941), and of the shrike, *Lanius ludovicianus* (from Miller, 1931), are given in table 4. They show a somewhat smaller range of values for the wing and tail lengths than do those of the drepaniids compared with them, but this may well be the result of the larger series of recent and probably better prepared material avail-

TABLE 3
SUMMARY OF COEFFICIENTS OF VARIATION (V) FROM TABLE 2

	Males			Females		
	Number of Coefficients	Range	Mean	Number of Coefficients	Range	Mean
Wing length	23	0.27-3.12	2.04	18	1.39-5.23	2.69
Tail length	24	0.36-4.45	2.61	15	1.80-5.11	3.31
Culmen length	5	3.16-5.80	4.37	2	3.33-4.86	4.09

birds, samples of fewer than 25 or so measurements will provide only very approximate values for σ and V . This is evident in the rather dissimilar values of V sometimes obtained for males and females of the same subspecies (table 2).

The tabulated values of V (table 3) suggest that females are slightly more variable than males. This is, of course, highly unlikely. The measurements of the "females" may often contain those of immatures or mis-sexed immature males, while adult males are usually unmistakable in color. Moreover, the considerable difference in this coefficient sometimes existing between the males and females of the same species or race suggests that much of the minor fluctuation evident is due to sampling error rather than to true differences in variability.

Table 3 also indicates that the tail is somewhat more variable than the wing. This distinction is probably valid, as it has been

able to Blanchard and to Miller.

Population geneticists have predicted that reduced genetic variability may be expected in small isolated populations because of random gene loss and fixation. Lack (1945, pp. 84-88) noticed a tendency in this direction among the Geospizinae, though it was usually too slight to be statistically significant in a given population. The average values of V for the drepaniids average little or no smaller than those of wide-ranging continental birds. As regards drepaniids from islands of differ-

TABLE 4
VALUE OF V FOR *Lanius* AND *Zonotrichia*
IN COMPARISON WITH DREPANIIDS

	Wing	Tail	Bill Length
<i>Zonotrichia</i>	2.09-2.46	2.20-3.20	3.53-4.63
<i>Lanius</i>	0.90-1.86	1.84-3.09	2.48-5.02
Drepaniids	0.27-5.23	0.36-5.11	3.16-5.80

ent size, the samples are too small to verify possible differences in variability. The small value for *V* for wing length in *Himatione sanguinea freethi* of Laysan may, however, be correlated with the small size of this population.

It is doubtful if the populations of most species of drepaniids were small enough for such population effects to be apparent. Even on tiny Laysan (2 square miles) Coultas estimated the population of *Psittirostra cantans* to be at least 1000 in 1938. This was probably much below its original figure. It also proved impossible to demonstrate differences in variability correlated with degree of specialization.

DIFFERENCES DUE TO AGE

Males of *Psittirostra palmeri* and of *Loxops maculata flammea* in immature or mixed immature-adult plumage average slightly smaller (about 3 per cent) than do adults (table 2).

A young female *Hemignathus procerus* shortly from the nest but with the juvenal wing and tail quills apparently fully grown has a bill length of only 42 mm. as compared with the minimum value of 51 mm. in adult females. The wing length of this specimen, 87 mm., is actually slightly greater than the minimum, 85 mm., for adult females. In this long-billed species the bill apparently takes longer to reach full length than do the wing and tail quills. This is usual in long-billed birds.

SEXUAL DIMORPHISM IN SIZE

In all Drepaniidae males exceed females in size. This is best shown by wing lengths (table 2), usually a fair index to general size. In two populations (*Psittirostra psittacea*, from Oahu only, and *Drepanis funerea*) the available wing lengths of females are greater than those of males. The four specimens of *P. psittacea* from Oahu are over a century old and in very poor condition. Only two specimens of *D. funerea* were measured, and but one of these is sexed. Adequate material of these two populations would doubtless reveal that males averaged larger than females.

The degree of sexual size dimorphism is not constant throughout the Drepaniidae. This

is shown by the ratios of mean wing and culmen lengths of females to those of the males for selected species gathered in table 5.

TABLE 5
RATIOS OF MEASUREMENTS OF FEMALES
TO THOSE OF MALES

	Wing	Culmen
<i>Loxops virens virens</i>	.98	.91
<i>Loxops virens chloris</i>	.93	.87
<i>Loxops sagittirostris</i>	.91	.94
<i>Hemignathus obscurus obscurus</i>	.94	.89
<i>Hemignathus procerus</i>	.95	.78
<i>Hemignathus wilsoni</i>	.94	.82
<i>Pseudonestor xanthophrys</i>	.91	.77
<i>Psittirostra kona</i>	.95	1.01
<i>Vestiaria coccinea</i> (Hawaii only)	.90	.85

In most species the wing of the female is approximately .95 that of the male. In a few, *Vestiaria*, *Pseudonestor*, *Loxops sagittirostris*, the ratio is about .90. In these the great difference in size of males and females is apparent upon casual examination and is further reflected in the absence of overlap in the measurements of the sexes (table 2).

Not to be confused with these significant differences in the magnitude of sexual size dimorphism are minor fluctuations such as that in *Loxops v. virens* as compared with *L. v. chloris*. This would probably prove to be nonexistent were enough specimens measured. It must be kept in mind that ratios may vary more widely than the measurements on which they are based. If one of the two measurements entering into a given ratio happens to be above the true (population) value and the other below it, these deviations will be exaggerated or minimized in the ratio, depending upon which is made the dividend in computing the ratio.

Similar trends are evident in the comparative tail lengths of the sexes. In two forms, *Loxops virens stejnegeri* and *L. maculata bairdi*, mean tail length is slightly longer for the females, but in view of the general trends in the family and even in the other measurements of these races, this is probably a result of sampling error.

Males of most forms also exceed females in tarsus length. Since this is a shorter measurement and one that is difficult to take accu-

rately, the sexual differences average less, and in some forms the females appear to average slightly larger, though probably more material would reverse this.

Sexual discrepancy in culmen length averages greater than that in wing length. This is particularly true in *Pseudonestor* and *Hemignathus procerus*; in these the culmen length of the females is only about .78 that of the male. In other forms of *Hemignathus*, in *Vestiaria*, and probably in *Drepanis*, the difference is almost or quite as great. In the heavy-billed genus *Psittirostra* there is no tendency towards increased sexual dimorphism in the bill; in *P. kona* the bills of the two sexes are almost identical in size.

The significance of this interspecific variation in relative size of the bill in the two sexes is obscure. In *Hemignathus procerus* it may be a simple result of allometric growth, as suggested elsewhere. What little is known of the habits of *Pseudonestor* does not suggest an explanation for the much smaller size, particularly as regards the bill, of the female.

GEOGRAPHICAL SIZE VARIATION WITHIN SPECIES

Given sufficient measurements it is probable that the members of every isolated population in the Drepaniidae could be shown to differ at least slightly from related ones in average measurements. This does not imply that all the minor fluctuations evident in table 2 are significant. Many of them are doubtless the result of sampling error, as shown by the opposing trends sometimes existing between males and females of the same form. These would almost surely equalize were enough material measured. The following comparisons are limited to the more pronounced, and hence presumably significant, geographic variation.

Loxops virens: The Kauai race, *stejnegeri*, is larger than the others, particularly in the bill, but has a slightly shorter tail. The adaptive significance of this is discussed later. No important size variation is apparent in the populations of *virens* on the other five islands, though the Maui birds appear to have slightly longer bills.

Loxops coccinea: The Hawaii and Maui races are of the same size. The Oahu race may have been smaller, though the three old speci-

mens available are in poor condition. The distinct Kauai race is of the same general size (wing) as those of Maui and Hawaii, but its tail averages 5 mm. longer. The relatively longer tail, characteristic of this entire species as compared with its congeners, is thus accentuated in the Kauai race.

Loxops maculata: This is the only drepaniid with distinct races on each of the six main islands. They are based on color, not size, and the somewhat longer bill of *flammea* of Molokai is the only convincing size difference among them.

Hemignathus obscurus (superspecies): There is progressive east-to-west increase in size in the forms *H. o. obscurus*, *H. o. lanaiensis*, and *H. procerus* (no satisfactory measurements of *H. o. ellisianus* are available). This increase is relatively greater in the length of the bill than in general size, as shown by the values for the ratio of culmen to wing length grouped in table 6.

TABLE 6
RATIO OF CULMEN TO WING IN
CERTAIN DREPANIIDS

Form	Wing	Culmen:Wing
<i>Loxops v. virens</i> (males)	65.2	.21
<i>Hemignathus o. obscurus</i> (males)	77.8	.56
<i>Hemignathus o. lanaiensis</i> (males)	82.0	.65
<i>Hemignathus procerus</i> (females)	86.1	.61
<i>Hemignathus procerus</i> (males)	90.4	.75

The increase in relative bill length exhibited in table 6 culminates in the huge and unwieldy bill of *H. procerus* (pl. 15). It seems doubtful that the great size of this bill is adaptive; more probably it reflects an unvarying pattern of differential growth. This suggestion is strengthened by the fact that the culmen is relatively shorter in females than in males of *procerus*, the former being somewhat smaller in general size also. There is no reason to suppose that the male of *procerus* has different feeding habits than the female or that its relatively larger bill is a secondary sexual character. (These possibilities cannot be ruled out, however, particu-

larly since there is also a striking sexual dimorphism in bill size in the related species, *Pseudonestor xanthophrys*.)

The number of forms compared in table 6 is not sufficient to permit a mathematical investigation of the possible presence of a consistent differential growth relationship. This is true even when the small but related species, *Loxops v. virens*, is included. The values do, however, approximate a straight line when graphed on linear coordinates (fig. 7). This suggests that one of the simpler linear growth relationships rather than the exponential one, $Y = bX^a$, is involved.

If the increase in relative bill length in *Hemignathus* is correctly attributed to allometry, a similar relationship should also exist between larger and smaller individuals. Large males of *H. procerus*, for example, should have relatively longer bills than small ones. Attempts to demonstrate this were unsuccessful, but the expected differences are so slight they might easily be masked by extraneous variation.

As mentioned elsewhere, the one female fledgling of *procerus* examined has a very short bill but a wing of adult size. Such ontogenetic differential growth of the bill may be taken for granted in a long-billed species like *procerus*. It need not and probably would not be of the same magnitude as the less definite phylogenetic allometric trend suggested above.

Hemignathus lucidus: *H. wilsoni* of Hawaii is a larger, more robust bird than its representatives on the other islands, but it has a shorter upper mandible, presumably associated with further specialization of the lower mandible for woodpecker-like use. The Kauai race, *hanapepe*, is somewhat larger than *affinis* of Maui both in size and bill length. The only specimen examined of the little known *lucidus* of Oahu, a supposed immature male, and the measurements of two or three others of this race given by Rothschild indicate that it was approximately the size of the Kauai race.

Psittirostra psittacea: This species seems to be uniform in size over the six islands.

Psittirostra cantans: The Nihoa race is much smaller than the Laysan one, so much so that it often has been considered a distinct species.

Himatione sanguinea: The nominate race is of quite uniform size throughout its range. *Freethii* of Laysan has a shorter bill and perhaps a slightly shorter wing, but its tail is apparently longer.

Palmeria dolei: The Maui and Molokai birds are alike in size as well as color.

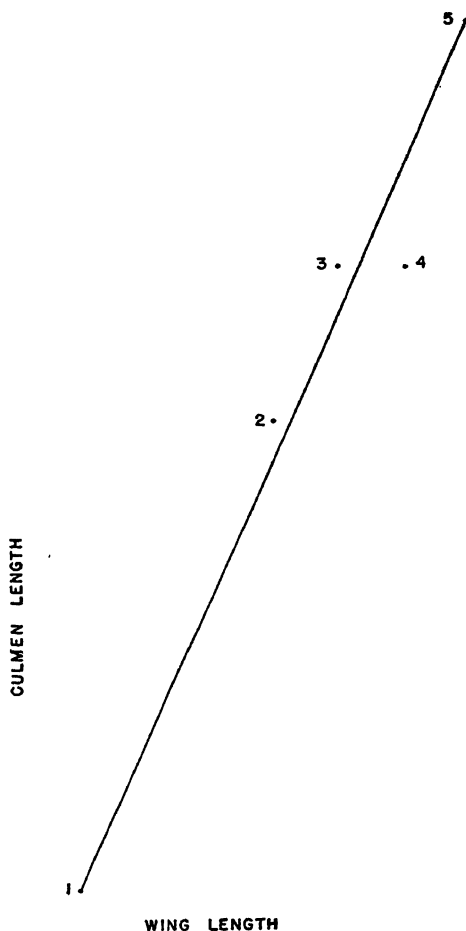


FIG. 7. Arithmetic graph of wing and culmen lengths. 1. *Loxops v. virens* (males). 2. *Hemignathus o. obscurus* (males). 3. *H. o. lanaiensis* (males). 4. *H. procerus* (females). 5. *H. procerus* (males).

Vestiaria coccinea: Possible size variation was considered in the preceding section.

TRENDS: No definite trends are apparent unless perhaps a tendency, when variation is present, for the largest or smallest forms of a given species to occur on one or the other of the terminal islands (Hawaii or Kauai). This

tendency, not very well established, might be attributed to reduced gene flow. The large size of Hawaii and the greater isolation of Kauai are other possible reasons.

Among non-drepaniids the Hawaii species of *Moho* is the largest; the Kauai species, the smallest. The Kauai race of *Phaeornis* is the largest, but there is a small sibling species on that island only (*palmeri*). The Kauai flycatcher, *Chasiempis*, is slightly smaller than the Hawaii race; the latter is about like the Oahu one.

the diagram are the following: Variation in bill length, even in this relatively primitive genus, is much greater than in the other measurements. The bill of *coccinea* is only about .75 that of *virens*, although their general size is nearly the same. *Sagittirostris* has a bill much longer than that of *virens*, but its tail and tarsus are relatively somewhat shorter. *L. coccinea* has a disproportionately long tail (about 1.11 that of *virens*); the possible significance of this is obscure. *L. parva* is the only species that does not vary signifi-

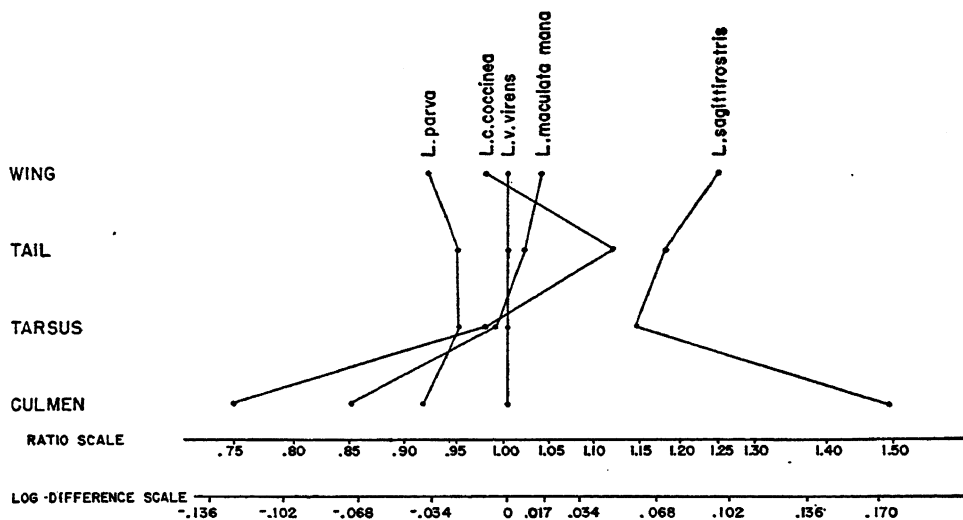


FIG. 8. Comparison of proportions of species of *Loxops* by ratio diagram (see text).

GEOGRAPHICAL SIZE VARIATION AMONG SPECIES OF A GENUS

Loxops: The relative proportions of males of the five species of *Loxops* are shown in the ratio diagram (fig. 8). (For species having more than one race, the Hawaii one was used). The construction of such diagrams, first proposed by Simpson (1941), is explained in Appendix 2. *L. v. virens* is used as a standard of comparison; the ratio scale at the bottom of the diagram gives the ratio of the other four species to it for each measurement.

Wing length may be assumed to be quite closely correlated with general size. The same may be true of the tarsus, though in *sagittirostris* it seems relatively short (about 1.14 that of *virens*, as compared with a corresponding ratio of 1.24 for wing length). Other significant differences in proportion evident from

cantly in proportions from *virens*. All its measurements fall between .90 and .95 of those of *virens*. This supports Perkins' conclusion that *parva* is closest to *virens*; is, in fact, the result of an early colonization of Kauai by *virens* stock. Rothschild and others, misled by its almost straight bill, allied *parva* with *maculata*.

The tail of *Loxops maculata* is rather short. This is a species that creeps over the trunks or branches of trees without using its tail as a support. In such species the tail is apt to be rather short; presumably this increases the bird's agility. The nuthatches, *Sitta*, are a good example of this (Richardson, 1942). Among the drepaniids, the species of *Hemignathus* show this tendency better than does *Loxops maculata*. The short tail of *Loxops sagittirostris* may be a similar adaptation,

though this species fed among foliage and vines rather than on the trunks and larger branches of trees. The somewhat shorter tail of *Loxops virens stejnegeri* as compared with the tail of other races of the species may reflect the fact that it shows an approach in feeding habits to the trunk-frequenting species of *Hemignathus*.

Hemignathus: The more important interspecific variation concerns the adaptive modification and allometry of the bill, discussed elsewhere. The relative proportions of wing, tail, and tarsus of a representative of each of the two superspecies are given in figure 10. They are very similar.

same general size, *funerea* has a considerably longer and somewhat more decurved bill than *pacifica*. Since both probed the deep flowers of lobelias for their principal sustenance, the adaptive significance, if any, of these distinctions is not apparent.

GEOGRAPHICAL SIZE VARIATION AMONG GENERA

Because of the variation in proportions that occurs among the species of some genera, it is not always possible to compare satisfactorily the proportions of the genera themselves. For a number of monotypic or less variable genera, however, it can be done

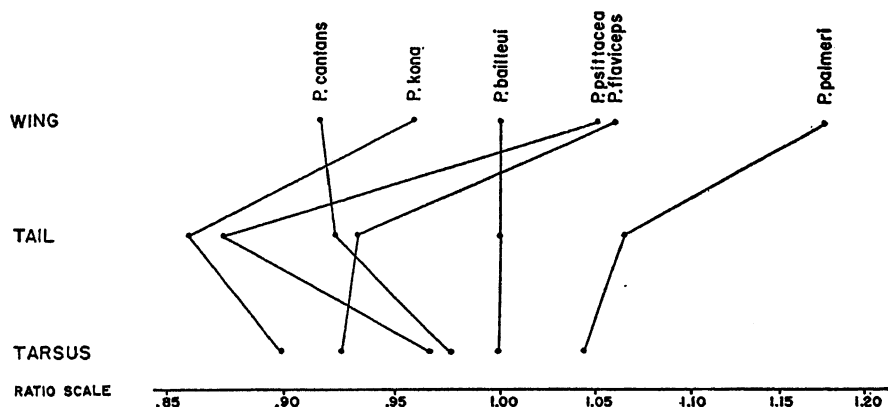


FIG. 9. Comparison of proportions of species of *Psittirostra* by ratio diagram (see text).

Psittirostra: The accompanying ratio diagram of the six species of this genus (fig. 9) does not include culmen length, since the significant variation in these birds is in the heaviness rather than the length of the bill. The scale of this diagram is rather large, so only the more pronounced deviations can be considered significant.

Of the three measurements used the tarsus is probably most closely related to general size. It will be noted that the wing length is relatively less in *cantans* than in the other species. As pointed out elsewhere (in the discussion of locomotion) this may be an adaptation to its semi-terrestrial existence on the low coral islet of Laysan. To be noted also is the similarity in the proportions of the sibling species *P. flaviceps* and *P. palmeri*.

Drepanis: Though apparently of about the

profitably. The relative proportions of selected species of the nine genera of the family are shown by a ratio diagram (fig. 10). Culmen lengths were too variable to be included on this diagram. Members of the Psittirostrinae are shown by solid lines, of the Drepaniinae by dotted lines.

Hemignathus wilsoni, the species used as a standard of comparison in figure 10 because of its intermediate size, belongs to a genus in which the tail is relatively short, an adaptation to tree-creeping habits, as noted above. The genera of Drepaniinae in particular (excepting the peculiar *Ciridops*) have relatively much longer tails than has *Hemignathus* or even than such less specialized members of the Psittirostrinae as *Loxops virens* or *Psittirostra palmeri*.

Most of the species have the tarsus rela-

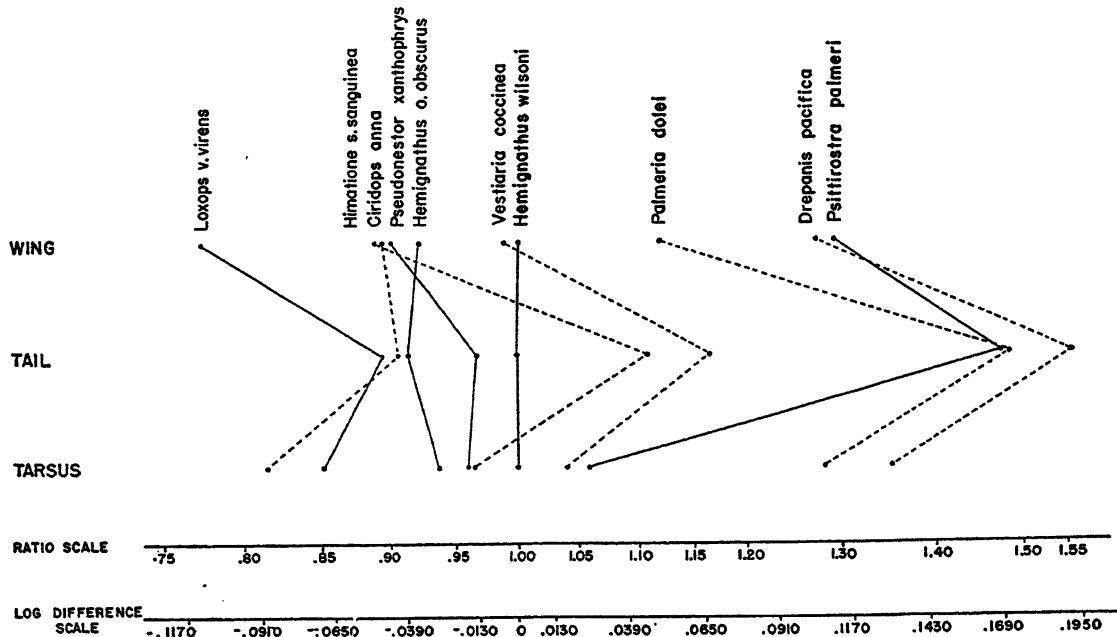


FIG. 10. Comparison of proportions of selected species of the Drepaniidae by ratio diagram (see text).

tively longer (as compared with wing length) than does *H. wilsoni*, but to a much slighter extent than is true of tail length. It is not unexpected for a species of woodpecker-like habits to have a short, heavy tarsus. *Ciridops* also has an exceptionally short tarsus as does, to an even greater degree, *Psittirostra palmeri*. To find whether or not all species of *Psittirostra* have a relatively short tarsus, tarsus:wing ratios were calculated (for convenience from males only) and grouped in table 7.

It will be noted that the tarsus is relatively short in *Ciridops* and in all the species of *Psittirostra* with the exception of the semi-terrestrial *P. cantans*. All these forms are fruit eaters, and this method of feeding seems often

TABLE 7
TARSUS:WING RATIOS OF SOME DREPANIIDAE

Species	Ratio
<i>Psittirostra flaviceps</i>	.24
<i>Psittirostra palmeri</i>	.25
<i>Psittirostra kona</i>	.26
<i>Psittirostra bailleui</i>	.28
<i>Psittirostra c. cantans</i>	.30
<i>Psittirostra psittacea</i>	.25
Other species of Psittirostrinae	.30-.33
<i>Ciridops anna</i>	.27
Other species of Drepaniinae	.31-.34

to be correlated with short legs, perhaps because it requires less hopping about than the pursuit of insects.

MOLTS AND PLUMAGES

MOLT OF IMMATURES

IN THE BETTER KNOWN MEMBERS of the Drepaniinae, adults are alike in color and are strikingly unlike the immatures. In the Psittirostrinae, on the other hand, there is usually less difference between the adult and immature plumages, especially those of the females, and molt is harder to detect. For this reason the molt of the Drepaniinae is considered first.

A preliminary study of *Vestiaria coccinea* based on the 158 skins of this species in the Bishop Museum was followed by more careful examination of 68 specimens in the American Museum of Natural History. Of these 226 birds, 131 (58 per cent) are in adult plumage; 39 (17 per cent) are in nearly adult plumage, but have a few scattered feathers of the juvenal body plumage and often juvenal wing and tail quills; 26 (12 per cent) are in mixed plumage with extensive patches of both adult and juvenal feathers; 12 (5 per cent) are in juvenal plumage with a few scattered red feathers of the adult plumage usually on the breast; while only 18 (8 per cent) are in full juvenal plumage.

The 18 specimens in full juvenal plumage were taken during the period between February 21 and September. In this plumage the throat, scapulars, upper back, and, less commonly, sides of the head are washed with red to a variable extent. In a small immature male shortly out of the nest and observed as it was fed by an adult (B.M. No. 6426, Perkins collector), no reddish feathers are visible in the scapulars, but upon being lifted a few red-tipped pin feathers are visible. This suggests that these reddish scapulars, which may be almost as bright as those of the adult plumage, are the last feathers of the juvenal plumage to appear. Their reddish color may be correlated with hormonal changes in a maturing bird. The fact that the throat feathers are usually tinged with red, although they appear when the bird is still very young, makes this theory doubtful, especially since the amount of red on the throat seems to be correlated with that on the scapulars.

As usual in passerine birds (Dwight, 1900,

p. 108), the post-juvenal molt begins on the breast. It proceeds rapidly on the under parts, less so on the back. Scattered red feathers appear on the chin and forehead at an early stage in the molt, and these areas gradually extend over the head. Usually an area on the nape remains in the green juvenal plumage after the body plumage is almost entirely adult. Even after the nape has molted, a few immature feathers may occasionally be found among the scapulars, wing coverts, or even on the abdomen and back. Individuals with a green patch on the nape and a few green feathers scattered elsewhere are common.

By the time the body plumage is molting, the juvenal wing and tail quills have become somewhat worn and brownish. They are not molted as a rule until after the body plumage has been nearly or quite replaced. In three specimens that still have a few immature feathers about the nape (February 18, March 26) the wing and tail feathers are beginning to be replaced. Perhaps some specimens with fully adult body plumage retain juvenal wing and tail quills. The difficulty of separating worn adults from immatures by the shape of the primaries makes it impossible to prove this from specimens. In individuals hatched late in the nesting season, a few immature feathers may still be present the following spring. Such individuals may breed. Thus B.M. No. 2814, a male taken in February, had a few green feathers on the nape and scapulars but was mated with a fully adult female and was nesting (Perkins, information from label). Two other males with a few green feathers on the breast and many on the back, collected by Henshaw on March 9, are labeled "testes, swollen, apparently breeding." The extreme of this tendency is a male with enlarged testes collected by Henshaw on February 21, still mostly in juvenal plumage but with scattered red feathers on the forehead, flanks, and back.

The post-juvenal molt of *Vestiaria* as just described produces a plumage fully adult in all details. In addition to the complete change in color from yellowish green to scarlet, the rounded juvenal primaries are replaced by the truncate ones of adults and the

unmodified throat feathers of the young by the semi-lanceolate ones of the adult.

Molt in *Himatione sanguinea* is the same as in *Vestiaria*. The 11 specimens of the nominate race in full juvenal plumage were collected between March 5 and June 15; two from Laysan on June 16 and September 1. One taken May 19 was just beginning the post-juvenal molt; one taken in September had almost finished the body molt, but the wing and tail quills are juvenal; while another September bird, in which a few juvenal feathers on the crown are the only signs of immaturity, was just finishing the wing molt, the outer two primaries being half grown and the others new. Its tail is apparently still in the juvenal plumage. One collected January 22 had nearly finished the body molt; its primaries were about half replaced.

The two specimens of *Palmeria dolei* in full juvenal plumage examined were collected on June 21 and August 13. Two others secured on August 13 and 16 were just beginning the post-juvenal molt.

To consider now the subfamily Psittirostrinae, *Loxops c. coccinea* was studied first, since the orange adult male is quite unlike the immature males (and females), thus making the post-juvenal molt more evident. Specimens in full juvenal plumage sexed as males were secured from February to November. A female in juvenal plumage taken on December 29 was labeled by Henshaw as "soon to breed." Eight males in mixed juvenal and adult plumage were taken in October, November, February, and March. In only one of these (November 20) could molt in the primaries be found, but some of the others may already have replaced the wing and tail feathers. It thus appears that the adult wing and tail feathers are acquired at the same time as the adult orange body plumage.

In *Loxops maculata flammea* also the brilliant plumage of adult males facilitates the study of molt. Eight males in mixed juvenal and adult plumage were collected in December, January, February, and June. All had abraded juvenal wing and tail quills without evident molt. Bryan (1906, p. 75) wrote of this race, "one is rather more apt to find pairs mated and settled before the male has assumed one-third of the conspicuous red plumage." This, as well as the testimony of col-

lectors as to the comparative scarcity of the scarlet males, suggests that the molt of *flammea* is a protracted process. Whether it proceeds by definite stages or gradually is uncertain. A long breeding season might account in part for the presence of intermediate males at all seasons.

A male of *Loxops m. maculata* taken January 28 was acquiring adult body plumage but still had the barred wing coverts of the juvenal male plumage as well as juvenal primaries and rectrices.

Two immature males of *Psittirostra psittacea* taken in January were acquiring the yellow head of the male, and in one of them the molt of the primaries had begun; another taken August 3 was in a similar stage of the post-juvenal molt. A specimen taken in June was assuming the yellow head; its wing and tail were almost through the molt but had several feathers still partially in the sheath. This species also may nest while yet in partially immature plumage, for a female collected in February was said to be mated with a male in "imperfect" plumage (Perkins, from label).

Fisher (1903, p. 387) published two photographs of a *Psittirostra cantans* at its nest. He wrote, "Both illustrations . . . show the species in the subadult, brownish, streaked feathering, which it will be seen is worn through the first nesting season."

Several males of *Psittirostra palmeri* taken between June 26 and October 6 have the forehead and throat orange but not the crown and breast as in (presumably) older specimens taken at the same time. Both types were in very worn plumage with no apparent molt. It is not certain if the wing and tail of these more dully colored males represent the juvenal plumage or an intermediate "first winter" or "first breeding" plumage. The true juvenal plumage, represented by September and October specimens, lacks orange and has the breast mottled with dusky. A male taken March 19 was acquiring the orange head feathers. Its wings were in molt, but it is impossible to say whether or not it would have gone into partial or fully adult male plumage.

MOLT OF ADULTS

Adult drepaniids, so far as determined, molt once annually: a complete post-breeding

molt. Body molt is difficult to detect in the material examined, so the following remarks refer chiefly to molt of the wing and tail. The primaries molt in regular sequence from the innermost (first) outward to the last (ninth) as in the immatures. Molt seems to proceed rather rapidly, for often two adjacent quills are replaced almost at the same time. Molt of the tail is even more rapid. It begins at the center of the tail, but often the old feathers are lost so rapidly that all the rectrices grow in more or less simultaneously. The molt of the tail usually occurs after that of the wing is well advanced. Molt of the body plumage may be even later. In *Psittirostra bairdii*, for instance, several specimens with the wing and tail molting were still in badly worn body plumage. The sequence of molt seems to be typical for song birds as summarized by Dwight (1900, pp. 84-97).

In discussing the plumage of *Loxops coccinea*, Perkins (1903, p. 420) wrote: "The red males of *L. coccinea* and probably of other species pass through a stage (non-breeding) when the plumage is largely of a greyish colour, a similar phase being shown by *Oreomyza* [= *Loxops maculata*] *flammea*. This phase is also more or less noticeable in many of the green-plumaged birds of other genera, though less striking than in the red species above-mentioned, and is probably pretty general in this section of the family, but I think not exhibited by the other section (*Himatione*, etc.)." I can find no evidence for such an eclipse or off-season plumage, though prolonged observation of individual birds might be required to disprove it positively. Probably Perkins confused immature or partially immature males for adult males in eclipse plumage. Of *Loxops c. coccinea*, for example, we have males in the bright orange plumage taken almost throughout the year, including the molting season. All the evidence indicates that this garb, once acquired, is retained permanently. The same seems to be true of the adult plumage in the entire family.

In the subfamily Drepaniinae the primaries usually molt in August, though averaging somewhat earlier, perhaps, in the genus *Palmeria*. A specimen of *Vestiaria* taken in August had already replaced its inner primaries; the sixth was growing in, while the

outer three were old. Its tail was molting, only the two outer pairs of old rectrices remaining. June specimens of *Himatione sanguinea* were in worn plumage but not molting. One taken August 5 was beginning to replace the primaries but not the rectrices. Others taken August 26, September 4, and September 11 had nearly finished the wing molt. October specimens were in fresh plumage.

A specimen of *Palmeria dolei* taken June 9 had molted the innermost two primaries; the next two were growing in and the others old; the tail was not molting. One taken August 16 had nearly completed the wing and tail molt; another taken the same date had completed this molt, as had several October specimens.

In the subfamily Psittirostrinae, too, the annual molt usually occurs in late summer or early fall. Because of individual variation in the time of beginning of the molt, the molting period of each species is prolonged over roughly three months. Some species of this subfamily molt later in the season than others.

Of 12 specimens of *Loxops v. virens* taken in August most had finished molting the primaries, but three or four had the outer primary still in the sheath. Of half a dozen September skins all but one had completed the wing molt, and the other had almost done so. October birds were in fresh plumage. One June specimen was badly worn but was not molting, while another taken June 15 was already replacing the inner primaries. Two mid-July birds had the wing half molted.

In the various races of *Loxops maculata* the molt usually occurs in July and August as in *virens*. A June 6 specimen was not molting, but one dated June 24 was finishing the wing molt. The latest date for the molt is a bird collected on October 3 which was just finishing the wing and tail molt. Molting dates for adults of *Loxops coccinea* all fall within the limits of the two congeneric species just discussed.

Series of *Hemignathus wilsoni* and *H. lucidus affinis* indicate a molt similar to that of *Loxops* but perhaps beginning even earlier, since two June specimens were molting the primaries. Although most early August specimens of *Hemignathus* had completed the molt, one taken as late as September 29 still

had one old primary (the outermost) remaining in each wing. *Pseudonestor* molts very early; a female taken June 15 and a male taken in May were both well advanced in the wing molt, while of half a dozen August birds all but one appear to have completed molt of the wing quills.

The molting period of the six species of *Psittirostra* is usually later than that of the other members of the subfamily and varies moreover from species to species. The several June and one July specimens of *P. bailleui* examined were not molting. One or two September birds appear not to have begun the molt, though most of a small series taken in that month were in the midst of it. One taken October 11 was just finishing the wing molt.

In *P. psittacea* the molting season is rather protracted. Although two June birds had started to molt the primaries, the main molting season seems to be from mid-August to mid-October. Much the same is true of *P. cantians*, in which only one (July 24) of several July birds had begun to molt. The only specimen of *P. kona* examined in the molt was in an early stage of replacing the primaries when taken on October 10.

Psittirostra palmeri and *P. flaviceps* molt the latest of all, judging from available specimens. Six *palmeri* taken from October 1 to 16 were all in very worn plumage and were not molting. These include birds in fully adult and in partially adult plumage but not juvenals of the year; they are in fresh plumage at that season. Three March adults of *palmeri* are in fresh unworn plumage, as compared with October birds. The type specimen of *P. flaviceps* was just replacing the innermost primary (October 1), but it was otherwise in very worn plumage. An adult female of *flaviceps* taken October 19 was not yet molting. Hence, in *P. palmeri* (and probably in *P. flaviceps*) molt seems normally to occur no

earlier than the first half of October. The worn condition of the October specimens and the initiation of molt in one specimen of *flaviceps* on October 1 suggest that November may have been the normal molting season in these two species. This is a month or two later than in some congeneric species and three or four months later than in such genera as *Pseudonestor*.

PLUMAGES

As will be evident from the above discussion of molt, many drepaniids seem to molt directly from the juvenal to the adult plumage without an intermediate "first winter" plumage. In this respect they resemble such birds as the Starling, *Sturnus vulgaris*, Cowbird, *Molothrus ater*, or Grackle, *Quiscalus quiscula*. In these species, the juvenal plumage, acquired when the young leaves the nest in early summer, may be retained until fall, when a complete molt into adult plumage occurs (Dwight, 1900). In the Drepaniinae the molt begins almost as soon as the young leave the nest and may be so protracted that birds in partially immature plumage breed. It is not known to what extent this greater variability and prolongation of the post-juvenal molt in the Drepaniidae are correlated with their rather lengthy breeding season.

Sutton (1935) by carefully studying captive young fringillids found that their juvenal plumages may be very transitory. Molt into the first winter plumage often begins before the juvenal plumage is completely acquired. In the cardinal, *Richmondia cardinalis*, which supposedly molts directly from the juvenal to the adult plumage, Sutton believes there is a transitory first winter plumage telescoped in between the other two. It is possible that careful study of developing drepaniids would reveal a similar situation.

COLOR AND COLOR PATTERN

COLOR DIFFERENCES AND AGE

IMMATURES OF THE PSITTIROSTRINAE are dull colored: brownish or grayish above, more whitish below, more or less washed with olive or green. The adult female is usually somewhat, and the adult male much, brighter than the immatures in color. In a few forms, often not closely related, such as *Loxops maculata bairdi* and *Psittirostra kona*, adults are almost as plainly colored as immatures. Exceptionally, as in *Psittirostra bailleui*, the juvenal plumage (and that of the adult female) shows an approach to the colorful adult male.

In the juvenal plumage there is often a white stripe in front of and above the eye. This in some species extends over and behind the eye to form a supra-ocular stripe. These eye stripes may be connected across the forehead. They are variously present or absent in the adult plumage. In *Loxops maculata bairdi*, for instance, such stripes are present in the young but absent in the adults. In *Loxops virens* and most forms of *Hemignathus*, they are present in both immatures and adults but yellow in the latter. In *Pseudonestor* they are particularly well developed. In forms with brilliantly colored males, e.g., *Loxops maculata flammea* and most races of *Loxops coccinea*, eye stripes are present in the juvenile male but lost in the uniformly colored adult male. They persist to some extent in the adult female.

Wing bars formed by white tips on the coverts are another common feature of the immature dress. These bars are almost always lacking in the adult plumage, but in one of the six races of *Loxops maculata*, that endemic to Oahu, they are retained by the adult female.

A number of species of this subfamily have black lores, but this character, unlike the two just mentioned, is best developed in adults and absent or but slightly indicated in juveniles.

A unique feature of the juvenal plumage of *Psittirostra cantans* is the blackish streaking (weakly indicated on the flanks and back of the adult female). This gives it a finch-like aspect that probably represents an adaptation

to the grassy, exposed environment that this bird frequents on Laysan and Nihoa.

In the Drepaniinae, the young of *Himatione* are washed, and those of *Vestiaria* spotted, with black. They are very unlike the brilliant red adults. Young of *Palmeria* are much like those of *Himatione*. Since the adults of *Palmeria* are extensively blackish also, the contrast between young and old birds is not so great. A specimen (A.M.N.H. No. 230275) of *Ciridops* in rather uniform olive green plumage washed with yellow probably represents the immature plumage of that species but may be that of the adult female. A male, not quite adult, of this species has a few brownish feathers in the wing coverts and elsewhere that might be remnants of the plumage just mentioned. The immature plumages of the two species of *Drepanis* are unknown.

SEXUAL DIMORPHISM IN COLOR

The immature plumages of the two sexes are alike. In the adult plumage of the Psittirostrinae the sexes may be alike and dully colored, or the female may be dull and the male brightly hued, or both may be brightly colored. The second condition is the usual one. The third is never fully achieved but is approached by *Psittirostra bailleui* and to a somewhat lesser extent by *P. cantans*.

In the better known genera of the Drepaniinae adults of both sexes are brightly colored. In *Ciridops* the situation is uncertain because of the specimen mentioned above that may be either an immature or an adult female. In *D. funerea* both sexes are black. This is not a reversion to an immature type of plumage but the culmination of a tendency perceptible in *Drepanis pacifica*, *Ciridops*, and *Palmeria*, as compared with *Himatione* and *Vestiaria*, which have only the wings and tail black.

The degree of color dimorphism often varies sharply in closely allied drepaniids. In *Loxops maculata flammea* the male is scarlet and the female brown; in two other races of this species both sexes are dully colored, while the three remaining races are intermediate in this respect. In *Psittirostra psittacea*, *P. palmeri*, and *P. flaviceps*, the female is drab,

the male colorful; in *P. kona*, otherwise the most specialized of the genus, both sexes are uniform green, while in *P. bairdii* the female is almost as brightly colored as the male. "Sexual dimorphism is extremely marked in all the [sub] species [of *Loxops coccinea*], except *L. caeruleirostris*, the male of which to a large extent preserves the green plumage exhibited only by the female and young of the other [sub] species" (Perkins, 1903, p. 420).

INDIVIDUAL VARIATION IN COLOR

In most of the Drepaniidae individual color variation falls within narrow limits. The male of *Loxops coccinea ochracea* of Maui is an exception. Highly colored males of this race are bright ochraceous orange while others are deep yellow, only sparingly washed with orange. Perkins (1903, p. 420) considers these two types of coloration to represent phases, though he admits that intermediates exist. Both types occur in males in breeding condition. The possibility that the yellowish birds are immature and would eventually become orange has not been entirely eliminated. More probably a high degree of individual variation exists, correlated perhaps with incipient racial loss of the orange coloration.

Males of *Loxops virens virens* are normally bright greenish yellow. One or two specimens in the series examined have a slight trace of orange, and Paul Baldwin showed me a specimen in which this is even more noticeable.

Of more pronounced variants or color "sports" the only one examined is a specimen of *Loxops virens wilsoni* collected on Maui on July 18, 1892, in which the eumelanins of the normal plumage are entirely lacking and only the yellow carotenoids remain. The wing and tail quills, only bordered with yellow in the normal plumage, are white in this specimen. This absence of pigment made the quills more subject to wear, and the rectrices are mere ragged stumps.

GEOGRAPHICAL COLOR VARIATION

Geographical color variation runs the gamut from subtle or doubtful distinctions to striking contrasts of red with green or yellow as in *Loxops maculata flammea* of Molokai. As

mentioned above, easily effected changes in the shade of red, orange, and yellow are involved. No trends are perceptible in the distribution of brightly or dully colored subspecies.

PHYLOGENETIC TRENDS

In the Drepaniinae the least specialized species, *Himatione sanguinea*, is brilliant red, as are most of the others. In the Psittirostriinae the only two species with red or orange forms (*Loxops maculata flammea* and three races of *Loxops coccinea*) occur in the least specialized genus, *Loxops*. This suggests that red coloration was basic in the family, at least by the time it split into subfamilies. If this view is correct, the orange wash occasionally found in males of *Loxops virens virens* probably is a throwback to a former orange plumage. Similarly we would assume that *Loxops coccinea caeruleirostris* has lost the orange of the other races of this species and does not represent the original condition.

The yellow or orange head of most species of *Psittirostra* is perhaps a new acquisition, foreshadowed in the yellowish head of *Hemignathus lucidus*. The absence of a yellow head in the otherwise specialized *Psittirostra kona* indicates that color differences of the kind under consideration take place so readily that they are of strictly limited value in showing relationships.

Within the Drepaniinae, a phylogenetic trend towards increase of black in the plumage is noticeable. In *Himatione* and *Vestiaria* only the wings and tail are black; in *Palmeria*, *Ciridops*, and *Drepanis pacifica*, much of the body plumage is as well; in *Drepanis funerea* the entire plumage.

Another trend, that towards the development of lanceolate feathers, characterizes the Drepaniinae. *Himatione* and *Vestiaria* represent initial stages in which such feathers are restricted to the crown and the throat, respectively. In *Ciridops* lanceolate feathers are of more general occurrence on the head, while in *Palmeria* they are present over most of the body as well. *Drepanis*, though otherwise rather specialized, is an exception to this trend and lacks lanceolate feathers altogether.

FEEDING HABITS

THE FEEDING HABITS of the Drepaniidae are of interest in the present study chiefly in relation to evolution and adaptive radiation. For this reason the arrangement follows the classification of the birds rather than the type of food eaten.

Porsch (1930) devoted one of his series of monographic studies of nectar-feeding birds to the Hawaiian Drepaniidae and Meliphagidae. It is primarily a compilation.

Plants that furnish food for drepaniids are listed below; scientific, common, and family names are given. The names are chiefly from Fagerlund and Mitchell (1944).

Freycinetia arborea (Pandanaceae), Climbing Screw-Pine, or Ieie: This vine grows over the trunks and branches of the Hawaiian forest trees, often in profusion. The female inflorescence is the preferred food of *Psittirostra psittacea*. *Hemignathus obscurus* often probed in the deep leaf axils of *Freycinetia* for insects, while various other drepaniids often searched for insects in this vine.

Pritchardia sp. (Palmaceae), Native Palm: The fruit of the native palm was said by natives to have been the preferred food of the extinct *Ciridops anna*.

Tribulus sp. (Zygophyllaceae), Puncture Weed: The thorny seeds of this widespread vine are eaten by *Psittirostra cantans* on Laysan. *Himatione sanguinea freethii* visited its flowers for nectar.

Boerhaavia sp. (Nyctaginaceae): The starchy root is eaten by *Psittirostra cantans* on Laysan.

Sesuvium sp. (Aizoaceae): A. K. Fisher said that the flowers of a *Sesuvium* were a source of nectar for *Himatione sanguinea freethii* on Laysan.

Portulaca sp. (Portulacaceae): It was, like the preceding, a source of insects and nectar for *H. s. freethii*.

Acacia koa (Leguminosae), Koa: This large tree is, after *Metrosideros*, the most important component of the Hawaiian forest. It has suffered greatly from inability to reproduce in areas grazed by livestock. The koa often occurs in almost pure stands and is of great importance to the Drepaniidae. *Psittirostra palmeri* and presumably *P. flaviceps* sub-

sisted largely on its seeds. *Pseudonestor* frequents koa groves where it feeds on cerambycid beetles infesting this tree. It has a short flowering season and is not important as a source of nectar. Many drepaniids hunt insects in the koa, and some, such as *Loxops coccinea*, are said to have a strong preference for it.

Sophora chrysophylla (Leguminosae), Mamani: The seeds of this tree are the preferred food of *Psittirostra bailleui*. Others, such as *Hemignathus wilsoni* and *Vestiaria*, frequent it in search of insects or nectar.

Pelea sp. (Rutaceae), Alani: *Pseudonestor* visits this tree in search of beetle larvae.

Aleurites moluccana (Euphorbiaceae), Kukui or Candlenut: Although considered by some a native species, this widespread tree



FIG. 11. Flower of *Metrosideros polymorpha*. After Porsch.

was probably introduced by the Hawaiian natives. It is of little importance to the native birds, but Perkins found *Loxops virens* feeding in it on scale-insects during an outbreak of these pests.

Dodonaea sp. (Sapindaceae), Aalii: Accord-

ing to Munro, *Psittirostra palmeri* fed on the seeds of this tree.

Wikstroemia sp. (Thymelaeaceae), Akia: According to Perkins, *Loxops virens stejnegeri* feeds on the berries of this plant.

Metrosideros collina (Myrtaceae), Ohia: The ohia is the dominant forest tree on all the islands. It assumes a variety of growth forms, sometimes occurring as a tall, stately tree, sometimes as a thick stand of scrubby growth pioneering on lava fields; while on windswept ridges its trunk may be prostrate. Its pompom-like blossoms are usually red (fig. 11). They are so shallow that even short-billed species like *Loxops parva* can extract the nectar. The ohia blooms profusely, usually over a long season. There are altitudinal variations in the flowering season, so trees in bloom may be found at all seasons. Most of the nectar-sucking drepaniids concentrate their attention on the blossoms of the ohia, and all of them obtain some nectar from it, even the long-billed species that prefer lobelias.

This tree belongs to a closely related group of species widespread in Polynesia from New Zealand to Hawaii. This, along with its great individual variability in the Hawaiian Is-



FIG. 12. Flower of *Clermontia grandiflora*. After Porsch.

lands, led Perkins to believe that *Metrosideros* is a relatively recent arrival there, notwithstanding its present abundance.

Ipomoea sp. (Convolvulaceae): *Himatione sanguinea freethii* visited the flowers of this species for nectar.

Physalis peruviana (Solanaceae), Poha: *Loxops v. virens* and *Psittirostra bailleui* eat the fruit of this species.

Myoporum sandwicense (Myoporaceae), Naio: *Psittirostra kona* was able to crush the hard seeds of this tree, obtaining thus its principal food. *P. bailleui* feeds to some extent on these seeds, when they are immature and softer.

Clermontia (and related genera) (Lobeliaceae), Lobelias: The endemic arborescent lobelias are among the most remarkable members of the endemic Hawaiian flora. They have deep, curved, tubular flowers (fig. 12). The two species of *Drepanis* exhibited a strong preference for them. The long-billed *Hemignathus obscurus* and *H. procerus*, though mainly insectivorous, preferred lobelias when they did supplement their diet with nectar.

Perkins and others believed these lobelias to be dependent upon drepaniids for fertilization. Dr. Harold St. John, botanist at the Bishop Museum, told me that the lobelias continue to set seed successfully on Hawaii, though both *Drepanis pacifica* and *Hemignathus obscurus* are extinct. On Maui where these genera were absent, so far as known, there are a number of endemic lobelias. Hence drepaniids cannot be their sole means of fertilization.

The berries of lobelias are a food of *Psittirostra psittacea*.

The feeding habits of the various species of the Drepaniidae will now be briefly summarized.

Loxops virens: On Oahu I frequently observed this species visiting the blossoms of *Metrosideros*. It also seeks insects among the foliage and sometimes on the branches of this and other trees. Munro (1944, pp. 101-102) wrote: "When feeding in the ohia flowers its action is different from that of the iiwi [*Vestiaria*] and apapane [*Himatione*] which pass over the flowers quickly. The amakihi [*L. virens*] is much more leisurely in its movements when feeding. It probes in the crevices of the bark and hunts in the folds of leaves. It will persevere for a considerable time in obtaining something from a folded leaf, a chrysalis or spider's egg-sac." He noted that it pierced the deep corollas of lobelias at their bases to get at nectar or insects. Munro thinks this species spends more time at each flower

than such species as *Vestiaria coccinea*, because it is in search of insects as well as nectar.

The Kauai race, *Loxops virens stejnegeri*, has a heavier bill than the others. This is correlated with differences in feeding habits. Perkins (1903, p. 409) said, "The larger Kauai species [*C. stejnegeri*], which is a stronger bird and has a stouter beak than the others, is more constant than these in its attention to the trunks and limbs of large forest trees. . . ."

Loxops virens also feeds upon berries. Perkins (1903, p. 409) wrote: "On occasion they are even fruit-eaters, for at times *C. stejnegeri* may be seen day after day feeding on the red berries of the Akia (*Wikstroemia*), and in the higher forests of Hawaii *C. virens* comes even to the ground for the berries of the Poha (*Physalis*). On Oahu the Amakihi took to feeding on a scale-insect (*Lecanium*), with which the leaves of the Kukui trees [*Aleurites*] were some years ago very much infested, and specimens shot in these trees had their stomachs entirely filled with these insects."

Loxops parva: The feeding habits of this small species are much like those of *L. virens*. Perkins (*loc. cit.*) remarked that it confined itself more to the foliage and to shallow blossoms such as those of the ohia, not frequenting the larger branches in search of insects as *L. virens* does at times.

Loxops sagittirostris: Perkins (1903, p. 412) described the feeding habits of this species as follows: "Nearly all the *Viridonia* seen by me were in the Ohia trees or more often in the dense masses of Ieie (*Freycinetia*) clothing the trunks of these trees. . . . In the eight examples that I dissected I found the small forest crickets of the genus *Paratrigonidium* to form a large part of this food. Caterpillars and spiders were also taken from the bird's stomach as well as a common carabid beetle, which lives at the base of the ieie leaves, where these are closely attached to the stem. For obtaining the latter and the crickets which live in the same situation, the strong beak of *Viridonia* is well adapted. Once only I saw one feeding at the flower of the Ohia. . . . I have little doubt that it was feeding on nectar, since its tongue is still unchanged from the form exhibited by that of the most persistent nectar-eaters."

Loxops coccinea: Perkins (1903, p. 418) wrote of this species: "In their general habits the species of *Loxops* [= *L. coccinea*] approach most nearly to *Chlorodrepanis* [= *L. virens*], since they obtain their food chiefly from the foliage of the trees. . . . They are largely eaters of caterpillars, feeding not only on the common exposed span-worms or loopers, but seeking also the more hidden smaller kinds, which feed in the leaf-buds, or are otherwise concealed. The abnormal structure of the mandible is clearly connected with the habit of seeking food in the closely imbricated buds of some of the forest trees. . . . two of the species of the genus also—*L. caeruleirostris* and *ochracea*—feed more or less rarely on the nectar of the Ohia blossoms. The thin, long, honey-sucking form of tongue is fully preserved in all, in spite of the small attention paid to such food, but with the distorted mandible it is obviously a very efficient help in procuring the larvae which feed in the terminal buds of trees. . . . The essential use of the distorted mandible of *Loxops* is without the least doubt for the extraction of insects living hidden in the leaf-buds of certain forest trees. These buds may not inaptly be compared to the pine cones from which *Loxias* [the true crossbill] procures its food, although their much softer substance by no means requires the more powerful implements of the crossbill. As has been already mentioned, the bill of *Loxops* is also useful in opening out the Koa phyllodes, when fastened together by certain caterpillars, or by some spiders. . . ."

Henshaw (1902, p. 62) apparently never saw this species take nectar, nor was he able to see that the twisted tips of the mandibles were of special use in procuring food, though at the time he was apparently unaware of Perkins' views on this subject.

Loxops maculata: This species receives its common name of Creeper from its habit of creeping over the trunks and branches of trees in search of insects. Henshaw (1902, p. 47) wrote: ". . . the present species creeps along the trunks and the larger branches, gleaning from the interstices of the bark and from the mosses and lichens its insect fare. Its food consists very largely of the larvae of beetles, which its sharp, straight bill enables it to procure with ease, provided they are not deeply hidden." It very rarely takes

nectar, though Perkins once or twice saw individuals of the Maui and Lanai subspecies visiting ohia flowers.

Hemignathus: The feeding habits of the members of this genus are given in some detail as they are important in understanding the adaptive radiation of the Drepaniidae.

Hemignathus obscurus+*procerus*: Perkins (1903, pp. 422-424) wrote as follows: "The two common species [of Hawaii and Kauai] are both partial to the nectar of some kinds of aborescent Lobeliaceae . . . especially to these with large corollas, while to certain kinds they pay no attention at all, however profusely they may be in flower. . . . At other times both the common species resort to the flowers of the Ohia with their exposed nectaries. The insects on which *Hemignathus* feeds are sought for . . . in or beneath the bark of trees and in decaying wood. . . . In the large Koa trees . . . the Akialoa could be traced by its audible tapping on the bark, the sound resembling that produced by the strokes of the beak of the Nukupuu [= *H. wilsoni*], except that it was less loud. In the excessively wet forests of windward Hawaii it was sometimes seen on the stems of the tree ferns, or amongst the masses of *Ieie* (*Freycinetia arborea*), exploring with its long beak in the first case the cavities of the stems of old fronds, broken off close to the caudex, and in the second the bases of the stiff clasping leaves and the debris found there, in both of which situations insects habitually harbour. . . . Several times, both on Kauai and Hawaii, I have killed a specimen when feeding woodpecker or creeper-like on the surface of a tree-trunk, and it has remained suspended from the tree by its beak alone, this organ at the moment of death having been thrust into some crevice or insect burrow, which it was probing for food. I have seen *Heterorhynchus wilsoni* suspended by the curved maxilla alone in similar fashion."

Other observers all emphasize that these species usually subsist on insects obtained by probing in crevices in the bark as they hop along the trunks and larger branches of trees. Henshaw, though he had much experience with *H. o. obscurus*, never saw it take nectar.

Hemignathus lucidus: Not so much is known of the feeding habits of this species as

we would like, for the Kauai and Maui races were always rather uncommon and local, while the Oahu race became extinct at an early date.

Perkins wrote (1903, p. 428): "In their manner of feeding both the Maui and Kauai species greatly resemble *H. wilsoni* [see below], but they are, though very active, less vigorous in their movements, when hunting their prey. Both hammer on the surface of trunk or branch and produce a tapping sound, audible at a distance, but it is generally much less loud than that of the Hawaii bird *H. affinis* on rare occasions sucks the nectar of the flowers of the Ohia." After mentioning various insects taken by members of this superspecies, Perkins continued: "But considering the various species of *Heterorhynchus*, as examined in all localities and at all seasons, their favourite food would appear to be the small brassy weevils of the genus *Oodemas*, a form not less peculiar than the birds themselves. . . . Though they habitually frequent trees infested with the native Cerambycid beetles they appear to trouble these rarely or not at all, either as larvae or as adult beetles. For this reason *H. affinis*, feeding side by side, as it sometimes does, with *Pseudonestor*, and constantly frequenting the same trees, enters but little into competition with this species, which is constantly on the hunt for these larvae."

Hemignathus wilsoni: This species is a geographical representative of *H. lucidus* and has in general similar feeding habits, but the greater modification of the mandible has allowed it to become even more woodpecker-like in its food getting. It never takes nectar. Munro (1944, p. 119) wrote of it: "All its muscles are well developed, especially those of the head and neck, and its skull is exceptionally thick. The head is larger than that of the Kauai species [*H. lucidus hanapepe*] and we had difficulty in getting the skin over it. The mandible seemed to extend further back than in most birds. I believe this has been brought about by its habit of using the lower mandible as a woodpecker does its bill. It uses great energy in beating at the bark and wood, breaking off pieces and dropping them. . . . It drives the lower mandible with considerable force into the crevices of the bark, the mouth kept open, the tapping noise being

plainly heard at a distance. . . . When it gets the lower mandible inserted it uses it as a lever. . . . The pieces which break off it takes with both mandibles and throws off, sweeping the long upper one into the crevices opened on the branch." Perkins (1903, p. 428) wrote: "Not infrequently it lays hold of a projecting piece of bark or the stump of some small broken branch, and shaking its head from side to side, and pulling in all directions, endeavours to tear it down. If unsuccessful in the attempt, it will alternate this treatment with a shower of blows from its gaping bill."

Pseudonestor xanthophrys: Of this remarkable bird Perkins' account is the most complete. He wrote (1903, p. 431): "It is extremely partial to the Koa [*Acacia koa*], and at most seasons obtains its food almost entirely from these. This food consists for a great part of the larvae, pupae and immature beetles of the native Cerambycidae, but more especially of *Clytarlus pennatus* and *modestus*, enormous quantities of which it destroys. It also visits other trees occasionally, especially some kinds of *Pelea*, whence it obtains the larvae of *Plagithymus*, leaving remarkable scars on the trees as a token of its visit."

"*Pseudonestor* is generally a sluggish bird, with little of the activity of the Nukupuu (*Heterorhynchus*) [= *Hemignathus wilsoni*], although in its movements it in many respects closely resembles the latter. Thus in hunting along a fallen tree-trunk it examines both sides in a single journey from end to end; in opening out the burrows of the *Clytarli* it often wrenches and pulls in a very similar manner; The twigs and smaller branches of the Koa, in which the *Clytarli* are found, are never rotten, but generally even drier and harder than the healthy, growing wood, and require enormous strength to open them. To perform this the branch is gripped by the curved upper mandible and the lower one opposed to it, and the burrow of the larva is exposed, either by the act of closing the beak or by wrenching with it, the somewhat slender tongue assisting in extracting the prey." He elsewhere spoke of the "great muscles" of its jaw.

Psittirostra psittacea: All observers seem agreed that the female inflorescence of the Climbing Screw-Pine or Ieie (*Freyinetia*

arborea) is the chosen food of this species and that its beak "is entirely formed and adapted for the purpose of picking out the component parts of this. . . ." (Perkins, 1903, p. 433). He continued: ". . . it also sometimes feeds on the male flowers as well as on parts of the . . . leaf-bracts. . . . It also in a lesser degree eats the fruits of several other trees, and in forests above the range of the Ieie is very partial to the berries of some of the arborescent Lobeliaceae. . . . In some localities the bird pays great attention to the red flowers of the Ohia. . . . Specimens shot while so engaged contained only much finely-divided green vegetable matter, so far as could be distinguished, . . . but I suspect that the exposed nectar of the flowers was really the attraction." This species also eats caterpillars and feeds them to its young.

Psittirostra cantans: The somewhat rigorous conditions on Laysan gave this species a generalized diet. Munro (1944, p. 129) wrote, "It has a wide dietary; insects, larvae, birds' eggs, dead birds, the starchy root of the *Boerhaavia*, seed of the seaside *Tribulus* which it cracks despite the protecting thorns."

W. K. Fisher (1903, p. 388) wrote: "*Tele-spiza* is not particular as to its food, but is fond of the soft parts of grass stems, tender shoots of bushes, seeds, and especially of sea-fowl eggs. I once frightened a tern off her 'nest,' and almost immediately a pair of Finches flew to the egg. One of them cracked a neat hole in the shell with a few strokes of its powerful beak, and began to feed, although I was hastily adjusting a camera only a yard or two away. . . ." The Nihoa race also feeds on eggs (Vanderbilt and deSchauensee, 1941, p. 13).

Psittirostra palmeri: Munro (1944, p. 126) wrote: "It fed largely on the green beans of the koa. The first one I saw was hanging back downwards evidently working on a bean pod after the manner of *Pseudonestor*. Old pods on the ground had a row of holes cut in them where the seeds had been. The seeds of these Hawaii koas were large and sometimes the birds' stomachs were stuffed with large pieces which had been cut up by their sharp-edged beaks. Some had a few smaller seeds in their stomachs and one small group was feeding in the low aalii trees (*Dodonaea*). They made quite a rustling in extracting the seed from

the dry shell surrounding it." Perkins (1903, p. 437) found that it occasionally takes caterpillars and "sometimes devours large quantities of gaudily coloured species, as well as the more sombre brown or green looper caterpillars."

Psittirostra flaviceps: The few known specimens were taken in association with *P. palmeri* and so far as known had similar habits.

Psittirostra bailleui: Perkins (1903, p. 436) stated: "The food of the Palila is to a very large extent derived from the Mamani trees [*Sophora*], on the seeds of which it chiefly feeds. I have frequently seen it cut off a pod and hold it down on a branch with its claws in order to extract the seeds. . . . It feeds its young on caterpillars, and is itself at some seasons most partial to such food. . . ." Munro (1944, p. 125) said it also eats the seed of the naio (*Myoporum*) while they are green and soft, and the fruit of the poha (*Physalis*).

Psittirostra kona: Munro (1944, p. 131) wrote of this, the most grosbeak-like of the drepaniids, as follows: "It frequented the naio (*Myoporum*) trees and in breaking the hard dry seeds with its strong heavy beak made a cracking sound which guided us to it. . . . Perkins found it a sluggish bird but I thought it active at times. When feeding it did seem sluggish, it sat still and cracked nuts, but it could move about with considerable alacrity. . . . Its food was almost entirely the little maggot-like germ from the center of the naio seeds but sometimes it cut up the green nuts and swallowed them. It also ate green leaves and at times caterpillars." It fed on more concentrated food than *P. palmeri* and had a much smaller stomach.

Himatione s. sanguinea: Perkins (1903, p. 407) wrote: "The Apapane is a great nectar eater, and this it procures mainly from the red flowers of the Ohia [*Metrosideros*], while of animal food, caterpillars, of which it is particularly fond, are obtained from many trees. . . . It can, and when necessary does, pass over a wide area in search of the Ohia blossoms, as well as making regular migrations when the flowering season demands. Vast numbers often collect in a favourite feeding ground."

Himatione s. freeihii: Fisher (1903, p. 389) wrote: "They are abundant in the interior of the island [Laysan] near the open plain bordering the lagoon. Here on the extensive

beds of succulent portulaca they may be seen throughout the day, busily walking about like pipits, either gathering insects or drinking honey from the numerous half-blown buds. The brush-like tongue . . . renders the gathering of honey, and such tiny insects as may infest the interior of corollas, an easy task. In fact it was no uncommon occurrence to see one go from flower to flower, and insert its bill between the petals of a nearly opened bud, with a certain precision and rapidity which suggested a hummingbird, except of course that the *Himatione* was on its feet. I also observed them catching green caterpillars from *Chenopodium sandwichicum*. . . . The Honey-eaters are partial to small brownish-gray moths or 'millers' which abound on the island. While we were at lunch, nearly every day a *Himatione* flew in and extracted these creatures from cracks between boards. It then grasped the miller with one foot, after the manner of a bird of prey, clinging with the other to the rough board wall, and ate the soft parts of its quarry. After a few moments the still fluttering victim was released." Munro (1944, p. 98) saw them visit the flowers of the nohu (*Tribulus*) and pohuehue (*Ipomoea*).

Palmeria dolei: Henshaw (1903, p. 54) stated that *Palmeria* has the same feeding habits as *Himatione*. It is an active, sprightly bird, frequenting the ohias for nectar and also taking insects. Perkins (1903, p. 406) noted that its crest is often filled with entangled pollen grains and that it sometimes hunts for caterpillars on dead branches as well as among foliage.

Vestiaria coccinea: The feeding habits of *Vestiaria* are similar to those of *Himatione*, but its longer bill enables it to obtain nectar from a greater variety of flowers. According to Perkins (1903, p. 403) it ". . . is extremely partial to many of the native campanulate or tubular flowers. . . . Besides the nectar of flowers, which on some occasions is the only food to be found in the stomach, this bird is especially fond of looper caterpillars, and so far as I have observed feeds its young entirely on these. It also feeds on those species of spiders which are so frequently found on the limbs of forest trees." Perkins believed its long bill was evolved to feed from tubular

flowers which are evidently an older element in the Hawaiian flora than the shallow-flowered *Metrosideros*. Henshaw (1902, p. 53) found it had learned to pierce the tubular corollas of some of the introduced nasturtiums at their base and thus obtain the nectar. This species wanders a great deal in search of flowers. It sometimes has regular local migrations, for Baldwin (1944) found that it frequents a particular tract of wet fern forest on Hawaii from August to March but is absent at other times.

Drepanis: Very few naturalists ever observed *Drepanis pacifica* in life. Henshaw (1902, p. 52) briefly observed two or more. They were very active in the tops of the tallest ohia trees, apparently hunting for insects. Some additional information on the feeding habits of this species is known from native reports. This may be omitted in view of our better knowledge of *D. funerea*.

W. A. Bryan wrote of the latter (1908, pp. 154-155): "The trees and vines were everywhere covered with thick wet moss, and although the bird hopped about from branch to branch, carefully inspecting each limb, I did not see it catch any insects, or even probe into the moss. Hopping from tree to tree, it worked its way around the head of the little side valley, up which it had come in answer to my call, to where a large purple-flowered lobelia was in profuse blossom, and began to feed. The ease and grace with which the feat was accomplished was indeed interesting, and left no doubt in my mind as to one of the probable causes of the remarkable development of the tongue and bill. The tongue was inserted with great precision, up to the nostrils, in the flower, while the bird balanced itself on the branches, assuming almost every imaginable attitude in its operations. In all three of the birds secured, the crown was smeared with the sticky purplish white pollen of this lobelia. . . . The chord of the largest of the curved tubular flowers of the lobelia on which the birds were feeding, is over two inches in length."

Perkins (1903, pp. 401-402) also saw *Drepanis funerea* exploring wet moss, darting its

tongue in and out so rapidly it appeared like a "liquid streak," but since not one of those he collected contained animal food he concluded they were taking water. "On one occasion only was the bird seen to visit the red flowers of the Ohia"; it preferred lobelias. "On one occasion. . . I saw three adult males of this bird in one low bush passing from flower to flower and spending only a few seconds over each. These were very tame, and I was able to watch their movements in this and neighbouring bushes for at least an hour. Even those flowers which were at a height of not more than a foot from the ground were carefully explored."

Ciridops anna: The native name of this bird was said to have been Ula-ai-hawane or "red bird that feeds on the Hawane," i.e., the fruit of the Hawaiian palms (*Pritchardia*). *Ciridops* was never observed in life by a naturalist, but its thick, short bill lends credence to the statement that it had departed from the nectar-feeding habits of its relatives and subsisted on fruit.

A summary of the food habits of the Drepaniidae according to type of food follows:

- Primarily nectar, some insects. Drepaniinae: *Himatione sanguinea*, *Vestiaria coccinea*, *Palmeria dolei*, *Drepanis pacifica*, *D. funerea*
- Primarily insects, considerable nectar. Psittirostrinae: *Loxops parva*, ?*L. sagittirostris*, *Hemignathus obscurus*, *H. procerus*
- Primarily insects, considerable nectar, some berries. Psittirostrinae: *Loxops virens*
- Primarily insects, very rarely nectar. Psittirostrinae: *Loxops maculata*, *L. coccinea*, *Hemignathus lucidus*
- Insects, no nectar. Psittirostrinae: *Hemignathus wilsoni*, *Pseudonestor xanthophrys*
- Primarily fruit or seeds, some insects. Drepaniinae: probably *Ciridops anna*. Psittirostrinae: all six species of *Psittirostra*

From the above it is evident that there is much greater diversity in feeding habits among the Psittirostrinae than among the Drepaniinae. The only genus of the latter subfamily that was not a typical nectar feeder was *Ciridops*, concerning which little was learned before it became extinct.

SONG, NESTING, AND LOCOMOTION

VOICE

THE SUBDIVISION of the Drepaniidae into two subfamilies is strongly supported by a difference in songs and call notes. Baldwin (1944) described this as follows: "The male amakihi [*Loxops v. virens*] has a slow, level 'trill' which it gives by itself or as a component of a complex song while fighting or singing for territory. The closely related olive-green creeper [*Loxops maculata mana*] has a similar male note given under like conditions, but it is more rapid and descends as does a whinny. I am certain that the akepa [*Loxops c. coccinea*] also has a similar but distinctive male 'trill,' though I have not been in the haunts of that rare bird enough to work it out fully. The close relationship of these Hawaiian birds is shown by these voice phenomena. Even the akiapolaau [*Hemignathus wilsoni*] with its so divergent bill structure has certain complex song elements almost indistinguishable from the three mentioned above and from what little I have heard of the ou's [*Psittirostra psittacea*] voice, I believe its notes may be likewise similar.

"The notes of the apapane [*Himatione*] and iiwi [*Vestiaria*] are totally different from the green group [=subfamily Psittirostrinae]. At least I can discern no similarity at all in the sound of the notes, the types of phrases, or corroboration of voice with behavior."

Perkins contrasted the songs of the Drepaniinae with those of the Psittirostrinae as follows (1903, p. 394): "The songs of the other group of Drepanids are quite different. That of the 'Iiwi' (*Vestiaria*) is harsh in the extreme. The song of the 'Apapane' is short, monotonous and often repeated, but not unpleasant. It has a singularly plaintive call-note. The 'Mamo' (*Drepanis*) and the allied form on Molokai have an identical cry, except that in the latter at its best it is probably much louder. The song of *Palmeria* is peculiar, as it makes a remarkable vibrating or gurgling sound. In spite of the dissimilarity in the normal songs or cries of the birds of this section, most of the different forms frequently utter calls or notes very similar to one another. They are more varied than the almost

universal squeak of the call or alarm-note of the green-feathered section [Psittirostrinae]."

The creaky notes of *Vestiaria* reminded me of a mixed flock of blackbirds, *Agelaius*, and cowbirds, *Molothrus*, of the family Icteridae. The song of *Loxops virens chloris* is a uniform series of notes that resembles that of the Swamp Sparrow, *Passerella georgiana* (Emberizinae). Howard Cogswell has likened it to the song of the Pileolated Warbler, *Wilsonia pusilla* (Parulidae). These resemblances are probably of no phylogenetic significance.

NESTING CYCLE

In *Himatione sanguinea* the male has been observed to spread its wings like a "strutting turkey cock" and "dance" on a limb in what was apparently a courtship performance (Seale, 1898, p. 43). There is some indication that the drepaniids, at least the Psittirostrinae, may be territorial. Perkins (1903, p. 414) wrote of *Loxops maculata*: "Apparently they sing only under stress of intense excitement, as for instance when one male has been successful in driving off another from its domain. On such occasions I have seen the victor rise spirally upwards to a height of twenty or thirty feet pouring out its little song while on the wing and then suddenly darting down again. . . ."

Most drepaniids nest in the spring, as do the birds of the Northern Hemisphere, but the nesting season may be rather protracted. Palmer even found *Himatione* and *Vestiaria* nesting in the fall. Baldwin (1944) wrote of his observations on Hawaii: "The longest nesting period I have observed belongs to the iiwi. In 1941 actual nesting had commenced early in January, as newly fledged young were seen in the park forests in the middle of February. The latest new fledglings were seen in July. Apapane (*Himatione*) and amakihi (*Loxops virens*) apparently started a few weeks later in the spring and continued through the early summer."

All drepaniids, so far as known, build rather loosely constructed, open, cup-shaped nests placed in trees, bushes, or (on Laysan) grass tussocks. A nest of *Loxops virens chloris* given to me by Howard Cogswell was placed

among the dense twigs of a small ohia lehua tree a few feet above the ground. It measures 53 mm. in diameter and 27 mm. in depth and was lined with fine rootlets and fibers. W. A. Bryan (1905b, p. 243) described the eggs and nest of this species as follows, "The eggs have a creamy white ground which is covered with pale lilac and smoke-grey freckles crowded together at the large end to form a cap-like zone." Of the nest he wrote: "Externally it is composed of fine twigs and bits of grass; the lining is of cream-colored lichens. . . . Into the coarse materials are woven a number of the balloon-shaped egg cases of certain species of spiders. . . . The structure is neat, compact and well made." The nests and eggs of other Hawaiian honeycreepers are all much the same.

There seems to be nothing in the nest and eggs of these birds sufficiently distinctive to be of much value in assessing their relationships. Some, if not most, species of the Fringillidae, Thraupidae, and Parulidae build similar open nests and lay spotted eggs. The more typical species of Coerebidae build domed nests with a side entrance, but *Eunornis campestris* and probably *Diglossa* make open nests. Moreover, the building of domed nests by some species of Fringillidae, Thraupidae, and even Parulidae makes it unwise to place too much emphasis on such habits. The pensile nests of typical members of the Icteridae also are rather unlike those of the Drepaniidae. Here again the occurrence of less specialized nests in the grackles, bobolinks, and meadowlarks (*Quiscalus*, *Dolichonyx*, and *Sturnella*) and the absence of nest building in some of the parasitic cowbirds, e.g., *Molothrus ater*, cast doubt on the value of such facts.

Little is known of the participation of the sexes in the various phases of the nesting activities. Perkins saw a male of *Psittirostra palmeri* carrying nesting material and found both members of a pair of *Loxops coccinea ochracea* engaged in nest building (1903, p. 420). There are several reports of a pair of drepaniids accompanied by a brood of young, so probably both sexes help to care for the young. It is not known if more than one brood is raised per season.

The numbers of each sex present in the material examined in certain species in which the

sexes are alike or nearly so in color (and hence less apt to be differentially collected) are presented in table 8. In a few, e.g., *Vestiaria coccinea*, the preponderance of males is sufficient to suggest that a real disparity exists in nature. It is possible, though, that the males are more active and vocal and hence are collected more often.

TABLE 8
SEX RATIOS OF SOME DREPANIIDAE
IN COLLECTIONS

Species or Subspecies	No. of Males	No. of Females
<i>Loxops parva</i>	14	9
<i>Loxops maculata bairdi</i>	13	9
<i>Loxops maculata mana</i>	21	21
<i>Loxops coccinea caeruleirostris</i>	11	10
<i>Psittirostra bailleui</i>	11	10
<i>Himatione s. sanguinea</i>	19	13
<i>Vestiaria coccinea</i> (American Museum)	16	12
<i>Vestiaria coccinea</i> (Bishop Museum)	73	27
<i>Vestiaria coccinea</i> (total)	89	39
<i>Palmeria dolei</i>	10	7
Total	188	118

Total ratio of females to males .63

LOCOMOTION

The ancestor of the Drepaniidae must have been a bird of strong flight to reach the Hawaiian Islands. Its descendants are arboreal and have retained average powers of flight. Munro (1944, p. 101) wrote of *Loxops virens stejnegeri*: "It is strong on the wing and on its feet. I was surprised at the way it could dash into a bush and alight without slackening speed at all." The truncate primaries of *Himatione* and *Vestiaria* produce a whirring sound audible for some distance. This is possibly of some use in courtship or in keeping a flock together, since these two species fly or circle above the tree tops more than do others.

The two drepaniids native to Laysan spent more time on the ground than the others, but their power of flight was not noticeably reduced. The wing length of these two, *Psittirostra cantans* and *Himatione sanguinea*

freethii, is, however, rather short, showing perhaps an incipient tendency in that direction (table 9). As a measure of general size for the comparison of relative wing lengths in table 9, "body length" was used. This was obtained by measuring specimens (skins) from the base of the tail to the base of the bill. While this length is highly variable because of variation in the preparation of specimens, it is believed that the average values used are sufficiently reliable to allow useful comparisons.

TABLE 9

RELATIVE WING LENGTHS IN SELECTED SPECIES
OF DREPANIIDAE, ARRANGED IN ORDER
OF DECREASING VALUES

Species	Relative Wing Length = (Wing Length: Body Length)
<i>Vestiaria coccinea</i>	1.22
<i>Loxops sagittirostris</i>	1.22
<i>Himatione s. sanguinea</i>	1.19
<i>Loxops v. virens</i>	1.18
<i>Psittirostra bailleui</i>	1.15
<i>Psittirostra psittacea</i>	1.11
<i>Drepanis pacifica</i>	1.11
<i>Hemignathus procerus</i>	1.10
<i>Psittirostra palmeri</i>	1.07
<i>Himatione sanguinea freethii</i>	1.07
<i>Pseudonestor xanthophrys</i>	1.06
<i>Psittirostra cantans</i>	0.98
<i>Psittirostra kona</i>	0.96

It will be evident from table 9 that species known to possess strong flight, such as *Himatione sanguinea*, have relatively long wings, but the same is true of some local or sedentary species, e.g., *Loxops sagittirostris* and *Psittirostra bailleui*. Species with long bills that might make flight difficult, like *Hemignathus procerus*, have the wing little if any reduced, but *Pseudonestor xanthophrys* and *Psittirostra kona*, both species with disproportionately heavy bills and of stocky build, have relatively short wings. The same, as already mentioned, is true of the two Laysan forms, *Himatione s. freethii* and *P. cantans*, particularly the latter which, judging from its greater differentiation (species rather than

subspecies), reached this small, windswept island at an earlier date.

The wings are slightly more pointed in *Himatione s. sanguinea* and *Vestiaria coccinea* (both strong-flying species) than in most other drepaniids.

The legs and feet in this family are typical for arboreal song birds. In species like *Loxops maculata* that creep along the trunks of trees the claws are strong and sharp.

The drepaniids of the main islands rarely come to the ground. The two forms of Laysan were of necessity confined to short vegetation or to the ground. It is interesting to find that they can walk rather than hop along the ground. Fisher (1906) wrote of *Himatione sanguinea freethii*: "... the proximity of broad patches, acres in fact, of a prostrate succulent portulaca with yellow and sesuvium with pink flowers has many attractions for the honey-eaters. Here they may be found throughout the day walking around after small insects or drinking honey from the blossoms." Of *Psittirostra cantans* he said, "They do not fly far, but prefer to alight soon, and run along the ground, or to elude pursuit by suddenly crouching under a grass tussock." He found, however, that they hopped about on the piazza of the residence on Laysan.

Walking rather than hopping progression may be acquired readily in species with terrestrial habits. Examples can be found in the Parulidae (*Seiurus*), Fringillidae (*Calcarius*, *Paroaria*), Corvidae, and other families. It is rarely of phylogenetic significance.

SOCIAL HABITS

Munro (1944, p. 94) wrote of *Vestiaria* and *Himatione* as encountered on Kauai in February and March, 1891: "The iiwi and apapane are so numerous that in their ceaseless activity, flying backwards and forwards their wings keep up a continual buzz. There will be half a dozen in a tree at a time, flitting from flower to flower and hopping about among the twigs and leaves in search of caterpillars." Several observers have noted that when a number of species of drepaniids are feeding together on nectar the birds are especially animated and vocal, as though stimulated by the sugar.

PARASITES, DISEASE, AND EXTINCTION

PARASITES

BIRD LICE: Perkins made a considerable collection of Mallophaga from Hawaiian birds but it was lost. Zimmerman (1948, pp. 71-72) lists five species of Mallophaga that he believes to be endemic on the Drepaniidae. The known host species are *Loxops virens*, *Himatione sanguinea*, and *Vestiaria coccinea*.

PARASITIC FLIES: Perkins (1893, p. 106; 1903, p. 410) found parasitic flies of the family Hippoboscidae on *Vestiaria* and on *Loxops virens*. The species of flies involved are considered non-endemic, as they occur also on some of the wide-ranging sea birds of Hawaii.

CESTODA: Baldwin (1948) found tapeworms in *Loxops virens*, *Himatione*, and *Vestiaria*. They have not yet been identified, and it is not known if they are endemic or introduced. The hosts appeared to be in good health when collected. Perkins (1913, p. ccxxviii) mentioned a very distinct tapeworm, "*Drepanidotaenia hemignathi*, belonging to an apodemic Cestode genus." This parasite was found in *Hemignathus procerus*.

ACANTHOCEPHALA: Perkins (*loc. cit.*) also cited "... the remarkable *Apororhynchus hemignathi*, taken from the drepaniid bird *Hemignathus procerus* on Kauai and forming the endemic family Apororhynchidae of the Acanthocephala." I do not know whether or not parasitologists still assign this parasite to an endemic Hawaiian family.

DISEASE

BUMBLEFOOT OR BIRD POX: It has long been known that the Drepaniidae are subject to foot infections of the type called "bumblefoot." It is not known whether or not this disease occurred before the advent of foreign birds in Hawaii.

Perkins (1893, p. 112), writing of the Kona district of Hawaii, said: "As on Oahu, many of the birds in Kona had swellings on the legs and feet; in some cases they had even lost one or more claws and parts of the toes. The species affected were *Himatione*, *Hemignathus*, *Chasiempis*, *Loxioides*, and *Rhodacanthus*. It is probably, I think, the result of damp, as in almost every case the birds affected were those shot within the rain-belt; while those

above, even of the same species, were almost if not quite always free of it." Henshaw (1902, pp. 20-21, 60-61) mentioned a number of other species that had bumblefoot. He, too, found it chiefly in rainy districts. The tumor-like swellings may occur at the corners of the mouth as well as on the feet. He wrote: "A specimen was forwarded to Washington for investigation, and the following report has been received from D. E. Salmon, Chief of the Bureau of Animal Industry: 'I am in receipt of your letter of September 11th together with a specimen of a bird, *Loxops coccinea*, affected with tumor-like growths on the head, feet and thighs. You state that this disease is very prevalent among the various woodland birds in the Hawaiian Islands, and request that you be furnished with information concerning the nature and cause of the disease.

"In reply I would say that a microscopical examination has demonstrated the presence within the degenerated tissues of numerous fungoid growths which closely resemble morphologically the blastomycetes described by Sanfelice in his article, "Über die pathogene wirkung der Blastomyceten," published in Zeit. für Hygiene und Infektionskrankheiten, 1897, page 298.

"These organisms have been demonstrated during the past summer in diseased chickens which were forwarded from Honolulu, and this fact adds to the probability of the same microphyte being the causative agent in the disease under consideration. This affection, commonly called chicken pox, sore head and bird pox, has been known for many years and is usually found in warm countries, especially in Southern Europe and the Gulf Section of the United States. It affects ordinary fowls, turkeys, pigeons and birds, and Bollinger, Virchow's Archiv. Bd. LVIII, S. 349, mentions an outbreak among hawks and pheasants.

"Further information concerning the disease may be found in Bulletin No. 1, of the Hawaii Agricultural Experiment Station, entitled "Chickens and their Diseases in Hawaii.""

Paul Baldwin showed me a specimen of

Himatione picked up dead in Hawaii National Park. It had a mild case of bumblefoot, which may or may not have been the cause of death. Whether or not this disease has played a perceptible role in the extermination of Hawaiian birds is unknown.

AVIAN MALARIA: Search for avian malaria was conducted by Baldwin while at Hawaii National Park. The results have not been fully published, but Munro quoted from an interim report. According to him (1944, p. 68): "In 1938 Dr. Joseph E. Alicata found pigeon malaria in pigeons in Honolulu ('Hawaii Farm and Home', April 15, 1938). And in 1941 two species of bird malaria were found in introduced birds in the Hawaii National Park. (Report of Paul H. Baldwin to the Superintendent dated August 2, 1941)." In his account of the introduced "Pekin Nightingale" (*Leiothrix lutea*, Timaliinae), Munro wrote (p. 167): "I quote from Paul H. Baldwin . . . regarding bird malaria which was 'discovered in blood smears from birds in Hawaii National Park in 1938 and 1939 by the writer and Donald P. Abott. . . . The ecological implications of this discovery may be far-reaching. In the first place, the cardinal fact that bird malaria is present in the Hawaiian Islands is established. While it cannot be stated with certainty that *Plasmodium* was not present in the native bird population before the practice of introducing and liberating perching birds from other parts of the world was started, the fact that what is considered to be *Plasmodium vaughani* has been reported from the babbler in Japan is a strong indication that infected birds were at one time imported to these islands. In the second place, it shows that, while there are no records as to mosquito hosts which serve as vectors for *P. vaughani*, mosquitoes capable of transmitting this parasite are present on the islands.'" Thus although malaria has not as yet been demonstrated in the Drepaniidae, they are probably infected with it.

All the mosquitoes found in Hawaii were introduced by man, so presumably avian malaria was not present originally. Unlike human malaria, avian malaria may be spread by genera of mosquitoes other than *Anopheles*; the latter is absent.

PREDATORS

The Hawaiian Hawk as do other buteos prefers open or semi-open country. It may occasionally catch a song bird or rob a nest, but there is no reason to suppose it was ever a serious enemy of the drepaniids.

The Short-eared Owl, *Asio flammeus sandwichensis*, is typically a bird of open country, though the Hawaiian race seems to frequent woodlands more than do the continental ones. Munro (1944, p. 67) wrote, "On Lanai some [owls] hunted over the trees in the small forest, searching for birds' nests, but the birds took precautions to hide their nests from them."

Perkins considered feral domestic cats an important enemy of song birds and during a morning's walk on Lanai found more than a dozen birds killed by cats. Munro considered this unusual and wondered if the birds had not been killed by a heavy storm a day or two before. It is doubtful if cats have been important in the decline of the Drepaniidae.

The introduced mongoose now swarms on all the main islands except Kauai and penetrates all the forests. Though a scourge to ground birds, its effect on the Drepaniidae is unknown. Like weasels or minks it hunts mostly on the ground though capable of climbing. The mongoose was probably not responsible for the extermination of any drepaniids.

The feathers of a few drepaniids, chiefly *Drepanis pacifica*, *Vestiaria coccinea*, and *Himatione sanguinea*, were used by the Hawaiian natives for ceremonial garments. The birds were usually captured alive and supposedly were released after the desired feathers were plucked. No serious inroads were made on the native birds by the Hawaiians. After the arrival of Europeans with firearms the feather traffic was more or less commercialized. *Moho nobilis* may have been wiped out on Hawaii by shooting. Of the drepaniids, only *Drepanis pacifica* was perhaps hastened towards extinction by shooting, but this is doubtful.

COMPETITION WITH INTRODUCED BIRDS

Most introduced birds like the Mynah, *Acridotheres tristis*, White-eye, *Zosterops ja-*

nica, and Skylark, *Alauda arvensis*, prefer open country and are absent or relatively common in the rain forest. A babbler, *Iothrix lutea*, is now abundant in the forest, but its spread is so recent the effect on drepaniids is uncertain. *Leiothrix* is more partial to undergrowth than are most drepaniids. Few other introduced birds occur in the forest but are comparatively uncommon. The chief harm to the Drepaniidae from introduced birds has probably come indirectly by the introduction of diseases and parasites. Many introduced birds swarm over the islands that some direct competition also occurs.

DESTRUCTION OF FOREST

According to Zimmerman (1948) only one-fourth of the Hawaiian forest remains. Much of the lowlands was cleared for agriculture. Though the mountain forest is of relatively little value for lumber, it has suffered seriously from livestock. Feral goats have overgrazed large areas; in others cattle, swine, and deer have thinned out the forest. The Drepaniidae are often very sensitive to such changes and, according to Perkins and others, many have disappeared as soon as cattle entered the tract of woods. The koa forest, valuable to many drepaniids, is destroyed by grazing. The vital importance of watersheds on these islands will serve to prevent further destruction of forests.

Even before the advent of white man the Hawaiian natives introduced chickens, pigs, rats, and the Pacific rat, *Rattus exulans waiiensis*. All these had an adverse influence on the Drepaniidae or their environment.

EXTINCTION

As is well known, large numbers of drepaniids are extinct. The present status of the species is summarized below so far as known, but recent field work, particularly on Kauai and to a lesser extent on Lanai, Molokai, and Maui, has been inadequate. Baldwin has worked Hawaii thoroughly and has visited some remote parts of Maui. He is fairly well known because of the concentration of bird students in Honolulu. Richardson (1949) in a recent survey of

Molokai found only the two common species, *Loxops virens* and *Himatione sanguinea*.

Loxops virens: This species has withstood civilization better than any other drepaniid. It probably still occurs on all the islands and is common in many places.

Loxops parva: Believed still to exist.

Loxops sagittirostris: Extinct, its former restricted range now largely planted to sugar (Baldwin).

Loxops maculata: Reduced in numbers and some of the races, e.g., the beautiful *flammea* of Molokai, perhaps extinct. It still occurs in small numbers even on Oahu.

Loxops coccinea: The Hawaii race is much reduced, rare, and local. The Maui race has not been found in many years, and the Oahu one is extinct. *Caeruleirostris* is believed still to occur on Kauai.

Hemignathus obscurus: All the races extinct except possibly *H. procerus* of Kauai (recent sight records of *ellisianus* of Oahu are extremely doubtful).

Hemignathus lucidus: *H. wilsoni* of Hawaii still occurs in modest numbers; the other representatives of this superspecies may be extinct, that of Oahu certainly is.

Pseudonestor xanthophrys: Not found by Baldwin, perhaps extinct.

Psittirostra psittacea: Much reduced; rare on Hawaii; extirpated on Oahu; existence on the other islands doubtful.

Psittirostra cantans: The Laysan population became extinct after the island was denuded by rabbits. Before this occurred the race had been introduced successfully on Midway. Birds from there were later reintroduced on Laysan, where Coultas estimated there were at least 1000 in 1938. The Midway colony was extirpated by rats during the war.

The Nihoa race is abundant, but this island is so small that the population is estimated at only 500 to 1000 birds (Vanderbilt and de Schauensee, 1941).

Psittirostra bairdii: Still exists (Baldwin).

Psittirostra palmeri, *P. flaviceps*, *P. kona*: These three species are extinct.

Himatione sanguinea: Next to *Loxops virens* the most successful species of drepaniid; still fairly common even on Oahu. The Laysan race is extinct.

Palmeria dolei: Rediscovered by Baldwin on Maui. Status on Molokai unknown, probably extirpated.

Ciridops anna: Extinct.

Vestiaria coccinea: Quite successful. There are a few on Oahu, and it is common locally on Maui and Hawaii, if not on the other islands.

REMARKS

As Henshaw and others pointed out, the widest ranging species of drepaniids usually have survived best. Three range throughout the main islands without racial variation: *Vestiaria coccinea*, *Himatione sanguinea*, and *Psittirostra psittacea*. None of them is extinct, though the last named disappeared long ago on Oahu and is now much reduced on the other islands. Two other species, *Loxops virens* and *Loxops maculata*, have representatives on each of the six islands, though they often vary racially from island to island. *L. virens* is the most successful and adaptable species of the family (and perhaps the most generalized). *L. maculata*, while it has declined, still persists on most of the islands, including even Oahu.

Three species, *Loxops coccinea* and the two superspecies of *Hemignathus*, each have representatives on four of the six main islands. All three have some extinct subspecies, and the present status of others is uncertain. Even on Hawaii, *Loxops coccinea* is now rare and local. Of *Hemignathus* the only form now in a reasonably flourishing condition seems to be *wilsoni*. Superficially it appears more specialized than the others (e.g., than its congener on Hawaii, *Hemignathus o. obscurus*), but its woodpecker-like adaptations may have aided it.

Drepanis had one species on Hawaii and one on Molokai; the former is extinct, and the latter is probably so. *Palmeria* also occurs on two islands, Maui and Molokai, in this

case without insular variation. It still persists on Maui, at least.

Considering now the species limited to a single island, five (*Loxops sagittirostris*, *Psittirostra kona*, *P. palmeri*, *P. flaviceps*, and *Ciridops anna*) are extinct. *Psittirostra bairdii* and, on Kauai, *Loxops parva*, still exist.

The same trends are found in other Hawaiian song birds. The widespread superspecies *Moho nobilis* persisted better than *Chaetoptila*, endemic on Hawaii. The widespread *Phaeornis obscurus* is still found on some islands, but *P. palmeri* of Kauai was always rare and is now probably extinct.

What do the above facts mean? Small oceanic islands foster rapid speciation but also rapid extinction. Species that evolve on separate islands may later overlap on the same island and compete severely for the small areas and limited food resources available. Of such species some survive by specializing, but they remain vulnerable to environmental changes and are usually limited to small areas where inbreeding may perhaps lead to loss of variability and even fixation of harmful genes. A widespread species, especially one of strong flight that renders occasional inter-island transfer likely, will escape such hazards.

The Drepaniidae are a rapidly evolving group living in a favorable and yet dynamic and at times cataclysmic environment. We might expect to find a considerable percentage of the endemic species declining through natural causes as others evolve. When adverse factors (deforestation, predators, and particularly disease) appeared with the advent of Europeans, the declining species quickly became very rare or extinct; the others survived with varying success. In only a few cases, notably Laysan, was the environment so thoroughly destroyed that the extinction of certain birds became inevitable for this reason alone.

COMPARATIVE ANATOMY

SKELETON

THE FAMILY DREPANIIDAE would furnish excellent material for the study of functional anatomy and adaptation, but insufficient material and field work limited the present study to comparative anatomy from a phylogenetic standpoint. There is now uniformity of opinion that the Drepaniidae are not related to such Old World nectar-eating birds as Australian honeyeaters (Meliphagidae), flowerpeckers (Dicaeidae), or sunbirds (Nectariniidae). Meliphagids differ from drepaniids in the structure of the tongue, in the 10-primaried rather than nine-primaried wing, and in so many other ways as to leave no doubt that they are not closely related even though both are found in Hawaii. Indeed, the Meliphagidae reached Hawaii via Australia, New Guinea, and Polynesia, while the ancestor of the Drepaniidae apparently came from America.

The closest relatives of the Hawaiian honeycreepers are to be found in the group of primarily American, mostly nine-primaried song birds. It is necessary to list these families here since they are frequently mentioned in the following pages. They include the vireos (Vireonidae), orioles and blackbirds (Icteridae), wood warblers (Parulidae), South American honeycreepers (Coerebidae), tanagers (Thraupidae), and finches (Fringillidae). Of these the Vireonidae are the only ones in which the tenth primary is not always vestigial. For this and other reasons the vireos seem less closely related to the Drepaniidae than are most of the others mentioned. The Icteridae stand somewhat apart, but the Parulidae, Coerebidae, and Thraupidae intergrade and are no more than subfamilies. The subfamily Richmondinae (cardinal grosbeaks), usually associated with the Fringillidae, also merges with the Thraupidae through such forms as *Saltator*. (The genus *Richmondia* is probably inseparable from *Pyrhuloxia*, an older name, so perhaps this subfamily should be called the Pyrrhuloxinae, not the Richmondinae.)

After the removal of the Richmondinae, the Fringillidae contain the subfamilies Fringillinae (genus *Fringilla* only), Cardueli-

nae (goldfinches, siskins, crossbills, etc.), and Emberizinae (buntings and American sparrows). The chaffinches (*Fringilla*) seem allied in many ways to the cardueline finches, and it may prove unnecessary to put them in separate subfamilies. Sushkin suggested such separation but never published his reasons. In this paper, however, the group Carduelinae, as understood by Sushkin, has been retained.

The family Fringillidae is the only one of this group of families that is found in the Old as well as the New World. *Fringilla* is an Old World genus, and the cardueline finches are better represented in the Old than in the New World. Although the genus *Emberiza* is Old World, the Emberizinae as a whole are more diversified in the New World. Only study of numerous American, chiefly South American, genera will determine whether the Emberizinae intergrade with the Richmondinae or really belong in different families.

Skeletons of the following species of the Drepaniidae were examined: *Loxops chloris*, *L. maculata*, *L. coccinea*, *Psittirostra cantans*, *Himatione sanguinea*, and *Vestiaria coccinea*. This material was borrowed from the Bishop Museum (courtesy of Dr. Peter H. Buck) and from the United States National Museum (courtesy of Dr. Herbert Friedmann). Some of it was in poor condition because of shot damage or for other reasons.

The significant features of the skull are discussed first. Figures that accompany the description are fully captioned and should serve to illustrate the points emphasized in the text without need for constant cross reference (figs. 13-15).

PALATO-MAXILLARIES

The palato-maxillaries when present are splint-like bones that adhere to the lateral edges of the prepalatines. In some of the Richmondinae (e.g., *Richmondia*, *Pheucticus*) they are quite large and protrude freely into the space between the diverging palatine and jugal. These bones are absent so far as known in the Drepaniidae, Carduelinae, and Ploceidae. They are present in at least some genera of the Richmondinae, Emberizinae,

Thraupidae, Coerebidae, and Parulidae. Other investigators have reported them in a few families obviously not close allies of the Drepaniidae, namely, the Pycnonotidae, Hirundinidae, Dicaeidae, and Picidae.

Even among individuals of the same species these small bones may be distinct in some and fused with the prepalatine bar in others (e.g., the Brazilian Cardinal, *Paroaria coronata*, of the Richmondeninae).

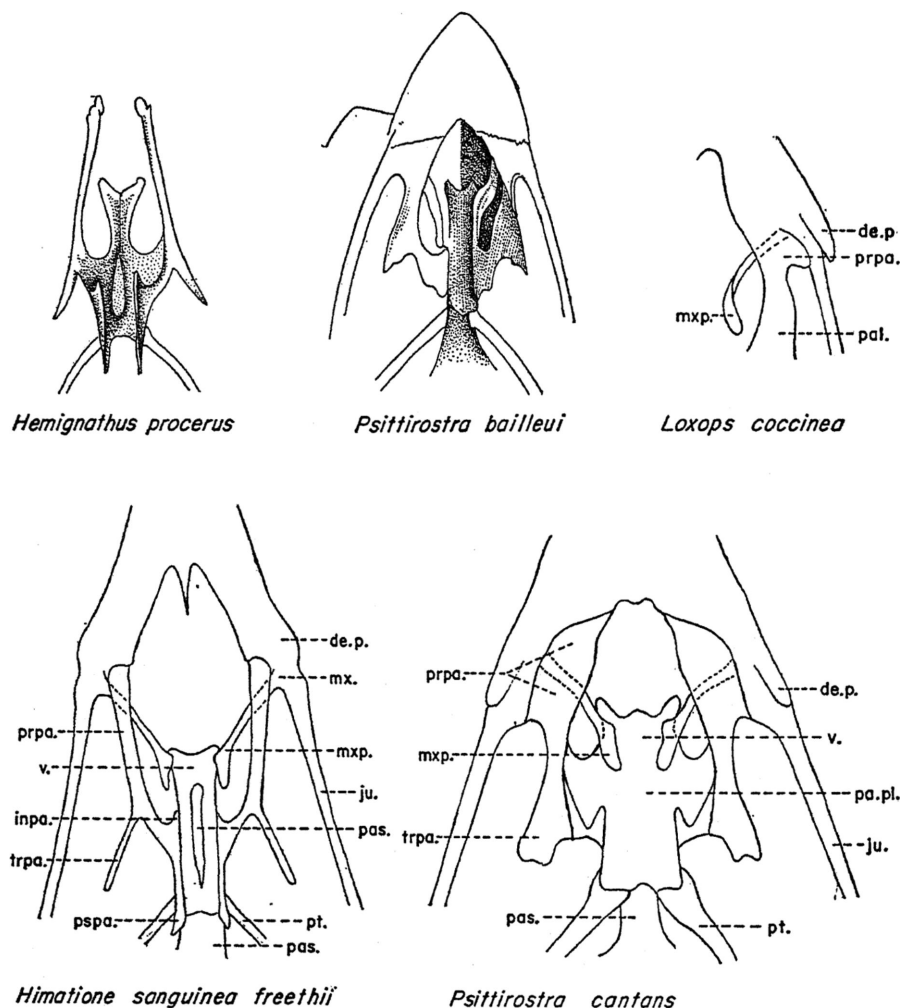


FIG. 13. Palates of some members of the Drepaniidae. *H. procerus* and *P. bailleui* after Gadow; others from specimens, semidiagrammatic. Abbreviations (figs. 13 and 14): de.p., dentary process of premaxilla; inpa., interpalatine process; j. mx., jugal process of maxilla; ju., jugal; mx., maxilla; mxp., maxillopalatine; pa. mx., palato-maxillary; pa. pl., palatal plate (palatines joined); pal., palatine; pas., parasphenoid; prpa., prepalatine bar; pspa., postpalatine process; pt., pterygoid; trpa., transpalatine process; v., vomer.

Palato-maxillaries may be present in some species of a genus and absent in others. According to Lucas this is true of *Dendroica* (Parulidae) and *Cyanerpes* (Coerebidae).

Parker figured two skulls of the Icteridae, one of *Icterus* sp.?, one of *Icterus "vulgaris"* (= *I. icterus*). On both he represented fair-sized palato-maxillary bones, though he re-

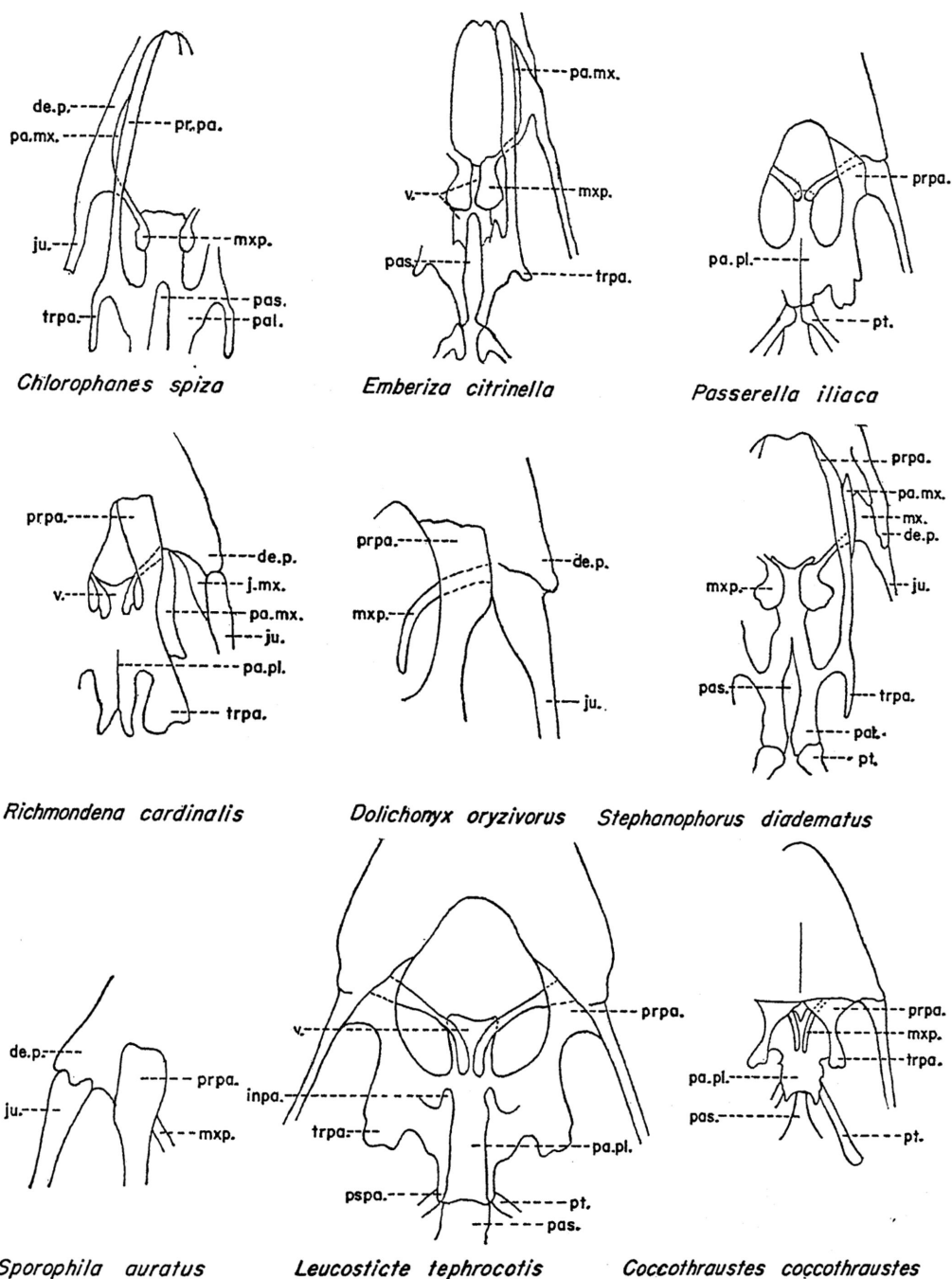


FIG. 14. Palates of forms possibly allied to the Drepaniidae. *Chlorophanes*, *Emberiza*, *Richmondia*, *Stephanophorus*, *Coccothraustes* modified from Parker; others from specimens, semidiagrammatic. See figure 13 for abbreviations.

marked for one of the species that these bones were somewhat fused with the palatines. I have examined 18 skulls of various species of *Icterus* (including *I. icterus*) and in only one or two of these (not *I. icterus*) is a palato-maxillary indicated, and then not very distinctly. Palato-maxillaries were not found in any of the several other genera of Icteridae. In many icterids the prepalatine bar does have a suggestion of a flange along its outer border which may represent a fused palato-maxillary. A similar flange is evident in some species of the Drepaniidae.

This infrequent occurrence of palato-maxillaries in the Icteridae makes it clear that should a similar condition exist in the Drepaniidae, examination of many additional skulls, including some immatures, would be necessary before it could definitely be concluded that these bones are always absent in the family. Nevertheless, the apparent absence of palatomaxillary bones in the Drepaniidae suggests that this group was derived from one in which they were also absent or vestigial. Since they are absent in some genera of most of the families where they do occur, it is necessary to assume only that the immediate ancestor of the Drepaniidae, and not the entire family to which it belonged, lacked them. Or it is possible that these bones were once present in the Drepaniidae but later were lost.

Little is known of the significance of the palato-maxillaries. They sometimes fuse with the prepalatines, but it is not meant to imply that this has happened generally in groups where they are lacking. According to Parker (1879) palato-maxillaries occupy the position filled by palatine processes of the premaxilla in the embryo.

TRANSPALATINE PROCESSES

Birds with slender, long bills, like the Coerebidae and Nectariniidae, often have thin, elongated, transpalatine processes. This is also true to an exceptional degree of the thin-billed drepaniids such as *Himatione*. The heavy-billed drepaniids like *Psittirostra cantans* have short, expanded transpalatine processes like those of the Emberizinae, Parulidae, etc.

This great variation of the transpalatine processes among the Drepaniidae makes it

difficult to assess their possible phylogenetic significance. This may not be true of other groups. In the Parulidae, for example, the transpalatine processes are shorter and blunter than might have been expected in such thin-billed birds. In the Thraupidae, on the other hand, they are almost as thin and elongated as in the Coerebidae, contrary to what would be anticipated in these heavy-billed birds. In other words, although heavy-billed birds tend to have short transpalatines and thin-billed birds to have long ones, frequent exceptions occur.

RELATION OF PALATINES TO EACH OTHER AND TO THE VOMER

In most passerine birds, including those under discussion, the mediopalatine processes of the right and left palatine bones do not meet in the mid-ventral line for their full lengths. In ventral view the sphenoid rostrum is visible through the aperture between the two palatine processes. Often the mediopalatine processes are in contact posteriorly at the point where they articulate with the pterygoids but diverge anteriorly to articulate or fuse with lateral posterior projections from the vomer. In other birds, such as most Icteridae, the palatines are widely separated posteriorly and converge anteriorly. Sometimes the gap between the two palatines is bridged by a thin, semitransparent, bony plate, seemingly not a part of the true palatines.

In certain birds, principally heavy-billed finches, the mediopalatine processes meet or fuse completely beneath the rostrum and also fuse with the vomer to form an imperforate bony palate. This strengthens the skull for crushing seeds.

The occurrence of these modifications can be summarized as follows:

1. Palatines not joined for their full length, but with an aperture between them: this condition exists in the Coerebidae, Parulidae, some Ploceidae, and most of the Emberizinae, Icteridae, and Thraupidae. For the Drepaniidae, Gadow figures *Hemignathus* with an aperture between the palatines which he says is covered with a thin sheet of bone. *Loxops maculata* has a narrow but long aperture between the palatines that did not appear to be mirrored with bone (unless it was

lost in preparation). *Himatione sanguinea* also has this kind of perforation in the palate. It consists of a very narrow gap extending back between the palatines and seems to be roofed over by thin bone.

2. Mediopalatine processes completely fused (or at least abutting against each other) and fused with the vomer: this type of palate is found in all the Carduelinae and in most or all of the Richmondinae (at least in the heavy-billed genera like *Sporophila*, *Richmondia*, and *Pheucticus*), and in a few of the heavier-billed Emberizinae like *Passerella*. Among the Thraupidae and Icteridae, some heavy-billed genera, e.g., *Molothrus*, approach this condition, but in the species examined the two palatines never are joined for their entire lengths. In the Ploceidae the palatines are frequently but by no means always as completely fused as in the Carduelinae (see figures in Sushkin, 1927).

In the Drepaniidae the palatines are completely joined beneath the rostrum in *Psittirostra cantans* (and presumably in the other heavy-billed species), in *Vestiaria*, and apparently in *Loxops coccinea caeruleirostris*, *Loxops virens*, and doubtless in some other species. Since many of the drepaniids are thin billed, it is surprising to find such a tendency for fusion of the palatines in the family. This is one of the few things that might be taken to indicate that the family is basically finch-like. It must be kept in mind, however, that several members of the family do have perforate palates. Furthermore, even those drepaniids that are not finch-like often have feeding habits that entail rather vigorous use of the bill and hence would favor strengthening of the palate.

ARTICULATION OF PTERYGOIDS, PALATINES, AND ROSTRUM

In birds the anterior ends of the pterygoids usually articulate with the pterygoid processes on the posterior margins of the palatines. Both pterygoids and palatines near their points of contact are dilated into thin, plate-like bones, which slide over the rostrum. The actual articulation of pterygoids and palatines is thus limited to the thin edges of these plates. In certain birds, such as most Drepaniidae, most Carduelinae, some Coerebidae (*Chlorophanes* and *Cyanerpes* but

not, according to Lucas, *Coereba*), some Parulidae (*Dendroica*, but not *Seiurus*), and some Ploceidae (*Poephila gouldiae*, *Steganura paradisea*, but not many others), the palatines and pterygoids are fused along their line of articulation. In the Drepaniidae, *Loxops maculata* was the only one of six species examined in which they apparently are not fused.

Fusion of the pterygoid-palatine articulation is thus not associated in any consistent way with the presence of a powerful, crushing type of bill. In the Carduelinae, as a matter of fact, the only species examined that did not have such fused palatines and pterygoids belong to the very heavy-billed hawfinch group, *Coccothraustes*. One examined skull of *C. coccothraustes* had the pterygoids and palatines fused; in two others they were not. In other related species (*Hesperiphona vespertina*, *Mycerobas carneipes*, *Coccothraustes personatus*) they were not fused in the few skulls examined.

The above findings do not lend support to Sushkin's statement that the relations of the pterygoids, palatines, and rostrum in the Drepaniidae show a particular resemblance to those of the Carduelinae.

PALATINE-PREMAXILLA ARTICULATION

Sushkin (1929b, p. 380) wrote: "Of the skeletal characters, the dilatation of the fore and of the anterior process of the palatine is highly characteristic. In the Fringilloid birds, it is proper only to the Cardueline group. In the Drepaniids, it is present in all genera which I have been able to compare, even in the most slender-billed as in *Oreomyza* [*Loxops maculata*], *Vestiaria*, and *Himatione*."

Some modifications of the prepalatine bar for articulation with the premaxilla and adjacent bones are shown in figures 13 and 14. In thin-billed birds, like parulids or coerebids, the slender, long prepalatines run forward with little increase in size, curving inward and almost meeting anteriorly.

In heavier-billed birds, like most icterids, emberizids, thraupids, many ploceids, etc., the prepalatines are somewhat heavier and shortened anteriorly and are bluntly truncate at the line of articulation with the premaxillae. Contrary to the impression given by Sushkin, this is the condition existing in

many of the thinner-billed drepaniids, e.g., *Vestiaria*, *Himatione*, *Hemignathus* (as figured by Gadow), *Loxops parva*, *Loxops virens*, and *Loxops maculata*.

Finally, the prepalatines are sometimes laterally expanded, or dilatated as Sushkin calls it. The articulation with the premaxilla then usually occurs on an oblique line (see figures of *Leucosticte* and *Psittirostra cantans*), though in *Coccothraustes*, a very heavy-billed genus, this is not the case.

An expanded prepalatine articulation is characteristic of all the cardueline finches and, among the drepaniids examined, of *Psittirostra cantans*, of *P. bailleui* (figured by Gadow), and, less markedly, of *Loxops coccinea caeruleirostris*. Doubtless the same is true of other species of *Psittirostra* and probably of *Pseudonestor*. This type of expanded, strong articulation of the palatine with the premaxilla is usually correlated with a heavy, seed-crushing bill. Among the Emberizinae it is approached by some of the heavy-billed genera and achieved by *Passerella* (and doubtless others) and by some of the heavier-billed Icteridae like *Dolichonyx*. In the Thraupidae, and more particularly in the Richmondeninae, some of the genera are heavy billed, but they usually have large or medium-sized palato-maxillary bones. These, by occupying and perhaps strengthening the lateral edges of the prepalatine bar, prevent extreme expansion of the latter.

From the above it is evident that Sushkin stated the case too strongly as regards resemblance of the Drepaniidae to the Carduelinae in this character. The dilated type of prepalatine bar is fully developed only in the heavier-billed Drepaniidae, not in all of them. This modification is not restricted to the Carduelinae and Drepaniidae but occurs in the Ploceidae and in some Richmondeninae and Emberizinae. It is clearly an adaptive feature associated with strengthening and foreshortening of the bill and presumably evolved independently several times.

It is true that the thin-billed Drepaniidae have a somewhat heavier, shorter prepalatine than would be expected in species of their general skull contour, but this cannot safely be accepted as evidence of derivation from finches, still less from one particular group of finches, the carduelines.

ECTETHMOID

Sushkin stated that the ectethmoid region of the Drepaniidae is like that of the Carduelinae. I was unable to find significant variation in the configuration of this region of the skull in any of the families under consideration.

ANGLE OF THE JAW

The lower mandible extends back beyond the quadrate articulation to permit additional muscular leverage in such birds as the starling, *Sturnus*, or the meadowlark, *Sturnella*,

TABLE 10
OCCURRENCE OF SKULL MODIFICATIONS IN THE DREPANIIDAE AND OTHER GROUPS

	Greatly Expanded Prepalatine Bars	Palatines Fused or Joined Below Rostrum	Attenuated Transpalatine Processes	Palato-Maxillary Bones	Fused Pterygoids and Palatines
Drepaniidae	XXO*	XXO	XO	O	XXO
Coerebidae	O	O	X	XO	XO
Parulidae	O	O	O	XO	XO
Icteridae	O (X)	OO (X)	O	OOX	O
Richmondeninae	O	XO	O	X	O
Emberizinae	OOX	OOX	O	XO	O
Carduelinae	X	X	O	O	XXO
Ploceidae	XO	XO	O	O	O
Thraupidae	O	OO (X)	X	XO	O

* Symbols as follows: O, absent; X, present; (X), not fully developed; XO, sometimes present, sometimes absent; XXO, more often present than absent; OOX, more often absent than present.

which have a rather long mandible capable of vigorous probing and of opening against the resistance of earth or fruit pulp. In grosbeak-like species with short powerful mandibles, the expanded muscle attachments

Hence the fact that Lucas found the angle of the jaw to be also slightly extended in the genus *Coereba* (but not in *Cyanerpes* or *Euneornis*) is of no phylogenetic significance.

The occurrence of some of the palatal

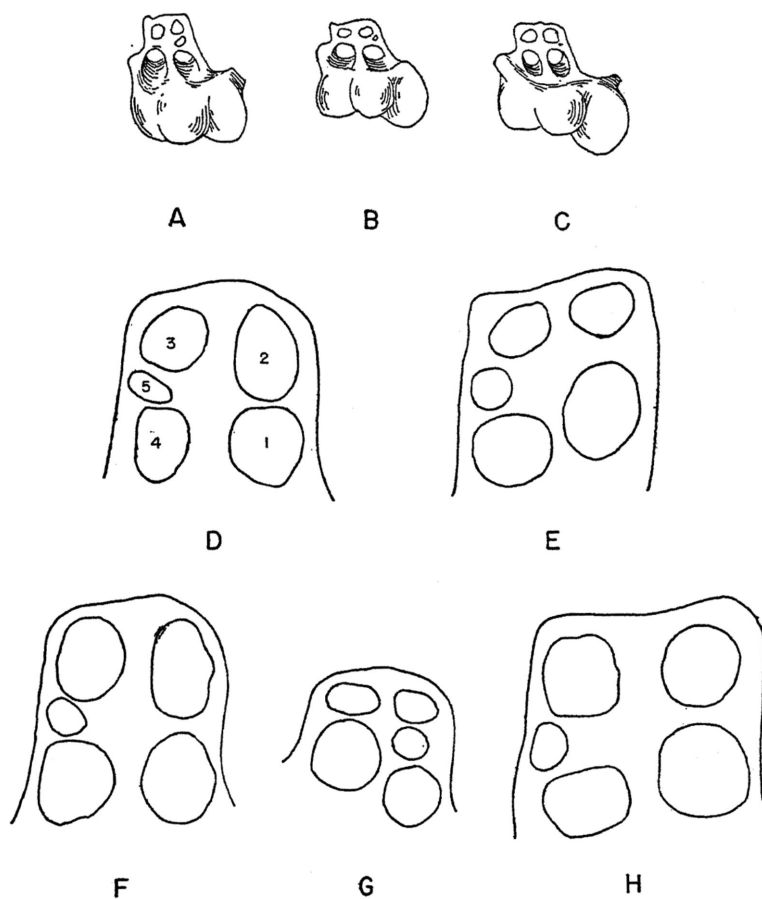


FIG. 15. Hypotarsi. A. *Turdus migratorius*. B. *Myadestes solitarius*. C. *Hemignathus obscurus*. D. *Piranga olivacea*. E. *Psittirostra cantans*. F. *Chlorophanes spiza*. G. *Gymnostinops montezumae*. H. *Coccothraustes coccothraustes*. A, B, and C from Lucas; others from specimens. Numbers on D correspond to foramina for tendons. 1. Flexor longus hallucis. 2. Flexor perforatus digiti IV and slip to base of first phalanx of digit III. 3. Flexor perforatus digiti III. 4. Flexor perforans digitorum profundus. 5. Flexor perforans et perforatus digiti II, and flexor perforatus digiti II. After Lucas.

permit sufficient leverage without such extension. This purely adaptive response explains why the angle of the jaw is not extended in *Psittirostra cantans* but is in *Loxops maculata*, *Vestiaria*, *Himatione*, and *Hemignathus obscurus* (Lucas, 1894, p. 305).

characters mentioned above is summarized in table 10.

HYPOTARSUS

At the proximal end of the posterior surface of the metatarsus the tendons of the foot

pass through bony or cartilaginous canals. This region, known as the hypotarsus, is, according to Sushkin, another point of resemblance between the Drepaniidae and the Carduelinae. Lucas, who compared the hypotarsi of Coerebidae, Drepaniidae, and allied groups, wrote (1894, p. 301), "The tendinal perforations of the upper end of the tarsus, while arranged on the same general plan in those passerine birds examined, show a number of variations in the execution of details. . . ."

Lucas (1894, p. 302) figured the hypotarsi of three thrushes, *Phaeornis*, *Myadestes*, *Turdus*, and of the drepaniid *Hemignathus obscurus*. Of the material examined by me, the only drepaniid with the hypotarsus preserved was a *Psittirostra cantans*. In addition, the hypotarsus of the following was examined: *Chlorophanes spiza* (Coerebidae); *Euphonia personata*, *Coccothraustes coccothraustes* (Carduelinae); *Piranga* (Thraupidae); *Gymnostinops montezumae* (Icteridae); *Dendroica* (Parulidae); *Passerella iliaca* (Emberizinae); *Sporophila* (Richmondeninae).

The arrangement of the foramina of the hypotarsus in all of these was found to be very similar, as will be evident from the examples reproduced herewith (fig. 15.) The terminology of the foramina is from Lucas.

Lucas found that foramen five varies in size and is sometimes merged with four (*Coereba*). In all the genera examined by me it was distinct. Lucas figured foramen five as very small in *Hemignathus*, but it is of medium size in *Psittirostra cantans*.

It seems quite evident that the variation in the hypotarsus in these birds is slight and of little or no significance for classification, at least above the level of genus. There seems to be no basis for Sushkin's statement that the Drepaniidae and Carduelinae show special resemblances in the hypotarsus.

REMARKS

The following comments on the skeleton of the Drepaniidae by various authors may be considered in the light of the above discussion. Some of the statements quoted are not true of all drepaniids.

Lucas (1894, p. 304) wrote: "The Drepanididae, as represented by *Vestiaria*, *Oreomyza* [= *Loxops maculata*], *Hemignathus* and

Himatione agree with the Coerebidae in the character of the transpalatine and interpalatine processes, and exceed them in the depth and production of the postpalatine. This feature is carried to its extreme in the Drepanididae and the same is true of the compression of the palatines, the free ventral edges of these bones approaching one another very closely, being in *Himatione sanguinea* almost in contact. The Drepanididae have the sphenoid covered by the palatine, a feature which is not found in the Coerebidae, but occurs in some, although by no means all, or even in a large majority, of the Fringillidae. Among the skulls examined those of *Certhiola* [= *Coereba*] and *Himatione* bear the closest general resemblance to one another." He concluded (p. 308), "To sum up, in the character of their palate the Coerebidae differ from the Mniotiltidae [= Parulidae] and resemble in some points the Drepanididae and some of the Tanagridae."

Gadow (1890-1899, p. 224) wrote: "According to Parker the palatine bones are not united with each other in the medio-ventral line in the Emberizine section of the Fringillidae (e.g. *Emberiza*, *Phrygilus*, *Plectrophanes lapponicus*) nor in *Icterus*. On the other hand, in the true Fringillinae (e.g. *Linaria*, *Estrilda*, *Coccothraustes*) the two palatine bones are broadened above the sphenoid bone into one continuous bony plate, which being also fused with the posterior end of the vomer, forms a single interpalatine plate. This is the case in *Psittacirostra* and in *Loxioides*, the latter of which much resembles *Pyrrhula* in the configuration of its palatine region; anteriorly the jugal bones are quite fused with the palatines; the maxillo-palatines are hollow, as in many Fringillidae, and (as a special feature) posteriorly almost touch the interpalatine spurs."

He continued on page 238, "That *Loxioides* and *Psittacirostra* differ so much in the configuration of their palatines from the Drepanididae is another weighty argument against their affinity to that family."

In a further supplement to the same work, Gadow accepted Perkins' contention that *Psittacirostra psittacea* and *P. (Loxioides) bailleui* do belong to the Drepaniidae, thus implying that the differences he had pointed out previously are not of great importance.

Of the palate of some of the thin-billed Drepaniidae Gadow (p. 238) wrote: "The bones of the palate of *Hemignathus* and in a less degree *Vestiaria* are most peculiar. The vomer is posteriorly completely fused with the palatines, and the lanceolate space between the two halves of the basal or dorsal parts of the palatines is closed by a transparent plate of bone, which covers, and rests upon, the sphenoid. Such a truly interpalatine plate occurs in many Fringillidae. The ventral palatine spurs (Parker's interpalatine spurs) are very high and slender, and posteriorly extended to such an extent that they project far beyond the level of the articulation of the pterygoids. The latter articulate with the palatines, and not with the sphenoid at all, by distinct cartilaginous feet, resembling in this respect again certain Fringillidae, e.g., *Coccothraustes*, although in the latter these feet are bony and liable to fuse with the palatines. The transpalatine or posterior lateral spurs are long and very slender. The maxillo-palatines are long and slender, passing ventrally over and past the anterior fork of the vomer and touching with their tips the anterior interpalatine spur; they rather resemble the same parts of *Loxioides* and of *Coccothraustes*; we must, however, bear in mind how much these little bones vary in shape, size and position even in the various Fringillidae; as a glance at the numerous illustrations in Parker's work on the Aegithognathous skull will show. The whole arrangement of the bones of palate of the Drepaniidae is totally different from that of the Meliphagidae, and other Cinnyrimorphae, and can only be compared with that which is indicated to a small extent in some Fringillidae (*Coccothraustes*, *Cardinalis*, *Estrilda*)."

Although interesting adaptive modifications can be found in the skeletons of song birds, there are few characters of phylogenetic significance. Lucas (1894, p. 300) wrote of the skeleton with reference to the Coerebidae, Drepaniidae, and related families, "It would almost seem that, aside from purely negative results, the skeleton can be relied upon to show but two things, very general and very close affinities, for the variation of parts is so infinite that between any 10 given birds we may find every intermediate stage and establish relationships in all direc-

tions."

So far as the skull itself is concerned, the difficulties of drawing sound conclusions can be further emphasized by a few quotations from Parker's (1879) monograph on the aegithognathous palate. Of the tanager, *Stephanophorus leucocephalus* [= *diadematus*] he said, "It shows in a charming manner that subgeneric modifications of the outer parts of birds are correlated with, or attended by, changes of structure in the most fundamental skeletal parts." Of the Old World Nectariniidae he wrote, "However that family may differ from the Tanagridae in external characters, osteologically they interblend." Of *Dicaeum aureolimbatus* of Celebes he wrote, "The palate shows nothing that is not Tanagerine in its modifications." He found that the palate of *Dendroica pensylvanica* (Parulidae) "comes very close" to that of *Sitta* [*Neositta*], an aberrant Australian nuthatch.

SOFT PARTS

THE TONGUE

The tongue of birds, like the bill, is highly adaptable. Though a good indicator of feeding habits, it is as a rule of little value in phylogenetic studies, as Lucas (1896) and Gardner (1925), among others, have concluded. In families that feed upon nectar, such as the Drepaniidae, Coerebidae, Nectariniidae, Meliphagidae, and Trochilidae, the tongue is tubular, probably as a result of independent evolution in each group. The structure of the tongue is somewhat different in each of these families and because of its specialization is of some diagnostic value. In the Drepaniidae the tongue is completely tubular in most of the species, but some of the insectivorous and granivorous species are exceptions. This makes the diagnosis of the family more difficult, but it is helpful in determining the phylogeny of the genera.

Tubular tongues often have a brush-like tip, though this is not true of the Nectariniidae and the related Dicaeidae. Bené (1946, p. 458) wrote of the tongue of hummingbirds (and the same is probably true of other groups having a tubular, brush-tipped tongue) that "... the primary, if not the sole function of the tubes is to procure liquids—nectar, sap, water—whereas the fimbriated portion is to entrap minute insects."

Gadow described and figured the tongues of a number of species of drepaniids. Rothschild figured the tongues of the now extinct *Ciridops anna* and *Drepanis pacifica*, as well as those of some better known species. Gardner (1925) described the tongue of a number of drepaniids and figured that of *Hemignathus procerus*. Some of these illustrations are reproduced herewith (fig. 16.) I have examined the tongues of a number of drepaniids collected by Henshaw. Unfortunately they were

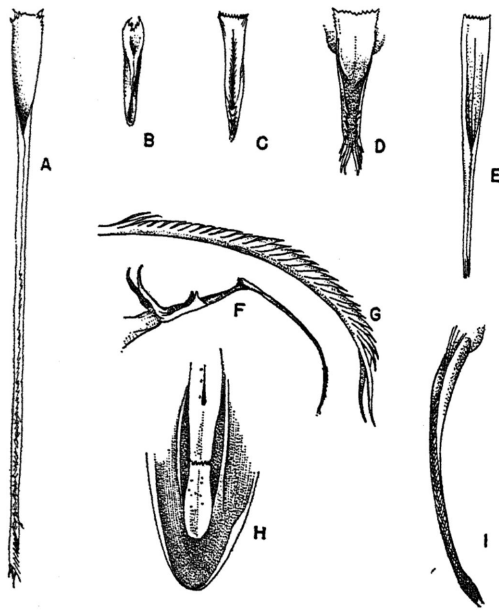


FIG. 16. Tongues of some species of Drepaniidae. A. *Hemignathus procerus*. B. *Psittirostra cantans*. C. *Loxops maculata bairdi*. D. *Pseudonestor xanthophrys*. E. *Himatione sanguinea*. F. *Drepanis pacifica*. G. Tip of same, enlarged. H. *Psittirostra bailleui* (tongue in place in lower mandible). I. *Ciridops anna*. A and B after Gardner; C, E, and H after Gadow; D, F, G, and I from Rothschild, drawn by Frohawk.

preserved dry for many years, but when returned to alcohol the structure is still quite evident. At the Royal Ontario Museum in Toronto, I noticed a skin of the most finch-like of the drepaniids, *Psittirostra kona*, with the tongue attached. I was able to study the latter through the courtesy of Mr. L. L. Snyder. The tongue of a specimen of *Himatione* preserved in fluid was also studied.

Gardner (1925, p. 27) described the typical

drepaniid tongue as follows: "These tongues are formed as are all tubular ones by an up-curling of the margins of the horny anterior part which constitutes the major portion of the tongue in these birds. The edges of the dorsally rolled sides meet in the midline and finally overlap. As the tip is approached the edges become broken up and split, forming delicate laciniae. At first one side completely overlaps the other but as these fimbriations become more prominent they interlace in a complex manner finally forming at the tip a whipped-out brush."

A description of the tongue of *Vestiaria* by Gadow (1890-1899, p. 230) gives further details: "The sharp dorso-lateral margins of the horny sheath of the tongue are raised upwards, and gradually meet each other in the middle line, without fusing with each other, but transforming the dorsal surface of the tapering tongue into a single semicanal. The distal halves of these raised margins are frayed out into numerous horny bristles or laciniae, which become longer towards the tip of the tongue, cross each other, or are even interlaced, and thus turn the end of the tongue into a brush. The whole tongue is as long as the bill, and, when the latter is shut, completely fills the space between the two mandibles. The tongue cannot be protruded far, because the hyoid horns do not

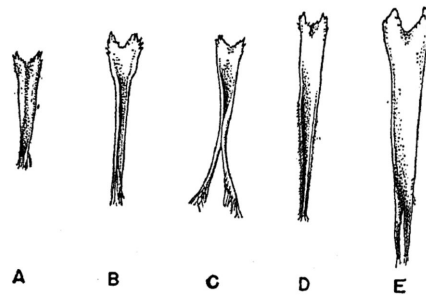


FIG. 17. Tongues of birds possibly allied to the Drepaniidae. A. *Dendroica tigrina*. B. *Chlorophanes spiza*. C. *Coereba flaveola*. D. *Cyanerpes cyaneus*. E. *Icterus icterus*. After Gardner.

project above or beyond the level of the eye; they are shorter than in *Nectarinia*, but resemble those of *Acrulocercus* [Maho]."

Even drepaniid tongues that have been dry for 50 years, tied to the legs of museum study skins, still have the edges of the tongue

tightly curled and overlapping. When placed in alcohol they still suck up the fluid by capillary attraction.

Fully tubular tongues are found in all six species of the subfamily Drepaniinae. In the Psittirostrinae this type of tongue occurs in all the species of *Loxops* except *L. maculata* and in all the species of *Hemignathus*. In such stubby-billed forms as *Loxops coccinea* the tongue is, of course, much shorter than in long-billed species, but the tubular modification is essentially the same. The tongue of *Ciridops* is said to be "intermediate" by Bryan and Greenway (1944, p. 141), but Rothschild's figure of it (fig. 16I) indicates a fully tubular tongue.

While some drepaniids that rarely or never take nectar, such as *Loxops coccinea*, *Hemignathus lucidus*, *H. wilsoni*, and *Ciridops anna*, still have a tubular tongue, others have a tongue that is only partly or not at all tubular. The tongues of such species will now be described.

Loxops maculata: Gadow's figure of the tongue of this insectivorous species is reproduced herewith. He described it as follows: "Tongue a little shorter than the bill, thin, and horny, but at first sight apparently different from that of the Drepanididae. However, the lateral horny margins are raised up dorsally and frayed out. The distal fourth of the horny part of the tongue is slightly split into a right and a left half, but far less than in *Coereba*. This broader, shorter, and less decidedly tubular tongue is in conformity with the slightly broader bill."

Pseudonestor xanthophrys: This species is entirely insectivorous. Gadow (p. 245) described the tongue of *Pseudonestor* as somewhat similar to that of *Psittirostra psittacea* but "... far less fleshy, more slender, more deeply split in the middle; the distal third of the horny sheath becomes gradually transparent towards the tip, is very slightly frayed out towards the tip and on the lateral edges, but shows no indication of curling up of the free margins." Yet in the enlarged figure of the tongue of this species published by Rothschild the tongue appears to be partially tubular (fig. 16D).

The species of the genus *Psittirostra* show the greatest deviation from the nectar-feeding type of tongue, as might be expected from

their seed- or fruit-eating habits.

Psittirostra psittacea: This species is less finch-like than the others. Gadow described its tongue as follows (p. 245): "The tongue is fleshy in its basal three-quarters, while the distal quarter is thin and horny, slightly split in the middle, and with the thin lateral edges turned up and inwards, forming a very imperfect half-tube, and slightly frayed out distally, i.e., at the anterior free end. It is consequently far less 'Fringilline' than the tongue of *Loxioides* [= *Psittirostra bailleui*]. On the other hand it resembles, or approaches, that of *Pseudonestor*...."

Psittirostra cantans: Clark (1912, p. 167) described the tongue of this species as follows: "In *Telespiza*, although the tongue resembles that of *Loxioides* [*P. bailleui*], the vertical thickness and fleshiness are remarkable. The tongue proper is 11 mm. long, scarcely 2 mm. wide and about 2.5 mm. in vertical thickness. The fleshy surface is quite papillose and the tip is not divided but is finely fringed as in *Loxioides*. As compared with *Pipilo* [Emberizinae], *Telespiza* has a much larger, thicker, fleshier and blunter tongue." Gardner (1925, p. 28) said that the heavy margins of the tongue are rolled up to form a tube.

Psittirostra bailleui: At the time he wrote the following description Gadow still believed this species to belong to the Fringillidae (p. 223): "Tongue thick and fleshy, much shorter than the bill, very slightly protractile; tip rounded off and ending in a neat horny scoop, which is formed by the lower horny covering of the tongue projecting a little; the brim of this scoop is slightly frayed out, as is the case in many Fringillidae. Each side of the tongue is accompanied by a high longitudinal fold of soft tissue, which arises sideways from the epiglottal region, extends forwards, and ultimately meets its fellow from the other side below the free end of the tongue, passing into the frenum linguae. Such guiding folds or projections of the lingual floor are frequently met with in birds which eat uncrushed seeds, and likewise in the Drepanididae."

Psittirostra palmeri: Gadow (p. 245) compared the tongue of this species with that of *P. psittacea* and of *P. bailleui* as follows: "The tongue of *Rhodacanthis* [= *P. palmeri*] ... is the most compact of all. Its upper

surface is slightly scooped out, while the whole under surface is covered with the usual thick and hard horny sheath, the thin lateral edges of which curl over upon the dorso-lateral sides, and are very slightly frayed out at the distal sixth only, where alone they form slightly sharp edges of the tongue, the tip of which is scarcely split at all."

Psittirostra kona: The tongue of this species seems to agree in every detail with the tongue of *P. palmeri*, as described by Gadow. The edges of the tongue of *kona* are somewhat upturned, giving a scoop-like effect, but possibly this is a result of drying. The horny portion of the tongue is only 5 mm. long.

As would be expected, *P. palmeri* and *P. kona*, the most grosbeak-like of the drepaniids, show the greatest departure from a tubular structure.

OTHER FAMILIES: The Old World song birds, some or all of whose members have tubular tongues, include the Nectariniidae, Dicaeidae, Zosteropidae, and Meliphagidae. None of these is a close relative of the Drepaniidae, as shown by a number of characters. Their tongues, too, are different. In the Nectariniidae and Dicaeidae, the tongue is not frayed and is often split at the tip. Usually each of these halves curls up to form a separate tube. In the Meliphagidae the tongue is deeply split at the tip, and each half is split again. The tongue is very feathery or brush-like (for figures, see Gadow, 1890-1899; Gardner, 1925; Mayr and Amadon, 1947).

Turning now to the nine-primaried families, the Coerebidae is the only one whose members sometimes have fully tubular tongues. The modification of the tongue varies considerably from genus to genus in this family; it is never the same in details as that of the Drepaniidae.

Among the Parulidae the Cape May Warbler, *Dendroica tigrina*, has a partially tubular tongue. I have observed this bird visiting the blossoms of wild cherry, presumably for nectar. Of the Icteridae, *Icterus cucullatus* has a somewhat tubular tongue. Among Old World birds more or less modification of the tongue for nectar feeding is found in some species of *Zosterops* and in *Chloropsis*. Such modification takes place rather readily once nectar enters the diet. The tongues of mem-

bers of some of these families are shown in figure 17.

CROP

Among non-passerine birds the Galliformes and Columbidae have a well-developed crop. In the latter, it is modified for the secretion of "pigeon milk" for feeding the young. A crop or crop-like dilation of the esophagus is also found in hawks, vultures, storks, and hummingbirds. Usually it is found in birds that consume bulky foods.

Considering now the Passeriformes, a crop is present to varying degrees in a number of families. It is best developed in certain seed-eating groups such as the Carduelinae and Ploceidae. I found *Pinicola* (Carduelinae) to have a crop with numerous longitudinal folds evident on its inner surface to permit expansion. In a specimen of *Serinus mozambicus* (Carduelinae) this was less evident. The Ploceidae also have distinct crops, though in the two examined, *Vidua serena* and *Ploceus st.-thomae*, longitudinal folds were not conspicuous. Among other finches (Emberizinae, Richmondinae) a crop is present, though apparently not usually so well developed as in the Carduelinae or Ploceidae. A specimen of *Richmondia* had a rather small crop with a few folds evident on its inner surface.

The waxwings (Bombycillidae) and the Bearded Titmouse, *Panurus* (Paradoxornithinae), are said to have a crop. I found a good-sized one in a white-eye, *Woodfordia* (Zosteropidae).

Lucas (1894) stated that the Parulidae and Thraupidae do not have a crop. This was true for one Scarlet Tanager, *Piranga*, that I examined. In the Coerebidae, Lucas (p. 303) found that *Coereba* lacks a crop but *Cyanerpes* "has a well-marked crop-like dilatation of the oesophagus, and *Glossoptila* [= *Eunornis*] has a good sized crop." This was confirmed by me for *Cyanerpes*; it has a distinct crop with longitudinal folds. A specimen of *Icterus dominicensis* also had a good-sized crop.

For information on the occurrence of a crop in the Drepaniidae, we are indebted chiefly to Gadow (1890-1899, pp. 223-233). The following notes are quoted from his account:

Psittirostra bailleui: "The oesophagus forms a capacious elongated dilatation, with-

out, however, assuming the shape of a distinct crop."

Psittirostra psittacea: "The oesophagus forms a very distinct pouch-like crop, which rests on the right side between the two clavicles."

Vestiaria coccinea: "The oesophagus forms a distinct ventral crop, which is lodged between the arms of the furcula; its width is nearly 1 centim.; while its walls are thin and smooth internally."

Himatione sanguinea: "The oesophagus forms a very distinct ventral crop."

Loxops coccinea: "The oesophagus forms no crop, but a distinctly marked long oval dilatation, which was full of soft small insects."

Loxops maculata bairdi: "The oesophagus has, as in *Loxops [coccinea]*, an oval dilatation."

Hemignathus procerus: "The oesophagus is thin-walled and has an elongated but not pouch-like dilatation, which internally is furnished with nearly twenty longitudinal ridges, apparently permanent."

Psittirostra cantans: Clark (1912, p. 168) examined the oesophagus of this species and wrote, "The crop-like dilatation of the lower end of the oesophagus is marked but there is no real crop."

It is apparent that a crop has evolved independently many times and to varying degrees. The presence of a crop in several species of the Drepaniidae thus cannot be considered as linking them with the Carduelinae or any other particular group of birds. Various species of the Icteridae, Coerebidae, Emberizinae, and Richmondininae have a crop similar to that of the Drepaniidae. In the latter, the degree of development of the crop is by no means closely correlated with modification for seed eating. Members of the thin-billed nectar- and insect-eating genera *Vestiaria*, *Himatione*, and *Hemignathus* have well-developed crops.

INTESTINAL CONVOLUTIONS

Gadow (1890-1899) figured and described the intestinal convolutions of several drepaniids but drew no phylogenetic conclusions therefrom. All the Passeriformes and even some related orders like the Piciformes

belong to one main group as regards the type of intestinal convolutions. Relatively minor variations are found among the passerine families, but they are of doubtful significance.

Lucas wrote (1894, pp. 300-306): "The convolutions of the intestine are in very much the same case as the pterylosis for, judging by Dr. Gadow's figures and my own limited number of dissections, they are subject to great specific variation. There is certainly a decided difference between the alimentary canal (including the stomach) of birds so nearly alike as *Coereba* [= *Cyanerpes*] *cyanea* and *C. caerulea*, and the genera of tanagers vary widely. . . . The alimentary canal of the Mnioiltidae [Parulidae] is, as a rule, comparatively simple, but in *Dendroica coronata* the convolutions of the intestine are almost exactly the same as in *Coereba* [*Cyanerpes*]. . . . The tanagers are fruit-eaters, are devoid of a crop, and have the largest intestine and simplest convolutions of any birds examined. In the complexity of the alimentary canal there is a parallel between *Certhiola* [*Coereba*] and the Drepaniidae, and the convolutions of *Hemignathus olivaceus* [*obscurus*] very nearly coincide with those of *C. caboti*.

"But in both groups there is varying complexity of convolution among the different species, and in neither is there any adherence to a given pattern. Among the Sandwich Islands birds there is, in the majority of specimens figured, a slight peculiarity in the manner in which the intestine begins to uncoil from the center. When looking from below at the right side of the viscera, the intestine is seen, roughly speaking, to start from the stomach and in a decreasing spiral or series of loops coil into a knot or short loop, whence it uncoils or unfolds in an increasing spiral. In *Loxioides*, *Psittacirostra*, *Himatione*, *Vestiaria*, and *Hemignathus* the first turn of the intestine from the center is to the left, while in the American species figured it is to the right. The point is one of little or no value, but among the species figured the difference exists" (see fig. 18).

According to Gadow (p. 225) *Psittirostra psittacea* has two functional caeca about a centimeter long, situated 2 centimeters from the vent. Functional caeca are very unusual in the Passeriformes. In the other drepaniids

examined by Gadow the caeca were rudimentary.

The variations in the alimentary tract of the Drepaniidae thus seem to provide no sure basis for phylogenetic inferences.

In the nectar-feeding drepaniids such as *Vestiaria* the opercula are very well developed. In primarily insectivorous species that also take nectar, such as *Loxops virens*, they are only slightly less conspicuous. *Psittirostra*

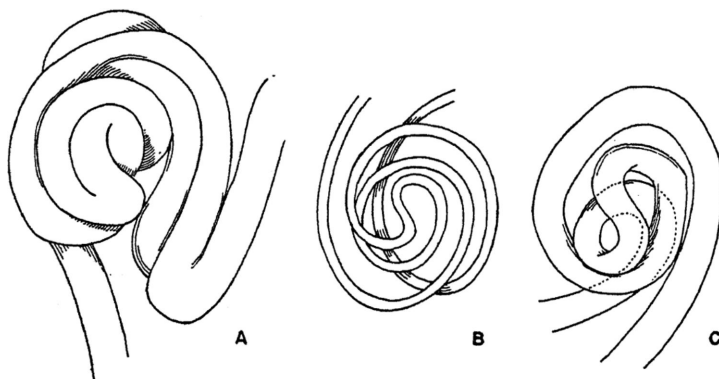


FIG. 18. Intestinal coils. A. *Hemignathus o. obscurus*. B. The same, with coils opened to show convolutions. C. *Coereba flaveola caboti* (central portion). After Lucas.

NASAL OPERCULUM

In birds that feed on nectar the nostrils are usually, if not always, covered by membranes (opercula) that extend from the upper border of the nostril and reduce the openings to narrow, lateral slits. They keep pollen, etc., out of the nostrils. Further protection is sometimes given by smaller opercula that



FIG. 19. Enlarged cross section of nostril of *Vestiaria*. After Gadow.

extend in from the lower rim of the nostril. The relation of these superior and inferior opercula will be evident from Gadow's cross section of the nostril of *Vestiaria*, reproduced as figure 19. In song birds that do not take nectar, the operculum is less fully developed, though often present. Sometimes the horny sheath of the bill extends to the edges of, or slightly into, the nostril, and there is no operculum.

psittacea, the least specialized member of this fruit- and seed-eating generic group, has a good-sized superior operculum, but it is smaller in the other species of the genus. Yet even the grosbeak-like *P. kona* has traces of superior and inferior opercula which are visible with the aid of a low-power microscope. The same is true of *Pseudonestor*, in which the opercula are even less evident, though not completely absent as sometimes stated.

Clark (1912), who compared *Psittirostra cantans* with a towhee, *Pipilo erythrophthalmus* (Emberizinae), considered the presence of nasal opercula in the former and their absence in *Pipilo* an important difference. He wrote: "The character of the nostrils is one of the most marked differences between *Telespiza* [*Psittirostra cantans*] and *Pipilo* or any other Fringilline bird with which I have compared it. The openings are large but each is provided above and on the posterior margin with a piece of thick bare skin, apparently corresponding to the opercular fold of many Hawaiian birds. A similar fold, less conspicuous because narrower and sloping inwards, is present on the lower margin also. . . . It may be that in life the nostrils can be quite closed by the movement of the bare

surrounding skin" (pp. 166-167).

In view of the obviously adaptive nature of the operculum it would seem that Clark overemphasized this difference. A fair-sized operculum is visible in some of the Emberizinae (including *Emberiza* itself), if not in *Pipilo erythrophthalmus*. The situation in *Psittirostra cantans* is, nevertheless, significant in suggesting its comparatively recent derivation from nectar-feeding drepaniids with a large operculum. This, in my opinion, explains why the operculum is better developed in the six species of *Psittirostra* than in most, if not all, heavy-billed finches.

NASAL PRECONCHA

In his discussion of the relationships of the Drepaniidae, Gadow (p. 246) wrote, "An absolute distinction between any of the thick-billed Hawaiian birds and the Fringillidae seems to be that in the latter the generally open and roundish nostril is blocked, so to speak, from the inside by the anterior little concha naris, which projects into the fundus of the nostril."

Stresemann (1927-1934, pp. 120-121) gave an excellent summary of the anatomy of the nasal region of birds. There is an anterior cavity or vestibulum and a posterior cavity. The vestibulum connects with the posterior cavity and also, through the nares, with the exterior. The posterior nasal cavity contains two cartilaginous structures, the middle and upper conchas. Continuing from Stresemann (translated): "The third nasal concha of the bird is the vestibulum-concha (preconcha) which, as its name suggests, is found in the vestibulum. It occurs in no other class of vertebrates and, since it does not possess the primordial sense epithelium, is not homologous with the true conchas [i.e., with the middle and upper conchas]. Usually it is a [cartilaginous] plate extending from the roof of the vestibulum and arching anteriorly and medially; or it may extend from the lateral wall of the cavity obliquely over to the septum. Its function is presumably to prevent the entrance of foreign bodies into the nasal cavity."

This cartilaginous preconcha shrinks and withdraws considerably in dry museum skins. It is often destroyed or damaged by sewing through the nostrils or obscured by dirt or

blood. Hence, it can be studied satisfactorily only in birds preserved in the flesh. Such material was examined by me as follows: Drepaniidae (*Himatione*), Coerebidae (*Cyanerpes*, *Coereba*, *Diglossa*), Parulidae (*Icteria*), Carduelinae (*Carpodacus*, *Pinicola*, *Serinus*), Emberizinae (*Zonotrichia*), Richmondeninae (*Richmondia*, *Paroaria*, *Sporophila*, *Saltator*), Icteridae (*Icterus*, *Molothrus*), Thraupidae (*Piranga*), Ploceidae (*Ploceus*, *Steganura*), and Nectariniidae (*Cyanomitra*).

In all these forms the preconcha is a conspicuous structure partly or largely obstructing the fundus or passage of the anterior nasal cavity (vestibulum). In the Purple Finch, *Carpodacus purpureus*, the preconcha is very conch-like, with rounded, scalloped anterior border and fluted upper surface. When the nasal feathers are pushed aside, it is visible just within the opening of the nostril, extending nearly across it. Even in some species with a well-developed nasal operculum, such as *Icterus* or *Zonotrichia*, the preconcha is easily visible beneath and behind the operculum.

In *Saltator* the concha is fleshier, less conch-like, and lies nearly at the bottom of the rather deep fundus of the vestibulum. In most other species it is much nearer the surface. In certain Ploceidae an open nostril makes the preconcha conspicuous from the exterior. The extreme of this is found in a rare weaverbird of the Congo, *Malimbus flavipes* Chapin, which has a large, unshielded nostril and exposed preconcha (figure in Chapin, 1916). For this reason, Gyldenstolpe proposed a new genus, *Rhinoploceus*, for this species.

In species with a fully operculate nostril the preconcha is often not visible externally even if the operculum is lifted, since in such species there is usually a smaller inferior operculum fitting under the upper one. This is the case in *Himatione*, *Coereba*, and *Cyanomitra*. Removal of the opercula in these species reveals medium-sized preconchas. In all of them, as it happens, the anterior margin of the preconcha is somewhat concave rather than rounded, as in *Carpodacus*, but every intermediate condition exists in other species. No specimens in the flesh of the finch-like drepaniids were available. There is no reason to believe they would have the pre-

concha smaller or less conspicuous than in *Himatione*, though perhaps it lies deeper within the fundus, for in these birds the heavy bill is presumably a rather recent modification. This may have produced a deep passageway or fundus of the vestibulum above the preconcha, thus agreeing with *Saltator* rather than with the cardueline finches. Since the preconcha is well developed in the Drepaniidae and all the related families, differing only in details of position and shape, the distinction Gadow would make on this basis between the Drepaniidae and the finches (Carduelinae) cannot be considered of great importance. For what it is worth, however, the evidence does not indicate that the Drepaniidae were derived from the Carduelinae.

MUSCULATURE

Beecher (in press) concluded that the type and arrangement of the jaw muscles are very conservative and highly useful in the classification of song birds at the family and subfamily level. After examining the jaw musculature of three drepaniids (*Vestiaria*, *Himatione*, and *Psittirostra cantans*) he concluded that the Drepaniidae are modified derivatives of the Thraupidae, and that a nectar-feeding type served as the transition. Since he considers the "Coerebidae" to be comprised mostly of thraupid genera modified for nectar-feeding, Gadow's earlier conclusion that the Drepaniidae are nearest the Coerebidae or the Thraupidae is thus not in disagreement with Beecher's findings.

PTERYLOSIS

In the so-called "nine-primaried" song birds the tenth, outermost primary is very minute and has shifted over to lie dorsal to the ninth primary, where it is concealed by the wing coverts. This is the condition in all drepaniids. Clark (1912, p. 167) said that there are 10 primaries in *Psittirostra cantans* but only nine in the towhee, *Pipilo*. This seems to be an error, as the latter, like all other song birds, does have a tenth primary. It happens to be slightly smaller than that of *P. cantans*.

The vestigial condition of the tenth primary is one of the characters in which the Drepaniidae agree with the group of predominantly American families, including the

tanagers, buntings, etc., and also with the great majority of the Carduelinae. This distinction, like so many others, is too variable to have any great significance. In certain families, such as the Vireonidae and Dicaeidae, some of the species have a functional tenth primary; others have a vestigial one. Such variation may exist even within a genus (*Vireo*). Reduction of the tenth primary is an adaptive change, at least in part. It has occurred independently in many families, e.g., the swallows, pipits, and white-eyes, in addition to those already mentioned. Even one genus of the cardueline finches (*Urocynchramus*) differs from all the others by having a well-developed tenth primary.

The configuration of the feather tracts is of considerable importance in the major classification of birds, but when the song birds are considered, great variation and intergradation occurs. In this connection Lucas (1894, p. 300) wrote: "The degree of value to be attached to the pterylosis is yet unsettled, and this can only be done by accumulating and comparing the facts in the case. It would be a great service if some one with ample time and unlimited patience would plot the pterylosis, or even the configuration of the dorsal tract, in as many small birds as could be obtained, for it would then be possible to ascertain what correlation, if any, there is between tract pattern and other characters.

"Between the continuous dorsal tract of a thrush and the inverted Y of a swallow there is a great difference, and this difference should have some definite meaning, exactly what meaning, is to my mind, not yet evident.

"All the birds examined during the preparation of this paper [Drepaniidae, Coerebidae, Thraupidae, Parulidae, Emberizinae, Carduelinae] have an uninterrupted dorsal tract whose shape appears to be specifically subject to great variation, but these variations are so slight and so innumerable that, except for general purposes, the pattern appears to be of little service."

Gadow gave brief comments on the pterylosis of several drepaniids, but he drew no phylogenetic conclusions.

Gadow's figures of the dorsal feather tracts of *Psittirostra psittacea* and the ventral tracts of *Hemignathus obscurus* are reproduced here (fig. 20). He also figured the dorsal tracts of

Psittirostra bailleui, *Hemignathus procerus*, and *Loxops maculata bairdi*, but they all appear to be virtually identical with the dorsal tract of *P. psittacea*.

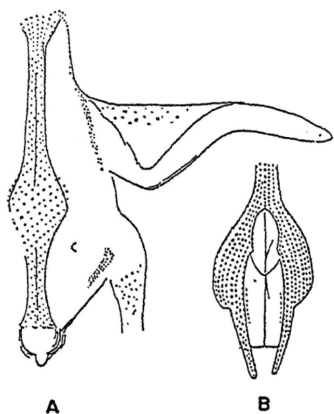


FIG. 20. Feather tracts. A. *Psittirostra psittacea*, dorsal. B. *Hemignathus obscurus*, ventral. After Gadow.

These figures can be compared with the following description of the feather tracts of *Psittirostra cantans* written by Clark (1912, p. 167): "The resemblance between *Tele-*

spiza and *Pipilo* in the general pterylosis is so striking as to be remarkable. The head is very fully feathered and has no apteria; above the eye there is more or less evidence of longitudinal rows in the arrangement of the feathers. The upper cervical tract is narrow and well defined and is continuous with the dorsal tract, which is characterized by a rhombic saddle of good size. The femoral tracts are narrow, about 10 mm. long and perfectly defined. The lower cervical tract forks well up on the throat and each branch connects very evidently over the shoulder with the narrow humeral tract. The sternal tracts are moderately wide and are slightly but distinctly separated posteriorly from the ventrals, which are moderately broad and end some distance anterior to the anus. In *Tele-spiza*, a narrow but quite distinct branch of the sternal tract runs directly upward on the side of the body under the wing for 6-8 mm., at right angles to the main tract; it contains 10-12 feathers. Indications of this tract are present in *Pipilo* but Gadow does not refer to its occurrence in any of the Hawaiian birds examined by him. Possibly its definiteness in *Tele-spiza* is associated with the ground-loving habits of the bird."

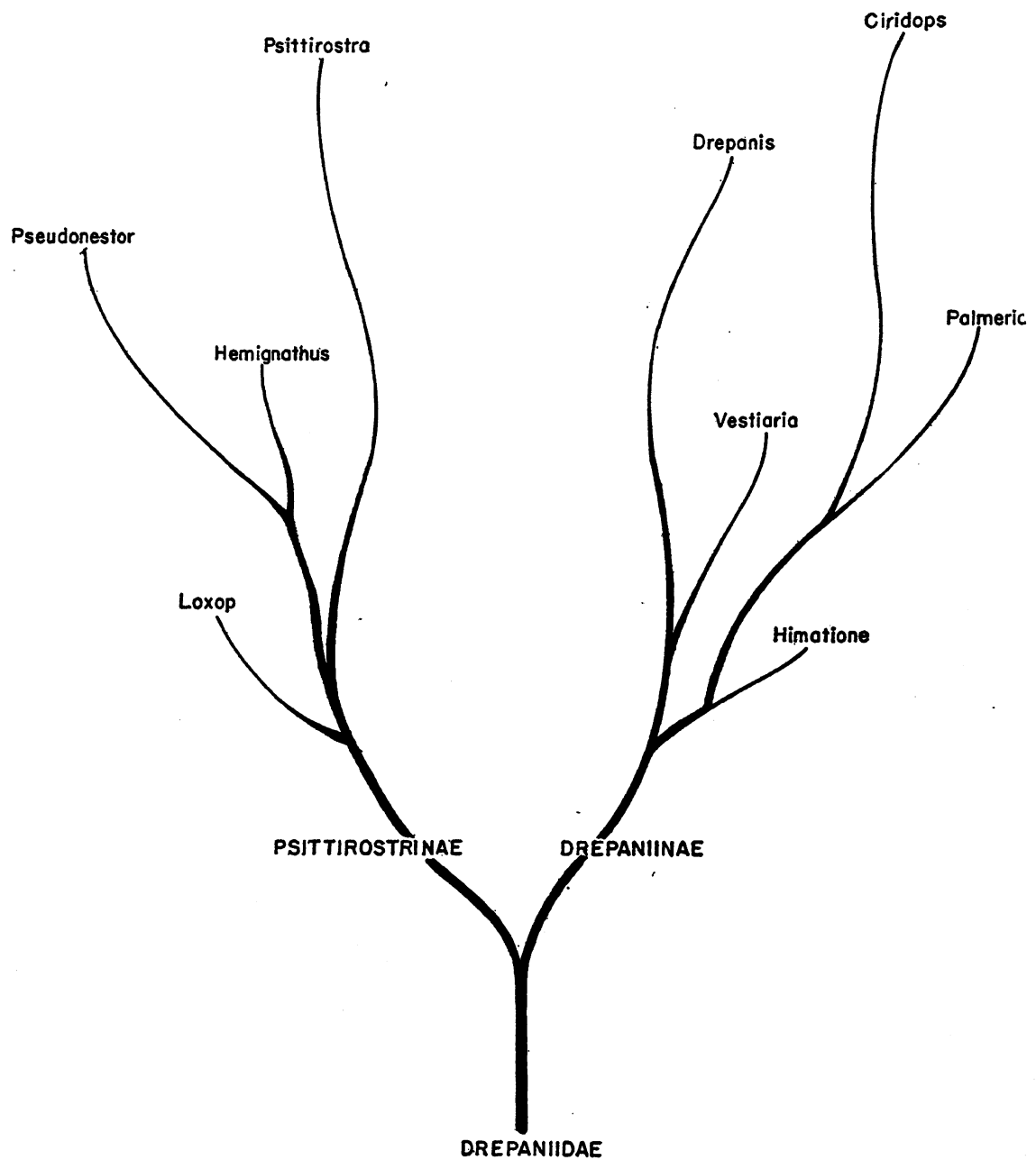


FIG. 21. Phylogeny of the genera of Drepaniidae.

PHYLOGENY OF THE GENERA AND OF THE FAMILY

THE SUPPOSED RELATIONSHIPS of the genera of Drepaniidae are diagrammed in figure 21. The following remarks on this arrangement are supplemental to the generic diagnoses given above.

PSITTIROSTRINAE: *Loxops* appears to be the most primitive genus of the family and subfamily. *Hemignathus*, particularly *H. obscurus*, differs from *Loxops virens* chiefly in its larger size and much longer bill. The latter is strongly decurved. In some forms of *Hemignathus* the bill is more specialized. The bill, coloration, and wing-to-tail proportions, as well as the notes and habits of the peculiar *Pseudonestor xanthophrys*, all ally it with *Hemignathus*. *Psittirostra* is the most specialized genus of this subfamily, but *Hemignathus wilsoni* and *Pseudonestor xanthophrys* show how the parrot- or finch-like bills of the various species of *Psittirostra* may have evolved from *Loxops*-like ancestors. The prevalent coloration of *Psittirostra*, particularly the yellow head, shows the affinity of this genus to *Hemignathus lucidus* and *H. wilsoni*.

DREPANIINAE: *Himatione* is the most primitive genus of this subfamily. It is sufficiently similar to *Loxops* so that some species of the latter were for many years placed in *Himatione*. *Palmeria dolei* is obviously related to *Himatione sanguinea* but much more specialized in color pattern and plumage; its crest is unique in the family. *Ciridops* is ecologically the most aberrant of this subfamily, since its tanager-like bill was probably used to eat fruit and was unsuited for probing after nectar, the mainstay of all the allied species. In coloration *Ciridops* definitely suggests *Palmeria*, with more distant indication of affinity to *Himatione*.

Vestiaria resembles *Himatione* in general coloration, in the sharply truncate primaries, and in the restriction of lanceolate feathers to the head. Such feathers occur on the throat in *Vestiaria*, but on the crown in *Himatione*. The strongly curved bill of *Vestiaria* is like that of *Drepanis*; indeed, as Perkins said, it is difficult to find arguments against uniting it with *Drepanis*. The latter differs from all other genera of the subfamily in the complete absence of lanceolate feathers. The extensive

black areas in the body plumage of *Drepanis* suggest *Palmeria* and *Ciridops*, not *Vestiaria*. Moreover, the bill in this family is so variable that such resemblances must be interpreted with caution. *Vestiaria* may well be closer to *Himatione* than to *Drepanis*.

The immature plumages of both species of *Drepanis* are unknown. In *Ciridops*, as explained elsewhere, it is uncertain whether the adult female resembled the adult male, as in other members of this subfamily, or whether the female had a greenish, immature-like plumage. These gaps in our information make the relationships of the genera more difficult to assess.

ORIGIN OF THE DREPANIIDAE

Gadow thought the Coerebidae the likeliest ancestors of the Drepaniidae. *Himatione* is probably the most coerebid-like genus of the family. Gadow also found similarities between the Thraupidae and Drepaniidae. *Ciridops* is perhaps the most tanager-like of the drepaniids. Some species of *Psittirostra* also resemble tanagers. The bill and skull in this genus (modified for crushing seeds) are like those of cardueline or weaver finches, not those of tanagers. This was the basis of Sushkin's (1929) conclusion that the Drepaniidae evolved from the Carduelinae. *Loxops coccinea* also bears a slight resemblance to some of the smaller cardueline finches, but this is surely superficial. The insectivorous diet, tubular tongue, and color pattern of this species all show its close affinity to *Loxops virens* and other congeneric species that are not at all finch-like.

Derivation of the Drepaniidae from a nectar-feeding coerebid-like ancestor offers no particular difficulties. *Loxops* and *Himatione*, the most primitive genera of the two subfamilies, are also the most coerebid-like. From these unspecialized genera it is relatively easy to derive the more specialized drepaniids. In the Psittirostrinae, in particular, one may visualize a sequence of successive stages that are rather well represented by *Loxops virens*, *Hemignathus obscurus*, *H. lucidus*, *H. wilsoni*, *Pseudonestor*, *Psittirostra psittacea*, *P. cantans*, and *P. kona* (pl. 11).

If, on the other hand, the Drepaniidae evolved from tanagers or finches, we must suppose the sequence was just the reverse: modification of a heavy-billed type like *Psittirostra* or *Ciridops* that terminated eventually in more generalized forms like *Loxops* or *Himatione*. This process is rather difficult to envisage in terms of functional anatomy. De-differentiation and "reversal of evolution" do occur, but as a rule evolution is from less to more specialized forms. In particular, a heavy, seed-crushing bill would seem to be something of an evolutionary dead end. The Galápagos finches might be considered an exception, but it is by no means proved that the thinner-billed geospizids (*Certhidea* and, more especially, *Pinaroloxias*) are not nearest the ancestral type. Moreover, bill variation in the Geospizinae is much less radical than in the Drepaniidae.

Further important evidence that the nectar- and insect-eating drepaniids such as *Loxops* antedate the highly specialized genera such as *Pseudonestor*, *Psittirostra*, and *Ciridops* is provided by the structure of the tongue. The tubular modification of the tongue is found not only in the drepaniids that eat nectar but also in others that do not, such as *Pseudonestor*, *Hemignathus wilsoni*, *Loxops maculata*, *Psittirostra psittacea*, and *Ciridops anna*. In some of these the tongue is not completely tubular, but in others, such as *Hemignathus wilsoni*, it is. The presence of a tubular tongue in such species can only be explained as an evolutionary lag in the loss or modification of a structure. Tubular tongues have evolved independently in half a dozen families of nectar-feeding birds; they are absent in all families that do not take nectar.

Since the bill is more important in food getting than the tongue, it is understandable that in a species like *Pseudonestor xanthophrys* the bill is completely transformed from the original nectar-feeding type while the tongue is only partially changed. The brushy tips of the tubular tongues of the Drepaniidae and of most other families of nectar eaters are believed to be of use in capturing minute insects. This feature of the drepaniid tongue, as well as its length, would still be of use to such an insectivorous species as *Hemignathus wilsoni*. Hence the tongue might be expected to change more slowly than the bill. Perkins

believed this continued utility of the tongue for insect catching to be the principal reason for the retention of a tubular, brush-tipped tongue in such species as *Pseudonestor*.

To summarize, comparison of the genera and species of drepaniids among themselves suggests that the ancestors of the family were generalized birds feeding on nectar and insects. They acquired a tubular tongue (if they did not originally possess one) at an early stage in the evolution of the family before its subdivision into two subfamilies. The least specialized members of each subfamily (*Loxops* and *Himatione*) answer this description. How does this conclusion fare in the light of evidence from comparative anatomy?

Gadow, as noted above, thought the Coerebidae the likeliest ancestors of the Drepaniidae, giving second choice to the Thraupidae. Clark (1912), after comparing *Psittirostra cantans* with a towhee, *Pipilo* (Emberizinae), concluded that resemblances between the finches and finch-like drepaniids are superficial.

Sushkin thought the Drepaniidae derived from the most specialized of the finches, the Carduelinae. Most of the characters he mentioned are not very weighty or occur in other allied families, but the genus *Psittirostra* has a skull modified for crushing seeds in almost the same way as that of the Carduelinae. Some of the other drepaniid genera show perhaps more tendency towards such strengthening of the skull than would be expected, but their feeding habits often are such as to employ the bill rather forcibly and hence possibly to lead to strengthening of the skull. By and large, it is easier to see how the skull of the more generalized drepaniids could be modified to result in a skull like that of *Psittirostra* than to postulate the opposite. For example, the transpalatine processes of such a genus as *Himatione* would presumably be blunt like those of the Parulidae rather than long and attenuated like those of the Coerebidae or Thraupidae if they had been derived from a cardueline-like skull such as that of *Psittirostra*.

Nasal opercula, along with a tubular tongue, are well developed in nectar-feeding birds. The opercula are larger in the genus *Psittirostra* (especially *P. psittacea*) than

would be expected in a true finch as compared with a modified nectar feeder.

The Thraupidae, so far as examined, have small palato-maxillary bones lacking in the Drepaniidae, but these may be present or absent in the Coerebidae. Almost every genus of the Coerebidae has a somewhat different tongue, so it is not difficult to consider the drepaniid type as just one more variant, even though it is not precisely the same as that of any coerebid.

As already noted, Beecher considers most of the Coerebidae to be nectar-feeding Thraupidae, though he thinks *Coereba* itself and a few others are nectar-feeding Parulidae. If he is correct (and the close relationship of the Thraupidae and Coerebidae has always been admitted) it is not of great significance whether one considers the Thraupidae or the Coerebidae (as represented by such genera as *Cyanerpes*) as nearest the Drepaniidae. Structurally and functionally, however, the thin-billed, nectar-feeding coerebids are nearer the more generalized drepaniids than are the heavy-billed, fruit-eating tanagers. One wonders, moreover, whether the insect- and nectar-feeding types (warblers, honeycreepers) are not more primitive than the fruit- or seed-eating ones (tanagers, finches).

Although the Thraupidae and Coerebidae are perhaps most like the Drepaniidae, the

other families of nine-primaried passerines are so similar that none of them, except the more specialized finches, can be ruled out as ancestors of the Drepaniidae. The tenuous characters separating these "families" may have been even less developed at the time the drepaniid ancestor reached Hawaii. Forms more or less adapted for feeding upon nectar occur in the Parulidae (*Dendroica tigrina*), the Icteridae (*Icterus cucullatus*), and the Vireonidae (*Hylophilus*). The Drepaniidae might have evolved from any of these families or their antecedents.

The diagnostic characters of the Drepaniidae and related families are so slight (when they can be determined at all) that there could be scant objection to reducing all of them to subfamily status. What groups to include in such an expanded family and how to arrange them are questions that should be answered before taking such action. The Hawaiian honeycreepers and many of the related groups are natural, monophyletic units that must be so designated in whatever system of classification is adopted. Comparative anatomists who suggest combining all song birds into "two or three families," without at the time providing an improved arrangement for the numerous subfamilies and tribes that must be recognized in such families, accomplish very little.

SPECIATION

A NUMBER OF SPECIES of Drepaniidae occur together on each of the main islands. From Hawaii proper no fewer than 15 are known. This led some writers (e.g., Mordvilko, 1937) to assume that these sympatric species evolved on the same island through some process of ecological speciation. However attractive such a theory may be, the evidence against it is very weighty (Mayr, 1947). Most significant is the fact that all subspecies in the family are geographically isolated on different islands. This suggests that when similar species now occur together it is the result of inter-island range extensions accomplished after, not before, speciation was completed.

Some species of Hawaiian birds fly, either by design or accident, from island to island frequently enough to prevent subspeciation. This is true not only of such large, mainly aquatic species as the Hawaiian Duck, Stilt, Coot, Gallinule, and Short-eared Owl (Appendix 1) but also of three species of drepaniids: *Psittirostra psittacea*, *Himatione sanguinea*, and *Vestiaria coccinea*. These drepaniids, we may be sure, get from island to island only by accident, e.g., when they become lost in the frequent fogs that engulf the Hawaiian forests or are carried away by storms.

There is evidence that the habits of the three species mentioned make them more subject to such accidental transfers than are other drepaniids. Wilson (Wilson and Evans, 1890-1899, p. 13) wrote of *Vestiaria*, "Mrs. Frances Sinclair informs me that after stormy weather she has seen numbers of these birds on the island of Niihau (where no forest now remains), to the uncongenial shores of which they had been driven by gales from the adjacent island of Kauai, separated by a channel 18 miles in width." Other authors have mentioned similar instances. Perkins (1903, pp. 389-391) wrote: "*Himatione*, *Vestiaria*, and *Psittirostra* are all birds which take extensive flights, often at a great height in the air, and frequently form small companies in these flights. If we stand on the main ridge of some of the islands the birds may be seen passing high overhead. . . . All freely traverse open country, in passing from one feeding-ground to another. Consequently when storms arise

they are extremely likely to be carried across the channels between the islands. The birds of the other class [i.e., those that vary from island to island] . . . do not take these extensive flights but keep closely to the forest.

. . . In short there is little doubt but that individuals of *Vestiaria* and its class are transferred from one island to another sufficiently often to prevent any true isolation.

. . . The only birds that I have myself picked up dead (sometimes in numbers) on the coast after . . . storms are of the genera *Vestiaria*, *Himatione*, and *Psittirostra*; in fact, the very forms which by their habits are most liable to be carried away by the wind. Further, it is well known that, after stormy weather, the two former sometimes reach the bare islands of Niihau, across the considerable channel which separates it from Kauai."

Further evidence of the unusual powers of flight of these three species was given by W. A. Bryan (1908, p. 169) who wrote: "The flight of the Ou [*Psittirostra psittacea*] is heavy, rapid and direct. During their more extended flights, as from one ridge to another, they are more often than otherwise in small flocks. . . . I have observed the Ou making long-sustained flights from the palis [cliffs] of the large valleys, that carried them readily from one valley to another. At such times they rarely, if ever, soar or circle about, but set off directly for the fresher fields with a show of knowledge and determination that makes them while on the wing, easily distinguished from their neighbors, as far as they can be seen." The same author noted that *Himatione* takes long daily flights for food, and he remarked on the strong flight of *Vestiaria* (pp. 155, 160).

These examples show that even among closely related song birds, differences in degree of subspeciation may be the result of differences in power of dispersal. Such explanations should be sought before invoking variation in mutation rates or other hypothetical explanations.

DEGREE OF ISOLATION AND SPECIATION

Laysan is by far the most isolated of the islands inhabited by Hawaiian land or freshwater birds. Of the five such species found

there, one belongs to an endemic genus (*Porzanula*); the other four have endemic subspecies on Laysan. Two of these four have representatives elsewhere only on the small island of Nihoa. The other two (*Anas*, *Himatione*) have races on the main islands. The fact that *Himatione sanguinea* and *Anas wyvilliana* range throughout the main islands without variation, yet developed distinct races on remote Laysan (the Laysan Teal is frequently considered a full species) is evidence of the potency of isolation. The small size of Laysan may also have contributed to this differentiation.

Of the main islands Kauai is by far the most isolated. This has evidently influenced the endemicity of its bird life, since three (*Loxops virens*, *L. coccinea*, *H. obscurus*) of the five polytypic species or superspecies of Drepaniidae and two (*Phaeornis obscurus*, *Moho nobilis*) of the three polytypic non-drepaniids have their most distinct form on Kauai. In *Loxops maculata* and in the flycatcher *Chasiempis sandwichensis*, the Kauai race is perhaps as well differentiated as any of the others but not more so. *Chasiempis* occurs only on Kauai, Oahu, and Hawaii, so the Kauai race is but little more isolated than that of Hawaii. Only in *Hemignathus lucidus* is the Kauai representative notably less differentiated than one of the others, namely, *H. wilsoni* of Hawaii. Perhaps this species is a relative newcomer on Kauai.

The isolation of Kauai is further emphasized by the only two clear-cut examples of speciation by double invasion to be found in the Hawaiian Islands. *Loxops parva* is evidently an earlier offshoot of the widespread *L. virens*. The latter reached Kauai again, giving rise to *L. virens stejnegeri* (fig. 3). The thrush *Phaeornis* is a more certain example, since the two species involved are the only Hawaiian thrushes. *Phaeornis obscurus* ranges throughout the main islands (except Maui), while the only other species, *P. palmeri*, is restricted to Kauai. Presumably after this genus spread over the islands, the Kauai population, because of its greater isolation, became differentiated to the species level, while on the other islands enough inter-island transfer of stragglers occurred to limit differentiation to the subspecific level. Later, *Phaeornis* again reached Kauai, but the

earlier arrival, *palmeri*, no longer interbred with the newcomers. Two sympatric species became established. The isolation of Kauai is thus sufficient to permit differentiation of some species of song birds to the specific level but not great enough to prevent occasional colonizations. Every species found on Oahu occurs also on Kauai.

Even in the species involved in the above double colonizations, the Kauai subspecies resulting from the second invasions have again become the most distinct of their species. By a repetition of the same process (triple or higher invasion), additional sympatric species might be produced until the available ecologic niches were exhausted. By this time some of the earlier arrivals on a particular island would doubtless differ generically from the later ones.

Negative evidence of the effect of degree of isolation is afforded by the similarity on near-by Maui, Lanai, and Molokai of certain species that show strong differentiation on the other islands. *Loxops virens* and *Phaeornis obscurus* are examples.

The direct effects of inter-island isolation are often more evident in invertebrates, principally because they are more sedentary than the birds. Perkins (1913) gave many examples both of this and of some other aspects of speciation discussed in this section. To mention only one example, the species-rich genus of snail, *Achatinella*, is very well represented on Oahu but never reached Kauai and has barely entered Hawaii.

ECOLOGICAL DIVERSITY AND SPECIATION

On a large island any given type of habitat is apt to occur over a wider area than on a small island. This may be of crucial importance to certain birds. The Hawaiian Hawk is found only on Hawaii, though it has occurred as a straggler on Maui. The absence of this strong-flying bird on the other islands presumably reflects lack of sufficient suitable habitat (semi-open country) to maintain a persistent population rather than inability to colonize the other islands. The Hawaiian Goose is partial to semi-barren lava fields. Such areas occur extensively on Hawaii and to a lesser degree on Maui, but they are virtually wanting on the other islands. This goose was common on Hawaii but very local

on Maui where it disappeared at an early date (Baldwin, 1945, p. 33). It was absent from the other islands.

The persistence of such species as *Psittirostra psittacea* and *Loxops coccinea* on Hawaii after they were extirpated on some of the other islands further reflects the importance of more extensive habitats and of the larger populations thereby made possible.

Large islands often possess types of habitat entirely lacking on smaller ones. This is particularly true if the large islands have greater elevations. When similar sympatric species compete, the more varied ecology of a large island may permit many of them to survive by occupying specialized or restricted ecological niches not available on small islands. This presumably explains how five species of *Psittirostra* have survived on Hawaii but no more than one on any of the other islands, or why two species of meliphagids occur on Hawaii but only one and sometimes none at all on the other islands.

A crude analogy with human society may clarify the above argument. On a small coral atoll most of the human inhabitants are perforce fishermen or fruit gatherers. On a continent the methods of making a livelihood are infinitely more varied, and many specialized vocations can arise.

Large islands present a bigger target to avian stragglers than do small islands and hence will tend to have more birds for this reason also. This factor is seemingly of no importance in the main Hawaiian Islands. They are so close together that irregularities in the distribution of birds are best attributed to ecological unsuitability or other causes rather than to failure of dispersal. All the song birds found on Oahu, for example, occur on isolated Kauai also. Perkins remarked that *Loxops coccinea* and *Hemignathus obscurus* surely would have flourished on Molokai had they reached it. Such assumptions are hazardous. In the past interspecific competition may have been more severe; the possibility of extinction, perhaps even before the arrival of man, must be kept in mind.

The Hawaiian Flycatcher, *Chasiempis*, is inexplicably lacking on Maui, Molokai, and Lanai, though abundant on the other islands. It was probably the last of the endemic

song birds to reach the Hawaiian Islands, and its absence from the central islands may be purely an accident of distribution. Yet, even in this instance, competition with insect-eating species of drepaniids, such as *Loxops maculata*, rather than failure of dispersal may have excluded *Chasiempis* from these islands.

The impoverished avifaunas of Nihoa and Laysan may stem in part from their isolation, but their small size also imposes rigid limits on the number of species they can support. The above remarks do not apply to more sedentary organisms; one group of snails, as noted above, is richly represented on Oahu but entirely lacking on Kauai.

Mayr (1940, pp. 214-215) in his analysis of the bird life of Polynesia cites similar evidence of the importance of the size of an island in the number of species of birds to become established: "New Caledonia, the largest of the islands, . . . has the largest number of species. Viti Levu [Fiji], the second largest island, has the second largest number. . . . Daly . . . holds that Tutuila is the oldest of the Samoan Islands, Upolu intermediate, and Savaii the most recent. On the basis of this age gradation one would expect an equivalent correlation of the number of species. Actually just the reverse order is true. . . . This latter gradient, however, runs exactly parallel to the size of the islands. Savaii has 730 sq. mi., Upolu 430 sq. mi., and Tutuila only 54 sq. mi."

The reasons suggested by Mayr to explain the greater number of bird species on large islands are essentially those given above. He emphasizes that large islands permit bigger populations that are less vulnerable to adverse factors, either ecological or genetical.

Occasional exceptions exist in the form of species that have become adjusted to small islands and avoid large ones. When such species are vagrants, sufficient mixing occurs to prevent any adverse genetic effects inherent in small populations. The Pacific Fruit Pigeon, *Ducula pacifica*, is such a species. The Laysan and Nihoa Miller Birds, *Acrocephalus familiaris*, belong to a superspecies widespread in the Pacific islands. It usually occurs on small atolls, but also on some high islands as in the Marquesas group. It is probable

that the absence of this excellent transocean colonizer in the main Hawaiian islands is the result of ecological unsuitability.

The Laysan and Nihoa Finch, *Psittirostra cantans*, though descended from the forest-inhabiting members of the same genus, is well adapted to conditions on these small islands. Were it to reënter the main islands it would probably restrict itself to semi-open areas of a type shunned by all the other drepaniids.

GEOLOGICAL AGE AND SPECIATION

As noted above, Hawaii is probably the youngest of these islands and Kauai the oldest. In most invertebrate groups this is reflected in the number of endemic species and genera present. Perkins (1903, p. 391) wrote of Hawaii, "... in other groups of animals [i.e., other than birds] with highly peculiar species it is frequently (though not invariably) extremely poor, as compared with the older islands of the group." Birds are an exception to this rule, presumably because of the importance to them of the greater area and ecological diversity of Hawaii. As noted above the same is true in the Samoan Islands. Birds have a high rate of accidental transfer from island to island. Any older or more primitive members of the Drepaniidae that once occurred on Kauai (assuming that that island was the home of the family for a time before Hawaii and Maui were inhabitable) were presumably later exterminated and replaced by widespread and aggressive species. In more recent time Hawaii, and to a lesser extent Maui, through their ecological diversity have provided a haven for specialized or declining species. The examples of double colonization on Kauai cited above are believed to be a result of greater isolation, not of greater age.

Although Hawaii still has active volcanoes, it is the largest of the islands and was perhaps the first to appear above the sea. Certain areas on this island may have been available to birds for as long as any part of Oahu or Kauai. The great mobility of birds would allow them to utilize now one and now another part of an island subject to periodic lava flows. Indeed, this condition continues to the present day on Hawaii.

Geological evidence as to the age of the species of Drepaniidae is still conflicting. Stearns (1946) and other Hawaiian geologists have suggested that this archipelago may have appeared above the waves as recently as late or middle Pliocene, but the recent borings on Bikini Atoll suggest a much greater age for Pacific islands. Perkins (1913) believed that the colonization of the Hawaiian Islands by plants and animals began as far back as the Eocene. Some biologists, particularly malacologists, have concluded that an even longer period was necessary for the evolution of this highly diversified and endemic fauna. Zimmerman (1948), however, has emphasized the rapidity of evolution possible in a tropical archipelago.

So far as speciation is concerned, the time factor presents no particular problem, since there is considerable evidence that it can proceed comparatively rapidly under insular conditions. The great ecological and morphological diversity of the genera of Drepaniidae would seem to require far more time. Yet some of the data indicate that adaptive radiation in this family (and probably in the insects and other diversified Hawaiian groups) has also taken place more rapidly than might be expected. It is safe to conclude that regardless of what further geological studies may reveal as to the age of the Hawaiian Islands, speciation and diversification have gone on at an accelerated pace in the Hawaiian honeycreepers because of the favorable and, at the same time, changing conditions under which they evolved. Yet it is difficult to believe that the history of the Drepaniidae and of many of the other endemic plants and animals does not extend back to the beginning of the Pliocene or before.

Much of the above data on speciation and endemism is summarized in the two maps (figs. 22-23) and in tables 11 and 12. On the maps, Roman numerals refer to the number of genera represented on the adjacent island. The number of such genera that are endemic is given in parentheses. The Arabic numerals give the number of species. The total number of species is broken down into the four following categories, always given in the same order in the parentheses: (1) endemic zoogeograph-

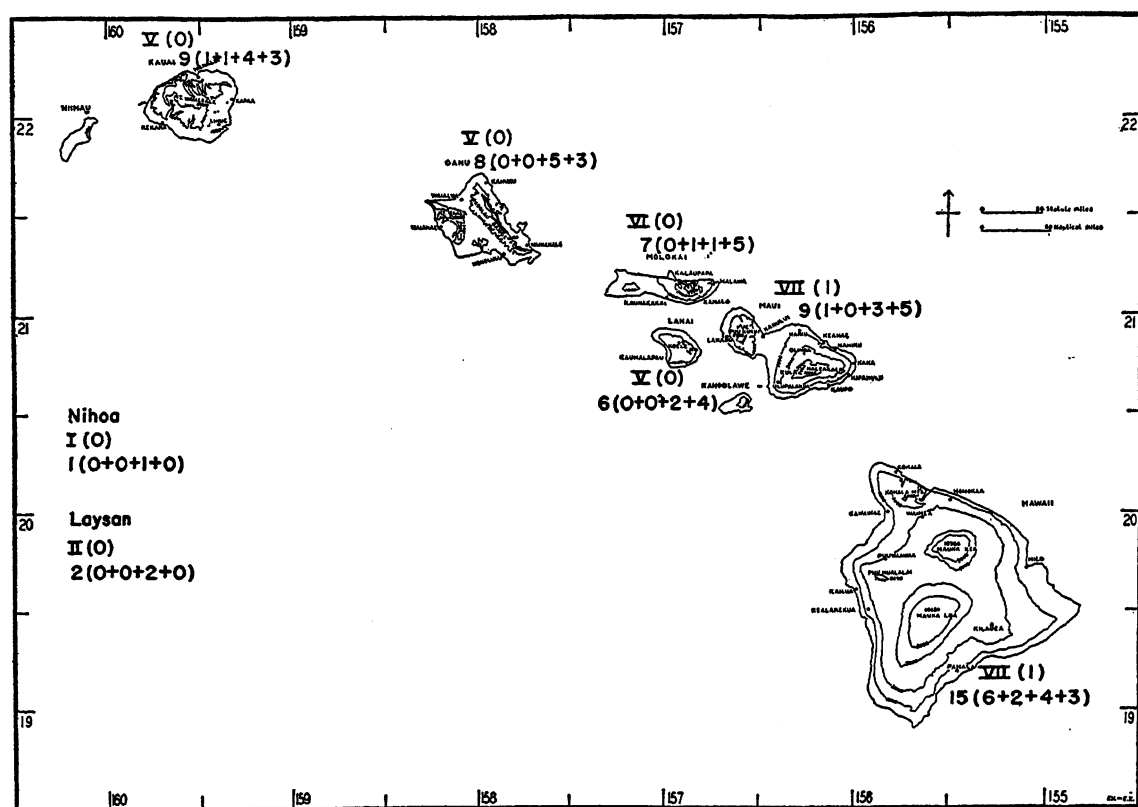


FIG. 22. Distribution and endemism of the Drepaniidae (see text).

TABLE 11
ENDEMISM OF THE DREPANIIDAE
BY ISLANDS

	Per Cent of Endemic Genera	Per Cent of Endemic Zooge- graphic Species	Per Cent of Endemic Species and Subspecies
Hawaii	1/7 = 14	6/15 = 40	12/15 = 80
Maui	1/7 = 14	1/9 = 11	4/9 = 44
Lanai	0	0	2/6 = 33
Molokai	0	0	2/7 = 29
Oahu	0	0	5/8 = 62
Kauai	0	1/9 = 11	6/9 = 67
Niihau	0	0	1/1 = 100
Laysan	0	0	2/2 = 100

ical species, i.e., species without representa-
tives on any other island, (2) endemic
semispecies, (3) endemic subspecies, (4)

non-endemic species or subspecies. Thus on
Hawaii VII genera of Drepaniidae are pres-
ent of which 1 (*Ciridops*) is endemic. Fif-
teen species are present, of which 6 are
endemic zoogeographic species (*Loxops sagi-
tirostris*, *Psittirostra bailleui*, *P. palmeri*, *P.
flaviceps*, *P. kona*, *Ciridops anna*), 2 are
endemic semispecies (*Hemignathus wilsoni*,
Drepanis pacifica), 4 are endemic subspecies
(*Loxops v. virens*, *L. maculata mana*, *L. c.
coccinea*, *Hemignathus o. obscurus*), and 3 are
non-endemic races or species (*Psittirostra
psittacea*, *Himatione s. sanguinea*, *Vestiaria
coccinea*). Some of the decisions involved in
such listings are arbitrary. Some students,
for example, would probably conclude that
species so different as *Drepanis pacifica* and
D. funerea should not be considered to form
a superspecies, even though they are the
only members of the genus and do not overlap
in range.

In addition to these data on endemism

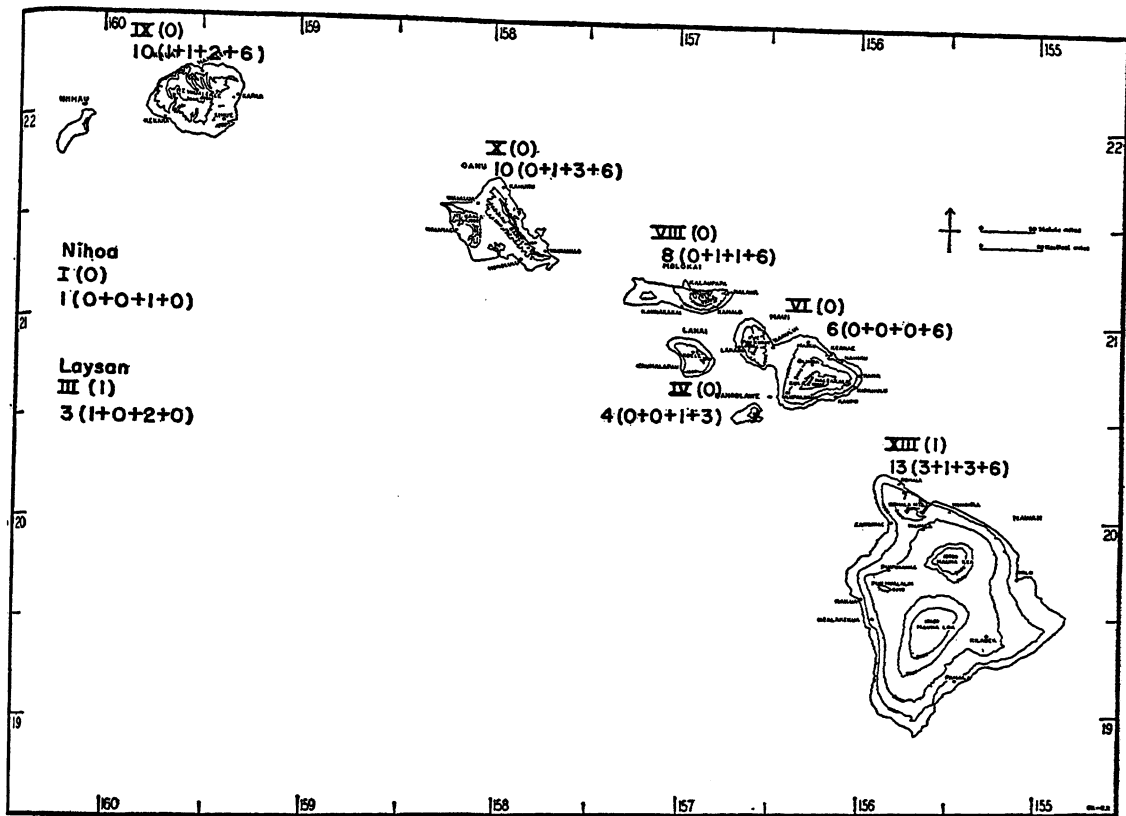


FIG. 23. Distribution and endemism of Hawaiian land and fresh-water birds other than Drepaniidae (see text).

for each island, it is sometimes instructive to consider groups of more than one island. Nihoa and Laysan together have two additional endemic species, *Psittirostra cantans* and *Acrocephalus familiaris*. The central islands, Molokai, Maui, Lanai, as a unit have an additional endemic, monotypic genus and species, *Palmeria dolei*, and an endemic race, *Loxops virens wilsoni*. Two species, *Anas wyvilliana* and *Himatione sanguinea*, do not vary in the main islands but have developed a race on Laysan.

Unfortunately, a number of Hawaiian birds probably disappeared before specimens were secured. Henshaw (1902) saw some form of *Moho* on Maui and had reports of a thrush, *Phaeornis*, there, but no specimens of either were secured. The rail *Pennula* is known only from Hawaii and doubtfully Oahu, but probably races occurred on the other islands (Munro, 1944, p. 51).

TABLE 12
ENDEMICITY OF HAWAIIAN LAND AND FRESH-WATER BIRDS OTHER THAN DREPANIIDAE
BY ISLANDS (SEE TEXT AND APPENDIX 1)

	Per Cent of Endemic Genera	Per Cent of Endemic Zoogeographic Species	Per Cent of Endemic Species and Subspecies
Hawaii	1/13 = 8	3/13 = 23	7/13 = 54
Maui	0	0	0
Lanai	0	0	1/4 = 25
Molokai	0	0	2/8 = 25
Oahu	0	0	4/10 = 40
Kauai	0	1/10 = 10	4/10 = 40
Nihoa	0	0	1/1 = 100
Laysan	1/3 = 33	1/3 = 33	3/3 = 100

The presence of a number of large, strong-flying, water birds, such as the Hawaiian

Stilt, among the Hawaiian non-drepaniids reduces the inter-island endemism of this group. On Maui all the non-drepaniids are of this kind; there are no song birds among them. The few non-drepaniid song birds show much the same pattern of endemism as the drepaniids themselves (Appendix 1).

HYBRIDIZATION AND SIBLING SPECIES

The high level of divergence of the Drepaniidae extends in most instances to the specific level. Only one specimen ("*Oreomyza perkinsi*") ever has been taken that appears to be an interspecific hybrid. Very similar sympatric species of the kind called sibling species by Mayr and others are also infrequent. *Psittirostra palmeri* and *P. flaviceps* may be considered as such, although they

differ in size and in the color of the head in the males. Unfortunately almost nothing definite is known of *flaviceps* except that the few known specimens were taken in the same forests as *palmeri* and were, in fact, considered by the collectors to be that species. On Kauai, *Loxops virens stejnegeri* and *Loxops parva* can be considered sibling species, as are the thrushes *Phaeornis obscurus myadestina* and *P. palmeri*. The concept of sibling species is at best indefinite, since subspecies (not to mention color phases) may be conspicuously different, while superficially similar species may be very different in requirements and behavior.

The rarity of hybridism and of sibling species in the Drepaniidae is very unlike the situation existing in the Galápagos finches (Lack, 1947).

MACRO-EVOLUTION

ADAPTIVE RADIATION

MAJOR DIVISIONS of the animal kingdom often contain subgroups differing widely in their mode of life and adaptive morphology. The diversity of avian families (penguins, albatrosses, hawks, warblers, etc.) is an example of this phenomenon, called "adaptive radiation" by the late H. F. Osborn. It occurs at different taxonomic levels. Thus, within the Order Falconiformes several adaptive types (eagles, fish hawks, bird-eating falcons, vultures, and others) are found. "Adaptive radiation is most obvious in the case of classes and sub-classes but may be traced both in higher and lower systematic units: however, in phyla and other units of high rank, the phenomenon is manifested only on very broad lines, while in small groups such as families the type is in general so much restricted that the radiation is neither so many-sided nor so obvious" (Huxley, 1943, pp. 486-487).

The Hawaiian honeycreepers are unique among birds as regards degree of adaptive radiation within a family. This radiation occurred rather recently and indeed is still not completed. Hence, the Drepaniidae furnish excellent material for the investigation of the crucial and rarely available early steps in this important type of evolution.

Although drastic changes in feeding habits have occurred repeatedly in the Drepaniidae, in continental families several sympatric species may coexist without developing major differences. This is true even of genera with a long evolutionary history, e.g., the diving ducks of the genus *Aythya* or the hawks of the genus *Buteo*.

The biotas of isolated, oceanic archipelagos are impoverished, and many families are absent. This is strikingly true of the Hawaiian Islands. Only five families or subfamilies of song birds are present (Appendix 1) as compared, for example, with 28 in the Malaysian region. These unbalanced insular biotas have been called "disharmonic" by Baur and by Gulick (1932). The few groups present tend to radiate into the empty ecological niches and in time to produce a secondarily balanced

or "harmonic" fauna. Thus the Drepaniidae have given rise to forms that to some extent replace such continental types as creepers, woodpeckers, finches, and tanagers. In continental faunas similar radiation took place long ago; the ecological niches are now occupied and the species find few opportunities for important ecological changes.

For radiation to occur, the absence of other competing groups is not enough. A variety of suitable environmental niches must be available. The Drepaniidae could not have evolved on the bleak Aleutian Islands.

Heavy predation or parasitism is thought to inhibit adaptive radiation by eliminating variant individuals. Selection resulting from predation will, however, promote the evolution of characters useful in escape or defense and sometimes these prove to be of importance. For example, the brown rat, *Rattus norvegicus*, and the black rat, *R. rattus* (both introduced in the Hawaiian Islands), compete with one another. The black rat escapes the more aggressive brown rat by its ability to climb and to live in trees or high in buildings. On the island of Maui, where the brown rat is not established, Eskey (1934) found that the black rat prefers to live on the ground in burrows beneath buildings. Predation by the brown rat might lead to further arboreal specialization by the black rat.

Zimmerman (1948) thinks many of the flightless or otherwise peculiar Hawaiian insects were produced not by selection but by the accumulation of mutations that could survive because of reduced selection pressure owing to the scarcity of predators and parasites. At first glance the same might appear to be true of the Drepaniidae, but upon closer scrutiny the unusual types of bill found in the family prove to be adapted (or in the process of being adapted) for particular sources of food.

The Hawaiian honeycreepers are the best example of recent adaptive radiation in a family of birds, but the Geospizinae of the Galápagos Islands exhibit similar tendencies (Lack, 1947). So far as mere diversity of bill structure is concerned, the Drepaniidae are rivaled by the Vangidae of Madagascar (pl.

13) and the Callaeidae of New Zealand (pl. 14). The latter family consists of only three genera, each monotypic, but they are very diverse. The family Vangidae contains 10 genera, some of them highly peculiar. Since the variation is in the bill, it is probably correlated with food habits, but this has not been demonstrated. New Zealand and Madagascar are much older than the Hawaiian or Galápagos Islands and their faunas are at an evolutionary level intermediate between those of continents and of young archipelagos. The same can be said of Australia and New Guinea. The birds of paradise (Paradisaeidae) of that region show much variation in the bill. This is, at least in part, adaptively correlated with feeding habits. Bourke and Austin (1947, p. 112) write of the Victoria Riflebird, *Ptilorhis victoriae*, a species with a heavy, curved bill, "... small parties may be seen energetically digging grubs and other insects from rotten logs and stumps." Most species of the family possess bills unsuited for such habits.

INCIPIENT ADAPTIVE RADIATION

A limited degree of divergent evolution is sometimes found even with a single population as in the castes of social insects. In the New Zealand Huia (*Neomorpha*) the male has a heavy bill for uncovering boring grubs and the female (pl. 14) a thin, curved one for extracting the grubs from their burrows. This divergence within a population cannot lead to adaptive radiation.

When a species is divided into isolated subgroups, adaptive divergence between populations is made possible. Mayr (1947) thinks it probable that all populations distinct enough to be considered subspecies possess minor ecological differences and adaptations. Such distinctions will tend to become greater with time, particularly when the representative populations have colonized dissimilar habitats. This is often the case when a species colonizes a small island and enters a less varied environment.

The effects of such a change upon behavior is often evident before morphological adaptations appear. The Red-winged Blackbird, *Agelaius phoeniceus*, normally nests in marsh vegetation. Yet on small islands in the Great Lakes it nests in conifers or even in tree cavi-

ties (Campbell, 1948). Lack (1942, pp. 20-21) found that seven species of British birds had altered their nesting habits after they colonized small coastal islands; several woodland species began to nest in open country.

A change involving the feeding habits of the king snake, *Lampropeltis*, was described by Barbour and Engels (1943). On the mainland it feeds upon other snakes, but on Ocracoke Island, off the Carolina coast, where there are no other snakes, a subspecies evolved that feeds on voles (*Microtus*). According to Ditmars (1933, p. 181) captive king snakes prefer other snakes as food, but they will eat rodents. Thus the change in habits found in the Ocracoke race was always potentially present in the species. Several examples of changes in habits on the part of voles (*Microtus*), peepers (*Hyla*), and other animals on islands in Lake Michigan are given by Hatt *et al.* (1948, pp. 137-139), and similar instances abound in the literature.

Species often differ in their ecological tolerance and hence in their capacity to colonize new environments.¹ This, as well as remoteness, is responsible for the poor avifaunas of distant islands. A large percentage of the birds straggling to such islands will be unable to survive. Species that can establish themselves, e.g., rails (Rallidae), become well represented even though they are weak fliers and hence less suited for island hopping than are many other birds.

Even closely related species may vary in their ecological tolerance. Lincoln's Sparrow, *Passerella lincolni*, occupies a narrow ecological niche and shows little geographical variation, though it is widespread in North America. The related Song Sparrow, *P. melodia*, occupies a broad ecological niche and by utilizing distinct subniches or habitats within it has broken up into almost thirty subspecies having minor, often adaptive, differences (Miller, 1942).

Among the Drepaniidae, ecological changes obviously correlated with colonization of different or more stringent environments are not numerous. The somewhat changed habits of *Psittirostra cantans* and to a less extent of *Himatione sanguinea freethii* on the atoll of

¹ The "tolerance" theory of plant distribution is an expression of this fact.

Laysan are exceptions. The longer tarsi and shorter wings of the Laysan Finch as compared with the related species of the larger islands are adaptive responses to the Laysan environment. On the main islands all the drepaniids are forest birds; the forests are quite similar on all six islands.

Considerable divergence exists in the Kauai meliphagid *Moho braccatus*, a semispecies of *M. nobilis*. Three of the four forms of this group, those of Hawaii, Molokai, and Oahu, are typical honeysucking meliphagids. The fourth, *M. braccatus*, has different habits. Perkins (1903, pp. 443-444) wrote: "It retains to a considerable extent a like fondness for the nectar of flowers. . . . But it is in being much more largely insectivorous that it strikingly differs from its congeners, and in accordance with these habits its structure is somewhat modified. Thus while the long weak plumes of the tail in the allied species are specially so modified for aesthetic [courtship] purposes, in the Oo-aa they are stiff and pointed and aid it greatly when climbing on the trunks of forest trees. . . . For insects it hunts freely on the trunks of the largest Ohias, to which its powerful legs and claws aided by the stiff tail enable it to cling woodpecker-like, while it searches on and beneath the bark."

There is no obvious ecological reason for these changes in the diet of the Kauai meliphagid. It is possible, of course, that competition with nectar-eating Drepaniidae is responsible, though why such competition would have been more severe or effective on Kauai than on the other islands is not apparent.

DIVERGENCE IN SYMPATRIC SPECIES

Ecological adaptations play an important part in the gradual differentiation of a population, first as a race, then as a species. Such ecological differences often enable two species that were formerly races to overlap in range after achieving reproductive isolation. In most instances the ecological isolation is by no means complete and the now sympatric species compete with one another.

Gause, followed by Lack (1944), concluded that two species occupying exactly the same ecological niche cannot exist together—one will displace the other. It might be argued

that if two such species are alike in reproductive potential and other basic respects as well as in food requirements, they could coexist just as, for example, two or more genetic alternates without selective value might persist indefinitely in a population in accordance with Hardy's formula. It is safe to assume, however, that two races never would diverge to the species level without acquiring differences affecting their relative abilities to survive when they enter the same area.

Up to 15 species of Drepaniidae occurred on a single island (Hawaii), though perhaps not more than eight or 10 were normally found together in any one part of the island. This condition presumably reflects much secondary overlap by range extensions of species from island to island. Four ecologically restricted species of *Psittirostra* (three of which are now extinct) occurred on the island of Hawaii, while a fifth, *P. psittacea*, was widespread both there and on the other islands. It is probable that some at least of the four endemic species of Hawaii were once more widespread but were eliminated on the smaller islands through competition with closely allied congeneric species. They managed to survive on Hawaii where the more varied ecology permitted specialization.

Many allopatric species that appeared during the evolution of the family doubtless proved to be too similar to exist together on the same island. When such a species enters the range of another it fails to become established or, if it happens to possess selective advantages, it displaces the first arrival. Continental species so similar ecologically as to be unable to invade each other's ranges are not infrequent. Mayr (1947, p. 265) cites such an example from Africa brought to his attention by R. E. Moreau: "*Cossypha heuglini* and *C. semirufa* occur in the same locality. The former is always restricted to its normal habitat, namely bush country outside the forest, while the latter is found only in the forest. In one or two mountain forests where *C. semirufa* is absent, the other bird replaces it." Moreau (1948) has since published other instances of this sort of replacement among African birds.

It sometimes would seem that the luxuriant Hawaiian rain forest with its teeming in-

vertebrate life presents song birds with an inexhaustible food supply. Yet Darwin was surely correct in accepting Malthus' conclusion that any species not otherwise checked will increase to the point where it exhausts its food supply. Since it is unlikely that diseases or predators put a serious check upon drepaniid populations before the arrival of man, competition for food might be expected. The adaptive radiation of the family is entirely one concerned with exploitation of new sources of food, an indication that competition for food did develop.

To have a selective effect competition need not be continuous. Every few years, perhaps, the building up of maximum populations of certain species of birds or the partial failure of important sources of food would result in heavy, selective mortality.

More definite evidence of competition exists. Henshaw (1902, p. 49) wrote of *Loxops maculata newtoni* of Maui: "When referring to the Hawaiian member of this genus (*mana*) [i.e., *L. maculata mana*], I laid special stress upon its habit of hunting almost exclusively along the main stems of the trees and upon the large limbs. . . . The Maui species is noticeable for the same habit, but, unlike *mana*, it much frequents also the undergrowth, and not rarely descends even to the ground in its hunting excursions. Such marked difference in habits between species so closely allied is extremely interesting, and I attribute it to the absence in Maui of the elepaio [*Chasiempis sandwichensis*, Muscipidae]. The elepaio is essentially a bird of the low undergrowth, though by no means exclusively confined to it. As the undergrowth in Maui is unoccupied by any bird, *Oreomyza* [*L. m. newtoni*] has changed its habits and extended its hunting grounds, being indeed far more an inhabitant of the scrub than of the trees. In other words, its habits are far less specialized in Maui than are those of its relatives upon Hawaii where competition is keener."

The same author wrote of *Palmeria dolei* (p. 55): "I noticed much animosity manifested by the individuals of this species towards the akakani [*Himatione*]. The habits of the two species are too much alike for friendly relations to exist, and the greater size and strength of *Palmeria* enable it to

drive away its smaller rivals from coveted feeding grounds. Even the half-grown birds successfully attack the akakani, and divide their time between sipping honey and in chasing their rival cousins."

Perkins wrote of an individual of *Drepanis funerea* that he observed feeding in an ohia (p. 401), "With that pugnacity which is said to be equally characteristic of the mamo [*D. pacifica*], it continually drove the smaller red birds [*Himatione* and *Palmeria*] from the bush, to be itself in turn driven off by the superior strength of the oo [*Moho bishopi*], but always returning after a few moments to the same flowers."

The Hawaiian meliphagids may compete with drepaniids since both feed on nectar. Perkins (p. 441) wrote of *Moho nobilis*: "It is very intolerant of the scarlet iiwi (*Vestiaria*) and will at intervals suspend its feeding to chase away any of these that have ventured into its own tree, or it will even leave this, however profuse be the blossoms, to drive from some distant tree one that it has chanced to spy there. This aggressiveness appears so wanton and unnecessary, and so frequently interrupts its own feeding, that one suspects it must be an ancient habit, which has survived from a time when either nectar-producing flowers were scarcer, or the birds which fed upon them were much more numerous."

Munro (1944, p. 104) noted that when the diminutive *Loxops parva* was chased out of the flowering trees by larger species it would quickly return, "almost at the tail of its pursuer." Baldwin (1940, p. 12) pointed out that "the iiwi (*Vestiaria*) and apapane (*Himatione*) consume similar types of food and inhabit the same level in the forest, thus they compete with each other."

Most of the above evidence for competition relates to the nectar-feeding species of drepaniids. Such pugnacious behavior may be characteristic of nectar-feeding birds in general as it occurs also in the Nectariniidae, the Trochilidae, and in some Meliphagidae. I have observed that wintering individuals of Costa's Hummingbird, *Calypte costae*, and Anna's Hummingbird, *C. anna*, in Sonora, Mexico, appear to have feeding territories. These they patrol regularly, vigorously ejecting other hummingbirds that may trespass.

Competition among insect- or fruit-eating species, although it may not often lead to the development of such overtly aggressive behavior towards other species or other individuals of the same species, may be just as effective in furthering ecological divergence.

COMPETITION AND MAJOR ADAPTIVE CHANGES

It remains to indicate the role of competition between sympatric species in adaptive radiation. This account is based in part on an earlier, brief discussion of this subject (Amadon, 1947). The Hawaiian thrushes are used as the first example, since the presence of only two species of this family (Turdidae) in the islands makes the problem less complex. Both species belong to the endemic genus *Phaeornis*. One of them, *P. obscurus*, is found throughout the islands except on Maui, where it probably also existed at one time. Each of the other five islands has a distinct subspecies. The second species, *P. palmeri*, occurs only on Kauai. Presumably the first *Phaeornis* stock to reach this remote island was so isolated that evolution to the specific level followed. On the other and less isolated islands one must assume that individuals of *Phaeornis obscurus* straggled from island to island frequently enough to keep differentiation at the subspecific level.

Phaeornis obscurus feeds on berries and fruits but sometimes takes insects, while *palmeri* is chiefly insectivorous. Perkins (1903, p. 377) found in the stomachs of specimens of the latter species "... the large hard weevils of the genus *Rhyncogonus*, and these unquestionably form a large part of their food. Spiders and caterpillars are also eaten, and the insectivorous habits of the species are strongly contrasted with the berry-eating propensity of the other members of the genus [i.e., the races of *obscurus*]. . . . Owing however to their totally different habits there is little or no competition between the two forms, as at present constituted." Since the five races of *obscurus* are all frugivorous, it is probable that the different feeding habits of *palmeri* were a result of competition for food with the congeneric species, following the second colonization of Kauai by this genus.

Phaeornis palmeri, even at the time of its

discovery, was a rare bird, restricted to the higher parts of the Kauai forest. *P. o. myadestina* was widespread and common throughout the range of *palmeri* and in other forested parts of Kauai as well. Although the difference in their food habits must reduce competition, perhaps their other requirements conflict enough to affect the status of *palmeri* adversely.

The dissimilarity in food habits of these thrushes must have existed to some extent at the time the genus colonized Kauai for the second time, or the two species would not have been able to coexist. There can be little doubt, however, that competition would enhance these incipient differences. Those members of either species that were most dissimilar in food habits would have the best chance of surviving. Thus selection would favor further divergence. The bill of *Phaeornis* is suitable for taking either berries or insects, and no morphological changes correlated with the unlike feeding habits of the two species are evident, at least superficially. As in many other closely related sympatric species there is a size difference (*palmeri* is smaller); this may be adaptive (Lack, 1944).

In the Drepaniidae, the genus *Loxops* presents an instance of speciation by double colonization upon Kauai similar to that of *Phaeornis*, except that adaptive changes in the bill are already perceptible. *Loxops virens* ranges throughout the main islands, while *L. parva* is restricted to Kauai. The former feeds chiefly upon insects sought among foliage and also, to a considerable extent, upon nectar. Occasionally it hunts upon the boughs of trees for insects, using its bill to tap or pry away bits of bark or lichens. The Kauai race, *Loxops virens stejnegeri*, of the widespread species, has a noticeably heavier bill than the races of the other five islands (pl. 9). Munro (1944, p. 100) wrote of *stejnegeri*: "I noted particularly in skinning that the muscles on the back of its head were more strongly developed than in the other Kauai birds and its skull more heavily built. This development was evidently occasioned by its habit of digging in the bark of trees to a greater extent than any of the other Kauai birds; or other amakihi [i.e., other races of *L. virens*]." *Loxops parva*, on the other hand, is a tiny bird, smaller than any race of *L.*

virens. It has a small, almost straight bill, very unlike the stout curved one of *stejnegeri*. Of *parva* Munro (p. 104) wrote: "It usually gathers its insect food among the twigs and leaves but sometimes in the loose bark. It is very fond of visiting the koa flowers." Perkins (1903, p. 409) also contrasted the habits of these two Kauai species and stated that in its manner of digging out concealed insects with its bill *stejnegeri* resembles *Hemignathus lucidus*.

To summarize, on the islands where but one species of this group (*Loxops virens*) occurs, it has generalized feeding habits. On Kauai where two species are present as a result of a double invasion, they have, so to speak, divided the ecological niche of the parental species between them (and extended it). *L. v. stejnegeri* has specialized for securing insects from beneath bark. Its bill has become strengthened by the natural selection resulting from such habits. *Loxops parva* restricts itself almost exclusively to food obtained from foliage and shallow flowers. Thus divergence and incipient specialization have resulted from competition between two similar species. Evidently their needs no longer conflict seriously since both are reasonably common.

Lack (1947) found a number of similar instances in the Geospizinae. When two sibling species occur on the same island in the Galápagos, they are adapted to slightly different ecological niches. On islands where only one member of such a pair is represented, often it is intermediate both morphologically and ecologically, sometimes to such a degree that it is impossible to tell which of the two species it represents.

A more striking example of divergence in the Drepaniidae is presented by the two superspecies of the genus *Hemignathus*. All members of this genus are primarily insectivorous. Their feeding habits will be briefly summarized here; they are given in more detail elsewhere in this paper.

Hemignathus obscurus hops along the trunks and limbs of trees, using its long, thin, decurved bill like a forceps to pick insects from crevices. Sometimes it taps with its bill to remove a bit of bark, but the tip of the bill is too slender and flexible to be of much use in this way. The lower mandible is appreci-

ably shorter than the upper; judging from the related species this may be the first step in adaptation for digging out grubs. In *Hemignathus lucidus* the bill is also decurved, but the lower mandible is much shorter and somewhat heavier than the upper (table 13). The feeding habits of this bird are similar to those of *obscurus*, but the heavier lower mandible is used more forcibly in chipping and prying away loose bits of bark. In *H. wilsoni* (the representative of *lucidus* on

TABLE 13
DECREASE IN LENGTH OF LOWER MANDIBLE
RELATIVE TO THE UPPER IN MALES OF
Hemignathus lucidus AND *H. wilsoni*
AS COMPARED WITH *H. obscurus*
(See table 2 for size of samples)

	Average Length of Upper Mandible	Average Length of Lower Mandible	Ratio of Lower to Upper Mandible
<i>Hemignathus o. obscurus</i>	43.2	38.6	.89
<i>Hemignathus lucidus affinis</i>	29.1	14.8	.51
<i>Hemignathus wilsoni</i>	26.9	14.7	.55

Hawaii and undoubtedly once only a subspecies of it) the modification of the lower mandible has progressed further. It is straight and heavy, resembling that of a woodpecker. Holding its bill open to keep the slender upper mandible out of harm's way, it pounds vigorously on bark or soft wood to expose insects.

Correlated with the modification of the bill in the genus *Hemignathus* is a progressive decrease in the use of nectar as food. *Hemignathus obscurus* not infrequently takes nectar, usually from the deep corollas of lobelias to which its long bill is well suited. Henshaw, who had much experience with *H. o. obscurus*, never saw it take nectar, and it must be emphasized that insects are the principal food of all members of this superspecies. *Hemignathus lucidus* very rarely takes nectar, its short lower mandible being unsuited for such feeding. *Hemignathus wilsoni* never feeds on nectar.

This remarkable modification of the bill in the genus *Hemignathus* would seem to be the result of competition between the two superspecies *H. obscurus* and *H. lucidus*. The heavier lower mandibles of *H. lucidus* and particularly of *H. wilsoni* enable them to knock or pry away bark, thus exposing insects not available to *obscurus*. The genus is of particular significance because the intermediate step (*H. lucidus*) of this important ecological and morphological change still exists. Since the bill of *Hemignathus* was specialized to begin with, the result of its modification as seen in *H. wilsoni* is somewhat grotesque. Yet it may be significant that *wilsoni* is the only one of the eight forms of *Hemignathus* surviving in fair numbers. Most or all of the others are extinct.

Presumably the heavy bills of *Pseudonestor*, *Psittirostra*, and *Ciridops* are the result of similar modification of slender decurved bills, but ones that were less elongated and specialized to begin with (i.e., of the type now found in *Loxops* or *Himatione*). The species grouped in plate 11 suggest how such transformations may have been accomplished.

MECHANISM OF ADAPTIVE RADIATION

The Hawaiian Islands are young geologically, and the radiation of the Drepaniidae must have been a comparatively rapid process. Probably it occurred within a period shorter than the known existence of some conservative avian genera like *Buteo* or *Grus*. *Hemignathus*, in particular, suggests how quickly important changes can occur when conditions are favorable. *Hemignathus wilsoni* is a geographical representative of *H. lucidus*; indeed Bryan and Greenway (1944, p. 129) treat them as subspecies. Yet a marked "qualitative" change in the lower mandible has occurred; that of *lucidus* is decurved; that of *wilsoni* is straight and chisel-like. This modification took place concurrently with the appearance of only minor "subspecific" differences in size and color (characters not subject to the strong selection affecting the bill) in these populations. The tongue is even now completely tubular in *H. lucidus* and *H. wilsoni*, though the latter, at least, never takes nectar. This is further evidence of their rapid evolution. Probably the other distinctive bill types in the Dre-

paniidae (those of *Pseudonestor*, *Psittirostra*, etc.) evolved with equal abruptness in response to strong selection favoring new feeding habits.

Paleontological data support the thesis that major evolutionary changes usually proceed with comparative rapidity. Simpson (1945) in his analysis of "Tempo and mode in evolution" emphasizes that important evolutionary advances usually involve a change from a given ecological niche to a very different one. The intermediate steps in such a process will usually be ill adapted for either the old or the new way of life. Hence, the change must be accomplished rapidly, if at all. To emphasize this, Simpson proposed the term "quantum evolution." Since this kind of evolutionary change presumably requires thousands or tens of thousands (as contrasted with hundreds of thousands, or millions) of years, the implied similarity to the instantaneous quantum phenomena of physics is somewhat misleading. This is especially true inasmuch as the term quantum evolution might seem to give comfort to now largely discredited theories of evolution by macrogenesis or "systemic" mutation.

The term "rapid divergent evolution" is perhaps not too cumbersome an equivalent for quantum evolution. To be sure, important evolutionary changes sometimes do not involve divergence in the sense of dichotomy between contemporary forms. In an historical sense divergence between ancestor and modified descendant does take place even then.

Simpson mentioned no examples of rapid divergent ("quantum") evolution among recent animals, but Davis (1949, p. 86) believes that "it may be studied to advantage in existing forms." Aside from *Hemignathus* other examples exist, particularly among invertebrates, in Hawaii and elsewhere. Zimmerman has emphasized the radical evolutionary changes that have occurred time after time among Hawaiian insects. A species of damselfly, *Megalagrion oahuense*, for example, differs from all other species of Odonata in that its larvae are terrestrial rather than aquatic and forage in the ground litter beneath ferns. "Is it not true that this peculiar species shows us how a new order of insects could arise?" (Zimmerman, 1948, p. 145.)

Hemignathus lucidus is an excellent example of the poorly adapted intermediates that Simpson predicated for the brief period when a species is undergoing radical changes in habits. The short lower mandible of this species is poorly adapted either for probing in flowers or crevices of bark (the habits of its less specialized relatives such as *Hemignathus obscurus*) or for digging away bark and wood (as does *H. wilsoni*, its contemporary "descendant" on Hawaii). *Lucidus* seems to be a poorly adapted intermediate between these very different methods of food-getting but is well enough adapted, nonetheless, to survive. In *Hemignathus* evolution appears to have been under the control of selection throughout. The habit of digging insects out of wood or bark, so fully established in *H. wilsoni*, is already foreshadowed in the habits of its much less specialized relatives, such as *Loxops virens*. Apparently competition for food with *H. obscurus* set in play the selection that led to specialization by *lucidus* and by *wilsoni*.

Davis (1949) doubts that truly inadaptable stages exist even in the most drastic evolutionary transformations. Some of the intermediate steps (e.g., *Hemignathus lucidus*) may merely appear inadaptable in comparison with later, better adapted stages.

Although divergent evolution is frequently an all-or-none process in which the poorly adapted intermediates must quickly complete the ecological break with the past or become extinct, exceptions seem to exist. In the auks (Alcidae) the wing is used for flying through the air and for propelling the bird through the water. Specialization for both of these functions cannot exist in the same wing, but a compromise has been achieved. In the penguins adaptation for aquatic progression gained the ascendancy and flight was lost.

In the genus *Dicaeum* of the flowerpeckers, a family of small arboreal birds, some of the species have thin decurved bills, others rather stout ones (Mayr and Amadon, 1947). The former are adapted for probing shallow flowers for nectar and minute insects; the latter for eating the berries of various species of mistletoe. These are the two principal methods of feeding of the genus; some species are adapted primarily for one, some for the

other. The trend of this adaptation has been reversed several times in the evolution of the genus. Several species have an intermediate type of bill. Even those that do not, usually manage to utilize both sources of food.

We can conclude that the powerful selective forces favoring generalization and use of a single structure, such as the bill, for many purposes tend to preserve intermediate types. This is less apt to prove possible when drastic ecological and morphological changes take place.

The genetic aspects of rapid divergent evolution have been discussed by Simpson (1945) and by Wright (1945) and others. In small populations genes of neutral or even adverse selective value may become established merely by chance. Exceptionally, such non-selective genetic changes may prove to be pre-adapted for a new ecological niche. Once the latter is entered selection becomes operative in perfecting adaptation.

As noted above, the major adaptive shift that took place in *Hemignathus lucidus* and *wilsoni* seems to have been under the direction of selection throughout. Significantly, the most radical change was in the form *wilsoni* of the large island of Hawaii. Its total population has probably always been well up in the thousands, too large for small population genetic effects to be effective.

Fundamental morphological changes probably require many successive gene mutations or recombinations. It is too much to expect that a single mutation established by chance will prove to be of great importance unless the circumstances are very exceptional, e.g., "negative" changes involving loss or degeneration of a character. Zimmerman (1948) shows that loss of flight has occurred again and again among Hawaiian insects. He believes that such flightless types have no selective advantages but are able to survive because of the scarcity of enemies and other unusual features of the Hawaiian environment. It is rather well established that a structure produced by selection will sooner or later "degenerate" if selection is relaxed. The complete or partial loss of flight in the Hawaiian and Laysan rails, as well as in many Hawaiian insects, is an instance as is the loss of vision and pigment in cave animals. But

whether the "Sewall Wright effect" is ever responsible for important new characters is debatable.

Simpson concluded that a certain amount of pre-adaptation must exist before a species can undergo a rapid major ecological (and morphological) change, since the transitional individuals must from the first be well enough adapted to the new way of life to survive. The thin decurved bill of *Hemignathus obscurus* is but slightly pre-adapted for chipping and prying away bark to expose insects. The ancestor of *H. lucidus* and *H. wilsoni* evidently had a bill like that of *obscurus* with but a minimum of pre-adaptation, yet natural selection in the direction of changed feeding habits led to a profound modification of the lower mandible.

Kosswig (1948) has discussed at length the role of pre-adaptation in macro-evolution, using the drepaniids as one of his principal examples. As a contemporary example he mentions the Kea, *Nestor notabilis*. The powerful hooked bill of this New Zealand parrot is adapted to grubbing out insects and roots. It proved to be pre-adapted to ripping open the backs of sheep to feed upon their fat and kidneys. Kosswig's assumption that this pre-adaptation is perfect and that no further adaptation (i.e., post-adaptation) would occur if the Kea were to adopt regularly such predatory habits is unjustified.

In a narrow sense every favorable mutation may be considered as "pre-adapted." This may mean only that a given mutation happens to coincide with the selective forces affecting a species. To give a crude analogy, in making a wall, stones "pre-adapted" for wall building are selected, but the stone wall itself is not an example of pre-adaptation.

Insofar as pre-adaptation is involved, change in form may precede change in function. In other instances, change in function or habits may precede adaptive morphological change. The ancestor of *Psittirostra cantans*, for example, was probably a short-legged species when it reached Laysan. There it perforce spent more time on the ground; selection favored those individuals with longer, stronger legs, and eventually adaptations in this direction occurred. In this sense change in function may precede change in

form without Lamarckian implications. But, in general, change in form and function may be considered as inseparable and usually simultaneous responses of the organism to its biological and physical environment. The recent emphasis on "functional" anatomy would seem to be another expression of this point of view.

Parallelism is rather subtly involved in the rapid divergent evolution of the Hawaiian honeycreepers. A long, thin, decurved bill evolved in *Drepanis* in connection with the probing of deep flowers for nectar and in *Hemignathus obscurus* and *procerus* as an aid in probing cavities in bark for insects. *Hemignathus* is apparently of later origin, and its evolution was favored by the existence of a curved, pointed though short bill in ancestors similar to the existing *Loxops virens*. Furthermore, *Hemignathus obscurus*, although primarily insectivorous, does probe the deep corollas of lobelias for nectar. That its adaptation is primarily for insect feeding is, however, evident both from its own food habits and from those of related species and genera.

Failure to recognize the parallelism between *Drepanis* and *Hemignathus* has led to their close association in some classifications, though they belong to different subfamilies.

One of the Neotropical wood-hewers, *Campylorhamphus*, has a bill similar to that of *Hemignathus procerus* and with a similar function, that of picking insects from deep crevices in bark as the bird hitches itself along the trunks of trees (pl. 15).

CORRELATION OF BEHAVIOR WITH MORPHOLOGY

It is generally assumed that feeding responses or behavior are inherited and basically "instinctive." Differences in behavior among related species prove that enough variation is present to furnish raw material for selection even in insects. In higher vertebrates, learning and conditioning become increasingly important in molding behavior. Cushing (1944) suggested that in birds non-inherited cultural or traditional feeding behavior passed on from parent to young may be stable enough to control the course of morphological adaptations for feeding. The

fishing behavior of the Fish Hawk, *Pandion*, he thinks, may have no basis more fundamental than the teaching of the young by their parents. Since young drepaniids follow their parents for some time after leaving the nest, Cushing suggests that traditional or learned behavior may have stabilized or controlled new feeding habits before or while the modification of the bill and other organs was occurring.

The problem of innate and learned behavior among vertebrates is so complex that Cushing's hypothesis cannot, perhaps, be evaluated without experimental work. In the white rat, for example, it has been shown recently that an individual reared on powdered food will not perform the "innate" behavior of nest building; it has never learned to handle objects with its teeth. Reared under "normal" circumstances, nest building appears to be innate. Similarly one must suppose that the feeding patterns of birds in their main outlines will develop without parental training in birds raised in normal surroundings. Thus, Lawrence (1949, pp. 22-25) related how young Pigeon Hawks, *Falco columbarius*, taken from the nest when half grown and never given live prey, learned to catch on the wing first insects and later birds. I have elsewhere published a somewhat similar experience with a young Great Horned Owl, *Bubo virginianus* (Amadon, 1943, pp. 257-258). This suggests that parental care of

young birds after they leave the nest lessens mortality while the young are perfecting the techniques of hunting, but it is not essential for the appearance of such techniques. In all Pelecaniformes, the young are abandoned by their parents before they leave the nest. Yet the pelicans, man-o'-war birds, and other members of this order have feeding methods involving much skill in diving or flying.

It must be admitted that imitative behavior, among adults or between parents and young, would aid in the establishment of a pronounced change in feeding habits such as that mentioned in the Kea. Another example is provided by certain game birds that for a time failed to utilize unfamiliar cultivated grains, only to begin doing so rather abruptly. Probably most changes in food, even in such a diverse family as the Drepaniidae, have taken place more gradually. It might be argued that failure of traditional or learned aspects of feeding behavior to prevent the utilization of new sources of food is more significant than their possible role in stabilizing patterns already present. The degree to which a given species is morphologically specialized for a particular food or foods will in itself usually limit the possibilities of further change. In this field, also, it would seem that a synthesizing point of view is best and insofar as necessary such problems may be approached from the standpoint of "psycho-functional anatomy."

SUMMARY

THE HAWAIIAN ISLANDS are very isolated oceanic islands of volcanic origin. Their great elevation and their position just within the Tropical Zone athwart the northeast trade winds assure much local variation in climate and rainfall. The climate is tropical and the rainfall in the mountains heavy, producing a luxuriant, though botanically rather undiversified, rain forest wherein the vast majority of the Hawaiian honeycreepers (Drepaniidae) find their home. Some believe the Hawaiian Islands date back to the Cretaceous or before; others believe that they are no older than late Pliocene. Recent research, particularly on Bikini, suggests that many Pacific islands are older than the volcanic cones now above sea level would indicate. Some elements of the Hawaiian biota may have arrived far back in the Tertiary. Vulcanism, subsidence, and other more or less catastrophic changes in the physical environment have since played a role (sometimes favorable, sometimes unfavorable) in their evolution.

The family Drepaniidae, as first noted by Perkins, is divisible into two well-defined subfamilies. In the present revision only nine genera are recognized, about half the usual number. Even so, five of the nine are monotypic and a sixth (*Drepanis*) is essentially so. These figures reflect the great morphological diversity of the family, which contains 18 "zoogeographical" species, and about 22 species in all when geographically representative species are counted separately. A number of forms are on the borderline between subspecies and species and must be classified somewhat arbitrarily. Seven of the 22 species break up into subspecies, varying from two to six per species. The total number of recognizable "forms" in the Drepaniidae is 39.

Measurements are tabulated for the drepaniids examined during the present study. Coefficients of variation for these birds seem to be of the same order of magnitude as for other birds. This is true even of the bill, which has undergone considerable recent adaptive change in several of the genera. As in most birds, the individual variability in bill length is greater than that in tail

length, and the latter slightly exceeds that in wing length. No effect on variability of small population size or of specialization could be demonstrated, but the available measurements were not extensive or precise enough to reveal slight differences. Males are larger than females in the Drepaniidae, sometimes rather markedly so. Sexual difference in bill size is, in some species, relatively greater than that in general size. There is some reason to believe that this is sometimes the result of non-selective positive allometry, especially in the genus *Hemignathus*. Variations in size and proportions among the races, species, and genera of the family are discussed and analyzed with the aid of graphs. Some of the differences seem definitely to be adaptive; others may or may not be.

Most drepaniids appear to molt directly from the juvenal to the adult plumage. In the subfamily Drepaniinae, at least, this molt may begin almost as soon as the young leave the nest and proceeds rapidly. Nevertheless, drepaniids sometimes nest in partially immature plumage; perhaps this is true chiefly of birds hatched late in the previous season. Further study may show that there is a partial first winter or intermediate plumage in some species.

Adult drepaniids molt once a year, following the nesting season. The period of molt varies somewhat from species to species, particularly in the Psittirostrinae and may come as early as June or as late as October or November. Perkins' belief that there is an eclipse or off-season plumage in some of the Psittirostrinae seems to be incorrect. The pattern of molt in drepaniids is typical for song birds.

Immature drepaniids are rather dull in color, adult females usually a little brighter, and adult males often brilliant red or orange. In the Drepaniinae, adult males and females are both brilliant red in several species. Degree of sexual dimorphism in color occasionally varies abruptly from species to species in a genus or even from race to race. Individual variation in color is usually slight, but in one or two forms an orange or yellowish tone may be present or absent. Geographical

variation in color, while occasionally striking, is no more so than in other insular song birds. Red plumage is most frequent in the less specialized members of both subfamilies, suggesting that it was characteristic of the earliest drepaniids. In the Drepaniinae a trend towards black plumage culminates in the entirely black *Drepanis funerea*.

The Hawaiian honeycreepers are notable for the adaptive radiation which permits them to utilize a variety of foods: nectar, insects (secured in many ways), fruits, and seeds. In one subfamily, the Drepaniinae, four of the five genera are primarily adapted to feeding upon nectar and small insects from flowers. The fifth genus, *Ciridops*, was evidently frugivorous (its only species became extinct very quickly). Some of the species of the other subfamily are adapted for digging insects from wood; others have very heavy, finch-like bills suitable for crushing seeds and fruit.

The song and call notes of the two subfamilies of the Drepaniidae are quite unlike. No detailed comparative studies of these birds during the nesting season have been made, and the information available is too general to be of much use in investigating the relationships of the family. Most of the species nest during the spring months and build an open nest of rootlets, moss, and similar material. It is placed among the twigs of bushes or trees at widely varying elevations. The eggs vary from two to four in number and are spotted. Apparently only one brood is raised, though more information is needed on this point. All the Hawaiian honeycreepers fly well, but there is slight evidence of incipient reduction of the wing in the two forms native to the little atoll of Laysan.

The Drepaniidae have a number of known parasites and are subject to various diseases, including bumblefoot, or bird pox, and probably avian malaria. Some or all of these diseases were brought in by introduced birds and may well be the most important factor in the decline and extinction of many of these birds. Other factors adverse to the endemic avifauna are destruction of the forest for agriculture or by livestock or other ruminants, competition with introduced birds, and predation by such introduced mammals as

the mongoose, cat, and three species of rats.

The small size of many of the insular populations probably tends to limit genetic variability and capacity for adaptive response to changing conditions. With the arrival of the Hawaiians and later of white man on the islands, the environment deteriorated, and widespread extinction of the more vulnerable components of the avifauna quickly ensued.

The occurrence of palatal characters of possible significance in classifying the Drepaniidae is given in table 10. Although the skull of the finch-like genus *Psittirostra* is very much like that of a cardueline finch, this is not true to any great extent of the thin-billed drepaniids. The attenuated post-palatal processes in the thin-billed species suggest the Thraupidae or Coerebidae. On the whole, the Drepaniidae have an assemblage of skull characters of their own, but the differences involved are slight and not always constant. This is equally true of the osteological characters of the related families.

The hypotarsus of the Drepaniidae is like that of all the Passeriformes examined and shows no special resemblance to that of the Carduelinae. Similarly the angle of the jaw seems to be of no phylogenetic significance.

In most Drepaniidae the tongue is elongated and its edges curl upward and overlap, forming a tube up which nectar ascends. The edges and tip of the tongue are frayed and brush-like. This type of tubular tongue is somewhat different from that of other nectar-feeding song birds, which show many variations among themselves. In some drepaniids that do not feed on nectar, the tongue is completely tubular but in others only partially so. In members of the fruit- and seed-eating genus *Psittirostra* the tongue is only slightly or, in the heaviest-billed species, not at all tubular.

Many drepaniids, including some nectar-feeding species, have a crop or crop-like dilation of the esophagus. Although among song birds the crop is as a rule best developed in seed eaters (Ploceidae, Carduelinae, etc.), some species of the Coerebidae and, among non-passerines, hummingbirds have a crop, so its presence in the Drepaniidae cannot be considered as establishing relationship to finches.

The pattern of intestinal convolutions seems to be of no value in classifying the family Drepaniidae. The concha of the nasal vestibulum is perhaps more like that of coerebids or thraupids than that of cardueline finches. The nasal opercula are very large in nectar-feeding drepaniids and not entirely lacking in the finch-like ones. This suggests that the latter are modified honeycreepers, not true finches.

The tenth primary of the Drepaniidae is vestigial. This is one of the characters allying them to the (chiefly) American group of nine-primaried song birds. Other details of the pterylosis seem not to be of value in classifying the family.

The supposed phylogeny of the genera of the Drepaniidae is diagrammed. The most primitive genus in each subfamily contains small, arboreal forms with moderately decurved bills and tubular tongues. They feed chiefly on nectar and insects. All the more specialized insect-, nectar-, fruit-, and seed-eating genera have evolved from such forms. Some species that no longer eat nectar still have a tubular, nectar-sucking tongue like that of the more generalized drepaniids. To suggest derivation of the family from finches or heavy-billed tanagers runs counter to this evidence and to some anatomical characters.

The primitive drepaniids are perhaps most like some of the Coerebidae, but the latter may be only thin-billed Thraupidae. The anatomical characters involved are so slight and inconstant that derivation of the Drepaniidae from any of the thinner-billed American groups of nine-primaried song birds, such as the Parulidae or Icteridae, cannot be ruled out.

In the Drepaniidae, as in other birds, speciation involves gradual differentiation of geographically isolated populations. The isolation has been on different islands, but

with much secondary overlap of species so that as many as 15 occurred on a single island (Hawaii). In some species inter-island stragglers are so frequent that differentiation does not occur or is held at the racial level. The more isolated islands receive fewer stragglers, and as a result endemism is very pronounced. The larger islands have a more varied ecology than do the smaller ones. This is reflected in a richer avifauna, apparently because many species are able to survive on the larger islands by utilizing ecological niches absent on the smaller ones. Birds straggle from island to island so frequently that the relative ages of the islands of the Hawaiian group are not reflected in the composition of the bird life. In this, birds differ from more sedentary groups such as mollusks.

Adaptive radiation, the occurrence of a number of very different ecological types within a taxonomic group, is usually best illustrated by families or orders, but in the Drepaniidae it occurs within the limits of a family. Competition among similar sympatric species places a selective premium upon divergence; if suitable empty ecological niches are available adaptive radiation may result. If they are not, one or the other of two such competing species will be exterminated, or both may survive by rigid specialization for only slightly different ecological niches. In major adaptive changes the intermediate steps will as a rule not be well adapted for either the old or new ecological niches. Hence, such transitions are usually abrupt. These principles are admirably illustrated by the genus *Hemignathus*. On geologically recent, isolated archipelagos adaptive radiation is now in progress; on continents evolution is usually in the later, more stabilized stage of minor adaptations and specializations.

APPENDIX 1. NATIVE LAND AND FRESH-WATER BIRDS (EXCEPT DREPANIIDAE) OF THE HAWAIIAN ISLANDS

MARINE BIRDS range widely over the Pacific. Their distribution is controlled by other factors than those for the land birds, factors that need not concern us here.

Fresh-water birds are intermediate between oceanic birds and land birds in their ability to cross the ocean. This is particularly true of species like certain rails and ducks that frequent coastal marshes or waters, at least seasonally.

In the following list species that are more or less generally distributed throughout the main Hawaiian Islands may be unrecorded on one or two of the islands for ecological reasons or because of lack of continuous observation. Lanai, for instance, has few or no coastal lagoons. Some of the fresh-water birds like *Gallinula* are apparently unrecorded there. Since the details of such minor gaps in distribution can be found in various works (Munro, 1944; Bryan and Greenway, 1944) they are not repeated here.

Mayr (1943) has reviewed the origin of the land and fresh-water birds of the Hawaiian Islands. They seem to be derived from only 14 colonizations, of which the Drepaniidae represent one. Mayr did not include Laysan and Nihoa. They would add two more genera, *Acrocephalus* and *Porzana*, though the latter may possibly be a result of the same colonization which produced *Pennula* of the main islands. Speciation and endemism in the Hawaiian non-drepaniids are considered in the section on Speciation above and are summarized in figure 23.

ARDEIDAE

HERONS

Nycticorax nycticorax hoactli

NIGHT HERON

Generally distributed. This is the only land or fresh-water bird not even subspecifically separable from the mainland (here North American) form.

ANATIDAE

GEESE AND DUCKS

Geochen rhuax

FOSSIL GOOSE

During well-drilling operations on Hawaii some charred, fragmentary leg bones of a bird were found at a depth of several hundred feet in volcanic ash. These, the only known vertebrate fossil or subfossil remains known from the Hawaiian Islands, have been described by Wetmore (1943) as a new genus and species of goose, *Geochen rhuax*. The age of these remains is presumably Pleistocene or even early Recent.

Wetmore believes that this goose was not closely related to the living Hawaiian Goose or Nene, *Branta (Nesochen) sandvicensis*, but was a member of the subfamily Cereopsinae. The only living representative of this group is the Cape Barren Goose of the southern coast of Australia, but the presence of another extinct member, *Cnemidornis*, in New Zealand suggests that the subfamily may once have been an important element in the Pacific avifauna.

Branta sandvicensis

NENE OR HAWAIIAN GOOSE

Hawaii and (formerly) Maui (Baldwin, 1945). This goose has usually been placed in a monotypic genus, *Nesochen*, but Delacour and Mayr (1945, p. 9) refer it to *Branta*. In view of the partial loss of the webbing of the toes and other adaptations for life away from water (Miller, 1937), *Nesochen* would seem to deserve at least subgeneric status.

Anas wyvilliana

HAWAIIAN DUCK

Anas wyvilliana wyvilliana

KOLOA

Generally distributed.

Anas wyvilliana laysanensis**LAYSAN TEAL**

Laysan only, perhaps extinct. Although very distinct, it is probably justifiable to consider the Laysan Teal a race of *wyvilliana*.

Delacour and Mayr (1945) have listed both forms of this species as races of the Mallard (*Anas platyrhynchos*). While there is no doubt that *wyvilliana* was derived from *platyrhynchos*, the pronounced changes in the former, including the almost complete loss of the distinctive male plumage of the Mallard, make it preferable, in my opinion, to retain *wyvilliana* as a species.

The Mallard has occurred in the Hawaiian Islands as a straggler and has been kept in semi-captivity there, but so far as known it shows no disposition to establish itself or to cross with *wyvilliana*. Quite probably the original colonization occurred during the glacial epoch when considerable fluctuations in climate occurred, as shown by the glaciation of Mauna Kea, Hawaii, and by pollen-count data (Selling, 1948).

ACCIPITRIDAE**HAWKS****Buteo solitarius****HAWAIIAN HAWK OR IO**

Hawaii only. The absence of this hawk on the other islands (it has occurred on Maui as a straggler) is difficult to explain. Perhaps it is a chance failure of a usually solitary bird to colonize the other islands, or the smaller islands may not have sufficient area to support a successful population of such a thinly dispersed species. Neither of these suggestions is particularly convincing, yet something has restricted this hawk to Hawaii.

Mayr (1943) states that *B. solitarius* is nearest to *B. swainsoni* of western North America, but evidence to support such a definite allocation in this difficult genus seems not to have been published.

RALLIDAE**RAILS, COOTS, AND GALLINULES****Fulica americana sandwichensis****HAWAIIAN COOT**

Generally distributed.

Gallinula chloropus sandwichensis**HAWAIIAN GALLINULE**

Generally distributed. Considered by Mayr (1943) as closest to the American race of this nearly cosmopolitan species which occurs also in the western Pacific as far east as Micronesia.

Pennula ?sandwichensis millsii**HAWAII RAIL**

Hawaii only; extinct. This race is known from five mounted specimens, all formerly in the collection of the taxidermist Mills of Hilo, Hawaii.

Pennula sandwichensis sandwichensis**(?OAHU) RAIL**

Known only from one old specimen of uncertain origin in the Leiden Museum. It differs from *millsii* in minor details of coloration and probably represents an extinct race of the same species, presumably from Oahu.

Munro (1944, p. 51) thinks there is good evidence that some form of this rail existed on Molokai. It may have been present on other islands before the introduction of the mongoose, but evidently was absent from Kauai. *Pennula* may be related to *Porzanula*.

Porzanula palmeri**LAYSAN RAIL**

Laysan only. It has long been extinct on Laysan but survived until recently on Midway, where it had been introduced. There is a remote possibility that the Laysan Rail still exists on other small islands in the Hawaiian Leeward group, but probably it is totally extinct.

Porzanula has only eight primaries, the smallest number known for any bird (W. de W. Miller, 1924, p. 313). The Laysan Rail was perhaps derived from the widespread genus *Porzana*.

RECURVIROSTRIDAE**STILTS****Himantopus himantopus knudseni****HAWAIIAN STILT**

Generally distributed. Considered by Mayr (1943) as closest to the American subspecies.

STRIGIDAE

OWLS

Asio flammeus sandwichensis

PUEO OR HAWAIIAN SHORT-EARED OWL

Generally distributed. A member of a widespread Holarctic species. Probably it arrived from North America. A race also occurs on Ponape in the Caroline Islands.

MUSCICAPIDAE

THRUSHES, OLD WORLD FLY-CATCHERS, AND ALLIES

SUBFAMILY TURDINAE

THRUSHES

This subfamily is represented by one endemic genus, *Phaeornis*, apparently derived from the American solitaires of the genus *Myadestes*, as Stejneger (1889) long ago concluded and emphasized by naming the Kauai form *Phaeornis myadestina*. As some recent authors have suggested that the Polynesian *Turdus poliocephalus* is the ancestor of *Phaeornis*, I reinvestigated the question (1942) and came to the same conclusion as Stejneger.

Phaeornis obscurus

OMAO

This species had races on Hawaii (*obscurus*), Lanai (*lanaiensis*), Molokai (*rutha*), Oahu (*oahuensis*), and Kauai (*myadestina*). The Oahu race has long been extinct, and no specimens exist. The genus is unknown from Maui, but Henshaw, while on that island, was told of a bird that he believed to be this species. The Molokai race is similar to that of Lanai but separable (type and others examined).

Phaeornis palmeri

This species occurred locally on Kauai along with *P. obscurus myadestina* but in much smaller numbers. It is probably extinct.

SUBFAMILY SYLVIINAE

OLD WORLD WARBLERS

Acrocephalus familiaris familiaris

LAYSAN MILLER BIRD

Extinct.

Acrocephalus familiaris kingi

NIHOA MILLER BIRD

This bird received its common name from the fondness of the Laysan race for a locally abundant "miller" moth. The species was restricted to Laysan and Nihoa but belongs to a widespread Polynesian super-species with representatives in the Marianas, Marquesas, Society, and other islands.

SUBFAMILY MUSCICAPINAE

OLD WORLD FLYCATCHERS

Chasiempis sandwichensis

ELEPAIO

This species belongs to an endemic, monotypic genus. There are races of the species on Hawaii (*sandwichensis*), Oahu (*gayi*), and Kauai (*sclateri*). The genus is of Polynesian derivation, related to *Monarcha* and *Pomaraea*. This species is absent from Molokai, Maui, and Lanai.

MELIPHAGIDAE

AUSTRALIAN HONEYEATERS

This family is represented by two endemic genera in the Hawaiian Islands.

Chaetoptila angustipluma

This greenish bird, almost as large as a crow, was endemic to Hawaii. It was one of the first Hawaiian birds to become extinct and is known only from the type specimen, described by Peale, and from two others from the Mills Collection. *Chaetoptila* is a close relative of *Gymnomyza* of Fiji and Samoa.

Moho (Acrolocercus auctt.)

This genus had representative forms on Hawaii (*nobilis*), Molokai (*bishopi*), Oahu (*apicalis*), and Kauai (*braccatus*), while Henshaw (1902, p. 74) saw an individual of some form of this genus on Maui, where it is otherwise unknown. The Hawaii and Oahu species are extinct; the Molokai one probably is, but there are recent sight records of *braccatus*. The species of this genus are striking,

glossy, black birds often with long, twisted tail feathers and with tufts of yellow plumes used by the natives for cloaks. There is perhaps enough difference in these plumes and other details to justify treating them as four species forming a superspecies rather than as races of a single species. The Kauai form, in particular, is much duller in color than the others.

Moho bears some resemblance to the Tui (*Prothemadera*) of New Zealand, both in habits and appearance (Munro, 1944, p. 831). Closer comparison, however, suggests that *Moho* and *Chaetoptila* are more nearly related than might appear at first glance. Probably they are both descendants of a single invasion of *Gymnomyza*-like stock and the resemblance of *Moho* to *Prothemadera* is only parallelism. The presence of yellow tufts of feathers in the plumage is widespread in the Meliphagidae.

CORVIDAE

CROWS

Corvus tropicus

The Hawaiian Crow is found only on Hawaii, where it is surprisingly local. It has been assumed to be of American origin, but a careful comparison with other species of this difficult genus is needed.

SUMMARY

The predominance of the Drepaniidae among Hawaiian Passeriformes is evident from the following comparison:

	NUMBER OF GENERA	NUMBER OF OF ZOOGEO- GRAPHICAL SPECIES	NUMBER OF RECOG- NIZABLE FORMS
Drepaniidae	9	18	39
All other Passeriformes	6	7	17

APPENDIX 2. EXPLANATION OF LOGARITHMIC RATIO DIAGRAMS

RATIO DIAGRAMS of the type used in figures 8 to 10 were first employed and explained by Simpson (1941). The following brief explanation of them is adopted and in part quoted from his paper. A logarithmic graphing of ratios has two advantages:

1. On a logarithmic graph, equal relative variation is represented by equal distance. For example, the difference between the logarithms of 10 and 100 is the same as that between those of 100 and 1000, and the ratios of these two pairs of numbers is the same. In figure 8, *Loxops v. virens* is taken as the standard of comparison (ratio 1.00). The ratio of a given measurement of any of the other species to the corresponding measurement of *L. v. virens* can be read directly from the ratio scale at the bottom of the graph.

"Although the differences are thus calculated from some one standard, the resulting diagram shows not only ratios to that standard but ratios of any combinations of observations. . . . By copying this scale on

a separate slip of paper, a movable scale can be made and the diagrams have the property that if 1.00 on the ratio scale be set at any specimen (whether the standard or not), the values of the ratios of all other specimens (set on the same horizontal) to this one can at once be read on the scale."

2. Logarithmic ratio diagrams are easily constructed without computing any of the numerous ratios represented thereon. The difference between the logarithms of two numbers corresponds to the ratio of the numbers, since division is performed by subtracting logarithms. Plotting logarithms on arithmetic graph paper is equivalent to plotting antilogarithms (arithmetic numbers) on logarithmic paper, so the logarithms of the ratios are plotted directly on arithmetic paper.

The actual calculation involved in plotting the diagram of figure 8 on graph paper for one measurement (culmen length) is given in table 14.

TABLE 14

Species	Culmen Length	Logarithm of Culmen	Difference from Logarithm of Standard (<i>L. v. virens</i>)	Log Differences Divided by Scale of Graph (.00170 = 1 mm.)
<i>L. v. virens</i>	13.9 mm.	1.14301	0	0
<i>L. parva</i>	12.7	1.10380	-.03921	- 23
<i>L. sagittirostris</i>	20.7	1.31597	+.17296	+102
<i>L. maculata mana</i>	11.8	1.07188	-.07113	- 42
<i>L. c. coccinea</i>	10.4	1.01703	-.12598	- 74

TABLE 15

Ratio	Logarithm of Ratio	Difference from 0 (= Logarithm of Standard)	Difference Divided by Scale of Graph (.00170 = 1 mm.)
.90	9.95424-10	-.04576	-27 mm.
.95	9.97772-10	-.02228	-13
1.00	0	0	0
1.05	.02119	+.02119	+12
1.10	.04139	+.04139	+24
etc.			

The scale ($.00170 = 1$ mm.) was chosen by dividing the greatest deviation above and below the standard of comparison in the logarithms by the number of millimeters on standard graph paper, thus allowing the maximum expansion. The procedure is similar for the other three measurements, the same scale being used, of course, for all of them.

To make a ratio scale for such a diagram,

ratios selected at suitable intervals are treated in exactly the same way as a series of measurements. The standard of comparison will have a ratio of 1 (logarithm 0), so again the deviations above and below the standard are found and plotted on the graph, using the same scale as for the measurements.

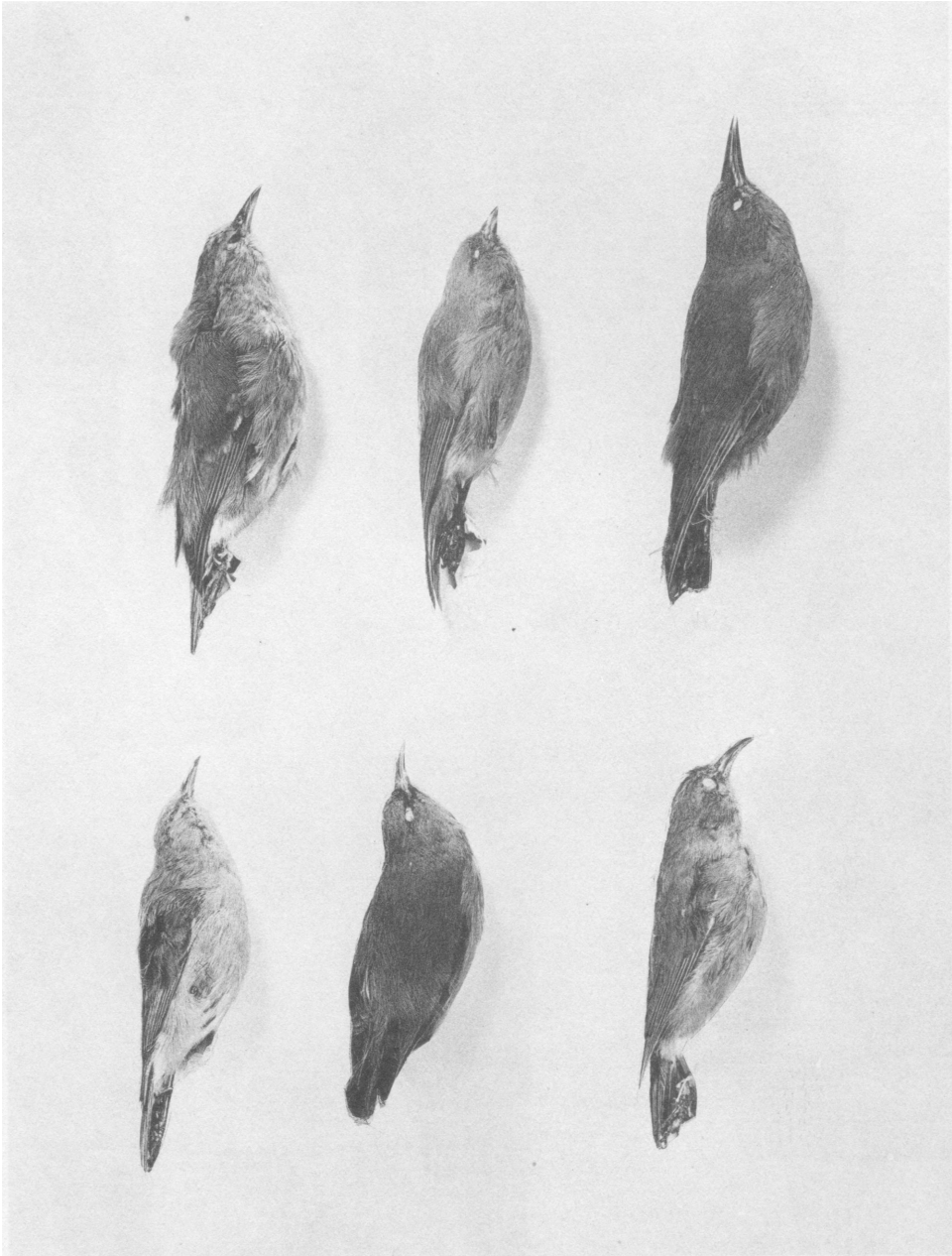
The procedure for a few sample ratios is given in table 15.

LITERATURE CITED

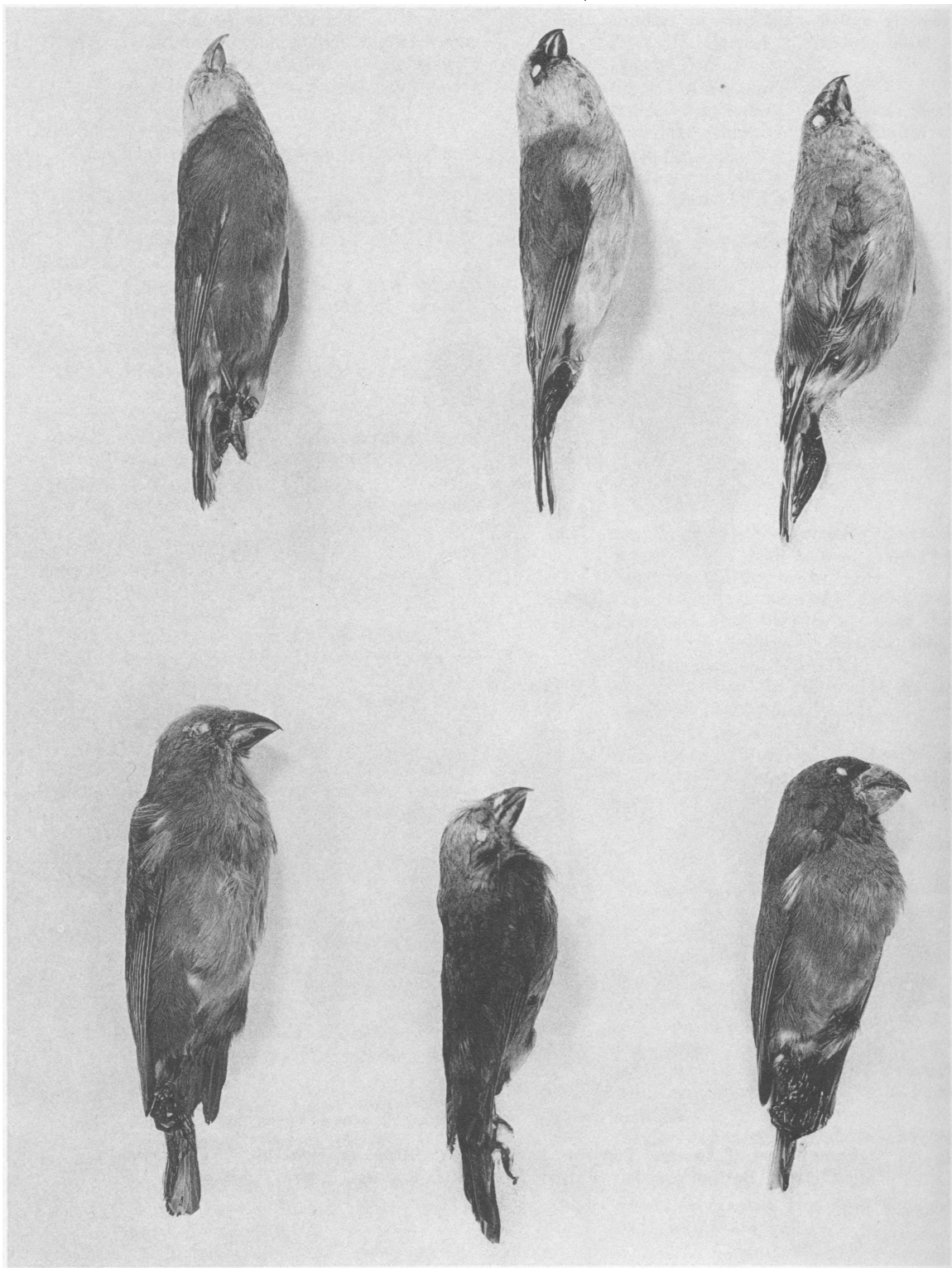
- AMADON, DEAN
 1942. Relationships of the Hawaiian avifauna. *Condor*, vol. 44, pp. 280-281.
 1943. Experiences with the great horned owl. *Univ. of State of New York Bull. to Schools*, vol. 29, pp. 255-258.
 1944. Sanford Ballard Dole: early Hawaiian ornithologist. *Elepaio*, Honolulu Audubon Soc., vol. 5, pp. 12-13.
 1947. Ecology and the evolution of some Hawaiian birds. *Evolution*, vol. 1, pp. 63-68.
- BALDWIN, PAUL H.
 1940. Environmental relationships of birds in the Kilauea section, Hawaii National Park. *Natl. Park Serv., Hawaii Natl. Park* (mimeographed).
 1944. Birds of Hawaii National Park. *Audubon Mag.*, vol. 46, pp. 147-154.
 1945. The Hawaiian goose, its distribution and reduction in numbers. *Condor*, vol. 47, pp. 27-37.
 1948. Discovery of tapeworm parasites in three genera of Hawaiian honey suckers. *Elepaio*, Honolulu Audubon Soc., vol. 9, p. 29.
- BANGS, OUTRAM
 1910. Unrecorded specimens of two rare Hawaiian birds. *Proc. Biol. Soc. Washington*, vol. 23, pp. 67-69.
- BARBOUR, THOMAS, AND WILLIAM L. ENGELS
 1942. Two interesting new snakes. *Proc. New England Zool. Club*, vol. 20, pp. 101-104.
- BEECHER, WILLIAM J.
 [MS.] On the relationships of the American nine-primaried passerines.
- BENÉ, FRANK
 1946. The feeding and related behavior of hummingbirds. *Mem. Boston Soc. Nat. Hist.*, vol. 9, pp. 395-478.
- BLANCHARD, BARBARA D.
 1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. California Publ. Zool.*, vol. 46, pp. 1-178.
- BOURKE, P. A., AND A. F. AUSTIN
 1947. The Atherton Tablelands and its avifauna. *Emu*, vol. 47, pp. 87-116.
- BRYAN, E. H., JR., AND J. C. GREENWAY, JR.
 1944. Contribution to the ornithology of the Hawaiian Islands. *Bull. Mus. Comp. Zool.*, vol. 94, no. 2, pp. 77-142.
- BRYAN, WILLIAM ALANSON
 1905a. Notes on the birds of the Waianae Mountains. *Occas. Papers Bishop Mus.*, vol. 2, pp. 229-241.
 1905b. Description of the nest and eggs of *Chlorodrepanis virens* (Gmel.). *Ibid.*, vol. 2, pp. 243-244.
 1905c. Two undescribed nests and an egg of a Hawaiian bird. *Ibid.*, vol. 2, pp. 251-252.
 1905d. Nest and eggs of *Heterorhynchus wilsoni* Roths. *Ibid.*, vol. 2, pp. 253-254.
 1908. Some birds of Molokai. *Ibid.*, vol. 4, pp. 133-176.
- BRYAN, WILLIAM ALANSON, AND ALVIN SEALE
 1901. Notes on the birds of Kauai. *Occas. Papers Bishop Mus.*, vol. 1, pp. 129-137.
- CAMPBELL, LOUIS W.
 1948. Nest-building adaptability of the Eastern Red-wing. *Wilson Bull.*, vol. 60 p. 244.
- CHAPIN, JAMES P.
 1916. Four new birds from the Belgian Congo. *Bull. Amer. Mus. Nat. Hist.*, vol. 35, pp. 23-29.
- CLANCEY, P. A.
 1948. Seasonal bill variation in tree sparrow [*Passer montanus*]. *Brit. Birds*, vol. 41, pp. 115-116.
- CLARK, HUBERT LYMAN
 1912. Notes on the Laysan finch. *Auk*, vol. 29, pp. 166-168.
- CUSHING, JOHN E., JR.
 1944. The relationships of non-heritable food habits to evolution. *Condor*, vol. 46, pp. 265-271.
- DAMMERMAN, K. W.
 1948. The fauna of Krakatau 1883-1933. *Verhandel. K. Nederlandsche Akad. Wetensch. afd. Naturk.*, sect. 20, vol. 44, pp. 1-594.
- DAVIS, D. DWIGHT
 1949. Comparative anatomy and the evolution of vertebrates. In Jepsen, Glenn L., Ernst Mayr, and George Gaylord Simpson (editors), *Genetics, paleontology and evolution*. Princeton, Princeton University Press, chap. 5.
- DELACOUR, JEAN
 1944. A revision of the family Nectariniidae (sunbirds). *Zoologica*, vol. 29, pp. 17-38.
- DELACOUR, JEAN, AND ERNST MAYR
 1945. The family Anatidae. *Wilson Bull.*, vol. 57, pp. 1-55.

- DITMARS, RAYMOND LEE
1933. Reptiles of the world. (New edition.) New York, Macmillan and Co.
- DOBRIN, M. B., BEAUREGARD PERKINS, JR., AND B. L. SNAVELY
1949. Subsurface constitution of Bikini Atoll as indicated by a seismic-refraction survey. Bull. Geol. Soc. Amer., vol. 60, pp. 807-828.
- DWIGHT, JONATHAN, JR.
1900. The sequence of plumages and moults of the passerine birds of New York. Ann. New York Acad. Sci., vol. 13, pp. 73-360.
- ESKEY, C. R.
1934. Epidemiological study of plague in the Hawaiian Islands. Public Health Bull., no. 213, Washington, D. C.
- FAGERLUND, GUNNAR O., AND ARTHUR L. MITCHELL
1944. A checklist of the plants of Hawaii National Park. Natl. Park Serv., Hawaii Natl. Park Nat. Hist. Bull. 9 (mimeographed).
- FISHER, HARVEY I.
1947. Bibliography of Hawaiian birds since 1890. Auk, vol. 64, pp. 78-97.
- FISHER, WALTER K.
1903. Notes on the birds peculiar to Laysan Island, Hawaiian group. Auk, vol. 20, pp. 384-397.
1906. Birds of Laysan and the Leeward Islands, Hawaiian group. Bull. U. S. Fish Comm. for 1903, vol. 23, pp. 767-807.
- GADOW, HANS
1890-1899. In Wilson, Scott B., and A. H. Evans, Aves Hawaiienses; the birds of the Sandwich Islands. London, R. H. Porter.
- GARDNER, LEON L.
1925. The adaptive modifications and the taxonomic value of the tongue in birds. Proc. U. S. Natl. Mus., vol. 67, pp. 1-49.
- GREENWAY, JAMES C., JR.
1939. *Dysmorodrepanis munroi* probably not a valid form. Auk, vol. 56, pp. 479-480.
- *GULICK, ADDISON
1932. Biological peculiarities of oceanic islands. Quart. Rev. Biol., vol. 7, pp. 405-427.
- HATT, ROBERT T., ET AL.
1948. Island life: a study of the land vertebrates of the islands of eastern Lake Michigan. Cranbrook Inst. of Sci. Bull. 27, xi+179 pp.
- HENSHAW, H. W.
1902. Birds of the Hawaiian Islands. Honolulu, Thomas G. Thrum.
- HUXLEY, JULIAN
1943. Evolution, the modern synthesis. New York, Harper and Brothers.
- KOSSWIG, CURT
1948. Genetische Beiträge zur Präadaptations-theorie. Rev. Fac. Sci. Univ. Istanbul, ser. B., vol. 13, pp. 176-209.
- LACK, DAVID
*1942. Ecological features of the bird faunas of British small islands. Jour. Animal Ecol., vol. 11, pp. 9-36.
*1944. Ecological aspects of species formation in passerine birds. Ibis, vol. 86, pp. 260-286.
1945. The Galapagos finches (Geospizinae). Occas. Papers California Acad. Sci., no. 21.
1947. Darwin's finches. New York; Cambridge, England, Macmillan and Co.
- LAWRENCE, LOUISE DE KIRILINE
1949. Notes on nesting pigeon hawks at Pimisi Bay, Ontario. Wilson Bull., vol. 61, pp. 15-25.
- LUCAS, FREDERIC A.
1894. Notes on the anatomy and affinities of the Coerebidae and other American birds. Proc. U. S. Natl. Mus., vol. 17, pp. 299-312.
1896. The taxonomic value of the tongue of birds. Auk, vol. 13, pp. 109-115.
- MAYR, ERNST
1940. The origin and the history of the bird fauna of Polynesia. Proc. Sixth Pacific Sci. Congr., vol. 4, pp. 197-216.
1942. Systematics and the origin of species. New York, Columbia University Press.
1943. The zoogeographic position of the Hawaiian Islands. Condor, vol. 45, pp. 45-48.
*1947. Ecological factors in speciation. Evolution, vol. 1, pp. 263-288.
- MAYR, ERNST, AND DEAN AMADON
1947. A review of the Dicaeidae. Amer. Mus. Novitates, no. 1360, pp. 1-32.
- MEISE, WILHELM
1938. Fortschritte der Ornithologischen Systematik seit 1920. Proc. 8th Internatl. Ornith. Congr. Oxford, pp. 49-189.
- MILLER, ALDEN H.
1931. Systematic revision and natural history of the American shrikes (*Lanius*). Univ. California Publ. Zool., vol. 38, pp. 11-242.
1937. Structural modifications in the Hawaiian Goose (*Nesochen sandvicensis*), a study in adaptive evolution. *Ibid.*, vol. 42, pp. 1-80.

1941. Speciation in the avian genus *Junco*. *Ibid.*, vol. 44, pp. 173-434.
1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. *Amer. Nat.*, vol. 76, pp. 25-35.
- MILLER, WALDRON DE W.
1924. Further notes on *Psittosis*. *Bull. Amer. Mus. Nat. Hist.*, vol. 50, pp. 305-331.
- MORDVILKO, A.
1937. Artbildung und Evolution. Teil II. *Biologia Generalis*, vol. 12, pp. 271-295.
- MOREAU, R. E.
1948. Ecological isolation in a rich tropical avifauna. *Jour. Animal Ecol.*, vol. 17, pp. 113-126.
- MUNRO, GEORGE C.
1944. *Birds of Hawaii*. Honolulu, Tongg Publishing Co.
- NEWTON, ALFRED
1892. Ornithology of the Sandwich Isles. *Nature*, vol. 45, pp. 465-469.
- PARKER, W. K.
1879. On the skull of the aegithognathous birds, part II. *Trans. Zool. Soc. London*, vol. 10, pp. 251-314.
- PERKINS, R. C. L.
1893. Notes on collecting in Kona, Hawaii. *Ibis*, pp. 101-112.
1903. *Fauna Hawaiiensis (Vertebrata)*. Cambridge, Cambridge University Press, vol. 1, pt. 4, pp. 365-466.
1913. *Fauna Hawaiiensis (Introduction)*. Cambridge, Cambridge University Press, vol. 1, pt. 6, pp. xv-ccxxviii.
- PORSCH, OTTO
1930. Kritische Quellenstudien über Blumenbesuch durch Vögel. V. *Biologia Generalis*, vol. 6, pp. 133-246.
- RICHARDSON, FRANK
1942. Adaptive modifications for tree-trunk foraging in birds. *Univ. California Publ. Zool.*, vol. 46, pp. 317-368.
1949. The status of native land birds on Molokai, Hawaiian Islands. *Pacific Sci.*, vol. 3, pp. 226-230.
- ROTHSCHILD, WALTER
1893-1900. The avifauna of Laysan and the Hawaiian possessions. London, R. H. Porter.
- SCLATER, P. L.
1871. Remarks on the avifauna of the Sandwich Islands. *Ibis*, pp. 356-362.
- SEALE, ALVIN
1900. Field notes on the birds of Oahu, H. I. *Occas. Papers Bishop Mus.*, vol. 1, no. 2, pp. 33-46.
- SELLING, OLOF H.
1948. Studies in Hawaiian pollen statistics. Part III. Bernice P. Bishop Museum, Special Publ. 39.
- SIMPSON, GEORGE GAYLORD
1941. Large Pleistocene felines of North America. *Amer. Mus. Novitates*, no. 1136, pp. 1-27.
1945. *Tempo and mode in evolution*. New York, Columbia University Press.
- STEARNS, HAROLD T.
1946. Geology of the Hawaiian Islands. *Terr. Hawaii, Div. Hydrography Bull.* 8.
- STEJNEGER, LEONHARD
1889. Notes on a third collection of birds made in Kauai, Hawaiian Islands, by Valdemar Knudsen. *Proc. U. S. Natl. Mus.*, vol. 12, pp. 377-386.
- STRESEMANN, ERWIN
1927-1934. *Sauropsida: Aves*. In Kükenthal and Krumbach, *Handbuch der Zoologie*. Berlin, Walter de Gruyter, vol. 7, 2d half.
- SUSHKIN, PETER P.
1927. On the anatomy and classification of the weaver-birds. *Bull. Amer. Mus. Nat. Hist.*, vol. 57, pp. 1-32.
- 1929a. On some peculiarities of adaptive radiation presented by insular fauna. *Verhandl. VI Internatl. Ornith. Kongr. Kopenhagen*, pp. 375-378.
- 1929b. On the systematic position of the Drepaniidae. *Ibid.*, pp. 379-381.
- SUTTON, GEORGE MIKSCHE
1935. The juvenal plumage and postjuvenal molt in several species of Michigan sparrows. *Cranbrook Inst. Sci. Bull.* 3, pp. 1-36.
- VANDERBILT, GEORGE, AND RODOLPHE MEYER DESCHAUENSEE
1941. Zoological results of the Vanderbilt Nihoa expedition, I. *Notulae Naturae*, no. 80, pp. 1-14.
- WETMORE, ALEXANDER
1943. An extinct goose from the island of Hawaii. *Condor*, vol. 45, pp. 146-148.
- WILSON, SCOTT B., AND A. H. EVANS
1890-1899. *Aves Hawaiienses: the birds of the Sandwich Islands (with supplements by Hans Gadow)*. London, R. H. Porter.
- WRIGHT, SEWALL
1945. *Tempo and mode in evolution: a critical review*. *Ecology*, vol. 26, pp. 415-419.
- ZIMMERMAN, ELWOOD C.
1948. *Insects of Hawaii*. Honolulu, University of Hawaii Press, vol. 1.



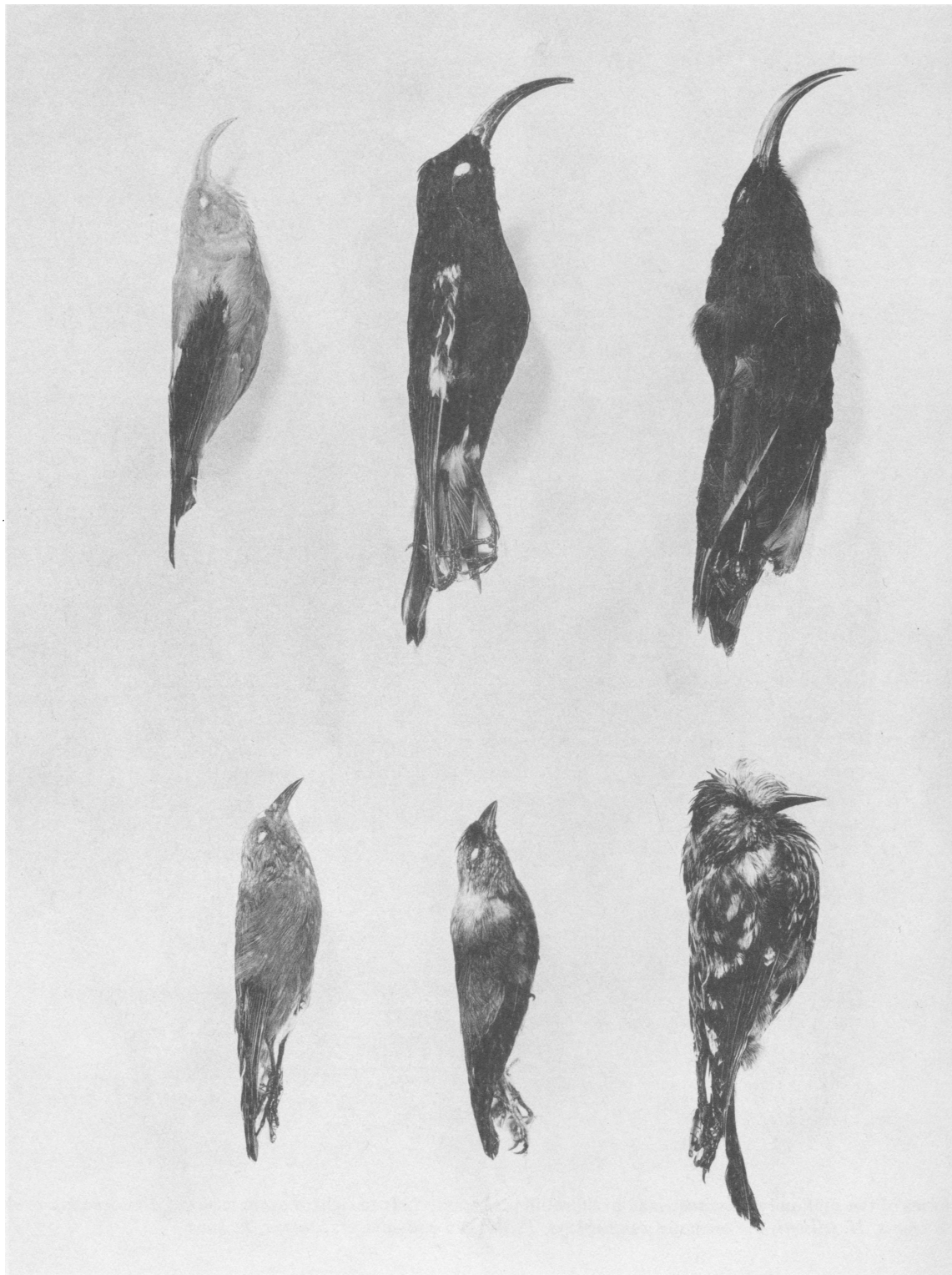
Some forms of *Loxops*. Top row, left to right: *Loxops m. maculata*, *L. c. coccinea*, *L. sagittirostris*. Bottom row, left to right: *L. parva*, *L. v. virens*, *L. virens stejnegeri*



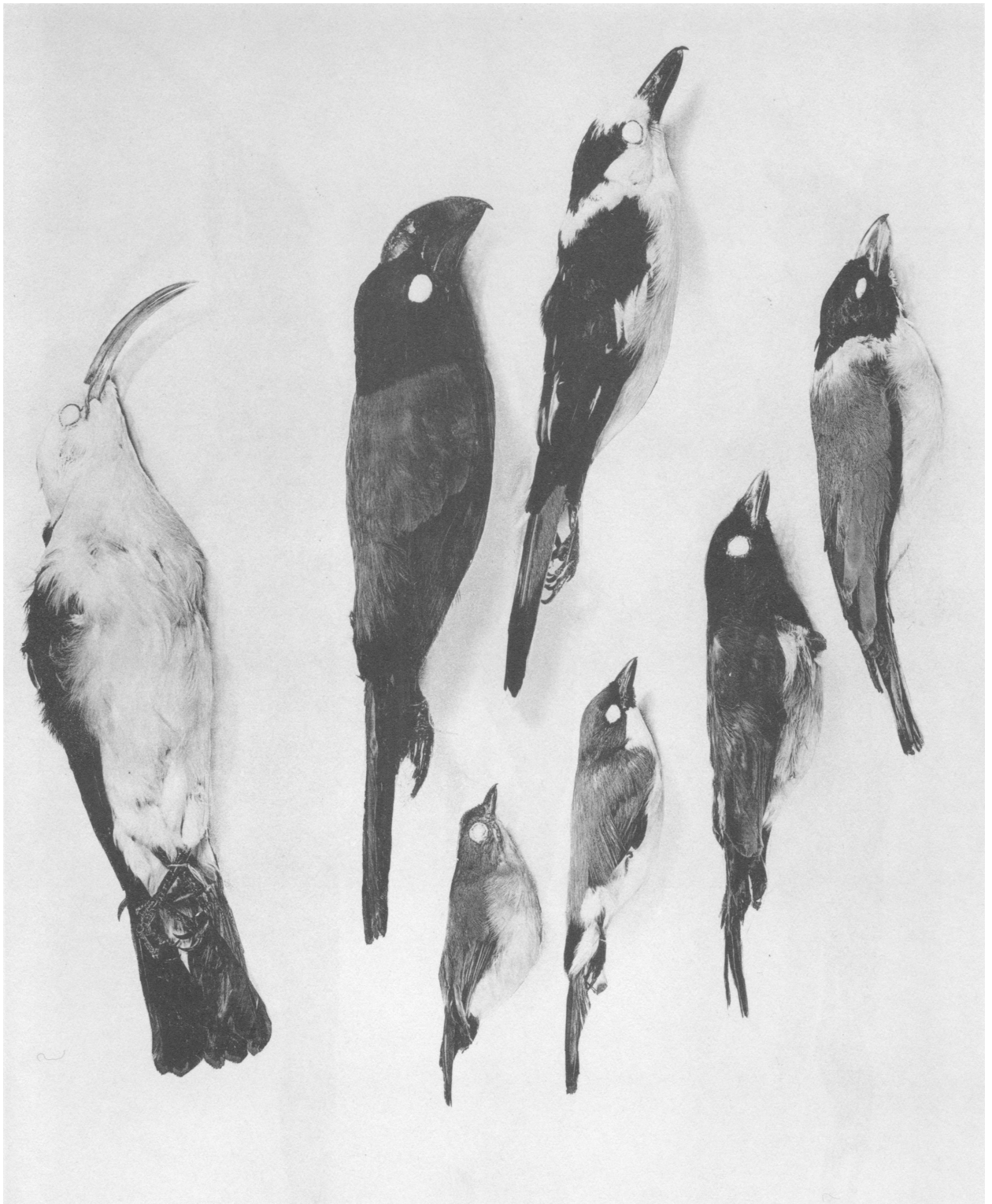
Species of *Psittirostra* (males). Top row, left to right: *P. psittacea*, *P. bailleui*, *P. cantans*. Bottom row, left to right: *P. palmeri*, *P. flaviceps* (type), *P. kona*



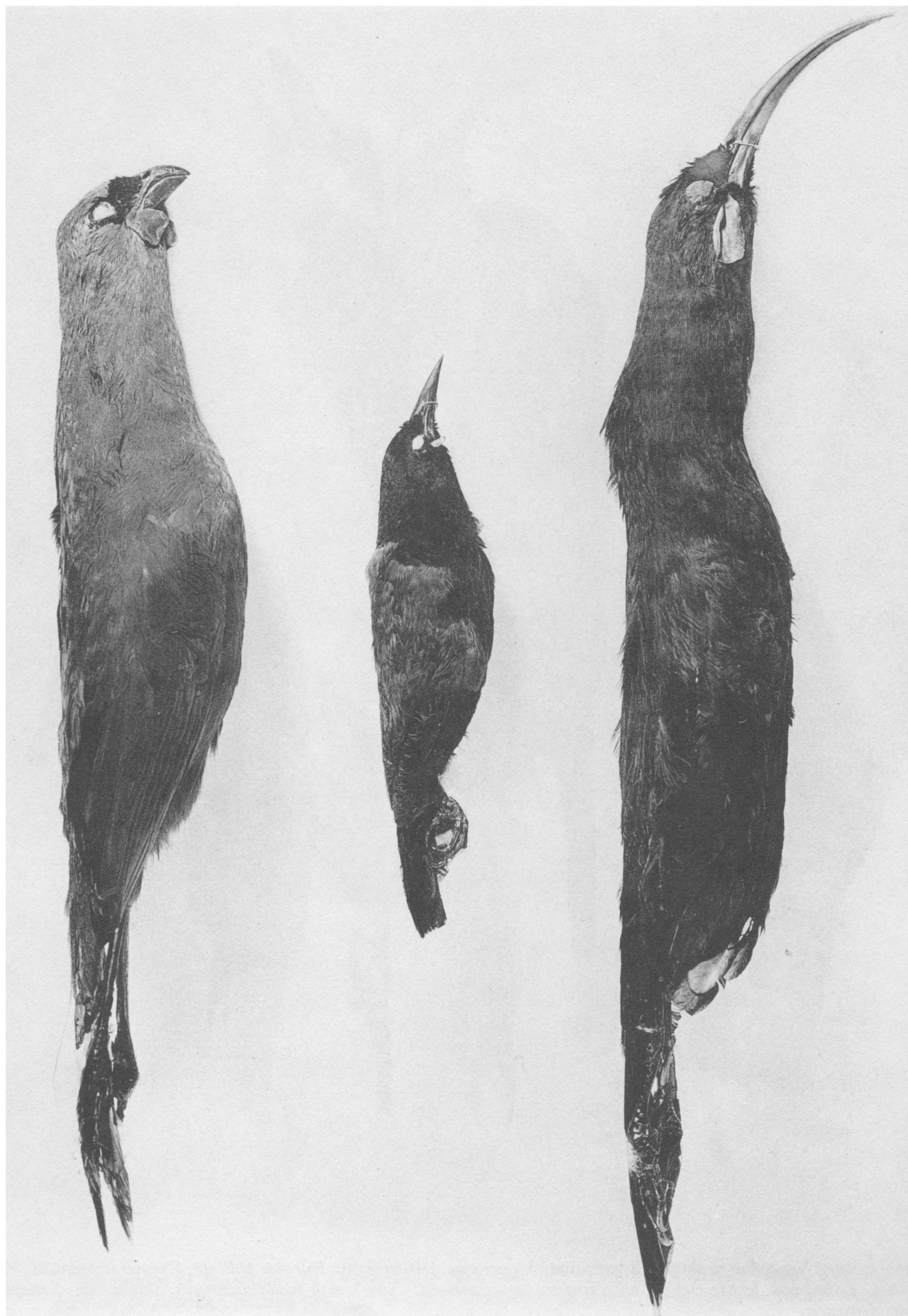
Some forms of the subfamily Psittirostrinae to show bill gradation. Left to right: *Loxops v. virens*, *Hemignathus o. obscurus*, *H. lucidus affinis*, *H. wilsoni*, *Pseudonestor xanthophrys*, *Psittirostra psittacea*, *P. cantans*, *P. kona*



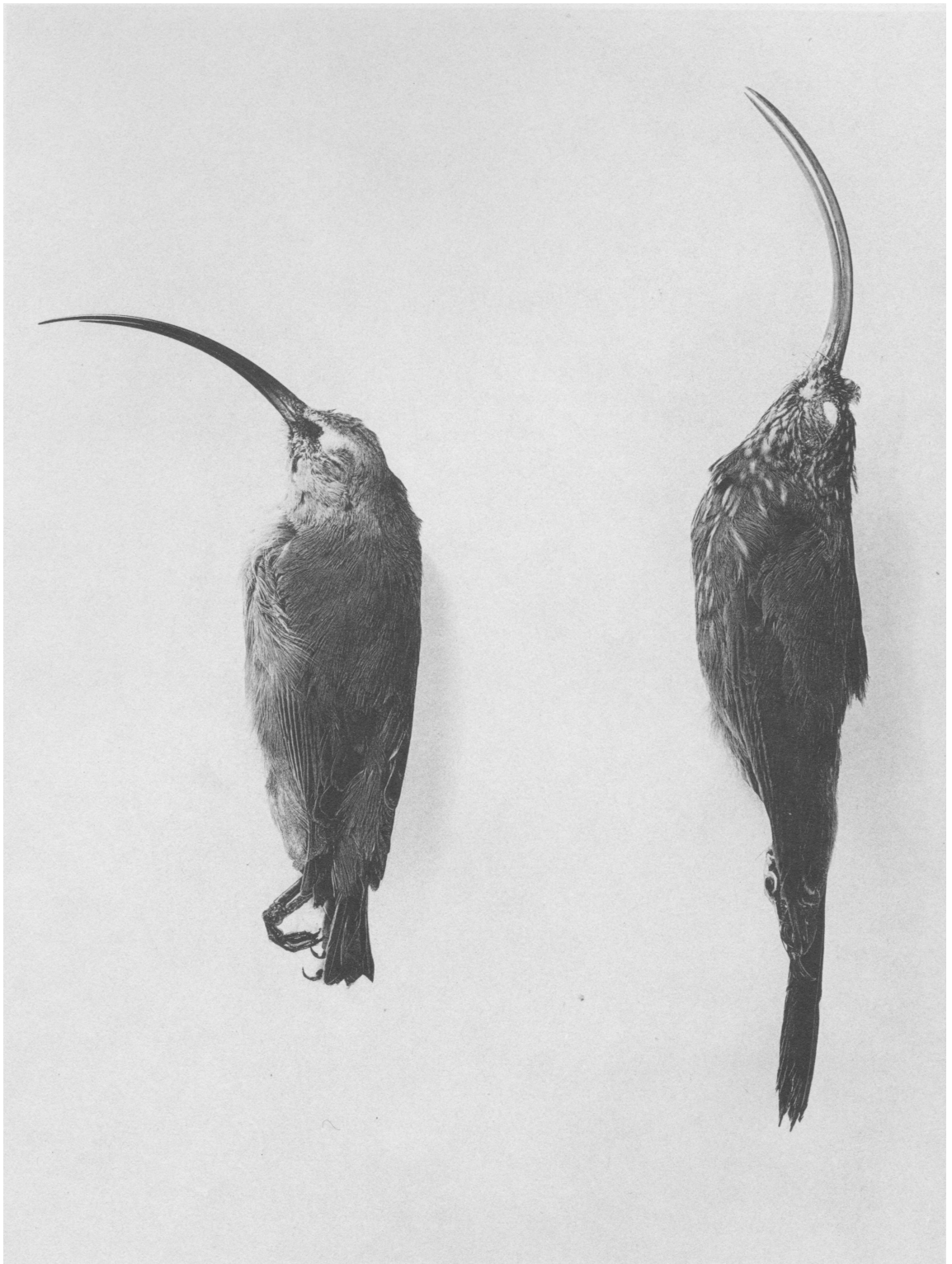
The species of the subfamily Drepaniinae. Top row, left to right: *Vestiaria coccinea*, *Drepanis pacifica*, *D. funerea*. Bottom row, left to right: *Himatione sanguinea*, *Ciridops anna*, *Palmeria dolei*



Some species of Vangidae to show bill variation. Upper row, left to right: *Falculea palliata*, *Euryceros prevostii*, *Vanga curvirostris*. Lower row, left to right: *Calicalicus madagascariensis*, *Cyanolanius madagascarinus*, *Shetba rufa*, *Xenopicrostris xenopicrostris*



The three species of the Callaeidae to show bill variation. Left to right: *Callaeas cinerea*, *Philesturnus carunculata*, *Neomorpha* [= *Heteralocha*] *acutirostris* (female)



Convergence in bills of *Hemignathus procerus* (Drepaniidae), left, and *Campylorhamphus trochilirostris* (Dendrocolaptidae), right