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Charles G. Sibley: A Commentary on 30 Years of Collaboration

JON AHLQUIST[1]
Department of Biochemistry and Molecular Biology, Medical University of South Carolina, Charleston, South Carolina 29425, USA

My association with Charles Sibley began in 1962. Perhaps there is no question regarding our relationship that has been posed to me more often than "Why did you stay with him for so long?" The answer is simple: we needed (and used) each other. Although we rarely discussed the topic, consciously or subconsciously, Charles must have been aware of his inability to maintain effective collaborations. He was an extremely effective operator, skilled at procuring research funds. Although he enjoyed tinkering with and constructing items for use in the lab, his great strength lay in his ability to persuade others to collect the all-important materials for our research: blood, tissues, and egg white. The number of letters that he wrote in pursuit of specimens was mind boggling. He constantly cajoled workers in the field to obtain critical species, keeping them apprized of the progress of the lab work and seeking to provide them compensation for their efforts. Charles remarked that it bothered him greatly if he did not respond *within a day* to every piece of correspondence he received.

The thread that held our relationship together was our common, overarching interest in the systematics of birds. People have frequently thought that I was remiss not to seek an independent career. My response is that it would have been impossible to accumulate the specimens needed to pursue the work. To investigate some other aspect of avian biology did not interest me. My abilities were in streamlining experimental protocols, reducing each to a block of time that fit easily into a technician's working day. Everyone in the lab knew how to perform each operation, so if someone was sick or on vacation, our schedule would not be interrupted. I maintained a pleasant ambiance in the lab, exerted pressure to hire the best people, and set up work schedules to maximize productivity. I gave up much in the way of professional advancement, salary, and academic perks. What I received from our research has to be reckoned in numbers of "eureka" experiences—the thrill of discovering something new and unprecedented.

Curiously enough, Charles and I never became "friends" in the usual application of the word. Perhaps the age difference of 27 years permanently cast us into the professor-student dichotomy. Perhaps Charles thought of me as a surrogate son. Perhaps at the core, we were both loners who fundamentally did not trust other people. Perhaps we were such manifestly different personalities that we found little common ground outside of research. We had opposite views on politics, religion, art, music, literature—virtually everything else one can think of. Charles, despite his outbursts of temper, was quite conservative and predictable in his behavior, once one learned how to gauge his actions in advance. On the other hand, I was mercurial, flamboyant, and moody.

In lighter moments, Charles referred to this as my "expansive" personality; at others, he called me a difficult manic-depressive. There were times that both of us had to bite our tongues to prevent a wholesale conflagration, and others in which we slugged it out verbally toe-to-toe. In retrospect, it is amazing that our collaboration persisted.

The story of how Charles began working with molecular methods has often been told. His reputation was built initially on studying natural hybridization in birds. The available methods of assessing hybrid individuals on the basis of plumage characteristics were fraught with difficulties. The scoring was subjective, and females or immatures often did not exhibit the variable features. In 1956, Charles became intrigued by the possibility that protein electrophoresis might yield a better characterization of hybrids. The first papers were published three years later (Sibley and Johnsgard 1959a, b). Whereas the blood proteins showed little usable variation (at least in paper electrophoresis), the egg-white proteins were informative. The surprise was that the variation proved insignificant at the species level but tantalizingly revealed information about the higher categories, an unprecedented windfall of opportunity at a time when hope for the solution to age-old systematic problems was at its nadir.

[1] Present address: P.O. Box 1037, 1563 East Ashley Avenue, Folly Beach, South Carolina 29439, USA. E-mail: ahlquist@musc.edu

Charles, along with Herbert C. Dessauer of the Louisiana State University School of Medicine, and Morris Goodman of Wayne State University School of Medicine, founded molecular systematics. Immediately succeeding them were Allan C. Wilson and Robert K. Selander, followed not long after by John C. Avise. Dessauer's main contributions have been in herpetology and Goodman's in primatology. Although Wilson, Selander, and Avise published numerous important papers on birds, their interests were not limited to birds or to systematics.

The early work using electrophoresis yielded important clues to relationships, but they were impossible to quantify and differed little from the traditional characters that they were intended to replace. A tactical blunder was that with each new technique, Charles' enthusiasm grew exponentially. Many in the ornithological community grew weary of hearing how the Holy Grail had been rediscovered once again.

Perhaps the most trying period of Charles' academic life was that of the so-called egg-white incident. In 1973, Charles was charged with six counts of violating the Lacey Act, pled no contest, and paid a fine. The Lacey Act of 1904 prohibits the importation of animals that were collected illegally. When the records of our collection were seized under subpoena, and the ramifications of the allegations began to unfurl, Charles went into a state of virtual tetanus. Not before nor since had I seen him so emotionally immobilized. Day after day he came into his office, shut the door, and sat at his desk. A curious array of colleagues rallied to his support; others shunned him. The details of these interactions could fill an article many times the size of the present one. He anticipated being fired. Kingman Brewster, Jr., President of Yale, chose not to reappoint him as Director of the Peabody Museum. He was asked to resign his membership in the British Ornithologists' Union, and he became unofficially *persona non grata* with the National Science Foundation.

Of the six charges, two were valid, two others questionable. The last two are the most interesting. One sample was from a species of parrot that had been bred in captivity in England; that the individual bird had been legally obtained, I believe, could have been established without much difficulty. The sixth charge concerned a sample from a bird called *Torpis oocleptica* (pers. obs.). Any avian systematist can attest that this is not the name for any living species of bird, nor have the names been used in the past! In fact, a rough translation of the bogus name is "lazy egg stealer." It was obvious to me that this was some sort of macabre joke. Several of us urged that he fight the charges. Why Charles chose the course he did is a mystery. He would not discuss it, replying only, "Jonny, you just wouldn't understand. . . ." Did he fear further personal reprisals if the Fish and Wildlife Service law enforcement decided to subpoena his correspondence? Was he concerned that his numerous collaborators would be hounded and persecuted? Was it because he was so crushed that he simply wanted to get the matter over with? How he solved it personally remains an enigma to this day.

Having worked with peptide mapping for my dissertation, I too, was weary of the continuing emphasis on electrophoretic techniques but not enthusiastic about resuming work on DNA-DNA hybridization. An earlier attempt (1963 to 1965) had met with overwhelming technical failures. The problems concerned radioactive labeling, growing avian cells in culture, the existence of repetitive DNA (unknown at the time), and other factors. In the intervening years, most of the technical problems were solved so that a couple of bird watchers could apply the method.

I recall discussions dating back to 1964 in which we yearned for a single genetic measurement, yielding clusters of related species, groups of related genera, and so on. Our first DNA data were so clear, so unambiguous, and so promising that any lingering doubts quickly disappeared. Here was a technique that provided simple numbers, reproducibility, reciprocity, and a range of resolution that encompassed all living birds. The early success of the DNA-DNA hybridization work more than anything else brought Charles out of his depression following the egg-white episode.

With his spirits lifted, Charles began to streamline the technique for comparative purposes. The culmination was our designing and building the automated apparatus that became known as the DNAlyzer. No sooner was the DNAlyzer complete and the lab producing data of significant quality and quantity, when Charles began to experience angina. His pace slowed to a crawl; the medications then available had disagreeable side effects. Ironically, at the same age Charles' mentor at Berkeley, Alden H. Miller, had succumbed to a heart attack. So had Miller's predecessor, Joseph Grinnell. Never one to be superstitious, Charles could not escape the coincidences of these events, and I think they troubled him more than he cared to admit.

The outpouring of comments demonstrated the magnitude of concern for Charles' health. Bypass surgery was successful; Charles was back to work within two weeks with a vengeance, his stamina greatly enhanced. The next time that he proposed a good idea, I congratulated him saying, "I guess the new plumbing improved the blood supply to your brain." Data poured forth; our confidence soared, perhaps too much!

No position is less appealing than being a prophet in one's own time. If the results of the DNA-DNA hybridization studies on birds generated controversy, they paled in comparison to what happened with the hominids. We had little interest in becoming involved in the controversy of human relationships, save for one factor. In the early 1980s, the molecular data (mainly immunological distances and mitochondrial DNA sequences) pointed to an unresolved trichotomy among humans, chimpanzees, and gorillas. Because we knew that DNA-DNA hybridization could distinguish, for example, the genera of birds-of-paradise; why not apply it to humans? Publication of our results immediately generated opposition. It came from a variety of sources and was fueled by the acquisition of some of our poor-quality data by those who immediately claimed fraud (see Lewin [1988] for some details; a follow-up article was never written). Here's what really happened.

Roy Britten of Cal Tech visited Yale in February 1986. Roy was a supporter of the DNA work from the outset; he had been a firm but impartial critic. During a discussion, he asked if we had any examples of thermal melting curves with spurious low temperature peaks. I replied that such peaks were common in mammalian data, but we had some from birds. A quick search of the files yielded enough for his interests. Some of the primate data and nearly all the bird data that I copied for him were substandard or marginal. They had been (or soon would be) replicated to give better results. Yet, these very data found their way into the hands of our antagonists and were publicized *without peer review* as fraud and bad science.

In retrospect, the phrase "bad science" was little more than a thinly veiled euphemism for character assassination and a specific political agenda. The matter could have been resolved with a civil phone call asking "How did you guys analyze these data, anyway?" Instead, a trial was carried out using innuendo, tabloid journalism, and licentiousness that would make the host of a TV talk show blush. There was empty talk about "truth," while any attempt at rational discussion was shouted down. The principal detractors have offered few data in the succeeding decade. A handful of young investigators has tested some of our phylogenetic hypotheses and in most cases corroborated or augmented them (e.g. the papers in Mindell 1997).

The only place of error concerned the matter of publication of our full procedures for data analysis. Briefly, this came about as follows. When our 1987 paper on the hominids was being written (Sibley and Ahlquist 1987), both Charles and I had left Yale and were confronted with new demands on our time. The original manuscript had been returned with a request to be shortened by one-fourth. Charles deleted much material from the lengthy historical review. I prepared a data analysis section, but this never was fully included in the paper because we anticipated that our book, *Phylogeny and Classification of Birds* would be published before the paper. Unfortunately, this did not happen for several years owing to a variety of reasons. In the interim, I presented our procedures for data analysis at numerous conferences and seminars. Not once did anyone question the methods we employed!

We have been criticized for our approach to research. Most of what we did and how we did it was dictated by time. Charles often spoke of life as being a series of "windows of opportunity" that must be taken advantage of, lest they be permanently closed. Our window of opportunity for significant research was from 1974 to 1986, the years of active work using DNA-DNA hybridization.

If we learned any lesson from the vast quantity of electrophoretic data, it was that all bets were off concerning existing classifications. Once we began accumulating data from DNA-DNA hybridization, surprises abounded. A simple reading of the sequence of experiments contained in our laboratory notebooks reveals that we jumped around from group to another—a shotgun approach. Although our detractors vociferously assailed us for this strategy, there were a number of dictates behind it. First, nobody, ourselves included, knew the limits of resolution of the technique for birds; thus, we had literally to find our own way. Second, sometimes, as with the still imperfectly resolved complex of waterbirds (i.e. our expanded order Ciconiiformes), we simply hit an impasse and turned our attention to taxa that were more tractable (in that instance, the passerines). Third, nearly every experiment revealed new questions, and we rarely resisted the temptation to follow these tangents. The studies of *Melampitta, Peltops,* and *Pityriasis* are examples. Given the number of surprises, neither of us had the discipline for constructing complete matrices nor performing adequate numbers of replicates. Would I advocate this procedure given 20/20 hindsight? Yes. There simply was not time or personnel to do all the niceties. I often remarked to Charles that if we had published 30 theoretical papers on DNA hybridization and computer simulations of data, and only one with actual data, the response would have been more positive. Lastly, the matter of the incomplete matrices demands one further point of clarification. Had we been offered in 1974 the opportunity to compare 2,000 species of birds in what would be characterized a haphazard fashion versus the opportunity to sequence 50 kilobases of a suitably conservative portion of the nuclear genome from 25 predetermined species, which would have been the better choice? Almost certainly the former. Why? Because our ignorance of avian phylogeny was so abysmal that *we would have chosen the wrong species.* In the process, we might have accumulated valuable sequence information, but we would likely have missed the Australo-Papuan radiation of songbirds and other significant discoveries.

We were excoriated for not using approximately 20% of our data by self-anointed popes of righteousness. Yet, we were always most interested in any method that would give the best representation of what we saw in the DNA melting curves. That is why we turned to the T50H statistic. Many individuals thought that delta values higher than 15°C were untrustworthy; a few, including ourselves, thought otherwise. Although we understood the importance of statistical tests on our data, neither of us was sufficiently interested in working out new procedures. Contrary to what some may think, Charles repeatedly engaged well-known statisticians who provided valuable input. That many of these efforts did not achieve maximum or lasting results was due again to the personality clashes that inevitably occurred. Subsequently, most of the technical and statistical criticisms of DNA hybridization have been answered in painstaking and elegant fashion by John A.W. Kirsch of the University of Wisconsin (Bleiweiss and Kirsch 1993a,b; Bleiweiss et al. 1994, 1995; Lapointe and Kirsch 1995).

The Sibley Legacy—Charles' work on natural hybridization in birds is classic. It will be recognized as long as researchers study the phenomenon. Like it or not, the Sibley-Ahlquist-Monroe (1988) classification and the volume by Sibley and Ahlquist (1990) will have to be reckoned with by anyone who studies avian systematics. Warts and all, it was a major pioneering effort.

How to assess Sibley's shortcomings? I will comment on some failures that I believe bothered him. The first was his inability to establish an enduring group in molecular systematics at Yale. Although he attracted several talented junior faculty members, I believe that his effort was doomed for three reasons. First, independent investigators have their own ideas and egos; they were unwilling to submit to Charles' penchant for control. Second, gaining tenure was not an easy matter at Yale. Not one of these individuals achieved it despite Charles' valiant efforts on their behalf. Third, it seems obvious that the focus of biology at Yale was moving inexorably toward the molecular. I think that Charles perceived this trend and gradually turned inward to his own personal agenda.

The second disappointment was the reception of the Sibley-Ahlquist-Monroe classification. Had anyone else proposed it, acceptance would have been wholehearted and instantaneous. I doubt that the vicious attacks would have been perpetrated on anyone else and that their persistence is due to the politics of envy and not the science itself. Evidence for this includes ignoring the corpus of molecular data by not citing it; making reference to the Sibley and Ahlquist oeuvre in a series of other references but mentioning it no further, or acknowledging its relevance but quickly deriding its value with one or more pejorative aspersions. It amuses me to read the linguistic contortions to which some scientists will resort in achieving these goals.

A third, and more personal aspect, may have been the lack of strong bond between Charles and his graduate students. Charles seemed to care little about the dissertations of his students, nor did he actively foster their careers. I am not aware of any festschrifts, symposia, or even the dedication of papers marking any of the common milestones of one's career. Nor do I recall Charles' mentioning any of his proteges with warmth and compassion. That these feelings were reciprocated is demonstrated by several of his former students joining the ranks of his detractors for their own personal gain. No one, myself included, came forth to organize a 75th birthday (or other) celebration for Charles.

I have much for which to be grateful, although the items I list may be surprising. First, there is what Charles called "the big picture." Every problem in ornithology had to be considered in the light of everything else. We dealt with birds on a global level. I learned birds on a worldwide basis, and not just systematics. All aspects mattered—morphology, behavior, ecology, biogeography, physiology, the fossil record. Charles may have given the impression that he was myopic in his interests, but he was widely read and knowledgeable about all areas of biology.

Second was his teaching ability, which was characterized by reducing complex subjects to clear, simple lectures. He advised me to learn to teach by emulating those teachers who did it well, and to learn what others (who were boring, prolix, obscurantist, etc.) did wrong. Our styles of teaching were different. Charles' approach was carefully controlled; mine was pure showmanship, carried to the limits of outrageous behavior.

Third was his predilection for organization. How I hated that word! He would repeat it over and over to the point that we used to make fun of it. Let's organize lunch at Burger King. Let's organize a movie tonight. But, he was right. Thorough, detailed organization is the key to successful research, teaching, and writing.

Epilogue—Charles did not take kindly to advancing years. From my perspective, he became more difficult. Perhaps this was due to his deteriorating health, or to his dwindling influence in ornithology. Charles did not have hobbies; he was not one to retire and watch birds. No doubt his inability to forge lasting or fruitful collaborations after 1986 troubled him. The premature death or physical incapacitation of some of his allies took its toll. Charles did not understand my shift in focus of interest, and my early retirement simply baffled him. To him, my failure to continue in the "Great Cause" was a cop-out. There is no mystery; academic ornithology simply ceased to be fun. The bureaucrats run the show, and professors are merely serfs. We get only one invitation to this party called life; when it turns ugly, it's time to make a new plan.

To conclude without a "Sibley story" or two would be unthinkable. Some are unprintable; most, unfortunately, are true. Our 20 years at Yale alone could yield a small volume of humorous episodes. Life was not all lived wearing a hair shirt.

Around the time that Charles Remington published his 1968 paper on hybrid "suture" zones (Remington 1968), we held a weekly discussion group on evolution. Both Charleses had studied the phenomenon of natural hybridization in wild species, and one would not expect them to hold identical views. One of Remington's remarks piqued Sibley sufficiently to bring him to his feet, "Dammit, Charlie;" he remonstrated, "you're wrong! It's obvious that you haven't thought long enough about this matter, *for if you had thought about it as long as I have, you would realize that I am right.*"

One of our long-standing arguments concerned rates of genome evolution in birds. Although we had supported a uniform rate in print, I never believed it, and over the years accumulated data demonstrating variable rates and correlating them with generation time. From the late 1970s until 1986, I would show Charles the various data, which I argued, showed variable rates. One day I was particularly obstreperous and pursued the argument well beyond the point of civility. Finally, Charles jumped up and left my office, slamming the door violently behind him. On the way out he shouted, "Dammit, Ahlquist, the trouble with you is that *you have no goddamn FAITH.*"

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