BILL SHAPE AS A GENERIC CHARACTER IN THE CARDINALS

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MANY genera in birds and other animal groups have been based essentially upon a single character. This character may be a single morphological feature, such as the presence or absence of the hallux, or it may be a complex of characters which are all closely correlated functionally, such as the bones, muscles, and ligaments of the jaw apparatus. The validity of many of these genera has been questioned in recent years with the general acceptance of the polytypic species concept and the increasing acknowledgment of the grouping service at low taxonomic levels provided by the genus. An example is the North American passerine genus *Pyrrhuloxia*, which is distinguished from *Richmondena* essentially on the basis of bill shape. The overall similarity of *Pyrrhuloxia sinuata* to the two species of *Richmondena* in morphology and in general life history (Gould, 1961) has led several recent authors to synonymize *Richmondena* with *Pyrrhuloxia*. Other workers have maintained the validity of the generic separation, basing their decision largely on the difference in bill shape. The object of this paper is to ascertain the importance of this difference as a taxonomic character and whether the difference if confirmed is of generic significance.

THE JAW APPARATUS

Ridgway (1901:624–625) described the bill of *P. sinuata* (see Figs. 1 and 2) as follows:

> "Bill very short, thick and deep, with culmen strongly convex and maxillary tomium deeply and angularly incised a little posterior to the middle portion: mandible deeper than the abruptly bent maxilla, with its distinctly toothed tomial angle about midway between base and tip; gonys straight, greatly ascending, shorter than distance from nostril to tip of maxilla; depth of bill at base much greater than its width."

He described (1901:629–630) the bill of *Richmondena* as:

> "Bill stout, conical, deeper than broad at base, where its depth is about equal to length of exposed culmen; culmen decidedly, sometimes strongly convex; gonys straight, shorter than distance from nostril to tip of maxilla; maxillary tomium situated a little anterior to or directly beneath nostril, with nearly obsolete subterminal notch or none at all; mandibular tomium either nearly straight or decidedly convex anterior to its subbasal angle, the latter more or less posterior to the middle portion and with or without a notch in front of it."

The differences between the genera can be summarized by noting that the bill of *P. sinuata* is shorter and more decurved than the more elongated bill of

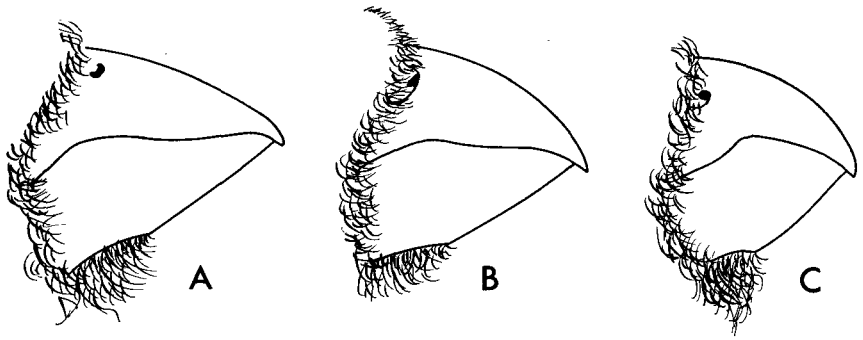

FIG. 1. Lateral view of the bills of (A) *Richmondena cardinalis*, (B) *R. phoenicea*, and (C) *Pyrrhuloxia sinuata*. The intermediate shape of the bill of *phoenicea* between those of *cardinalis* and *sinuata* can be readily appreciated.

R. cardinalis. This distinction is most evident in the mandible which is deeper in *sinuata* with a decided ventral bony boss at the gonys of the mandible, and in the strongly decurved, almost parrot-like, upper jaw of *sinuata*. The morphological difference between the bills of *sinuata* and *cardinalis* is essentially bridged (Fig. 1) by that of *R. phoenicea* found in northern South America. The upper jaw of *phoenicea* is less elongated and more decurved than that of *cardinalis* and closely approaches that seen in *sinuata*. Although the mandible of *phoenicea* is much deeper than that of *cardinalis*, it lacks the heavy ventral bony boss found in *sinuata*. If the bills of the three species are superimposed on one another (Fig. 2D), the intermediate position of *phoenicea* between *cardinalis* and *sinuata* is clearly shown. Ridgway (1901: 630) pointed out many years ago that: "The evident gap between *Cardinalis* and *Pyrrhuloxia* is nearly bridged by *C. phoeniceus*. . . ."

The jaw muscles of *sinuata* and *cardinalis* reflect the differences in their skull morphology, although the basic pattern of musculature is the same in the two species. The skull of *cardinalis* is larger absolutely than that of *sinuata* and hence one could expect the jaw muscles to be larger, which is the case. Moreover, the jaw muscles of *cardinalis* appear, in general, to be larger, relatively, than those of *sinuata*. Another general difference is that the major dorsal adductors have a more anterior insertion on the mandible in *cardinalis* than in *sinuata*. Detailed differences and similarities in the jaw muscles of these birds are as follows. M. depressor mandibulae is much the same in both species, in size as well as shape. M. adductor mandibulae externus is larger in *cardinalis*, but not uniformly. The temporal part of M. adductor mandibulae externus rostralis is about 25% larger in *cardinalis* and has a small posteroventral pinnate bundle that is lacking in *sinuata*. Similarly, the medial segment of the pars rostralis which originates from the posterior wall of the orbit is about 20% larger in *cardinalis*. The lateral bundle arising from the tip of the zygomatic process and from the external surface of the underlying M. adductor mandibulae externus ventralis is about the same relative size in both species, although a thin sheet of parallel fibers extends farther ventrally in *sinuata*. The M.

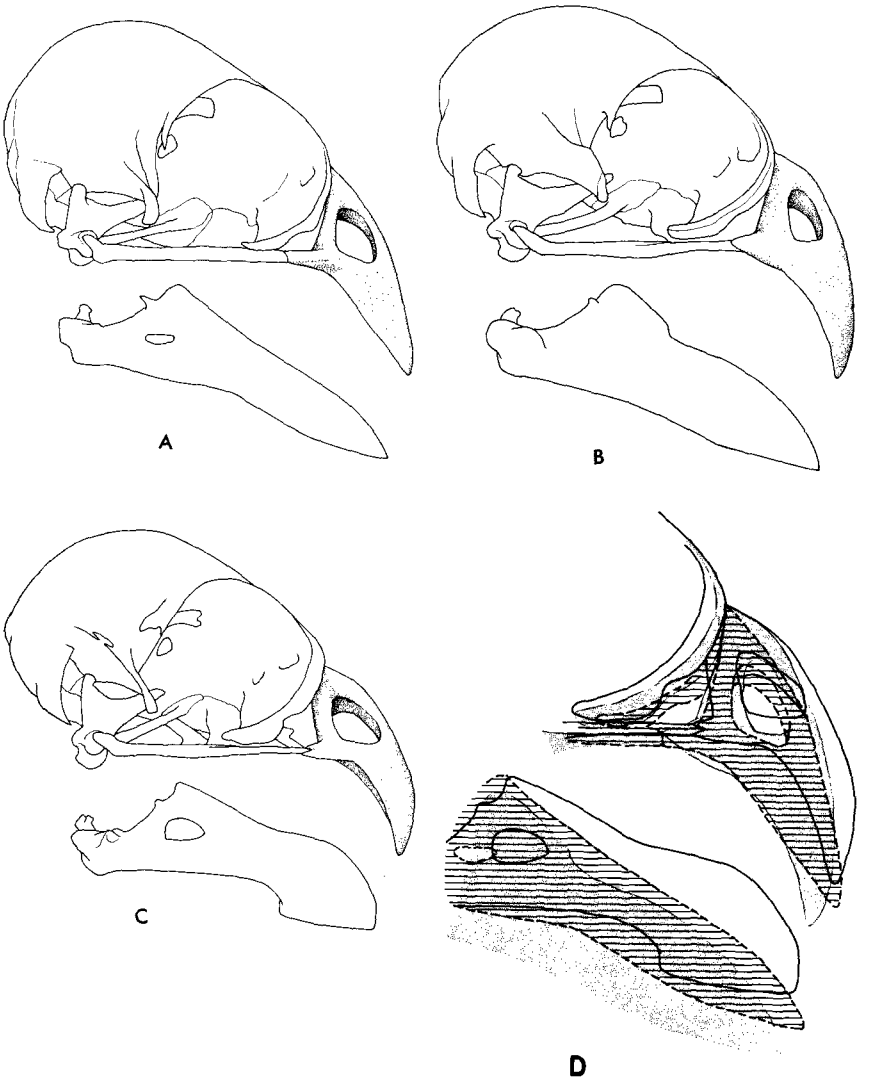

FIG. 2. Lateral view of the skull of (A) *Richmondena cardinalis*, (B) *R. phoenicea*, and (C) *Pyrrhuloxia sinuata*. Note especially the differences in the shape of the upper jaw and of the mandible. Other differences, such as the shape of the zygomatic process and the structure of the quadrate, are of lesser importance and have not been emphasized in the drawings. The jaws of the three species have been superimposed upon each other (D) to show the intermediate position of *R. phoenicea* in this morphological series. The bill of *cardinalis* is indicated by horizontal lines, that of *phoenicea* by stippling, and that of *sinuata* is blank.

adductor mandibulae externus ventralis is slightly larger in *cardinalis*, perhaps about 10–20%. The posterior and deep-lying M. adductor mandibulae externus caudalis is about the same size in both, perhaps slightly smaller in *cardinalis*. All parts of the M. adductor mandibulae externus have a more anterior insertion in *cardinalis* than in *sinuata*. The M. adductor mandibulae posterior is about 30–40% larger in *sinuata*, but it does not add greatly to the force of the adducting muscles because this muscle is relatively small compared to the other jaw muscles. The M. pseudotemporalis superficialis is considerably larger in *cardinalis*, at least twice as large as in *sinuata*, and inserts much farther forward on the mandible. It covers much of the M. pseudotemporalis profundus in *cardinalis*, while this latter muscle is largely exposed in *sinuata*. M. pseudotemporalis profundus is about the same size in both species or perhaps a bit larger in *cardinalis*. All parts of M. pterygoideus are similar morphologically in the two species; the entire muscle seems to be larger in *cardinalis*. The superficial part (ventralmost) of M. pterygoideus ventralis lateralis that originates from the free palatine process of the premaxilla cannot be easily separated from the rest of the ventralis lateralis. A substantial bundle of fibers from M. pterygoideus dorsalis medialis and from M. pterygoideus ventralis medialis runs directly posterior and inserts on the base of the skull. M. protractor pterygoidei is similar in both species.

A most interesting aspect of the jaw apparatus is that the postorbital ligament has almost completely disappeared in both species. All that remains is a faint strand of connective tissue that can be overlooked easily even when special attention is given to it. Without doubt this ligament is functionless in these finches and has no role in cranial kinesis.

The differences in the jaw morphology and in the musculature of *sinuata* and *cardinalis* appear to be correlated mainly with the difference in elongation of the bill. In *cardinalis*, the upper jaw is not as deep at its base and is less decurved. The mandible is correspondingly straighter and thinner. The jaw muscles, especially the dorsal set of mandibular adductors, are larger and have a more anterior insertion. This combination of features suggests that these muscles provide a stronger and more effective force to the mandible when the bird is cracking seeds. Hence, the Cardinal would be able to feed upon larger seeds or to hold the seeds in a more anterior position in the bill when they are crushed.

The Pyrrhuloxia has a shorter, deeper, and more decurved bill. In appearance the bill of the Pyrrhuloxia is quite reminiscent of a parrot's bill. Corresponding to the short, decurved upper jaw, the mandible is shorter and deeper with a ventral boss at the gonys. This reinforcing mass of bone lies ventral to the heavy postnasal bar of the upper jaw when the bill is closed. Presumably the major stresses on the bill occur at its posterior end between the postnasal bar and the ventral boss of the mandible. The more posterior insertion of the dorsal adductors suggests either that smaller seeds are eaten by the Pyrrhuloxia or that the seeds are held farther back in the bill when crushed. The latter possibility is in closer agreement with the structure of the underlying skeleton. If the Pyrrhuloxia were to be able to crush larger

or harder seeds than the Cardinal in spite of its smaller jaw muscles, the seeds would have to be held far back in the bill. This would reduce the required forces that must be applied to the system by the jaw muscles. Such a reduction may be significant although exact figures are not available. A reduction in required forces would permit the Pyrrhuloxia to have smaller muscles inserting closer to the articulation. A more posterior insertion would reduce the mechanical advantage of the jaw muscles, but their angle of insertion would be larger and thus increase the useful component of force. Without knowing the physical properties of the seeds eaten by the two species and the position the seed is held in the bill, it is not feasible to speculate further on the relative adaptations of their jaw apparatus. To judge from the differences in the jaw apparatus of these forms, one can conclude with assurance that these species feed upon different seeds which are cracked in somewhat different methods.

The South American Cardinal, *R. phoenicea*, is clearly intermediate between *cardinalis* and *sinuata* in the structure of its bill. Specimens for dissection were not available; it can only be presumed that the jaw muscles are well developed, perhaps larger than in *cardinalis* but with a more posterior insertion. It may be postulated that *phoenicea* uses a feeding method intermediate between those used by *cardinalis* and by *sinuata*. It may also be suggested that *cardinalis* and the *sinuata* bill structure and jaw muscles could both be derived from a *phoenicea*-like condition.

TAXONOMIC IMPLICATIONS

Judgment of generic limits and of the taxonomic significance of observable differences is a most subjective inquiry depending upon the philosophy of classification accepted by the individual worker. No proof can be offered for or against any particular philosophy (e.g., advocating taxonomic categories embracing a wide adaptive range or a narrow adaptive range), no matter how radical or how widely accepted it may be. As a general principle, no a priori means of ascertaining specific, generic, etc., characters are known, nor can a certain difference be evaluated a priori as generic, familial, and so forth. It is, thus, futile to argue whether the differences between *Richmondena* and *Pyrrhuloxia* are or are not of generic value. It should be stressed that many genera contain one or two species which deviate quite strikingly from their congeners in one character or one character complex, but that this deviation does not justify generic separation.

No question exists on the close relationship between the Cardinal and the Pyrrhuloxia. The species *cardinalis*, *phoenicea*, and *sinuata* form a natural group separated by a distinct gap from all other cardinaline finches. Yet in spite of the overall resemblance in many aspects of the plumage, behavior,

ecology, and anatomy, certain differences do exist, some of them being quite striking. The question, then, is how can one judge whether the differences between *Richmondena* and *Pyrrhuloxia* warrant generic separation. Only two alternatives are seriously possible. Either the genera *Richmondena* and *Pyrrhuloxia* should be maintained as separate genera or they should be merged into one genus. A third possibility—to place the intermediate species *Richmondena phoenicea* in a separate genus—has not been supported by anyone in recent years and can be ignored. Another principle of classification, independent of the degree of difference accepted for generic distinction, must be applied. No matter what degree of difference is accepted as the basis for distinction at any taxonomic level, this measure must be applied consistently to all taxa belonging to the taxon of at least the next higher rank. Hence, whatever degree of difference is chosen as a measure of generic distinction, this measure should be applied consistently to all genera belonging to the same family or subfamily. Ideally then, the question of the distinction between *Richmondena* and *Pyrrhuloxia* should not be answered until a comparison is made between all genera of the subfamily of cardinals. Such a study is not possible at this time because the limits of the subfamilies of the Fringillidae and even the limits between the Fringillidae and closely related families are still quite indefinite. An extensive investigation of the entire New World nine-primaried oscine complex, especially of the tropical forms, is needed before all the problem genera can be allocated to the correct family group. But the urgency of the nomenclatural problem associated with the generic names of these forms and the name of the subfamily (Mayr, MS) justifies the use of less intensive methods. The differences between the cardinals and Pyrrhuloxia can be evaluated by a comparison with the range of bill variation in a few select genera. The genera chosen are ones that are fairly closely related to the *Richmondena–Pyrrhuloxia* complex and ones whose limits are accepted by a majority of workers including many who advocate narrower generic limits.

The differences in the shape of the bills in the extreme forms *cardinalis* and *sinuata* are reflected in a series of differences in the structure of the skull and in the configuration of the jaw muscles. If all of these differences were listed, the ledger would be quite impressive, but would not present an accurate picture of the evolutionary divergence of the two species. These differences do not represent a series of independent evolutionary adaptations. All of the characteristics of the skull and of the jaw muscles which differ between these species (see above) are associated with the same modification in function, presumably resulting from a difference in the seeds utilized by these forms. These cranial features belong to the same character complex (= functional unit of structures) and should be treated as a single taxonomic character.

The fact that *phoenicea* bridges the morphological gap in the jaw apparatus of *cardinalis* and *sinuata* is suggestive, but not conclusive as far as generic separation is concerned. It should be noted that *phoenicea* is not intermediate in all of the features separating the extreme species, but is intermediate in the apparent adaptive significance of the bill; this does not affect its relevancy to the taxonomic argument. Certainly the distinctive gap between *cardinalis* and *sinuata* is greatly reduced, but a decided difference still exists between *phoenicea* and *sinuata*. This latter difference may still be sufficient to warrant generic recognition of *Richmondena* and *Pyrrhuloxia*. The mandible of *P. sinuata* is quite unique for the group, suggesting that this bird differs from *phoenicea* as well as *cardinalis* in feeding habits. Actually the differences between individual species of this complex are not as important as the total adaptive range embraced by the complex. Judgment of generic limits in the Cardinal–Pyrrhuloxia complex should be made by comparing the adaptive range embraced by these birds with the adaptive range of other closely related genera. The total range of the variation of bill structure may be used as an index to the adaptive range of the group in feeding methods.

The bills of *cardinalis*, *phoenicea*, and *sinuata* are shown in Fig. 1, which illustrates clearly the shift from an elongated bill in *cardinalis* to a short, parrot-shaped one in *sinuata*. The bills of the four species of *Paroaria* are shown in Fig. 3. These birds differ somewhat in the thickness of their elongated bill although they exhibit less variation in shape than in the *Richmondena–Pyrrhuloxia* complex. However, the range of bill shape in the genus *Saltator* (Fig. 4) is much greater than in the Cardinal–Pyrrhuloxia group, although the limits of *Saltator* are accepted by most, if not all, ornithologists. The extreme forms in this genus, *maxillosus* (Fig. 4A) and *a. atripennis* (Fig. 4G) or *maximus* (Fig. 4I), are certainly more different in bill shape than are *R. cardinalis* and *P. sinuata*. Another example, although of a more distantly related genus, is *Geospiza*. The difference in the shape of the bill between *G. magnirostris* and *G. scandens* (Lack, 1947) is greater than between the Cardinal and Pyrrhuloxia. The variation in the relative size of the bill within *Geospiza* aside from any difference in configuration is alone far

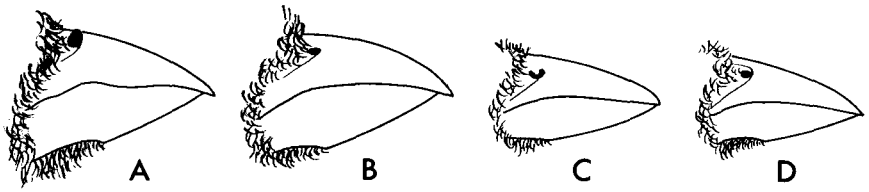

FIG. 3. Lateral view of the bills of (A) *Paroaria dominicana*, (B) *P. coronata*, (C) *P. capitata*, and (D) *P. gularis* to show the variation of the bill in this genus.

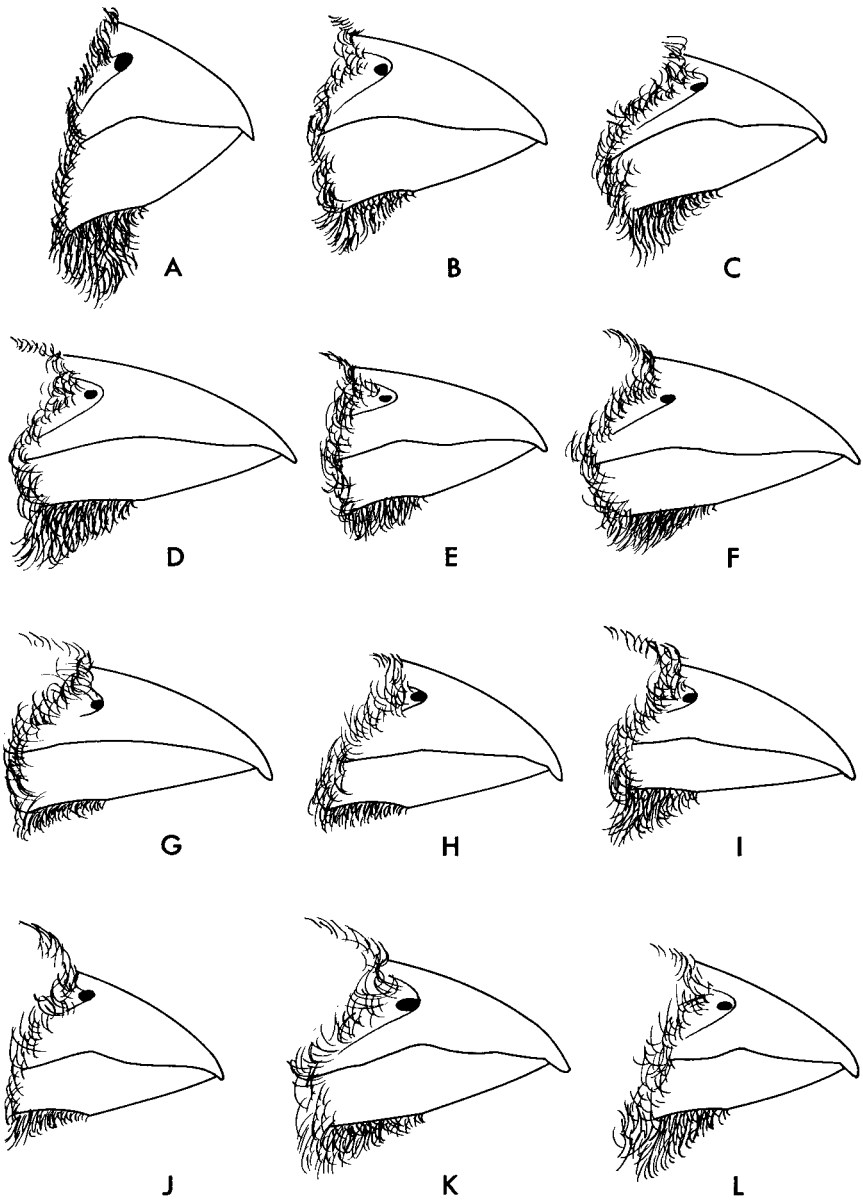

FIG. 4. Lateral view of the bills of (A) *Saltator maxillosus*, (B) *S. sinilis*, (C) *S. atricollis*, (D) *S. coerulescens hesperis*, (E) *S. c. grandis*, (F) *S. atriceps raptor*, (G) *S. atripennis atripennis*, (H) *S. a. atripennis*, (I) *S. maximus intermedius*, (J) *S. aurantiirostris*, (K) *S. albicollis guadelupensis*, and (L) *S. a. isthmicus* to show the great variation in the shape of the bill in a closely knit genus. Note especially the differences between the extreme forms *maxillosus*, *atripennis*, and *maximus*, and compare this difference with that seen between *R. cardinalis* and *P. sinuata*.

greater in adaptive significance than the difference in either *Saltator* or the *Richmondena–Pyrrhuloxia* complex.

The evolution of the differences in the bills of *cardinalis* and *sinuata* may provide additional evidence for determination of the degree of relationship between these birds. The essential similarity of these species suggests that their divergence was recent. The nature of their differences suggests that most of the divergence was a result of direct competition between these species. The major differences are (a) the morphology of the bill and the jaw muscles; (b) the color of the bill; (c) the male plumage; and (d) the general ecology and distribution. The Pyrrhuloxia appears to be restricted to the dry mesquite plains of the Southwest while the Cardinal appears to require a slightly more mesophytic habitat. This ecological difference between the two species may form the basis for their general geographic separation. Gould (1961) concluded that these species did not differ in their ecology in his study area, but it seems likely that the habitat in this study area was disturbed by previous cutting and agricultural practices. Certainly these species differ in their climatic tolerances and hence in their distribution as noted by Gould. This present-day lack of geographic overlap is the major snag for the hypothesis that the divergence between *cardinalis* and *sinuata* resulted from competition. Yet there is no reason to assume that these species were always separated geographically in the recent past. During the periods of glacial advance, one of the greatest changes in the climate of the Southwest was an increase in rainfall. Thus, it is quite conceivable that the Cardinal was able to extend farther into the now dry plains of the Southwest and overlap broadly the range of the Pyrrhuloxia during periods of glacial advance.

Assuming that the ranges of the Cardinal and the Pyrrhuloxia did overlap at one time, two major changes had to evolve if these closely related birds were to coexist in the same habitat. Little doubt exists that these birds descended from the same immediate common ancestor and hence were, at some time in the past, more similar in plumage, bill structure, and ecological requirements. A difference in feeding methods must have developed. This could account for the divergence in the morphology of the bill and jaw muscles. Different and distinct species recognition marks were essential. The great difference in the male plumage could be the result of this requirement, especially if the female chooses the singing male as in most passerine birds. Yet it is interesting that the songs of these species are so similar. The silhouette of a singing Cardinal is almost indistinguishable from that of a singing Pyrrhuloxia to the human observer and presumably also to the females of these species, and it is difficult to separate them by song. The females of these species are even more similar. However, the shape and color of the bill of each species are quite distinct, so much so that these birds can be

identified at a long distance if the bill can be seen. Lack (1947) has shown that the various sympatric species of *Geospiza* use the bill as species recognition marks. It is thus reasonable to suggest that the disparity in shape in the bills of the Cardinal and the Pyrrhuloxia serves as species recognition marks as well as enabling these birds to feed on different seeds. The present-day differences in habital preferences which account for the geographical separation could have also evolved through competition. Although these species may have overlapped broadly, they may have segregated out into different parts of the habitat, the Cardinal to the more mesophytic areas along river bottoms and the Pyrrhuloxia to the xerophytic uplands.

With the retreat of the ice fronts and the general drying of the climate in the Southwest, the Cardinal may have been forced out of the drier sections. The xerophytic mesquite plains were left to the Pyrrhuloxia. The Cardinal is still spreading north and northeast, which may be a continuation of the range expansion that started with the retreat of the glaciers (see Beddall, 1963, for a discussion of this point).

The hypothesis that the divergence between the Cardinal and the Pyrrhuloxia resulted from competition between these species is important owing to its taxonomic consequences. In general, specific differences that are the result of ad hoc selection to mitigate interspecific competition are of lower taxonomic relevance than differences that are the result of a general genetic divergence. The fact that these differences resulting from interspecific competition may appear striking to the ornithologist does not affect the validity of this general conclusion. Indeed, this category of differences constitutes one of the special cases for which the general rule that taxonomic distinction is correlated closely with morphological divergence cannot be applied. Closely related species may be more distinct in a few special characters (ones that are often extremely important for the species) than is usually the case. This special situation has been shown, on one hand, for species-specific recognization features (see Sibley, 1957). On the other hand, it has been shown for feeding methods and other ecological preferences by Lack (1947), Vaurie (1951), Brown and Wilson (1956), and others under the general heading of character displacement.

As a general conclusion, it can be stated that generic distinctions should not be based upon morphological and other differences which have resulted from competition or other types of direct interaction between closely related species.

CONCLUSION

The evidence and arguments presented allow only the conclusion that the three species *cardinalis*, *phoenicea*, and *sinuata* are congeneric. The reasons

supporting this conclusion are: (1) Many good genera of birds contain one or two species that are strikingly different in a character or character complex without justifying generic separation; (2) these species form a natural group separated by a distinct gap from other cardinaline finches; (3) differences resulting from ad hoc selection to mitigate interspecific selection have less taxonomic value; (4) the adaptive range encompassed by this group is no greater than by *Saltator* and *Geospiza*; and (5) the gap between the two extreme species *cardinalis* and *sinuata* is bridged by an essentially intermediate species—*phoenicea*. If *Richmondena* and *Pyrrhuloxia* are maintained as separate genera, then the principle of consistency would require that genera such as *Saltator* and *Geospiza* be divided into several smaller genera. Such action would greatly decrease the usefulness of our taxonomic system and in particular would decrease the utility of the genus as a taxonomic category beween the species and the family. Thus the species *cardinalis*, *phoenicea*, and *sinuata* would be placed in the genus *Pyrrhuloxia* with *Richmondena* in synonymy.

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NEW LIFE MEMBER

Francis M. Uhler, of Laurel, Maryland has become a Life Member of The Wilson Ornithological Society, which he first joined in 1931. Mr. Uhler, a graduate of Gustavus Adolphus College, is a biologist with the U.S. Fish and Wildlife Service, specializing in waterfowl habitat management. His principal ornithological interest is in the food habits of waterfowl, and the picture shows Mr. Uhler harvesting wild millet for the seeding of duck impoundments. Mr. Uhler is the co-author of a Fish and Wildlife Service report on "Food of Game Ducks of United States and Canada" as well as various other papers on aquatic wildlife. Mr. Uhler is a member of the American Ornithologists' Union, the Cooper Ornithological Society, The Washington Academy of Science, as well as of other biological societies. His hobbies are canoeing, photography, and the study of wetland ecology.