Charles Michener, 1918–2015

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Charles D. Michener passed away in November 2015. Mich, as he was known to his students, friends, and colleagues, had a truly impressive career in evolutionary biology, systematics, and behavior. Mich wrote a memoire (2007a) in which he discusses both his personal and scientific history; here I give my own perspective on the influence of his scientific thought.

Mich's professional career spanned ten decades. He first published on bees when he was a high school student and his last paper was published just this year. He became interested in bees as a child, when he observed them visiting flowers that he was painting. The bee systematists P. H. Timberlake and T. D. A. Cockerell encouraged his passion for bees while he was still in high school, and Mich spent a formative summer with Cockerell and his wife in Boulder, CO, where Cockerell was curator of entomology at the University of Colorado Museum of Natural History. The generosity of the Cockerells in hosting a promising high school student helped to shape Mich's own magnanimity as a mentor.

In 1936, Mich moved from his childhood home in Pasadena to the University of California, Berkeley, where he made a quick passage through his undergraduate degree. Still at Berkeley, he



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then produced a doctoral dissertation on the systematics of bees that is recognized as a classic work. The publication resulting from his dissertation (Michener 1944) served as the basis for bee taxonomy until his own *Bees of the World* (most recent version, Michener 2007b) supplanted it as the definitive work on bee systematics. Mich guided numerous masters and doctoral students through genus-level studies of bees, as well as continuing his own deep line of thinking about



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bee evolution. Of his work on bee systematics and evolution, my favorite publication is his monograph on the biogeography of bees (1979), which is definitive—a gem of precision and a fount of information.

Mich enlisted in the army as an officer in its medical research corps during World War II. While in Panama, he worked out the life cycle of a chigger mite. The army assignment took him to the tropics before it was common to work there and his *Bees of Panama* paved the way for understanding neotropical bees (Michener 1954). His continued study of bees during his spare time while in the army illustrates a lifelong pattern of wise time management. He never wasted an opportunity.

Jobs in academia were scarce after the war, and his first position, at the American Museum of Natural History, was as a curator and researcher of Lepidoptera. This job caused him to detour his interests from bees to saturniid moths (Michener 1949). But his clear preference was working with bees. In 1948, he moved to a faculty position at the University of Kansas, in Lawrence, enabling his return to studies of bees (this move was against the advice of Theodosius Dobzhansky, who felt Mich could do better at a more well-know university). Mich came to love Lawrence and eastern Kansas, but a scientist of his accomplishments could certainly have had opportunities to move to academic positions elsewhere, had he wished.

In the course of his work on systematics, he became fascinated by discoveries of social behavior in diverse and unexpected taxa within the bee phylogeny. Guggenheim fellowships allowed him to travel to Africa and Australia to pursue work on allodapines. He also spent time in Brazil working on halictid social behavior. He coalesced his interest in bee behavior with his book *Comparative Social Behavior of the Bees* (Michener 1974). This book was a masterpiece for a number of reasons, including its comprehensiveness, clarity of writing, and depth of conceptual thought. For many scholars of bees, it was their first introduction to the rich palette of social behavior presented by bees other than honeybees.

It was also notable that Mich's student Suzanne Batra first used the term eusocial in print and that Mich initiated what would become a decades-long discussion of how to define eusociality (Michener 1969). He recognized the importance of kin recognition in testing the principles proposed by W. D. Hamilton for the evolution of social behavior. With Ed Barrows, Mich introduced in the mid 1970s the first evidence of individual recognition in invertebrates and set the stage for what became an explosion of research into kin recognition (Barrows et al. 1975). Mich and David J. C. Fletcher edited a book on kin recognition that largely defined the field and shaped the questions and methods for decades of later researchers (Fletcher and Michener 1987). I don't think Mich ever viewed social behavior as the core of his scientific pursuits, but he definitely believed that the richness of social behavior in bees added a valuable dimension to their study.

Mich thought deeply about the intellectual processes involved in the study of systematics. He was interested in accurate, useful species descriptions as well as how higher level taxonomic units could be used to inform analyses of evolutionary processes. I credit him with the co-invention of numerical taxonomy with Robert Sokal (Michener and Sokal 1957), but he was never an ardent pheneticist. In a second paper, Sokal and Michener (1958) developed UPGMA (Unweighted Pair Group Method with Arithmetic Mean), which became the standard statistical technique for finding hierarchical clusters in numerical data. A Web of Science search using UPGMA as the topic yields over 14,000 papers, most of which employ this approach in data analysis. I believe that he was a coconspirator in Camin's development of the Caminalcules, an imaginary set of organisms used to test hypotheses about how systematic technique interacts with evolutionary hypothesis (Sokal 1983). He was an early advocate of the use of cladistics in systematic analyses. Ultimately he was a thoughtful and flexible systematist, using tools such as numerical taxonomy and cladistics where appropriate, but also relying on applying his immense knowledge of bees and his remarkable powers of integrative thinking to his work on bee classification.

Google Scholar credits him with over 16,000 citations. This is even more impressive when considering that Mich never appended his name to



work by his students; he only recorded authorship on papers where he actually did much of the work. He was elected to the US National Academy of Sciences and the American Academy of Arts and Sciences. He held a Watkins Distinguished Professorship at the University of Kansas. He was a fellow of several large scientific societies, including the Entomological Society of America and the Animal Behavior Society. He received the Hamilton Award from the International Union for the Study of Social Insects (IUSSI). He was the editor of the journal Evolution during its formative years and edited the Annual Review of Ecology and Systematics for many years. He was president of the IUSSI and of the American Society of Naturalists. He chaired the Department of Entomology at the University of Kansas during its heyday in the 1960s and 1970s.

Mich rarely turned his focus towards honeybees. I think he viewed the introduction of the honeybee to the Americas as an unfortunate disruption of natural pollination systems and that he felt that more than adequate scientific effort was being directed to understanding honeybees. Two issues, though, took his attention to Apis. One was the spread of the Africanized honeybee in the Americas. In the late 1960s and early 1970s, lurid stories of bee attacks on humans and livestock in South America made their way into news stories in the USA. The emerging issue of Africanized honeybees and their possible impact in the USA gained the attention of the scientific community, and Mich was asked to chair a National Research Council committee to study the situation. The committee traveled to Brazil and its report (Anon. 1972) prompted a generation of scientific inquiry into the problem. Mich was concerned about getting the scientific message out in a more general way, so he published a summary of the committee's findings in *Bioscience* (1973) and in Annual Review of Entomology (1975). His conclusions in the *Bioscience* article include this amazingly prescient statement about Africanized bees: "...the forms spreading northward through equatorial Brazil are thoroughly undesirable. As there is no obvious barrier to northward spread, it may affect the beekeeping and pollination industries as well as enjoyment of the out-of-doors in the southern United States."

The other attraction of Apis was the very interesting question of whether the phylogeny of the Apidae supports the hypothesis that eusociality evolved a single time in the Apini (the tribe including Bombus, the stingless bees, and the honeybees). This interest led, via a larger study of the evolution of bee mouthparts, to a paper with Mark Winston that argued for two independent origins of eusociality in the stingless bees and the honeybees (Winston and Michener 1977). This argument has led to ongoing investigations, with the intriguing picture emerging that morphological and DNA evidence lead to contradictory conclusions about the origins of eusociality in the Apidae (Cameron and Mardulyn 2001; Cardinal and Danforth 2011).

In addition to all of these scientific accomplishments, Mich was a dedicated husband and father. He and his wife, Mary, were married for over fifty years, with Mary passing away a few years before Mich. Their home, an old farmhouse on the outskirts of Lawrence, was inviting and comfortable. Mary owned and managed a bookstore that for many years was an intellectual center in the small town of Lawrence.

Mich was unfailing in his support for his graduate students. By his count (2007a), he advised 42 doctoral students. He leaves a legacy of scientific accomplishment, facilitation of communication among scientists by promoting the IUSSI and other scientific societies, and numerous academic children, grandchildren, and great-grandchildren. But most of all, he will be remembered for his kindness and thoughtfulness about both personal and scientific questions and his commitment to the careful and considered application of scientific thinking to important questions in evolution and behavior.

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REFERENCES

Anon (1972) Final Report, Committee on the African Honey Bee. Div. of Biol. and Agric. N.R.C., National Acad. Sci, Washington



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Barrows, E.M., Bell, W.J., Michener, C.D. (1975) Individual odor differences and their social functions in insect. Proc. Natl. Acad. Sci. U. S. A. 72, 2824–2828

- Cameron, S.A., Mardulyn, P. (2001) Multiple molecular data sets suggest independent origins of highly eusocial behavior in bees (Hymenoptera: Apinae). Syst. Biol. 50, 194–214
- Cardinal, S., Danforth, B.N. (2011) The antiquity and evolutionary history of social behavior in bees. PLoS ONE 6, e21086
- Fletcher, D.J.C., Michener, C.D. (1987) Kin recognition in animals. Wiley, New York
- Michener, C.D. (1944) Comparative external morphology, phylogeny, and a classification of the bees. Bull. Amer. Mus. Nat. Hist. **82**, 151–326
- Michener, C.D. (1949) Parallelisms in the evolution of the saturniid moths. Evolution 3, 129–141
- Michener, C.D. (1954) The bees of Panama. Bull. Am. Mus. Natu. Hist. **104**, 1–176
- Michener, C.D. (1969) Comparative social behavior of bees. Ann. Rev. Entomol. 14, 299–342
- Michener, C.D. (1973) Brazilian honeybee. Bioscience 23, 523–527

- Michener, C.D. (1974) The social behavior of the bees. Belknap Press of Harvard University Press. Massachusetts, Cambridge
- Michener, C.D. (1975) The Brazilian bee problem. Ann. Rev. Entomol. **20**, 399–416
- Michener, C.D. (1979) Biogeography of the bees. Ann. Missouri Bot. Garden **66**, 277–347
- Michener, C.D. (2007a) The professional development of an entomologist. Ann. Rev. Entomol. **52**, 1–15
- Michener, C.D. (2007b) The bees of the world, 2nd edn. Johns Hopkins University Press, Baltimore
- Michener, C.D., Sokal, R.R. (1957) A quantitative approach to a problem in classification. Evolution 11, 130–162
- Sokal, R.R. (1983) A phylogenetic analysis of the Caminalcules I. The data base. Syst. Zool. 32, 159– 184
- Sokal, R.R., Michener, C.D. (1958) A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull. 38, 1409–1438
- Winston, M.L., Michener, C.D. (1977) Dual origin of highly social-behavior among bees Proc. Nat. Acad. Sci. U. S. A. 74, 1135–1137

