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ALAN H. BRUSH

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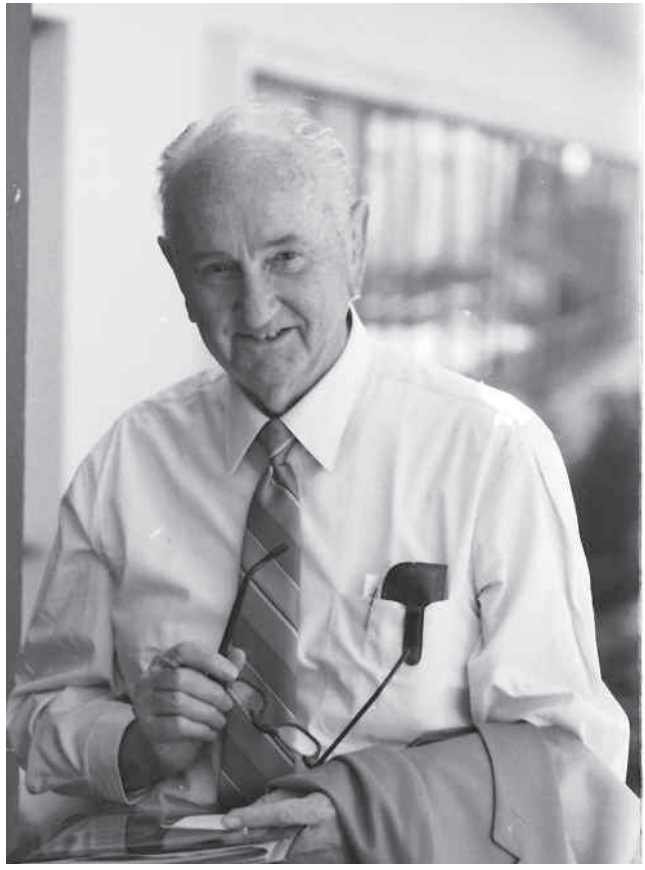

Peter Stettenheim, Plainfield, New Hampshire

Charles Sibley

CHARLES GALD SIBLEY

August 7, 1917–April 12, 1998

BY ALAN H. BRUSH

CHARLES GALD SIBLEY WAS born in Fresno, California, on August 7, 1917, and died at age 80 in Santa Rosa, California. He was not a small-town boy who simply moved upstate. Between his early years in Fresno and his ultimate move to Santa Rosa, Charles traveled worldwide to conduct and report on his research. He was one of the leading ornithologists during the latter half of the twentieth century, one of the founders and a major player in the emerging field of molecular systematics, and contributed significantly to our knowledge of the evolutionary relationships among the higher avian taxa.

Charles's intellectual intensity and excitement touched the lives of many of his contemporaries in ways both good and bad, and he influenced several generations of students. Few ornithologists have so polarized their students and colleagues. Ultimately his greatest impact may be the transmission of his ideas and intellectual fervor to students, which he did with an evangelical intensity, sometimes threatening his wrath but usually with the grace of a master communicator.

Charles was an exceptionally well-organized person, blessed with a fine intellect and an unyielding belief in himself. Those at the receiving end of one of his famous

verbal debates or attacks may not have looked beyond their own bruised egos to appreciate his finer qualities. He was a generous person, giving freely and frequently of his time to students and colleagues, particularly if it involved discussions of science. He took pride in his broad understanding of biology and its processes, but he stuck to his own beliefs and understanding of biological "facts" until presented with unequivocal information that he was wrong. Then, immediately, he would champion the new information, never looking back to dwell on the fact that he may have been wrong. This contrary nature of being dogmatic on the one hand, while always welcoming new information on the other, made it difficult for some people to deal with Charles and his science, but for his students he was an endlessly variable, fascinating, and challenging role model.

Charles was associated with six universities over the course of his academic career. His first appointment was a one-year assistant professorship in 1948 at the University of Kansas. A year later he returned to his native state to join the faculty of San Jose State College (now California State University at San Jose) as an assistant professor of zoology. In 1953 he went to Cornell University as curator of birds and associate professor of zoology in the Department of Conservation. During his 12 years there Charles advanced to professor, taught ornithology to overflowing classes of both graduate and undergraduate students, developed Cornell's scientific collection of bird specimens, and mentored nine graduate students and one postdoctoral fellow. In 1959-60 he took a sabbatical year at Oxford University as a Guggenheim fellow. Back on the Cornell campus during the summer of 1962, he oversaw the activities of the 13th International Ornithological Congress. Broadly speaking, his research during the Cornell years dealt with hybridization between species-pairs and the molecular systematics of avian orders and families.

Charles, who prided himself as an ornithologist, joined the American Ornithologists' Union (AOU) in 1939, became an elected member in 1949, and a fellow in 1955. He served as treasurer for 11 years, from 1953 to 1963, and as president during the 1986-88 term. Before becoming president Charles served twice as vice-president and was elected to several terms on the Council. In 1971 he was awarded the Brewster Memorial Medal by the AOU, and in 1986 both he and his wife, Frances, became patrons of the organization he had served so often and well.

In addition to his AOU activities Charles was a secretary of the Cooper Ornithological Society, a fellow or corresponding fellow of six foreign societies, and an officer or council member of five societies. From 1958 to 1962 he served as the secretary-general of the 13th International Ornithological Congress, and from 1986 to 1990 he was president of the 20th International Ornithological Congress. Altogether he was a member of about 15 scientific societies, including all major ornithological societies of the United States, as well as Deutsche Ornithologen-Gesellschaft, Société Ornithologique de France, Asociación Ornitologíca del Plata, and Suomen Lintutieteellinen Yhdistys. He served on the editorial boards of *Evolution*, *Journal of Molecular Evolution*, and *Molecular Biology and Evolution*.

In 1965 Charles moved to Yale University as a professor of biology, the William Robertson Coe Professor of Ornithology, and curator of birds of the Peabody Museum of Natural History. In 1970 he was appointed director of the Peabody Museum of Natural History. During his years at Yale Charles advised another seven graduate students and three postdoctoral fellows. In 1986 he was elected to the National Academy of Sciences. That same year Charles retired and was named a professor emeritus of Yale University. Later that year he and Fran again moved back to California. There

he became affiliated with San Francisco State University as a Dean's Professor of Science and Professor of Biology. In 1988 Charles and colleague Jon E. Ahlquist received the Daniel Giraud Elliot Medal from the National Academy of Sciences in recognition of their contributions to our knowledge of avian systematics, and in 1991 Charles was awarded the Alessandro Ghigi Medal by the National Institute of Wildlife Biology (Italy). His final appointment occurred in March 1993 after moving to Santa Rosa. There he was named adjunct professor of biology at Sonoma State University, in part so that he could have continued access to his extensive personal library that he had given to the university.

In his conversations with students and colleagues Charles could generate great excitement about the potential of his research. He delighted in invitations as plenary or keynote speaker and he occasionally organized mini-symposia at scientific meetings, where he and his students would give papers updating their current research. Throughout his career he attracted individuals upon whose lives he made an indelible mark. Among those who studied with him are four AOU elective members, eight AOU fellows, an AOU secretary, an editor of *The Auk*, and an AOU treasurer.

Every project that Charles undertook demonstrated his talent for enlisting the help of an extraordinary diversity of people and expertise. For example, in 1961 when he first conceived of a DNA hybridization facility at Cornell, he sent K. W. Corbin to Bethesda to learn the techniques from the three investigators who had only months earlier developed the methodology. In 1966 when Sibley wanted avian blood samples from European species, he contacted a number of friends who would be at that year's International Ornithological Congress in Oxford, asking for their aid in that early work on hemoglobin; Charles was never hesitant

to enlist knowledgeable individuals well outside academia in order to achieve his goals in fieldwork.

No fieldwork of his illustrates this better than the immense effort he put into planning for the 1969 National Science Foundation expedition to Papua-New Guinea aboard the research vessel *Alpha Helix*. A year prior to that expedition Sibley and Prof. George A. Bartholomew (of the University of California, Los Angeles) made a comprehensive assessment of the potential field facilities, logistics, and personal contacts in that vast region. There they enlisted the cooperation and help of an amazing group of individuals, some of whom were local officials, administrators, ministers of either the Lutheran or Catholic churches, an archbishop, ranchers, pilots, local scientists and educators associated with the Australian National University facilities, members of the Australian Bush Patrol, telegraph operators, directors of sanctuaries, and native Papua-New Guineans.

As a youngster Charles was an avid birder and kept precise records of his observations very early on. He was introduced to natural history by reading John Burroughs and Ernest Thompson Seton. Close friend Robert Failing encouraged his interest in birds, and high-school teacher Jean M. Nelson was particularly supportive of his interests in natural history. Together they founded the natural sciences club at Oakland High School. In the mid 1930s as an undergraduate at the University of California, Berkeley, he gravitated to the Museum of Vertebrate Zoology (MVZ). MVZ had become a major center for the study of natural history under the direction of Joseph Grinnell, whose field notebook methods Charles would later use to fill 15 volumes that detailed years of fieldwork in his precise, unedited script. The MVZ maintained an emphasis on the fauna of the region, as well as an association with the museum of paleontology. Accordingly,

his first publications were on fossil birds obtained from the tar pits at Rancho La Brea in Los Angeles.

After graduation from Berkeley in 1940 (A.B. in zoology), Charles worked one year for the U.S. Public Health Service on plague suppressive measures. Military service intervened, and he was commissioned as an ensign in the U.S. Navy reserves. During the later stages of World War II he was called for active duty and rose to lieutenant as a communications officer in the Pacific theater during the last 19 months of the war. His primary station was on Emiru Island in the St. Matthias group, 75 miles off the northern tip of the Bismarck Archipelago. During his off-duty time he collected locally and sent scientific specimens back to the MVZ. That effort on Emiru was supplemented while on rest-and-relaxation expeditions to the Solomon Islands and the Philippines.

This combination of travel and the collection of scientific specimens was pure pleasure for Charles and would typify family travel experiences over his lifetime. As the years passed, his collection of museum specimens was replaced by the collection of egg-white and blood samples for serum, hemoglobin, and ultimately the extraction of DNA. For example, following the 14th International Ornithological Congress in Oxford, England, Charles organized a month-long European vacation around visits to zoological gardens, aviaries, and the homes of European colleagues in an ongoing effort to obtain critical species for his research.

After the war and now married, Charles returned to Berkeley in 1946 to pursue a doctoral degree under the direction of Alden H. Miller, who was himself a protégé of Joseph Grinnell. By the mid-1940s Miller had followed Grinnell into the directorship of the MVZ and was particularly interested in species-level taxonomic problems. At that time Charles met John Davis, another incoming Miller doc-

toral student, whom he joined on a series of collecting trips to Mexico. As a result Charles became fluent in Spanish, learned the ropes of carrying out fieldwork in Mexico, and was introduced to some peculiar Mexican bird specimens collected by Helmuth Wagner.

Those specimens turned out to be hybrids between two species of towhee in the genus *Pipilo*. Subsequently, for his doctoral research Charles decided to examine the complex patterns of plumage variation caused by hybridization and the breakdown of species-specific reproductive isolating mechanisms between the red-eyed towhee, *P. erythrophthalmus,* and the collared towhee, *P. ocai,* along the transvolcanic plateau of Mexico. This was a zone of hybridization that stretched nearly 500 miles from southeastern Jalisco to the states of Veracruz and Puebla. His thesis "Species Formation in the Red-eyed Towhees of Mexico" was published as volume 50 of the University of California Publications in Zoology and was the first of 17 of his publications that dealt with avian hybridization.

A major contribution of his doctoral work was the application of a method for summarizing the plumage variation among hybridizing individuals as a single number, a hybrid index value. The establishment of a species-specific hybrid index scale was an extraordinarily powerful and ingenious method for analyzing complex, multigenic traits whose morphological patterns shifted geographically due to hybridization between incipient species. The method was later used by his first group of graduate students to study the complex patterns of hybridization between species-pairs in the Great Plains of North America. In retrospect, Charles's doctoral research can best be described as an early descriptive stage in the development of his understanding of the role played by hybridization, both during the process of speciation and as a result of the breakdown of reproductive isolating mecha-

nisms. These were significant conceptual and methodological contributions to our understanding of hybridization as a mechanism of evolution.

After Sibley moved to Cornell University the hybridization studies were extended to include other species-pairs that hybridized throughout the Great Plains of North America. They included Bullock's and Baltimore orioles, yellow-shafted and red-shafted flickers, indigo and lazuli buntings, and rose-breasted and black-headed grosbeaks. Those years were heady, exciting times for him, involving his first graduate students, David A. West, Lester L. Short, Fred C. Sibley (unrelated), and Paul A. Johnsgard in many field trips to collect hybrids along the Platte River and elsewhere in Colorado, Kansas, Nebraska, and the Dakotas. In addition he revisited the Mexican highlands to extend his earlier work there.

Although the hybrid index method had proven to be a powerful tool for studying the complexities of hybridization for the breakdown of reproductive isolation, by 1958 Charles was looking for better ways to quantify the degree of introgression between species-pairs. Simultaneously Paul Johnsgard was in need of financial support to complete his own doctoral thesis. In an attempt to resolve both issues Charles wrote a small proposal to the National Science Foundation to examine the possibility of using the new technique of paper electrophoresis to study species-specific variation in the serum proteins of game birds. If successful, it might be applied to the analysis of genetic variation in hybrid populations.

As the research assistant in this small study Johnsgard followed Charles's instructions to the *n*th degree—almost. It was the "almost" that would prove to be serendipitous. Like most of Charles's students both then and subsequently, Paul stood in mortal fear of invoking his wrath. Departure

from the laboratory protocols was a cardinal sin. Paul, however, had read McCabe and Deutsch's earlier paper on the electrophoresis of egg-white proteins. Out of curiosity and a broader interest, but without Charles's consent, Paul included a few egg-white samples along with the serum samples during his electrophoretic analyses.

At it turned out, even with the crude technique of paper electrophoresis, the serum protein electrophoretic patterns seemed much too variable among individuals to be applied to the hybridization studies. (Recall that at that time nothing was known about protein variation, either within or between species.) Lamenting this and greatly discouraged, Charles began to write up the results as a report to the National Science Foundation. It was then that Paul mustered the courage to reveal his covert analyses. The egg-white electrophoretic patterns were consistent among individuals of a species and differed among the few species that had been examined. Charles instantly recognized the implications of those observations. A powerful new tool and a new set of characters were awaiting application by systematists. Almost overnight he put aside his plans for using serum proteins to study the variation among hybrids and began to lay plans for an electrophoretic study of egg-white protein variation in birds. Over the subsequent decade and a half that research would become a massive comparative taxonomic study of the higher avian taxa. Indeed, the relationships among avian orders and families would be at the forefront of his research interests for the remainder of his life. Thus began the next phase of Charles's research, which would overshadow the earlier work throughout the 1960s and into the early 1970s.

The move to electrophoretic analyses of egg-white proteins involved a major shift in Charles's career. Along with Herb Dessauer of Louisiana State University, who studied reptiles and amphibians, and Morris Goodman of Wayne

State University, who studied primates, Charles became one of the founders of molecular systematics. For each of these men this shift required a great deal of retooling both mentally and in the laboratory. The transition involved a move from activities that primarily used classic fieldwork coupled with comparative morphology to one of daily laboratory analyses using the methods of comparative biochemistry. As one might expect, the new approach was also encumbered with some of the old thinking.

A peculiar bias that Charles carried concerned the genetic variation of structural proteins versus enzymes and the ways that natural selection would constrain the latter. He, along with one of his colleagues at Cornell, believed that enzymes would be invariant in their amino acid sequences due to evolutionary constraints on their activity. Enzymes, in their view, functioned only at specific temperatures and pH values, and natural selection would weed out all but the most effective structure for each enzyme and species. Indeed, during the early 1960s Charles and his colleague believed that an enzyme's primary structure might prove to be identical both within and among species. Any variation in an enzyme's structure would render it inactive according to their logic, and they knew little about the newly discovered phenomenon of allozymes being studied by Allan C. Wilson at the University of California, Berkeley, and Clement C. Markert at Johns Hopkins University. Thus, in their view enzymes would be unlikely to carry phylogenetic information and would be useless for both systematic and population genetic studies. Throughout much of the 1960s, informal debates on this issue occurred between Charles and Wilson.

Wilson's careful studies of allozyme variation, coupled with Markert's research on picine lactate dehydrogenases, eventually convinced Charles that enzymes did in fact vary within species. This conversion provided the basis for another

attempt to study the hybrids of the Great Plains. Though the shift in research was tangential to his main interests, it began in 1969 during the *Alpha Helix* expedition to Papua-New Guinea, where the laboratory work took place aboard the ship. Though the primary thrust of that expedition was to be a general sampling of the fauna of the world's second largest island, Charles's team also carried out some population genetic studies. Among other research problems, these included both hybridizing species-pairs (birds of paradise of the genus *Paradisaea*) and non-hybridizing species complexes (starlings of the genus *Aplonis*). In fact, of the 22 members of that expedition, 9 subsequently focused their activities on different studies of allozyme variation within and among populations. In addition to Charles, who was the prime mover and organizer of the expedition, the molecular systematists were H. C. Dessauer, A. C. Wilson, K. W. Corbin, A. H. Brush, A. Ferguson, J. E. Ahlquist, R. Storez, and V. M. Sarich.

From the outset of that work Charles was impressed by the analytical results involving two classes of enzymes, the esterases and the dehydrogenases. Both were variable within and among populations, and the frequencies of their variants (i.e., alleles) could be used to characterize individual populations. Within a few weeks of seeing the first electrophoretic results aboard the *Alpha Helix*, Charles began to think about applying the new methods to the hybrids of the Great Plains. The approach would be to sample populations of hybridizing species-pairs at intervals across the hybrid zone, just as in the earlier studies of plumage variation. This time, however, in addition to the construction of hybrid indexes, polymorphic enzymes, esterases perhaps, would be analyzed for their variation by means of electrophoresis. In contrast to the introgression of complex multigenic traits as quantified by hybrid indexes, the electrophoretic studies

of gene flow would involve single gene traits with simple patterns of inheritance.

The following year those plans began to unfold. The research vessel would be a modern prairie schooner, an Airstream trailer, outfitted with all essential electrophoretic equipment. A full crew was put in the field. After the first week the collecting focused on orioles and a study of the introgression of genetic variation caused by hybridization between the Bullock's and Baltimore orioles. The results flowed in. Specimens were collected in the mornings and late afternoons; during the midday periods enzymes were extracted and analyzed by means of starch gel electrophoresis. The database mounted and soon became impressive, encouraging the collecting party westward in 50-mile leaps across the zone of hybridization, and then back eastward, filling in the gaps between the initial collecting localities.

The collecting continued in 1971 and 1974. The results of the population genetic analyses confirmed the earlier morphological studies. Gene flow across the Great Plains was extensive, at least among populations of orioles. Alleles at esterase loci were being exchanged between the eastern and western populations, just as the plumage characters flowed eastward and westward through the filter of the zone of hybrids along the Platte River in Nebraska and Colorado. Presumably gene flow was comparable in the other riparian habitats stretching across the plains, although Charles's studies of the patterns of hybridization in the Mexican towhees showed that such assumptions might be unwarranted. Nevertheless, these studies and those by others revealed that the species of these hybridizing species-pairs might in fact be subspecies. This recognition was reflected in later versions of the *AOU Checklist of North American Birds.*

By 1974 Charles was already a decade and a half into

the taxonomic comparison of the egg-white proteins. The early electrophoretic methods for the separations of proteins on paper strips soon became obsolete. Paper electrophoresis gave way to starch gel electrophoresis, whose relatively crude resolution potential was supplanted by polyacrylamide gel electrophoresis and eventually by isoelectric focusing in either polyacrylamide gels or agarose plates. In an ongoing attempt to refine and improve his comparative data, Charles adopted each new improvement almost as soon as it became commercially available.

Early on he was convinced that the comparative study of protein variation could aid significantly in determining avian phylogenetic relationships at the higher levels of classification. He was equally certain that the methods would not be much help at the levels of species and genera. Although protein differences were basically phenotypic characters, they differed in one significant way from the traditional morphological characters used by most systematists at that time. Namely, protein structure, determined by amino acid sequences, was only one step removed from the genetic code itself. Consequently, differences among proteins were a more direct reflection of the underlying genetic similarities and differences among species than was gross morphology. It was this relationship between genes and the traits they encoded, in this case the primary structure of proteins, that convinced Charles he was on the right track.

The first results of the early electrophoretic studies suggested that the relationships among the higher taxa might be determined with relative ease. The protocols were simple: obtain egg white from the species of interest, separate the proteins of each sample on either starch or polyacrylamide gels under appropriate controls and standard electrophoretic conditions of wattage and time, stain the gels with amido blue black, photograph the gels, and then compare the

resulting patterns. Voila! Evolutionary relationships were revealed like never before. It was a heady time, and the world was watching and waiting for the results. Some were envious that Charles was making such headway in solving age-old taxonomic problems, others were bitter that their own expertise was being eclipsed, but most ornithologists were enthusiastic about the progress being made.

By as early as 1959 the Cornell laboratory was deeply involved in a comparative study of the egg-white proteins by means of acrylamide gel electrophoresis in small glass tubes. Soon thereafter, and with his usual skill, energy, and enthusiasm, Charles was extolling the virtues of those data in resolving longstanding systematic problems. At annual scientific meetings and through invited lectures in North America and Europe he spread the message about the wonders of the new comparative methods. In 1960 he eagerly presented data that demonstrated the affinities of the Old World sylviids and muscicapids in contrast to their more distant New World cousins, the parulids. By the time of the 13th International Ornithological Congress, which was held in 1962 in Ithaca with Sibley as secretary-general, there were electrophoretic data bearing upon the relationships of many more avian families.

The methods of electrophoretic analysis may have been relatively uncomplicated, but the effort to examine the evolutionary relationships of all the higher avian taxa by means of electrophoresis was daunting. There were the nests of thousands of species to find. Each egg-white specimen had to be compared electrophoretically over and over again. Thousands of analyses were carried out over almost two decades. Nothing but unequivocal data would satisfy Charles's objectives. How else could one compare all of the higher avian taxa by means of this new technology? The museums of the world housed the scientific specimens needed for

comparative morphological studies, but there were no depositories of egg-white specimens. Every species used in Charles's research program had to be collected by him and his collaborators.

Charles set out to do that, encouraging volunteers from throughout the world to collect samples and ship them to Cornell University. The effort was massive and profoundly successful. For over a decade the samples came in from every continent. Willing students acquired collecting permits, risked their necks climbing trees and cliff faces, combed forests, prairies, and tundra, all in search of samples from both common and rare species. Hosts of both professional ornithologists and amateur birders collaborated in the effort. Along the way more than a dozen technicians carried out the lab work that was completed at Cornell and Yale. The effort was monumental and culminated in two monographs published by the Peabody Museum of Natural History at Yale University: the first authored by Charles alone (1970) and the second coauthored with J. E. Ahlquist (1972). Charles was proud of these publications, as well he should have been. Many taxonomic problems were resolved, although others remained.

In addition to the egg-white protein studies there were side excursions to utilize other protein systems either by way of confirmation or for specific taxonomic problems. One of these, coauthored with A. H. Brush, involved an extensive study based on the electrophoretic variation of eye lens proteins. Another, coauthored with H. T. Hendrickson, involved the plasma proteins. Two particularly intractable taxonomic problems, one involving the relationships of the flamingoes and the other the relationships of the seed snipe, were tackled by using ion-exchange column chromatographic techniques to examine variation in the tryptic peptides of hemoglobins. Other studies were never published. The most

important of these was a massive database developed at Yale dealing with the electrophoretic variation of avian hemoglobins Sanples were obtained from over half of the then recognized bird species. Another study involved the use of serology to examine the blood serum proteins of muscicapids and sylviids. Ultimately it was the study of the egg-white proteins that paid the highest dividends.

The egg-white studies of the birds of the world, following those of avian hybridization on the Great Plains, would have been a life's work for most individuals in academia, but not for Charles. As the successes of the electrophoretic analyses of the egg-white proteins began to accumulate, a new technique was being tested in his laboratories at Cornell and later at Yale. The method's early development by others was an attempt to examine differences in DNA molecules by means of annealing, or hybridizing, short fragments of DNA to one another. The technique soon became known as DNA-DNA hybridization. Although Charles's laboratory at Cornell began to explore the potential of the method as early as 1963, another decade would pass before Charles had perfected the "DNA machine" in his laboratories at Yale.

The DNA-DNA hybridization studies involved the development of another tissue collection. Initially, while at Cornell, an attempt was made to use tissue culture methods to grow avian fibroblasts obtained from embryos. This method was soon abandoned due to technical problems and the availability of a more direct method. Because birds have nucleated red blood cells, blood samples were the obvious and expedient source of DNA. By the mid-1970s studies of the proteins of egg white, blood, and eye lenses were all but complete; it was time for the DNA studies to begin in earnest.

The years at Yale were some of the best for Charles and some of his worst. The best saw the publication of his egg-white monographs by the Peabody Museum of Natural His-

tory and the development of the DNA-DNA hybridization database. By 1986 the latter was being used to piece together a comprehensive phylogeny of the orders and families of the birds of the world. In printed form the dendrogram spanned more than 20 feet along the walls of poster sessions held in conjunction with annual scientific meetings during the 1980s. It thus became known as the tapestry and was a phenomenon in itself, as groups of people simultaneously examined its details.

The worst moments at Yale involved allegations against Charles for two kinds of scientific impropriety. The first was a federal indictment alleging that he had illegally imported the egg white of six European species, including one that was wholly fictitious and contrived by unknown individuals, either within or outside the U.S. Fish and Wildlife Service. After a good deal of media attention and the paying of a substantial fine, this episode eventually led to Charles's resignation of the directorship of the Peabody Museum of Natural History. It was a sad moment, indeed, for a man who had prided himself for following the federal guidelines regarding the necessary scientific collecting permits here and abroad. It was simultaneously a black mark against the scientific community that did so little to protest this injustice. Sibley never explained why he chose to pay the fine uncontested.

From a scientific point of view the second allegation was much more serious. It involved the informal charge that the analyses of DNA-DNA hybridization data had been manipulated to yield results that conformed with preconceived notions of phylogenetic relationships. One could argue that the methods of data analysis were not as rigorous as they might have been. There were certainly differences of opinion among the members of Sibley's own research group on how best to quantify and summarize the data; however,

this was an aspect of natural growth and did not constitute fraud. In fact, the issue probably would never have arisen if Charles and his group had not ventured into the treacherous waters involving human evolution. The debates in that arena are legendary, beginning with Raymond Dart and leading up to today's antagonists. In Sibley's case the issue revolved around rates of genetic change along different phylogenetic lineages: specifically, the one that led to the genus *Homo*, the other leading to the remaining higher primates. It was this debate that focused the attention of the scientific community on Charles's preferred methods of analysis of the DNA hybridization data. At its heart the issue was whether the entire genome of an organism evolved at a constant average rate, as Charles maintained. Although there is solid evidence to suggest that rates of change do differ among different lineages, the issue is still unresolved.

As in all other matters of his life Charles believed in himself. He believed unequivocally that his analyses of the relationships of the birds of the world were correct. In 1990 Yale University Press published two massive scientific contributions. One, in collaboration with his close friend and colleague Burt Monroe, Jr., was *Distribution and Taxonomy of the Birds of the World,* a comprehensive treatment of all avian species recognized as of 1990. The other, with his longtime associate Jon E. Ahlquist, was *Phylogeny and Classification of the Birds of the World: A Study in Molecular Evolution.* This was the tapestry, along with all of the supporting data.

Charles knew the history of systematics well. He knew better than most that classifications were always under review and modification, and he did not delude himself into believing that his classification would be the final word on avian taxonomy. One of his dreams, however, during the early phase of the DNA research was to be able to read off

nucleotide sequences from a DNA molecule. That was the kind of precision he sought, knowing full well that the technology of the 1970s and 1980s was not up to that task. Today automatic DNA-sequencing methods produce long sequences of nucleotides, and several genome projects are at or nearing completion. Already his students and their students have built upon the contributions made by Sibley and his group. The possibility of eventually reaching a consensus with regard to the phylogenetic relationships of birds is certainly obtainable, something that would give Sibley immense satisfaction.

Charles passed away at his home in Santa Rosa on Easter Sunday, April 12, 1998, from myelogenous leukemia. He is survived by Frances, his wife of 56 years, whom he met as Frances Louise Kelly, and their daughters, Barbara Susanne, Dorothy Ellen, and Carol Nadine.

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