

THE CONDOR

VOLUME 45

MARCH-APRIL, 1943

NUMBER 2

THE ZOOGEOGRAPHIC POSITION OF THE HAWAIIAN ISLANDS

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Islands offer a special problem to the zoogeographer. As long as they are small and not too far offshore, they can safely be included in the same zoogeographic region with the nearest mainland. Doubts, however, arise in regard to the larger and more isolated islands. Most of the birds of New Zealand, for example, apparently arrived there from Australia. But some of the endemics are so unique and the unchanged Australian element is so small, that it seems hardly justified to include New Zealand in the Australian Region. The same is true for Madagascar. In addition to an unquestionable African element the bird fauna of this island has a large endemic element (including eight families) and a surprisingly large Oriental element (Rand, Bull. Amer. Mus. Nat Hist., 72, 1936:294-299). An island with such a faunal composition obviously cannot be included with the Ethiopian Region, as strictly defined.

Another island group which causes difficulties, at least to the ornithologist, is the Hawaiian Archipelago. For about one hundred years zoogeographers have associated these islands with Polynesia, apparently for reasons of geographical position and because the native humans are Polynesians. The fauna was practically unknown at the time when this classification was first proposed. In more formal zoogeographic studies the archipelago was either included in the "Polynesian Subregion of the Australian Region" or it was accorded the rank of an "Hawaiian Subregion," a course which I followed in my recent study of the borders of the Polynesian Subregion (Proc. Sixth Pac. Sci. Congr. (1939), 4, 1941:132-133).

Since then I have made a more thorough analysis of the Hawaiian bird fauna and have found that its relationship with the Polynesian fauna is slight indeed. The total number of species of native Hawaiian land birds is open to doubt, since many of them are geographic representatives of each other and are considered full species by some authors, subspecies by others. There is, however, little doubt that these birds owe their origin to 14 separate invasions. These invasions are the following, here listed according to their probable age with indication of relationships and sources:

Endemic family

- (1) Drepaniidae; related to cardueline finches or tanagers (American or Palearctic).

Endemic genera

- (2) *Pennula*, rail; relationship unknown.
- (3) *Moho*, *Chaetoptila*—honeyeaters; related to *Amoromyza* and other honeyeaters (Australasian).
- (4a) *Phaeornis*, thrush; related to *Myadestes* (American).
- (4b) *Chasiempsis*, flycatcher; related to the *Monarcha* group (*Pomarea*, *Mayrornis*, etc.) (Polynesian).
- (4c) *Nesochen*, goose; related to *Branta* (American).

Endemic species

- (5a) *Corvus tropicus*, crow; related to continental *Corvus* (Holarctic).
 (5b) *Buteo solitarius*, hawk; related to *Buteo swainsoni* (American).
 (5c) *Anas wyvilliana*, duck; related to *Anas platyrhynchos* (Holarctic).

Endemic subspecies

- (6a) *Asio flammeus sandwichensis*, Short-eared Owl (Holarctic).
 (6b) *Himantopus himantopus knudseni*, Stilt (American).
 (6c) *Gallinula chloropus sandwichensis*, Waterhen or Gallinule (American).
 (6d) *Fulica americana alai*, Coot (American).

Not endemic

- (7) *Nycticorax nycticorax hoactli*, Black-crowned Night Heron (American).

THE TAXONOMIC POSITION OF SOME OF THE HAWAIIAN ENDEMICIS

The reliability of zoogeographic conclusions depends to a large extent on the soundness of the taxonomic work carried out on the groups studied. It is, therefore, of primary importance to determine the taxonomic position and nearest relatives of the Hawaiian endemics. There is no difficulty in regard to 7, 6d, 5b, and 4c of the preceding list; they are unquestionable American elements. The species to which 6b and 6c belong are widespread, but the endemic Hawaiian subspecies are closer to the American than to the Eurasian forms. One glance at the map is sufficient to convince one that the Holarctic immigrants (Drepaniidae, *Corvus*, *Anas*, *Asio*) probably also came from North America, since it is considerably closer to Hawaii than is Asia. The Hawaiian thrushes (*Phaeornis*) are descendants of the American *Myadestes* (Amadon, Condor, 44, 1942:280).

The taxonomic position of the Hawaiian Flightless Rail (*Pennula*) is and will probably remain doubtful. This genus has lost all distinctive characters and is now merely a nondescript-looking, small, brownish rail with a reduced wing. It is possibly related to the Polynesian *Aphanolimnas-Porzanoidea-Nesophylax* stock, but it seems equally possible that it is a descendant of one of the genera of Holarctic rails (*Porzana*, *Rallus*).

The Hawaiian Crow has certain peculiar characters that have appeared repeatedly in island forms of the genus *Corvus*. (Compare, for example, *C. jamaicensis* with *C. ossifragus*, and *C. fuscicapillus* with *C. validus*.) The plumage has lost its gloss and the individual feathers tend to be looser, more decomposed. The deep bill and the graduated tail suggest that the raven might be its nearest relative on the American mainland. However, according to Peale, the voice resembles that of the Fish Crow (*C. ossifragus*). North America is almost certainly the home of the ancestor of the Hawaiian Crow, even though the exact ancestral species may be in doubt.

All the genera and families mentioned up to now are represented in Hawaii by only one or two species. All of them together do not add up to the number by which the single family Drepaniidae is represented on the Hawaiian Islands. (*Drepanis* comes from the Greek word *δρεπανη*, the sickle. The latinized stem of this word is drepani and by adding the family ending -idae, we get Drepaniidae. Gadow used the spelling Drepanididae, Sushkin Drepanidae; neither one seems to be formed correctly.) The exact determination of the relationship of this diversified family is obviously of paramount importance. This group has had a tortuous taxonomic history. The genera belonging to it were originally scattered among the Fringillidae, Dicaeidae, Nectariniidae and Meliphagidae. Gadow (in Wilson and Evans, *Aves Hawaiiensis*, 1891-1899:219-249) finally united them in the family Drepanididae, on the insistence of the field naturalist Perkins, whose observations of live birds had convinced him that the thick-billed and long-billed forms were closely related. Gadow concluded that they were more

closely related to the Coerebidae than to the Tanagridae, but he did not make a very good case for this assumption since he did not compare them with typical tanagers. Sushkin (Verh. VI Int. Ornith. Kongr., 1929:379), on the other hand, presented some seemingly strong arguments in favor of a cardueline relationship. Birds like the goldfinches, purple finches, pine grosbeaks and crossbills would, according to him, be the nearest relatives of the Drepaniidae. Sushkin, however, fails to answer some of Gadow's objections against a cardueline relationship (nasal apertures, crop, etc.) and it seems, therefore, as if the last word had not yet been said. So much is certain that America or Northern Asia must be the home of the ancestors of the Drepaniidae, since tanagers as well as cardueline finches are entirely absent from Polynesia and from the Australian-Papuan Region.

TIME OF SETTLEMENT

The Hawaiian fauna has all the earmarks of that of an oceanic island. There is not a single serious modern student (I use the term *serious* advisedly) who believes in the former existence of land bridges between America and Hawaii, or between Polynesia and Hawaii. Oceanic islands are colonized at different times by accidental stragglers. The different degree of distinctness which the descendants of the bird settlers on Hawaii have attained can be considered as irrefutable proof for the fact that they did not reach the islands simultaneously.

FAUNAL ORIGIN OF THE HAWAIIAN BIRDS

Summary

American: 4a, 4c, 5b, 6b, 6c, 6d, 7.....	7
(numbers refer to preceding tabulation)	
Holarctic: 1, 5a, 5c, 6a	4
Polynesian: 3, 4b	2
Unknown: 2	1
Total	14

Eliminating the single doubtful element (*Pennula*), we find that eleven of the thirteen colonizations of Hawaiian birds probably came from North America and only two from Polynesia (Honeyeaters, *Chasiempsis*). All non-passerine immigrants came from America, whereas the five colonizations of song birds are rather evenly divided (2 from Polynesia, 3 from America). Both Polynesian colonizations must be of considerable antiquity, since one of them produced an endemic genus and the other evolved even into two endemic genera (*Moho*, *Chaetoptila*). The oldest and most diversified group of Hawaiian birds, the Drepaniidae, has branched out into about 12 genera, 22 species and a total of 42 recognizable species and subspecies.

THE ZOOGEOGRAPHIC POSITION OF HAWAII

It is self-evident from the preceding remarks that the Hawaiian avifauna shows an overwhelming preponderance of North American, that is, Holarctic elements. The Polynesian element consists merely of one monotypic species of honeyeaters (*Chaetoptila angustipluma*), of one superspecies of honeyeaters (*Moho nobilis*), of one polytypic species of Old World flycatchers (*Chasiempsis sandvicensis*), and possibly of a single polytypic species of rails (*Pennula sandwichensis*). The American or Holarctic element consists of at least 32 species or superspecies. On this basis the Hawaiian Islands should be included with the Nearctic Region, in fact a case might even be made for including them in the next "A.O.U. Check-list"! However, it seems that the case

of the birds is unique. All the workers on plants, insects, arachnids, and mollusks agree that the Hawaiian fauna of these groups is overwhelmingly Polynesian. It will, therefore, be wisest to evaluate the ornithological data in conjunction with the evidence from all the other groups, and to associate the Hawaiian Islands with the Australian Region, provided one believes at all in the principle of zoogeographic regions. There is, of course, a growing school of students who deny the validity of zoogeographic regions (see Dunn, *Science*, 56, 1922:336-338, for an early reference). They claim that there are faunas, but not regions. They say that one can speak of Nearctic and Palearctic faunas, but not of Palearctic or Nearctic regions. This is true for continents but even truer for islands.

I would now like to revert to the discussion at the beginning of this paper. Should the West Indies be included with the Neotropical or with the Holarctic Region, should Madagascar be associated with the Ethiopian or with the Oriental Region, should Celebes or New Guinea be included with the Oriental or with the Australian Region, or should perhaps all of these islands be raised to the rank of separate regions, in addition to New Zealand and perhaps Hawaii? In each case, no decisive answer can be given. One can prepare a faunal analysis of all these islands but it shows in each case that the fauna is very heterogeneous. The faunas of these islands consist of a strong endemic element, as well as of immigrant components of various derivation. The same is true for all continental regions that are geographically intermediate between other major continents, as for example North America or the East Indies. A faunal analysis will permit in such cases a much more accurate representation of facts than a regional analysis. Most of the "regions" of the regional zoogeographer coincide anyhow more or less with the major geographic subdivisions of the earth. To say that the bird fauna of North America consists of 23 per cent Neotropical, 46 per cent Nearctic, and 31 per cent Palearctic elements gives a much more accurate picture of the composition of its fauna than to say that the Nearctic Subregion is part of the Holarctic Region. The time seems to have come to revise our zoogeographic classifications on the basis of this new concept. Its application by Stegmann (*Faune d. l' URSS, Oiseaux*, vol. 1, no. 2, 1938) to the birds of the Palearctic Region and by Stresemann (*Jour. für Ornith.*, 87, 1939:312-425) to the birds of Celebes has been extremely fruitful.

American Museum of Natural History, January 21, 1943.