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The Professional Development of an Entomologist

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Abstract

An account of the development of biological interest, and specifically interest in bees, by Charles D. Michener. Included topics are the role of graduate students and the relationship between behavioral studies and systematics. Sections are (*a*) upbringing, including initiation of biological interests, (*b*) early studies of bees, (*c*) student work at the University of California, Berkeley, (*d*) work at the American Museum of Natural History and in the U.S. Army, and (*e*) work at the University of Kansas, especially wild bee behavior and bee systematics.

INTRODUCTION

The Editorial Committee has asked me to write an account of my life as a biologist, the reasons for and planning behind what successes I have had, perhaps with the objective of helping young biologists to navigate the ecosystem in which we develop as biologists. I must admit at the outset that most of my development as a biologist was not a result of thoughtful planning that could help others. On the contrary, it was the result of being born to the right parents, being brought up in the right environment, and being lucky in my subsequent decisions. However, it is true that somehow I knew how to take advantage of opportunities, and clearly from an early age I was ambitious to become a professional biologist, a fact that undoubtedly helped a lot. So I will try to give you some possibly interesting insights into my career.

Biologists can be divided (with much intergradation) into two groups: those who enjoy laboratory work and reductionist methods for learning about biology and those who enjoy natural history and learning about the diversity of kinds of animals and plants. Those of the first group have experienced wonderful recent achievements at the cellular and molecular levels. As they seek to contribute to principles and theory, they select the kind of organism best suited to solving whatever is their current topic. Therefore they select their problem first and then the best organism to elucidate it. Of course these biologists are interested in how organisms work; they are physiologists, biochemists, molecular biologists, among others.

Biologists of the second group tend to be field or museum naturalists who enjoy work in the outdoors, who often collect some favorite group of organisms for themselves or for a museum, and who study systematics, ecology, behavior, and the like. They usually work with whole organisms. Comparative examination of organisms or phenomena and study of experiments set up by nature are their most common methods. They tend to special-

ize, sometimes for irrational reasons, on one favorite group of organisms. They often engage in rather descriptive work (e.g., on morphology, systematics, or behavior). Of course they also enjoy developing theories and principles (e.g., on evolution and various ecological theories). Significant contributions have been made (and continue to be made) by interested amateurs (Charles Darwin, for one). Almost all biologists were of this style until a couple of centuries ago.

As indicated above, many biologists are intermediate between my sketches of the extremes of a continuum. Indeed some of the greatest contributions are by persons comfortable in both camps, e.g., many geneticists.

UPBRINGING

My upbringing and subsequent development placed me strongly in the second group. I have liked to watch a bee's activities, compare nests of different kinds of bees, review the systematics and comparative morphology of a group, and make keys for identification, maps of their distributions, and phylogenetic hypotheses.

I was born in 1918 to Harold and Josephine Michener and grew up in Pasadena, California. My mother nearly completed a PhD from the University of California, Berkeley, working on systematics of marine dinoflagellate protozoa. She quit her studies after marriage. In those days women rarely had professional careers while they married and raised families. My father was an electrical engineer for a power company but was strongly interested in birds, as was my mother. The two of them banded some 45,000 birds captured and released in our large and densely treed yard in Pasadena. They carried on various studies made possible by large populations of individually recognized (by band numbers) birds and published about 30 papers from 1925 to 1953. For example, they published on molts in free wild birds, possible because the same individual birds returned repeatedly to the traps,

and using birds with different colored band combinations, they were among those who early recognized the existence of and investigated territorial behavior in wild birds.

Even as a small child I helped by watching color-banded mockingbirds and writing down their locations and often their individualistic behaviors. During the same years my mother took me on many short trips to interesting places—museums, beaches, a stream full of aquatic life, and the chaparral-covered nearby mountains. [My only sibling was six years older and often doing other things; my father was severely afflicted with rheumatoid arthritis and so needed rest and relaxation whenever possible in order to continue his professional work. Thus it was chiefly my mother who went out with me.] I remember particularly a small moist gully at the nearby foot of the San Gabriel Mountains overhung by trees and covered with a layer of their leaves. We visited it repeatedly and found mushrooms we had not seen before on every visit. We called it Fungus Canyon.

I remember annual one-week family vacations during 1927 to 1929 to a lake in the Sierra Nevada, a lagoon on the coast, and the desert near Palm Springs. I have liked deserts ever since. On all such trips we looked at, collected, and, with my mother's help, identified so far as possible the organisms we found. An upstairs room in our big old house came to be known as The Museum, because we kept there seashells, bottles of soft-bodied creatures, insects, and skulls of roadkills.

My mother knew or learned what books to buy or borrow from the library to learn about various taxa—plants, fungi, insects, spiders, and intertidal invertebrates—in addition to the near-professional literature on birds. In early years when I did not read freely, she read relevant descriptions and keys for me. I must have acquired an early appreciation for identifying and naming organisms.

Some of my mother's former graduate student associates stopped at our house occasionally for dinner or overnight. The ones that I recall were by then faculty members at univer-

sities and colleges. They often showed interest in my interests and, for example, showed me how to pin insects or to put small ones on points. Similar help came from an entomologist advisor to my father, who, although an engineer, had the job of figuring out what to do about termite damage to power poles.

The first organisms in which I became seriously interested were flowering plants. Beginning in 1927 and continuing through 1930, I made watercolor drawings of as many kinds of native flowering plants (in bloom) as I could find. We had no car, so collecting trips were limited, but friends often brought flowers from the desert or mountains. I painted about 130 species, all identified with the help of my mother and W.L. Jepson's *Manual of the Flowering Plants of California* (1925). I still have this stack of paintings.

My work place was the kitchen/dining room table, so I had to retreat at mealtimes. One would have thought I could work in The Museum upstairs, but I did not do so. Likely my folks thought it was better if my mother and I were close together, and she spent most of her time in the kitchen and bird-banding room. Eventually my parents had a small addition built off the kitchen, a room for my work!

It soon became difficult for me to find species of native plants in bloom that I had not already painted. So, as early as 1928 and continuing in reduced numbers to 1933, I began to collect and draw insects. These were mostly line drawings in ink. I used watercolors only for a few butterflies and colorful wasps. Through drawing and J.H. Comstock's *Introduction to Entomology* (1920), I learned a lot. With some help I was usually able to identify insects and other forms of animal life (which I also illustrated) to at least the family level. The drawings were often detailed, with wings and other parts shown in special drawings. Notes (descriptive or about food or life cycles, details of where the insect was found) accompanied many of the drawings. I have just revisited these drawings; the number to me is astounding, about 1200 sheets of drawings of insects and accompanying notes, plus perhaps

100 arachnids and a similar number of intertidal invertebrates, small fish, frogs, fungi, and slime molds. I remember the principal of my primary school wanted me to fill in the drawings with crayon color to make them more conspicuous so that he could have an impressive exhibit; he had no interest in details that would be obscured. I refused. Most insects were identified only to family, so I had Ichneumonidae 1, Ichneumonidae 2, etc. Of course I became more sophisticated about insects as time went on. No doubt I had less time for insects as I went through junior high school and high school. I have never resumed making drawings on such a large scale.

It may not be entirely out of place in an account of professional development to remark that although I was undoubtedly nerdish, I had friends of my age, mostly in Pasadena public schools, from first grade to high school. We played and talked together. None shared my intense interest in natural history but neither did they make fun of me for having such an interest. They were all good students who shared my dislike for athletics and coaches. As I write this I realize for the first time that I had few close friends during the years when I devoted so much time to illustrating flowers and insects. The remark above about friends applies primarily to the time before and after the period 1928 to 1932.

I do not remember making a conscious decision that I wanted to become an entomologist and a professor. It was just obvious that that was what I wanted to do. I remember that several times lying in bed before going to sleep, I imagined myself giving a great lecture on some, probably entomological, topic to a large audience. Unfortunately I never became a spell-binding lecturer, although I did enjoy teaching for many years, mostly with small groups.

For a budding systematist, an essential decision is the taxon to be studied. I have no clear recollection of how this occurred. I do recall being charmed by ichneumonids with their long, flexible abdomens and often long ovipositors. Hymenoptera are strongly rep-

resented in the drawings and notes described above. I suspect that my early fixation on bees, however, had to do in part with *Perdita rbois* Cockerell, a beautiful, minute, yellow-and-black insect that appeared each summer in small numbers on Shasta daisies in our yard in Pasadena. The male, in particular, is so unbee-like that I did not identify it as a bee for several years; it was a puzzle and a frustration, and through it I became more proficient in running various small Hymenoptera, including bees, through the keys in Comstock's *Introduction to Entomology*. I did not have a microscope and instead used a hand lens mounted on a stand; I probably could not see the plumose hairs that characterize bees on a tiny, smooth bee such as *P. rbois*.

EARLY STUDIES OF BEES

Southern California has a rich bee fauna, and as I collected more species from different flowers, of course I wanted to identify them to the genus or species level. From one of the university visitors I learned that T.D.A. Cockerell at the University of Colorado was the principal bee specialist active at the time. Probably at about age 14, I wrote to him, asking about how to identify bees. He responded with interest, saying that H.L. Viereck's *Hymenoptera of Connecticut* (1916) (which I obtained for \$2.00) was not very useful in the West. E.T. Cresson's *Synopsis* (1887) was ancient even in the 1930s but was available for \$10.00. With these inadequate works I identified to genus a box full of bees, pinned and labeled, and sent them to Cockerell for checking. He returned them, with identifications corrected as needed, and some specimens even identified to species.

Moreover, Cockerell wrote supporting comments about work on bees and invited me to meet him and P.H. Timberlake at Riverside, California, where the Cockerells would be visiting. Timberlake, a faculty member at the University of California Citrus Experiment Station, was interested in my catches because, although I lived only 60 miles from Riverside,

I had collected several species of bees that he had never seen. Later, he invited me to accompany him on collecting trips to the Mojave and Colorado deserts and elsewhere.

Professor and Mrs. Cockerell also invited me to spend the next summer (before my last year in high school) in Boulder, Colorado, with them, where I could work with him and learn about bees. Cockerell was an especially charming man who, lacking a university degree, was in some ways a second-class citizen among the university faculty members. He never had many graduate students who became seriously interested in bees, in spite of his long career as the principal bee taxonomist in North America, if not the world; his publications on bees span the years 1895 to 1949. Probably for this reason he was especially enthusiastic about my interest and encouraged the preparation and publication of my first taxonomic papers. Thus I was clearly hooked on bees well before beginning my undergraduate work at the University of California, Berkeley.

BERKELEY

Cockerell was a superb teacher but both a good and bad mentor or example for a developing entomologist. He was good as an understanding, intelligent man who recognized the major problems in biology at the time, lectured on problems of conservation and human population, and published freely. From 1882 to 1949 he published 3904 papers on diverse topics, including many on bees. He was a bad mentor in that he often rushed to publish, rarely provided keys (almost never illustrations), and never provided proper bibliographical references. Thus he did not contribute as he could have to the work of subsequent generations of bee specialists. His comment was, "I have gathered the wood; it is up to you to build the house," that is, I have found and named the species, and it is up to you to study them in detail and develop a classification for them. In any case, in 1935 I published in the *Pan-Pacific Ento-*

mologist my first scientific contribution (8), a short paper on the hitherto unknown nest of a species of resin bee, *Dianthidium*. In subsequent years (especially 1935 and 1936) I published several taxonomic papers on Western bees, describing new species and sometimes providing keys to species. Although inexperienced, I recognized some of the shortcomings of Cockerell's ways. Nevertheless, I was in some danger of imitating him too much.

In 1936, my last year in high school, I decided to go to the University of California, Berkeley, as an undergraduate. At that time it had the best-known entomology department in the West, which was my main consideration. I clearly remember this was my thought about it, even though no one there at the time was studying bees or Hymenoptera. I intended to work on bees, however; I must have thought I did not need help (beyond that from Timberlake and Cockerell, both far away)! Anyway, it was the right decision for me.

From this point on, much of my career as a biologist can be understood from a selected list of scientific publications, presented in the literature cited below. Of 427 publications, 58 serve as exemplars of my research activities.

As a prospective entomologist I was welcomed in Berkeley and given space to work among graduate students, even though I was only a freshman. Soon I learned to prepare revisional papers with keys and illustrations (9, 10) rather than with merely descriptions of new species. Probably I was not welcome among the graduate students—a kid just out of high school occupying space and using facilities that they should have had. However, they never made this attitude clear to me; we got on well and made joint collecting trips from time to time and talked a lot about taxonomic and evolutionary problems. During my undergraduate and graduate career, interacting with faculty and other students, I became a comparative morphologist and systematist of bees and prepared a dissertation (1942) on these topics published with some additions in 1944. I began my dissertation work while still

an undergraduate and moved fast, largely because it was wartime and I did not want to get drafted in the midst of thesis preparation. The published version of my thesis (13) included a key to the North American bee genera, the lack of which had sent me to Professor Cockerell for help a few years before.

Especially important to me during my student years at U.C. Berkeley were E. Gorton Linsley and Robert L. Usinger. They were young faculty or prefaculty members and essentially replaced my major professor, E.O. Essig, in mentoring for me. Linsley, a coleopterist, became interested in bees, I think because of my enthusiasm for them, and later wrote extensively on them, including joint papers (6). One summer he, Usinger, and I made a trip by car from Berkeley to all the major eastern museums, examining types and other material relevant to our studies.

Deciding to stay at U.C. Berkeley for graduate work should have been a major matter. I tell students that their decisions of where and with whom to undertake graduate work may be one of the few really important decisions in their lives because it will probably determine the direction of their lifetime research. But I scarcely remember considering other places for graduate work. I suppose this made sense at the time because, in fact, I was already doing thesis work in my last undergraduate year. I did not know that later I would urge students to move to new institutions, either after a bachelor's degree or after a master's degree. I have said, "You probably have heard most of the bright ideas of the faculty here; your experience will be best if you go to another good entomology program and learn about a new batch of good ideas."

As a graduate student I was a teaching assistant in entomology courses offered by Professor Essig and by E.G. Linsley. I learned a lot from helping in these courses, which was good preparation for the weeklong written comprehensive examination followed by orals. But for me the most significant benefit of the teaching assistant job came from one of my students, Mary Hastings, who after a semester

became my wife. She understood and continues after 65 years to support and to have an interest in my entomological activities. With our four children she has traveled with me to all continents except Antarctica including, in addition to shorter trips, a year each in Brazil, Australia, and Africa.

AMNH AND MEDICAL ENTOMOLOGY

As my PhD program at U.C. Berkeley neared completion in 1942, I looked for jobs. People told me that, as a bee specialist, I would find difficulties because bees (except for the honey bee) attract no attention because they have no economic significance. [Fortunately this attitude has now changed.] I took the matter seriously and studied ichneumonids for a while, believing that, as parasitoids, they might have more practical importance. The result was three small papers on systematics of ichneumonids (11), with of course no influence on job opportunities. I was offered a tenure-track faculty position at one of the California State Colleges (now universities). A wise and thoughtful mentor, Professor S.F. Light, who gave courses in invertebrate zoology, urged me not to take it, emphasizing that research opportunities and prestige were better elsewhere. I finally also turned down a one-year-only postdoctoral fellowship in favor of an opening as a lepidopterist at the American Museum of Natural History (AMNH) in New York.

I had little choice at the time, but this proved to be a wise move. I was not opposed to research on an entirely different group of insects; I maintained an interest and completed a few papers on bees (17) but worked full time on systematics of butterflies (12) and saturniid moths (20). I found them interesting and exciting. Thanks to Frank Johnson, a saturniid enthusiast and museum benefactor, I had an assistant who helped with preparations and drawings. Above all, at AMNH I had as associates Ernst Mayr (ornithology) and G.G. Simpson (paleontology), famous

and influential evolutionary biologists, and as a neighbor, at Columbia University, Theodosius Dobzhansky (genetics). This combination made for an exciting time for systematic and evolutionary biologists, enhanced by T.C. Schneirla (behavior) and his work on army ants. The association with AMNH led me to certain studies related to evolutionary problems (16, 19).

After nearly two years at the AMNH, with military service looming, I volunteered in 1943 for service in the Army Sanitary Corps; this was entomological work, and contrary to my expectations, it proved to be professionally valuable. Actually, I think I was successful at finding things to do that benefited the Army's program and at the same time my professional development. I was first sent to do mosquito survey and control work on and around Camp Shelby, Mississippi. While there I wrote on mosquitoes (14), including a long paper (finished later) on seasonality and relative abundance of the numerous species of mosquitoes (18) based largely on our weekly surveys of a large area. On weekends and even while surveying mosquitoes I collected bees, an activity that made possible a paper on the bees of the area, the first such account for any area in the South except for an early paper on bees of Miami, Florida, and vicinity.

After about a year and a half dealing with mosquitoes and their control in Mississippi, I was sent to the Gorgas Memorial Laboratory in Panama to investigate chigger mites (Trombiculidae) because they were transmitting scrub typhus in the Pacific, often with fatal results. As was known, chigger larvae are the parasitic stage; they bite only once. If the *Rickettsia* that causes scrub typhus is acquired, from biting a rat or other vertebrate, it must survive in the nonparasitic nymphal and adult stages of the mite in soil or litter. Then the *Rickettsia*, in female mites, can be transferred by transovarian transmission to the eggs and thence to the larvae of the next generation in order for larvae to be infective. It is therefore necessary to rear the vector through its entire life cycle in order to investigate trans-

mission. Among other things, we learned that the free-living stages feed on eggs of soil insects (even on *Anopheles* eggs when they were conveniently available in the lab).

In Panama, my first tropical experience, I was happy to see *Trigona* (stingless bees) everywhere and male *Euglossa* (which I later called orchid bees) visiting orchid flowers on a rack by the back door of our house—my first experience with living neotropical bees. I had the good fortune to work with Marshall Hertig and A.G.B. Fairchild, who were experienced in tropical studies of medically important insect vectors, such as *Phlebotomus*. They were fine associates at the Gorgas Memorial Laboratory and were most helpful in furthering my work under conditions at first unfamiliar to me. While I wrote papers on chigger biology (15), host ranges, and clothing treatments to prevent bites, I was also able to collect bees, forming the basis for a later work entitled "The Bees of Panamá" (23).

Although my experience in the Army proved interesting and professionally valuable, I rejected suggestions that I remain as a medical entomologist and returned to the AMNH as a lepidopterist (but with some opportunity for research on bees). There I discussed bee problems with Herbert F. Schwarz, well known for his studies of stingless bees and anthidiine bees. He was a wealthy volunteer, very knowledgeable, who worked every day like an AMNH curator.

In many ways my position at the AMNH was wonderful. I had much of my time for research, although there were some curatorial responsibilities. I had a full-time secretarial assistant funded by the Museum, as well as a research assistant for work on moths. There were opportunities for field work (I went on a three-month trip to Mexico with others from Entomology in the AMNH) and excellent publication outlets. I had no plans to leave or seek employment elsewhere. However, there were ways in which I thought that the AMNH was less than optimal for me. One was life in New York City for me and my family. We lived in New Jersey and I spent one hour each way,

each day, on bus and subway commuting to the AMNH. More important, I had always felt an affinity for university life and the opportunity to train graduate students, that is, to leave professional progeny. I liked work with Lepidoptera but would prefer to give my full research attention to bees. Finally, the director of the AMNH was not concerned about, or did not know how to prevent, departure of some of the best known curators for university positions. The result was that the AMNH became a less interesting place to work. Still, the AMNH job was in many ways ideal and my objective was to improve the AMNH, not to leave it.

KANSAS

However, in 1947 and 1948, H.B. Hungerford met me and urged me to come to the University of Kansas (KU) to take the position from which he would soon retire. I considered it carefully and, after visits, decided to move. Because it had a major insect collection and several systematic entomologists, I was already familiar with KU, having visited there as a student while at U.C. Berkeley. It was probably a less prestigious position than at the AMNH. I would have teaching activities and of course committee responsibilities, but the advantages seemed to outweigh the disadvantages. Although Dobzhansky told me to "let the Kansans stew in their own juices," I moved to Lawrence in August 1948 and have never looked back. I finished a few papers on moths after leaving the AMNH, and by way of graduate students and military funding because of the Korean War, I resumed my interest in chiggers, but for the most part I returned to my long-established interest in the systematics of bees.

The department which I joined and, by prior agreement, soon chaired was one of very few entomology departments in the United States not in a school of agriculture and hence without agricultural responsibilities. The research-active faculty members were all systematists and they and most of their gradu-

ate students were working on Hemiptera (including Homoptera). It was highly inbred, with all the faculty members having one or more degrees from KU. I had an agreement with the administration to the effect that, as opportunity arose, we would find applicants from other institutions. (In those days, wide advertisement of openings was not required; one found promising applicants largely by reviewing journals and talking to one's friends at national meetings.)

When considering a move to Kansas, I realized that if I were to undertake year-long investigations of bee biology, Kansas would be a better place than the AMNH. As time went on in Kansas, I decided that I needed experience in wild bee behavior and nesting biology. This embryonic interest was strengthened by the realization that such work could contribute to the solution of pollination problems (especially with alfalfa) and that funding for students and equipment might therefore become available. So both out of curiosity and for practical considerations, I began serious thought about bee biology.

BEE BEHAVIOR AND SYSTEMATICS

Behavior and ecology, together with systematics of bees or, as my associates said, whatever I could learn about solitary and primitively social bees, continued as my chief research activity until I retired. On average I spent about half my research time on behavior (along with ecology) and half on systematics (including comparative anatomy and phylogeny). The two go together very well, each field contributing to the understanding of the other.

Until 1950 I knew about bee behavior and nesting biology almost entirely from reading, having devoted myself to systematics, comparative morphology, and floral relationships, the last mostly because the flowers help one find the bees. In 1950, however, I began studies of bee larvae (21, 34) to see what their characters would contribute to systematics, and of

leafcutter bee biology (22). A few years later I began a long series of studies of nesting biology and social organization of bees, with emphasis on primitively social forms and on the origin and evolution of social behavior. I abandoned research relating to the practical solution of pollination problems. Much was known about solitary bees (50) and about the social behavior of highly social bees such as *Apis* and the stingless bees (24), but little was known of the great many weakly social bee species living in colonies of two bees to a few dozen. I supposed that by studying the several extant levels of such scarcely social or weakly social forms, one might learn about the evolutionary steps through which the ancestors of *Apis* must have passed during their development of elaborately social lives. Primitively social halictid bees occur worldwide, with different groups of course in different continents and with a wide spectrum of behaviors (3, 26, 38, 42, 45, 46, 48, 51). Similar behavior is found in allodapine bees in Africa, southern Asia, and Australia (7, 30, 31, 37). To take advantage of such bees, which developed social behavior and also often lost it, reverting to solitary life, I spent, in addition to shorter trips, over a year each in Brazil, Australia, and Africa thanks to fellowships, grants, and University money. With many talented graduate students to assist, this went on for 40 years, until 1990, and involved the publication in 1974 of *The Social Behavior of the Bees: A Comparative Study* (32).

During these many years I also continued systematic work on various bee groups but especially on those whose behavior I was also studying—Halictidae and Allodapini. Naturally I collected bees for the KU Entomology Museum (now part of the KU Natural History Museum).

During the 41 years from my arrival at KU (1948) until retirement (1989) I was involved in diverse nonresearch activities. Of course, formal teaching was one: At various times I gave or helped with courses in entomology such as introductory courses and *Insects and Man* (now *Insects and Human Affairs*)

and with the course on evolutionary mechanisms (not an entomology course). During these years I also attended numerous national and international meetings. The only one that seems worth mentioning in the present context is the first Editorial Committee meeting for the *Annual Review of Entomology*, at the Natural History Survey and the University of Illinois, where we discussed and selected topics and authors for the first volume, published in 1956.

I have had numerous talented graduate students (42 PhD students, some of them retired years ago!). Several of them were essential to the parts of my program concerning social behavior and nestmate recognition in halictid bees, and we published numerous studies in coauthorship as well as under their own names. I have written about my views on training graduate students along the following lines: One of my great pleasures has been having graduate students who now occupy responsible positions in diverse states and countries and who continue to contribute to science. Of course one hopes that graduate students learn from faculty, in addition to the methods and content of the field, appropriate professional attitudes and philosophies. However, learning should be a two-way street. The graduate student who becomes a clone of his or her major professor may be a useful contributor to the field, but that field will not be advanced greatly. The most interesting and rewarding graduate student has skills and academic background different from those of the professor. The professor learns a lot from the student, and that learning can later be transmitted to other students. Such students can bring methods and ideas new to the field to bear upon its problems and should be the most welcome students. The students become colleagues of their major professors, trusted like other colleagues; the principal differences are that graduate students have less experience and near-subsistence-level salaries.

After discussion of problems, the important thing, while not letting the student feel abandoned, is to leave him or her alone. The

professor's door should be open to encourage discussion of problems. Such discussion ordinarily occurs at the student's initiative or at the professor's; it should rarely occur in the manner of supervising or directing the student. (Naturally, if a student is uncommunicative, a review of progress is appropriate.)

A professor should help fashion professionalism in students by enthusiasm, hard work, writing style, preparation of results for publication, honesty, and fairness in dealing with peers and students. Such values are best transmitted through examples, by frequent informal interactions among colleagues and friends, not by courses, formal requirements, and the like. We must encourage students before they receive the doctorate to publish, present papers at major meetings, and otherwise become known as doing professional work.

Teaching, including training of graduate students, went on through all the years. My own research largely followed the two major lines outlined above, systematics and behavior, but with deviations based on decisions that may be of some interest. When research can profit from travel (which often leads to new directions), one should apply for appropriate funds (e.g., Fulbright, Guggenheim, sabbaticals) and go with family and remain abroad as long as useful for the study. It is essential to plan in advance, apply early, and arrange for the survival of students at home. Rushed trips are frustrating. In my case, I was able to study primitively social bee behavior and also to collect specimens for future systematic work.

Decisions to follow new research paths naturally influence one's career. I have already mentioned deciding to investigate nesting and social biology of bees after a start in systematics. This involved the need to keep bees indoors and therefore to construct properly lighted bee rooms and observation nests for ground-nesting, burrowing bees (46). It was in such rooms that major studies of primitively social behavior of halictid bees were made by me and graduate students. The site was an abandoned schoolhouse and later a tempo-

rary wooden building. When we wanted to have the bees go outside to forage, we could just bore a hole in the wall and connect the nest container, something impossible in regular university or museum buildings.

My interests in bee behavior have always been to compare nest structures and to watch and record behavior, to see what bees are really doing, and to compare behavior among species (3, 22, 25, 31, 42, 45, 48, 50, 54, 55). Thus I am not a theoretician, although working in an area replete with theories, largely because of the problem noted by Darwin that it is difficult to understand how selection could promote the evolution of a worker caste with reduced reproductivity. I am skeptical about observations or experiments designed to show that a particular theory is correct. What items are missed or ignored because of concentration on a particular objective? I have, however, claimed that social behavior in Hymenoptera might have arisen as a result of mutual benefit that could outweigh in importance the standard altruism explanation. (Other papers related to evolutionary or social concepts are References 2, 5, 26, 36–38, 44, and 52.) I even played with ways of improving our system of nomenclature (27).

A deviation from strict bee studies had to do with individual recognition in animals (4). It was an easy step, because in halictid bees we found that males avoided mating with closely related females. Moreover, guards at nest entrances admitted nestmates and close relatives of nestmates, but not other bees. Recognition of classes of individuals was shown; evidently recognition was due at least in part to molecules (macrocyclic lactones and cuticular hydrocarbons) on the surfaces of the bees. These findings led to the book *Kin Recognition in Animals*, edited by David Fletcher and me in 1987 (52). For a field that we thought was ripe for a comprehensive review, surprisingly little attention was given to this book by biologists; I suppose it was largely a failure from the viewpoint of my professional development, but the several research papers related to the topic are significant (see References 2, 52).

In addition to studies of bees, I have made various efforts at more general contributions. All required decisions to put aside for a time revisions of various bee taxa in favor of projects of broader application. One such, done jointly with Robert R. Sokal (53), was the development of phenotypically based classifications, widely known as numerical taxonomy. We knew that most classifications had been based largely on intuition as to relationships, such that it was difficult to defend many decisions. Taxa were (are) supposed to be monophyletic, but how could one ascertain that status, given clear evidence of convergence and parallel evolution? Classifications were unstable because they were based on beliefs about relationships not supported by scientific evidence and not agreed to by all specialists.

We therefore thought that by tabulating numerous characters and classifying on the basis of degree of difference (or similarity), more stable classifications would be achieved. Hardly anyone was really satisfied by this method because people wanted classification to be based on phylogeny. Yet in the absence of dependable phylogenetic evidence, phenetics was an alternative. The method would soon be largely abandoned by systematists, but it accomplished useful objectives: It often stimulated discussion and, for the first time, it forced systematists to record and tabulate the status of all known characters for all the taxa under consideration.

Thus when phylogenetic methods became well known (about 1966) and computerized methods were developed later, collection of data largely appropriate for use was already being done. Although I use phylogenetic methods, I am by no means sure that the stability of nomenclature has been promoted. The phylogeny used in developing a classification is a hypothesis; it is not factual. With new characters or additional taxa, phylogeny often changes. Its great merit is that one can explain how it was developed, but it is always a hypothesis subject to challenge, perhaps to change, with resulting changes in nomenclature and classifications.

In spite of diversions such as the ones described above, most of my research time that was devoted to systematics was used for the preparation of revisions and regional studies. An early one, "The Bees of Panamá" (23), proved frustrating because in order to be certain of the proper specific names of the included species one must almost revise all the included genera, a practical impossibility. Later regional works (Australia; 28) dealt only with the genus and subgenus levels, with species names only listed. As time went on I selected especially groups that I understood poorly and that needed clarification in preparation for a general systematic study of bees worldwide. This idea entered my consciousness as a possibility by about 1988. Also, I selected for systematic investigation groups on which I had made or was making behavioral or ecological studies (33, 35). To discover more characters for use in studying relationships among families and genera, I investigated particular structures (e.g., glossa and midcoxa) across all families of bees (43), as well as nest features in diverse families of bees (24, 29, 51, 58). During fieldwork I came across interesting items to investigate, such as nests, nest sites, and floral relationships. Taking advantage of such findings resulted in various papers not closely related to my general research plans (24, 25, 29, 49, 55). Moreover, one of the best advantages of travel was the opportunity to work with foreign bee specialists, e.g., Padre Jesus S. Moure in Brazil, and often to coauthor papers with them (49, 51, 56). Other papers that did relate to the plans for a worldwide systematic treatment were studies of cleptoparasitic and socially parasitic bees (unrelated forms, often convergent; 30, 35) and of fossil bees (47). Of special importance in preparing for a general systematic treatment were two large studies of phylogenetic relationships written with Arturo Roig-Alsina (57) on long-tongued bees and with the late Byron Alexander (1) on short-tongued bees. Such studies made possible phylogenetic investigations of bees at the family and subfamily levels (39, 40).

CONCLUDING REMARKS

Some people enjoy and do well with administrative responsibilities. Often people are surprised at their own reactions; some hate, whereas some enjoy and thrive. I tolerated such responsibilities as Chair of the Department of Entomology and as Director of the Entomology Museum (now part of the Natural History Museum), but I did not do an outstanding job. An outstandingly effective chair needs to demand things that would improve the unit while not antagonizing his superiors too much. I have always been timid when faced with higher-level administrators (deans and the like) and therefore was only moderately successful. I think it is important that administrative activity by a researcher and teacher have a termination date; it should not be a life sentence. Some people should not accept such jobs at all. I am told that Dobzhansky, when urged to take the department chair at Columbia University, said "If you make me chair, I will make this department the laughing stock of the nation." He escaped the job.

I retired from teaching and most committees in 1989, but thanks to the Entomology Division of the KU Natural History Museum and, for several years, to an NSF grant, I kept right on with studies of bee systematics. Owing to lack of funds and especially to less than good eyesight for watching minute bees, I

dropped behavioral studies at about that time, so my research since retirement has been in systematics (41).

In 2000 I published a large work, *The Bees of the World* (39), which is a detailed, primarily systematic account of all taxa from family to subgenus; species are largely ignored. People tell me I was just finishing and updating my PhD thesis (published in 1944)! I am often asked how long it took me to write *The Bees of the World*; I really do not know because many parts depend on genus-level revisions and other comparative studies written long ago. It was, however, a major activity from 1989 to 1999, and it is now being revised.

Clearly I have had a very satisfying professional career as a member of the second group of biologists as distinguished at the outset, and I have had a very happy family life; the two are really intertwined as each has influenced the other. I greatly doubt if I have written anything here that would help young or aspiring professional entomologists make their life decisions. I think important qualities to develop, especially for those in academic life, are (a) the ability to return seamlessly to what you were doing or thinking after being interrupted by someone with an entirely different problem and (b) the resolve to keep doing and publishing the research that you enjoy even when most of your time has to be devoted to something else.

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