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THE RELATIONSHIPS OF CERTAIN BIRDS AS INDICATED BY THEIR EGG WHITE PROTEINS

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INTRODUCTION

THIS paper attempts to forge a new taxonomic tool from techniques used in chemistry and field ornithology.

Mayr (1942: 45), speaking about the phenomena of geographic variation in relation to systematics, stated that "Small physiological differences between populations, subspecies and species are often more important biologically than the accompanying structural differences." The basic premise to be developed in this paper is that the protein composition of egg white is a physiological character that can be used in the study of avian taxonomy.

The method utilized in this study of the protein composition of egg white is termed electrophoresis. It may be briefly defined as the migration of charged colloidal particles to the pole of opposite charge when solutions of colloidal materials such as proteins are placed in an electric field.

Inasmuch as this paper is directed to an ornithological audience, further clarification on method and chemical terminology is in order. The electrophoretic study of the protein composition of a given egg white is carried out by the moving boundary method (Tiselius, 1937). This implies in part that the individual molecules of a solution of egg white proteins at a given pH in an electric field will move at different rates toward either the positive or negative pole. The speed of movement of each kind of protein molecule depends in part on its electric charge. Likewise, the quantity of the components is recorded photographically as a refractive index function and represented as a series of peaks, each of which will arbitrarily be expressed as a curve similar in configuration to a frequency distribution curve (Figs. 1 through 7). The ordinates on the electrophoretic pattern represent gradients in

THE CAHOW, *Pterodroma cahow*, PAINTED BY ROGER TORY PETERSON.

refractive indices, *i. e.* protein concentration, and the abscissae indicate the position of each protein component in respect to the total distance moved in the course of an experiment. The electrophoretic pattern can be enlarged and the area below each peak planimetered to give a rough measure of each component. For taxonomic purposes this is (as yet) unimportant. Likewise we need not concern ourselves with the salt boundaries (anomalies) in the patterns which are labeled with the Greek letters δ and ϵ for the ascending (left) and descending (right) patterns respectively. They represent the approximate starting points for all of the protein molecules. Further detailed information on electrophoresis was adequately given in the papers of Longsworth (1942) and of Alberty (1948).

Previous electrophoretic work on the egg white proteins of wild birds was carried out by Bain and Deutsch (1947). Proteins of several closely related species were compared, but no mention was made by these or previous investigators of the possible taxonomic value of the results. They did however point out greater similarities among closely related species. Our earliest suspicion of phylogenetic relationships came with the examination of the electrophoretic patterns of the egg white proteins of the Coot, *Fulica americana*, and Florida Gallinule, *Gallinula chloropus cachinnans* (Fig. 2B), two birds from separate genera of the family Rallidae. A close relationship of the various proteins as indicated by similarities of their electrophoretic patterns showed that the two birds were in this respect physiologically similar. Despite over-all similarity, there were sufficient differences to make each pattern distinct. With this and the previous work as an incentive, we made further comparisons of egg white proteins to check this method with those based on orthodox taxonomic characters.

ACKNOWLEDGMENTS

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METHODS

The first step in the analysis was to obtain fresh eggs from wild birds. It is here that the techniques of field ornithology are brought to bear. A knowledge of the nesting habits, phenology, and the breeding cycle of each species is essential. It is inherent in wild birds to disguise, conceal, or secrete their nests, so that to obtain eggs the nests must first be located. The difficulties in all but the commonest species need no elaboration.

Completed clutches were first thought to be undesirable because in most species one or more of the eggs would have had some incubation. This is evidenced by the irregular time (*i. e.* on successive days) of hatching in most songbirds. It was further thought that incubation, even for a short period, might drastically alter the protein structure in the albumin. Recent work by Marshall and Deutsch (1950) on chicken egg white showed, however, that this was not the case. They stated (p. 160) "During the development of the chick embryo, the proteins of the egg white and of the amniotic fluid appear to remain in the same relative proportion in which they are present in fresh egg white." In this study, however, no eggs from completed clutches were used and to our knowledge all eggs were fresh.

The egg shell was punctured around the middle and the contents run onto a clean chemical watch glass. If the vitelline membrane surrounding the yolk ruptured, the egg was not used. Special care was taken to remove as thoroughly as possible the egg white adhering to the inner surface of the shell and to the vitelline membrane. This was accomplished by means of a small pipette. This material was then mixed with three volumes of a diethyl barbiturate buffer (pH 8.6 and ionic strength of 0.1) and gently homogenized. The buffer maintains a constant pH which is necessary to the electrophoretic processing. Unless the sample was used immediately, it was quick-frozen with the help of a dry ice and alcohol bath and stored at $-10°$ to $-15°$ C. When needed, the material was brought back to a liquid state and dialyzed from 48 to 96 hours at 0° to 2° C. against changes of buffer and then analyzed electrophoretically. The insoluble mucous strands and chalazae were removed after an initial 48-hour dialysis and discarded. The duration of the experiment was usually 10,800 seconds with a constant potential gradient of between 5.8 and 6.3 volts per cm.

The photographs of the protein composition by the electrophoretic apparatus were taken on small plates. These were enlarged, redrawn, and blocked in with India ink, as shown in the various figures. All

discernible peaks were regarded as separate protein components, analyzed,[1] and numbered in order of increasing electrophoretic mobility. It must be recognized that the selection of components is at times arbitrary, particularly in cases showing poor electrophoretic separation. The numbers on the patterns are not to be compared between diagrams, but merely represent protein molecules of an electrophoretic mobility within a restricted range. The width of each pattern is dependent on the duration of the experiment, the amount of current utilized, and the electrophoretic mobility of the proteins. The important function for a given protein molecule is its electrophoretic mobility, and the unequal widths of the various diagrams in no way invalidate the comparisons.

The electrophoretic diagrams for the egg white proteins of the Domestic Chicken, Turkey, and Guinea Hen, the Muscovy and common Mallard Duck, Ring-necked Pheasant, Coot, Black Tern, English Sparrow, Rock Dove, and Ringed Turtle Dove were presented previously by Bain and Deutsch (1947). These diagrams were reanalyzed for the greatest number of discernible components and not as was done previously, for entities supposedly related to known proteins of chicken egg white. The inclusion of these electrophoretic diagrams is important for a consideration of their relationships to many of the other egg white systems reported here for the first time.

The number of eggs used in each sample varied. Only one egg was available for the large exotic gallinaceous birds. The ducks were represented by two to six eggs per sample and the songbirds by four to eight eggs.

Larger numbers of eggs would seem desirable, but interpolating from the Domestic Chicken, there appears to be virtually no variation in egg white proteins among eggs of a clutch or between clutches of different chickens. Many dozens of chicken eggs have been analyzed electrophoretically in the process of purification of their egg white protein components so that variations, if they existed, would have been detected.

The nomenclature and taxonomy unless otherwise stated were taken from the fourth edition of the A.O.U. 'Check-list of North American Birds' (1931) and Peters' 'Check-list Birds of the World,' Volume 2 (1934), for the remaining foreign species.

DISCUSSION

Delacour and Mayr (1945) reclassified the duck family Anatidae "to arrange the species in related groups and in a natural sequence,

[1] The analytical data showing the quantity of each component and its mobility rating for each species can be obtained in tabular form by writing H. F. Deutsch, Department of Physiological Chemistry, University of Wisconsin, Madison, Wisconsin.

and to adjust the nomenclature of species and genera to progressive concepts of these categories." A review of that paper will reveal that these ends were thoroughly and effectively accomplished. The ducks were regrouped by the use of morphology and also by characters available to the ecologist, behaviorist, and field worker. The basis for the reclassification was in part the bird's general behavior and courtship, its living and nesting habits, and the down pattern of the young. Such criteria can readily be seen by the nonsystematist.

The Delacour-Mayr grouping of the "river ducks" puts all but four "aberrant" species (each in a monotypic genus) into the genus *Anas*. With this single genus as a base datum, we electrophoretically examined the egg white proteins of five species of river ducks. The electrophoretic patterns are shown in Figure 1A. It is at once clear that the five river ducks show strikingly similar electrophoretic patterns, yet each is sufficiently distinct so that the patterns are not confused. Thus it appears from examination of a comparable physiological character (egg white protein) that the river ducks are *very* closely related; therefore, limited as our evidence may be, it shows that the justification for a single genus as proposed by Delacour and Mayr is well-founded. It might also mean that the method employed here is most useful above the generic level.

Unfortunately we have only one member of the pochard group to add to the comparison. The pattern for the Redhead, *Aythya americana*, is shown in Figure 1B. This pattern is so much like that of the river ducks that it might well be considered as being from that group. What this means we cannot say until more experiments on the egg whites of other species of this genus are run. From this single instance it might be inferred that pochards are more closely related to river ducks than to any other group. This is further emphasized when the egg white pattern of the Redhead is compared with that of a perching duck, the Muscovy, *Cairina moschata*, and that of a stiff-tailed duck, the North American Ruddy Duck, *Oxyura jamaicensis* (Fig. 2A). In these comparisons it is likewise plain that the egg white diagram for the Muscovy is intermediate in configuration between those of the river ducks and that of the radically different Ruddy Duck. All this, including the close resemblance of the Redhead to the river ducks, further substantiates the division of the Anatidae made by Delacour and Mayr.

From the family Rallidae we have the electrophoretic patterns for the egg white proteins of the Florida Gallinule and the American Coot. The patterns (Fig. 2B) show the two are quite similar and also that the suspected protein components are the same in number. The

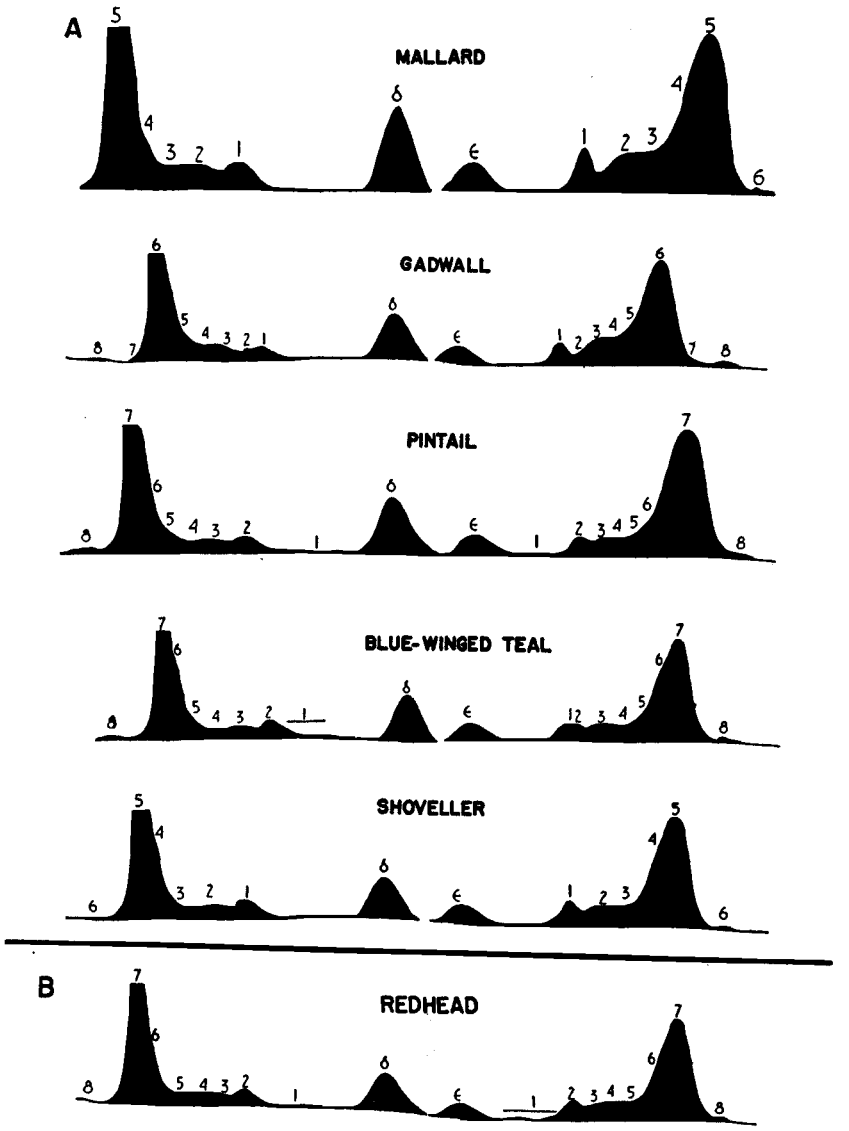

FIGURE 1. Electrophoretic patterns for some species of waterfowl.

patterns for the Purple Gallinule, *Porphyrula martinica*, and the European Coot, *Fulica atra*, when made will present interesting inter- and intra-generic comparisons.

The two other water birds for which we have patterns (Fig. 3A) are the Black Tern, *Chlidonias nigra*, and the Pied-billed Grebe, *Podilym-*

bus podiceps. These are presented merely to show the differences between distantly related groups.

The patterns (Fig. 3B) of the Ringed Turtle Dove, *Streptopelia risoria*, and the Rock Dove, *Columba livia*, show less inter-generic similarity than any others we examined. In general the physiology, morphology, behavior, and life history of these two doves imply a closer relationship than their egg white patterns indicate.

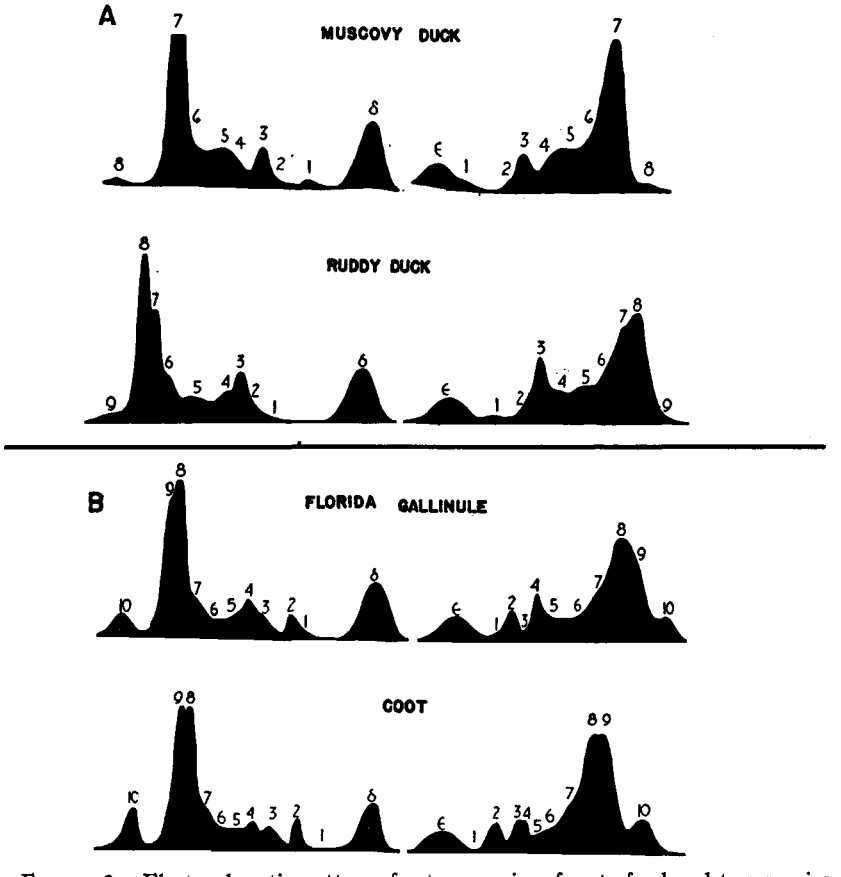

FIGURE 2. Electrophoretic patterns for two species of waterfowl and two species of marsh birds.

Collections of birds' eggs for this study were governed primarily by availability and expedience. We have, however, seven patterns to compare among the passerine birds. The first (Fig. 4A) is an inter-generic comparison between the Catbird, *Dumetella carolinensis*, and the Brown Thrasher, *Toxostoma rufum*. The resemblance between

the two is very clear despite definite analytical differences. It would be interesting to have an analysis for the remaining member (in eastern United States) of the family Mimidae for comparison, namely the Eastern Mockingbird, *Mimus polyglottos*. From the closely related family Turdidae the electrophoretic patterns for the Robin, *Turdus migratorius*, and Bluebird, *Sialia sialis*, are shown in Figure 4B. The interfamily comparison shows a definite affinity of the two groups. The Bluebird pattern bears a closer relationship to the patterns of the two species of Mimidae than to that of the Robin.

The two generic patterns in the thrush group show wider differences than are found between the two mimid genera. Note the plateau between the peak components on both sides of the pattern in the Robin, which is wanting in the Bluebird pattern. From appearances alone it would seem that there is a closer phylogenetic relationship between the Brown Thrasher and Catbird than between the Robin and Bluebird. This seems to agree with the morphological evidence which shows the Catbird to be a slightly aberrant thrasher. The Robin and Bluebird are morphologically dissimilar in many ways. In the latter case again we would like to have been able to present the egg white patterns for the Varied Thrush, *Ixoreus naevius*, and the "brown-backed" thrushes, *Hylocichla* spp., to mention but two genera.

A European weaver finch (the English Sparrow—*Passer domesticus*), and the Eastern Goldfinch, *Spinus tristis*, show very little conformity in egg white patterns (Fig. 4D), despite their being classed phylogenetically as "advanced" bird families. This fact, however, need not imply close relationship. The Cedar Waxwing, *Bombycilla cedrorum* (Fig. 4C) and Goldfinch patterns are not too dissimilar as an interfamily relation.

The remaining large group for which we have patterns is that of the galliform birds, representing three families, Phasianidae, Numididae, and Meleagrididae. In the family Phasianidae eight genera are represented, four of these by a single species. Of the genera with two or more species for comparison, the first (Fig. 5A) is between the Chukar Partridge, *Alectoris graeca*, and the French Red-legged Partridge, *Alectoris rufa*. The electrophoretic pattern for the latter species is somewhat more complex, but the similarities are obvious. The taxonomic juxtaposition appears justifiable when these patterns are compared with that of the Bobwhite Quail, *Colinus virginianus* (Fig. 5B) where the similarities are less pronounced, as they should be since the comparison is between genera of two subfamilies. *Colinus* is in the subfamily of American quails, Odontophorinae, and *Alectoris* is in the subfamily of partridges, quails, and pheasants, Phasianinae.

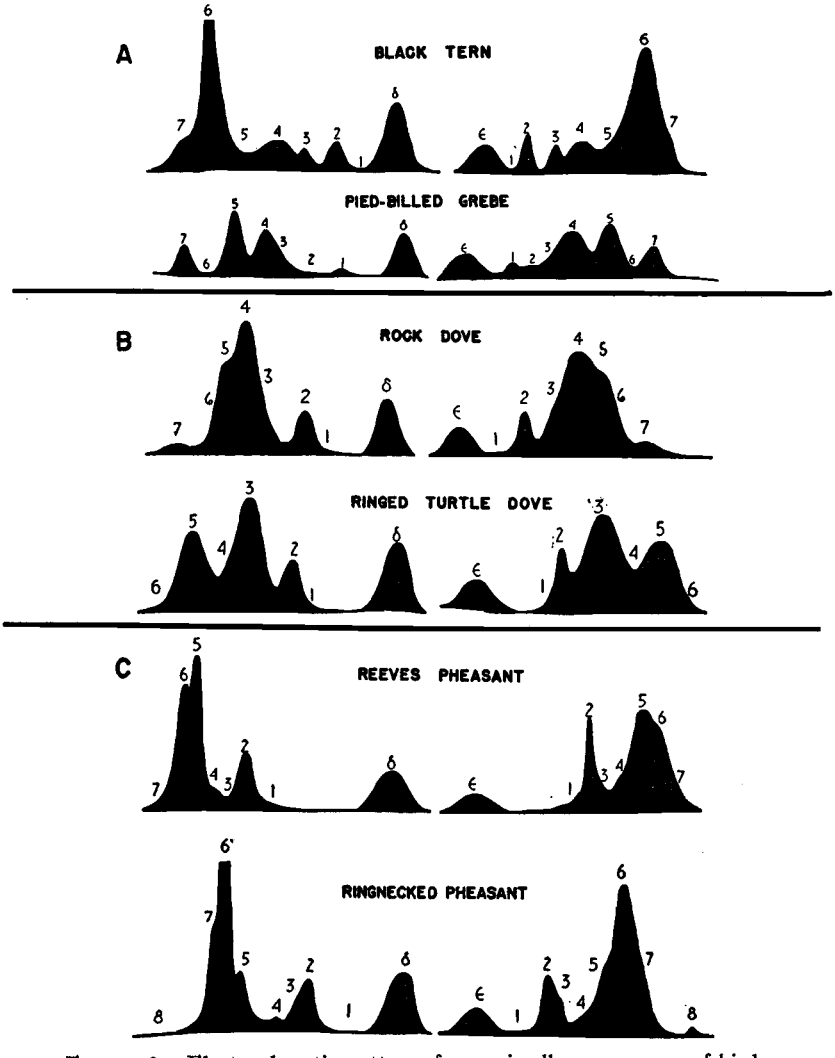

FIGURE 3. Electrophoretic patterns for a miscellaneous group of birds.

The *Alectoris* group lies taxonomically between the genus *Gennaeus* and the genus *Colinus*, but shows no closer affinity to one than the other. Beebe (1921) treated the Nepal and White-crested kaleeges and the Silver Pheasant as separate species, *Gennaeus leucomelanus*, *G. albocristatus*, and *G. nycthemerus*. Peters (1934) considered the two kaleeges as subspecies and the Silver Pheasant as a distinct species, that is, *Gennaeus l. leucomelanos*, *G. l. hamiltonii*, and *G. nycthemerus*. Delacour (1949) reclassified these birds into the genus *Lophura* and

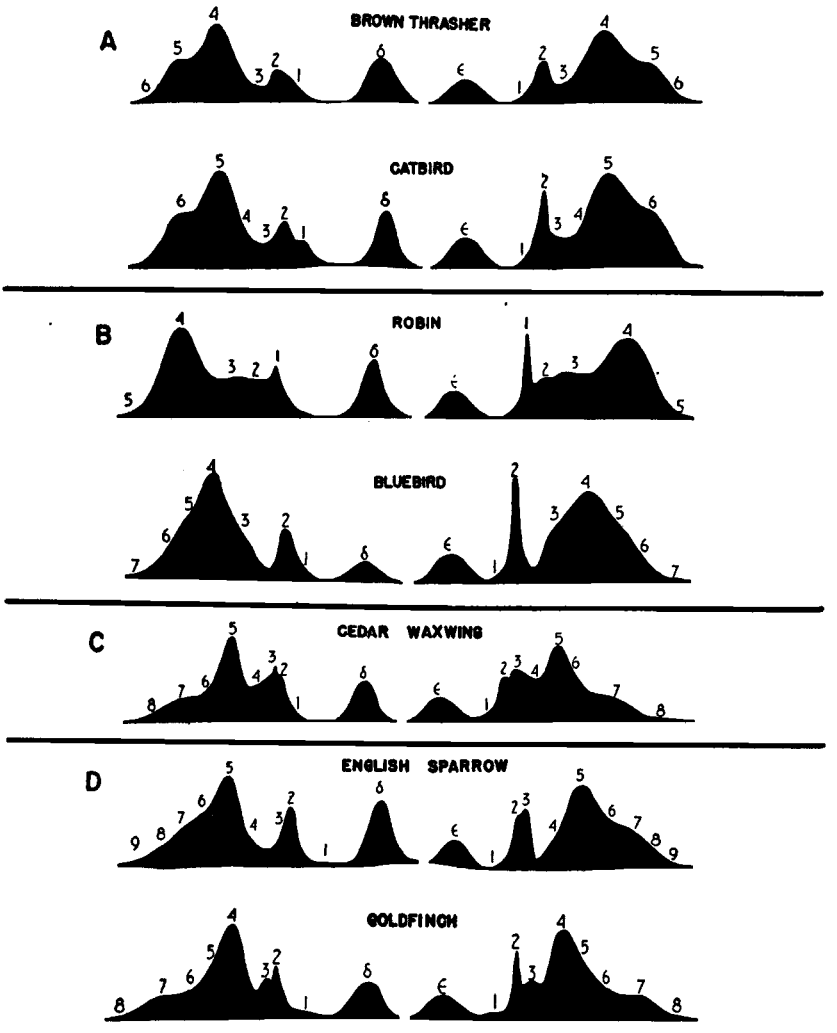

FIGURE 4. Electrophoretic patterns for a group of passerine birds.

as members of a superspecies, *L. leucomelana-nycthemera*. The two kaleeges are treated as subspecies, *L. l. leucomelana* and *L. l. hamiltoni*, and the Silver Pheasant as a species, *L. n. nycthemera*. Delacour (1949: 188) stated of the early classification of the gallopheasants "Such splitting was then perfectly understandable in accordance with the fashion of the day." By the same token one might consider the present day "lumping" tendencies to be a fashion also, awaiting to be split again by taxonomists in the future. Regardless of the published

taxonomic treatments, this much is clear from the electrophoretic patterns—the two kaleege patterns (Fig. 6A) are neither easily grouped nor readily contrasted with the Silver Pheasant. It might even be said that the pattern of the White-crested Kaleege is more like that of the Silver Pheasant than that of the Nepal Kaleege. As members of a genus, this trio has egg white proteins whose electrophoretic properties are surprisingly uniform.

The next three genera, *Gallus*, *Phasianus*, and *Syrmaticus*, are represented by the Red Jungle Fowl (*Gallus gallus*), the Ring-necked Pheasant (*Phasianus colchicus*), and the Reeves Pheasant (*Syrmaticus reevesii*), respectively. Each of these patterns is distinct, showing only enough similarity to be associated at a family level. Two patterns are shown in Figure 3C; the Red Jungle Fowl (Fig. 5C) will be used in a later comparison.

The patterns (Fig. 6B) for the Golden Pheasant, *Chrysolophus pictus*, and the Lady Amherst Pheasant, *Chrysolophus amherstiae*, show a marked similarity despite the presence of the component of high mobility in the latter pattern. It would not have been surprising in view of the present evidence had these two birds been classed as subspecies.

The Green Peafowl, *Pavo muticus*, and the Blue Peafowl, *Pavo cristatus* (Fig. 7A) show differences sufficient that a species classification seems logical. When the peafowl eggs were received from the State Game Farm one of the egg-sample labels read *Green or Black-shouldered Peafowl.* This was an obvious mislabeling since the Black-shouldered Peafowl is a mutation of the Blue Peafowl. This mutation was discussed in detail by Delacour (1951). The rather distinct differences between this pattern and that of the Blue Peafowl led us to suspect that the egg white sample came from the Green Peafowl. The Golden and Lady Amherst pheasants appear to be more closely related to the kaleeges than to members of the genus *Gallus*, *Phasianus*, *Syrmaticus*, or *Pavo*, according to the respective patterns.

The Guinea Hen, *Numida meleagris*, of the family Numididae is surprisingly similar in its pattern to the genus *Pavo* of the family Phasianidae. The number of suspected proteins is greater in the Peafowl, but the conformity is obvious, even to the split in the main peak on the left half of the pattern. No such similarity is apparent in the comparison (Fig. 7B) with the Domestic Turkey, *Meleagris gallopavo*, of the family Meleagrididea. The physiochemical evidence indicates a closer relationship of the Guinea Hen with the Peafowl than with the Turkey. On the basis of egg white proteins alone, the Guinea Hen could be placed in the genus *Pavo* of the family Phasi-

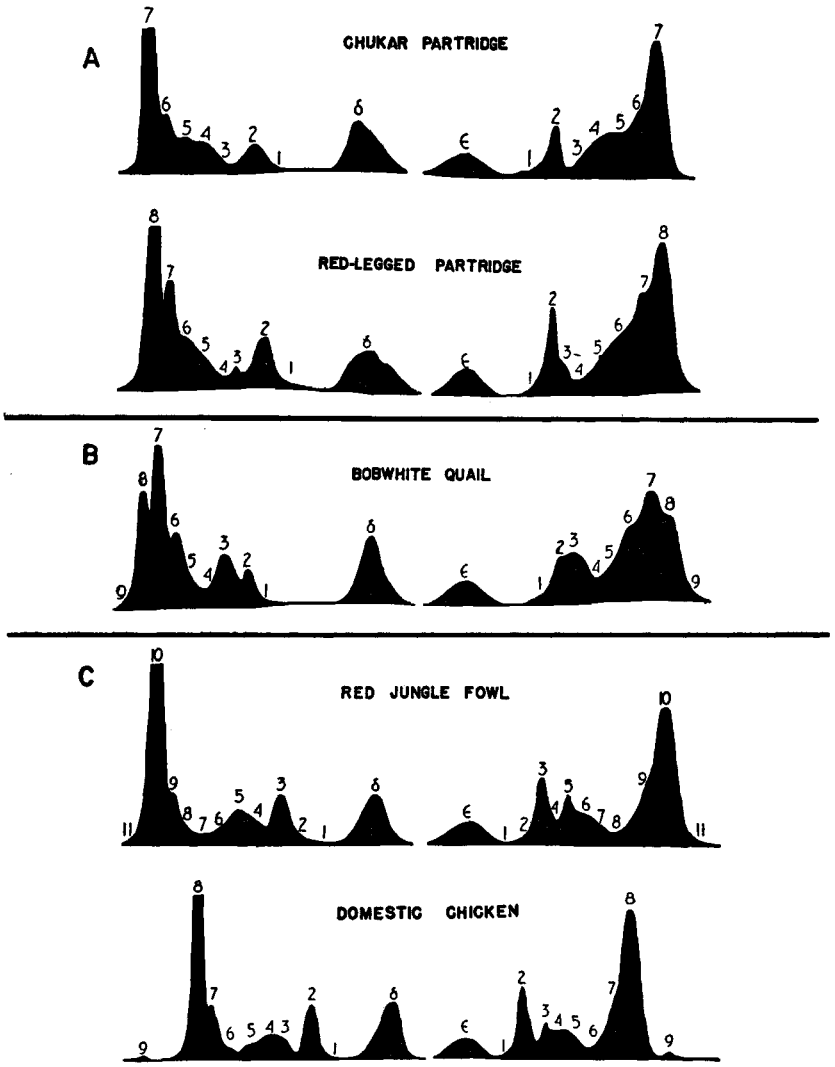

FIGURE 5. Electrophoretic patterns for a group of gallinaceous birds.

anidae. Greater inter-generic differences exist in other patterns than was indicated between these members of different families.

No systematic study has been made of the differences between the egg whites in all varieties of domestic fowl, but sample runs from several varieties indicate there is little or no difference among the commercial egg-producing chickens. The pattern used here (Fig. 5C) was made from pooled egg whites of White Leghorns.

Color, size, shape, etc. are characters, selected for in poultry husbandry, that make for morphological differences among the numerous varieties of chickens. If this selectivity can be considered rapid and relatively recent, then the composition of the egg white proteins for which there is apparently no selection should retain a pattern similar to that of the Red Jungle Fowl, *Gallus gallus*, which is generally considered to be the parent stock from which the Domestic Chicken has been developed. The comparison of patterns (Fig. 5C) shows a marked similarity between the two, despite the sharp peaks and numerous components involved. Here is an instance of known, although artificial, selection producing changes (*i. e.*, color, size, etc.) that are likewise known to be taking place in other birds in the wild through natural selection.

The conformity of the egg white patterns of the Domestic Chicken and the Red Jungle Fowl is clearly evident.

We found, as stated earlier, that some of the results of this electrophoretic process substantiate the taxonomy based primarily on morphology and also the more recent use of behavior, nidiology, down pattern of the young, etc. This outcome was not surprising. Hinton (1940), for example, found that his classification of the Mexican Water Beetles, *Elmidae*, based on internal anatomy, corroborated most of the taxonomy based on external morphology. In our work complete agreement was not hoped for or achieved.

In some cases the results suggest a closer relationship than is now shown by morphological criteria, *e. g.* the genus *Aythya* with the "river ducks" or the Guinea Fowl, *Numida*, with the Peafowl, *Pavo*. In other instances the relationship appears to be more distant, as between the Rock Dove, *Columba livia*, and the Turtle Dove, *Streptopelia risoria*, and between the Robin, *Turdus migratorius*, and the Bluebird, *Sialia sialis*.

One point that appears obvious from the electrophoretic studies is that the method is more sensitive above the level of the genus than below. Differences between families are clearly indicated, *e. g.* Anatidae and Phasianidae. Despite the apparent utility of this check on avian taxonomy, further work on its relative reliability is necessary before it can be accepted as a standard tool.

Some of the avian groups that might profit from a comparative study of the electrophoretic properties of the egg white proteins are as follows: Mockingbird family with the wrens; the Goldfinch, *Spinus tristis*, and Purple Finches, *Carpodacus purpureus*, with the American buntings; the sandpipers with the phalaropes; the nuthatches with the bush-tits and wren-tits; the goatsuckers with the owls; the cuckoos with

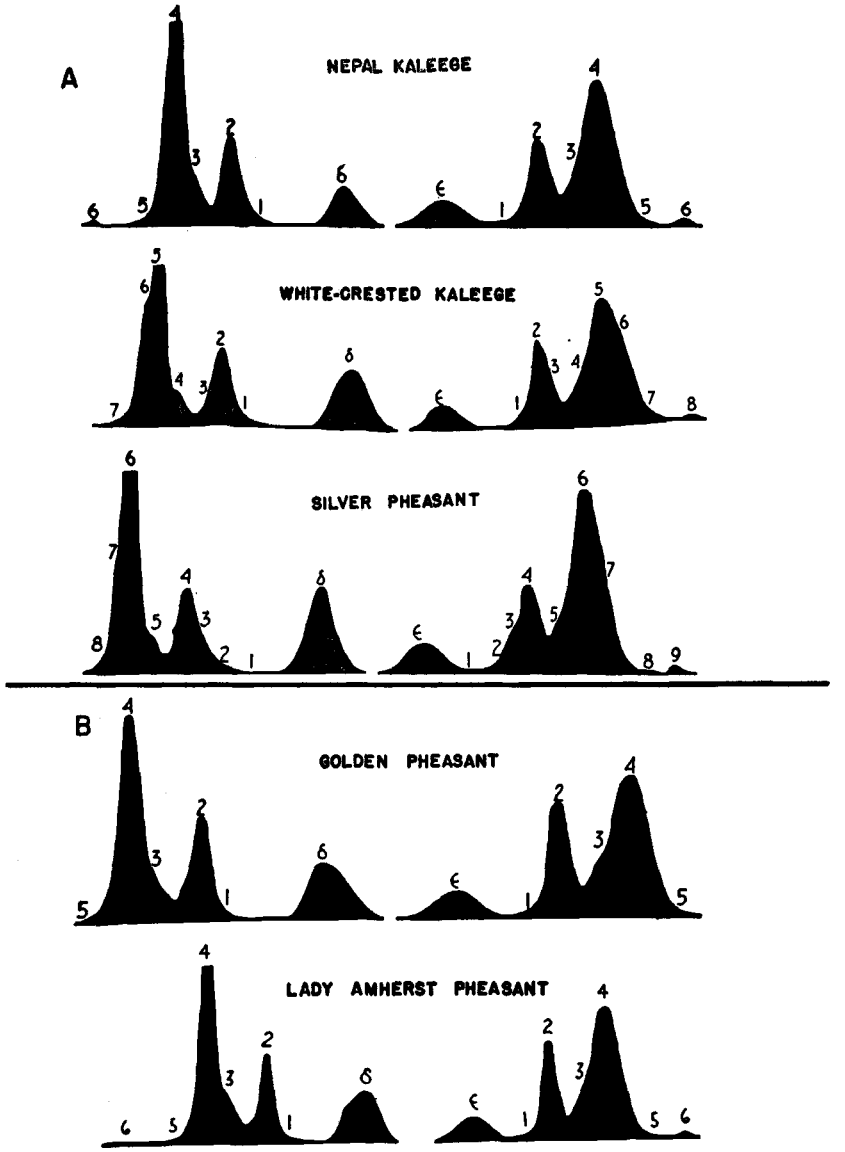

FIGURE 6. Electrophoretic patterns for some birds of the genera *Gennaeus* and *Chrysolophus*.

the gallinaceous birds; and American vultures with the hawks. Some individual comparisons worthy of investigation are: the Wood Duck, *Aix sponsa*, with the Muscovy Duck, *Cairina moschata;* the Song Sparrow, *Melospiza melodia*, with the Field Sparrow, *Spizella pusilla*, and Chipping Sparrow, *Spizella passerina*, and Old World buntings; the Cardinal, *Richmondena cardinalis*, with the Indigo Bunting, *Passerina cyanea*, and tanagers; and the Yellow-breasted Chat, *Icteria virens*, with the tanagers and wood warblers. This list is by no means complete, but does indicate that the problems are many and are not confined to any one taxonomic group.

Taxonomic relationships deduced from the comparison of the electrophoretic properties of egg white protein must be regarded as indicative only because of the extreme complexity of this protein system. There may exist many more proteins than are indicated under the present experimental conditions, *i. e.*, certain numbered components may consist of two or more proteins. Studies and recognition of the function of the individual proteins in the various species will be essential to this problem. Moreover, the number of egg whites studied electrophoretically to date is comparatively small.

The nature of the data, however, encourages speculation. The following discussion may serve to stimulate thinking and uncover leads for future work along these lines.

The use of egg white proteins as a common denominator to show relationships among birds need not and likely could not replace morphological characters, but it would clarify at a more fundamental level those groups or individuals that appear aberrant by present taxonomic standards. It seems possible that the physiochemical character of an egg retains more of its incipient phylogeny than the more superficial aspects of the bird's adult morphology. The survival value of a stout bill, wing size, particular coloration, and the like appear to be of greater importance than the protein composition of the egg white (at least as of our present state of knowledge regarding egg white proteins). Selective factors very likely operate rapidly and drastically at a morphological level and thus divergence may become apparent in a relatively short space of evolutionary time. The selection for factors affecting egg white proteins is probably slow, indirect, and less drastic. This, if true, would allow the various branches of a given phylogenetic stalk to retain a physiological lineage with the parent stalk, while the external modifications among the species tend to mask that relationship; witness the Galapagos finches. These finches bring up still another point. Lack (1947) mentioned that there is considerable doubt as to the nearest mainland relative of these island finches. An

investigation of egg white proteins might shed light on this and other aspects of the relationships among these birds.

The problem of avian affinities on archipelagos has been further investigated by Amadon (1950) on the Hawaiian Islands. His work was done on a family of Honey Creepers (Drepaniidae). This fine

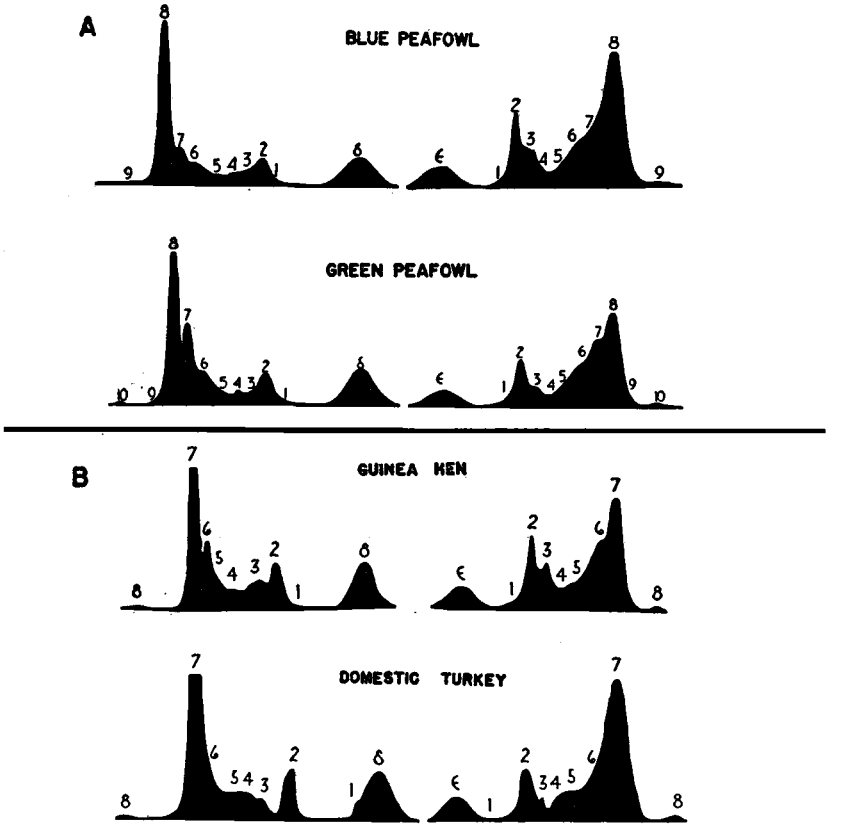

FIGURE 7. Electrophoretic patterns for members of the family Phasianidae (A); and the families Numididae and Meleagrididae (B).

work notwithstanding, Amadon stated (p. 253), "The primitive Drepanids 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." Here then is a case where morphology and anatomy have failed to give a systematist sufficient evidence to indicate the proper taxonomic posi-

tion of a group of birds. We suggest that a relationship may be evident on examination of the egg white proteins of these birds.

It is not inconceivable that relationships among birds may be studied by an interchange of albumin or the addition and subtraction of fractionated components between closely grouped forms. This type of experimentation could also test whether the albumin with its various components has any effect on gene action. If growth and differentiation of the embryonic chick are in part dependent on the albumin for food and environment, then any change in the ecology of the minute embryo could alter the appearance or functioning of the end product, namely the young bird.

Many of the components of chicken egg white have been isolated, studied and some functions made known. Research has already been carried out on various domestic birds as regards immunological relationships of some of the egg white components (Landsteiner, 1945; and Wetter, L. R., M. Cohn, and H. F. Deutsch, unpubl. data Univ. of Wis.). Other recent work in the field of immunology has uncovered some important facts that bear on this general problem. Irwin (1949: 119) stated "It is interesting that these species [doves of the genus *Streptopelia*] can be differentiated sharply by antigenic substances in either cells or serum, whereas certain measurable morphological characteristics—such as over-all length and extent, length of wing, beak, tarsus, middle toe, and tail feathers—do not permit a differentiation except on statistical bases." Although the above research was not concerned with taxonomy the indications are that, like the electrophoresis of egg white proteins, the antigenic substance in the blood, egg white, and tissues could serve to help clarify the taxonomic position of forms not readily classified by morphological characters.

Although we realize that this discussion section is largely speculation and that our data are limited, we hope the speculation has been provocative. It must be kept in mind that this approach to taxonomy and evolution is in a pilot stage and that no claims are made as to its eventual practicability.

SUMMARY

Electrophoresis, which is a method for studying certain properties of soluble proteins, was used to study the egg white composition of 37 species of birds' eggs. The results, which are expressed as blocked-in line graphs and commonly referred to as electrophoretic patterns, show similarities in configuration between some of the birds that are considered closely related taxonomically. In other instances these

patterns indicate a more distant relationship than is indicated in the present taxonomic position. No patterns were completely identical. Thus, each species has a distinct pattern of its own, which may show marked similarities to the pattern of other species. This relationship among birds using the egg white proteins as a common denominator is thought by the writers to be a tool in augmenting the present taxonomic procedure.

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