Mechanisms of major evolutionary change have remained one of the more vexing problems in evolutionary biology. The long time periods associated with their operation preclude the use of experiments and direct observations for the elucidation of the mechanisms underlying transspecific changes. Paleontologists have supplied most of the direct observations of major phyletic evolution in plants and animals, but they have been severely limited in their efforts to clarify the associated evolutionary mechanisms because of the nature of the fossil record. Evolutionists are restricted to analogies and assumptions as the main bases for the formulation of theories explaining large evolutionary changes. Most earlier students assumed that evolution of new taxa or of new complex adaptive features resulted from some type of saltation; hence they believed that the mechanisms of transpecific evolution differed from those acting at the species level. They also believed that the known methods of microevolution could not explain the "fundamental differences" associated with the origin of a new complex adaptation or the rise of a new major taxon. These views mirrored the large gaps in the known fossil record at that time and still undiscovered or inadequately studied adaptations among living organisms. With the development of the synthetic theory of evolution beginning in the 1930's, many workers claimed that major evolutionary change occurred by the same mechanisms responsible for microevolutionary change at or below the species level. This change of interpretation stemmed from the better known fossil record with gaps being nearly obliterated in several groups (e.g., the mammals) and from the continued failure to discover special transspecific mechanisms of evolution. Differences between microevolution and macroevolution were held to be quantitative rather than qualitative. Simpson (1944, 1953), who was largely instrumental in establishing the belief that macroevolution and microevolution constitute a continuum of change, showed that the events and changes observed in the fossil record are in harmony with this assumption.

Schaeffer and Hecht (1965) reviewed many of the recent studies based on this belief as well as some of the noteworthy objections to the synthetic theory. They and the other contributors to a symposium on "The origin of higher levels of organization" (Systematic Zoology, volume 14(4), 1965) developed their ideas on the basic assumption that the microevolution and macroevolution continuum is indeed correct. However, a careful review of this symposium and much other recent literature in which the authors advocate the same idea reveals very little supporting documentation for this assumption at the critical species level. Simpson (1944, 1953) develops this basic idea in a most convincing fashion but fails to present adequate supporting examples.

Schaeffer, Hecht and their associates, including myself (Bock, 1965), develop many fundamental aspects involved in the idea that macroevolution does not differ

1 I would like to dedicate this paper to Julian Huxley, ornithologist and evolutionist, in recognition of his pioneering contributions to the synthetic theory of evolution that had its origins in his book "Evolution, the Modern Synthesis" published three decades ago.

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qualitatively from microevolution, but fail completely to provide the needed critical support for their claims. Most of the examples cited as support for this assumption provide equally good support for the concept of special transpecific evolutionary mechanisms. The necessary critical support must come from the species level. Sequences of change illustrated by series of fossil genera are unsufficient because they do not preclude small superspecific saltations and hence mechanisms different from infraspecific evolutionary ones. A rare exception to this general pattern is Mayr's (1963: 589-592) discussion of the occasional rise of new genera by extreme geographic variation for which he provides a number of supporting examples.

A second and equally serious difficulty in many earlier papers stems from the ambiguity in the meaning of macroevolutionary change and in relating definite microevolutionary mechanisms to major evolutionary changes.

The general lack of documentation has been one of the points seized upon by opponents of the synthetic theory (e.g., Russell, 1962) although the conclusions reached by these workers suffer from the same lack of documentation. Nevertheless the shortage of supporting examples for the synthetic assumption remains a decided weakness that must be corrected before a truly coherent and convincing set of macroevolutionary mechanisms can be postulated.

At the onset, I should like to emphasize that I accept completely the hypothesis that major evolutionary change takes place by the mechanisms of microevolutionary modifications and that there is no evidence for any additional special transspecific evolutionary mechanisms. In an earlier study (Bock, 1965), I used this hypothesis as the foundation for a discussion of whether or not the origin of new major forms of organization is adaptive in its entirety and whether or not this change can be explained fully in terms of known mechanisms of biological adaptation. A careful reappraisal of this paper has shown that the examples of adaptive changes and the proposed mechanisms did not necessarily have to occur by known evolutionary mechanisms acting on or below the species level. The entire discussion is equally consistent with a hypothesis that small adaptive saltations occurred at the superspecific levels. All I demonstrated in that paper was that the evolutionary mechanisms leading to major changes are adaptive, but I failed to demonstrate that they are the same mechanisms involved in infraspecific modifications.

In this study, I would like to present a more definite statement of the correlation between microevolution and macroevolution including a clearer enumeration of the main microevolutionary mechanisms that are involved in major evolutionary changes and most importantly to analyze an example that appears to support the synthetic assumption. This study will also serve as the vehicle to present a series of scaled drawings of the bill in lateral view of all species of the Drepanididae from specimens in the American Museum of Natural History.

The Synthetic Assumption

The synthetic assumption, as I would like to term this fundamental cornerstone of the synthetic theory of evolution, is that macroevolutionary changes can be explained completely by known microevolutionary mechanisms and that no additional or special macroevolutionary mechanisms exist. Microevolution and macroevolution constitute a continuum of change. Possibly the only unique aspect of macroevolution, or at least the study of large evolutionary changes, is that the probable sequence of events and changes must be established with extraordinary care before discussing the evolutionary mechanisms responsible for these transspecific modifications. Sequences are probably equally important in microevolutionary studies, but they are more apparent in transspecific evolution. The importance of establishing series of events is stressed in my earlier paper (Bock, 1965:274) in which sequences constituted a major foundation for the model describing
the origin of new taxa via adaptive mechanisms.

By macroevolutionary change, I mean the appearance of new distinctive adaptive features or the origin of new taxa at the generic level or higher; I am not here concerned with a precise delimitation of the lower level of macroevolutionary change.

Of greater importance are the particular microevolutionary mechanisms by which large phyletic changes occur. I will not discuss here the mechanisms of adaptation which I treated earlier (Bock, 1965, 1969), or with roles of the environment or behavior which have been covered by von Wahlert (1965), or with the concept of experimentation as advocated by Schaeffer (1965); these topics have been well covered by these authors. Rather, I wish to emphasize those mechanisms acting at the species level and below that are subject to verification by experiments and/or by direct observation, and that are responsible for large evolutionary change by their successive cumulative action. These are: (a) the dual mechanisms of the generation of genetical variation and of natural selection which are responsible for geographic variation within the limits of a species; (b) the processes involved in the allopatric phase of speciation (multiplication of species) by means of geographic speciation (e.g., Mayr, 1963), polyplody (e.g., Stebbins, 1950), or other demonstrated methods by which intrinsic isolating mechanisms evolve; (c) the processes involved in the sympatric phase of speciation following secondary overlap of the newly isolated species (e.g. double invasions) in which character displacement of ecological features and of ethological (and all other isolating mechanisms that would reduce reproductive wastage) features frequently follows as a result of competition and other interactions between these species (e.g., Lack, 1944, 1947; Brown and Wilson, 1956; Mayr, 1963:82–86; Keast, 1968); (d) range extension resulting in more extensive sympatry between the newly evolved species; and (e) extinction (see Warner, 1968, for extinction of Hawaiian birds).

All of these microevolutionary mechanisms act on or below the species level and all are well established either by experimental verification or by extensive comparative observations. According to the synthetic assumption, successive operation of these mechanisms could result in major evolutionary change. Verification or rejection of this assumption depends upon the enumeration of actual examples that possess several properties, namely: (a) they demonstrate a major evolutionary change; (b) they are explicable by the above cited mechanisms; (c) they require few, and preferably no, hypothetical intermediate steps (i.e. hypothetical species) for a convincing explanation; and (d) they are discussed on the level of species (i.e., maximum differences and changes are those between species and all mechanisms are on the species level).

By one step in the continuum of evolutionary change, I mean precisely that series of events and associated mechanisms necessary to evolve a pair of sympatric species (at the completion of the sympatric phase of speciation with its character displacement) from a parental species. Basically one step is a full cycle of speciation including the sympatric phase; this is admittedly an arbitrary but useful division for discussion of large evolutionary changes. I shall adhere to this meaning of a single step when discussing the minimum number of steps required for particular evolutionary changes in the Hawaiian honeycreepers later in this study.

The importance for transspecific evolution of character displacement of ecological and ethological features during the sympatric phase of speciation has not received the emphasis it deserves. It is quite likely that a large portion of any major evolutionary modification is an accumulation of character displacements during the sympatric phases of successive speciations, and the aggregated change from the allopatric phases contributing only a minor amount to the total change. Moreover, the strength
A SUPPORTING EXAMPLE

The Hawaiian honeycreepers (Drepanididae), which constitute one of the best known examples of adaptive radiation among recent vertebrates, provide an outstanding case history supporting the synthetic assumption. Many aspects of the adaptive radiation of the Drepanididae have been reviewed by Amadon (1950) in his now classic study; his classification and suggested phylogeny will be followed closely herein. Ecological factors influencing the evolution of some species of honeycreepers were discussed in an earlier paper by Amadon (1947). More recently, Richards and Bock, (ms.) described the functional morphology, adaptation and evolution of the feeding apparatus in the genus Loxops. These papers provide the factual basis for the present discussion which will consider the adaptive radiation of only the bill morphology and feeding habits in the Hawaiian honeycreepers with emphasis on the subfamily Psittirostrinae. The tongue is specifically excluded from this analysis because the detailed information required is insufficient at this time. Although evolution of the feeding apparatus is the most spectac-
The subfamily Drepanidinae contains five genera (*Ciridops, Himatone, Palmeria, Vestiaria*, and *Drepanis*) which represent an interesting example of adaptive radiation in bill structure and feeding habits. Changes within this taxon are associated with feeding on fruits (the short-billed *Ciridops*), on various insects and on nectar from diverse flowers (the other four genera). The suggested phylogeny of the Drepanidinae (Fig. 1) is quite controversial and differs considerably from that advocated by Amadon (1950:230). He regards *Ciridops* as an advanced frugivorous member of the subfamily while it is here considered as a primitive form following Richards and Bock (ms.). Each of the five genera in this subfamily contains only a single species or superspecies and most species are monotypic; the genus *Drepanis* contains two monotypic species comprising a single superspecies, and the species *Himatone sanguinea*, found on the six main islands with no geographic variation, has a weakly differentiated race (*freethii*) on the small leeward island of Laysan which lies...
800 statute miles northwest of the nearest main island (Kauai). Thus, the Drepanidinae lack one of the essential requirements of a good supporting example for the synthetic assumption—namely, a continuum of intermediate species—and will not be discussed further.

The other subfamily, the Psittirostrinae, contains four genera (*Loxops, Hemignathus, Pseudonester, and Psittirostra*) which exhibit a wide range of bill structure and feeding habits and which include a number of polytypic species, many of which are broadly sympatric throughout the main Hawaiian islands. Both properties are desirable ones for an example supporting the synthetic assumption. The generic and specific limits advocated by Amadon (1950) for this subfamily are accepted by me as are most of the basic aspects of his phylogeny for this group (1950:230). The evolutionary sequences to be discussed represent morphological sequences or "pseudophylogenies" arranged for the purposes of this study. The actual phylogeny of the existing genera and species of the Psittirostrinae presumably did not include the living species as intermediate steps in the evolution of other living species. For example, the living taxon *Loxops virens stejnegeri* probably evolved after the time a presumably "stejnegeri-like" intermediate form existed in the evolution of the subfamily. Most likely, the actual series of evolutionary changes in the phylogeny of the Psittirostrinae was reasonably similar to the "pseudophylogenies" of living taxa used in this discussion. Some earlier taxa compris-
Fig. 4. Bill length (culmen in mm) of the *Loxops virens* complex following the same system as in Figure 3. Data taken from Amadon (1950).

The actual steps in the evolution of this subfamily could have become extinct, which is a common phenomenon of insular birds, and replaced by the later evolution of similar forms.

Most workers (e.g., Amadon, 1950; Richards and Bock, ms.) accept *Loxops* as representing the most primitive stock of the subfamily with *Loxops virens* as most similar to the probable primitive species. *Loxops* contains three widespread polytypic species (*virens*, *maculata*, and *coccinea*) which are sympatric on most of the main Hawaiian islands (Fig. 2). The two remaining species (*parva* and *sagittirostris*) are recent offshoots of *virens*. Each of the widespread species exhibits considerable geographic variation in bill size (e.g., Fig. 3 for *maculata* and Fig. 4 for *virens*). The difference between the bills of *L. maculata newtoni* and of *L. m. mana* is reflected in a large number of differences in cranial osteology and jaw musculature (Richards and Bock, ms.) with the small-billed *L. m. newtoni* being more similar in numerous features to *L. v. virens* than to *L. m. mana*. Similar geographic variation is seen in most other widespread species of the Psittirostrinae (Amadon, 1950:179–185). With chance double invasion of the same island by different populations of the same species, the basis for ecological divergence of the two
populations already exists, provided that these populations had developed intrinsic reproductive isolating mechanisms by the time of their sympatry (e.g., Mayr, 1963; Lack, 1944, 1947). For example, the populations of *Loxops maculata* on the neighboring islands of Maui and Molokai are quite dissimilar in bill size. If *L. m. flammea* (large bill) invaded Maui where *L. m. newtoni* (small bill) already existed and if the two taxa were already reproductively isolated, then it seems probable that they could coexist, divide the habitat available to these bark probing, insectivorous creepers, and presumably diverge from each other because of mutual selection forces on one another resulting from ecological competition.

This pattern of double invasion, competition and resulting character displacement in the newly sympatric species has occurred twice in the *Loxops virens* complex (Richards and Bock, ms.; Figs. 4 and 5). *Loxops virens* is a small, thin-billed bird with a tubular, fringed tongue; it takes some nectar from Ohia flowers and rarely fruit, but the main part of its diet is small insects gleaned from leaf surfaces and small twigs, or extracted from bark crevices by weak probing. On the island of Hawaii, one member of the double invasion, *L. v. virens* has maintained the original feeding habits although becoming smaller in bill size than most other races of virens. The other invader, *L. sagittirostris*, which presumably had a larger bill at the time the original sympatry was established, evolved a larger, straighter and stronger bill associated with its feeding on larger insects obtained by powerful probing. A similar double invasion took place on the island of Kauai as noted previously by Amadon (1947, 1950: 245–246). In this case, the small billed insect gleaner is considered as the separate species, *L. parva* (Amadon, 1950:165), on the basis of plumage color. The large
decurred-billed insect prober is classified as a race, stejnegeri, of Loxops virens. It should be noted that L. v. stejnegeri represents a case of extreme geographic variation in L. virens (Mayr, 1963:589–592). Moreover, it is a rather moot point whether stejnegeri should be classified as a subspecies of L. virens or as a monotypic species. Loxops parva is a leaf gleaner and L. v. stejnegeri probes into crevices in the trunk and branches of large forest trees for its insect prey; both species also take nectar. It is interesting to note first that the small-billed member of each pair of double invaders is smaller in bill size than the populations of L. virens found alone on other islands (Fig. 4), or conversely virens when found alone is intermediate in bill size between the small and large billed members of the double invaders. One may suspect that virens when alone on an island does more probing into bark crevices for insects. This general phenomenon of intermediacy in size of the ancestral population compared to both members of a double invasion has been described and well documented by Lack (1944, 1947). Second is that each large-billed member of each pair is a bark prober for insect prey, but that one has a straight bill and the other has a decurred bill. The difference in shape of these probing bills results from the action of accidental evolutionary mechanisms (Mayr, 1962; Bock, 1967, 1969) and represents different paradaptations for probing. Each type of probing bill suggests the beginning stage of a different evolutionary line, one leading to bark probing tree creepers (e.g., L. maculata) and the other to bark probing “heterobills” (e.g., Hemignathus lucidus). Lastly,
the probable recency of both double invasions is indicated by the failure of the divergent forms to spread to other islands of the Hawaiian archipelago.

Evolution of the species in the entire genus *Loxops* was presumably the result of a series of repeated double invasions, competitions and resulting character displacements; the ancestral *L. virens* gave rise to (a) a creeper-like bark prober, *L. maculata*, with a straighter stronger bill, and (b) a leaf bud and legume pod opener, *L. coccinea*, with a short, siskin-like bill with crossed tips (Fig. 6). Both descendent species are primarily or purely insectivorous and differ from *virens* mainly in their methods of obtaining insects which has resulted in the adaptive modifications in bill shape and other features of the feeding apparatus (Richards and Bock, ms.). It is important to note that the differences in bill shape between *virens* and *maculata* or between *virens* and *coccinea* are no greater than between *v. virens* and *sagittirostris* or even between *v. virens* and *v. stejnegeri*. Indeed, the difference between *v. virens* and *v. stejnegeri* is larger than between *v. virens* and *v. maculata* newtoni. Moreover, the probing method used by *sagittirostris* is very similar to that used by *maculata*. The origins of *maculata* and *coccinea* were probably earlier in time than *sagittirostris* and *parva* because the former species have spread over the main Hawaiian Islands and subsequently have evolved considerable geographical variation in bill size.

*Loxops coccinea* deserves a brief comment because it possesses one of the most bizarre feeding apparatus in the Drepanididae despite its apparently unstriking bill (Richards and Bock, ms.). The crossing of its bill is restricted to the tips of its rhamphotheca; the bony jaws are symmetrical. Yet the mandible-quadrato articulations and most of the jaw muscles are highly asymmetrical. This bird can develop large laterally directed forces to counter the lateral external forces acting on its bill tips during the twisting motions which are presumably used when opening leaf buds and legume pods in search for its insect prey.

Up to this point in the “phylogeny” of the Psittirostrinae, the evolutionary changes have been within the limits of a single genus and of a magnitude that cannot be regarded as truly macroevolutionary although some of the differences, e.g. between *virens* and *coccinea*, are greater than apparent at first glance. The total amount of change in the evolution of the genera *Hemignathus* and *Pseudonestor* from *L. virens stejnegeri* (Fig. 7) is far greater than the change within *Loxops*, but the change in each individual step may represent a smaller magnitude than that seen between *virens* and *coccinea*.

*Loxops virens stejnegeri* uses its stout decurved bill to probe into bark crevices of tree trunks and large branches for insects. Presumably it also feeds on nectar. The change from a bird like *L. v. stejnegeri* to a bird similar to *Hemignathus lucidus* involves little more than lengthening the decurved upper jaw along its original arc of curvature; this modification is no greater than many seen within the genus *Loxops*. Had no additional species evolved from *Hemignathus lucidus*, it could be included within *Loxops* without any undue stretching of the width of the genera within the Drepanididae. *Hemignathus lucidus* feeds on insects obtained by probing and prying under bark and by tapping with its bill, and on the nectar of the Ohia tree, a favorite of many species of *Loxops* and *Hemignathus*. The methods used by *L. v. stejnegeri* and *H. lucidus* to dig out concealed insects are very similar (Amadon, 1950:246). Moreover, *L. v. stejnegeri* and *H. lucidus hanapepe* are sympatric on Kauai, and *hanapepe* is the largest billed race of *H. lucidus* suggesting that character displacement following competition has occurred between these species.

The interesting species, *H. wilsoni* is a geographic representative of *H. lucidus* (Amadon, 1947, 1950:169, 202–203). Its lower jaw became straight and woodpecker-like and is used as a chisel to cut open bark and wood to expose insects. The chiselling of *H. wilsoni* is simply an extension of the tapping used by all members of *Hemignathus* in their search for insects. In *H.*
wilsoni, the decurved upper jaw is raised out of the way of the mandible when the bird is pecking. After a hole has been cut and the insect exposed, the longer decurved upper jaw is then used to probe for the insects. The combination of straight chisel-like mandible and a long decurved upper jaw for probing is an unusual, and perhaps unique, example of the two jaws in a single avian species being adapted for two quite different actions, both of which are essential for the feeding method of this species. Thus, H. wilsoni is an outstanding example of considerable evolutionary change arising from geographical variation as noted previously by Amadon (1947, 1950) and Mayr (1963:589–592).

A second phyletic line in Hemignathus led to the long sickle-billed H. obscurus-procerus superspecies from H. lucidus by lengthening the lower jaw until it was equal to the upper jaw and then elongation of the entire bill. These long billed species obscurus and procerus feed by probing for insects in crevices in bark and broken twigs, and by sucking nectar from flowers with large corollas. Change in bill structure may have been largely associated with a greater use of nectar by obscurus in comparison to the occasional or rare feeding on nectar by lucidus, or it may have resulted from a difference in probing methods used by these birds. In any case, the change in bill structure from lucidus to obscurus is of the same magnitude as that from v. stejnegeri to lucidus or from lucidus to wilsoni. The superspecies lucidus-wilsoni is broadly sympatric with the superspecies obscurus-procerus on several of the main Hawaiian islands. Of greatest interest is that the longest sicklebilled taxon, procerus, is found on Kauai where it is sympatric with hana-
pepe, the largest billed member of H. lucidus. Possibly, hanapepe and procerus have undergone competition and character displacement with evolution toward large bill size in procerus. Thus, the presence of a small curved billed prober, L. v. stejnegeri, on Kauai resulted in displacement of bill size in the Kauai population of lucidus to the larger billed form H. l. hanapepe which in turn resulted in displacement of bill size in the Kauai population of obscurus to the larger billed species H. procerus. These observations on relative bill size in Loxops virens, Hemignathus lucidus, and H. obscurus-procerus complex are important because they suggest that these species have interacted (competed) with each other, giving rise to character displacement, in spite of the great difference in bill morphology between the extreme forms of stejnegeri and procerus. Thus it is reasonable to assume that the origin of Hemignathus and the evolution of its several species resulted from a small series of steps each including a double invasion and character displacement following competition.

A third phyletic line leading from Hemignathus lucidus ends in the shorter, heavy billed Pseudonestor xanthophrys, an insectivorous bird in spite of its stout bill. Pseudonestor obtains its insect prey by chewing or tearing into insect burrows in twigs and branches; it crushes rather than probes or pries and hence is able to exploit a source of insects closed to members of Hemignathus. Its feeding method is readily derived from a bird like H. lucidus that probes or pries into branches for insects. The shorter, heavier bill of Pseudonestor represents the obvious adaptations from a mechanical point of view for a bird that chews or crushes wood to expose insect burrows. Interestingly, the shape of the upper and lower jaws of Pseudonestor resembles those of Hemignathus lucidus; the longer, decurved upper jaw is not a necessary requirement mechanically for the feeding methods employed by Pseudonestor. And this bird still possesses a partly tubular tongue (Amadon, 1950:169) although it does not take nectar. Pseudonestor xanthophrys is found on only one island (Maui) but it is sympatric there with H. lucidus affinis. Although its short heavy bill appears quite distinct from that of H. lucidus, Pseudonestor could have evolved from it as a result of character displacement because of competition with H. lucidus affinis on Maui. By chewing and tearing into wood, Pseudonestor can obtain insects not available to H. lucidus. And the evolutionary change undertaken by the ancestors of Pseudonestor is one of the few avenues available to an insectivorous prober descended from and in competition with a closely related form (i.e., Hemignathus lucidus). An already existing long sicklebilled prober, Hemignathus obscurus, would have closed that possible avenue of evolutionary change. Similar changes have been observed in other passerine groups (Keast, 1968). Although Pseudonestor has a considerably heavier bill than any species of Hemignathus, I do not regard the magnitude of change between H. lucidus and Pseudonestor xanthophrys as significantly greater than that between L. v. stejnegeri and H. lucidus or between H. lucidus and H. obscurus. Moreover, the change between H. lucidus and Pseudonestor is of the same magnitude or perhaps even less than that between Loxops virens and L. coccinea when the total degree of asymmetries in the jaw articulations and jaw muscles is considered (Richards and Bock, ms.).

Thus far, all evolutionary changes in the Psittirostrinae have been associated with insectivorous and nectarivorous feeding habits. The major adaptations in bill shape and in associated features of the jaw apparatus evolved because of differences in methods of obtaining food and feeding sites rather than because of differences in the food objects themselves. However, the next step in the evolution of this subfamily involves a real change in food objects rather than a modification in feeding methods which are quite similar in Pseudonestor and Psittirostra.

Pseudonestor xanthophrys is an obvious intermediate form between the thin-billed insectivorous and nectarivorous Loxops and
Hemignathus and the heavy billed phytophagous and insectivorous Psittirostra (Figs. 8 and 9). The heavy bill of Pseudonestor evolved to open tunnels of insects in wood associated with continued insectivorous feeding is an obvious preadaptation for phytophagous food habits in which large forces are needed to open or otherwise break hard plant parts. Indeed the morphological change between Pseudonestor and Psittirostra, including the functional properties of the bill, is far smaller than that between Hemignathus lucidus and Pseudonestor or even that between some species within Hemignathus or Loxops, but it has resulted in a major feeding change from insectivorous to primarily phytophagous with the taking of some insects. Psittirostra psittacea is found on all the main Hawaiian islands and could have evolved from Pseudonestor as a geographic variant or as a result of character displacement following double invasion. The Maui race of P. psittacea, which is sympatric with Pseudonestor, is not different in bill size from conspecific populations on other islands. A difference would not be expected because the radically different food habits of Pseudonestor and P. psittacea would preclude competition between them and hence displacement of the population of P. psittacea sympatric with Pseudonestor would not be expected.

Psittirostra cantans of the leeward islands is a geographic representative of P. psittacea, which has a diversified diet of insects,
larvae, bird's eggs, dead birds, the starchy root of *Boerhavia* and seeds of the seaside *Tribulus* (Amadon, 1950:203). This diversity can be related to the rigorous conditions on Laysan, lack of an abundant continuous single food supply to which *Psittirostra cantans* is primarily adapted and, finally, lack of other land birds that could compete with it.

The array of *Psittirostra* species found on the island of Hawaii—*psittacea, flaviceps, palmeri, bailleui*, and *kona*—appears to be the result of multiple invasions and character displacements following competition (Figs. 8 and 9); indeed, these finches represent one of the most extreme cases of congeneric species of birds found on a single oceanic island. It may be possible that some *Psittirostra* species arose on Hawaii via geographic isolation on different mountains, or the entire series of species arose by repeated invasions. Apparently none of the derived species reinvaded the other Hawaiian islands. The pair of species *flaviceps* (small bill) and *palmeri* (large bill) are most similar to one another and to *psittacea*. The other pair *bailleui* (smallest) and *kona* (heaviest) have broad conical bills that differ considerably in shape from that of *psittacea*, but are also not very similar to one another. The Hawaiian population of *psittacea* does not differ from other island populations in bill size and is intermediate between the small billed *bail-
leui and the large billed flaviceps, palmeri, and kona. The exact details of the feeding habits of the Psittirostra species on Hawaii are not well known because three of the four endemic species are extinct. However, they all fed on seeds of various trees and on insects (Amadon, 1950:203–204). Sufficient differences in feeding habits apparently existed to permit coexistence of the five species of Psittirostra on Hawaii. P. baileui may be altitudinally separate from other species of Psittirostra.

Discussion

The range in bill shape in the Psittirostrinae extends from the small thin bill of Loxops virens and L. parva, to the crossbill of Loxops coccinea with its asymmetrical jaw articulations and jaw musculature, to the “heterobill” of Hemignathus wilsoni with its decurved upper jaw and straight “woodpecker-like” mandible, to the extremely long sicklebill of Hemignathus procerus, and to the heavy conical grosbeak bill of Psittirostra kona. This range of variation is only slightly less than that found in the entire order of perching birds. Flycatching bills and heavy crow and shrike bills are absent, but not much else. (The tongues of the psittirostrines are equally variable, including fringed tubular tongues, flat stiff tongues and thick, fleshy seed handling tongues which span much of the range of tongue structure in the perching birds.) The evolution from the short thin bill of Loxops virens to the long sicklebill of Hemignathus procerus or to the heavy grosbeak bill of Psittirostra kona and the associated change in feeding habits represent without question major evolutionary changes. The documented sequences of steps responsible for these macroevolutionary changes are ones that can be explained completely on the basis of the evolutionary mechanisms of geographical variation, allopatric phase of speciation, secondary overlap with competition and resulting character displacement. Indeed each step in the several sequences can be discussed in terms of known existing species and subspecies. No hypothetical intermediate species have to be deduced to bridge the observed steps between the existing bill shapes and feeding methods.

I am not concerned in this analysis with the details of the adaptations in the morphology of the feeding apparatus. Some of these adaptations have been analyzed in Loxops (Richards and Bock, ms.) and we hope to study the other genera. The morphology of the feeding apparatus and the feeding methods in the species of Loxops are adapted to their environments. I know of no reason to assume that any species of drepanidid has a bill morphology poorly adapted for its feeding methods. Moreover, it does not appear likely that extinction in the Drepanididae resulted from poor feeding adaptations (Richards and Bock, ms.) or because of drastic changes in the habitat. Rather the widespread recent extinction of Hawaiian birds appears to be mainly the consequences of introduced diseases and/or insect vectors (Warner, 1968), with feeding adaptations being quite irrelevant.

Although it is not possible at this time to discuss in detail the exact pattern of mosaic evolution in the Psittirostrinae, clear indications exist of this ubiquitous evolutionary pattern. Modifications in the lengths and shapes of the upper jaw and of the lower jaw occurred separately in Hemignathus, Pseudonestor, and Psittirostra. Moreover, evolution of tongue structure is quite independent of the evolution of bill shape because many of these species are insectivorous and nectarivorous to quite different degrees.

Lastly, it is of some interest to ascertain the minimum number of species level steps needed for the observed major evolutionary changes within the Psittirostrinae. By a step, I mean a full cycle of speciation including the sympatric phase with character displacement following competition. From Loxops virens to Hemignathus procerus a minimum of four steps are required—stejnegeri, lucidus, obscurus, and procerus; from Loxops virens to Hemignathus wilsoni, only three steps are needed—stejnegeri, lucidus, and wilsoni; and from Loxops
to *Psittirostra kona*, five steps are needed—*stjnegeri*, *lucidus*, *xanthophrys*, *psittacea*, and *kona*. More steps may have occurred in the actual phylogeny of these taxa, but I am considering here the minimum number of necessary steps. Estimating a minimum of 100,000 years and a maximum of 1,000,000 years for each step, then a range of 500,000 years to 5,000,000 years can be calculated for the evolution of these changes, and probably only a little more time would be required for the evolution of the entire subfamily. On the basis of these estimates, the evolution of the Drepanididae could have taken place well within a time span of 10,000,000 years which is in good agreement with other estimates and with datings of the age of the Hawaiian islands.

Of greater interest is the possibility that the evolution of the Drepanididae may have required only 1,000,000 years which is a minimum, but not impossible, period using an estimate of 100,000 years for each step. Yet I hasten to add that the radiation of the Drepanididae within a time span of 10,000,000 years, or even 1,000,000 years, does not imply "rapid" evolution. The evolutionary mechanisms used to explain the steps in the suggested history of the Psittirostrinae are the generally accepted ones postulated for speciation and other microevolutionary events as are the estimates for the time required for each step. And the rates for the evolutionary change required for radiation of the known Drepanididae in a time span of 1,000,000 to 10,000,000 years are those existing in typical microevolutionary change; they need not be considered as excessively high rates. Probably the most severe selection forces and the fastest evolutionary changes occurred during the period of initial sympatry and ecological competition between newly established species. Again the large contribution of the change during successive sympatric phases of speciation to the total macroevolutionary change cannot be underestimated. Macroevolution, or at least rapid macroevolutionary change, may be no more than a sequence of character displacements. Decline in the occurrence of character displacements, perhaps in continental areas lacking geographical barriers and other requirements for speciation, may result in a decline in the rate of macroevolutionary change. A close positive correlation between the rates of double overlaps with character displacement and of macroevolutionary change would provide additional support for the notion that major evolutionary changes and the origin of new taxa result from adaptive radiations, not as continued evolution in a single phyletic line (Bock, 1965).

**CONCLUSION**

The single important factor in this analysis of the radiation of the Psittirostrinae was to arrange the changes into probable sequences and then to discuss the evolutionary changes and the mechanisms responsible for them in the order indicated by these sequences. The macroevolutionary modifications in the psittirostrines can be shown to be the consequence of a repeated
series of the same microevolutionary modifications (Fig. 10) resulting in an increase in the number of species and in an accumulation of differences. But this accumulation of differences developed in a very definite pattern and can be studied properly only in the same pattern. Failure to recognize the paramount importance of the sequence of events in macroevolution has been a major weakness in many earlier studies. Most of these studies, both those advocating the synthetic assumption and those arguing for the existence of special trans-specific evolutionary mechanisms, use a nonsequential approach. The set of differences between two major taxa or between the onset and endpoint of a macroevolutionary change are listed and described first, and then these differences are discussed at random or as if they all evolved simultaneously. No approach could be further from reality as shown by the mosaic nature of
well documented phylogenies, and it is not surprising that the nonsequential approach has not permitted a sound appreciation of macroevolutionary mechanisms. The general conclusion that may be reached from this analysis is that: If the sequence of events in a major evolutionary change is outlined properly, then the known mechanisms of microevolution will provide a complete explanation for the macroevolutionary change. Solution of transspecific phenomena does not lie in the search for special mechanisms or for special operation of known evolutionary mechanisms but in a thorough understanding of the sequences of events involved in major evolutionary changes.

Finally, what is needed at this time are additional well analyzed examples which support the synthetic assumption. These examples should document a major evolutionary change and preferably not require the deduction of unknown intermediate steps (i.e., species). Most likely, the best supporting examples will be found in groups of living organisms which have undergone recent adaptive radiation and still possess sufficient species and subspecies to permit the arrangement of reasonable "pseudophyletic" sequences without species-level gaps.

Summary

The synthetic assumption that macroevolutionary changes can be explained completely by known microevolutionary mechanisms is widely accepted, but it still lacks supporting evidence at the species level. The radiation of the subfamily Psittirostrinae of the Hawaiian honeycreepers is described as a supporting example in which major changes in their bill structure and feeding habits have occurred by a series of steps involving modifications on the species level and can be illustrated by existing taxa. The core concept for development of general macroevolutionary theory and for understanding particular cases of major evolutionary change is the arrangement of events and associated modifications into a probable sequence followed by the analysis of this sequence using known evolutionary mechanisms. The exact sequence or the choice of one of several possible sequences is not important. Rather it is the concept that major evolutionary changes, being the consequence of a series of events each of which dependent upon previous ones, can be analyzed properly only within the framework of a plausible sequence of events, changes and controlling evolutionary mechanisms.

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Literature Cited


WARNER, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70:101–120.