Letters from

Michigan Herpetology

edited by Greg Schneider and Linda Trueb

Special Publication No. 3
The University of Michigan Museum of Zoology
Ann Arbor, Michigan
November 15, 2021

ISBN 978-1-946681-02-7

PUBLICATIONS OF THE
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

Special Publication Number 3

GERALD SMITH, *Editor*

The publications of the Museum of Zoology, The University of Michigan, consist primarily of two series—the *Miscellaneous Publications* and the *Occasional Papers.* Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb. Occasionally the Museum publishes contributions outside of these series. Beginning in 1990 these are titled *Special Publications* and *Circulars,* and each is sequentially numbered. All submitted manuscripts to any of the Museum's publications receive external peer review.

The *Occasional Papers*, begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When enough pages have been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The *Miscellaneous Publications*, initiated in 1916, include monographic studies, papers on field and museum techniques, and other contributions not within the scope of the *Occasional Papers,* and are published separately. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Mammals, Birds, Reptiles and Amphibians, Fishes, Insects, Mollusks, and other topics is available. Address inquiries to Publications, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079.

RECENT *SPECIAL PUBLICATIONS* AND *OCCASIONAL PAPERS*

Smith, G. R., editor, Collected Papers, 2020. Science with a Passion and a Moral Compass: John Vandermeer, The Dialects of Ecology: Biological, Historical, and Political Intersections. *Special Pap. Mus. Zool., Univ. Michigan.*

Kraus, Fred. 2015. A new species of the miniaturized frog genus *Paedophryne* (Anura: Microhylidae) from Papua New Guinea. *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 745, pp. 1–11, 2 figs., 1 table, 1 map.

Wilkinson, M., A. O'Connor, and R. A. Nussbaum. 2013. Taxonomic status of the neotropical caecilian genera *Brasilotyphlus* Taylor, 1968, *Microcaecilia* Taylor, 1968 and *Parvicaecilia* Taylor, 1968 (Amphibia: Gymnophiona: Siphonopidae). *Occ. Pap. Mus. Zool., Univ. Michigan,* No. 744, pp. 1–10, 2 figs., 1 table.

Dedicated to the memory of two

herpetological pioneers:

Helen T. Gaige
and
Alexander G. Ruthven

Cover Design and Timeline
by
John Megahan
Biological Illustrator, University of Michigan

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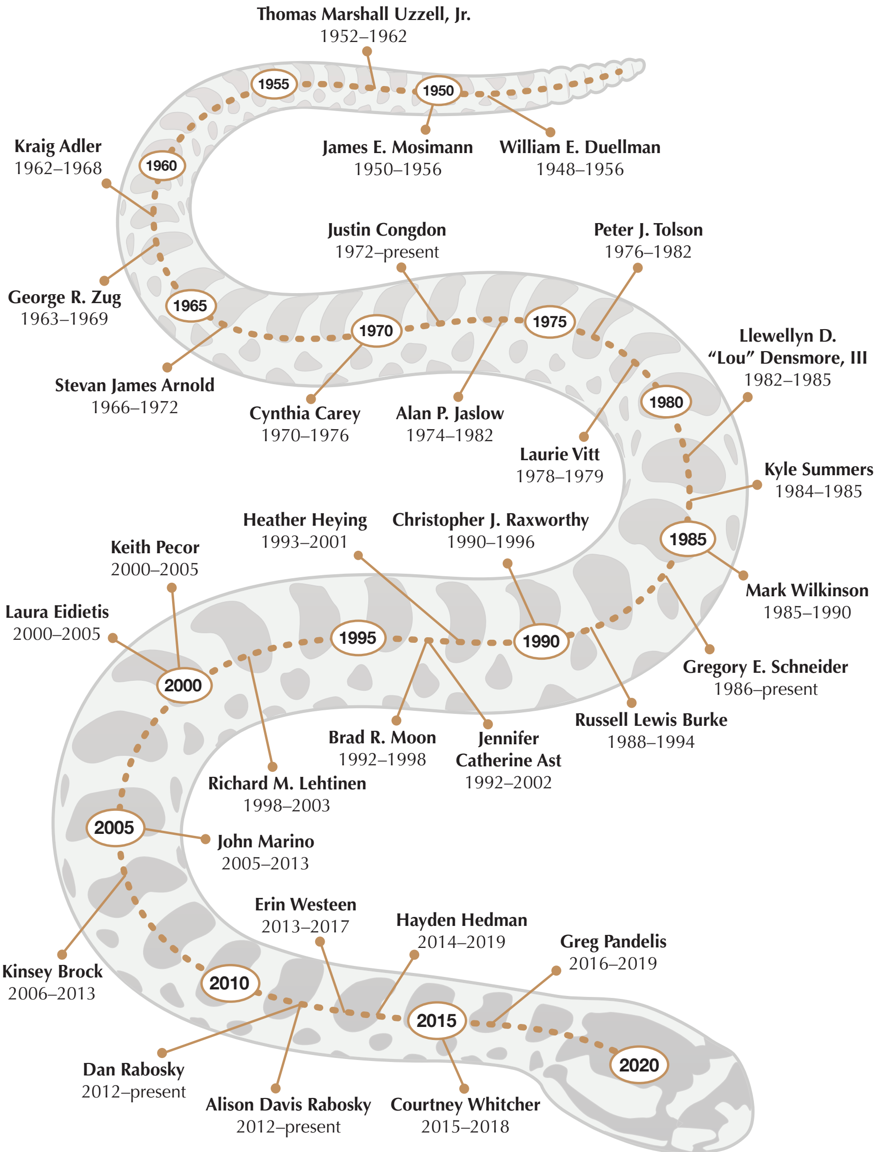
Timeline of Authors to Letters from Michigan Herpetology



This timeline of contributors to the volume spans nearly 75 years, post WW II. Representatives include University of Michigan Ph.D.'s, postdoctoral researchers, faculty, staff, and undergraduate students from each decade since whose research encompasses a diversity of herpetological topics.

Prologue: The Book to Commemorate the Meeting that Never Was Held

This book chronicles the last 75 years of the herpetological program at the University of Michigan, one of America's leading public research universities. The prologue attempts to answer several key questions about the planning and scheduling of an upcoming herpetological meeting on the Michigan campus and the publication details of this related commemorative volume. Coincidentally, the meeting and book have also served to renew ties between two of the great American graduate programs devoted to the biology of amphibians and reptiles.

SSAR Invited to Meet at the University of Michigan

The Society for the Study of Amphibians and Reptiles (SSAR) often sponsors books, poster, and special activities to commemorate its meetings, both those held together with other organizations (e.g., Joint Meeting of Ichthyologists [JMIH] and the World Congress of Herpetology) and those organized separately. The last such independent meeting, co-hosted by Partners in Amphibian and Reptile Conservation (PARC), was held at the University of Kansas in 2015. Besides a souvenir poster that year, SSAR published a new, 346-page book, *Herpetology at Kansas*, which recounts the first century of one of the leading graduate research and education programs on amphibians and reptiles. The book was written by the person who led the Kansas program for half a century, a person who by no accident happened to be a graduate of the herpetology program at Michigan.

The Kansas meeting itself, which attracted nearly 500 delegates, was recognized in the moment to be one of the most successful herpetological conferences in many years, so much so that it inspired the leaders of two university-based herpetological programs to approach SSAR officers on the spot and invite them to meet on their campuses in the near future. One of these invitations was extended by Daniel Rabosky, then an assistant professor of ecology and evolutionary biology at Michigan, together with his wife, Alison Davis Rabosky, later also an assistant professor in the same department. Concurrently, they are both curators in the Division of Reptiles and Amphibians in the university's Museum of Zoology, which is the hub of herpetological activities across the Ann Arbor campus. Such meetings have been held on the Michigan campus several times, beginning in 1929 and including a joint meeting in 1988 that SSAR co-hosted, but SSAR was now being invited to sponsor a meeting of its own. Because of the long and outstanding tradition of the herpetological program at Michigan and the availability of its modern conference facilities, the SSAR Board promptly accepted the offer. Rabosky and Davis Rabosky were appointed co-chairs of the local committee that would plan and run the SSAR meeting. (See announcement on page xiv.)

Conceptualizing the Commemorative Book

It was soon decided to produce a commemorative book about the Michigan herpetological program as a giveaway volume at the conference, which was announced for August 5–9, 2021. Unlike the Kansas book that had been written by someone who had led that program for half its history, there was no such faculty member at Michigan who was able to produce a comparable volume. Thus, the local committee, which included the co-chairs and Gregory E. Schneider, the longtime Research Museum Collections Manager for herpetology and a Master's graduate from the University of California at Santa Barbara, had to develop a different concept for the Michigan volume. They eventually settled on a collection of personal historical essays about the Michigan herpetology program by several former doctoral students, postdoctoral fellows, faculty, and staff, as well as a few undergraduates. Their contributions cover the program since the end of World War II. (The period before 1945 produced 20 Ph.D. graduates among whom were some of the most illustrious American herpetologists of the 20th century; see Appendix.)

The mid-1940s is a convenient dividing point within the longer history of herpetology at the University of Michigan because it marks the retirement of the last of the original leaders of the formal program—Helen T. Gaige—who retired as curator of herpetology in 1945. The essays were requested by invitation so that every decade and the diversity of research topics could be represented. The complete list of individuals who earned Ph.D.'s at Michigan's Ann Arbor campus with dissertations on amphibians and/or reptiles is recorded in the Appendix of this book and begins with William Henry Smith in 1876. (Coincidentally, Smith is thought to be the first person to be awarded a Ph.D. degree in the United States for a strictly herpetological dissertation.)

Links Between the Programs at Michigan and Kansas

Schneider has been responsible for making publication arrangements for the book, as well as handling all correspondence related to it. He, together with Rabosky and Davis Rabosky, invited the contributors. Because he has access to archival materials at Michigan, he was an invaluable help to his co-editor, Linda Trueb, in fact-checking and assembling historical data. Trueb is a graduate of the University of

Kansas herpetological program. Now retired, she served as curator (in collaboration with Bill Duellman) of the Division of Herpetology, professor, editor of museum publications, and associate director of the Biodiversity Institute. In addition to editing this volume with Schneider, Trueb designed the volume and typeset it in Adobe InDesign Ver. 16.3.2. As Duellman's former student, Trueb's participation in the present book project completes the circle of connections between the Michigan and Kansas herpetological programs. (Additionally, the co-chairs of the Kansas meeting—Rafe Brown and Rich Glor—have offered advice and every possible assistance to the Raboskys in planning the Michigan event.)

In reality, the Michigan-Kansas connection was preordained when E. Raymond Hall, a mammalogist who was both museum director and zoology department chair at Kansas, decided to hire the museum's new curator of herpetology *exclusively from among doctoral graduates of the University of Michigan.* He was determined to import the practices developed in the herpetology program at the University of Michigan Museum of Zoology because of the quality of its former students, its development of new technologies for museum-based research, and the democratic social atmosphere that had been developed there by Mrs. Gaige. In fact, all three of the candidates for the open position had been students of the same person—Gaige's former student and successor as curator-in-charge, Norman Hartweg. Hall was also director of the Kansas Biological Survey and the official State Zoologist at the time. He had real autocratic power in his hands and he used it. Although he had been a graduate and former faculty member at a major research university in California, he nevertheless chose a Michigan-trained herpetologist to rejuvenate and improve the Kansas program. (Duellman was hired in 1959. It is practically inconceivable to structure an academic search like this today.)

Why an On-campus Meeting?

It has been SSAR Board policy since 2011 to have an on-campus meeting every 5 years (or once during an undergraduate or graduate career), mainly for the benefit of the students. From its founding in 1958, about 70% of the Society's annual meetings have been held at universities, museums, and biological field stations—the Society's predominate meeting model before JMIH. Such independent meetings in academic environments are SSAR's way to expose students to the natural habitat of most professional herpetologists and to introduce them to the major graduate research programs in our field. Kansas and Michigan certainly qualify, and other campuses are under consideration for future years. By being on a research campus, students can see for themselves the special facilities and collections, explore local habitats available for field research, meet the faculty, students, and staff, and see the broader institutional context. And so it will be for Ann Arbor in 2024. This experience is far better than reading a description or even having a virtual tour. This commitment by SSAR requires a great deal of extra effort and expense, but the Society thinks that it is a critical investment in the future of our discipline.

Scheduling and Rescheduling the Michigan Meeting

The SSAR meeting at Michigan had originally been set for the summer of 2020, exactly 5 years after the Kansas meeting and on schedule according to the SSAR Board policy to have occasional independent, on-campus meetings. However, subsequently, it was announced that the 9th WCH was going to be held in New Zealand in January of that year. It was thought that this might create a financial burden for many delegates who planned to attend both events; so, SSAR and the local committee decided to delay the meeting by a year until August 2021. Little did anyone know at the time that the world crisis that would develop in January 2020 would put both the 2020 and 2021 dates in jeopardy. The SARS-CoV-2 pandemic (or "Covid-19") began its steep rise during the spring and summer of 2020, and its potential impact on the Michigan meeting scheduled for August 2021 was being constantly evaluated by the SSAR Board, the local committee, and SSAR's official liaison to the local committee, Aaron M. Bauer. There was no certainty that a vaccine could be developed, and inoculations completed in time for the meeting to take place safely, nor could the local committee seriously plan the overall meeting and get commitments from key participants. A decision to postpone the meeting by the SSAR Board in October 2020. As it turned out, the vaccine first became available for public use in January 2021, but the vaccination of the American public was not complete even by the summer of 2021. The University of Michigan later canceled all on-campus meetings for the summer of 2021, so no facilities would have been available in any case. The Board had made the right decision, painful though it was, and it did so in a timely manner. The Board furthermore decided to postpone the meeting to the summer of 2024, the earliest year it could have chosen under its rolling contract with the JIMH group of societies.

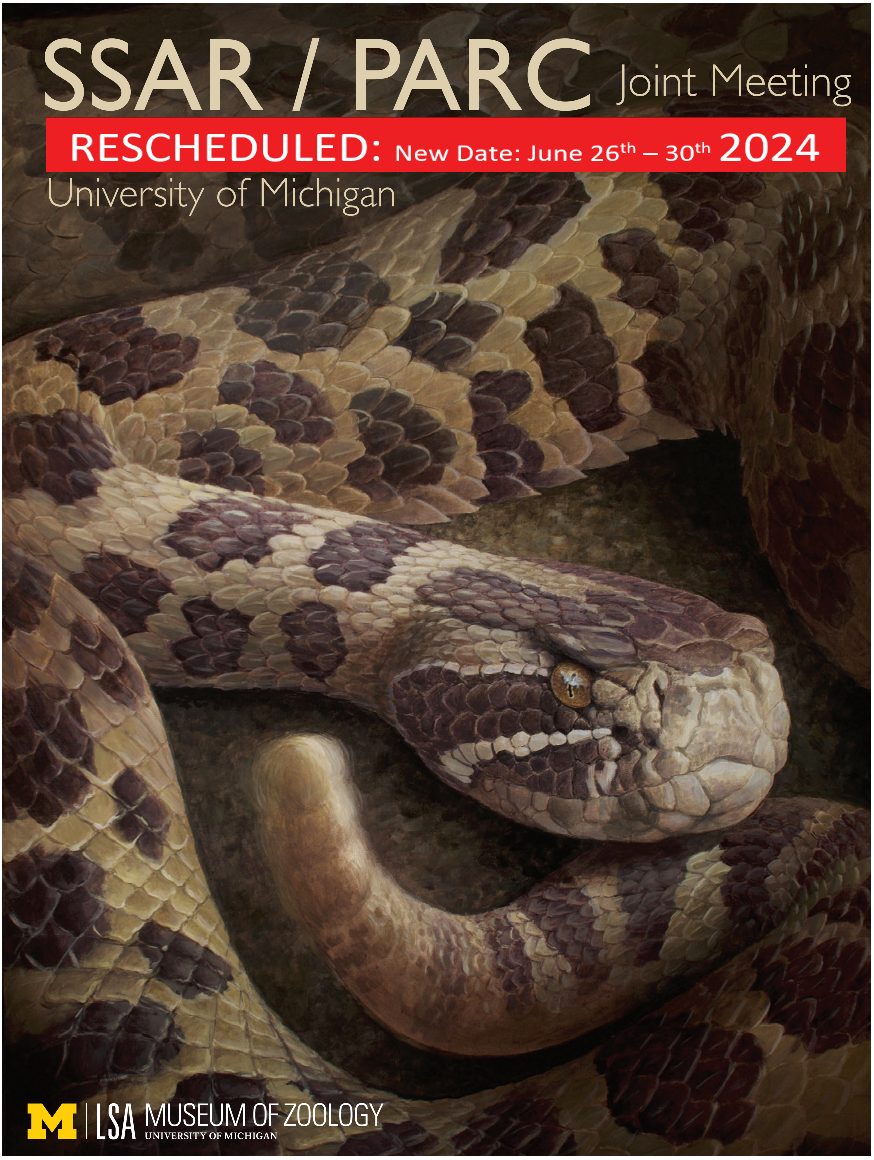
Publication and Distribution of the Book

It was originally assumed that the book's publication would also be delayed until 2024, but in fact issuance of the book was not directly linked to the meeting—the meeting of 2021 that never was held. Several authors and organizers urged that the book be published when ready and not pushed off to 2024. It was thought that by doing so now would give SSAR a great opportunity to promote the postponed meeting more broadly. Consequently, it was decided to publish the book in 2021 while it would still be fresh, and distribute it directly to members of the Society. The aid of a generous grant from the Gans Charitable Fund has made it possible to do so. (Carl Gans, in fact, was once part of the Michigan herpetological program—as a faculty member and department chair in Biological Sciences between 1970 and 1997; see Brad Moon's essay, page 183.) SSAR and the Department of Ecology and Evolutionary Biology also contributed to publication costs.

The Future of the Michigan Program

Here, then, following an historical overview by Linda Trueb, we introduce more than 30 personal recollections about the Michigan herpetological program of the recent past as told by the actual participants. Michigan graduates will be particularly eager to read the final two chapters by Rabosky and Davis Rabosky, for they give insight into the research interests and goals of the two people who will lead the Michigan herpetological program for the foreseeable future. In several respects, they are akin the renowned team of Alexander G. Ruthven and Helen T. Gaige, who developed the original program more than a century ago. Rabosky and Davis Rabosky—trained at Cornell University and the University of California–Santa Cruz, respectively, and with postdoctoral fellowships at the University of California–Berkeley—are conversant with observational, as well as experimental research modes, use the most modern methodologies and technologies, and conduct research both in the field and in the lab. They are committed to building the collections—the largest university-based museum of amphibians and reptiles in the world—and to using them in exciting ways. They are also fully aware of, and respect, the deep history of the program that they now lead. They already have successfully supervised a wide range of student projects and demonstrably adhere to the highest academic standards. There is great enthusiasm, therefore, about the future of "Michigan Herpetology" and the key role that this program will continue to play as a leader in the progress of our discipline and biology generally.

Kraig Adler
July 2021


SSAR / PARC Joint Meeting
RESCHEDULED: New Date: June 26th – 30th 2024
University of Michigan
LSA MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN

LINDA TRUEB

Introduction: Building on a Legacy

As I began assembling the contributions for this volume, I considered myself to be an unbiased observer—one who was introduced to herpetology at UC–Berkeley in the late 50s before undertaking graduate studies at the University of Kansas in the early 60s. How difficult could it be (with the outstanding help of co-editor Greg Schneider) to assemble some 31 letters composed by professionals who were trained in, or are the current curators of, herpetology at the University of Michigan Museum of Zoology (UMMZ) during the past 72 years? In the spirit of a research challenge, I looked for similarities and differences, and tried to identify patterns of change through time in these reported experiences. Were there any insights into the causes of programmatic successes that influenced the profile of Michigan's herpetology program on the national and international landscapes? The first thing that became obvious was that reflections of the older herpetologists are set in a broader historical and geographic context than those of the more recent graduates; thus, viewed through the lens of changing times and breadth of experience, the accounts are not directly comparable. The older reader has much to learn about the future of herpetology from the younger scientists, and the younger, in turn, have an opportunity to evaluate their place in the history of the discipline from their elders.

Ancient History

An overview of history indicates that the legacy of collections is probably as old as humankind, suggesting that humans are, and always have been, inveterate collectors. From Stone Age hunter-gatherers in 50,000 BCE, humans transitioned through the next 38,000 years to the Neolithic Period, dating from about 12,000 years BCE until about 4500 years BCE. This period was characterized by refinement of tools, use of pottery and textiles, and the appearance of agriculture and development of more permanent settlements. Beginning in about 5000 BCE, urban cultures emerged and there is evidence of the development of metallurgy and manufacturing in Egypt, Mesopotamia, what is now Pakistan, and India. This marks the beginning of collections and museums. In Mesopotamia, in the remains of what may have been a warehouse or library of clay tablets, one tablet was recovered that listed the titles of other tablets—the first collection catalog? And Egypt, of course, is renowned for its massive collections of funerary objects—i.e., collections of items that were to accompany the deceased on the journey ahead.

The first collections not associated with funerary objects emerged in the period 2000–700 BCE when trade routes were established, and novel raw materials became available. In Egypt, pharaohs collected specimens of plants and animals, as well as art, antiquities, and examples of flora and fauna from Asia. The first zoo usually is credited to Egypt, specifically to Queen Hatshepsut (1473–1458 BCE). Other Egyptian collections contained rings, gemstones, and fine pottery; caches of fossil bones from local herbivores and crocodiles also were found. Late in the 1st millennium BCE, Homer's *Illiad* and *Odyssey* were transcribed from oral to written form; these epic poems reveal that the Greeks understood the history and use of historical objects—in other words, they developed the concept of an object's provenance.

Arguably, one of the most significant contributions of the Greeks to collections is the association of objects and knowledge. Collections during this period (ca. 500 BCE – 500 CE) were housed in public sanctuaries and techniques were developed to preserve fragile objects. One such collection was the Temple of the Muses in Alexandria, Egypt. The holdings focused on texts, but included a room devoted to anatomy. Collection objects in the Temple (*Musaeum*) were considered to be sources of knowledge that were studied by a school of scholars. The whole—i.e., scholars, research institute, and library—were protected by the Muses. This is thought to be the Hellenistic forerunner of a university and is the source of the name "museum."

The contributions of Plato and Aristotle are central to collections development during this period. Plato's (428–347 BCE) philosophical Theory of Forms hypothesizes that all objects that we see are imperfect and ephemeral representations of ideal archetypes; hence, a universal classification of objects based on ideal standards and patterns could be applied to collections. Plato's student, Aristotle (384–322 BCE), tutored young Alexander the Great (356–323 BCE). While conducting military campaigns in western Asia and northeastern Africa, Alexander sent specimens and descriptions of things he saw to Aristotle, who included them in his compendium, *Historia Animalium,* which was written ~350 BCE, with the first printed edition appearing in 1476 CE. Aristotle organized all known species of animals in a staged progression (*scala naturae*) in their perceived degree of perfection—a classification scheme that prevailed in collections arrangement up to the mid-18th to the 19th century until after Darwinian evolution was widely accepted.

The Roman Republic (27 BCE–286 CE) preceded the establishment of the Roman Empire; the western portion lasted until about 500 CE, whereas the eastern part prevailed until 1453 CE. Collecting the odd and unusual was common and items were displayed in homes. No institutions housing collections existed, save for the city of Rome, which is a monumental outdoor museum in, and of, itself. Nevertheless, some of the private collections eventually found their way into Medieval Europe (400–1400 CE) owing to travelers, pilgrims, merchants, and soldiers crisscrossing the region. Churches became the centers of intellectual life, and church treasuries became depositories of many collections.

The Renaissance

The first universities were founded as early as 859 and 970 CE in Morocco and Egypt, respectively. European universities followed beginning in 1088 (Bologna, Italy), 1096 (Oxford, UK), 1134 (Salamanca, Spain), 1160 (Paris, France), 1209 (Cambridge, UK), and 1222–40 (Padua, Naples, and Siena in Italy). With the beginning of the Renaissance in the 1300s, these institutions were well positioned to replace churches as intellectual centers. Science was recognized as a process of discovery leading to an accumulation of knowledge (Francis Bacon, 1561–1626 CE), which justified the collection and study of objects in museums and universities. A noteworthy early private collection was that of an Italian naturalist, Ulisse Aldrovandi (1522–1605), in Bologna in the 1550s. Aldrovandi is acknowledged to be the world's first professor of natural history, and on his death, his collection of some 7000 botanical and zoological specimens was given to the Senate of Bologna; it became the nucleus of a public display—the world's first public natural history museum that was conserved as a unit until 1742. Aldrovandi also established a public medicinal herb garden in Bologna in 1568; today, this garden is maintained by the University of Bologna as the Orto Botanico di Bologna.

Several factors contributed to the development of Renaissance collections. Perhaps most significant is the emergence of a global economy fueled by maritime trade around the world. Given the influx of collected objects to European private collections, the need arose to document or catalog their contents and organize the arrangement of objects. The invention of the printing press (1440s) in Europe led to the publication of collection catalogs. Near the end of the Renaissance, the raison d'être for collections shifted from gathering oddities to more rational assemblages of natural, environmental objects. This, in turn, led to expansion of private collections and their eventual consolidation into museums open to the public.

The Age of Enlightenment

The early 1600s ushered in the scientific revolution marked by empiricism, experimentation, and inductive reasoning, and a period of intense geographical and political imperialism. Natural consequences included: consolidation of private collections, which grew and eventually specialized (e.g., historical, art, scientific); a proliferation of collections; and the establishment of scientific societies (e.g., Royal Society of London). It is noteworthy that the first printing press in the American colonies was in Cambridge, Massachusetts, in 1638; it was financially supported by Harvard College.

The 1700s is characterized by scholarly interest in the development of universal languages and systems of order that could be applied to collections—specifically, the binomial system of Carl Linnaeus (1707–1778), which prevailed over the zoogeographic system proposed by Comte de Buffon (1761, 1776) and led to Lamarck's (1809) theory of evolution. In the late 1700s, the first museums were established in the American colonies. The oldest was founded by the Charleston Library Society, which founded the College of Charleston in 1770 and the Charleston Museum in 1773 in Charleston, South Carolina. In 1782, a Swiss artist, Pierre Eugene Du Simitiere, opened a public natural history museum in Philadelphia, which was purchased by Charles Wilson Peale in 1785 and opened to the public. Peale (1742–1827) was a naturalist and portrait artist who organized the first U.S. scientific expedition funded by the American Philosophical Society in 1801. Peale's "American Museum" was among the first to adopt Linnaean taxonomy. The collections were sold after Peale's death and eventually were purchased by John Scudder in 1809 for "Scudder's American Museum." In 1841, P. T. Barnum purchased Scudder's collection for "Barnum's American Museum," which opened in 1842 in New York

City and closed in 1865.

Modern U.S. Museums: 1800s

The **Academy of Natural Sciences of Philadelphia** is the second oldest U.S. museum; it was founded in 1812 by amateur naturalists who donated library materials and specimens to establish the collections. The Academy was opened to the public in 1828. It participated in many explorations and came to house Thomas Jefferson's fossils, Lewis and Clark's plants, and many of the birds collected by John James Audubon.

The industrial economy of the last half of the 19th century witnessed a proliferation of public museums and the publication of Darwin's *Origin of Species* in 1859, which had a profound impact on the rationalization, importance, and use of collections. Museums and their collections came to be recognized as educational resources that underpinned scholarly research. Darwin's theory of evolution displaced the typological constructs that underlay collections of this period. Instead of an anagenetic progression to perfection (*scala naturae*), species arise by diverse branching from a common ancestor in response to natural selection (i.e., descent with modification). To understand the diversity and relationships of organisms, the variations within and between species had to be examined. Modern museums, then, are repositories for preserved, catalogued specimens of verifiable provenance, as well as their associated documents and library materials—all of which can be studied by scientists.

Most of the first U.S. museums were established in the 13 former British colonies along the Eastern Seaboard in the second half of the 19th century. Notable exceptions are two West Coast institutions: (1) The **California Academy of Sciences,** a research institute and society that was founded in 1853; the museum officially opened in 1874 and was destroyed in 1906 by the San Francisco earthquake and fire, but later was rebuilt; and (2) the **San Diego Natural History Museum,** which was established by the San Diego Society of Natural History in 1874 and is the second oldest museum west of the Mississippi River. Among the early American museums are the **Smithsonian Institution** (1846), which included collections that were to become the **National Museum of Natural History** in 1911. The **Museum of Comparative Zoology** at Harvard College was founded in 1859 by Louis Agassiz; it is a consolidation of collections that had been held in different university departments. The **Peabody Museum of Natural History** at

Yale University and New York's **Cornell University Museum of Vertebrates** were both established 1866, shortly before the **American Museum of Natural History** opened in New York City in 1869.

As immigrants pressed westward from the territory of the 13 original colonies and across the Louisiana Purchase (1803), settlements flourished, and states were established. Admission to statehood required authorization by Congress, which in turn, required the petitioners to formulate a government and adopt a constitution in compliance with the U.S. Constitution. As part of this process, two kinds of institutions commonly were chartered—viz., biological and geological surveys and state universities, which in turn, frequently established "cabinets of natural history" (not to be confused with "cabinets of curiosities") to accommodate the research collections of university students and professors in the biological sciences.

The histories of these collections, their organizations, and their names evolved through the 20th century in response to the economy, the development of research and funding, and the changing attitude of university administrations. As technology advanced, many administrations came to view "cabinets" and museums as the pastime of dilettante organismal "stamp-collectors" and ceased to support them. This resulted in the abandonment of many collections or occasionally, their rebranding under the rubrics of "centers" and "institutes" as the focus for research and graduate education. For many university administrators, the substantial extramural funding garnered by these organizations justified their existence.

Herpetology at the University of Michigan

This is the legacy upon which the collections and graduate program at the University of Michigan were built. Much of the following account is drawn from Arnold Kluge's "History of the Collections" and "Reptile & Amphibian History"—contributions prepared for publication on the web accessible at https://webapps.lsa.umich.edu/ummz/herps/history/default.asp.

The Early Years: 1837–1900.—The cultural and economic context of the mid- to late-19th century was the Second Industrial Revolution and so-called Gilded Age in the U.S. Technological advances included generation of electricity, development of transformers, and appearance of gasoline-powered automobiles. The 1890s witnessed a severe economic depression, widespread strikes by industrial workers, the

Klondike Gold Rush, the Spanish American War, and the discovery of radioactivity. In 1893, the World's Columbian Exposition was held in Chicago, Illinois. The **Field Museum** opened in 1894 to house some 50,000 artifacts that had been on exhibition at the fair.

When Michigan was admitted to the Union in 1837, the Michigan State Legislature budgeted for a Cabinet of Natural History, which was renamed the Museum of Natural History in 1881. The core of the initial holdings was the Trowbridge Collection, which was donated by the Smithsonian Institution in 1859; Lieutenant William Petit Trowbridge, a Michigan professor, had collected specimens along the Pacific Coast from San Diego to Puget Sound from 1853–1856. Another significant source of early specimens was the Beal Steere Collections. Joseph Beal Steere (1842–1940) received his degree (B.A.; B. of Law) from Michigan in 1870. Upon graduating, Steere, who was an ornithologist, spent 18 months on the Amazon River and collected in Peru before sailing to China. In 1887, he mounted a 5-year expedition to the Philippines and Moluccas, returning to the U.S. by way of the Suez Canal and Great Britain. Steere was awarded an honorary Ph.D. by the university in 1875 and joined the Michigan zoology/paleontology faculties in 1876. In 1876, William Henry Smith received a Ph.D. from Michigan. Smith's thesis is thought to be the first strictly herpetological thesis in America. It was published in 1877 under the title *The Tailed Amphibians including the Caecilians. A thesis: Presented to the Faculty of Michigan University.* Many members of the faculty contributed to, and had curatorial responsibilities associated with, the cabinet (e.g., Asa Gray, botanist; Alexander Winchell, geologist; Charles C. Adams, zoologist).

It is important to understand the duties of curators during the 19th century and up to the mid-20th century. The word *curator* is derived from the Latin *curatus,* the past participle of *curare,* which means "to take care of." Thus, until the middle of the 20th century, herpetological curators were hands-on managers of dried and fluid-preserved specimens of amphibians and reptiles. They were responsible for identifying specimens, arranging them taxonomically in the collection, maintaining fluid levels, and registering their data in handwritten catalogues. In addition, curators associated with universities were expected to have a specimen-based research program, train students, and usually to teach courses in the biological sciences.

The Establishment of the University of Michigan Museum of Zoology: 1900–1929.—With the 1900s came numerous inventions (e.g., the typewriter, nickel-alkaline storage battery, steam and diesel engines), the first controlled flight (Wright brothers), and mass production of automobiles. By far the most significant scientific advances were in physics with the contributions of Albert Einstein, who explained the photoelectric effect, Brownian motion, and advanced the theory of special relativity. The first photostat machine appeared and Bakelite was invented (from which the ubiquitous black Bakelite lids for jars of fluid in collections were made) in 1907.

1910–1930 was a dynamic period marked by events such as World War I (1914–1918), the economic boom after the war, the Wall Street Crash in 1929, and scientific advances that affected research and collections. The Smithsonian Institution opened its Natural History building to the public, and Thomas Hunt Morgan discovered that genes are located on chromosomes (1910). In the following year, the first international treaty to address wildlife conservation was signed, the first explorers reached the South Pole, and superconductivity was discovered. In 1912 Alfred Wegener proposed his theory of Continental Drift, and in 1913, mass spectrometry was developed, the ozone layer was discovered, and the quantum model of the atom developed. Important 1915 publications included Einstein's theory of General Relativity, Wegener's theory of Pangea, and T. H. Morgan's documentation of non-inherited genetic mutation in *Drosophila*. Toward the end of the decade, Ernest Rutherford first observed a nuclear reaction, and R. A. Fisher advanced a genetic model that demonstrated that continuous variation could be the result of Mendelian inheritance.

At the University of Michigan, Alexander Grant Ruthven (curator from 1906–1936) was the first professionally trained herpetologist to curate the collections of amphibians and reptiles. Ruthven received his Ph.D. in 1906 for his research on garter-snake systematics under the mentorship of Charles Adams. He had a positive and far-reaching, effect on the collections, as well as the university as a whole. Ruthven's fieldwork resulted in large collections of local amphibians and reptiles, in addition to specimens from some 18 expeditions in the U.S., Mexico, Colombia, and British Guiana. In 1913, Ruthven was appointed as the first director of the museum, which then was renamed as the Museum of Zoology. In 1918, he secured funds for the Museums Building, which opened in 1928. The following year, Ruthven resigned as director of the museum to become president of the university; however, he retained his curatorship of the Division of Reptiles and Amphibians until 1936. Early in his curatorial career, Ruthven was assisted by two women, Helen Thompson (1912–1918) and Crystal Thompson (1914–1918). Helen (along with Frank Blanchard) had been a student of Ruthven's. All of the early collections were registered in the same numbered series; however, in 1916, four separate vertebrate catalogues were begun, with each starting at the number 52001. The first reptile and amphibian catalogue is Volume II.

In 1919, Helen Gaige (née Thompson, but no relation to Crystal Thompson) was appointed as an assistant curator. The importance of Helen Gaige's role in Michigan herpetology has not received the recognition that it deserves. As Ruthven assumed more administrative responsibilities, he obviously had less time for research and student mentorship; these activities were assumed by Helen Gaige. Charles Walker (Ph.D. 1935) ostensibly was a student of Ruthven's. However, in an undated conversation with Kraig Adler, Walker said that he had only met with Ruthven twice during his graduate studies—once when he first arrived and again at his thesis defense; otherwise, Mrs. Gaige directed his studies (Adler, pers. com.). Apparently, this was the case for most of Ruthven's students after 1930. Although Ruthven continued to publish research, most of it was conducted by Helen Gaige, who was not listed as a co-author on earlier works. Helen Gaige had a profound impact on herpetology at Michigan and nationally. She was one of the organizers of the American Society of Ichthyologists and Herpetologists and was named as an honorary president of the organization in 1946. From 1937–1950, Gaige served as the Editor-in-chief of *Copeia,* which quickly became the premier journal for fishes, amphibians and reptiles during this period. And probably most important, Helen and her husband (entomologist, Frederick McMahon Gaige) were responsible for establishing a family-like atmosphere in the Division of Reptiles and Amphibians—a tradition cherished and carried on by generations of Michigan graduate students.

Ruthven chaired the Ph.D. committees of a total of nine students, the first four of which were Frank N. Blanchard (1919), Frieda Cobb (Blanchard; 1920), Arthur I. Ortenburger (1925), and Olive G. Stull (1930). Blanchard, Ortenburger, and Stull completed research on the systematics of snakes, whereas Cobb studied genetics of primroses. Ruthven also chaired Carl Hubb's (1927), Josselyn van Tyne's (1928), and Laurence C. Stuart's (1933) committees. Hubbs first served as assistant curator of fish, amphibians, and reptiles at the Field Museum of Natural History before accepting the position of curator of fishes at Michigan in 1920, where he received his Ph.D. Van Tyne, an ornithologist, became curator of birds at the UMMZ. Stuart completed his undergraduate, as well as his graduate degrees at Michigan, and subsequently became a faculty member. He maintained his association with Michigan until 1969, after which he and his wife, Kate (Ruthven's daughter), retired to live in Panajachel, Guatemala. Although considered by some to have been somewhat of an outlier in the museum community, Stuart made tremendous contributions to the collections through his fieldwork and studies on the distributions and taxonomy of amphibians and reptiles of Central American, particularly Guatemala. He was one of the most versatile and productive herpetologists of the Michigan cohort at the time.

Herpetological Traditions Established During Tough Times: 1930s & 1940s.—The 1930s brought global economic and political crises that culminated in World War II (1939–1945)—not an especially favorable climate for herpetological research and the growth of collections. The Great Depression followed the crash of the stock market and lasted until 1941, when the U.S. entered World War II. Technological advances included the invention of radar and the discovery of nuclear fission in 1938, which in turn, led to the creation of a nuclear chain reaction, and ultimately the development of nuclear reactors and atomic bombs in the early 1940s. The first digital computational devices appeared, along with primitive jet aircraft.

Helen Gaige was the divisional curator until 1945. However, by maintaining his curatorial title, Ruthven cast a long shadow on the development of research and graduate-training, and the future of the herpetological program at the University of Michigan. His first graduate student, Frank Blanchard, was hired as a zoology professor at the University of Michigan in 1920. Blanchard, in turn, directed the doctoral research of Charles E. Burt (1930), Howard K. Gloyd (1936), William M. Clay (1937), Ira D. George (1940), Hugh D. Clark (1941), and chaired the committee of Lucille Farrier Stickel (1949) until his death. Another Ruthven student, Laurence C. Stuart (1933), was appointed Instructor in Zoology and Research Associate in the Museum of Zoology when he completed his Ph.D. Likewise, Norman Hartweg received both his undergraduate and graduate training at Michigan and was appointed as an assistant curator in Herpetology in 1934 on receiving his Ph.D., Charles F. Walker, who received his AB and MS degrees from Ohio State University and his Ph.D. from Michigan in 1935, returned to Michigan as a curator of amphibians and reptiles in 1947.

Three students of Ruthven's did not return to Michigan—Arthur Ortenburger (1925) joined the faculty of the University of Oklahoma and was appointed curator of the Museum of Zoology (now the Sam Noble Museum of Natural History) in 1924. Joseph Bailey (1940), and James Oliver (1941) pursued careers at Duke University and the American Museum of Natural History, respectively. Although preceded by Ortenburger's departure many years earlier, Bailey and Oliver's departures mark the first of a cascade of Michigan graduates who populated positions across the U.S., as well as a departure from previous hiring practices. Universities began to seek faculty who were trained at peer institutions, rather than hiring their own graduates. In 1940, Frederick H. Test—an ecologist and amphibian biologist—was hired by the zoology faculty at Michigan; Test arrived by way of Purdue (B.S.), Cornell (M.A.), and UC–Berkeley (Ph.D.), adding another dimension to the herpetology program.

World War II obviously interrupted undergraduate and graduate studies at the university. Nevertheless, Norman Hartweg mentored two graduate students—Fred Cagle and Grace Orton, who received their degrees in 1943 and 1944, respectively.

Windows of Opportunity: Michigan Herpetology in the 1950s and 1960s.—Despite the backdrop of the Cold War between the U.S. and the Soviet Union, the Korean War (1950–1953), the Vietnam War (1955–1975), and revolutions in Cuba and Hungary, as well as conflicts in Algeria and Indochina, herpetology prospered at Michigan. In no small measure, this probably reflected two major events. The first was the implementation of the G.I. Bill that provided educational benefits to veterans returning from WWII, and the Korean and Vietnam wars. And the second was the creation, in 1950, of the National Science Foundation (NSF), the purpose of which was "to promote the progress of science; the advance the national health, prosperity and welfare; to secure the national defense; and for other purposes" (https://www.nsf.gov/about/history/overview-50.jsp). During the 1960s, the NSF supported basic research (primarily in the natural sciences) performed by individuals who, by creating knowledge, would transform the future. In its initial program (1960), NSF provided matching funds for building or renovating research laboratories at 1st-tier, graduate degree–granting universities. In an effort to increase the number of institutions of recognized excellence and widen the geographical dispersion of funds, the NSF launched its Institutional Grants for Science to institutions other than those in the 1st tier in 1961. Significant advances in technology signaled the onset of the Space Race with the launch of Sputnik 1 in 1957 and the moon landing in 1969; the first use of passenger jets and the first transistor computer appeared in the early 50s and was followed by the founding of NASA (National Aeronautics and Space Administration) in 1958. Doubtless the single most important biological milestone was the discovery of the double helix structure of DNA, popularly credited to Francis Crick and James Watson, but also including Rosalind Franklin and Maurice Wilkins in 1953.

The first of the series of recollections begins in this decade with essays by William E. Duellman (1930–) and James E. Mosimann (1930–), both of whom received their undergraduate and graduate degrees from Michigan. In their essays, both speak to the challenges and advantages of their associations with fellow graduate students who were veterans—viz., James A. Peters (1922–1972), Herndon Dowling (1921–2015), Thomas Uzzell (1932–), Harold Dundee (1924–2018), Charles Carpenter (1921–2016), Owen J. Sexton (1926–2018), James Organ (1931–2015), and Richard Etheridge (1930–2019). Many of these museum-based students served as curatorial assistants to curators Hartweg and Walker. The remainder of the herpetological cohort was composed of Arthur E. "Jack" Dammann (1920–2007), Paul Martin (1928–2010), Priscilla Starrett (1929–1997), George Rabb (1930–2017), and Harold Heatwole (1935–). This dynamic group of students was mentored by Norman Hartweg, Charles Walker, Frederick Test, and Nelson Hairston, Sr. (who joined the zoology faculty in 1948). The diversity of research endeavors of these students is impressive—systematics, ecology, life-history, population biology, morphology, morphometrics, as well as regional and distributional studies of lizards, snakes, turtles, frogs, and salamanders. Nearly all of these projects involved extensive fieldwork and collections of voucher specimens from across the U.S., as well as Mexico and Central and South America. During the 60s, Michigan was one of the institutions that garnered support from the NSF, which funded the addition of a new research wing on the museum. This wing housed modern biological laboratories with live animal-holding rooms, environmental chambers, and biochemical facilities—all of which expanded the research horizons of the graduate students into experimental biology and led to a productive integration of faculty from both the department and museum on graduate-student committees.

Although not members of the herpetology group (*sensu stricto*), other graduate students contributed to the herpetological core at Michigan. For example, there are the following dissertations: Emanuel Hertzler (1951) on pigmentation in salamanders; George Baxter (1952) on the relation of temperature to altitudinal distribution in toads; Kenneth Fitch (1957) on the development of the salamander, *Necturus;* and Albert Schwartz, a student in mammalogy (Ph.D., 1952), who participated in many field excursions with the students in herpetology, and later conducted ground-breaking systematic research on Antillean amphibians and reptiles before turning his attention to lepidopterans.

These Michigan graduates of the 1950s marked the beginning of a herpetological diaspora. They and those who followed during the 1960s populated major universities, many of which housed collections of amphibians and reptiles, free-standing museums, and federal organizations such as the National Institutes of Health. Thus, Michigan Herpetology made its mark on the national landscape at a time when basic research was generously funded by the NSF—the so-called "Golden Age of Science" funding.

The addition of physiological ecologist William R. "Bill" Dawson, who published many herpetological papers, in 1953 to the Michigan faculty brought another dimension to herpetological research—that of ecophysiology. Dawson served as chair of biology (1974–1982) and director of the Museum of Zoology (1982–1993) and mentored a total of 19 graduate students. Among these were Calvin Boyd Dewitt (1963), Paul Licht (1963), Vaughan H. Shoemaker (1964), William A. Dunson (1965), Walter R. Moberly (1966) and John E. Minnich (1968). Another significant addition to the faculty was Donald W. Tinkle, who developed life-history theory in reptiles. Tinkle had been a student of an early Michigan graduate, Fred Cagle. He joined the Michigan faculty in 1965 and served as Curator of the Division of Reptiles and Amphibians until 1975, when he was appointed director of the museum. His first two students were Gary W. Ferguson (1969) and Charles O. Kinney (1969).

During the 1960s, a plethora of students completed their degrees under the mentorship of Charles Walker, Norman Hartweg, Frederick Test, and Nelson G. Hairston. Among these were Harold Heatwole (1960), Tom Uzzell (1962), Jim W. Dole (1963), Marilyn Bachman (1964), Floyd L. Downs (1965), William R. Healy (1966), Priscilla H. Starrett (1968), Kraig Adler (1968), Warren Y. Brockelman (1968), and George

R. Zug (1969). Both Adler and Zug have contributed to this volume of recollections and offer interesting insights into the personalities of the faculty and their devoted mentorship of graduate students during the decade.

The 1970s and the Pivot of Change.—This decade often is referred to as the "Pivot of Change." Economic upheavals followed the end of the economic boom at the end of the Vietnam War. Nevertheless, there were tremendous technological advances in science and scientific instrumentation, fueled largely by the National Science Foundation's initiative to support applied research that was focused on national problems (e.g., environmental quality, and urban growth and management). This focus shifted funding from institutional and educational programs in the sciences to "socially relevant scientific research," which had major consequences for the growing number of institutions competing for support of their facilities and instrumentation.

Among the notable scientific events were the development of the integrated circuit (e.g., Intel 4004), the first desktop computer (Xerox, 1973), e-mail (1971), lasers, C-programming language, and the first genetically engineered organism (a mouse). The first fiber optics, microwave ovens, and cell phones appeared, and the Apple Computer Company was established in 1976. Stephen Hawking developed the Black Hole Theory, and Stephen J. Gould and Niles Eldredge posited the Punctuated Equilibrium Theory of Evolution. Elsewhere in biology, molecular biology, bacteriology, virology, and genetics emerged. And there was growing concern (as evidenced by the first Earth Day in 1970) about habitat destruction and diminishing species diversity. During this decade, herpetological collections continued to grow at a rapid pace as more and more herpetologists pursued fieldwork around the world. It became increasingly challenging to manage these collections and retrieve their data; so, it was no surprise that we began to hear about "computerizing collections."

Meanwhile, at Michigan, the herpetological pursuits of graduate students were focused primarily on population ecology, courtship behavior, reproductive ecology, and life-history and metabolic studies of amphibians and reptiles in the U.S. Don Tinkle mentored nine students (Stephen Tilley, 1970; Ronald Flaspohler, 1970; Marian Vinegar, 1973; James Collins, 1975; Wayne Van Devender, 1975; Douglas Ruby, 1976; Michael Devine, 1977; David Smith, 1977, and Arthur Dunham, 1978), and Bill Dawson another three (Albert Bennett, 1971; Robert

Gatten, Jr., 1973, and Cynthia Carey, 1976). Charles Walker had two students (Albert Allen, Jr., 1970; and Henry Wilbur, 1971), and Richard Alexander and Frederick Test each had one herp student. Two new curators were added to the docket—Arnold Kluge (Zoology Department faculty, 1965; museum, 1967) and Ronald Nussbaum in 1974. Kluge mentored Stevan Arnold (1972) and Nussbaum mentored Paul Feaver (1977). Much of the herpetological flavor of this decade at Michigan is captured in Steve Arnold's informative account, Cynthia Carey's recollections, and Justin Congdon's contribution about his postdoctoral fellowship at the E. S. George Reserve with Don Tinkle. Likewise, the recollections of Alan Jaslow and Peter Tolson, neither of whom received their degrees until 1982, are most relevant to this decade, as is the essay of Laurie Vitt, who undertook a post-doctoral fellowship in 1978.

Although he did not graduate any Michigan students during the 1970s, an extremely influential addition was made to the faculty in 1971—viz., Carl Gans, who was hired as Professor and Chair of the Department of Zoology. Armed with engineering degrees from New York University and Columbia University, and a Ph.D. in Zoology from Harvard, Gans brought novel expertise and a new program to graduate studies at Michigan—that of functional morphology, primarily of amphibians and reptiles. This research was an obvious asset to the herpetological program, but the interactions of herpetological principals (Gans, Kluge, and Nussbaum) were not always harmonious. Gans was committed to specimen-based systematic and empirical research, whereas Kluge was a systematist involved in the philosophical underpinnings of phylogenetic methodology; both were noted for their strong personalities, a combination that one might have predicted would lead to the Perfect Storm. Nussbaum, in contrast, quietly pursued his research interests on caecilians and his fieldwork on amphibians and reptiles of the Seychelles Archipelago and Madagascar. He also served as Director of the E. S. George Reserve between 1983 and 2006.

Collection Managers and the 1980s at Michigan.—Genetic research and digital technology forever altered the scientific landscape. The first genetically modified crops were developed. Personal computers, powered by operating systems engineered by IBM, Microsoft, and later, Apple, became common mainstays of laboratories and offices, and in the second half of the 1980s, groundwork for the Internet and World Wide Web was established. The world population increased explosively, and toward the end of the decade, there was a severe global economic depression marked in the U.S. by the Black Monday stock-market crash in 1987. The NSF initiated its Biotic Surveys and Inventories Program in 1989, which supported herpetological fieldwork globally and led to the meteoric growth of collections. Another significant change in collections was the shift in their physical management from academic curators to collections managers. Aside from technicians employed at the National Museum of Natural History, John E. Simmons in the Department of Herpetology at the California Academy of Sciences and José Rosado at the Museum of Comparative Zoology at Harvard were the first professional herpetological collections managers; both were appointed in 1977. During the 1980s, collection managers became a museum staple, and Michigan hired its first professionally trained collection manager—Greg Schneider—in 1986. Schneider's account in this book is an excellent, unparalleled history of digital transformation of collections data in herpetology.

Ten students received their doctoral degrees in the 1980s under the guidance of five faculty members. Kluge mentored four students (Scott Moody, 1980; Alan Jaslow, 1982; Peter Tolson, 1982; and Edward Kraus, 1987), three of whom completed phylogenetic studies. Ron Nussbaum graduated two (Edward Hover, 1982; and Peter Ducey, 1988), both of whom studied behavioral ecology. Carl Gans had two graduates (Thomas Scanlon, 1982; and David Carrier, 1988), and Richard Alexander and William Dawson each mentored one herpetological student—Cynthia Sherman (1980) and Kenneth Crawford (1988), respectively. Alan Jaslow, Peter Tolson, and post-doctoral fellow, Lou Densmore, chronicle divisional activities during this decade.

A Seismic Shift Toward Molecular Biology: The 1990s and Beyond.—Although not especially evident in the research of the graduate students in herpetology at Michigan, during the 80s and 90s, growing numbers of U.S. herpetologists were applying new tools to generate data for phylogenetic studies. The molecular work on amphibians and reptiles that was carried out at Michigan was done primarily in the late 80s and 90s in the laboratory of Wesley Brown in the Department of Molecular, Cellular and Developmental Biology; he mentored several herpetological postdocs (e.g., Lou Densmore, Craig Moritz) and some herp graduate students (e.g., Fred Kraus, Jennifer Ast, Matthew Chatfield). Beginning in the 80s, electrophoretic techniques were used to generate data from allozymes and albumin immunological distances to study similarities and differences between closely related taxa of amphibians and reptiles. It wasn't until the 90s that DNA sequence data were used widely in studies of higher-level systematic relationships of amphibians and reptiles. Initially, mitochondrial genes, which were relatively easy to amplify and sequence, were used in studies of genetic variation among closely related species and conspecific populations. But to probe deeper phylogenetic levels, genetic data needed to be gathered from nuclear genes that have a lower mutation rate and evolve more slowly than mitochondrial genes.

Application of DNA sequence data to phylogenetic studies became nearly ubiquitous for several reasons—increased grant support, decreasing costs of instrumentation, development of sophisticated computer hardware and software, and rapidly advancing computational tools for analyses of data. But acquisition of these data also came at a cost to collectors and collections. The pace of biotic surveys and inventories grew amid increased concerns about climate change and threats to biological diversity. As a consequence, collections grew both in numbers and kinds of preparations (e.g., fluid-preserved, dry, skeletal, histological, acoustic, digital images) and the addition of a new class entirely—tissues. Tissues had to be collected in the field and usually stored in liquid nitrogen for transport back to the host institution, where they were associated with their preserved voucher specimens. Once accessioned, tissues had to be stored in cryogenic freezers at temperatures of –150° to –190°. Thus, collecting became more complex for the collectors; collections had to add cryogenic facilities at a substantial expense; and collection managers had to grapple with an entirely new dimension of specimen care and accessibility.

The significant expansion of collections during the 80s and 90s had several corollaries. Increasing numbers of collection managers were hired and their international professional organization, the Society for the Preservation of Natural History Collections, was founded in 1985. Institutions had to expand and diversify their storage facilities. In many cases, collections were moved to new sites physically removed from the central campuses; thus, curators were separated from collections, which were managed by the collection managers. In the case of Michigan, this occurred in 2012. The separation had some unintended and arguably, unfortunate consequences. Although involved in collections policy and funding issues, curators were no longer training graduate students how to use and care for collections—that fell under the purview of the collection managers. And perhaps most unfortunately, students could access tissues from collections and sequence data from GenBank without ever leaving their laboratories; thus, they could complete dissertations, without handling specimens, conducting fieldwork, and observing the habitat and natural history of the organisms.

Perusal of the herpetological Ph.D.'s at Michigan from 1990 onward reveals that molecular systematics did not gain a strong herpetological foothold. Some 35 students were graduated between 1990 and 2020. Only four of these students—Kraus, Ast, Fox, and Chatfield—incorporated molecular data into their dissertations. (However, no data were provided by Rabosky and Davis Rabosky about their students in time to be included in this text.) Of the 35 students, Arnold Kluge mentored five—Kyle Summers (1990), Alan Wolf (1996), Heather Heying (2001), Jennifer Ast (2002), and Glenn Fox (2006). Ron Nussbaum advised eight (co-chairing the last 3)—Russell Burke (1994), Shenghai Wu (1994), Daniel York (1995), Richard Lehtinen (2003), Keith Pecor (2005), Corinne Richards (2008), Matthew Chatfield (2009), and Jay Reed (2014)—before his retirement in 2016. Carl Gans mentored Brad Moon (1998). Six of these students have contributed chapters that provide insights as to the atmosphere and activities in the division and department at the time—viz., Summers, Heying, Ast, Lehtinen, Pecor, and Moon.

Ecologist Earl Werner, who retired from the Department of Ecology and Evolutionary Biology at Michigan in 2014, made substantial contributions to the herpetology program during the late 90s and up to 2013. Werner's research focused on larval amphibian communities as model systems in which to study species interactions and their consequences to ecological community structure. He chaired nine doctoral committees of students working primarily with larval salamanders and frogs. They are David Skelly (1992), Rick Relyea (1998), Scott Peacor (2001), Kerry Yurewicz (2002), Luis Schiesari (2004), Michael Fraker (2007), Amanda Zellmer (2010), Jessica Middlemis Maher (2011), and John Marino (2013), who has contributed a chapter to the present volume.

In 2012, Michigan hired Daniel Rabosky as the curator of herpetology in preparation for the retirement of Ron Nussbaum in 2015. Rabosky was accompanied by his spouse, Alison Davis Rabosky, who was appointed as an assistant professor in the Department of Ecology and Evolutionary Biology. She received a curatorial appointment in 2016. Dan Rabosky is a macroevolutionary herpetologist interested in the evolution and ecology of Australian reptiles, and development of software to analyze macroevolutionary dynamics on phylogenetic trees. Alison Davis Rabosky is also an evolutionary biologist; she combines molecular, field, and laboratory data to study systematics, animal behavior, and conservation and management of herpetological island endemics. Thus far, Alison and Dan have mentored four students who have received their degrees as of 2020. Pascal Title (2018), Joanna Larson (2020) and Mike Grundler (2020) were mentored by Dan, whereas Iris Holmes (2020) was mentored by Alison. Pascal Title is a Research Assistant Professor in the Department of Ecology and Evolutionary Biology at Stony Brook University, where he is an evolutionary macroecologist who studies large-scale patterns of diversity. Each of the three other Michigan graduates has secured a postdoctoral fellowship. Joanna Larson joined the Rohr Laboratory of Ecology and Public Health at the University of Notre Dame, where she is investigating the variation in the intestinal microbial communities across the frog tree of life and exploring its correlation with interspecific ecological differences among anurans. Mike Grundler is a postdoc in the Zapata Laboratory in the Department of Ecology and Evolutionary Biology at the University of California–Los Angeles. Mike, who studies multivariate ecological phenotypes using phylogenies, will be investigating the phylogenomics, systematics, and historical biogeography of Hawaiian plants. Iris Holmes, who uses genetic methods and modeling to explore the ways in which host-parasite-mutualist interactions change through space and time, has joined the Hendry Lab in the Department of Microbiology at Cornell University.

The legacy that Dan Rabosky and Alison Davis Rabosky have inherited is indeed rich and diverse. The success of their first generation of students suggests that they are leveraging this heritage, adapting aspects of it to meet emerging challenges and adding to the strength of this foundation to train forthcoming generations of herpetologists. Most important, they are formulating relevant research objectives for their students that will ensure the viability and utility of biodiversity collections for the future. You are invited to read about their insights, priorities, and visions in the final two chapters of this volume.

Acknowledgments. The bulk of this work was accomplished during the Covid-19 pandemic. While I don't feel obliged to be thank-

ful for this event, it did provide an unparalleled opportunity to assemble and edit the many contributions while in lock down. I am grateful for the Internet, and the cheerful cooperation of all of the authors. One in particular deserves special mention. My spouse, Bill Duellman, first suggested that I undertake this project because it would be "fun." He reaped his just reward as I hunkered down in my office for hours and days on end, only to emerge and ask him to read what had been written that day while he ate his late lunch.

I am indebted to two persons in particular. The first is John E. Simmons—a valued collaborator, collection manager, and personal friend of many years. Much of the inspiration for this Introduction came from reading his book, *Museums – A History* (2016. Rowman & Littlefield, Lanham. 308 pp.). John also reviewed and improved an earlier draft of this document. Likewise, I am grateful to Kraig Adler who date- and fact-checked this manuscript and offered many constructive suggestions for its improvement. Special thanks to both of these colleagues.

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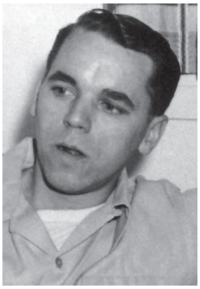
WILLIAM E. DUELLMAN

Herpetology at Michigan Post World War II

1948–

Just after my 18th birthday at the beginning of my freshman year in September 1948 at the University of Michigan, I met my undergraduate advisor, Assistant Professor Frederick E. Smith; when he asked what my goals at Michigan were, he seemed dumbfounded by my reply that I intended to get a Ph.D. in herpetology. This marked the beginning of a long-term relationship, inasmuch as Fred Smith served on my Ph.D. committee. I visited the "herp division" in the Museum of Zoology where I had a satisfying discussion with the jovial Norman E. Hartweg, and also met the seemingly more serious Charles F. Walker, along with two graduate students—Herndon G. Dowling and James A. Peters—both World War II veterans. In the fall of 1948, veterans predominated the graduate-student population in the UMMZ—Charles O. Handley, Jr. and William Quay in mammalogy; Philip S. Humphrey, Robert M. Mengel, and Harrison B. Tordoff in ornithology; George W. Byers in entomology, and Clarence L. Smith in ichthyology, among others. Byers, Humphrey,

Bill Duellman



Herndon Dowling

James Peters

and Mengel became colleagues with me at the University of Kansas. These students were supported by the GI Bill. They were serious and determined to complete their education and the requirements for their Ph.D.'s. Despite their greater experience, they accepted a fuzzy-cheeked teenager into their ranks and did their best to mentor him in the ways of the world, as well as herpetology.

Alexander Ruthven

Helen Gaige

I hung around the herp division as much as possible, mostly looking at books and reprints in the library. One day, when I was on my hands and knees looking for a specimen on the bottom shelf in the reptile range, an imposingly large man nearly stepped on me; fortunately for both of us, he managed to keep his balance and grunted, "Who the Hell are you?" That was my introduction to Prof. Laurence C. (Pancho) Stuart. My introductions to Alexander G. Ruthven and Helen T. Gaige were far more civilized. Ruthven had been director of, and curator of herpetology in, the Museum of Zoology until 1928, when he became president of the U of M. For several years in the 1920s and early 1930s Gaige had effectively run the Division of Herpetology in the museum.

Walker seemed to warm to my herpetological aspirations when I showed him my data on two species of salamanders from southern Ohio, and subsequently, Hartweg offered me a job as an undergraduate assistant in Herpetology. I accepted enthusiastically; after all, the pay was 40¢ per hour and by the beginning of my sophomore year, I made 50¢ an hour. Don't laugh—who today would not be delighted to receive a 25% increase in salary? In the late 1940s, 50¢ could go a long way. For example, a ticket to a movie was 25¢; the popcorn was 10¢ and a coke 5¢, and there was still a dime in your pocket. On completing my undergraduate degree in 1952, I "graduated" to the graduate research assistantship in Herpetology—a position vacated by Jim Peters when he finished his degree in that year—with a whopping monthly salary of $150, but no tuition and fees.

In 1949, James E. Mosimann transferred as a sophomore from Charleston College to the U of M. Soon thereafter he was hired as an undergraduate assistant in Herpetology. We became close friends and worked together mostly under the direction of Jim Peters, who was a relentless task master. During the next two years the herpetological community changed drastically with the addition of George Rabb and

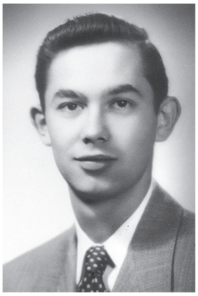
Thomas Uzzell from Charleston, Paul S. Martin from Cornell, Richard Etheridge from Tulane, Priscilla (Holly) Starrett from Connecticut, and Arthur E. (Jack) Dammann from Arizona State. Similarly, there were changes in the Department of Zoology. Charles Carpenter completed his Ph.D. under the direction of Frederick H. Test, who took on two new graduate students—Owen J. Sexton from Oberlin College and Harold F. Heatwole from Goshen College in Indiana. Nelson G. Hairston, Sr. joined the faculty in the department in 1948 and shared bag lunches with Duellman in Hairston's office while discussing plethodontid salamanders in the Appalachian Mountains. Hairston had two graduate students: Harold A. Dundee from Kansas and James A. Organ from Rutgers. Somewhat afield was Thomas M. Oelrich in the medical school; his dissertation on the anatomy of the head of *Ctenosaura pectinata* was based on specimens collected by Duellman in Mexico in 1951. Thus, in the early 1950s Michigan was a dynamic center of herpetology with diverse faculty and an even more diverse group of graduate students. A major factor in this diversity was the fact that students picked their own dissertation projects. Published results were by the student alone; professors almost never put their names on such publications and then only when collaborating on the actual research.

James Mosimann

George Rabb

With the exception of Oelrich and Starrett, all of the research projects by the graduate students involved field work. Some of this was local by Heatwole, Sexton, and Uzzell, and ranged from painted turtles to the *Ambystoma jeffersonianum* Complex, in which Uzzell discovered

Thomas Uzzell

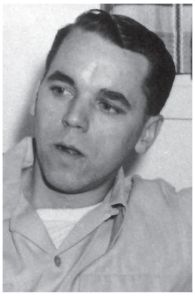


Richard Etheridge

Priscilla (Holly) Starrett

Arthur (Jack) Dammann


Fred Test


Charles Carpenter

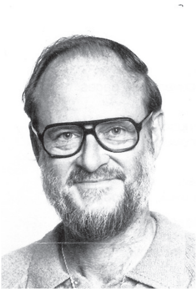

Nelson Hairston


James Organ

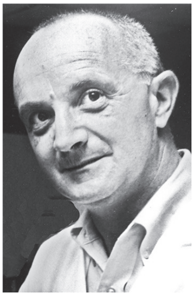
unisexual species. Mosimann's work on growth in turtles involved collecting series of several species; on several occasions Duellman accompanied him to collect turtles, and once Edward H. Taylor joined them. George Rabb began his graduate studies working on the systematics of salamanders of the genus *Chiropterotriton;* supported by Walker, Rabb and Mosimann spent several weeks collecting these salamanders in eastern Mexico. Rabb was frustrated by his inability to identify meaningful morphological characters in these small salamanders, and turned his attention to lizards, namely *Leiocephalus* in the Bahamas, for his Ph.D. dissertation.

Most of my summers were spent in the field. In 1950, Albert Schwartz introduced me to the western United States; although he was working on mammals at the time, he shifted his interests to amphibians and reptiles and went on to become a well-known herpetologist. In 1951, I accompanied Donald D. Brand and four of his graduate students from the Department of Geography at the University of Texas to Mexico; we spent 10 weeks in the field, mostly in Michoacán where we traveled on mule back. The summers of 1953 and 1954 were spent with Al Schwartz in southern Florida, and in 1955, four of us collected snails, fishes, mammals, and of course herps in western Mexico. In September 1955 I submitted a grant proposal to the American Philosophical Society to


Harold Dundee


Harold Heatwole


Owen Sexton

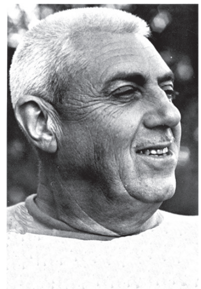

Albert Schwartz

support seven months of field studies in Mexico. On October 31st, I received a telegram awarding me a grant of $1500 and notifying me that I had to complete my Ph.D. before initiating the field work on February 1, 1956. I had not written word one of my dissertation. After many long days and nights of typing, I submitted my dissertation of 274 pages and passed my final examination with three days to spare. Hartweg arranged for a university field vehicle, and on February 1st, I departed Ann Arbor in a snow storm with my wife, Ann. Richard Etheridge joined us for two months and we returned to Ann Arbor on August 31st with more than 3700 specimens.

In addition to the collections, we returned with an idea—viz., establishment of a tropical biology field station. We presented our idea to the curators in the UMMZ. The director, Theodore H. Hubbell, and some others, including Hartweg and Stuart, were intrigued. The original idea was for a station in Mexico. When that did not pan out, Hartweg moved the idea to Costa Rica and added Jay Savage's existing field course to it. After several years of intense effort, especially by Hartweg, the Organization for Tropical Studies was founded, and La Selva Field Station was established in Costa Rica. In August 1963 I was in Washington DC and met with Hartweg, who was all smiles when he returned from the NSF with news that they would fund the program for the next 2 years. We celebrated without my knowing that Hartweg was dying of pancreatic cancer.

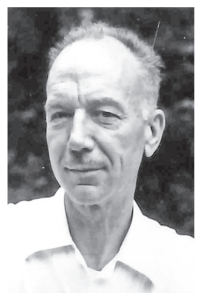
Although the students kept in close touch with one another, they had diverse academic programs. For example, my undergraduate minor was geography; Master's and Ph.D. minors were geology and botany, respectively. In the latter field I encountered the finest teacher of my career at Michigan—Pierre Dansereau. He taught challenging courses in plant ecology and plant biogeography, both of which were characterized by problem solving and some three-hour lectures that resulted in few notes because Dansereau was so engaging. Vertebrate paleontology taught by Claude W. Hibbard was a two-semester undertaking during which "Hibbie" brought fossils to life. Naturally, we all took Hartweg's course on reptiles and Walker's on amphibians; both of these consisted mainly of memorizing characteristics of families and learning to identify specimens in the spare "teaching collection." In the reptile class, Hartweg began with his favorites—turtles; they lasted for more than two months; squamates were covered in about a month, and crocodilians and rhynchocephalians were omitted.

Stuart taught two courses with lectures at 8 am. On the first day of class, Stuart ambled into the room and announced: "I am Mister Stuart, and this is zoogeography." While checking the roster of students, he would call out names of enrollees; then he pulled a pack of cigarettes



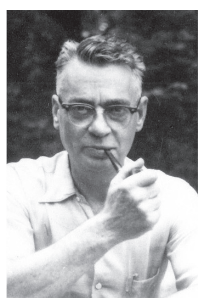
Laurence (Pancho) Stuart

from his pocket and lit up. In one of his classes, he started to light his cigarette and commented: "Hope my smoking won't bother anyone." A young woman replied, "smoke bothers me." Stuart took a long drag and said emphatically "then you better get the hell out of here"; she immediately left the room, never to return. Zoogeography in the early 1950s emphasized Matthew's proposition of northern origins and southward dispersal of mammals; Wegener's idea of continental drift was barely mentioned. Emmett R. Dunn's paper on the American herpetofauna based on Matthewsian principals was accepted as gospel. A term paper was required. I received an "A" on my paper that critiqued Dunn's arrangement of colubrid snakes; however, Stuart disagreed with me—a fact that he reminded me of daily for next 2 years by sticking his head in my office door first thing in the morning and grumbling "Duellman, you're full of shit." Stuart's second course was History of Biology, which closely followed Erik Nordenskiöld's book by the same name. This thick book became my bedtime companion; reading 10 pages could guarantee immediate sleep.



Charles Walker

We students quickly learned possible ways of socialization with the herp faculty in the UMMZ. Charles Walker was a confirmed bachelor who lived in an apartment near the museum and seldom invited guests to his abode. However, he played an important role in graduate-student life; after several hours of labor in their respective offices, the students would gather at about 10 pm to go to Metzger's Restaurant for beer and discussion of the day's accomplishments. Walker commonly was in his office at such an hour, and usually accepted an invitation to join the students. Sometimes his participation was a financial necessity; after all, a pitcher of Michelob was 75¢!



Norman (Kibe) Hartweg

The Hartweg family lived in a nice house on Geddes Road. If there was a notable visitor in town (e.g., Fred Cagle, Karl P. Schmidt), Hartweg usually hosted a herp gathering at his home, so that the students had an opportunity to have informal discussions with visitors. At least once a year on a Saturday in spring or fall, Hartweg would provide an ample amount of beer and grill hamburgers covered with Taliachigoo, a sauce that according to Hartweg was a recipe from an Italian by the name of Goo. One of Hartweg's plans did not turn out well. He had asked the students to help him construct a wall on one side of his driveway. We showed up on a hot Saturday morning to find a pile of rocks on the driveway. On the heels of a lengthy discussion about the appropriate way to proceed, the heat and anticipated physical labor suggested that a round of cold beer was in order; this, of course, was followed by another round, and others until there was no beer left, so we went home. On Monday Hartweg engaged a contractor.

Stuart and his wife Kate (Alexander Ruthven's daughter) lived at the end of Geddes Road just across the Huron River. They entertained infrequently. Larry Stuart, who had graduated from the Waldorf Astoria Chefs School, prepared excellent meals that only could be enjoyed if one drank no more than two of his martinis only kissed by a fragrance of vermouth. As necessary, women were directed to the bathroom on the second floor, whereas men were directed to the back porch from which Stuart peed year-round.

Many of us in the herp division were avid fans of the Michigan ice hockey team; typically, we were joined by Harold and Dee Dundee, Harry Walters, and Andy Starrett. We arranged for two or three persons to enter the rink as soon as it opened and buy tickets for all of us. The early birds would reserve appropriate space a few rows up from the opponent's box. As the teams warmed up on the ice, we would pick one individual to heckle during the game. This could annoy some players; one threatened us with his stick from the box. Usually it was a raucous bunch of fans at these games, and it was not unusual for someone who disagreed with a call made by a referee to throw something at him; surely the most outrageous item was a live octopus. The games were only the beginning of the evening because a post-game party was held at someone's residence. Everyone brought something to eat and/or drink, including anything left from the last party. Harry Walters guitar stylings always encouraged party participants to dance or stomp their feet. On at least one occasion, the exuberant dancers dislodged the blocks supporting one corner of the Starrett's trailer, resulting in a significant shift of the pitch of the floor . Yes, hockey games were lots of fun.

Not all parties were like those. For example, when some of us noted that Walker's birthday was coming up in a week, we decided to stage a surprise birthday party for him—but the challenge was where to have it and how to surprise Walker. We were discussing the matter when Paul Martin came down the hall; with a gleam in his eye, George Rabb said, "I got it." Paul and Marion Martin had a new baby; we, but mostly George, convinced Paul that he should ask Walker to baby sit the next Saturday evening. Later that day after several minutes of Paul's pleading, Walker agreed. The Martins lived in the country; all of us had hidden our cars behind structures, placed party supplies in the kitchen, and awaited Walker's arrival. He showed up on time and was greeted by the Martins. Walker's grim expression gave way to one of relief and happiness when we burst into the living room. Soon plates and bowls of food were placed on a runner on the dining room table, and cold beer was brought in from the back porch. The party terminated shortly after Martin's pet coati raced around the house and under the dining room table where it snatched the end of the overhanging table runner and pulled all of the dishes and food on to the floor. Happy birthday, Charles Walker.

Despite (or perhaps, partly because of) the parties, hockey games, beer at Metzger's, and other diversions, each of us finished our Ph.D. These individual achievements were realized in an academically and socially unique collective atmosphere that probably will never be duplicated. I think that I can speak for the group, as well as myself, in thanking our obliging professors for their faith in our abilities to become accomplished professionals and carry on the Michigan tradition for the past several decades.

Acknowledgments. I am grateful to James E. Mosimann for providing his picture for this contribution. Kraig Adler and Linda Trueb commented on an earlier draft this essay and Kraig generously provided most of the photographs, except for a few that I took.

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Bill is a 1956 Michigan graduate whose career focused on the systematics, biogeography, and ecology of amphibians and reptiles of Meso- and South America. His extensive fieldwork and research resulted in the publication of 10 books and more than 300 other publications. He will be remembered for fostering an extraordinary graduate program in herpetology at the Biodiversity Institute at the University of Kansas—one that produced some 80 graduates, many of whom are active research scientists in the U.S., overseas, and in many Latin American countries.

Although retired and living in New Hampshire now, Bill continues his neotropical research in collaboration with Luis Coloma of Quito, Ecuador, with whom he is authoring a forthcoming book on the amphibians of Ecuador.

JAMES E. MOSIMANN

The Herpetology Division at the UMMZ in the Early Fifties

1950–

What can I say? It's been many years but looking back, it was truly an exciting time for students. The war had ended 5 years earlier and we were a real mix of aspiring herpetologists, ex-GIs like Jim Peters (Air Force, South Pacific), Herndon Dowling (Marines, at Iwo Jima), Al Schwartz (in mammalogy, but a herp man at heart), and a youthful corps that included Bill Duellman from Ohio, myself, George Rabb and Tom Uzzell (fellow Carolinians from the herp-rich Low Country), and Paul and Marian Martin fresh from Cornell. All were very stimulating and knowledgeable Ph.D. candidates under the careful and excellent guidance of either Norman Hartweg or Charles F. Walker. And the Pan-Am highway had recently opened, so many of us, regardless of age, turned our eyes to Mexico and its remarkable assemblage of reptiles and amphibians as subjects for our respective theses.

I arrived at Michigan in September 1950 as a junior transferring from the Catholic University of America. That summer had been spent with George Rabb camped in Montana on an archaeological dig. (We published an article in *Copeia* on the herps we collected there.) But my memory was of 90 straight days in a sleeping bag, and yes, I counted them. At my arrival in the herp division, Bill Duellman, also a junior, had seniority over me as a prior member, so I started out washing bottles. He had just returned from a highly successful trip to the Southwest where unusual deluges had brought out a remarkable assembly of amphibians that Dr. Walker examined relentlessly.

Although at Catholic U. I had the good fortune of studying comparative anatomy under an excellent biologist and sometimes herpetologist, Dr. W. Gardner Lynn; I was addicted to herpetology. One afternoon after visiting the collections at the Smithsonian, I was talking with Dr. Doris Cochran, the curator of herpetology. I mentioned that I had a scholarship that could be used at any university. My memory does not allow a direct quote, but I recall her words as "Well, if you want to study herpetology, there's no choice, go to Michigan."

And that was sufficient reason for me. And I never regretted following her advice, ever!

At Michigan, I had the privilege of studying under, and being formed by, two professors—Norman Hartweg and Charles F. Walker. Norman Hartweg was my thesis advisor; Dr. Walker was the advisor of George Rabb, Paul Martin, and Tom Uzzell. All of us received Ph.D.'s from Michigan.

But at least in my case, the degree was second to what I learned from the example of two excellent scholars, Walker and Hartweg. And not from their words so much as their example. Each had a measure of dedication to the truth and possessed the integrity to make that dedication come alive in their teaching, something that I strove to emulate. I was under their tutelage and guidance for 6 years, from 1950–1956. Other professors made their teaching subordinate to their professional achievements, but I can truthfully state that these two men cared more that we achieve success than they. While originally, I was drawn to study with Dr. Walker because my interest in frogs and salamanders (soft bodies), after taking a course in statistics in Angell Hall, I sought subjects with hard bodies that allowed repeatable measurements (turtles, Dr. Hartweg's specialty). He appeared worried that I was doing this because of his own interests, which he did not want to influence my own. For my part I was worried that he did not approve of my use of statistics, and that he might think I would be more interested in statistics than biology. (A worry that later proved to be partially justified.)

Whatever the case, I spent several years with him finishing one "biostatistical" paper on a large sample of *Kinosternon integrum* collected in 1950 by Jim Peters and in 1951 by Bill Duellman in Michoacán, Mexico. After that, I finally finished my thesis in 1956, "An Analysis of Allometry in the Chelonian Shell" which later appeared in

La Revue Canadienne de Biologie and got favorable comments by Stephen J. Gould in *Biological Reviews.*

Only after submitting my own thesis, did I think to look up Dr. Hartweg's thesis in the Rackham Graduate School records. Many years earlier (about 20) he had written his thesis on measurements of the shell of the painted turtle *Chrysemys picta* in which he also commended the analysis of numerical data! And never a word from him to me about that!

When I accosted him to tell him that I had seen his thesis and (to me) it had the same goals as mine, he gave me a wry smile and changed the subject. What I had thought was a disapproving attitude towards my statistical efforts, was simply his desire for me to be objective, and not to do something simply because it would please him. A real lesson in his dedication to maintain objectivity, taught by example.

Finally, a lesson in real tolerance. I was born Catholic and came near to abandoning that religion at Michigan. However, after my undergraduate degree I returned to Catholic U. to study philosophy and renewed my beliefs. That Fall I returned to the herp division. It is, and was then, my understanding that Dr. Hartweg had once been Catholic himself. On several occasions he privately indicated to me his displeasure with my beliefs, but never did he let that influence his judgment of my work. In one instance I remember him supporting me silently, but staunchly, while another professor (not a herpetologist) disrespected me because of my beliefs. As a professor, he taught me true objectivity, not with words and platitudes but with his life typified by Dr. Hartweg, along with his wife and son, supporting a relative who was unable to work in their Ann Arbor home.

Yes too, the diverse students mentioned above flourished under the exceptional and tolerant direction of Drs. Hartweg and Walker. Paul Martin (a life-long collaborator) excelled in the study of past climates and human-caused extinction. While George Rabb may have preferred a thesis on Mexican salamanders with Dr. Walker, he chose to study variation in the iguanid lizard *Leiocephalus,* and went on to establish zoos as instruments of conservation. Jim Peters became curator of herpetology at the National Museum (Dr. Cochran' s old position) but suffered an untimely death. (I was with him in the hospital the day before he died. He had just been to Australia's Great Barrier Reef, and wanted to finish his studies, but that was not to be.) I lost track of Herndon Dowling after his Ph.D., but later learned that he had been stranded when his pickup boat forgot him on the Galapagos and had been near death when recovered. Bill Duellman had a highly successful career at Kansas. He has his own essay here, as likewise, does Tom Uzzell. I can't resist adding a comment made to me by Dr. Walker in the 60s at a party at Jim Peter's house in Rockville, Maryland (near where I lived.) He told me Tom's thesis was the best he had seen come out of the Division of Herpetology. Right on, Tom!

Yes, after teaching biostatistics at the University of Montreal, I went to Johns Hopkins and obtained a Masters in Biostatistics from that institution. In 1970 or so I was named a Fellow of the American Statistical Society, but my most cited papers on the mathematics of allometry and the study of proportional data derive from (and apply to) the earlier studies of allometry in turtles. I retired in 1995 after many years with the Computer Division of the National Institutes of Health. My last years in the government were spent with the Office of Research Integrity using statistics to examine questioned data for fabrication. During those last years I often wondered what Dr. Walker and Dr. Hartweg would have thought of my work there. They could not have imagined the need for an ORI. Never would they have believed that trained academic scientists would fake data in research, and on such a scale as occurs today.

I will forever be grateful to those two human beings who formed in me an attitude to truth, research, and integrity—an attitude that has sustained me through the years. And yes, I am grateful to my fellow students, George Rabb, Tom Uzzell, Bill Duellman, Paul Martin, Herndon Dowling, Jim Peters (sometime also a mentor) and other zoologists who shared those exciting times in the UMMZ, and whose lives likewise benefited from working with and/or under two extraordinary men who also were our professors.

To Dr. Walker and Dr. Hartweg, and to the UMMZ, a final belated "Thanks."

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After receiving his Ph.D. from the University of Michigan in 1956 Jim taught Biostatistics at the French-speaking Université de Montréal until 1962 and obtained a Master's degree in Biostatistics from the Johns Hopkins University. He held two postdoctoral fellowships before joining the National Institutes of Health where Mosimann spent more than 30 years in computers and statistical consulting. In 1970, he became a Fellow of the American Statistical Association, and in 1974, the Chief of the Laboratory of Statistical and Mathematical Methodology of the Computer Division. Mosimann also was an adjunct professor in Mathematics and Statistics at the American University in Washington, D.C. In 1991, after receiving training at the Federal Law Enforcement Training Center, Jim joined the Office of Research Integrity of Public Health Service, as Senior Biostatistician to develop and use statistical methods to detect falsified data. When he retired from that office in 1995, he became a private consultant with ABL Associates of Bethesda Maryland. After consulting for a number of years, Jim really retired and devoted himself to his family (Jean and eight children) and writing novels the heroine of which is a female statistician who uses statistics to detect falsified data and expose various nefarious schemes.

Prepared for the Future

1952–

I first encountered the UMMZ in my junior year, 1952. I had transferred from The University of North Carolina to Michigan to join my fellow Charlestonians and comrades who were already there as graduate students, George B. Rabb (Ph.D., 1957) and James E. Mosimann (Ph.D., 1956). Michigan was the place to study systematic herpetology at the time. We three had done extensive herpetological fieldwork together in South Carolina and had made a summer collecting trip to northeastern Mexico, on which we concentrated especially on plethodontid salamanders. Prof. Edward Taylor (University of Kansas) had described many new species, and Prof. Charles Walker was eager to see as many of them as we could find. I was accepted in the herpetology spaces at the UMMZ, but didn't have much time there. I was supported by an NROTC (Naval Reserve Officers Training Corp) scholarship, and when I graduated, I had more academic credits in Naval Science than in Zoology. On graduation, I served 3 years as a Junior Officer in the U.S. Navy and returned to Michigan when discharged (1956). Again, I was generously supported, this time for 4 years by the GI bill. Many of the graduate students at UMMZ at this time had served during World War II; they were exceptionally mature and motivated, and GI bill support for their war service was well justified.

So much had changed: old students gone, and new ones admitted. In my undergraduate courses, the argument had been whether or not DNA was the genetic material. When I returned we had double helices and not long thereafter, a genetic code. I had basic courses to take that I'd missed because of NROTC commitments: organic chemistry and comparative anatomy, for examples.

Michigan was an excellent place to learn biology given the excellent instructors and the wide array of courses from which to choose. Fellow students also taught me; one student's explaining to me how to balance equations in organic chemistry helped me go from a "C" or a "D" in the course to an "A." I tried to help other students. I hope I did help. One of the best learning experiences, though, was serving as Teaching Assistant in Zoology Department courses. The Museum was becoming more integrated with the Department, a good change for both. I served in comparative physiology for Prof. William Dawson and in comparative endocrinology for Prof. John Allen. I believe I was one of the first museum students to participate in this activity, although many did so later.

I trained under Charles Walker, one of the curators of Herpetology at Michigan. Before he accepted me as a student, he asked me to look at some lizards that Prof. Test had brought back from Venezuela. I enjoyed this task, and published several papers on the group to which they belonged. Eventually, though, I studied mole salamanders related to *Ambystoma jeffersonianum* for my dissertation research. Dr. Walker had long puzzled about these animals, and showed me a paper describing an unusual population in Indiana and an intriguing technique used for capturing breeding adults. Using this technique and examining as many museum specimens of the group as I could borrow, I could see that the males fell into two distinct groups, with several quite distinct morphological features. The females, which were far more numerous in collections, formed almost a continuum between the males in these characters. This was a puzzle.

For living samples, additional critical data were possible. Examination of red blood cell size and nuclear dimensions, combined with knowledge that many of the females were triploid, was a critical part of the solution. Briefly, the males belong to two distinct species. The combined range of the two species stretches as far south as Kentucky, and almost as far north as Hudson Bay, east to the Atlantic Ocean and west to Iowa. Very, very roughly, males north of a line from Boston to Chicago belong to one species (*Ambystoma laterale,* Blue-spotted Salamanders), those from the south belong to the other (*A. jeffersonianum,* Jefferson Salamander). Females with small red blood cells and small nuclei from north of the line are also Blue-spotted Salamanders; females from south of the line are Jefferson Salamanders. Females with larger cells and nuclei from north of the line look mainly like Blue-spotted Salamanders, but with hints of Jefferson Salamander. Females with larger cells and nuclei from south of the line look mainly like Jefferson Salamander, but with hints of Blue-spotted Salamander.

The easy interpretation of these basic patterns is that in the past, Blue-spotted and Jefferson salamanders have hybridized, and that large-celled salamanders from north of the line have more genes of Blue-spotted salamanders, whereas those from south of the line have more genes from Jefferson Salamander. Later use of molecular techniques, breeding experiments, and examination of lampbrush chromosomes largely confirm this pattern. Northern large-celled salamanders have two nuclear genomes of Blue-spotted Salamanders, one of Jefferson Salamander, whereas southern large-celled salamanders have two nuclear genomes of Jefferson Salamander, one of the Blue-spotted Salamander. I called the northern triploids Tremblay's Salamander (*A. tremblayi*), and the southern ones Silvery Salamanders (*A. platineum*). Some taxonomists object to using these names, but like all scientific names for organisms, they provide easy access to much useful information.

This new understanding explains many biological oddities of these organisms. The triploid salamanders lay numerous eggs, but many of them do not develop into larvae. That any of the eggs develop is itself a surprise: meiosis in triploid organisms is usually impaired because synapsis of chromosomes in triploids is difficult. The triploid salamanders cheat; at the last premeiotic division, the two newly replicated chromosomes stay together in "pseudobivalents." The cells that produce ova thus go through a hexaploid level with six sets of chromosomes. After two nuclear divisions, triploid ova are produced, with exactly the genotype of the female.

The reproductive system of these triploids, gynogenesis, is more complex yet. The eggs of mole salamanders must be activated (as they are in most organisms) by sperm. There is this important difference, though. The ova of the triploid salamanders are rarely fertilized by sperm; the sperm serve only to activate the eggs to go through cell divisions and develop into larvae and eventually full-grown salamanders. Because the ova are derived from a hexaploid stage, there are as a first approximation only half as many of them. They are also larger, just as the red blood cells are larger. All of the ova that develop normally produce females; thus, males are exceedingly rare. This partly explains the excess of females in museum collections and in samples collected at breeding ponds.

Because the ova of triploid salamanders must be activated, males are essential parts of the system. The courtship of these salamanders involves a prolonged clasp and is accompanied by a limited production of spermatophores, the mechanism for sperm transfer from male to female. Because spermatophore production is limited, you would expect males of this group to be very selective in choosing mates, and they are. In breeding experiments, Blue-spotted and Jefferson salamanders produce most spermatophores when courting conspecific females. When courting the similar triploids, they produce fewer spermatophores; and when courting the dissimilar triploids, even fewer spermatophores are produced. The production of spermatophores when males are confined with females of the other species is nil; actual courtship is rarely observed. The biology of the clonal hybrids among mole salamanders stimulated a long-lasting broader interest in such systems in other vertebrates.

Although I used no molecular techniques in my dissertation research, such techniques developed rapidly in the following years. I first used protein electrophoresis in acrylamide gels, and then enzymes in starch gels. There was a brief flurry of microcomplement fixation of serum albumin, and finally, work with DNA, almost all of it with Dr. Christina Spolsky. At first we separated by electrophoresis mitochondrial DNA fragments produced by site-specific restriction enzyme cleavage. Then we used DNA sequence analysis in long acrylamide gels with painstaking manual reading of the sequences, and then simple automated sequencing, and finally reached our present state—purify some DNA and send it to a commercial lab for sequencing. In early sequencing, 300–500 base pairs was a long read; now tens of thousands of bases are routinely read. All the detailed techniques that I learned along the way are no longer used and are almost forgotten.

I tried many of these molecular techniques. It was fun and intellectually rewarding to introduce a series of foreign taxonomists to these techniques, which were completely unknown to them. I worked first with Prof. Ilya Darevsky, Soviet Academy of Sciences, on Caucasian Rock Lizards, now *Darevskia,* in which he had discovered several all-female parthenogenetic lineages. In these lineages, matings with males result in fertilized eggs that usually fail. Prof. Darevsky could identify these lizards, which to my eye are rather similar, at long distances. Starch gel electrophoresis, together with careful consideration of geographic distributions, revealed to us that there were several distinct and largely allopatric sexual species; and that the parthenogenetic lineages originated as hybrids of distinct pairs of sexual species. The data also helped clarify the relationships of the sexual species.

I had a similar experience working with Prof. Leszek Berger of the Polish Academy of Sciences. Using traditional morphology coupled with crossing experiments, he had determined that most of the edible frogs of Europe, both male and female (*Pelophylax,* water frogs), are interspecies hybrids. (His Ph.D. was in plant science, because Polish academic zoologists at the time couldn't accept what he was saying.) Although Prof. Berger could identify by sight a partly submerged water frog with great accuracy, electrophoresis of proteins revealed great complexity in the group. Prof. Heinz Tunner, University of Vienna, identified the usual inheritance pattern of the hybrids to be hybridogenesis; in this clonal system chromosomes of only one parental species are incorporated into gametes, whether ova or sperm, but the hybrids normally mate with the other parental species, so that hybridity is restored. Working with Prof. Berger, and then with a wide diversity of European biologists, additional patterns of inheritance were discovered, as were populations of two kinds of triploid water frogs. More continuing research continues to reveal new complexity.

All along, my research on mole salamanders, always with Dr. Spolsky, has continued. Mitochondrial DNA of the clonal *Ambysto-*

ma lineages comes from neither of the parental species present in the soma. It is apparently closest to the mtDNA of the distantly related *Ambystoma texanum* or a close relative of that species. Dr. Walker had always felt that *A. texanum* was involved with this group. Dr. Spolsky and I were particularly surprised to discover populations of the southern triploid that depended on *A. texanum* for activation of its eggs.

These experiences were particularly relevant, both to my job at the Academy of Natural Sciences of Drexel University and to the state of taxonomic research throughout the country and probably across the world; many of the curators at the Academy knew their organisms extremely well, but their understandings of the phylogeny of those organisms was less secure. I told them, and I tell you, dear reader, that extensive DNA sequencing can produce elaborate phylogenetic reconstructions, but without the knowledge of traditional taxonomy, often based on morphology, such phylogenies are empty, meaningless. What kinds of organisms are they phylogenies of? How has morphology, physiology, and behavior changed, and under what selection pressure?

Looking back over my research career, it is obvious that in many instances conclusions that I drew were too simple, although they fit the data available to me at the time. I don't know whether this is just my experience or a more general phenomenon, but I suspect the latter. For example, among the small primarily South American lizards that I studied after working on the problem that Charles Walker had started me on, few taxa were represented by long series and broad geographical samples.

Much more material is now available, and the group is far more complex than I could tell at the time. Many new species and genera have been discovered, although some of the species groupings that I reported remain. The group itself, recognized more than a century before my work, remains, but at a higher taxonomic level. Geographic ranges of southeastern U.S. species, for which I reported new ranges, have been extended even farther. It's been fun to see these changes, although my interests had changed and I was not involved. The groups that I spent most of my career working on (mole salamanders related to *Ambystoma jeffersonianum*, frogs of the genus *Pelophylax*, lizards of the genus *Darevskia*) have all grown increasingly complex as more was learned about them. Much of science advances by small steps; much depends on accretion, not merely falsification.

For the most part, I have shared research on these organisms with a wonderful set of people, far too many to list here. At this remove in time, I know fewer of the students of these groups. I sit on the sideline and watch. I must again acknowledge my wife Christina Spolsky, with whom I have shared both life and research since 1974.

About the Author

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After graduating from Michigan in 1953, Tom served in the U. S. Navy for 3 years and completed his dissertation in 1962. He held faculty positions at The University of Chicago, Yale University, the Academy of Natural Sciences, and the University of Illinois at Champaign-Urbana, where he was Director of the Museum of Natural History. He built on his dissertation research, emphasizing amphibians and reptiles with clonal or hemiclonal reproduction, and helped introduce molecular techniques (electrophoretic analysis of enzymes and DNA restriction fragments, DNA sequencing) to the study of vertebrate evolution in museum settings. Tom's long-term research projects focused on teiid lizards, *Ambystoma, Darevskya,* and *Pelophylax.* His most important paper, co-authored with Kendall Corbin in 1971, concerned the probability of evolutionary changes in protein sequences. On retiring from the University of Illinois, Tom returned to Philadelphia area as a research associate at Magainin Pharmaceuticals in Plymouth Meeting, PA. Tom has provided editorial assistance with written English to many foreign colleagues.

KRAIG ADLER

Herpetology at Michigan in the Nineteen Sixties

1962 –

This commemorative book might be a herpetologist's version of *Canterbury Tales,* which chronicled a diverse group of pilgrims from many places who traveled to the same location for a period of study together before dispersing. Each one of us has a different story to tell from our pilgrimage to Ann Arbor. Although

we spent part of the decade of the 1960s working and studying together, we have had a diversity of careers spent in many different places across the continent and even beyond. Ours could have been a very different experience with just a few changes in the composition of characters, both students and faculty alike, but it turned out very well for us. Unfortunately, there is no Chaucer among us to record our Michigan days in his iambic pentameter style, so these essays will have to suffice as our joint story of the idyllic years we spent at the University of Michigan.

Why Michigan?

Each person will have his or her own answer to this simple question. In retrospect, I can see clearly now the key events leading up to my own decision to attend Michigan. Reptiles were a boyhood passion for me. As a young teenager in Ohio, I spent a lot of time on field trips with my buddy, Dave Dennis. We first explored central Ohio as far as we could walk or our bicycles could carry us, but when Dave got his driver's license (he's older) we spent almost every warm weekend driving throughout Ohio to find reptiles (amphibians came later). Running out of adventure there, after beginning college we headed south to the Appalachian Mountains of West Virginia, Kentucky, Virginia, and finally to that heaven-on-earth—the Blue Ridge Mountains of North Carolina. Starting in high school, I began to collect publications on reptiles and regularly purchased back issues in affordable lots from Michigan, Harvard, Kansas, Berkeley, and other places. From reading these articles, I got a sense of the style of research done in each institution. I liked the fact that faculty and students spent a lot of time on expeditions to exotic locations. This was when Michigan—that is, the University of Michigan Museum of Zoology (UMMZ)—came to my attention as a viable place for graduate school. And soon it became the *only* place I really wanted to go.

I had to finagle a way to visit the museum, meet some faculty and students, and see the facilities. This opportunity arose during my sophomore year in college (Spring 1960). I had acquired a specimen of a rare Ohio watersnake (called *Natrix erythrogaster neglecta* at the time) that I offered to one of the UMMZ curators, Charles F. Walker. He was already known to Dave and me as the author of the book, *Frogs and Toads of Ohio,* which had become one of our field guides. He invited me to visit (with the snake, of course). Steve Tilley, who was also to become a UMMZ Herpetology student but was then still in high school, accompanied me. We had been collecting snakes in northwestern Ohio in June of that year and so just popped across the border to Ann Arbor. I don't think we made the right first impression, however, for we came directly from the field and tracked mud all over the usually spotless, polished-cement floors of the museum. (Maybe this is why we were not asked to sign the guest register?) Anyway, the snake was turned over and I accomplished my object to see UMMZ for myself. For me, it solidified my earlier plan, but there were two confirming events.

Dave and I attended the June 1960 ASIH meeting in Chicago where we met lots of people and heard many exciting lectures. I could compare the talks by Michigan herpetologists to those from other places and they seemed to be among the best. The other key event came the next fall when I got a message from Tom Uzzell, then a student of

Walker's. He needed some help in setting up a drift fence to monitor a population of *Ambystoma jeffersonianum* located just north of where I was attending college in central Ohio. I had already switched to salamanders by this time, so this was a great opportunity to learn more about Michigan and also about Tom's research on gynogenesis in ambystomatids. It was then Michigan or bust for me!

Becoming Immersed in Michigan Herpetology

When I arrived for grad school in August 1962, the local situation had already changed from that observed during my 1960 visit. The original, nearly V-shaped building—called University Museums—was getting ready to add a new wing, funded by NSF, obliterating a small zoo that once exhibited a collection of Michigan birds, mammals and, occasionally, reptiles. (This new wing was recently torn down and replaced with a teaching facility. The original museum building, because of its architectural splendor, has been refurbished for use by the Michigan senior administration. Its exterior is ornamented with portraits of American naturalists and animals in *bas-relief* on the spandrels between floors. Questions about these effigies sometimes appeared during our oral candidacy exams.) This new wing was a visible sign that the nature of the museum's research programs was changing from systematics and biogeographical studies, which had originally attracted me. Alexander Ruthven, the herp program's principal founder, had initiated a new style of doctoral dissertation in 1906—an in-depth monograph devoted to the systematics, relationships, and distribution of a single, well-defined genus. (The

Main entrance of the University of Michigan Museum of Zoology. *May 1964. This building, occupied in 1928 and ornamented with images of American naturalists and animals, has now become the offices of the President of the University of Michigan. (Photo by Kraig Adler.)*

last one at Michigan was Floyd Downs's dissertation on *Geophis* in 1965.) The new wing, with its modern research labs, environmental chambers, etc., allowed students to choose research topics from across a much broader spectrum in behavior, evolution, and ecology. The faculty were the same as before, so it was the grad students who were primarily responsible for setting off in new research directions Some of us decided to use experimental methodologies to answer questions. At about this same time, academic connections with the other Zoology grad students and faculty, located two blocks away in the Natural Sciences Building, were improving due to efforts by Dugald E. S. Brown, the department chair, and his well-liked staff assistant, Ursula Freimark. These connections had broad implications for the graduate students in the UMMZ.

My first job in the Division of Herpetology was Research Assistant, something like today's collections manager but really more of an untrained gofer for the managing curator, Dr. Walker. Little did I know what priceless experience I was going to get in this role. Yes, I handled loans of specimens and kept the alcohol topped up in the bottles, but as a result I also got introduced to many herpetologists around the world and was exposed to the Michigan herp collections, which are still the largest university-based collections in the world. Here were the specimens that previous faculty and students had used in their own doctoral research—Ruthven's garter snakes, Frank Blanchard's kingsnakes, Grace Orton's tadpoles, Richard Etheridge's anoles, Jim Organ's dusky salamanders. (I was to have daily interactions with Organ a few years later. More below.) I learned how the division and museum operated, interacted with students and faculty throughout the building, spent time in the division and museum libraries reading literature and examining the herp classics, helped to identify incoming collections, etc. I never took the courses "Amphibians" and "Reptiles," partly because of this rich experience in the herp division and partly because I felt I needed other courses more to broaden my biological education. Visitors to the division were also partly my responsibility. Just two examples. I got to meet Ernst Mayr one day when he came to talk with Walker. Another visitor, Harold Voris, then a grad student at the University of Chicago and the Field Museum, had come to be trained to use our soft X-ray machine and this introduction resulted in a lifelong friendship.

Norman Hartweg, the other curator of herpetology who was then also assistant director of the museum, assigned me to tag and identify to species all of the preserved reptiles in the teaching collections. I was to give him the numbered list for use with students in his "Reptiles" course. These were specimens that had accumulated over many decades from multiple sources. Now this was a real challenge for a first-year grad student who wanted to demonstrate his knowledge of herps. Most of the work went smoothly using various keys, photographs in books, and already-identified specimens in the collection, until I got to the snakes. I had real trouble with them and, finally admitting defeat with a large fraction of them, I took the list to Hartweg, expecting a scowl. His response: "Oh, I forgot to tell you that many of the snakes were aberrant specimens." These had been sent to Blanchard, who had been an earlier Michigan grad student and faculty member, because they did not key out to the correct species in his *Key to the Snakes of the United States* (1925). Whew! The level of my ignorance was not yet to be revealed.

The Curators and Other Faculty

The two curators of herpetology—Hartweg and Walker—had been fellow grad students at Michigan in the 1930s, both officially supervised by Ruthven but actually trained on a daily basis by Ruthven's associate, Mrs. Helen T. Gaige. Ruthven and Gaige had founded the division and were still alive and living in Ann Arbor when I arrived. Bill Duellman, who arrived as a freshman in 1948, writes that he got to meet both of them, but I did not. They never, ever came into the museum and I was too shy to go out to their homes (they were next-door neighbors) and knock on their doors. Hartweg and Walker were like best friends. To our student eyes and ears they never differed on any action that was taken. There was total agreement on how the division was to be run and, moreover, on how grad students were to be supervised. They both gave their students free rein on choice of thesis research. Neither of them had ever had a federal grant, so their students were not focused on the next grant renewal. Their roles were to curate the collections and to support their students. Yes, they had their own research programs, but these were decidedly secondary to the collections and their students. (This tradition was to change with their replacements as curators.) Laurence C. Stuart, also a former Ruthven/Gaige student during the same era as Hartweg and Walker, was not a curator but was often in the museum working on Central American collections. He was a professor of zoology and housed in the Laboratory of Vertebrate Biology across a now non-existent street adjacent to the museum. He was pretty much a loner and never had grad students.

Another curator, but of paleontology, was Claude W. Hibbard, located in the Museum of Paleontology in the other wing of the Museums building. Many of us in the Museum of Zoology, especially in Herpetology, took his course in "Vertebrate Paleontology." Much of his work in late Cenozoic deposits of North America was with herps. The only A-plus I ever got in a course was from Hibbie and my pleasure was not diminished when I learned that everybody got the same grade. He was not interested in grades, but in sucking everybody into his own research program. He would bring unidentified fossils to class to pass around for ideas. One day a nondescript piece of bone made the rounds and got back to Hibbie. He said, "Can't figure the damn thing out myself," and then promptly crushed it under his shoe. As a result of Hibbie's enthusiasm for paleontology and inferring paleoclimates, I became interested in fossil and prehistoric turtle remains. I got to know James B. Griffin, director of the Museum of Anthropology upstairs from Herpetology, who opened to me his accumulated collections of turtle bones recovered from Native American middens. This led to several publications. The faculty in the several museums of the University Museums building were like this. They were eager to have students from other units interact with their own. Reeve M. Bailey, in Fishes, who was also interested in herps, and Theodore H. Hubbell, in Insects, an expert on cave crickets (which sometimes live together with salamanders), were especially important to my personal development.

In the Department of Zoology during the 1960s there were a number of faculty who were interested in herps and who often supervised graduate students who worked with amphibians or reptiles. Nelson G. Hairston, Sr., a parasitologist and population ecologist, had worked on plethodontid salamander systematics and ecology prior to (and after) his tenure at Michigan, supervised several herp students (Warren Brockelman, Douglas Gill, James Organ, Wayne VanDevender). Frederick H. Test, a vertebrate ecologist, also had doctoral students in the 1960s working on herps (Marilyn Bachman, Jim Dole, Harold Heatwole) as did William R. Dawson, a physiological ecologist (Calvin DeWitt, William Dunson, Paul Licht, Walter Moberly, Vaughn Shoemaker). The Herpetology students in the museum regularly interacted with these Zoology grad students and took courses from their professors. Later on, Hairston and Dawson each served as director of the Museum of Zoology. This large number of professors with different research specialties became a valuable resource to us in the Division of Herpetology and many of them served on our doctoral committees.

Hairston and Hibbard, and William H. Burt in the museum's Division of Mammals, were on mine.

Later in the 1960s, there were significant changes for the herp community following the untimely death of Hartweg from pancreatic cancer in February 1964. He had spent his final years focused on the founding of the Organization for Tropical Studies, a multi-institutional teaching program in Costa Rica, and sometimes even slept at the office to conserve his dwindling time and energy. As the only unmarried grad student in the division at the time, I was in the museum almost every night and once watched the custodian mop around Hartweg while he was asleep on the cement floor in his darkened office. Observing someone show such selfless devotion to an important academic goal under extremely stressful circumstances makes a powerful impression on a student. One upshot of Hartweg's death was that George Zug, my office mate, and I were hired on Hartweg's salary line as "temporary curators" to rearrange the collection of lizards and snakes that was still organized according to the classification proposed 75 years earlier by George A. Boulenger at the British Museum. This task was an unexpected treat for me and was made all the more enjoyable to have accomplished it with my friend George, but it taught me that a museum curatorship was probably not a wise career choice for me. It was better to find this out earlier rather than later.

George Zug, *a Walker student, dissecting a turtle under a stereomicroscope in our shared office in the University of Michigan. (Photo by Kraig Adler.)*

Donald W. Tinkle was hired in 1965 to be Hartweg's successor as curator of herpetology. Arnold G. Kluge had been a candidate for the same job but was hired instead by the Department of Zoology to teach comparative anatomy. (Kluge also became a curator in 1967, but only later did he move over to the museum from Zoology.) Both were supported by federal grants which impacted the nature of their research programs and the training of their grad students. The contrast to the styles of Hartweg and Walker was dramatic. Tinkle, for example, had had scant training in museology. He and his students had little understanding of how the collections worked or how specimens were accessioned. Sometimes they would put bottles of uncatalogued specimens on the shelves in the collection ranges but not in the proper places and with only a simple paper label on the bottle with the species name scrawled in pencil. Walker's students were under strict orders to remove any such jars that we found and to unobtrusively bring them to him for proper cataloguing. No one was to be embarrassed. I never knew whether Tinkle found out what Walker was doing because it was never mentioned again.

Despite their extreme differences in operating procedures, to say nothing of their personalities, Walker and Tinkle worked together extremely well and we students never observed any upset. I know from his comments to me that Walker developed great respect for Don Tinkle and his research program. Tinkle, in his obituary for Walker in *Copeia* in 1979, noted that he was an acknowledged world authority on amphibians. He remarked about his "insistence upon excellence" and that Walker was for him "the quintessential colleague." This was an object lesson for us students, who had been in Herpetology from the era of Hartweg and Walker, to witness the ways in which faculty trained in such different ways and with such different academic goals, could nevertheless coexist and thrive in the same unit. Each one added value to the program. These lessons learned were the more valuable to me when I was a faculty member myself, a department chair on multiple occasions, and a senior university administrator.

Grad Student Academic and Social Life

Throughout my career at Cornell I have advised undergrads aspiring to attend grad school to carefully check out the total environment at prospective Ph.D. institutions. Not just the professors and the facilities, but also the grad students because they are going to spend far more time interacting with them than with the faculty. This advice was informed by my own graduate experience at Michigan, which was even more beneficial than I had expected. I am speaking about both the academic and social environments. The opportunity to teach undergrads, as lab instructors or lecture assistants—and to be part of a cadre of bright and dedicated grad students interacting daily to create the best possible learning environment—was instrumental to my develop-

Douglas Futuyma *demonstrating his expert lizard-collecting technique in the parking lot behind the museum. May 1964. Futuyma was a budding herpetologist from New York City who joined the Division of Herpetology in 1963 via Cornell. He later drifted over to join the ecologists in Zoology and a career as an evolutionary biologist. (Photo by Kraig Adler.)*

ment as a university teacher. We debated pedagogy, helped one another when necessary, and learned together; fast friendships developed that still exist. Not all experiences were fun, however. We suffered together through the day-long, written, comprehensive exams. One got two chances to pass, otherwise you were out of the program. We also stuck together when confronted with pettiness. Once, the professor in charge of the introductory labs insisted that we all wear white lab coats to look the part of a scientist. We demurred on the grounds that none of us ever wore one to do our own research. The professor insisted and induced the department chair to order us to wear the jackets. With the departmental picnic coming up, we decided to wear the white jackets all day even when we were flipping the hamburgers. The department chair got the message and rescinded his order the next week. In a more serious incident, I was one of four teaching assistants in Donald M. Maynard's course, "Neuromuscular Basis of Animal Behavior." Maynard had told the students the first day of class, in writing, exactly how they were going to be graded, but then changed his mind near the end without ever informing them. We four sent a signed protest letter to Maynard who promptly put a letter of reprimand in each of our grad files. This black mark I was proud to earn.

The Zoology grad students had a very active steering committee called "The Brownian Movement," named for the department chair. Sometimes, museum students were members; I was one of them. They organized events including a weekly grad seminar for us to present our current research, represented us on university-wide petitions to the administration (turned out we Zoology students had it pretty good), helped to host Zoology's external review committee (I got paired up with E. O. Wilson), relayed suggestions (complaints really) to the faculty executive committee, etc. The museum grad students also had a weekly seminar to discuss and debate current research papers and new books, usually held at the museum in the evening. Ernst Mayr's *Animal Species and Evolution* and George C. Williams's *Adaptation and Natural Selection* were published during the mid-1960s and generated a lot of heated discussions. Sympatric speciation, group selection, and other hot topics. These sessions were grad-students-only and the discussions were sophisticated, often intense, and even heated; included

Stevan Arnold, *a student of Kluge's, collecting specimens of* Plethodon nettingi *in the dense spruce forests on Cheat Mountain, West Virginia, for his dissertation on courtship behavior in salamanders. Summer 1969. (Photo by Kraig Adler.)*

Henry Wilbur *and his wife,* ***Dorothy "Dot" Wilbur*** *during a frigid walk along Bullhead Trail to Mt. LeConte, Great Smoky Mountains, Tennessee. April 1967. Henry was Charles Walker's last PhD student and did his postdoc with Tinkle. (Photo by Steve Tilley.)*

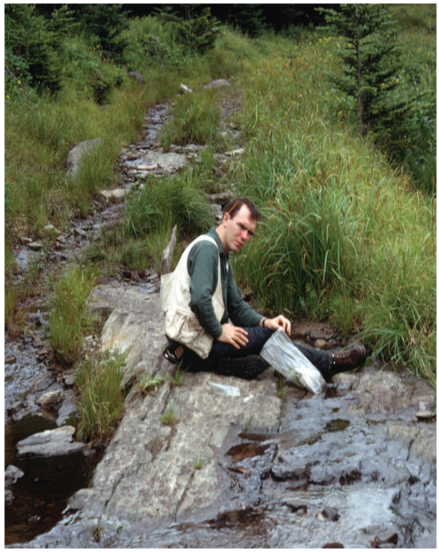
in this group were three future members of the U.S. National Academy of Sciences. Students from throughout the museum were regular participants: Mary Jane West (-Eberhard), Ted Cohen, and Ann Pace from Insects; Steve Emlen, Frank Gill, and Al Feduccia from Birds; Ted Fleming, Tim Lawler, Guy Musser, and Jim Brown from Mammals; John Lundberg and Steve (we called him Jim) Farris from Fishes; and Doug Futuyma, Steve Arnold, Henry Wilbur, and others of us from Herps. (Mollusks was a world unto itself and almost never attended museum-wide functions. Each division had its own culture.) We all remember the exchanges between Brown and Farris, which never disappointed! Despite the arguments, many in the group would afterwards go to Metzger's German Restaurant to share a beer.

Almost every weekend the Zoology grad students, most especially including those in the museum, had a party at someone's home or apartment, often in the basement or dining room where there was space to dance (Pat and George Zug were our most energetic dancers! I met my future wife, Dolores, at one of those dances). These events would normally last until well after midnight, and sometimes extended until after sun-up. Breakfast was served. These social gatherings further cemented our already-close ties. Sometimes a faculty member would show up (bad form!), which would always sober the group a bit. Science was often discussed, too. It was a relaxed atmosphere that helped further develop friendships which, in turn, supported our academic work during the day. Grad school turned out to be a total-immersion sport.

Choosing One's Doctoral Research Project

How a doctoral research program was chosen varied from lab to lab. Some professors, especially those with federal grants, suggested questions, but most faculty in the museum allowed their students a great deal of flexibility. Hartweg and Walker were extreme in this regard and always expected their students to make their own choices. This can often take a long time, as students move from one idea to another to test the waters. For me, I had always thought that I would do a systematics thesis on some group of Mexican herps. I went on expedition to Mexico during the summer of 1964 with Guy Musser and Jim Brown. I made some nice discoveries of new species and wrote them up, but the work left me unfulfilled. Next, I spent a summer in Colombia with Walt Moberly, one of Dawson's students who was working on diving physiology in iguanas. I was hoping to work on brooding

Charles McKinney, Gary Ferguson, and Donald Tinkle *filming* Uta stansburiana *at Colorado National Monument, Colorado. June 1966. (Photo by Steve Tilley.)*



Steve Tilley, *a Tinkle student, conducting field studies with* Desmognathus carolinensis *on the Maple Camp Bald Trail at Mt. Mitchell, North Carolina. July 1968. (Photo courtesy Steve Tilley.)*

behavior in marsupial frogs but couldn't find enough of them to make a go of it. I toyed with turtle paleontology and paleoarcheology for a bit, then moved into behavior. I fiddled with odor-cued orientation using Y-shaped mazes that I had crafted from sheets of acrylic (plexiglas), but the results were not sufficiently repeatable. Throughout this multi-year process my major professor, Dr. Walker, never once asked me how my research was going. Not once. If there was something that I needed to ask him, he was always willing to sit down and talk about it at length, but he never initiated an inquiry. And I spent a lot of time with him. Unmarried and a man of fixed patterns, Walker ate breakfast every morning in The Michigan League, located one block from the museum. Unmarried and living in a rooming house just off campus, I ate breakfast with Walker almost every morning for several years. He would get his *New York Times* first, then his scrambled eggs. We would sit, eat, and usually talk about research or science, but if his newspaper had not yet arrived or his favorite cook was not there, then it was mostly stone silence—and it was going to be a bad day. (Other grad students, knowing all this, would sometimes ask me, "Would today be a good time to talk with Dr. Walker?")

Eventually, I did choose a topic—environmental control of locomotor behavior in salamanders. Experimental research appealed to me. I did the field work at Mountain Lake Biological Station in western Virginia, consisting of all-night transects along the lakeshore in company with the denizens of the night (deer, an overly inquisitive skunk, white-footed mice that learned to take food from my fingertips, flying squirrels that started playing exactly on schedule every night, and a black bear that once bathed in the lake 50 feet away) and did most of the lab work in the environmental chambers in the museum's new wing (where I jury-rigged event recorders to monitor locomotor activity under shifting photoperiods). Among other papers, this research led to my first article in *Science*, on the discovery of extraocular photoreceptors and entrainment of circadian rhythms, so it all worked out OK, but Walker never hurried me along. I will be eternally grateful for the time and emotional space he gave me to find my own way and at my own speed. I have tried to emulate his style of supervision by being patient with my own students.

Early on, Don Tinkle's grad students all worked on some aspect of the ecology of *Uta stansburiana* and questions related to Don's grant-supported research program. All but one. That exception was Steve Tilley, who had been imprinted to dusky salamanders by Barry Valentine as an undergrad at Ohio State University. (Oh, sorry, *The* Ohio State University). Steve was devoted to the study of these animals and, in fact, spent his entire career milking those little brown sallies for a long series of excellent research papers. To his great credit, Steve worked almost entirely independently because Don did not understand salamanders. Over beer at Metzger's he once confessed that he didn't grasp how a tiny little salamander, which would be dead by age two were it one of his lizards, was in fact not even close to being sexually mature. Steve would explain but Don, for all his considerable smarts, could never fully get his head around it. As time went on, he became more willing to have his students' research diverge more significantly from his own. Even professors can learn.

Making Academic Connections

Starting with my first UMMZ job as research assistant, I was constantly meeting and interacting with new people while at Michigan—other students, staff, faculty, correspondents, people at scientific meetings, students and faculty in other departments, and so forth. For the most part, these were smart people who were highly dedicated to their work. It is easy to like people like that. You see your own failings and shortcomings more clearly when you are around really competent people and it makes you want to be better. Of course, you also get lots of good ideas by hanging out with them and, hopefully, give proper credit where it is due. Grad seminars and evenings at Metzger's were almost equally important in considering new ideas and different points of view. The Michigan experience was an incredibly rich learning environment in so many ways.

To mention a few specific experiences, during my year as research assistant I suggested to Dr. Walker that we might increase the diversity of the collections by making some strategic exchanges of specimens on a one-for-one basis with people working in other parts of the world. He gave the idea his OK. One of those I approached was Ilya S. Darevsky in the (then) Soviet Union because the UMMZ had virtually nothing from that vast country. I had learned about his classic papers on parthenogenesis in lizards and could read enough of one in German to know that his work was important. He eagerly accepted the offer, so we exchanged several hundred specimens and obtained Michigan's first *Ranodon* (a hynobiid) and unisexual species of *Lacerta,* among many others. As a byproduct of this exchange, I suggested to Ilya that he might consider publishing some of his research in English because few scientists in America knew about it. He agreed and I became his editor. His

James Organ, *a Hairston student, his wife* ***Della Organ,*** *and* ***Kraig Adler,*** *a Walker student, at the Organs' cabin at Mountain Lake Biological Station, University of Virginia. The student assistant at the left is unidentified. July 1967. (Photo courtesy David Dennis.)*

long paper, published in 1965, was the first introduction to Darevsky's work for most Americans and other English-speaking herpetologists. We became close friends and, together with Carl Gans, I was able to host Ilya and his associate, Natalia Ananjeva, on their first visit to America, in 1988, first to Ann Arbor for the herp meetings, then to Cornell and several museums along the East Coast. We became life-long friends and Ilya's cooperation became essential to the success of the First World Congress of Herpetology in the UK (1989). Without his active participation we probably would not have had Russians or even participants from eastern European countries in attendance. All because of an exchange of some herp specimens back in 1963.

Another example. Because my doctoral thesis research became experimental in nature and Dr. Walker had never conducted experiments, I had to reach out to others for advice on my experimental designs. I entered into correspondence with Victor Twitty at Stanford, a renowned developmental biologist who also worked on newt orientation. He was most generous in offering advice, sent publications I had not seen, and put me in touch with members of his field research team, especially David Grant, who knew the details of their displacement experiments. I also needed advice to analyze circadian rhythms, so I wrote to one of the leaders of this field, Colin Pittendrigh, a British-born physiologist then at Princeton. Like Twitty, he was most generous with his time and advice, and shepherded my first *Science* paper through that journal's byzantine editorial process. These were object lessons for me as a budding scientist. Be generous with your time to others even when they are not your own students or even at your own institution. Their help to me as senior colleagues also allowed me to function almost as an independent investigator would, rather than as a graduate student under regular professorial supervision.

Final example, with a Michigan connection hinted at earlier. During my first summer at Mountain Lake Biological Station in western Virginia, by happy accident I shared a laboratory space with James Organ of City University of New York. Organ had been one of Hairston's PhD students but finished up two years before my arrival at Michigan. He had conducted studies on the population dynamics of five species of *Desmognathus* salamanders and amassed a truly immense collection of specimens, of all life stages, that were placed at UMMZ. I knew his collection from my year as research assistant and I already knew about his studies, so our relationship had a big head start because of our Michigan connections. While working in our shared lab we constantly talked about salamander biology. I learned a lot from him, and from some work we did together in the field. I also became friends with his family, Della Organ and their two daughters, and we even took a weekend vacation together. But not all of our discussions in the lab were about research. At that time, The Ohio Herpetological Society was about to transition into a national society and was having difficulty choosing its new name. Based on the example of the Society for the Study of Evolution, Jim suggested the name "Society for the Study of Reptiles and Amphibians," but I massaged it a little bit. We thus have Jim Organ to thank for SSAR's rather long but eminently descriptive name. Two years later, Organ served as co-chair of the local committee for the SSAR meeting held at Mountain Lake. When I was looking for a job, Organ, who was by then chair of his department, offered me an interview. I declined on the grounds that we wanted to stay in the Midwest and would probably not enjoy living in a big city. Connections can be very important to one's research program and they should be nurtured. They can also have potential practical benefits, as Organ's friendship also turned out to have. Ideally, these connections should have reciprocal benefits, but that is not always possible especially when the individuals involved are at very different stages of their career. But gestures still matter. My appreciation for the importance of these kinds of connections really began at Michigan.

How Did Michigan Prepare Me for My Academic Career?

My 6 years in grad school (M.S., Ph.D.) provided me with a wealth of experiences that, looking back after more than half a century, come more fully into focus. Of course, my primary educational goals were to learn how to do modern biological research independently and to learn the multitude of skills necessary to be an effective teacher and mentor. How does one encourage students to become innovative researchers and inspiring teachers? As an undergraduate student I was not aware of all the numerous elements that combine to make for good research and teaching. You learn best by actually doing something but learning also depends on a nurturing environment. The faculty and my fellow grad students were essential to my development as an academic. Sometimes you mature best by having a patient, hands-off supervisor. You also learn to pay attention to what is going on around you, both the good and the bad, and you observe results and consequences, too.

In the various examples described in this essay I have recounted just a few of the situations I faced as a student in the Division of Herpetology in the UMMZ and in the Zoology Department. Each one of us who passed through this program in the 1960s can describe many unique experiences but also some shared ones that contributed to our training. Having been in the herp division at a time of major transition was a great advantage in understanding the evolution of the program. For me, the opportunities I had as a research assistant, teaching fellow, and temporary curator, on museum expeditions to Mexico and Colombia, as an NIH Trainee and Rackham Fellow, or as a member of the steering committee of The Brownian Movement and in other leadership roles were defining elements in my academic development and the career I had at Notre Dame and Cornell. I suppose that I would have become a very different person had I attended another program. My story, of course, is certainly not comparable to *Canterbury Tales*, but it is my own personal tale anyway. I am deeply grateful to the faculty, grad students, and staff at Michigan for their generosity of spirit, their extreme patience and devotion to excellence, and for making it a lot of fun. I would do it all over again. And happily, too.

Acknowledgments. I am grateful to George Zug, William Duellman, and Robert Hansen for reading and commenting on my manuscript. I thank Stephen Tilley and David Dennis for photographs.

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Now retired, Kraig Adler's research program focused on exploring the sensory basis of long-distance orientation and navigation in field and laboratory studies. He used amphibians and reptiles as model systems because of their local abundance and the ease with which they could be manipulated. His laboratory discovered that amphibians and reptiles can detect and use skylight polarization patterns for orientation (polarotaxis) and that the critical receptors for this cue are extraocular (pineal and related structures). They were also the first to demonstrate detection of the earth's magnetic field by amphibians and reptiles for use in orientation and that true navigation behavior exists in amphibians. Other studies investigated the importance of individual variability, time-dependent orientation mechanisms, the role of environmental stress in orientation, and the function of melatonin in re-setting internal clocks used for orientation. Adler and one of his students also discovered kin recognition behavior in frog tadpoles.

Equally significant as his research is Adler's long-standing development and support of herpetological professional societies—in particular, the Society for the Study of Amphibians and Reptiles (SSAR). The SSAR is now the largest professional herpetological society in the world and publishes the *Journal of Herpetology*, along with *Herpetological Review* and an impressive array of books and other publications. He was the founding Secretary-General of the World Congress of Herpetology that over three decades has sponsored nine congresses around the globe. Largely in response to Kraig's numerous proactive contributions to the study of the history and bibliography of herpetology, he was awarded the 2018 Founders' Medal of the London-based Society for the History of Natural History. At Cornell, he served as chair of his academic department on three separate occasions and was also the university's first vice provost for life sciences.

GEORGE ZUG

A New Beginning: September 1963–November 1968

1963–

Into my second year at the University of Florida, I knew that I needed something different, but what was it? Unformulated in my mind, it was a greater intellectual challenge and broadening. Whatever it was, Michigan seemed to offer it, and once there, I discovered what it was and that it was there "in spades." The difficulty in course work was not different between Florida and Michigan, but the level of scholastic interaction was multiple times greater at Michigan.

The latter was evident within a month on campus and was present throughout the department (Zoology). Obviously, I gravitated to the museum and amphibian and reptile division. As I arrived without a fellowship, Dr. Charles F. Walker quickly found a curatorial assistantship for me. I was immediately welcomed by my fellow herp students and became a member of the lunch group in the division's catalog room, a habit/routine that continued throughout my Michigan stay. I also soon discovered afternoon tea in the museum director's office/conference room—well attended by students and faculty—with discussions wide ranging but seldom without a biological undertone.

In the department, there were weekly graduate student seminars. Here my memory is failing me but certainly a couple a month. This activity derived from the graduate student body's formal organization "The Brownian Movement," an organization which was relatively new (a couple of years old??)

organized initially to fight some onerous decrees announced by Prof. Brown, the departmental chairman. Apparently, the decrees were intentionally oppressive to stir a lackadaisical graduate student body into organizing and interacting. It worked, certainly during my Michigan tenure, in nurturing a high level of interchange among us with diverse biological interests. The seminars and other activities certainly broaden my appreciation and knowledge of the diversity of biological research. Wasn't that what I came for?

Well, yes, but also with the intent of working on kinosternid systematics with Dr. Norman Hartweg. That was not to be! Upon my Michigan arrival, he was traveling in Central America for the Organization for Tropical Studies. Returning home at Thanksgiving, he fell sick, and he and I never had an opportunity to discuss my plans. Early in the winter semester his kinosternid notes were handed to me. I spent many hours in the basement turtle tank room comparing his data with those that I was gathering. It became clear that I could not integrate the two sets of notes. Additionally, his thoughts on population relationships in *Kinosternon* were not well documented in his notes. Later, in the summer of 1965, I traveled to northern Mexico to determine my ability to sample the *Kinosternon* population. The trip was not overly successful and led me to abandon my plans for a project with these turtles. The trip was supported by a small personal grant from Dr. Walker. His financial assistance for research activities was not confined to herp students; I am aware of such grants for the study of insects and birds.

With the death of Hartweg in February 1964 and my increasing familiarity with curatorial needs, my duties increased. One was self-imposed. The reptile collection was organized in a Boulenger catalog arrangement that was frustrating to us "younger types" unfamiliar with that particular ordering. Kraig Adler and I decided that an alphabetic by a family-genus arrangement would be more practical. We approached Dr. Walker with the suggestion. He reluctantly agreed. The rearrangement was begun and completed, retaining the Michigan counties first arrangement within the Michigan herpetofauna.

Other duties included helping Tom Uzzell, then at University of Chicago, to erect a salamander fence around his study pond in the woods at Zeeb Road. Another included meeting visiting herpetologists, most of whom were former graduate students but not all. In my first summer (1964) at Michigan while Dr. Walker was in the field, I remember "hosting" Edward H. Taylor and Allen Greer. Taylor was working on his caecilian monograph but would break to tell one of his adventures. I can still see him in the visitor's lab surrounded by bottles of specimens taking a break by studying Russian flashcards to enable him to read the Russian literature on caecilians. Allen had begun his lifelong study of skinks. I had no research interest in skinks then. Only later when working in the South Pacific did my interest in those lizards develop. Subsequently, we developed a close friendship during my visits to Australian Museum in Sydney in the 1990s researching systematics of *Nactus* and *Carlia*. My curatorial duties continued in subsequent years when I held graduate assistantships, teaching comparative anatomy labs for Dr. Cather and then Dr. Kluge. I also assisted with Dr. F. Test's natural history of vertebrate labs.

Having lost my presumed advisor, I asked Dr. Walker to serve. He requested that I await the arrival of Don Tinkle and Arnold Kluge to see if they were willing and appropriate. They were the candidates for the curatorial vacancy. Both gave impressive seminars. Arnold was offered a position in the Department, specifically to teach comparative anatomy and Don received the offer for the curatorship. Both arrived prior to the fall semester. By that time, I had begun the preliminaries on a morphological and behavioral study of turtles for my doctoral research. Don was fully immersed in lizard ecology studies and lacked an interest in my proposed research. Arnold supported my research plans, but both of us decided that our developing friendship was a potential negative for an advisor although he willingly served as a committee member.

My interaction with museum and departmental colleagues was wide, with far too many names to mention. I must, however, mention Kraig Adler, my officemate, who became and remains a close friend. Although a bit older than he, Kraig was more administratively astute and regularly offered good advice. I did serve as a sounding board as he converted The Ohio Herpetological Society into the Society for the Study of Amphibians and Reptiles. These interactions prepped and encouraged me in my subsequent volunteer work for the SSAR and American Society of Ichthyologists and Herpetologists.

This broad level of interaction between students and between students and faculty may be common at other universities but was new to me. It was also my impression that it was a relatively recent thing for the students housed in the department and those in the museum to be integrated into a single interacting and cooperating group. It was certainly a great benefit to me while a Michigan student and subsequently in my career.

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George Zug is an Emeritus Research Zoologist in the Division of Amphibians & Reptiles, Department of Vertebrate Zoology, National Museum of Natural History – Smithsonian Institution. He joined the museum staff in January 1969 and retired in January 2007, serving in various capacities, such as Curator-in-Charge of the division and chairman of the department. His research interests have been broad including research in locomotion and its association with morphology in turtles and anurans, systematics of Pacific area amphibians and reptiles (especially lizards), skeletochronology and growth in sea turtles, and currently systematics and biology of amphibians and reptiles of Myanmar (Burma). He remains an active researcher in the latter area.

STEVAN J. ARNOLD

Graduate Student Experiences at The University of Michigan Museum of Zoology, 1966–1972

1966–

Below, I describe my experiences as a graduate student in the Department of Zoology and in the Museum of Zoology at the University of Michigan from 1966–1972. During those years, I metamorphosed from an undergraduate to a scientist capable of designing, executing, and publishing research projects. I also learned how to conduct experiments and statistical analyses. Many people guided and helped me during these professional transformations. I focus on these people in this essay and only briefly mention others who had major effects on my social life and maturation.

From Berkeley to OTS to Ann Arbor

Some events in Ann Arbor will make more sense if I begin by recounting some of my experiences as an undergraduate Zoology major at UC–Berkeley, 1962–66. Even before arriving at Berkeley in the fall of 1962, I had an avid interest in herpetology. Beginning in junior high school in Arcadia, CA, I teamed up with Tim Clarke, a like-aged herpetology enthusiast who lived in the neighboring town of Monrovia. Together, Tim and I roamed the nearby San Gabriel Mountains looking for amphibians and reptiles. Later, as car-mobile high school students, we were joined by Richard D. Sage as we scoured the deserts of Southern California, Utah, and Arizona for lizards and snakes. We were mentored by

Arcadia natives Richard and Norman J. Scott Jr. who were herpetology graduate students at Humboldt State University and the University of Southern California. We considered ourselves serious herpetologists. We subscribed to the *Bulletin of the Philadelphia Herpetological Society* and *Copeia*, kept field notes, viewed Stebbins[1] as a bible and Stebbins himself as a god. We also visited Laurence M. Klauber in San Diego and once called him from the road to report a particularly significant range extension. When I arrived at Berkeley as an undergraduate, I had already visited the herpetology lab in the Museum of Vertebrate Zoology (MVZ), met one of Prof. Robert Stebbins' graduate students (Robert G. Crippen), and corresponded with Stebbins himself. Soon after my arrival, I was hired to work part-time in the herpetology lab doing routine curatorial work (tying tags on specimens, topping up alcohol levels in jars, cataloging new entries into the collection). I didn't even stop to think that my herpetologist self-image had been validated.

Work in the herp lab also gave me an entree into the social life of the museum. I gradually became comfortable chatting with graduate students and some of the curators (e.g., Seth B. Benson). I also regularly attended seminars (e.g., by C. S. Holling, Julian Huxley, and Richard C. Lewontin) and doctoral defenses (e.g., by Dale R. McCullough, Richard B. Root, Vince M. Sarich, and Thomas T. Struhsaker). I filled up my curriculum with courses heavily slanted towards organismal biology and did well enough that graduate school was a natural next step. Evolution courses by G. Ledyard Stebbins and Herbert G. Baker and an animal behavior course by Peter Marler convinced me to head in those directions for graduate research.

In my senior year I convinced Robert Stebbins to sponsor my senior research project on courtship behavior in plethodontid salamanders. I got the inspiration for doing research on amphibian reproduction while working at my other part-time job, as a stock-keeper and salesman for Jones-Stanley Tropical Fish in Oakland, next door to Berkeley. As a stock-keeper, I learned how to breed a number of tropical fish (e.g., *Apolcheilus*, *Discus*, *Trichogaster*), as well as a small African pipid frog, *Hymenochirus.* I was fascinated by their elaborate mating behavior, and they became my lead candidate for a senior research project. However, in the library I discovered that George and Mary Rabb had just published detailed descriptions of breeding behavior in *Hymenochirus*[2] and *Pipa pipa.*[3] From William Z. Lidicker's course in Vertebrate Reproduction (with teaching assistant, Mercedes S.

Foster), I remembered that *Ensatina* had elaborate courtship behavior, as described in a well-illustrated account by Stebbins.[4] More work in the library revealed that courtship behavior had not been described in any other plethodontid in the western U.S.—*Aneides*, *Batrachoseps*, *Hydromantes*, and *Plethodon* were all virgin territory. Stebbins was on board with my proposal for a descriptive account of courtship in any of these genera, so I got to work in February 1965.

For the next few months I put my field skills to work searching the Berkeley Hills and beyond for plethodontids with well-developed mental glands (a sign of sexual competency in males). I housed my captives in a small (3 × 8 ft), cork-lined, live-animal room adjacent to the herp lab and observed them by night under dim red light. *Aneides* and *Batrachoseps* were available within walking distance of the campus, but to secure *Hydromantes* and *Plethodon*, I went on weekend trips further north in California with Richard D. Sage (my Berkeley roommate) and fellow Zoology major A. Ross Kiester. Those trips were memorable, but in the end, I was able to observe courtship in just one plethodontid, *Ensatina*. Nevertheless, I became a patient observer of animal behavior and developed my own system for making notes and drawings in the dark. I also concocted a scheme for how *Ensatina* partners used tactile cues in sexual communication and discovered that I had original perspectives on the literature on salamander courtship.[5] Those ideas later blossomed into a plan for doctoral research in Ann Arbor.

I drove roundtrip from California to Costa Rica in the summer of 1965 and again in the summer of 1966. The drive was an arduous journey in those days. Although the two-lane road was passable the whole way, it was impractical to drive at night because of livestock on the highway. Consequently, it took 11 days just to drive the length of Mexico. The common denominator for these trips was the Organization for Tropical Studies (OTS), a newly created consortium of universities that offered a 10-week course in tropical ecology in Costa Rica. In 1965, Dick Sage and I made the trip as part of a 3-month effort to obtain data and specimens for Berkeley entomology professor Paul D. Hurd, who had an NSF grant to study carpenter bees (*Xylocopa*) in Middle America. As a favor to Berkeley Ph.D. Daniel H. Janzen, we agreed to transport equipment and supplies to the OTS course, which was underway in Costa Rica. The next year I was admitted to the OTS course and made the trip by truck with UCLA ornithology graduate student F. Gary Stiles, again transporting equipment and supplies for the course.

Figure 1. Organization for Tropical Studies *course near Guapiles, Limon Prov., Costa Rica in 1966. Rob Colwell is in the center of the photo with a camera around his neck: Doug Futuyma is to the right of Colwell, Steve Arnold is to the right of Futuyma, and Steve Tilley is directly below Colwell.*

The structure of the OTS course was to visit a series of field stations in a variety of tropical biomes. At each location, we did field exercises by day and listened to lectures in the evenings. An astounding amount of tropical natural history unfolded before our eyes—stinging ants protecting their host plants from herbivores; iridescent bees that collected scent from orchids to use in mate attraction; bot flies that captured mosquitoes and deposited larvae on them, as well as plenty of snakes (e.g., *Boa, Bothrops, Clelia, Lachesis*) and lizards (e.g., *Corytophanes, Ctenosaura, Iguana, Lepidophyma*).[6] Near the end of the course, we spent two weeks doing independent research projects. Mine was an experimental study of competition between species of stingless bees (*Trigona*). On top of all this, I became life-long friends with a diverse cadre of young systematists and ecologists, including four graduate students from Ann Arbor—viz., Douglas J. Futuyma (a course instructor), Robert K. Colwell, Douglas E. Gill, and Stephen G. Tilley (Figure 1).

War, Love, and the Graduate Exam

I arrived in Ann Arbor at the end of the summer of 1966 to find a dark cloud hanging over the entire graduate program and especially over me. A letter from my draft board was waiting for me which read "report for your physical examination…in Panama City." I had forgotten to tell them that I was planning to spend two months out of the country. I quickly arranged to take the physical in Detroit and did obtain a student deferment, but like every other male graduate student, I was in the cross-hairs of the Selective Service. The war in Vietnam was ratcheting up and sweeping thousands of young men into the armed forces.

Early in the fall of 1966, a Department of Zoology meeting was convened to announce new procedures regarding the draft. Previously, the department chair had responded to Selective Service queries about the status of male graduate students, but now a small faculty committee would take over the job. No one mentioned whether graduate students could participate on the committee, so I raised my hand and asked if one or more graduate students could be included. "No," came the response, the faculty were fully capable of representing the interests of the graduate students. I wasn't ready to let the matter rest. "Well," I said, "the hard fact is that the graduate students are going to Vietnam and dying, not the faculty!" This outburst didn't change any faculty minds. I remember that Prof. Donald Maynard puffed up and retorted that some of the faculty had served in the armed forces during WWII. I suppose I came across as a Berkeley firebrand, even though I hadn't participated in the notorious Free Speech Movement. Nevertheless, I had been to quite a few rallies and Vietnam War protests.

In Ann Arbor, my monastic life as an undergraduate ended, and I found myself on an emotional roller coaster. With the war in the background, my graduate student group seemed to seize on every opportunity to throw a party. Dancing to the accompaniment of Motown, the Beatles, the Stones, and Bob Dylan was a big part of these events. A popular local bar, The Flame, was also a standard hangout in the evening, but here serious discussions of ecology and evolution were part of the scene. Everyone knew everyone in the Department of Zoology/Museum groups, but I focused on one graduate student in particular, Rudi C. Berkelhamer. By the end of October, we were an item. But then my roller coaster began a rapid descent. The occasion for my crash was the graduate exam.

The graduate examination almost knocked me out of graduate school. This comprehensive written exam was given at the end of your first term and was meant to diagnose gaps in background that might be plugged with coursework. You had two shots at passing, so when I failed on the first try, I resolved to study so that I wouldn't fail the second time. Adding to the tension, Rudi and I were pregnant by early spring. We got married in May 1967. When we got the news that twins were on the way, I asked the obstetrician if there might be some mistake. "When I hear horse's hooves, I don't expect zebras," he replied. Neither of us laughed, but we were thrilled when Hilary and Laura were born in December 1967 (Figure 2). As a side issue, I passed the Graduate Exam with a high score that same month. I was now on a roll with a new family, a clear path to a Ph.D., and an iron-clad deferment from the draft board.

Figure 2. ***Rudi Berkelhamer*** *(holding Hilary) and* ***Steve Arnold*** *(holding Laura) at Mountain Lake Biological Station in July, 1968.*

Pedagogy with Cigarettes, Cigars, and the Sensory Homunculus

With both my home life and relationship with the draft resolved, I turned my attention to coursework. Passing the graduate exam meant that I had free rein to choose courses; consequently, in the next few semesters, I signed up for statistics, ecology, and neurophysiology. The most eye-opening course was Frederick E. Smith's statistics course (with teaching assistant, J. David Allan). Sokal and Rohlf's influential Biometry text[7] did not appear until 1981; thus, Smith taught his course with a text designed for students of agricultural science.[8] The accounts for methods such as ANOVA and regression were designed for students doing calculations on a Marchant desktop calculator with a pull arm to power the wheels spinning inside. The hours spent doing homework in a room full of noisy calculators did have a big payoff. Concepts like "sums of squares" and "sums of cross products" were not hypotheticals. They were real computational endpoints that could take an hour or more to grind out and confirm on the calculator. Even today, I have lingering muscle-memories associated with those concepts. An independent project was required for Smith's course, and my project produced an unanticipated benefit, my first publication.

The cause of tropical species diversity was a hot topic in the 1960s, constantly discussed in the literature, seminars, and even at The Flame. In the spirit of the time, my Berkeley undergraduate colleague Ross Kiester had worked up a herpetological version of G. G. Simpson's mammalian species density map for North America.[9, 10] Ross's work was still unpublished when I was seeking a project for Smith's course, but I knew about the project and his results. With Ross's idea as a launch point, I began thinking about how the specialized diets of snakes might be used as a wedge to understand species diversity gradients. Smith and Allan taught us the concept of partial regression, and I realized that it provided a framework to analyze data on the species diversity of snakes and their prey. But I needed information on snake diets, which usually couldn't be found in the field guides (the source used by Kiester); therefore, I burrowed deeply into the herpetological library down the hall from my office. Soon I was grinding away on a Marchant calculator, computing sums of squares and cross products and converting them into partial regression and path coefficients. A few years later, I published my project in the *American Naturalist*[11] but was surprised to find that UM professors seemed unimpressed by both my results and their publication. Don Tinkle told me that if "I told a Kansas farmer that there were more lizard-eating snakes where there are more lizards, he wouldn't be surprised." Fortunately, Eric Pianka (my editor at the *American Naturalist*) and Robert Sokal (a fan of Sewall Wright's path analysis) were supportive and helped my ego recover. But, the biggest benefit from the project in Smith's course didn't arrive until the 1980s. Because of the time I spent calculating partial correlation coefficients, I had a deep memory of the corresponding formula. Because of that memory, I recognized Russ Lande's concept of a selection gradient[12] was essentially a partial correlation coefficient. The resulting paper[13] turned out to be the most-cited paper that either of us ever published.

The other two courses that most influenced me were Lawrence B. Slobodkin's ecology course and Donald M. Maynard's neurophysiology course. I am grateful to Slobodkin for a gentle introduction to life tables and exponential functions. I also remember an incident from his course that seems almost inconceivable today. Sitting in the front row during a lecture, I lit up a cigarette as I took notes. Slobodkin stopped in midsentence, not to reprimand me, but to ask for a cigarette, which I lit for him. In the 1960s, it was taken for granted that one could smoke in any social situation, including during class, although it was unusual for a professor to bum a smoke. Maynard's class was most memorable for the neurophysiological preparations in the lab that accompanied his lectures. Imagine arriving at lab to find a 2-m rattlesnake (*Crotalus adamanteus*) anesthetized and stretched out on a counter top with recording wires coming out of its head and running to an oscilloscope and a loud-speaker. Still in shock from this spectacle, we watched as Maynard calmly lit a cigar and—using it as a heat source—proceeded to illustrate all the basic principles of sensory physiology, as we listened to neural output snake's heat-sensing organ on a loud speaker and watched sensory neurons fire on the oscilloscope. Later in the course, Albert F. Bennett (my lab partner) and I won a prize when the class drew straws to determine who-would-get-which lab demonstration project. Our prize was to anesthetize a squirrel monkey and remove the top of its skull. These procedures enabled us to expose the monkey's sensorimotor cortex, which integrates tactile information. By moving a monitoring probe in a grid-pattern over the cortex, while touching different regions of the monkey's body, we confirmed that a map of the body was laid out on the surface of the brain. Both of these adrenaline-fueled experiences created indelible memories. Maybe drama should be part of all learning.

Joining the Herpetology Division in the Museum of Zoology

Another consequence of passing the graduate exam was that I was free to seek a doctoral advisor. Up until this point, I shared an office on the first floor the Natural Science Building with fellow graduate student Donald B. Heckenlively. During that first year, in addition to visiting Rudi Berkelhamer in her office on the third floor, I also spent a lot of time hanging out with Larry Slobodkin's group on the fourth floor. There, Doug Futuyma, Rob Colwell, and Armand Kuris held court, and lively discussions were always underway on issues large and small, occasionally punctuated by the appearance of Larry himself. But when Arnold G. Kluge took me on as a graduate student, I moved to the museum and thereafter spent most of my time there.

Once ensconced in the Museum, I quickly learned that museum tea was the best place to meet people and find out what was going on. Museum inhabitants assembled at 3 pm each week day for a ritual in which we all served ourselves tea or coffee and sat around huge square table. The tea room was adjacent to the director's office in the new wing. The director (Nelson Hairston) usually attended, as well as representatives of all the divisions in the museum and visitors from the department. The participants whom I especially remember are (curators indicated in boldface and listed in order of seniority):

- *Birds:* **Robert W. Storer**, **Harrison B. Tordoff**, Frank B. Gill, J. David Ligon, J. Alan Feduccia.
- *Insects:* **Theodore H. Hubbell** (one of the founders of OTS), **Richard**

D. Alexander, **Thomas E. Moore**, Daniel Otte, Jonathan Waage, Ann Pace.

- *Amphibians & Reptiles:* **Laurence C. Stuart**, **Charles F. Walker, Arnold G. Kluge**, **Donald Tinkle**, Kraig Adler, George R. Zug, Dale L. Hoyt, Floyd L. Downs, Henry M. Wilbur, Gary W. Ferguson, Charles O. McKinney, Stephen G. Tilley, James P. Collins, W. Charles Kerfoot, and postdocs J. Whitfield Gibbons and Orlando Cuellar.
- *Fishes:* **Robert Rush Miller**, **Reeve Bailey**, **Gerald Smith**, John G. Lundberg, James S. Farris.
- *Mammals:* **William H. Burt**, **Emmett T. Hooper**, **Douglas M. Lay**, Timothy E. Lawlor, Guy G. Musser, Warren Y. Brockleman
- *Mollusks:* **Jack B. Burch, Elmer G. Berry**.
- *Departmental Visitors:* Douglas J. Futuyma, John H. Vandermeer, Douglas E. Gill.

Attendance varied from day to day and not everyone was a regular. The younger curators (e.g., Tinkle and Kluge) seldom attended, but the emeritus curators were nearly always on hand.

Commonly 10–20 people sat around the tea table and—as a group—discussed an almost random succession of topics (e.g., recent seminars, hot issues in systematics and ecology, recent field work). I can't remember the serious discussions that took place, but I do remember some examples of trivia. For example, I learned that the father of the actress Julie Andrews was a squirrel enthusiast who had funded some of Guy Musser's field work. One day Bud Tordoff got kidded for publishing an almost facetious note on the unusual death of a Gouldian Finch (but later, all of us requested a reprint[14]). In other words, the atmosphere was generally friendly and supportive. No one wanted to return to their office with indigestion. Nevertheless, the tea was a challenging situation for a new graduate student to find his voice. I didn't say much for a couple of years. Eventually I did voice my opinions, and occasionally, I even brought a live specimen to tea for show and tell. Once, having just returned from field work in California, I brought two west coast endemics, a Jerusalem cricket (*Stenopelmatus*) and a Banana Slug (*Ariolimax*). I was tickled to see Hubbell and Burch perk up and tell us about these specimens.

When I arrived at the Herpetology Division in the Museum, I was surprised to find four curators instead of one, as was the case at Berkeley. The senior curator was Laurence C. Stuart, who had spent most of his career working on the herpetofauna of Middle America. He was especially well known for deducing a dispersal corridor through Guatemala that connected the dry forests and thus, the faunas of Costa Rica with Mexico. Stuart, about to retire, was packing up his library and giving away mementos of a long career. I mocked the supplicants who often clustered about his office door hoping for reprints or books. As I walked down the hall, I held my arms perpendicular to my body, tilting them as I swirled like a vulture. I remember Tinkle's post doc Orlando Cuellar being amused. In 1974, Lynne Houck and I visited Larry at his retirement home in Panajachel, Guatemala, on the shores of Lake Atitlán to report on recent work in Guatemala by Dave Wake's group. Larry said that he made annual car trips to Veracruz, Mexico, to eat seafood and every few years continued north to visit friends in Ann Arbor. I remember thinking at the time that Larry must really enjoy seafood and prize his friendships. From Panajachel, it's 1100

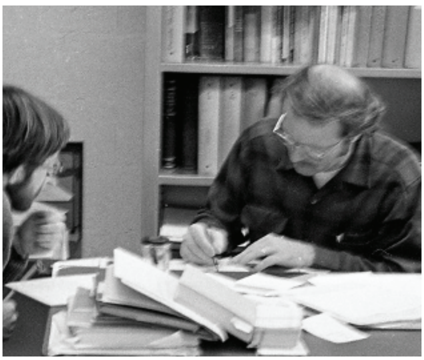

Figure 3.* *Arnold Kluge *(right) and* ***Jim Collins,*** *ca. 1969. Photo by author.*

Figure 4.* *Don Tinkle, *ca. 1969. Photo by author.*

km to Veracruz and another 3600 km to Ann Arbor, and those aren't freeway kilometers.

The other senior curator, Charles F. Walker, was best known for his 1946 book[15] on the amphibians of Ohio. Despite his low profile, Walker was doctoral supervisor for a cadre of seven students in various stages of finishing their theses—viz., Kraig Adler, Floyd Downs, Dale Hoyt, William R. Healy, Henry Wilbur, and George Zug. I knew Walker mainly in his role of supervising the students who were tying tags on specimens and entering them into the specimen catalog. I was part of that cataloging team. The other two curators, Arnold G. Kluge (Figure 3) and Donald W. Tinkle (Figure 4), were 1965 hires and between them supervised another eight doctoral students and a couple of postdocs.

Tinkle's taxonomic expertise centered on lizards and turtles, but his conceptual interest was evolutionary demography. The conspicuous element in Tinkle's research when I arrived was his long running project on the lizard genus *Uta*, which had a few species spread across the southwestern U.S. and several more in Baja California, including many of the islands in the Sea of Cortez. Tinkle's group had studied and sampled the entire complex in the field. When I arrived, graduate students Gary W. Ferguson and Charles O. McKinney were finishing up their doctoral work on this complex. Among other things, Ferguson and McKinney were working on mating and push-up displays in *Sceloporus*, as well as in *Uta*.[16, 17, 18] These topics were close to my own interests. They used a 16-mm movie camera to film push-up displays and a Vanguard motion picture analyzer to review and analyze their film. I was particularly fascinated by the Vanguard analyzer which projected film images onto a tilted screen so that extent and rate of movement could be measured. They showed me how to use both the camera and the analyzer, and Tinkle gave his blessing for me to use them in my own research. My research plans were also shaped by two other doctoral students, Henry M. Wilbur and Stephen G. Tilley.

The first time Henry Wilbur gave me a tour his field sites at the Edwin S. George Reserve (ESGR), 25 km NW of Ann Arbor, I was stunned (Figure 5). Passing through the gated entrance to the reserve, I marveled at 500 hectares of landscape exposed when the Wisconsin glaciation retreated 10,000 years ago and graced with dozens of ponds that brimmed with wildlife. Henry was an expert on the natural history of the reserve, and its fauna and its flora. On that first tour, Henry asked me if I had ever seen a flying squirrel. When I said no, he took me to a nearby tree with a dead trunk studded with holes and explained that flying squirrels nested in such isolated trees because red squirrels could not jump to them. Henry stationed me at the closest tree about 10 m away and banged on the nesting tree with a stick. A flying squirrel emerged from one of the holes, ran to the top of the stump and launched itself toward my tree. The squirrel had a panicked look on its face as I caught it in midair (Figure 5C). On that first tour, I also got a good introduction to the study system Henry was using for his doctoral research.

Henry had adapted an ESGR tradition of using aquatic field enclosures to design his own study of the roles of competition and

Figure 5. Henry M. Wilbur *at the E. S. George Reserve about 1969. (**A**) Enclosures at Burt Pond for studying competition and predation in the* Ambystoma-Rana *community. (**B**) Henry and his drift fence for capturing amphibians as they migrate to and away from a breeding pond. (**C**) Henry holding a recently captured Flying Squirrel (*Glaucomys*). (**D**) Henry contemplating an ant (*Formica*) nest. Photos by the author.*

predation in shaping amphibian (*Ambystoma* and *Rana*) communities.[19] The Wilbur version of such an enclosure was 8 × 2 × 2 ft and covered with window screen. On that first tour, several dozens of these enclosures were laid out around Burt Pond (Figure 5) near the main house, where Henry lived with his wife Dot on the reserve. The idea of the enclosure was to control and manipulate what went in (eggs or larvae of Species *X*, *Y*, and/or *Z*) and then record what came out at the end of the growing season (metamorphs of *X*, *Y*, and/or *Z*). By executing replicated experimental designs, Henry could isolate and test the competitive and predatory effects of Species *X* on *Y*, etc. Henry also used drift fences to trap amphibians as they migrated to ponds in the spring and that meant that he could stage matings in enclosures to yield the fertilized eggs he needed for his experiments. Later, I adapted his mating enclosures to conduct my thesis experiments on male-male

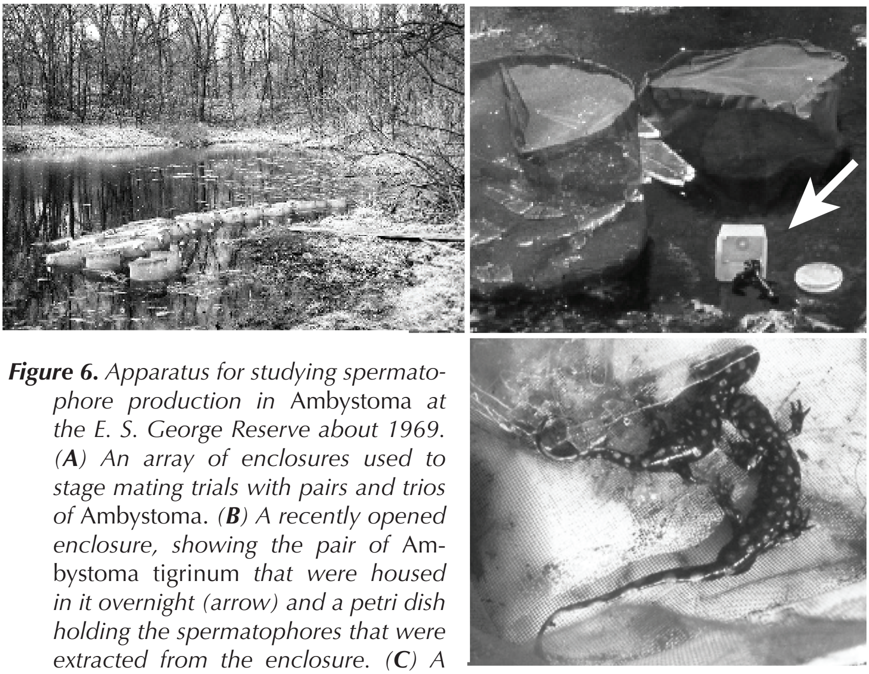

Figure 6. *Apparatus for studying spermatophore production in* Ambystoma *at the E. S. George Reserve about 1969. (**A**) An array of enclosures used to stage mating trials with pairs and trios of* Ambystoma. *(**B**) A recently opened enclosure, showing the pair of* Ambystoma tigrinum *that were housed in it overnight (arrow) and a petri dish holding the spermatophores that were extracted from the enclosure. (**C**) A male (below) and female (above)* Ambystoma tigrinum *inside an enclosure that has been removed from the pond. A few spermatophores are visible by virtue of their white, apical sperm masses. Photos by author.*

competition and sexual communication in *Ambysoma* (Figure 6).[20]

Steve Tilley was another graduate student who made a huge contribution to my doctoral research. Steve was exploring reproductive investment, one of the hot topics in the Tinkle Group, by documenting size-fecundity relationships in five species of *Desmognathus* salamanders in the Appalachians.[21] In the course of that work, Steve helped me establish the feasibility of my developing plans for a doctoral dissertation by supplying live animals at a crucial juncture. In the summer of 1967, Steve and his wife Mary returned from North Carolina with a gift for me—a sample of mature, sexually active *Plethodon shermani*, which at that time were considered to be a subspecies of *P. jordani*. I soon found that, in contrast to *Ensatina* and other west coast plethodontids, courtship in the large eastern *Plethodon* was easy to observe, photograph, and film. My plans for doctoral research began to form around those successes.

Years after graduate school, my colleagues were often surprised to learn that Arnold Kluge (Figure 3) was my doctoral advisor. Kluge's reputation is in cladistics methods, whereas mine is in sexual selection and evolutionary quantitative genetics. We were not so far apart when I approached Kluge in 1967 to see if he would sponsor doctoral research on salamander courtship. I had just spent two summers in Costa Rica and six other Middle American countries. Kluge had made several trips to Middle America when he was a graduate student of Jay Savage at the University of Southern California. More importantly, Kluge was opened-minded about my proposal and later turned out to be a responsive sounding-board for my developing plans and ideas. Kluge also had an engaging curiosity about herpetological natural history and liked to puzzle over unsolved problems and mysteries. For example, one afternoon he pulled a large photograph of a gecko out of a drawer in his desk and asked if I knew what it was. "*Eublepharis?*" I answered, referring to a large gecko from Pakistan which was common in the pet trade. "No," replied Kluge. "Years ago, someone captured this *Eublepharis*-sized gecko in the Anza Borrego Desert and brought it to Charles Shaw at the San Diego Zoo." It wasn't a *Eublepharis*. Nobody knew what it was, and no additional specimens had been seen in the years that followed. To make matters worse, the specimen had been lost. We scratched our heads and marveled at this little mystery. The mystery wasn't solved until the 1970s, when additional specimens were found in Southern California and Baja California. The new gecko was named *Anarbylus switaki*[22] but was later assigned to the genus *Coleonyx*. Mysteries aside, Kluge often had good advice, which included steering me to appropriate literature. One day he suggested George Gaylord Simpson's books,[23, 24] which I admitted I had not read. I followed his advice, but only skimmed the books and did not get hooked. Later, when I got interested in evolution in deep time, I carefully read Simpson's books and was inspired by their perspectives.[25, 26]

In the 1960s, Kluge and Steve Farris met regularly to discuss phylogenetics and the manuscripts that they were working on. One day I found them huddled around the large work table in the herp commons room that was flanked by Kluge and Walker's offices. The lively discussion between Kluge and Farris was punctuated by a new phrase that I had never heard before. "What's a patristic centroid," I asked. "Patristic centroid? You don't know what a patristic centroid is?" exclaimed Farris. "No, I have no idea what it is,", I replied. "Well there is no reason you should know," snorted Farris. "We just coined the term 5 minutes ago." In this manner, my tutoring in phylogenetics continued week after week for the next few years. This topic was not a major shtick for me, but I learned enough to incorporate the use of a Wagner network in one of my thesis chapters.

A Thesis on Salamander Courtship

I pushed forward with the idea of doing a doctoral thesis on salamander courtship, ensconced in the Herpetology Division, with Kluge looking over my shoulder. The thesis as a whole was not driven by a central question but rather by my fascination with the phenomenology of salamander courtship and my growing interest in sexual selection. Even though I lacked an overall rationale, I devised a plan in which the two parts of my thesis were organized around different issues. The first part was a detailed comparison of courtship in three species (*Plethodon jordani*, *Ambystoma maculatum*, and *A. tigrinum*) that had contrasting courtship strategies (e.g., a few spermatophores per courtship with much male investment in each versus many spermatophores, produced in rapid succession with little behavioral investment). Here the focus was on the operation of sexual selection, traditionally viewed as having two aspects—mate choice and contests between sexual rivals. I tried using information theory and Markov chains as organizing principles for this part of my thesis, but without much success. Instead, I focused on the intricate choreography of courtship which involved coordination between sexual partners.[27, 28, 29] This aspect of courtship was not a hot topic then or even now, but I later argued that it was the key to understanding long-term evolutionary stasis in salamander courtship.[30]

In the second part of my thesis, I adopted a comparative ethological perspective and tried to analyze courtship evolution across the entire salamander radiation which consists of 10 families and about 70 genera. Here, I was influenced by the work of Robert Hinde[31] and other comparative ethologists who were cataloging modes of evolution in behavioral displays. (How did one display evolve from another? What were the non-display precursors of displays?) Diving into the literature with Salthe's review[32] as a guide, I found that while something was known about courtship in about 20 genera, in many genera and species, the accounts were very brief. Furthermore, illustrations were rare, and photographs were almost nonexistent. I resolved to observe courtship in as many genera and species as possible and to make detailed descriptions illustrated with photographs and motion pictures.

Although I was excited and enthusiastic about my thesis and the immediate progress that I was able to make, my graduate student colleagues seemed lukewarm at best. I didn't seem to be tackling one of the big issues of day. Indeed, several years later when I was interviewing for a job at an elite university, a former graduate student colleague (who was now an assistant professor) took me aside and told me that I was NOT being invited because of my work on salamander courtship! I think his complaint was that I didn't have an over-arching framework to organize the themes in my work on salamander courtship. Nevertheless, when my University of Chicago colleague Russell Lande began working on a model of evolution by sexual selection,[33] I knew that his model had the potential to pull together the loose coceptual strands of my thesis work. Using Lande's model as a launching point, I later built models to organize my work with Steve Tilley on sexual isolation in *Desmognathus*,[34, 35] as well as my work with Lynne Houck on salamander pheromone and courtship evolution.[30, 36, 37]

Getting Live Animals in the Field and Through the Mail

In the late 1960s, however, I was hard at work obtaining salamanders from Europe, Asia, and North and Middle America and coaxing them to court in the laboratory in front of my movie camera. To obtain the salamanders I needed, I relied on the kindness of colleagues as well as my own fieldwork. University of Michigan Prof. George W. Nace had established an NIH-funded breeding colony of amphibians to supply embryos to developmental biologists. The manager of the Amphibian Facility, Christina Richards, loaned me key taxa (*Ambystoma mexicanum* and *Cynops pyrrhogaster*), introduced me to visiting Hiroshima scientist Toshijiro Kawamura, and put me in touch with John Taylor at Wayne State University who let me observe and film his *Pleurodeles waltl*, an Iberian and North African species. European animal dealers and Luxemborg colleague Robert Thorn sent me live *Salamandra* and *Triturus*. West Coast colleagues (David B. Wake, Edmund Brodie Jr. and Ronald Nussbaum) sent me *Bolitoglossa*, *Taricha*, and *Rhyacotriton*. Meanwhile, I launched collecting expeditions in the Appalachians (West Virginia, Virginia, North Carolina), and Ouachitas, and Ozark mountains.

Graduate student colleagues from the department and museum came along on some of these expeditions. Doug Futuyma accompanied me on my first trip to North Carolina, which had the goal of renewing my supply of *Plethodon shermani*. Much of the collecting was done at night, and that first night in North Carolina, I had a terrifying experience. Doug and I were working in a rhododendron thicket along a small stream and got separated. Realizing that we were out of contact and with no sense of direction, I called Doug's name in a loud voice but got no response. Literally guessing at the correct direction, I moved along, periodically calling to Doug, not knowing whether I was headed back to the road or deeper into the woods toward Georgia. Eventually, I heard response so faint that it did not confirm or deny my guess at direction. Luckily, the response grew loader and loader, confirming a correct guess and so, we were reunited. A total of only 60 minutes had elapsed but that was long enough to produce a huge surge of adrenalin. We struggled into Andrews, North Carolina, the next morning to get breakfast at a small café. The waitress looked us over and asked "Say, are you boys with the circus?"

Many collecting trips in the Appalachians were based out of Mountain Lake Biological Station (MLBS) in southwestern Virginia. Rudi and I took our twin daughters there in the summer of 1968, so that I could work on *Plethodon* and other local salamanders (Figure 2). James Organ and his wife Della were also at MLBS that first summer and had established a room for housing and observing salamanders in the basement of the main laboratory. Jim had done his thesis work on the demography of *Desmognathus*[38] with Nelson Hairston at UM and had published a series of papers on the courtship of plethodontid salamanders.[39, 40, 41] Jim and Della showed me the ropes. They took me to their field sites at Whitetop and Mt. Rogers and regaled me with stories of the old days. Jim said that when he first started working in and around Whitetop in the 1950s, it was routine to wear a sidearm. When you encountered another adult male, the standard greeting was "Howdy, what ya packin'?," whereupon pistols were exchanged and inspected. Jim also introduced me to plastic shoe boxes, a handy alternative to glass aquaria for housing and observing salamanders. I felt foolish for hauling 20 aquaria to MLBS that first summer, and I used plastic boxes for the rest of my career.

Kraig Adler was also working at MLBS, and he also took me under his wing. I especially remember trips we made to West Virginia in pursuit of *Aneides*, *Plethodon*, *Gyrinophilus*, and *Eurycea*. At one locality, we went into a cave with a wide entrance to look for salamanders. Shining our lights to the back of the cave we were startled to see dozens of large eyes. Then sound erupted. We pressed ourselves against the cave walls as a herd of cattle came thundering past us and out of the cave, which they had been using as a retreat from the summer heat.

One summer, Dawson graduate student Al Bennett visited MLBS, and I took him to Tawney's Cave at the base of the mountain to look for *Eurycea lucifuga*. As we walked back to our car, an old pickup truck slowed down as it approached us from the other direction. The movie *Easy Rider* had just been released and featured an unfortunate incident in a circumstance just like this (i.e., a shotgun fired out the window of a pickup in the South). As the pickup truck stopped, the driver stuck his head out the window and said "Howdy boys. Why y'all must be COMMUNISTS!" We must have had startled, horrified expressions on our faces, even though no shotgun appeared. Instead, the driver laughed and explained that he was a chemistry professor at Blacksburg. He didn't have to explain that he knew how to scare the hell out of Yankees.

Live-animal facilities on and off campus helped me launch my observational studies of courtship. At first, I used a small constant-temperature room in the new wing in the museum. I soon realized that the vibration of the metal shelves was upsetting my animals, and the room was too small for photography, much less for cinematography. Botany Professor Warren L. Wagner came to the rescue and let me use a large root room in the Matthaei Botanical Gardens, which were situated a few kilometers west of campus. I knew Wagner from summers at Mountain Lake and had complained that I needed a subterranean room in Ann Arbor like the one at MLBS. I now had all the room I needed and set up dozens of glass aquaria and plastic boxes. I kept my animals on a natural photoperiod and spent many evenings in the root room. The new wing of the museum did have a good-sized aquarium room that I used to photograph and film the courtship of aquatic salamanders. Some of these species (e.g., *Taricha*, *Notophthalmus*) would court by day, which meant that I sometimes walked through the museum during business hours, taking photographs as I went (e.g., Figures 3, 4). Recently I digitized my 16-mm movies of salamander courtship from the 1960s and 1970s. They are now available for viewing on my YouTube Channel, "Salamander Courtship."

In 1969, I made a late summer trip to Whitetop, an Appalachian peak in southwestern Virginia, accompanied by Al Bennett, Jim Collins, and Thomas Yocum. The Vietnam War was still in full swing, as well as the draft. We were all happy to put the war and our academic issues on a back burner for a long weekend. In route, we picked up groceries (which included a small watermelon and a few bottles of Three

Bears wine) and stopped at a stream to collect a few dozen crayfish to cook for dinner. After dinner we set up our tents in a clearing on Whitetop and collapsed in our sleeping bags, exhausted from the 12-hour drive. But sleep was interrupted almost immediately by a party at a nearby campfire. Suffering in silence for a few sleepless hours, we finally yelled out but were ignored. The next morning, we found the campfire abandoned and discovered that we were the only campers in the clearing. We spent that day collecting *Plethodon*, *Desmognathus*, *Eurycea*, and *Pseudotriton* for my courtship project. We returned to our campsite to find our tents pulled down and their contents strewn about. At first, we were paralyzed and outraged by the spectacle, but then one of us exclaimed "Where's Edgar?", using the pet name we had given our watermelon. We found him smashed on the road. Who were the mystery perpetrators and how dare they violate Edgar?

That night as we sat around the campfire, we were surprised when six or eight local guys walked into the fire light. Apologies were offered and introductions were made. We soon learned that the clearing was a regular meeting/drinking place. Our hosts had brought beer, but soon that was exhausted, as well as our small stock of Three Bears wine. "Have y'all ever tried white lightning?" Of course, we hadn't, so one of our hosts went on a liquor run and soon returned. Drinking continued. The main topic of discussion was the war. As first we worried that we would be scorned as draft resisters and evaders, but we soon discovered that everyone was of the same mind. The war was stupid, and no one wanted to serve in it, and especially none of us wanted to get killed in it. That night we fell asleep thinking that resistance to the war must be uniform across the country, at least for all the distance between Ann Arbor and Whitetop.

Not all my fieldwork was so far afield, some was in the immediate vicinity of Ann Arbor. Aside from the ESGR, I also worked Goss Pond near the Matthaei Botanical Gardens and a pond on Zeeb Road that been the study site used by E. L. Husting[42] in the 1950s. In the spring, these ponds were alive with breeding *Ambystoma* (*A. maculatum*, *A. tigrium*, *A. texanum*, *A. laterale*) and *Notophthalmus*. All of these became grist for my ethological mill. One night I returned to the Zeeb Road pond to find that most of the hardwoods had been cut down. I was stunned by the sacrilege. Walnut trees had towered over the pond, creating a cathedral like atmosphere, especially at night. After a while I was joined by a farmer who saw my light through his window. I asked why the trees had been cut. He said that he had promised his grandfather that he would never cut the trees, but the property taxes had gotten to be too much.

Two plethodontids were also the focus of field expeditions near Ann Arbor. One of these was *Plethodon cinereus*, which was easy to find during the fall courtship season. My other quarry was *Hemidactylium*, but it was not so easy to find in the fall. Nace graduate student Daniel Rittschoff teamed up with me on several unsuccessful trips to find *Hemidactylium*. We tried to approach the problem scientifically by studying papers by Frank Blanchard[43, 44, 45,46], but he was vague about his localities. Finally, Charles Walker mentioned that Frank's wife Frieda still lived in Ann Arbor. Maybe she knew the location of Frank's study sites. We called Frieda Blanchard and were invited over to her house. We explained our predicament, but she just shook her head. She didn't have any relevant recollections. She did, however, have a lot to tell us about her work with Frank on the inheritance of melanism in *Thamnophis sirtalis.*[47] They tried to deduce the mode of inheritance from coloration of mothers and their offspring, but what they really needed was data on the coloration of fathers as well. Frieda decided that artificial insemination might provide the needed data. She killed a male and fixed his everted hemipenis in formalin. With that reference specimen, she approached a watchmaker in town and asked him to make a facsimile out of brass. She also had him drill a hole through the brass model and attach a tube and a small rubber bulb. Using this apparatus, Frieda loaded the bulb with a sperm suspension and inseminated several females. But to no avail. None of the females ever produced litters. Dan and I were spellbound by Frieda's tale. We decided she was as one of the unsung female heroes of Michigan herpetology!

Models, Encouragement, and a Validation

Another war was being waged besides the one in Vietnam. This other war was the conceptual struggle to establish modeling as a legitimate approach in ecology and evolution. This struggle seems strange now, but in the 1960s many of the professors in the museum took a dim view of models, as well as the journals that published them (e.g., *The American Naturalist*). Tinkle once told me that models were just window dressing. Likewise, Richard Alexander was a fan of the George Williams approach[48] that featured verbal models, but he had no patience for formal models of the evolutionary process. Hairston also seemed to be in the anti-modeling camp and often leveled harsh verbal criticism of Robert MacArthur and his approach to community ecology. On the other side of the issue, a group of graduate students embraced the modeling approach while avoiding confrontation with Tinkle, Alexander, and Hairston. This group included Futuyma, Colwell, Vandermeer, Wilbur, and me, as well as a few young faculty (e.g., Stephen P. Hubbell, George F. Estabrook, and Brian A. Hazlett). Although this group never succeeded in bringing MacArthur to campus, we were able to host Chicago professors Richard C. Lewontin and Richard Levins. These two were admired for their rigorous theoretical approach to problems at the ecology-evolution interface. We also organized seminars that excluded faculty, so that we could we could tutor each other on the new theory being spun in Chicago and elsewhere. I remember sitting around in a post-seminar event for Dick Levins and marveling at the remarkable sentiments that he dropped into the conversation (e.g., "Beware of the dull hand of competence in pursuit of a narrow empiricism"; "Truth is the intersection of independent lies"). These practitioners of the modeler's art were also important consultants. When Lewontin came to town, I signed up for some time to meet with him and get his reactions to a model[49] I was working on. A little encouragement, especially from an idol, went a long way. In the coming decades, model-bashing became less and less respectable, and it became standard practice to encourage graduate students to make modeling a part of their training.

Other seminar speakers and visitors also had big impact on my outlook. I especially remember seminars by Murray Littlejohn (ethological isolation in frogs) and Richard F. Johnston (rapid evolution of house sparrows in the New World). Thomas Uzzell drifted through the Museum one day. I had read Uzzell's papers[50, 51] on triploid *Ambystoma* and we immediately discovered that we saw eye-to-eye on ambystomatid biology. Later Tom invited me to the Philadelphia Academy of Science to give a seminar. Likewise, I met David B. Wake as a graduate student, and that helped pave the way for a postdoc at the MVZ. Toward the end of my graduate career, Jeanne Altmann gave a seminar on sampling methods for observational studies of behavior. Her approach was statistical and perplexing at the time because of its complete novelty. As I walked out at the end of the seminar, a faculty member next to me remarked "Well that was a complete waste of time." I am sure Jeanne didn't hear this remark, but if she had, she would have had the last laugh because her 1974 contribution[52] became one of the most influential and highly-cited papers in behavioral biology (more than 14,000 citations in Google Scholar by September 2018).

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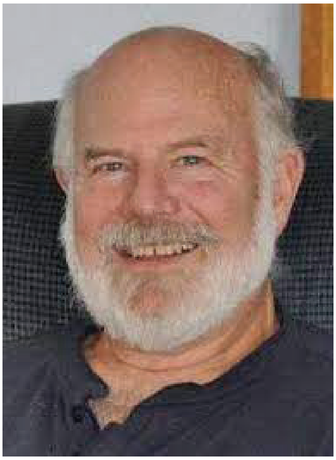

Steve received his B.A. in Zoology from the University of California – Berkeley in 1966, and his Ph.D. from the University of Michigan in 1972.

In his own words, he is "…generally interested in evolutionary biology, and especially in the evolution of phenotypic traits such as body size and sexually-dimorphic behaviors and structures. Much of my work is on theoretical aspects of phenotypic evolution, for example, the measurement of selection and the evolutionary stability of inheritance and mutational processes. My empirical work has been focused on the evolutionary ecology of garter snakes and on the evolution of sexual communication in salamanders."

CYNTHIA CAREY

Toad Research in the Colorado Rockies

1970–

I was graduate student of Bill Dawson's in Natural Sciences. Despite my never having been in the Herp Division, I appreciate the invitation to submit some remarks on my experiences at University of Michigan and to give a shout-out to all the former herp students whom I knew.

After a traumatic first year with the challenge of the Grad Exam and my first cloudy, gray, and cold Michigan winter, I decided that if I was to survive at Michigan, I needed to spend my summers doing field work elsewhere. Curt Adkisson, a Bird Division grad student, told me about the Rocky Mountain Biological Laboratory (RMBL) near Crested Butte, CO. I discovered in Robert Stebbins' book on herps of the western United States that boreal toads, *Bufo boreas,* had been studied at RMBL. I knew that the choice of a topic for a Ph.D. dissertation should be made on more consequential grounds, such as on important, unanswered, frontier-defining topics, than the need to get out of town, but it worked out. Because grad students from Harvard, Yale, Kansas, and Stanford were working at RMBL, I felt as though I benefitted from two graduate educations—one at the RMBL and the other at the Michigan. At student talks and conversations with faculty at both institutions, I heard alternate versions of "What was True." Both RMBL and Zoology at Michigan had graduate student seminars and I would say that the atmosphere at the Brownian Movement meetings was much more critical and contentious than the seminars at RMBL. However, an older grad student told me that the more critical students were toward each other's research, the better their Ph.D. research would be and the better they would enhance the reputations of Zoology graduate students overall.

When I started field research in 1970, populations of boreal toads in the mountains of Colorado above 9000 ft. were robust. By 1973, I began seeing carcasses in the field and by 1976, there was no breeding (and no, I didn't kill them all for my physiological research). I couldn't find any boreal toads anywhere I searched in the appropriate habitats in Colorado. Some toads I brought back to Michigan from the previous fall were sick; the campus vet diagnosed them as having "red leg," which was thought to be caused by a bacterium, *Aeromonas hydrophila.*

I was hired at the University of Colorado in 1976. Tenure, of course, depended on productive research, which was not possible if your study organism is extinct. So for the next 15 years, I studied birds breeding at high altitudes. For this research, I studied gas exchange of bird eggs first in the environs of RMBL, and later at altitudes up to 17,000 ft in the Peruvian Andes.

At the First World Herpetological Congress in England in 1989, I was surprised to learn that the population declines and extinctions of toads and frogs was a world-wide phenomenon. NSF hosted a symposium on possible causes of amphibian declines, including ultraviolet B-rays (UVB, acid rain, pesticides, and habitat destruction. Some proponents of these theories were quite adamant that their theory (e.g., UVB) was correct with little thought toward proving cause and effect. I presented my ideas on disease as the proximal factor, possibly with some ultimate involvement of one or more distal environmental factor(s), causing immunosuppression and increased vulnerability to pathogens.

The National Aeronautics and Space Administration (NASA) awarded a grant to the Declining Amphibian Populations Task Force (DAPTF) to determine if environmental correlates measured by satellites coincided with declines at particular localities. Ron Heyer, director of the DAPTF, called about 15 scientists to ask them to head up the project and all refused. I was the 16th recipient of the call and agreed, although I knew nothing about satellite data. I invited researchers who had been in the field during the die-offs of amphibians in their localities, including Costa Rica, Australia, U.S. (Sierras and Rockies), and the mountains of eastern Brazil. We noticed that all of these die-offs fit the same pattern—i.e., relatively high altitudes and colder areas than the surrounding environs; males died first; etc. We hired some researchers from NASA, the National Oceanic and Atmospheric Administration (NOAA), and the United States Geological Survey (USGS) to run their data sets of climatic or UVB variables for analysis of environmental correlates preceding or simultaneously with the die-offs. They found no consistent pattern among the various study sites.

NSF awarded me a small grant to host a meeting of concerned individuals about the possible role of disease in amphibian declines. At that meeting, Karen Lips and others revealed that the infectious culprit causing population declines and extinctions was a fungus, *Batrachochytrium dendrobatidis*. The scramble was then on (and continues to date) to find out: how the fungus killed amphibians; why some populations seemed immune to it; how the fungus was transmitted; what was the evolutionary history of the fungus, etc. This group has continued to work on the problem with the leadership of Jim Collins, whom some of you remember from Michigan. One hopeful sign from ongoing research is that remnants of some populations have developed immunity to the fungus and populations are growing.

While I thoroughly enjoyed my research on bird reproduction at high altitudes and survival of cold climates, I felt good about working with a highly congenial, collaborative group of scientists on a world-wide problem with serious ramifications for biodiversity.

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Born and raised in Denver, Colorado, Cynthia earned her Ph.D. from the University of Michigan in 1976 after receiving an AB and MA in Biology at Occidental College, Los Angeles, in 1969 and 1970 respectively. Since then, she has been on the faculty at the University of Colorado (now Emerita) where she received the Brewster Medal for excellence in ornithological research as well as two awards for teaching excellence. As one of the first scientists to work with the Declining Amphibian Populations Task Force, she has maintained a career-long interest in this worldwide problem.

JUSTIN D. CONGDON

Recollections of Thirty-six Years of Turtle Research on the E. S. George Reserve

1972–

My association, and that of a fellow graduate student (Laurie Vitt), with the University of Michigan as postdocs began in 1972. Both of us attended an Evolutionary Ecology class taught by Dr. Donald Tinkle, Director of the Museum of Zoology, while he was a visiting Maytag Professor at the Arizona State University. I volunteered to work on Don's lizard studies in Utah and Arizona and subsequently, was hired to continue the field work and to conduct bomb calorimetry for a study of energetics of lizards. That was when Don asked me if I would be interested in a post-doc at the UMMZ to participate in a 20-year study ("or whatever it would take") of the life histories and ecology of three species of long-lived freshwater turtles on the E. S. George Reserve (ESGR). I tried my best to look like I was considering the offer before I accepted. Working with Don Tinkle while he was director of the UMMZ and PI of the ESGR turtle research formed a big part of my perception of the UMMZ. The early hint of things to come started the morning Nancy and I arrived at the ESGR with a U-haul truck and a 1964 Peugeot station wagon in tow, we were greeted by Dick Wiltse (manager) who helped us start unloading the truck. Don showed up and announced that we had to check the turtle traps because he was leaving for the southwest to conduct his lizard studies and I needed to know where the traps were (a stickler for details). We left Nancy and Dick to finish unloading with some guilt on my part, but Don was the boss. The next morning, I headed out to check traps and found myself at an unfamiliar gate (Problem #1), I reversed course and found Southwest Swamp, canoe, and traps. After two days on the ESGR, Nancy and I were beginning to appreciate that our association with the UMMZ and the ESGR would be an adventure, but not that it would continue for more than four decades.

For the next four years, while we lived in the Hill 'n' Dale House in the center of the ESGR, I had an office (Don's lab) and met many of the scientists whom I'd known previously only through the literature. Two interactions are worthy of note. After Bill Hamilton moved to Ann Arbor from England, Don asked me to help him buy his first vehicle (a Ford van). I spent a full day involved in the altruistic behavior of finding him a vehicle interspersed with bouts of panic while teaching him to drive on the "correct" side of the road. Other notable highlights were spending four days with John Maynard Smith at the Hill 'n' Dale House on the ESGR. We spent daylight exploring, birding, and turtling and evenings talking life (e.g., he read the entire Tolkien Trilogy to his children), evolutionary biology, and now and again the life history of turtles. When he told me that he liked fishing, but had never caught a bass, we went to Sayles Lake where he caught two bass, and a northern pike. Now how fine was that?

My wife Nancy and I formed enduring friendships with the Tinkle family (Don, Margie, Donna, Randy, Steve, and Melanie), Dick and Lorie Alexander, Jerry Smith, and Ron Nussbaum that have lasted until present. Another friendship of note developed in my early years at the UMMZ with Arthur Dunham who had an unusual professor-student experience on the ESGR. While we were upgrading the Southwest Swamp grid stakes in February, Art fell through the apparently thin ice and Don went to help and also fell through the ice; I remained on thicker ice to rescue them. After Don's untimely death in February 1980, Art and I collaborated on finishing papers from Don's lizard research, and we co-authored papers on life-history topics while Art was on the faculty at the University of Pennsylvania where I spent a sabbatical in1990.

A brief history of the ESGR turtle research will help put this letter in perspective. Painted and Blanding's turtles had been studied on the ESGR by Owen Sexton (1953–1957) and Henry Wilbur (1968–1973) with a total of ~1600 Painted and Blanding's turtles marked (apparently, they were afraid of snappers). Don recognized that building on the previous studies would provide empirically robust data on their longevities and life histories. I worked full time managing the research. Despite Don's many administrative and teaching responsibilities in addition to his winding down his lizard research, he managed to be involved with the turtle project to an amazing extent. Together, we fell out of canoes, learned turtle telemetry, developed protocols for studying nesting ecology, and strangest of all, during a discussion of the possible functions of the waxy material secreted along the bridge of Snapping Turtles, we tasted it (apparently, despite the rather earthy bouquet, it was a particularly good year for flavor and not toxic). Most of all, we watched the data roll in at an exciting rate. Near the end of Don's life, he convinced NSF to let me continue the study for the remaining years on his grant and Dick Alexander stepped forward to take faculty responsibility. Don also advised me to maintain the emphasis on the nesting ecology and reproductive traits of females. I did. At the end of the study in 2007 (plus results from a follow up population survey from 2016–2018), we marked approximately 14,000 individuals, made approximately 48,000 total captures, and recorded clutch size and egg widths from 5700 x-radiographs of gravid females.

Justin Congdon *drawing blood from a Snapping Turtle ca. 2017.*

The administrative help of Robert Storer (Director of the UMMZ) during the years of transition from Don's leadership to my taking over the ESGR turtle study was certainly important to the success of the project. I was called into his office and told that Carl Gans had approached him about doing turtle studies on the ESGR, and what did I think of that. After a moment of what I am sure looked like a deer in the headlights, I answered that we were doing an intensive life history study and a second researcher, particularly one that outranked me (in military talk…"him general, me lieutenant"), would inevitably lead to problems, but I would try to accommodate if I had to (he waffled). My next interaction with Carl started off with "Well Justin, I just heard that you had me banned for life from doing research on the ESGR." I can't imagine how different the ESGR turtle research could have been without Bob's help. There were six directors of the ESGR who followed Don Tinkle (Dick Alexander, Jerry Smith, Ron Nussbaum, Earl Werner, Chris Dick and Robyn Burnham). During the same period, the turtle research was enthusiastically helped by four ESGR managers (Dick Wiltse, Jack Haynes, Jeff Bolgis, and Alex Wenner and their crews. They all were genuinely interested in what we and other researchers were doing. (They often assigned colorful nicknames to researchers, but I never found out if I had one.) When problems arose, the crews built equipment boxes at the "Turtle HQ" in the East Marsh, removed fallen trees out of roads, fixed things, pulled field vehicles out of sandy and muddy areas and sometimes out of wetlands. They also observed us and then showed us how to do things. While the manager's crew, operating at code red, repaired a failed well and later a failed drain field, they also arranged for us to use facilities at the Fresh Air Camp. It was not convenient but allowed six to eight turtle researchers to continue working through two nesting seasons.

I still find it amazing that the number of problems through decades of research on the ESGR were so few and so minor. The common theme of the directors and managers questions was, "Is there anything we can do to help?" At the University of Michigan's Star Party at Kit Peak in 2016, Nancy and I met Martha Pollack the Provost of the University; during a lull in admiring the Milky Way, other galaxies and star clusters, I offered to tell her something she probably seldom got to hear as a problem solver. After she assessed the potential threats, she indicated that I should go on. I related how well I had been treated by the UMMZ and recently by the Department of Ecology and Evolutionary Biology throughout decades of research on the ESGR. She thanked me, and then the bigger picture of the universes reclaimed our attention. Later that evening, she told me that she had thought over our conversation and realized how seldom that someone just wanted her to hear a positive story and how much she appreciated it.

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Congdon, now retired from his position as a research scientist at the University of Georgia's Savannah River Ecology Laboratory, lives in Arizona. He received his Ph.D. from Arizona State University where he researched methods to measure the reproductive efforts of lizards in the Chiricahua Mountains of southeastern Arizona. He has authored some 180 publications dealing with the physiology, life histories, and conservation of turtles—in particular, Snapping Turtles, Blanding's Turtles, Sonoran Mud Turtles, Northern Map Turtles, and Painted Turtles. His work also includes ecological studies of snakes, lizards, frogs, and fish, and the environmental effects of deposition of coal-combustion residues on aquatic ecosystems and their inhabitants.

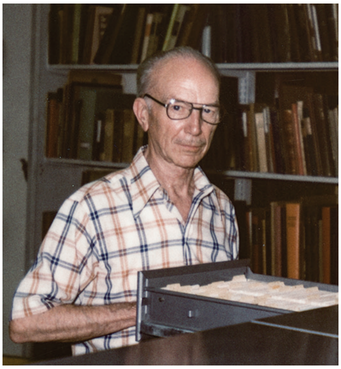
ALAN JASLOW

My Years in the Ruthven Museum

1974–

The Herp Division was so very important to me, and my memories and stories are all a blend of place, people, and knowledge. To me, the Herp Division was the Ruthven Museum—old wood, tall-ceilinged halls, with newer wings, and lots of rooms with different purposes and lots places we grad students could access. I first saw the museum exhibit halls as an elementary school student on a field trip from Northville, MI. I remember animals on the landing of the first flight of stairs—either a boa or Gila monsters—I've mixed up which lived there earlier and then later. Museums were always a place of joy for me from exhibits to collections. After moving to the D.C. area, I volunteered and hung out at the U.S. National Museum's Herpetology Division (USNM) as a junior-high and high-school student. I would take an occasional personal day (probably counted as skipping school) to come into the museum when famous herpetologists were in town for a weekday only. My mentor curators there, James Peters, and a later hire, George Zug, were both from the University of Michigan herp division. I appreciated their Michigan stories and their introductions to visiting Michigan herpetologists.

Needless to say, I was thrilled to come to the University of Michigan (UMMZ) and join the UMMZ Herp Division. I was put to work curating the turtle collection housed in tanks in the basement. I was to make sure the turtles were not rotting away, prepare a new inventory, replace tags, and rearrange some of the specimens in an updated systematic scheme. I had done this with caecilians at the USNM and later, garter snakes at UMMZ. If you followed me and had to repeat these tasks and could not imagine why such a dated classification was used or how it might have been pieced together—just remember, someone else is coming after you and doubtless will have the same questions. I loved having a job, a purpose, and learning about a group or groups about which I knew very little. I especially enjoyed the history of researchers revealed in the specimen catalogue accounts, field notes, and publications.



Charles Walker *in library of UMMZ Herp Division*

I remember having access to most parts of the museum—both collections and exhibits—although, perhaps I misremember night access to exhibits. Access to both the museum and Herp Division libraries was an incredible joy. Browsing my way through shelves and journals reading anything that caught my eye was both interesting and empowering. As mentors had told me it had been for them, I found my grad years a time to read wide-ranging literature freely. I foraged these shelves and cabinets mostly at night, which paralleled nocturnal work recording frog calls during many summers and years. I went through past collectors' field notes that were lined up on the divisional library shelves and felt part of a long chain of scholars hoping someday to place my own field notes among them.

One basement room held a few supplies and items in storage. My first summer I was told I could use Norman Hartweg's cold-weather sleeping bag. I have no idea why it was made of packed wool or cotton stuffing and heavy as all get out, as I know down has been around as long as birds. No doubt this was the only wet enduring insulation of his day. I used it under other bedding in my tent as I traveled around the state that summer surveying Gray Tree Frogs. Later it was my pallet for naps in my office in Ann Arbor and later, Chicago. I'm only sorry that the tag with Hartweg's name was lost in my travels. We grad students had access to the museum roof. One roof section had *Daphnia* cultures for one or more fish-division student-feeding projects. Another was used occasionally for drying fresh mammal material, but maybe that was just during an emergency overflow. More than a few clear summer nights, after returning from surveying frog choruses in nearby counties or when I was just too tired to head home, I hauled Dr. Hartweg's futon of a sleeping bag up to the roof to sleep. One morning as I woke at the crack of dawn, I saw another soul sitting on some sort of scaffolding on the CCL (Clarence Cook Little) roof, across the street lifting a mug in greeting.

Some fellow museum workers were steady night owls and others came and went. Night times gave me comradeship and access to some visiting scientists, as well as the crepuscular curators and students. Robert Sokal was in residence for a sabbatical term. All of the grad students had a copy of Sokal and Rohlf among their statistics books. I had a question about the appropriateness of regression assumptions as used for temperature relationships to frog-call parameters. Sokal was all about his research and the use and utilities of Path Coefficients during his sabbatical and that is all he wanted to talk about. He pushed me to use these with several ways to measure a frog's temperature that had been used as proxies for CNS and throat temperatures. It was an interesting idea and my first attempt at modeling, but not a quick success or one that yielded any better way to do quick field temperature recordings. Sokal never would answer my question about simple regression assumptions, always insisting that I had to use path coefficients for this frog work—a very focused man.

During his sabbatical residency, John Maynard Smith would sometimes seek out my company after he was done writing for the night. He was great fun and had many terrific stories. I lost his companionship when I asked him if he would sign a copy of his book—Models in Ecology,1974—an exceedingly thin and expensive hardbound book of 146 pages. In the way that one remembers the biggest bound book that you have seen, grad students often pointed to Smith's book as the most expensive and small hardbound biology book one could find. But boy was he pissed when I handed him my xerographic copy of his book to sign. I mistakenly assumed he would realize how unlikely it was that a grad student to could afford to buy his book. He never was as friendly toward me after that. In retrospect, I'm quite embarrassed by my rudeness and my lack of respect. By the way, his signature on my photocopy of Smith's book is totally illegible, but I still value it.

Murray Littlejohn from Australia visited one or more times during my graduate tenure. We spent one special night together working on our own sonographs.[1] He taught me many refined and quick tricks to use with these Kay Sonograph machines, as well as helping me to understand some of their internal works. This came in handy years later when I was able to repair and rehab a machine in Panama. It was an education beyond the instructions most students get. He was a kind, generous, and genuine human. It was eventually figured out that electric etching or burning chemically treated paper in a closed room was hazardous; so, exhaust systems were added to sound-analysis rooms around the country before we all switched to computer and digital capture.

When I started at Michigan, we were still punching code onto punch cards and hauling those cards to computer card readers across the way at a computing facility on the main campus. Later, we had dumb terminals with which to enter code and finally, near the end of my student tenure, interactive terminals with the dawn of PCs. In those early days, one's program for statistical analysis would run as per priority time and then inevitably, the output would be an error message caused by a missing comma or other character for the starting cards. Computer science grad students were assigned to help find unnoticed errors in code. It seemed to me that having a job of looking for other folks' typos was bad deal in contrast to the very engaging teaching assistant and research assistant positions that funded our graduate studies in biology and at the museum. Nevertheless, these computer science grad students, along with similar grad students staffing the statistics help pools, provided some of the most important assistance I had for my research and the eventual completion of my dissertation. I know I never thanked them enough and only ever knew one statistics student by name.

To produce figures for said dissertation, another great night activity was to head to North Campus computer center where the only graphic terminal display existed. This Tektronix 11-inch green screen monitor, in my memory, popped and screeched through its rapid linear line by line addition to plot a graph or chart, like an electronic Etch A Sketch on speed. If the plot looked OK (and in truth it was really was too small to tell), we could plot on paper with the Calcomp plotter. They'd run it with felt tip pens, most time for speed and cost savings; for publication figures, one could request printing during a special overnight period, when they set it up with India-ink pens. What you need to understand is that although the Calcomp was better than the guided-pen–stencil lettering of the Leroy system and sticky plastic tape lines, along with transfer letters and dots that were pressed onto paper, any computer assistance at that time in this task was tediously basic. We had to specify every line, length, and position. None of this "do a correlation; now let's "change the axis" of a few years later and today. Each attempt always seemed to end up with an extra millimeter line, or such, extending somewhere. I remember bonding with other nocturnal grad students over our shared curses to our wasted efforts.

There were so many wonderful fellow grad students about by night, and more during the day. The Herp Division was a large group when I arrived. I learned about office politics. I got answers to phylogenetic and statistical questions, and was introduced to many new reptiles and amphibians. I garnered many life lessons from all of these. I watched an otherwise quiet, older student work a room of scientists at a meeting; he told me about using his theater background to market himself for post-doctoral positions, which I hadn't thought of as a possibility before. I certainly tried to emulate him later in my life. Another older student helped move a resident emeritus professor out of the office we'd been assigned. Prior to the student's return from a year in the field, I had just waited politely each day to see if this was the day our elder states person would move, hah! Other students and post-docs, who conscientiously teased my younger newbie self, became steadfast supporters at many future professional meetings when our paths crossed. Those relationships mean a lot to me and have guided me in my own mentoring. Then, there were herpetological grad students not associated with UMMZ Herp Division, and students working on other organisms who were interested in the research questions and problems that we shared. There was no shortage of young, intelligent, energetic students in all sorts of areas with whom to associate.

Looking back, I realize how easily professors and curators who didn't work with me directly or with whom I hadn't had a class, welcomed me and my questions. They taught me a great deal about evolution, ploidy, sound recording and analysis, to mention only a few topics. My older self realizes how this might have been rare at other places or in other times. The years I lived in Panama certainly were a highlight of my grad school years. These experiences and the people I met there also formed who I was to be in my life. Naturally, I had many adventures in Panama, but they were separate from Michigan herpetology. I did travel with an old altimeter that was attributed to Charles Walker. This was long before GPS and before cloud-cover–free topo maps of Panama. I always set the Charles Walker Memorial Altimeter, as I called it, with a known reference as I left the Canal Zone to head to the mountains, but between the altimeter's limitations, the topo map limitations (missing mountain tops and ranges), and no doubt my limitations, it was often quite a challenge to figure out where I was, at least until better topo maps were available years later.

Those were heady years in the Herp Division, with many fond memories. Most weeks in my later life, one of those memories returns to me, and I am grateful.

Endnotes

[1] Sonographs are early mechanical analog machines that produce illustration of a tape-recorded sound's frequency versus time, electrically etching by burning special paper surfaces. I understood that this technology originated during WWII and was used analyze underwater sounds.

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PETER J. TOLSON

Graduate Study in Herpetology the Land of the Lotus Eaters

1976–

Although I came to study herpetology at Michigan by a rather circuitous route, it was one the wisest—and luckiest—decisions I made during my academic career. I actually applied to the Rackham School of Graduate Studies after the application deadline had passed. With funding secured to study protein chemistry at UCLA, I asked myself a fundamental question: Could I spend the next 5 years at a bench—away from the field and my beloved West Indian boas? The answer was "no." With encouragement from my early mentor, Albert Schwartz, I requested a meeting with Donald Tinkle, then Professor and Curator of Amphibians and Reptiles at the Museum of Zoology. I explained my plight, and somehow, magically, I was able to begin my graduate career at Michigan.

Michigan was unequaled for herpetological studies. The faculty was peerless—Arnold Kluge, Carl Gans, Donald Tinkle, William Dawson, George Nace, Ronald Nussbaum—most were at the top of their professional careers when I arrived. Visiting professors such as Richard Alexander, William Hamilton, and Wes Brown exposed us to ideas regarding behavior, speciation, altruism, and group selection that were almost unimaginable a decade before. The old paradigms of evolutionary theory were being rapidly replaced or modified. And there were always the ghosts haunting the hallways of the University of Michigan Museum of Zoology (UMMZ): Charles Walker, Larry Stuart, Nelson

Hairston, and other faculty retirees who, along with the rest of us, viewed the UMMZ as the one fixed point in the universe of our existence. The herpetological tradition of that place filled every space at the UMMZ, from the holotypes in the ranges to the photographs, books, reprints, and field logs embellished with the names of those that had gone before: Helen Thompson Gaige, Major Chapman Grant, Alexander Ruthven, Albert Schwartz, and Olive Griffith Stull.

But I believe what I valued most was (with a few exceptions) the collegial atmosphere of the UMMZ and the Department of Biological Sciences. I never found a faculty member too busy or unwilling to help with my dissertation research. I owe a great debt to Arnold Kluge, my major professor, who devised a Ph.D. program for me that married my love of biochemistry with Caribbean field work on West Indian boas that took me to each of the Greater Antilles and the two major Bahamian Banks.

The quality of graduate students in the division was so high that we learned as much from our peers as we did from course work. Not that all was sweetness and light; standards were high, and competition was fierce. Some fell beneath the wheel. The most stressful time was the brutal testing for the graduate qualifying examinations—which, appropriately, were held over Halloween weekend for my cohort. During the following week the halls of the UMMZ were either illuminated by the smiles of those that passed or darkened by the shocked expressions of those whose careers at Michigan would be terminated shortly. Even the herpetological seminars could resemble bloodbaths as the unfortunate presenter was confronted by other graduate students eager to cement what they thought was their alpha status. I'll always remember a hapless, shaking, stammering, graduate student in Professor Gans' lab making a presentation as the bull-necked *Herr Doktor Professor* sat in the rear of the room, pursing his lips and shaking his head negatively as the victim attempted to make a point. There were no "safe spaces" in the Division of Herpetology—rather a respect for critical thinking and hypotheses based on empirical evidence rather than social constructs. But we did have fun in the UMMZ (sometimes too much, apparently)![1]

The support facilities were wonderful. Library holdings were exceptional, and not only did we have the normal graduate and undergraduate stacks, but we had a Natural Science Library, the Museum Library, and individual Divisional Libraries for Herpetology and the other vertebrate divisions. In the days before the Internet at Michigan, one rarely had to go through the tedious process of interlibrary loans to obtain a needed publication. The laboratories of the Medical Sciences Buildings and the Herbarium were a few steps away. Fully equipped animal rooms in the UMMZ and the Natural Science Building facilitated large living research holdings—including my collection of more than 150 West Indian boas. In my case, the opportunity to curate such a large living collection led directly to my subsequent employment at the Toledo Zoo as a Curator.

But no student that I knew was eager to leave Michigan. We jokingly referred to it as the "Land of the Lotus Eaters." Like the sailors of the Homeric ship in The Odyssey, once having tasted the fruit of the UMMZ, few of us wanted to leave.

Now I, like Charles Walker so many years ago, am a ghost myself. But I won't have the luxury of haunting the ranges and libraries of the UMMZ. The range collections, managers, and technicians (now served by state-of-the-art infrastructure and protected by fire-suppression systems) have been transplanted to a cavernous warehouse at the outer regions, along with the vertebrate division libraries and their precious paper reprints. And now the UMMZ itself is to be re-purposed, its contents moved to a new Biological Sciences Building. In the new era of political correctness at the University, one can be certain that the stone puma guardians of the UMMZ—now recast in bronze and moved to the new Natural Sciences Building—will never again roar when a virgin passes between them.

Endnotes

[1]At one point, while working as a research assistant in the Herpetology Division Professor Kluge banished me to my office to work, because so much cutting up occurred between me, technician Susan Rhodine, and Inteflex medical student (now M.D., Ph.D.) Amy Lowechik.

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Aside from chasing the local snakes in Cleveland, Ohio, as a child, my herpetological odyssey really began in 1968, the year I was sent Guantánamo Bay, Cuba as a young Marine. I found the Cuban herpetofauna fascinating, especially the Cuban Boa. Luckily, I was introduced to Dr. Albert Schwarz, a Michigan grad and a renowned expert in West Indian herpetology. Under Al's mentorship, I realized one could actually earn a living as a herpetologist, and with his advice began planning for my future education. I left GTMO and the Marine Corps to pursue a degree in zoology at Michigan State University, before earning a doctoral degree in ecology and evolution from the University of Michigan—working with West Indian boas. After graduating, I was hired as the Curator of Amphibians and Reptiles at the Toledo Zoo. West Indian boas were my first love, and my position at the Zoo allowed me to initiate conservation programs for the endangered Virgin Islands Boa. Over the years, I was promoted to Conservation Biologist, then the Director of Conservation and Research, which allowed me to expand my research and conservation work to virtually all the Antillean forms of Epicrates (= Chilabothrus). I "retired" in 2016, but am blessed to be able to continue my boa research and conservation work under the auspices of the Toledo Zoo as Director Emeritus, Conservation and Research, and as a contractor for the U.S. Navy at Naval Station Guantánamo Bay.

LAURIE J. VITT

A Year in the Life of the UMMZ

1978–

I arrived at the Museum of Zoology at Michigan (UMMZ) in fall of 1978. I was brought in to replace Wayne Van Devender on a Department of Natural Resources grant that Don Tinkle was administering. I had spent the previous year collecting a massive amount of data on the ecology of tropical lizards in the semi-arid Caatinga of northeastern Brazil, and I was chomping at the bit to share some of those findings. At the time, lizard ecology and systematics were hot at the UMMZ, which made it a very exciting place to be (aside from the weather!).

First, the people. As you might imagine, I was humbled by the likes of Don Tinkle (who I already knew), Arnold Kluge, Ron Nussbaum, and the non-herp curators at the UMMZ, as well as some of the collection managers, graduate students, and post-docs (e.g., Justin Congdon, Art Dunham, Phil Rosen, Gary Breitenbach, and others). The often-lengthy discussions that we had over coffee in the UMMZ led to many new insights and no doubt influenced how I approached research.

The postdoc—I was essentially part of a team (first myself and Paul Feaver followed by Gary Breitenbach) that was to survey the state of Michigan and produce a report on the status of reptiles and amphibians of the state. We visited every county in the lower peninsula, and our findings likely mirrored findings from other state herp surveys: If decent habitat existed, reptiles and amphibians were there, and if decent habitat did not exist (most of the state), then herp populations were either down or gone.

Stories from the shelves—nearly everyone has stories that they tell repeatedly, and we all embellish them a little. Here are a couple of mine from those wonderful days involving Don Tinkle.

When I first returned from the field, I was excited because I had sampled every lizard species in the area over an entire year. Based just on examination of reproductive organs, I had found every known lizard life history pattern at one place and during one time period. This flew in the face of the notion that the local environment was the primary driver behind lizard life-history traits, which had been a central theme in some of Tinkle's research. He was skeptical at the time, and to this day I don't know what he thought about it, but future analyses would show that in fact, I was right. The local environment impacts lizard life-history traits, but at a much lower level than previously thought. With the advent of molecular systematics, it became possible to examine lizard life histories in an historical framework. Work that I was involved in many years later with Daniel Mesquita, Renato Faria, Guarino Colli, Gabriel Costa, Tais Costa, Donald Shepard, and Eric Pianka revealed that history (phylogeny), as well as climatic variables, contributed significantly to patterns of lizard life histories.

I had also discovered a lizard that seemed to have the most advanced placenta known in reptiles. My boxes of samples that had been sent to me by Paulo Vanzolini, were sitting in the basement (where my office was) unopened. I cornered Don, and when I told him that I had found a lizard with an apparent placenta similar to that of mammals—his response was "no you didn't." I was taken aback, for the second time (actually the third, but the second at UMMZ). I responded by saying, I'll go get the samples and you can look at them. I headed to the basement, unpacked about 5000 vials with either stomachs or reproductive organs, and finally located those for the skink *Brasiliscincus heathi.* We dug out a dissecting scope and began examining the samples. When he finally realized what I had, he told me that I should write an article and send it to *Science.* I got together with Dan Blackburn and Carol Beuchat and we did submit the paper to *Science.* Although it received great reviews, Science didn't take it and we published it in *PNAS.* What I discovered was that as dogmatic as Don could be, a few data would easily change his mind.

It was at Michigan that I came to realize how important history was in the evolution of life-history traits, based largely on my own data. I really didn't know how to show that at the time, but I could make a pretty good story based on lizard foraging mode. I would learn later that foraging mode itself was simply a trait carried through time from temporally distant ancestors. I love to be proven wrong, especially by myself! The natural history data were clear, but it would require use of well supported phylogenies to sort out the impact of history in a meaningful way. Based on other ecological data, I also knew that within-clade variation of ecological traits seemed to be much less that between clade variation. Many years later, in collaboration with Eric Pianka, we were able to demonstrate key differences in diets between lizard clades.

Working in the field in Michigan had some classic moments as well. Gary Breitenbach and I had camped along a lake and set out a bunch of turtle traps as part of our survey. When we checked the traps in the morning, we had several nice crappie (*Pomoxis* sp., North American freshwater fish), in addition to turtles. We didn't realize it, but it was opening day of crappie season. As we were frying our breakfast of crappie, a couple of fishermen came by, and apparently assumed that we were fishermen. They had thus far caught no fish. When they asked us what we used for bait, we pulled a few small lures out of our lure box (we did do some fishing while in the field) and told the fishermen that we had caught the fish using those lures. They went happily on their way excited to try lures. After breakfast, we quickly packed up our gear and moved on.

Because I was involved in a survey of Michigan's reptiles and amphibians, I had many memorable experiences while in the field. In a very nice peat bog, while searching for four-toed salamanders, I dug through some roots under a fallen log. Unbeknown to me, the roots were poison ivy, and I am highly allergic. That night I slept in my Ford van with my arm across my chest. In the morning I had a nearly perfect arm and hand print of blisters across my chest, as well as blisters in several other places. We were close to

Michigan State University so I went to their infirmary and asked if I could see a physician. I was told that my University of Michigan health insurance was not good at Michigan State and that I would have to see a private physician. I then lifted my shirt up exposing my youthful abs, but also exposing the arm and hand print of blisters across my chest. The attendant immediately called a doctor in, and I went back with him and received some sort of corticosteroid injection. I blistered and itched for several more days, but in the end, I learned something very important—viz., poison ivy roots are just as bad as leaves when it comes to producing rashes.

Like most herpetologists, I have always been fascinated with snakes, and I am pretty good at finding them. In southern Michigan, we lifted a large piece of plywood and found a beautiful female Fox Snake with a clutch of 12 eggs. We took the eggs back to the lab, hatched them, took a bunch of measurements, and then took the snakes back where we had found them. This was my one and only experience with fox snakes. For a hard-core "snaker," it was a thrill to see these.

Five-lined Skink (Plestiodon fasciatus) *brooding eggs. This is one of the species surveyed in Michigan. Photo by Laurie Vitt.*

I also had the opportunity to see and collect some Five-lined Skinks in Michigan. Surprisingly, they were most common along railroad tracks and in places that had been logged in the distant past, leaving large rotting trunks of hardwood trees. Everything about these colorful lizards fascinated me, and years later, William Cooper, Jr., and I would initiate a series of studies on the three North American members of the five-lined skink clade. Our studies included everything from chemical communication and social behavior, to nest attendance and tail loss.

My stay at Michigan was rather brief, only about 11 months. I had been offered a post-doc at the University of Georgia and would be moving on. Nevertheless, my time at the UMMZ was right at the top of my list of best experiences. The halls of the UMMZ bustled with excitement about research. Those "guys in the museum" were considered attack dogs during seminars and I did witness some of that. In defense of the UMMZ, I have to say that questions raised by the likes of Kluge, Tinkle, and Dunham (the pit bulls) at seminars were always right on, and often generated thorough discussion of whatever the topic might be. I had the opportunity to experience some of the most critical people in herpetology at the time. The single most revealing observation that came out of that 11 months at the UMMZ was the importance of basic research—i.e., learning what animals do and why they do it. Much basic research at the time was driven by our apparent innate desire to understand a little piece of the world that we live in, not by whether or not funding was available.

About the Author

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Laurie Vitt's research focuses on the evolutionary history of ecological traits of reptiles, particularly squamates. He is a Curator and George Lynn Cross Professor Emeritus from the Sam Noble Museum and the University of Oklahoma. He was a research ecologist at the Savannah River Ecology Lab; in 1982, he joined the faculty at UCLA and in 1990, he accepted a position at the Sam Noble Museum. Laurie's research accomplishments include more than 270 peer-reviewed publications and 7 books, including three editions of a herpetology textbook. Vitt currently lives in Tubac, Arizona, and continues with collaborative research.

LLEWELLYN D. "LOU" DENSMORE, III

Memories of Herpetology at the University of Michigan 1982–1985

1982– I was fortunate enough to be a postdoc in the lab of Wesley M. Brown between 1982 and 1985. I had worked on the biochemical and immunological systematics of crocodylians at the LSU Medical School under Herbert C. Dessauer. Herb was the first major research scientist to use techniques such as starch gel electrophoresis and microcomplement fixation to study the population genetics and systematics of reptiles. Because of the training I received in Dessauer's lab, I was able to get my "foot in the door" after having presented a seminar to Wes's group in the spring of 1982, and I joined the lab in the fall of that year. The lab already had two excellent postdocs Rodney Honeycutt and Steve Sherwood, as well as Jim Hixson, a Ph.D. student. I have never witnessed or been privy to better discussions about biology in general and specifically a number of aspects of molecular evolutionary biology than during those first 12–18 months. Furthermore, Jeff Palmer was just down the hall. At that time, the Division of Biological Sciences boasted one of the top three animal mitochondrial DNA evolution labs and probably the top plant organellar DNA evolution lab in the world about two floors and 50 meters apart.

Wes and his major herpetological collaborator, John W. Wright from the L. A. County Museum (and a Research Associate at the UM Museum of Natural History), were studying racerunners/whiptails from the southwestern United States (then in the genus *Cnemidophorus*, now *Aspidocelis*). John supplied the herpetological knowledge and collected the lizards that we studied and Wes the molecular expertise, primarily using mitochondrial DNA fragment and mapping analysis. I came into a rather interesting situation, as there had been little progress from the previous postdoc on a fair number of "cnemi" samples collected on an NSF grant to Wes and John. The grant dealt with investigating the diploid and triploid parthenogenetic lizard populations that were first recognized as almost completely female by Richard Zweifel of the American Museum of Natural History.

John Wright was one of the most interesting people whom I have ever known. A classically trained herpetologist who was without doubt one of the two or three most knowledgeable "cnemidophrologists"(his word not mine) in the world, he would often send us collected samples that were double-blind. Although he respected Wes and considered him a good scientist, he was very covetous of the information about his samples and often did not want to reveal to us collection localities or even in some cases, the identities of presumptive species or subspecies samples that he had collected. These animals were extremely difficult to identify in the hand, and while John sent them to us alive, we were unable to identify many of them morphologically (especially without locality data, which would have made it much easier). That made it considerably more complicated and difficult for me (and more than once frustrated Wes). We were trying to determine which bisexual species were contributing maternal genomes to either diploid or triploid parthenogens and then ascertain if we could differentiate among the several all-female clones. My genetic analysis of the samples was made more difficult by size variability within and between the mitochondrial DNAs that eventually was found to be in the D-loop. Ultimately, we were able to publish the first example of mitochondrial heteroplasmy in any wild population of vertebrates,[1] as well as several other papers on the relationships among a number of the diploid and triploid populations.

This work (and Wes's reputation) attracted interest from several other people, including a young Australian doctoral student who was working on parthenogenesis in the gekko *Heteronotia.* His name was Craig Moritz. Wes had served as a reviewer on the 1983 Science paper that Craig had submitted and the two began communicating. Within a year or so, Craig had joined the lab as another postdoc and it was obvious from the outset that he was a very special researcher. I have never known another scientist who could work on so many different projects so efficiently. He is one of those people whom you only rarely have the pleasure of knowing, much less working with, and I was fortunate enough to get to work with him on several projects and publications. Craig did have his "less than Moritzean moments" however—I well remember the time that he flew from Australia, landed in California, and then realized he did not have his wallet or passport. Even though a day or two later he had his documents, we worked him over pretty well for that situation, clearly one that could not possibly happen in today's world. Frankly, I still do not know how he managed to get on the plane even during the decade of 80s (some of us "decided" that it was probably because his wife Fiona was the daughter of a high- ranking Australian politician).

Another postdoc who joined the lab while I was in Ann Arbor, Thomas Dowling was a fish biologist that had come from Wayne State. Tom turned out to be an excellent population geneticist, my claim to fame with him was to teach him as many of the techniques as I could. He had an excellent career at Arizona State University and returned to Wayne State about 4 years ago.

During my tenure at UM, I got to know Carl Gans, one of the great functional morphologists of the 20th Century. I got along very well with Carl, who was known to be a bit short and gruff with people. In fact, one of my first experiences with Wes (and Carl) was outside of the symposium of the 25th annual meeting of SSAR in Raleigh. I had already been invited by Wes and had accepted to be a post-doc in the Brown lab, but I was also one of a couple of graduate students invited to speak at the symposium. During a coffee break, Wes was outside and I think he may have been smoking a marijuana cigarette because when Carl walked by, Wes asked: "Carl, do you want a toke?" Carl answered with his typical Teutonic brevity "NO" and walked on I was behind them when this exchange took place and had to stifle my laughter with my arm. You must remember, at this time Wes was still not tenured. It is a credit to Carl that even if he did not want a "toke" he did not hold that against Wes (or his lab). In fact, Carl had a tuatara that he had kept in captivity for years, which was beginning to show signs of aging. Because of the animal's state, Carl was given authority by the IUCN and Endangered Species office to sacrifice, dissect and then prepare the tuatara. I was actually invited to attend and help in that event (which was one of the coolest things that I was able to do while at UM), and I collected organ tissue and isolated such a significant amount of mitochondrial DNA to supply researchers studying tuataras around the world for the next decade.

Outside of the Division, there were of course a number of people who worked on herps in the UM Museum, most importantly Arnold Kluge and his students. For me, the person who was most memorable is Fred Kraus. I met Fred in the Laboratory of Molecular Systematics that Wes started in about 1984 and he is one of the brightest and most unusual people whom I have ever known. There are many stories that I could tell about Fred, most of which could not be published in a work such as this. Fred worked on the brown tree snake that was driving Guam rails to extinction, primarily working out of the University of Hawaii Museum. I believe that he is now back at UM. Suffice it to say, that Fred was the primary instigator in a number of fascinating "events" that occurred during my tenure at UM, including one in which he put a fully articulated skeleton in Arnold's chair in his museum office for Halloween. When the door to Arnold's office opened, the movement of the door caused the skeleton to wave. We never knew what Arnold said about this gag. Fred was also the catalyst for a large butcher paper sign on Wes's garage door that "welcomed" me back to give a seminar and work on some manuscripts after I was at Texas Tech. I still have the sign, of course autographed by Wes, Jim Hixson, Craig Moritz and many other folks; it is still not suitable for public scrutiny.

Another Museum person whom I was fortunate to meet when he was a graduate student was Jacques Gauthier. Although we approached the topic from quite different perspectives and analysis, Jacques and I both worked on crocodyliforms. Jacques was interested in cladistic analyses of vertebrate evolution and my future was going to be involved with the molecular systematics and population genetics of the extant crocodilians. Jacques has gone on to a great career and remains one of the premier vertebrate paleontologists in the world.

Although I did not get to know him well, Ronald Nussbaum was at one time one the world's authorities on caecilian biology and in fact, I saw my first caecilian in his lab.

My time at the University of Michigan from 1982–1985 was critical to my development as a research scientist and a mentor. I met many important scientists who either visited our lab or gave seminars in the Division. Most importantly, I was fortunate to be able to work with Wes. Although an Assistant Professor when I arrived, it was clear that Wes had an incredibly keen mind and was an outstanding writer of both grants and papers. He also emphasized the idea of quality over quantity in publications, echoing the advice that Herb Dessauer had given me. That philosophy has stayed with me throughout my career at Texas Tech and I hope that I have passed it on to the 18 Ph.D. (and 14 MS) students that I have graduated.

Ultimately and for those of us that knew him, Wes did it his way, retiring in 2001 to the eastern shore of Virginia. In 2015, he moved to Gamboa, Panamá, where he continues to live today. His impact on the discipline of molecular systematics and evolution in the 1980s and 1990s cannot be overstated. He was one of the initial research mentors who produced a generation of scientists who have had major influences on vertebrate evolutionary biology in general and particularly on herpetology by applying the most modern techniques of the period.

Endnote

[1]Densmore, L. D., J. W. Wright, and W. M. Brown. 1985. Length variation and heteroplasmy are frequent in mitochondrial DNA from parthenogenetic and bisexual lizards (genus *Cnemidophorus*). Genetics 110 (4): 689–707.

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Lou's lab pursues studies of vertebrate molecular systematics, population genetics, ecology, and molecular toxicology. His vertebrates of choice are crocodylians. After studying the phylogeogeaphy of of the American crocodile, he is working on dietary and spatial ecology and species distribution models for crocodiles and caimans in Central and South America, heavy metal concentrations in crocodylians, and parasites in alligators.

KYLE SUMMERS

Toxic Jewels: Poison Frogs of the Rainforest

1984–

My fascination with amphibians and reptiles has always seemed to me to be "innate," appearing without any encouragement and minimal opportunity for observation. (I grew up in New York City.) I did not have the opportunity to see many amphibians or reptiles in the wild until I traveled to Central America as an 11-year-old. As a child, I did not envision myself as a biologist, and so did not think of herps in a career context. But when I did decide to pursue biology as an undergraduate (after several years of "wandering in the wilderness" with no firm idea of what I wanted to do for the rest of my life), I became captivated with the prospect of studying my favorite organisms as part of my career path. I recall spending most of my time on desert field trips in my mammalogy class at the University of California at Santa Cruz (UCSC), where herpetology was not offered, searching for lizards and snakes. Fortunately, the major professor was a tolerant and flexible fellow. Eventually, I chose to do my honors research project at UCSC on lizards. In fact, I chose to work on the population genetics of *Uta stansburiana* on the Channel Islands and nearby mainland in Southern California. However, I remained ignorant of the seminal contributions of Donald Tinkle (former curator in the Division of Herpetology at Michigan) to the study of the life history of this fascinating lizard, and of course knew nothing of the evolutionary treasure trove this species would become in the capable hands of one Barry Sinervo! My advisor at UCSC was Robert L. Trivers, one of the great minds working on the evolution of behavior, and he instilled in me an enduring fascination with evolution and animal behavior. He encouraged my pursuit of graduate research in this area and given the diverse and fascinating reproductive strategies of frogs, this got me thinking about possible projects focused on anuran life history and reproductive behavior.

When I finished my degree at UCSC in 1984, I applied to graduate school at the University of Michigan with the encouragement of my friend (and fellow UCSC undergraduate) Richard Connor, who studies dolphins and had gone to Michigan the year before to work with Richard D. Alexander in zoology and Richard Wrangham in anthropology. Richard Connor currently is a professor at the University of Massachusetts in Dartmouth. Fun fact: were it not for some fortuitous encounters with marine mammals, Richard might have become a herpetologist. He showed me one his earliest written documents (from age 6) in which he expounded "When I grow up, I want to be a herpurtologist [sic], so I can study about animals"! Following in Richard's footsteps, I moved on to the Division of Biological Sciences (later to become the Department of Biology) at the University of Michigan in the fall of 1984, where I made my home at the Museum of Zoology, under the tutelage of Professor Arnold Kluge, Curator of Herpetology. Kluge was well known for his work on the systematics of reptiles, although as he was usually the first to point out, this is not actually a real group. One of his favorite stories was that when his friend and colleague William Fink (in ichthyology) interviewed for a job, he asked Kluge what he worked on—"reptiles" replied Kluge. "How do you know?" quipped Fink. A bold joke for an interview, but one that earned Kluge's respect, along with a hearty laugh.

The University of Michigan and the Museum of Zoology were a revelation to me. The graduate students in the department and museum were so serious and so accomplished that it was both inspiring and intimidating. My cohort was small but included Michael Nachman (director of the Museum of Vertebrate Zoology at UC–Berkeley), Eileen Lacey (professor in the MVZ at UC–Berkeley), and Richard Prum (professor and former chair of the department at Yale University), among others. Walking the halls one could not help but run into brilliant students who would go on to stellar careers, such as Trevor Price (University of Chicago), Bernard Crespi (Simon Fraser University), Beverly Strassman (University of Michigan), Steven Frank (UC

–Irvine), Marlene Zuk (University of Minnesota) and Geoffrey Hill (Auburn University).

The more senior graduate students in herpetology when I arrived, especially Fred Kraus (Bishop Museum, Hawaii; University of Michigan) and Peter Ducey (SUNY at Cortland), were patient and kind to me in spite of my naiveté, for which I am grateful. Fred was a fierce proponent of cladistics, in the mold of Kluge, whereas Peter was an expert in all things salamander, working with Ron Nussbaum, another curator in the Herpetology Division. I came into the department at about the same time as Mark Wilkinson (a curator at the British Natural History Museum), who worked with Nussbaum on caecilians. We shared an office for a while, and I remember on several occasions coming into the office late at night to find Mark perched over a dissection tray, carefully dissecting what looked like a worm but was, in fact, a caecilian. I credit Mark with instilling in me an appreciation of these fascinating beasts and have been fortunate to find them in the field in the tropics on several occasions. Mark's work on these curious creatures made a splash when he published a *Nature* paper illustrating how mother caecilians provide maternal care by allowing their offspring to eat their skin—now that is motherly devotion!

While Arnold Kluge was best known as a systematist (and specifically, a devoted cladist), he also had a soft spot in his heart for frog behavior. In fact, he had worked extensively with Richard Howard (now retired from Purdue University) on bullfrog reproductive strategies and had also written a monumental monograph on his research on the reproductive behavior of Gladiator Frogs in Panama. He was happy to take on a student with an interest in frog behavior, although I suspect he viewed me and my research as something of a "pet project," as opposed to the serious business of reconstructing phylogenetic relationships. Being in the lab was highly educational for me because it gave me the chance to become familiar with the various methods used to reconstruct phylogenetic relationships, not to mention the intense controversies surrounding these methods. It is well known that Kluge played a central role in these controversies as a vigorous (some might say too vigorous) proponent of cladistic methods, and I often heard extensive critiques of alternate methods, such as numerical taxonomy and maximum likelihood. These experiences may have colored my early perceptions of appropriate phylogenetic methods, although I later came to appreciate the methods typically employed in statistical phylogenetics (e.g., maximum likelihood and Bayesian inference) and have used them extensively in my research. When (later in my career) I came into contact with leaders in the field of statistical phylogenetics (e.g., Joseph Felsenstein, David Swofford), there was often a moment of awkward silence after I revealed the identity of my major advisor, although this usually dissipated quickly. Although I am not a systematist by trade, I have watched the "taxonomy wars" from afar, and my impression is that the cladists have in large part lost the argument with the statistical phylogeneticists (having previously defeated the numerical taxonomists), although I realize that "pockets of resistance" remain (especially at the American Museum of Natural History). I view this as an intriguing episode in the history of science, and of course I am not the only one to see it that way—I refer interested readers to David Hull's fascinating book *Science as a Process.*[1]

At the museum, I also became associated with Richard Alexander's group. Alexander was fascinated with both non-human animal and human behavior, and attracted a large group of brilliant students, postdocs, and faculty from across the university to his orbit. My association with this group provided a stimulating forum for discussion of many aspects of evolutionary ecology and behavior and was instrumental in the development of my thesis proposal, and indeed, of the course of my career and focus of my research interests ever since.


Dendrobates auratus.

After considering various options, I eventually settled on a project on the reproductive strategies of *Dendrobates auratus,* the Green and Black Poison Dart Frog. My undergraduate advisor, the aforementioned Robert Trivers, had cited this species as a possible example of sex role reversal in his classic 1972 paper[2] on parental investment and sexual selection. Fieldwork by Kentwood Wells (from the University of Connecticut) in Panama had yielded results consistent with this hypothesis, but the work was not conclusive, and much remained to be done. I applied for a fellowship from the Smithsonian

Tropical Research Institute and was fortunate to receive support to travel to Panama and carry out research on this species.

In the summer of 1985, I flew to Panama for the first time. It was not my first time in Central America; as an 11-year-old, I had traveled first to Costa Rica with my mother, and then later in the same summer, to Guatemala with my father. Those trips may well have influenced me vis-à-vis my fascination with tropical biology in general and tropical herpetofauna in particular. My mother and I journeyed to a remote house in the north, near Puerto Viejo de Sarapiqui, and near the site of the La Selva Biological Station. I was immediately fascinated by the diverse life forms that were visible as we cruised upriver to the house in a motorized dugout canoe and then walked through the rainforest. I remember being enthralled as I watched a tarantula hawk (a spider wasp) paralyzing a tarantula and dragging it to her burrow. This was only the first of many fascinating encounters with wildlife there. We were fortunate to be able to visit the La Selva Station and walk the grounds, which was an amazing experience. I specifically recall seeing a tiny, bright red frog with dark blue legs hop out from behind a huge tree buttress—my first encounter with a Neotropical poison frog (which as the reader may guess, was a Strawberry Poison Frog, *Oophaga pumilio*). I was thrilled to see this gorgeous little living jewel—little did I know that many years later I would study this very family of frogs for my thesis research, and this very species as a postdoc.[3] After this trip, I went on another with an elderly acquaintance of my mother (my mother stayed in San Jose, the capital city) to Tortugero, famous as a breeding site for sea turtles. After an 8-hour journey along a canal in a motorized dugout, we arrived at the field station. Much to my elderly guardian's dismay, I immediately went out to explore the forest. ("Come back or you'll be dead before dinner!" was her parting shot.) In short order, I found a rather large (for an 11-year-old) *Boa constrictor* (about 6 ft long). I grabbed it behind the head (having heard somewhere that this was the thing to do) and brought it back into to station to show my prize to my guardian. Unfortunately, I lost my grip and the snake fell to the floor, then quickly slithered out of sight into a crack in the wall before I could recapture it. Not knowing what to do, I went to find the field station manager. I found him fairly quickly, but before I could explain the situation, we were startled by piercing screams coming from my guardian's room. We raced there, at which point she bolted out of the room, her face ashen, saying that she had been attacked by a giant snake! The station manager calmly went into the room and captured the snake, after which I explained what had happened. He was amused, but my guardian was not, and I doubt she ever forgave me. That night we went out to see the sea turtles laying their eggs on the beach—another amazing sight that I will never forget. After returning from Tortugero, my mother flew home and I flew to Guatemala City to meet my father, who was traveling in a VW van with his partner at the time. Our travels in Guatemala were amazing, but from a herpetological perspective the highlight was a trip we took to Tikal in the province of Petén. This is an extensive series of Mayan ruins rising from the middle of the jungle. We hiked through the rainforest and overgrown ruins for several days and saw a stunning variety of wildlife, from mysterious trapdoor spiders to noisy and smelly herds of peccaries, and from raucous troops of monkeys to gaudy treefrogs. By the time I returned home, the forests of Central America were firmly fixed in my mind as a paradise of nature, home to an unrivaled menagerie of amphibians and reptiles.

And so, when I arrived in Panama, I was not entirely unfamiliar with the tropics or Latin America. Nevertheless, it was a thrilling experience to see Panama and meet the scientists working there. The Smithsonian Tropical Research Institute (STRI) is a tropical biologist's dream. Supported by the Smithsonian Institution, and hence the U.S. Government, STRI has amazing facilities located a short drive from large tracts of pristine rainforest. In the case of Barro Colorado Island, the facilities are actually in pristine rainforest! After arriving in Panama, I soon met my mentor-away-from-home, Stanley Rand. Dr. Rand, the only herpetologist among the staff scientists at STRI, was a legendary figure in tropical herpetology. He had wide ranging interests, from anoles to iguanas, and from Red-eyed Tree Frogs to Tungara Frogs. Of course, he was particularly well known for his work on Tungara Frogs in collaboration with Michael Ryan. Together, they carried out a multitude of experiments over multiple decades that have become an iconic example of research on the evolution of communication in the context of the trade off between sexual selection and predation. Although Rand passed away in 2005, Ryan has continued the work, and has trained a cadre of tropical biologists who have further expanded research on this fascinating system (and others). Much of this work has been done in Gamboa, a town at the confluence of the Chagres River and the Panama Canal, originally created to house workers employed by the dredging division of the Canal Commission.

My interactions with Stan Rand were inspiring and helpful—he was always upbeat and engaging, with a wry sense of humor and an infectious enthusiasm for tropical herpetology. He and his wife, Pat, had lived in the tropics for many decades by the time I got there, and knew the herpetofauna of the forests around Gamboa better than anyone. I was also fortunate that when I arrived, Kentwood Wells and his student, Josh Schwartz, were in Gamboa, working on mate choice in *Dendrosophus ebraccata.* They generously let me observe their mate-choice experiments, which were a wonderful introduction to the key role of opportunism in tropical biology. They set up these experiments in the middle of the living room of their apartment in Gamboa, with the female frog placed strategically in the middle of the floor (under a paper cup with a string glued to the top), and the speakers broadcasting different calls carefully placed on either side of the living room. This impressed upon me the value of using what is locally available to design and carry out experiments in the field, an approach that has served me well in a number of remote field sites.

Angel Falls *in the Guyana Highlands of Venezuela.*

After consulting with Wells and Rand, I decided to pursue my research on Taboga Island, off the Pacific coast near the entrance to the Panama Canal. Wells had visited the island years previously and had seen dense populations of this species of poison frog on the forested slopes of this small, mountainous island. STRI arranged housing for me on the

A ***ferrocarril,*** *or "bus on tracks" in Ecuador.*

island and I began my work. I ended up working on Taboga Island during three long (4-month) field seasons, which yielded a treasure trove of behavioral and ecological data and came to comprise the bulk of my thesis. My observations and experiments were designed to test the sex-role-reversal hypothesis, but I found that the reproductive strategies of males and females in this species were better explained by the sexual conflict hypothesis,[4] which was just becoming recognized as important explanation for reproductive strategies in a variety of taxa.[5]

After conducting fieldwork in Panama for several years, I decided to undertake comparative research on two related species of poison frogs, *Dendrobates leucomelas* in Venezuela and *Dendrobates histrionicus* (now *Oophaga sylvatica*) in Ecuador. In Venezuela, I worked in the hills around Guri (a large hydroelectric station) and in the Guyana Highlands near Auyan-Tepui, one of the largest tepuis (table-top mountains) in the region, and home to Angel Falls, the highest waterfall in the world. I was fortunate to make contact with a British biologist (Steven Gorzula), who had been living in Venezuela for years and worked for the electric company (EDELCA) conducting surveys of the herpetofauna in various parts of the country. He kindly put me up in his house during my several-month stay and gave me invaluable assistance and advice on my project. My research on *Dendrobates leucomelas* (the Yellow-banded Poison Frog) revealed parental and mating strategies that were remarkably similar to those of *Dendrobates auratus,* which supported my arguments concerning the role of sexual conflict.

I next went to Ecuador to study a species with the opposite pattern of parental care (*Oophaga sylvatica* [formerly *Dendrobates histrionica*]). This species lives on the lush, forested slopes of the western side of the country, and my assistant (Michael Barry) and I chose to work in the forest near the small town of San Lorenzo on the coast. San Lorenzo is an Afro-Ecuadorian community built by descendants of Africans brought to work on the coast. When we worked there, the town could only be reached by the *ferrocarril,* a single car train or a kind of "bus on tracks." We lived in the coastal town and each day hiked several miles into the forest to work on *O. sylvatica* (the Little Devil Poison Frog). This species has female parental care and provided a fascinating contrast with the other two species.[6] The area was highly diverse, and we found many different species of amphibians and reptiles while working in the forest. One day we came across a beautiful, large (6-foot) *Boa constrictor.* I grabbed the snake behind the head, but then we realized we had neglected to bring a camera that day. Michael begged me to wait while he ran back to town to get a camera, and so I spent an hour or so waiting for him to return, which he finally did in time to take some pictures.

I planned to work in Panama in my final field season, but my plans were disrupted by the increasing tensions between the Panamanian dictator, Manuel Noriega, and the U.S. Government under President George H. W. Bush. After *Time* magazine published a cover picture of the vice presidential candidate for the opposition being beaten with an iron bar by some of Noriega's thugs, tensions between the U.S. and Panama became so intense that STRI advised researchers from the U.S. to go elsewhere for the time being. Hence, I ended up going to Corcovado National Park in Costa Rica for my last field season. This turned out to be an amazing experience because Corcovado Park has an incredibly diverse range of wildlife that is remarkably accessible. I could study four different species—*Phyllobates vittatus, Dendrobates granuliferus* (currently *Oophaga granulifera*), *Colostethus talamancae,* and *C. nubicola.* This research yielded interesting results[7] but involved some risks. One of my field sites had the highest density of Fer-de-lances (*Bothops asper*) I have ever seen. The frogs often lived in small arroyos, where a Fer-de-lance could easily hide among the tangled roots covering the arroyo banks, and this resulted in some nervous scan-sampling. In fact, the famous ecologist Roy Caldwell had been bitten (in the shoulder!) in Corcovado several years before. There were also killer bees swarming through the canopy, large crocodiles in the rivers, and large sharks along the coast and in the brackish waters where the rivers meet the ocean. Sizable herds of large white-lipped peccaries patrolled the pathways, and the males would loudly clack their tusk-like teeth at anyone with whom they came into contact. Jaguars, in turn, would hunt the peccaries. In fact, both jaguars and pumas were relatively common (for big cats) in the park. Yet in spite of the various forms of dangerous wildlife, my only real problem came from handling a small frog.

While most poison frogs have a variety of different alkaloid toxins in their skin, members of the genus *Phyllobates* have batrachotoxin, one of the most toxic alkaloids known to humankind. The species I was working with, *P. vittatus,* only has small amounts of this toxin in its skin, but nevertheless it is highly potent. I carelessly handled a frog without gloves one day, and without noticing that I had a cut on my hand. Afterward, the cut began to throb and hurt. Rather than dissipating, the pain began, to work its way up my wrist and then my arm (over a period of several days), and coincidentally I started to feel very sick—dizzy, nauseous and lethargic. After several days, I hitched a ride with some tourists on a single engine plane back to San Jose (the capital city in Costa Rica) and went to the hospital for tests. They told me they did not find any signs of poison, but that I did have amoebic dysentery. I think the hospital personnel were quite perplexed when I let out a sigh of relief upon learning that my symptoms were associated with amoebic dysentery!

After finishing my degree at Michigan in 1990, I was fortunate to receive two postdoctoral fellowships (a NATO NSF and a STRI postdoctoral fellowship) and was even more fortunate to be able to take them back-to-back. My experience at Michigan, with years of fieldwork under my belt, prepared me well to pursue a career as a tropical evolutionary biologist, and I have been working in South and Central America ever since. Of course, I am in no way unusual in this regard—the Museum of Zoology was chock full of world travelers, going to far-flung regions to study all manner of species in their native habitats.

In 1996, I took a position as an evolutionary biologist at East Carolina University in North Carolina. My students and I have continued to work in South and Central America since then, although for the last 18 years or so, we have concentrated on research in Peru, which is ground zero for poison frog diversity. Speaking of diversity, I have tried to support a diverse array of students at both the graduate and undergraduate levels. For example, I took Lonnie Gonsalves, an African American who had never been out of North Carolina, with me to Peru as a field assistant in 2000. This experience inspired Gonsalves to pursue a career in ecology; he completed a doctoral thesis at Elizabeth State University and is currently employed as a fisheries biologist by the National Oceanic and Atmospheric Administration. I have also been lucky to encounter and work with some remarkable Peruvian scientists, such as Pablo Venegas, Karen Sui Ting, Andy Barboza and Thomas Valqui of the Center for Ornithology and Biodiversity in Lima, and Victor Morales of Ricardo Palma University. It is difficult for Peruvians to pursue careers in herpetology, given the constraints on support faced at many levels. I am particularly proud that I have been able to help one very promising Peruvian achieve his dream of becoming an evolutionary biologist. Rudolf von May first worked with me between his undergraduate work in Peru and his graduate work in the states on a project on the reproductive strategies of *Ranitomeya biolat* (a bamboo-breeding species) in southern Amazonian Peru that was funded (in part) by a grant from the National Geographic Society.[8] I was privileged to be an external member on his thesis committee when he attended Florida International University, and I have followed his career with pleasure as he has accumulated an excellent research and publication record while successfully pursuing postdoctoral fellowships at the Museum of Vertebrate Zoology of the University of California at Berkeley (working with Craig Moritz), and then at the University of Michigan Museum of Zoology(!) working with Dan Rabosky.[9]

Endnotes

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[9] Rudi currently is an assistant professor at California State University Channel Islands.

About the Author

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Kyle Summers completed his undergraduate degree in 1984 at the University of California at Santa Cruz and his Ph.D. at the University of Michigan in 1990. He was a postdoctoral researcher at the Smithsonian Tropical Research Institute, Queen's University, Cambridge University, and the University of California at Davis before accepting a position at East Carolina University in Greenville, North Carolina in 1996. Currently he is a full professor in the Department of Biology. He has broad interests in evolutionary biology, particularly evolutionary ecology and molecular evolutionary genetics, especially in amphibians. Most of his field and laboratory research has focused on poison frogs in the family Dendrobatidae, a group of toxic frogs in Central and South America. These frogs vary in diet, coloration and toxicity, making them excellent subjects for research on aposematism and mimicry. The reproductive strategies of these frogs are also interesting, involving territoriality, intra- and inter-sexual conflict, complex courtship, mate choice, extensive parental care by one or both sexes, trophic egg-feeding and larval cannibalism. The wide spectrum of variation in life histories across the poison frog family make this group an excellent system for comparative studies. Dr. Summers also does research on human health and disease, using data from medical and genomic databases in combination with statistical methods from molecular evolutionary genetics.

MARK WILKINSON

Michigan, Herpetology, and I

1985 —

I spent 4½-years in the late 1980s as a graduate student at the University of Michigan. My stay was interrupted by a year spent back in London completing a Master's in History and Philosophy of Science and Mathematics to satisfy my cognate requirements for the Michigan Ph.D. Program in the then Department of Ecology and Evolutionary Biology (DEEB). The following is an account of some of my recollections of how I came to be in Michigan, what the experience was like, and what it meant to me.

Because my father was in the submarine service, I was born and raised in Portsmouth, on the south coast of England, which is both the home of the British Navy and an area with substantial natural diversity and beauty. Growing up, I spent considerable time outside, bird watching, beach combing, and developing my interests in, and knowledge of, natural history. I don't recall why I developed an early and strong affinity for reptiles and amphibians, given the paucity of the UK's herpetofauna. Nevertheless, by the time I was 14 years old, my avid reading of herpetological texts had piqued my interest in caecilians, and I was frustrated at being unable to learn much about these mysterious tropical amphibians. In retrospect, it is probably fair to say that I became obsessed with caecilians, going so far as to arrange a loan of Taylor's 1968 taxonomic monograph, *The Caecilians of the World,* from the British Library and transcribing substantial portions of its more than 800 pages. My friends in the Portsmouth

Aquarist Society knew about my interest and in 1978, I received a surprise telephone call from Steve Crabtree, a leading member of the society's Herpetology Section, alerting me that he had just seen an aquatic caecilian in a local pet store. It was a Saturday and after sufficient pestering, my parents drove me to store and gave me the princely sum of £10 to purchase said caecilian. This was a lot of money for my modest parents and suggests that they considered my preoccupation to be a healthy one. The caecilian died a year and a half later. I preserved it and donated it to what was then the British Museum (Natural History) where it remains to this day. My observations on this specimen were published in 1980; this improved my CV and helped me secure a place to read Zoology at New College, Oxford. Throughout my undergraduate studies, I knew that what I really wanted to do was research on caecilians and it was this desire that led me to Michigan.

Of the few authorities on caecilians, I was most impressed by the exemplary works of Ronald A. Nussbaum of the University of Michigan on caecilian systematics and evolution. In my final year at Oxford, I wrote to Professor Nussbaum seeking his advice on what might be a worthwhile and tractable research project for graduate studies. Once, again, I was surprised by another phone call, this one from Ron, who suggested that I should try to enroll at Michigan to work under his supervision. With his help and promise to keep a place open for me until I could complete the required GRE examination, that is what I did.

It is probably worth mentioning that the American education system was, at that time, different in many important respects from that with which I was familiar in the UK. Completion of the GRE was the least profound of these differences, and I did not become aware of the full force of the more important ones until I was in Ann Arbor. In the UK in the 1980s, tertiary education was essentially free. I had not paid for my undergraduate tuition and had received a stipend to cover my living costs. I cannot lessen the importance of this. Along with many others of my age, I was the first generation in my family to receive a university education. With the transition from under- to postgraduate, I would be eligible for 3 more years of funding and a more substantial funding to cover my living costs. Most Ph.D. students devoted all their time to research, while perhaps supplementing their perfectly adequate stipends and improving their CVs with a modicum of teaching; consequently, most finished their Ph.D.'s in fewer than 4 years. I understood that at the University of Michigan I would be paid by the

University for teaching and that would provide the funds for my education and living expenses. (I clearly remember my father's incredulity that I was going to be paid for teaching when I had no experience!) But I was quite unprepared for the financial struggles ahead. I was also unprepared for the substantial academic differences. In the UK, virtually the sole requirement for the award of a doctorate was the production of sufficiently meritorious dissertation of original research, and graduate students set about this task from day one. Imagine my surprise then when I discovered that a thesis was only a part of the requirements for a Ph.D. Additionally, I would have to accumulate (and pay for) more than 60 credits, mostly by taking courses. The Ph.D. I hoped to earn would have an unanticipated financial cost. I took umbrage at this, protesting to those who would listen, that even Darwin's Origin would not have gotten him a Ph.D. from Michigan. (In retrospect, I realize that the well-heeled Darwin could have afforded it, but Wallace would have struggled!)

At my first meeting with academic staff, I sat down with Phil Myers to learn that, despite 8 years of French at school, I was "deficient" in college-level foreign language and that I would have to take courses to fulfill this and other requirements. Taking more courses so soon after completing my finals at Oxford was anathema to me and I found ways to avoid it as far as possible. I opted out of my French classes and satisfied the requirement by passing an exam. I enrolled in scarcely any traditional courses, opting instead to earn credits through independent study, mostly with Ron Nussbaum, who seemed happy enough with my plans. Independent study was where the fun was to be had.

It took a few weeks before Ron and I knew each other sufficiently well to be comfortable. I later learned that he had a reputation for being somewhat reclusive; for example, he did not attend the Ichs and Herps (ASIH) meetings. "Why go to meetings when you could be doing fieldwork?" he would ask. His influence must have been profound—more than 30 years later, I still have never attended an ASIH meeting and I would rather be doing fieldwork. Once acquainted with Ron, I found myself in my element. I wanted nothing more than to learn about caecilians, and here I was learning from the master. I should not speak for Ron, but I think that he also got a big kick out of having someone around who shared his fascination for caecilians. I remember in our first telephone conversation, he told me that I was the first student who had expressed a sincere interest in caecilians in his 15 years of as a major professor.

Michigan proved to be a wonderland for me. A first-class University with all the associated social and academic vibrancy, it was sufficiently diverse to include a foreigner such as myself. (Biology's International Society was great for newcomers.) There was a great local music and art scene where I got to see many fine local bands and more famous artists (including Buddy Guy and J. J. Cale) whom I never would have seen in the UK. More importantly, I was embedded in an academic unit devoted to herpetology, something that did not exist in the UK outside of the British Museum. The Herpetology Division of the UMMZ had an impressive, diverse, well-organized, and accessible specimen collection, a marvelous library with reprints, transparencies, and a wall of doctoral theses, a decent prep lab, two curators (Ron Nussbaum and Arnold Kluge), a collections manager (Bob Kessey), a secretary (Susan Morseau), and some incumbent graduate students (Pete Ducey, Fred Kraus, and Kyle Summers). As if that was not enough, the herpetology community also included staff in the Biology Department and the Natural Resources Department. There was Carl Gans, the former Head of Department, George Nace, Earl Werner, and Wes Brown. I don't recall exactly when they arrived, but several postdocs, including David Carrier, Craig Moritz, Jacques Gauthier, and Tom Jones, and visiting Academics (Yang Datong, and fellow Brit Ian Swingland) came and went. My dear departed friend Sheng-Hai Wu was in my cohort and subsequently, newer grad students Russ Burke, Joe Newsome, and Brad Moon also added to the critical mass and diversity of expertise of this academic community, as did Greg Schneider when he became the collection manager and started to take the Division's organization to the next level. I have fond memories of the lunchtime social and discussion meetings that took place for a while at the Brown Jug. We'd take over a back room and someone would present a paper for discussion. I think I kicked off the series while still a newbie with a discussion of Felsenstein's now classic 1985 *American Naturalist* paper "Phylogenies and the Comparative Method." I probably failed to appreciate how important the paper was, perhaps having already been well-primed in the topic by Mark Ridley's "The Explanation of Organic Diversity" (a bit like Felsenstein without the Brownian motion).

There were other great facilities too. On the ground floor of the "new wing" (1960 addition to the Museums building), there was the

DNA lab and the dark room where I spent so much time developing several hundred X-ray plates. On the fourth floor, there were labs set aside for maintenance and study of live animals. Here, Pete Ducey had a room full of salamanders, each lovingly housed in a plastic shoe box, on moist unbleached paper towels with toilet-paper roll homes. Next door, Ron had a room full of caecilians, housed in large aquaria filled with soil. The collection kept growing during my time in Ann Arbor, bolstered by his collecting on trips to Seychelles, Ecuador, São Tomé, and China, and eventually needed more dedicated support to maintain in good order. Jim O'Reilly, whom I had taught in Comparative Anatomy, ably stepped up to the plate and did a great job of taking care of the caecilians. Another undergraduate, Mike Pfrender, also got hooked by caecilians and accompanied Ron to Seychelles and São Tomé. On the fourth-floor animal rooms, I started a project with Dan York, a TA in Bill Dawson's physiology course. We set up a chamber in which we could vary the ratio of oxygen and nitrogen to see what impact this had on the throat movements of caecilians, which seemed to be of two kinds, small-scale fluttering that we thought was "sniffing" and less frequent series of deep throat expansions that ventilated the lungs. We had some results, but this was one of numerous projects from which the results are unpublished.

From left: ***Mike Pfrender, Mark Wilkinson,*** *and* ***Jim O'Reilly*** *with a live* Caecilia *collected by Ron Nussbaum in Ecuador.*

Also on the fourth floor, there was a lab I used for histology work. Despite the fume hood, my memories of it are infused with excessive inhalation of xylene, and panicky moments when I realized I really had to stop and get some fresh air. I had some previous experience with histology from my undergraduate honors research project on the morphology of the anuran pelvic girdle, but I sought the help of Norm Kemp. Norm was an old timer—unpretentious, gentleman naturalist, whose office had an air of a paraffin waxworks and who helped me get started with embedding, sectioning, and staining samples. I also spent some time sectioning the brain of a *Typhlonectes* with Thomas Schilling, a fellow TA in Comparative Anatomy, and student in Glenn Northcutt's lab. Further afield within the University, I was able to investigate caecilian teeth using the scanning electron microscope (SEM) in the Geology Department. And, I attempted to examine the cranial morphology of the giant lungless caecilian, *Atretochoana eiselti*, with a CT scan at the medical school, however, the resolution was poor.

Pete Ducey was assigned as my "Big Sib"—a pairing program designed to make life easier for newbies. Mostly, that is exactly what Pete did. However, on one occasion he nearly got me into big trouble. At some point I had qualifying exams covering a scholarly literature review (caecilian taxonomy), an oral exam that I don't really recall, and my first research seminar (on mite pockets in lizards). Immediately after concluding the seminar (about 11 am), Pete and Bob Kessey took me to Rick's American Cafe (of all the bars in all the world) and plied me

From left: ***Simon Maddock, David Gower, Keith Pecor, Greg Schneider, Gary Casper, Tom Beauvais,*** *and* ***Mark Wilkinson*** *at Grizzly Peak Brewing Company in Ann Arbor on November 11, 2011.*

with strong liquor and the only proper cigar I ever smoked. Unlike Bill Clinton, I couldn't stop myself from inhaling and by the time we left, I was in no state to teach the lab for Carl Gans' Comparative Anatomy lab that afternoon. I turned up there only to ask the other TAs to cover for me before leaving to sleep it off. The next day, as I walked along the ground floor of the Biology Department, I saw Carl up ahead, I was in immediate fear of his possible reaction to my unauthorized absence. I knew there was no way Carl would not know the truth because he always turned up to the labs, and at this point I knew Carl much more from his somewhat fearsome reputation than for who he really was. I probably visibly cringed as he approached, only for him to break into a disarming smile, hold out his hand and quietly say "I hear you passed your qualification exams, congratulations." As well as holding him in the highest regard as a scientist, from that day I always enjoyed being in Carl's company. I fondly remember his treating his teaching assistants to unlimited "garbage" pizza while we stayed up to the small hours marking the practical and theory papers from the midterms and final exams until the job was done. Whereas Pete Ducey only occasionally led me astray, the other senior graduate student in the Division, Fred Kraus was more of a serial offender. I don't really remember how it happened, but Fred and I hit it off, mostly in association with ritualistic and, occasionally excessive, consumption of port, mostly in his office. Fred is a hugely knowledgeable, plain-speaking, opinionated, and committed scientist, and I took a lot of pleasure in his company and the many wide-ranging conversations and discussions we had. It's always a great pleasure when we get to catch up.

In addition to Herpetology, Michigan was a center of development and application of phylogenetics, a rapidly advancing field with much exciting controversy, which proved to be really important to me. There were leading figures in phylogenetics, Arnold Kluge of course, and Bill Fink, in the Museum of Zoology, and Dan Fischer and Phil Gingerich in the Museum of Palaeontology, all of whom were influential in one way or another. However, my biggest influence was the late George Estabrook in the University Herbarium. George made excellent use of mathematics to clarify and explain emerging concepts in phylogenetics and I found his papers (and those of his former UM student, Chris Meacham) particularly clear and helpful. So, I sought him out. A one-credit independent study with him consisted of George giving me a floppy disc with a Turbo Pascal compiler, a recommendation for an introductory textbook on Pascal programming, and the instruction to go away and teach myself how to represent phylogenetic trees with pointers. My programming skills remain basic but have been sufficient to allow me to have made headway with some of the theoretical work, that, since Michigan, has competed with caecilians, for my attention. Much later, together with Mike Frohlich, George was to name a measure "Wilkinson Support." The measure is not much used, but I remain flattered by this "salute" from a much-missed personal hero.

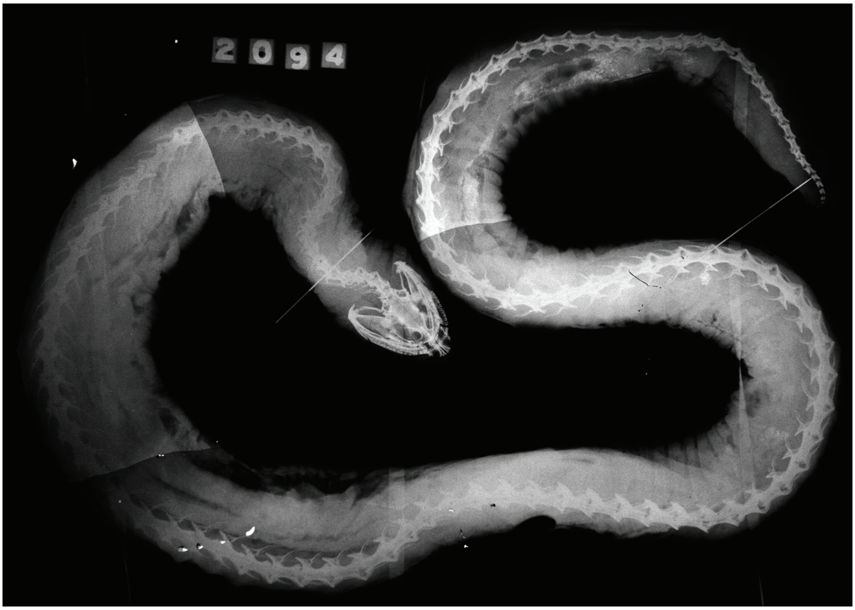
There were other graduate students and faculty whom I remember well for their camaraderie and contributions to exciting scientific and political discussions. Among faculty, Gerry Smith and Jack Burch stood out for their friendliness, and I was also a big fan of Barry O'Connor and Dick Alexander. Among graduate students, I always enjoyed chatting with Randy Hoeh, Tim Pierce, Brian Dyer, and with Rajiv Modi in Julian Adams' lab in the Biology Department. I regularly socialized (snooker at the Union, and beer and science at Ashley's) with James Cresswell. Though I knew them less well, I also enjoyed substantial interactions with Doug Begle, Michael Nachman, Rick Prum, and Bernie Crespi, and appreciated not being invisible to these impressive individuals. Apologies to the many others I rubbed shoulders with that I have not mentioned here.

One person who stands out for their importance to me in Michigan, is the late Sheng-Hai Wu. We arrived in Michigan at the same time, were accommodated in (and played soccer for) the same dormitory, taught together in Introductory Biology and Comparative Anatomy, talked loads about science and life, and were generally there for each other. On one occasion, a large group of us was invited to Carl Gans' house and were treated to a home-prepared feast, good company, and conversation. I recall feeling somewhat uneasy as the conversation veered towards matters of personal hygiene and cultural differences therein. I tried to use humor to defuse the unfavorable comparison of Europeans with Americans "When I grew up, my mother ensured I had a bath once a week, whether I needed it or not." As my feeble defense was failing, Sheng-Hai Wu came to my rescue. "In some places in China, a person has only three baths," he interjected "once when they are born, once when they marry, and once when they die." I came up for air and broke the brief silence that followed "it seems to me that between the extremes of America and China, we Europeans have got it about right!" I'm very thankful that Michigan brought our paths together.

Of course, my most intense interactions were with Ron Nussbaum.

As my mentor, Ron generously shared his knowledge and had a profound effect upon my development as a caecilian biologist. Beyond that, I was truly amazed at Ron's general knowledge of natural history and his deep understanding of evolutionary biology. We spent innumerable hours together because I used the high-quality binocular microscope in his office for much of my detailed dissection work. I sat at that scope while Ron, no more than a couple of meters away, was at his computer doing his myriad professorial tasks. Ron once told me toward the end of my time in Ann Arbor, of a recent dream in which he had been castigated by then museum director Bill Dawson for no longer doing sufficient hands-on research, to which Ron's defense had been something like, "But now I have Mark Wilkinson doing that for me." The graduate students' freedom from professorial duties had indeed seen me outstrip Ron in the amount of time I had for hands-on research (though he remained no slouch) in which Ron was keenly interested, fully debriefed, and consistently challenging on what I thought I might have discovered. Early in my time in Michigan, I described my first new species with Ron, and set about publishing some of my taxonomic work on caecilians separately. I worked closely with Ron on two big projects. The first arose in response to reviewers' comments on our species descriptions—why we were not using the revised caecilian classification of Lescure et al. published in 1986? The reviews made us realize that we could not simply ignore the work, because as ill-founded as it seemed, it presented a serious obstacle to progress in the field. We set about a critical review of caecilian classification and phylogeny in which we attempted to expose the flaws in several recent works and proposed a conservative classification that we thought appropriate to the rudimentary level of knowledge of caecilian biodiversity. More than any of my works in Michigan, this authoritative work helped establish me as a leading caecilian researcher. Combined with the cut and thrust of critical discussion that existed at the University of Michigan, especially in the Museum of Zoology, this exercise helped to instill a long-held belief, that scientific errors, factual or interpretative, should not be politely ignored, but rather, should be exposed and eliminated, lest they mislead future workers and impede the progress of science and the growth of knowledge. That individual scientists might be upset, embarrassed, or aggrieved that their work (not them) has attracted criticism is simply irrelevant.

The second major project initiated in Michigan, but only completed after I had left, was the discovery, description, and interpretation of



Radiograph of the holotype of **Atretochoana eiselti.** *Pins indicate the position of the vent and the end of the nuchal collars*

the evolution of a giant (and the only) lungless caecilian now known as *Atretochoana eiselti.* I could write an entire chapter on this extended episode, which included numerous eureka moments, but I want to mention just one. I had already discovered that this caecilian was lungless, having been granted permission to open the coelom of the holotype, and at that time, the only known specimen, and I had X-rayed it and set about counting its vertebrae from the radiograph. I started counting from the tail end and when I got to the head my jaw dropped, the radiograph revealed a cranial morphology quite unlike that of any other caecilian. I still remember the excitement and the adrenaline and, hormonally emboldened, I rushed out of my office and knocked on Ron's office door. Rather than offering any pleasantries, I entered and issued a command "come with me!"—not how you usually talk to your supervisor! As we walked down the hall to my office, Ron turned to me and said, "This better be good." I didn't reply; I knew that it was. I sat Ron down at the light table with a magnifier positioned over the head of the caecilian on the radiograph, and I asked, "What is that?" "It's a snake," came the reply. Of course, Ron knew that it wasn't a snake, but his answer reflected that the skull of this caecilian was snakelike. I'm not sure how to spell it but I think Ron's second comment was "Oskeewahwah." Our shared excitement was intoxicating and unforgettable.

I started teaching at Michigan immediately, despite having no prior experience. Like most newbies, I taught labs for Introductory Biology. At an age of 22, I was younger than many of my students and I noticed a distinct change in formality once the students realized this. I confess that I found the teaching assistant workload substantial and attending all the lectures a bit painful. In the UK, my contemporaries were enjoying 8-week terms and full-time research, whereas in Michigan, getting through a 16-week semester was tough for the uninitiated. Subsequently, I taught Comparative Anatomy, a required course for pre-meds that was not marked on a curve, and had the important role of winnowing those seemingly not fitted to keeping us all fit and healthy. I had a couple of stints as the Herp Division's Research Assistant, helping Greg Schneider with curatorial tasks that (with the exception the re-spiriting of the stinky turtle-tank collection in the poorly ventilated basement store) were both interesting and enjoyable. My strongest teaching memories were from being the resident TA in the Biology Study Center. The center was an innovative teaching resource developed by Lewis Kleinsmith, and available to students of any biology course. It had some textbooks, a suite of computers with practice tests for the Intro Biology courses, and most importantly, a TA was always on hand to help answer any questions. All introductory biology TAs had to staff the center for 6 hours a week (2 shifts), and one TA ran the center in the evenings, 5 days a week from 6 to either 9 or 10 pm. I landed that job twice. Most of the time I was alone, but as exams approached, the demand increased and peaked just before the exams; lines of students stretched down the hall, each student awaiting personal tutoring. During the quiet periods, I completed some major tasks, including translating important texts and drafting my parts of a review of caecilian classification that Ron and I published. When it was busy, there was scarcely time to breathe, and it was challenging to field such diverse questions and to find ways to explain to a diversity of students, but the experience was fantastic and formative.

One year, I taught several weeks of Ron Nussbaum's Herpetology course, which freed him up for some fieldwork in Seychelles. This was a valuable first experience at lecturing, but best of all, I could participate in the class field trip to the Smoky Mountains in North Carolina. Sheng-Hai Wu was the TA, and I think that the undergraduates included Jim O'Reilly and Mike Pfrender. I hadn't had much opportunity to travel outside of Ann Arbor, and this was a highlight—spectacular natural beauty and so many salamanders. It was the only time I ever spent in the field with Ron. The first and only time I've seen Hellbenders was when we paused on the drive back to Ann Arbor to wade into an icy river and work in teams at lifting and feeling under large slabs of submerged rocks. I remember being quite unable to cope with the cold. (I am better suited to fieldwork in the tropics.) I remember Ron wading in his jeans and cowboy boots. As I recall, he emptied the boots and put them back on before driving soaked through, all the way home.

In contrast to my academic work and social life, I struggled financially in Michigan. Throughout my time in Ann Arbor, I had sustained a relationship with my partner from back home, Jo, and her young daughter Chloe. But, after years of a long-distance relationship, she was perfectly reasonable in asking that either I come back to the UK or arrange for her and Chloe to come and live with me in Ann Arbor. We attempted the latter, but in the absence of a full tuition waver, my graduate student stipend proved insufficient to support myself, and my family. Six months after they had joined me in Ann Arbor, we all turned tail and returned to the UK to begin a new chapter in our lives.

I left Michigan without a formal degree, but profoundly changed by my experience. I was privileged to study in Michigan when its herpetological community was so impressively strong and diverse, to be exposed to so many excellent scientists and inquiring minds, to have the scientific collections at my disposal, and to be a part of and contribute in my own small way to the academic excellence. I left Michigan a reasonably experienced teacher, phylogeneticist, computer user, and emerging expert on caecilians with a network of professional colleagues and the beginnings of a reputation for my scholarly works. I remember seeing myself listed in the first volume of the *Contributions to the History of Herpetology,* edited by Kraig Adler, with my pride at having "made it" mixed with chagrin that I was apparently American. I'd like to take the belated opportunity to set that straight. I am in fact an earthling, a human being, a scientist, and a citizen of the world. Michigan played no small part in making me the last two of these. I also left Michigan with many projects under way, some of which were completed, and carried with me lasting friendships and, as writing this reminds me, so many good memories. I have returned many times, and hope to again, to visit the collection, and to catch up with dear friends and colleagues and just to keep an eye on the place.

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Mark read Zoology at Oxford, did graduate studies on caecilian amphibians at the University of Michigan Museum of Zoology, a Master's in the History and Philosophy of Science and Mathematics at King's College, London, and a Ph.D. in phylogenetic inference in the Geology Department of the University of Bristol.

After a Postdoc in Molecular Systematics at the Natural History Museum (NHM) London, Mark was the Lecturer in Taxonomy at the University of Glasgow and then Lecturer in Biological Sciences at the University of Bristol before becoming Associate Keeper (Deputy Head) of Zoology at the NHM. In 2004, he obtained an Individual Merit Promotion allowing him to concentrate on research. This was renewed in 2009, 2014 and 2019. At the NHM Mark served as Head of the Vertebrates Division until 2016, and as Interim Head of Life Sciences in 2019-2020. He holds honorary professorial positions at University College London, the University of Nottingham and the Vrije Universiteit Brussel.

Wilkinson's research is divided between his primary interests in the theory and methods of phylogenetic and other evolutionary inference and the biology of caecilian amphibians (Gymnophiona). He likes to think of himself as "Her Majesty's caecilian collector."

GREGORY SCHNEIDER

Collection Management in the Age of Information Technology

1986–

I began work as the Collections Manager for the University of Michigan Museum of Zoology, Division of Reptiles and Amphibians in January 1986. Of course, I knew wherever I went after completing my Master's research with Sam Sweet at the University of California–Santa Barbara (UCSB), the weather would probably be worse (Figure 1). But I was excited to start work at a top-notch university with a long and glorious history of herpe-

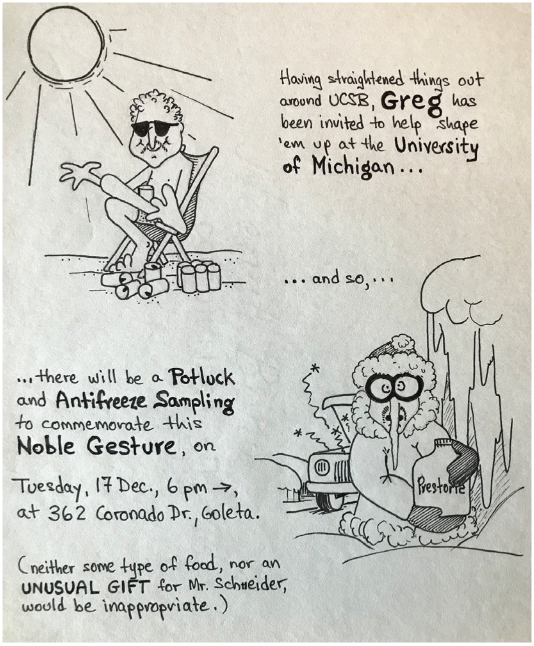

***Figure 1.** Invitation and artwork courtesy of Samuel S. Sweet.*

tological research and to manage the second largest research collection of preserved amphibians and reptiles in the world. (The U.S. National Museum–Smithsonian Institution has the largest.) The curators at that time, Arnold Kluge and Ron Nussbaum, were my direct supervisors at the museum. I was welcomed by all, including Arnold's post-doc Jacques Gauthier, and Herp Division graduate students: Fred Kraus, Mark Wilkinson, Pete Ducey, Kyle Summers, and Sheng-hai Wu. Other herpetologists with whom I initially interacted regularly included Craig Moritz, working with Wes Brown in our molecular systematics lab, and Carl Gans in the Department of Biology. Sam Sweet had apprised me of the "dynamics" of herpetology at Michigan, yet I felt I was well qualified to make the move. I had had quite a lot of experience working in all aspects in the UCSB Vertebrate Museum, done a fair amount of field work for my Master's research on geographic variation in southern California rattlesnakes, *Crotalus viridis*, and had some experience manipulating large datasets on a mainframe computer for multivariate statistical analyses. I think my computer experience may have been one of the most important assets involved in the hiring decision.

There certainly is a multitude of topics and approaches that could be presented in an essay of this nature regarding the history, growth, diversity, maintenance, and stewardship of the UMMZ herpetology collections for nearly three and half decades. Some of particular interest might be about the people and politics (faculty, students, visitors, etc.), the research cycles (cladistics, molecular genetics, functional morphology and morphometrics, ecology and niche modeling), the field work and expeditions and the collections, specimen preparation and auxiliary collections (osteology both dry and cleared-and-stained, frozen tissues, radiographs, histology, and imaging of all types including CT Scan), or the physical plant including several moves and renovations as well as building new facilities—the Research Museums Center (RMC) and the Biological Sciences Building (BSB). But, one of the most significant, game-changing chapters in the history of the UMMZ Division of Reptiles and Amphibians has been computerization and digitization and the emergence of the age of information. With that in mind, I would like to focus on the evolution of computerization and digitization in our collection spanning a time period of more than three decades. This has been an extremely important time for natural history collections, and one of exceedingly rapid technological change.

I think it is an extremely important era of our history to document, and a perspective that may be of interest to a variety of age groups. While computers did not necessarily completely change the way we do business, digitization revolutionized the way we think about our natural history museum collections, transitioning from research projects on archives of vouchers, to a much more dynamic, integrative approach to specimen-based scientific inquiry.

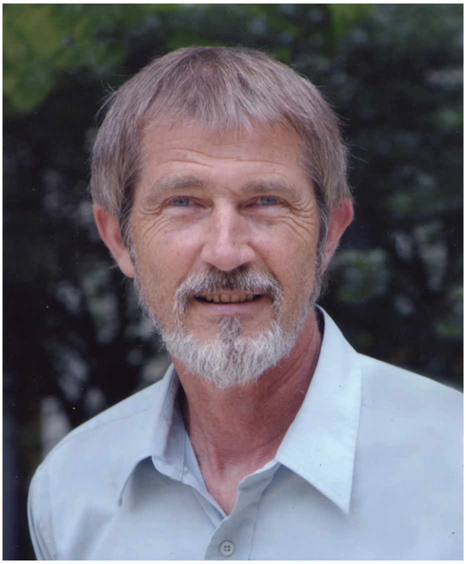

Figure 2. George Estabrook, *a specialist in the diversity and evolution of economic plants and a pioneer in applying quantitative techniques to taxonomy and other facets of the life sciences. He used statistics, information theory, and the theory of lattices to resolve phylogenetic relationships and analyze rates of evolution and speciation.*

The University of Michigan Herpetology collection was one of the first large museum collections to computerize its main catalogue. The process began as a pilot project in 1975 with National Science Foundation support. The hand-written catalogue ledgers of specimen records were entered on keypunch cards solely by Kerri Hyrns, who completed the task in 1978. NSF sponsored a workshop here in 1977 (more than 40 years ago!) to showcase our Electronic Data Processing (EDP) system using the TAXIR (Taximetrics Information Retrieval) system. TAXIR was developed by mathematician and botanist, George Estabrook (Figure 2) and Bob Brill at University of Colorado–Boulder. They both brought it to Michigan in the early 1970s and developed it at the Michigan Computing Center (although TAXIR also evolved independently at UC Berkeley and Washington State University). TAXIR was deployed at several dozen sites here running on the Michigan Terminal System (MTS). It was likely the first database to use bitwise storage. The discussion topics in the 1977 workshop included: "community needs" and whether EDP fulfills them; "interest"; "standardization"; "legal and ethical problems"; and "what EDP projects would be most beneficial to the community."

Two major conclusions emerged from the discussions: (1) A primary role of museum collections is to make information associated with the contents of collections available to users; and (2) EDP is an economical and quick way to make these data available. Interestingly, we are still discussing the same topics today, but on a much grander scale.

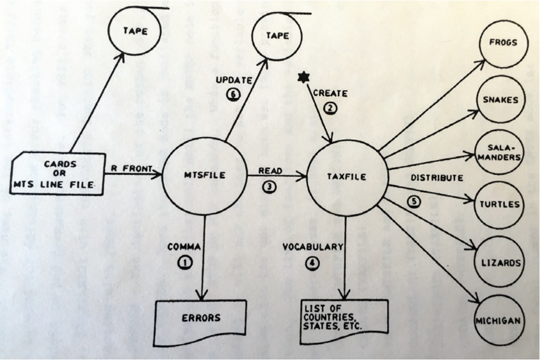

***Figure 3.** Original Electronic Data Processing (EDP) system on MTS using TAXIR.*

Upon my arrival in January 1986, Arnold Kluge began teaching me how to use our "Front End" program that interacted with TAXIR on the mainframe computer using the MTS operating system. We sat together in the Herp Division office on the second floor of the Alexander G. Ruthven Museums Building, in front of the big black screen with a dull green cursor of a dummy terminal monitor that communicated with MTS via a dial-up modem (those old style dial-up telephones weighing about 5 pounds) that could transmit at 600–1200 baud (one bit per second). The database was split up into six files (data banks): Frogs, Salamanders (including caecilians), Lizards, Snakes, Turtles (including rynchocephalians), and Michigan. Only 12 of the 18 fields we kept were "queriable descriptors," whereas the other six were stored as text on magnetic tape (Figure 3).

Although state of the art at the time, the system and "Front End" program were cumbersome and the learning curve was steep. Arnold was quite patient with me and made sure I understood how to "create comma-delimited line files" for data entry and distribute them to the data banks, as well as run queries and process information requests. In those days, computer time cost money, so we met at the divisional office on weekends when costs were deferred. I think it is noteworthy to mention that while perhaps known to be overzealous at times, Arnold was an excellent teacher, excellent anatomist and preparator, hands-on curator, and a wonderful host and family man. I learned a lot from him.

The Herp Division migrated the databases to FoxPro 2.6 in 1994. The mainframe computing environment was being phased out in favor of desktop computers. (My first Zenith desk-top computer was outfitted with two hard drives, 500 MB each, to accommodate our extra storage needs.) Perhaps the University wanted to divest itself of the management responsibility, although the Literature, Science, and the Arts (LS&A) College offered us an option to build a grand database in Oracle at a cost of about $10,000. One consideration for our choice was that we did not want to be reliant on the College for our computing needs. Likewise, having attended the MUSE meetings at the Museum of Vertebrate Zoology in Berkeley in 1993, we decided not to participate in the MUSE effort of networking ichthyological collections because we would have to rely on the MUSE team (which began with our own UMMZ Fish Collection in 1989). I chose FoxPro 2.6 software as a powerful collections management tool because it was relational, robust (accommodating 1 billion records in 252 tables), stable (because it ran on a dbase platform) and could run external programs (especially in dbase). In addition, the program was inexpensive ($99), multi-platform (PC and Mac), and it was versatile with importing and exporting capabilities using different programs such as Microsoft Excel. I worked directly with the Michigan computing consultant, Steve Burling, who wrote a simple program to migrate all the data from the TAXIR databases, matched with record strings extracted from our 9-track magnetic tapes, converted into comma-delimited line files, and appended into FoxPro. The learning curve in FoxPro was steep, but I could add records, build queries, and import and export data. I was fortunate that Earl Werner's (Department of Biology) graduate student, Rick Relyea, came to work for the Division that year as the Divisional Research Assistant. (Each semester, the Division was able to hire a graduate student curatorial assistant, someone who had advanced to candidacy, to help with curation of the collections.) Rick had outstanding computer experience and skills. I showed him all that I had developed in FoxPro to that point and asked him to learn as much as he could and then teach me. Together, we developed data entry screens, loan programs, various reports, etc. (This arrangement proved to be hugely beneficial to me many years later when we acquired Earl Werner's collections of ecological vouchers from the Edwin S. George Reserve. Rick had been managing all of the ESGR collection records—samples from

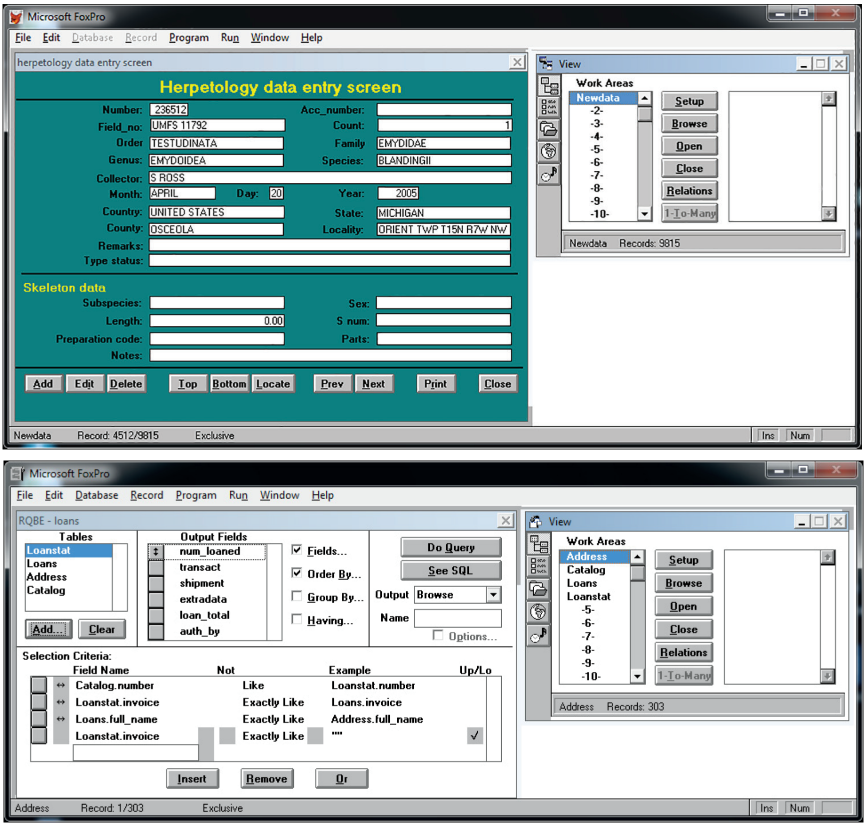

Figure 4. *Data entry screen for Newdata with pick lists and lookup table (upper). Loan Progam relating addressee and specimen data summarized on an Invoice Report (lower).*

about 30 ponds for more than 18 years—in FoxPro 2.6, and I still had the program running on an older 32-bit PC.). Most importantly, FoxPro was customizable and could accommodate any computing needs that arose (Figure 4). It was a powerful tool for collection management; we were not reliant on others for our computing needs, and, there was no cost. It was actually saving us money because by this time, we had started using e-mail, and I could fill information requests by sending Excel files as e-mail attachments (rather than sending printouts in the mail and trying to get reimbursed for the cost of computer time as we had done previously when using the mainframe environment). I don't know if I adequately expressed my gratitude to Rick for helping me, but by developing our loan program in FoxPro, I was able to learn about, and tap some of the powers of, using relational databases to facilitate work on new projects in the collection.

During the next 10 years, I used the powerful indexing, filtering, and relational capabilities of FoxPro to accomplish a variety of database tasks including proofreading and standardizing vocabulary, especially in geography and taxonomy. This also entailed the inventory and reorganization of collections to match the organization of the database. Imagine how valuable that would be when having to move collections out of, and back into, storage rooms to accommodate renovations. But one of the most valuable aspects of managing our own database in FoxPro was the ease and especially the versatility of adding records and importing data.

During the 1990s, our Fish Division was deeply submerged in the development of the MUSE databasing project and also began the Neodat project, assigning latitude and longitude coordinates to museum records of neotropical fish across a consortium of museum collections to map fish distributions. It was suggested that the Herp Division also should assign coordinates, minimally to Michigan records, to take advantage of some of the developing mapping software. Although we had more than 30,000 herp records from Michigan in our FoxPro database, indexing, sorting, and filtering revealed that there were only about 3000 unique localities. My work-study student at the time, Cori Richards-Zawacki, an undergraduate from Engineering (also interested in biology) was pretty handy with computers. Using downloaded look-up tables, one for the center of every section in Michigan (ordered by townships and ranges in each county) and another for Michigan place names, and using our extensive map collection, Cori assigned (i.e., copied and pasted) geographical coordinates to our Michigan localities in about 6 weeks. The relational capabilities of the FoxPro database made it simple to distribute the coordinates from the 3000 locality records, updating the newly created fields for the >30,000 individual specimen records. That was completed in 1999. By 2000, I figured out how to plot the distributions of UMMZ Michigan species in ArcView 3.2 and export the maps as JPEG files for presentation as web pages.

Ron Nussbaum and his postdoc, Chris Raxworthy, were sufficiently impressed with this work to ask me to do the same for about 25,000 UMMZ specimen records that had accumulated from their work in Madagascar. Some results based on that project were published in *Letters to Nature* (2003), "Predicting distributions of known and unknown reptile species in Madagascar."

Concurrently (late 1990s–early 2000s), photography was transitioning to digital formats, and the cost of good quality digital cameras was decreasing. Around 2003, we began a project to assemble digital images of Primary Type specimens in the collection for eventual inclusion on our website. (I should note that my memory is a little fuzzy about those years as my wife and I had twins in 1999, the year following a family tragedy.) But I recall that our work-study student, Dave Lamb, was an accomplished user of a digital SLR camera. Using a ring-light set up, he captured digital images of our amphibian types that were subsequently included on our website in early 2004. Shortly thereafter (May 14th, 2004), renowned biologist, Edward O. Wilson, presented the keynote address for the grand opening convocation of our University of Michigan Life Sciences Institute (Figure 5).

Figure 5. E. O. Wilson *"Exploring the Complexity of Life" Life Sciences Grand Opening Convocation May 14, 2004.*

In his address Wilson talked about the "exploration of biodiversity and how the prospect of that initiative has now been accelerated greatly by new technology, in particular high-resolution digital photography, Internet publication, and rapid DNA sequencing." The presentation also introduced the idea of an "Encyclopedia of Life" with electronic pages for each species including high-resolution digital images. This made a huge impression on me, and because I had already been doing some of this kind of work, it occurred to me that I could make a significant contribution. I thought that a website with an image of every type specimen linked to the published description was a realistic and attainable goal that would be of use to researchers everywhere. Within a few years, the Type Imaging Project was completed with the help of a several divisional employees, including John Emmerick (biology undergraduate) and Cristy Watkins (a Ph.D. research assistant from the School of Natural Resources), as well as several others. That original collection of digital images now is hosted by the University of Michigan Digital Library.

Desktop computer technology accelerated rapidly. Along with the increased speed of processing and storage, database software also evolved. Because FoxPro 2.6 (a dbase program) could not run on the new 64-bit machines, we transitioned to FileMaker Pro in 2004–2005. (Nevertheless, I maintain an old 32-bit machine with the old version of FoxPro 2.6 and WordPerfect 3.2; it comes in handy occasionally for conversions.) It was easy to make the transition, as FileMaker can import DBF files, as well as any file from Excel. My management strategy remained basically the same with look-up tables that came directly from the existing catalogue vocabulary and a relational loan program that functioned the same as it had in FoxPro. I also transferred all our auxiliary collections (tissues, radiographs, kodachromes, etc.) into FileMaker tables with relational cross referencing as needed. The "layout" feature in FileMaker was powerful and versatile. I easily could improve upon my FoxPro reports, including various transaction invoices. But one exceptional feature of FileMaker is its use of container fields and the ability to import a folder of files such as audio or image files, assign numbers to them by auto increment, and create and store a thumbnail, file name, and file path, all in a single import command. This feature would prove to be exceedingly important in automating and streamlining future digitization projects.

I wanted to digitize all of the division's auxiliary collections as a way of preserving and archiving them, but also to make them more accessible for research. In 2008, I started cataloguing digital images, assigning them UMMZ Division of Reptile and Amphibian Digital Image Numbers, curating the image files, and storing the metadata in a FileMaker database which displayed thumbnails, but could refer to the stored image file and open it in another application. This started out as a way to archive images of some newly discovered Michigan herps from Murphy Lake State Game Area in Tuscola County (especially the habitat and eggs of *Eurycea bislinata,* and also *Desmoganthus fuscus,* and *Cnemidophorus sexlineatus*) and to be able to refer to these catalogued images in talks and publications. These species were thought to have been introduced at Murphy Lake; my personal and e-mail correspondence with Max Nickerson in 2014 (Appendix 1) supports the notion that the introductions were intentional and were made around 1970 by Jack Beelman, a high school teacher from Saginaw Michigan, who visited the Nickerson Farm in Miller County, Missouri. Jack apparently told Max of his collecting plans in Missouri and of his plan to take animals back to Michigan.

In the fall of 2008, Matt Chatfield joined us as our divisional curatorial assistant. In our initial conversation about work, I mentioned (as I do with all the Divisional Research/Curatorial Assistants) that designing a project that could simultaneously benefit his research and be beneficial to the collections is ideal. Matt described that he wanted to archive his tail tips of the *Plethodon jordani* Species Complex in the Herp Division frozen tissue collection, but the only vouchers he had were digital images, because collecting specimens in the Great Smoky Mountain National Park was not permitted. I think he was impressed when I said not to worry, I've got just the solution. Our FileMaker Digital Image database handles this with ease (Figure 6). Once Matt created Excel files of metadata for the tail tips and organized them by "Box Number" and "Cell Number" within each box, updating the

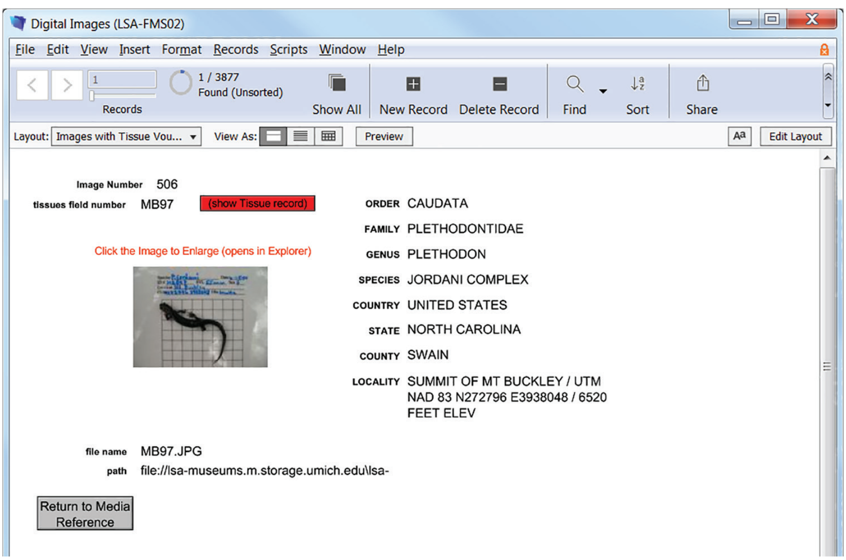

***Figure 6.** Screen shot of our FileMaker Pro Digital Image database displaying a thumbnail (1 kb) and file location of the higher resolution image.*

Digital Image database in FileMaker was a simple, automated matter.

During the next decade, I submitted digital projects to our Digital Library (formerly Digital Library Production Services or DLPS) for archiving and serving up as digital collections via their web site. The primary focus was to preserve and archive our auxiliary collections and to make them accessible for research. The project began with a version of our specimen catalog and included images of our primary types. We had a collection of 37 audio tapes of more than 100 anuran vocalizations recorded in the field on reel-to-reel tapes. These were digitized in audio-mixing sound board at the Duderstadt Media Center on north campus and output as WAV files that were accessible to researchers. The Digital Library was a better choice for a repository because the University of Michigan computing environment for Libraries (and Engineering) was more stable than our College of LS&A computing environment. Our fragile and extremely valuable field notebook collection was scanned and saved as PDF files, mostly by Kinsey Brock starting in 2010 (and finished by Hayden Hedman) and became available online in 2016. To help our caecilian researchers with vertebral counts, we (with the help of Jason Good) began digitizing our caecilian radiograph film collection in 2014. This required the ability to view scanned "maps" of specimens side by side with the digitized film plates simultaneously for specimen identification. The Digital Library acquired new software to accommodate this "two-up" feature. Jason did such a good job documenting his methodology and procedures (in our Divisional "Procedures and Methods" archive) that we were able to continue his work and add pygopod radiographs to the project. An enhanced version of the "two-up" software was added in 2018 to accommodate Mike Grundler's research (UMMZ Ph.D., 2020), an image database of Snake Predators and Prey.

In 2013, our computing climate started to change. Many factors were considered in the decision for the college to resume control of the computing environment. Some were related to safety and expense (whereas others related to the politics of the situation are intentionally omitted from this discussion). An institutional decision was made to have one database for all. After considering Arctos, KeEMU, and Specify (software being used at peer institutions), the College decided that all LS&A Museums would use a common database solution in KeEMU. The College's project goals included: cross collections searching; archival security; appropriate interaction/integration with UMDL (Digital Library); promotion of data to other institutions/peer organizations; promotion of college assets/resources and institutional prowess; and expectations at the organizational level for the future development and support needs of these collections. However, KeEMU met with considerable resistance, and shortly, Zoology and the Herbarium opted for Specify instead. Fortunately, during these transitions, I still maintained FileMaker Pro databases for the "nuts and bolts" daily work of the Reptile and Amphibian Division (including new digital projects that had been started); thus, when our curators, Dan Rabosky and Alison Davis Rabosky, hired georeferencing interns in 2015, we were able to assign coordinates to more than 90% of our records in less than a year using FileMaker (as was previously done for Michigan and Madagascar). But, to preserve verbatim latitude/longitude coordinates that had been recorded in our "locality" field, our curatorial assistant, Pascal Title, wrote a program in R language that searched the entire database, recognized coordinates written as text, converted them to decimal degrees, and entered them into the appropriate verbatim coordinate fields.

At the time of this writing (December 2018), we were still in the process of transitioning to Specify with the help of our laboratory assistant, Courtney Whitcher. (Courtney wrote an undergraduate honors thesis in the division and contributed to this volume.) Most of the college's goals should be realized—with the possible exception of "institutional prowess," which is achieved in so many other ways at the University of Michigan—especially auto uploading and sharing data with Internet aggregators. However, adequate management of the division's auxiliary collections, including our newly acquired and extensive CT Scan collections, is an on-going developmental task. The Scan all Snakes project is producing massive amounts of data, perhaps several gigabytes per specimen, that will have to be archived and curated along with specimens.

New and developing technologies continue to challenge the limits of databases and digitization, but software development, necessarily, is keeping up. In the past 35 years, the UMMZ Division of Reptiles and Amphibians has employed five different database solutions: TAXIR, FoxPro, FileMaker Pro, KeEMU, and Specify (and utilized continual upgrades of each as needed). It seems the life expectancy of an individual database software might be about 10 years, or perhaps less. Today, museum specimen-based research envisions incorporation of many different kinds of data including physical, ecological, genetic, and historical aspects of each of these. We seem to be in the early stages of

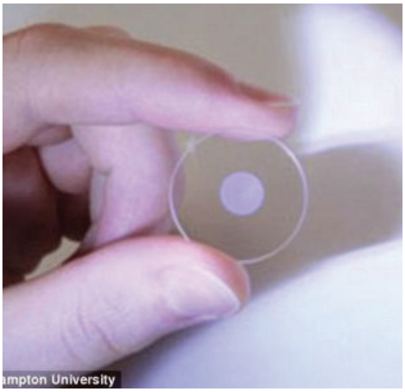

Figure 7. *Memory crystal.*

building a massive information network, with museums and libraries contributing significantly. Given the rapidly accelerating technological advances, there is no reason to think that the next new colossal database solution is not just on the horizon. History has shown repeatedly that the science fiction of today becomes the technology of tomorrow. Certainly, many readers will recall Superman's "Fortress of Solitude," constructed from Kryptonian "crystals of knowledge" and equipped as a digital library and database of the history of his planet, a storehouse for all of the knowledge of the universe gathered by Kryptonians, and manned by holographic robotic librarians. Perhaps inspired by these "crystals of knowledge," researchers at the University of Southampton have developed what they are now calling "the superman memory crystal," a new form of data storage on a coin-sized crystal disc, recording data in five dimensions and written to with lasers that store up to 360 terabytes with a practically unlimited lifetime! Could this be the future of data storage? (Figure 7)

In conclusion, I think it is important to keep building and managing our databases and digitization projects with open minds and the flexibility and versatility to avail ourselves of rapidly developing technological opportunities. Seemingly, our computing technology has begun to overcome initial hurdles limiting digital storage space coupled with processing speed. During the past several decades, I have tried to build digital projects that archive our division's assets, as well as aid in herpetological research by increasing the organization and accessibility of data and digital media. Last, with respect to institutional prowess, my work here at the UMMZ has been possible through the vast resources the University has to offer and with the help of the many undergraduate and graduate students who have been employed during my tenure as laboratory assistants and curatorial assistants in the Division of Reptiles and Amphibians (Appendix 2 for alphabetical list). I have always been proud to work in Ruthven's collections and it is an honor to be included as part of the legacy.

Appendix 1: Michigan Race Runners

Correspondence with Max Nickerson 8/7/2014 and 8/28/2015 pursuing the origin of the population of *Cnemidophorus sexlineatus* in Tuscola County, Michigan (e-mails on file in UMMZ, Division of Reptile and Amphibian correspondence).

> "Jack Beelman, 2245 Gaylord, in Saginaw, 48602 (e-mail from Max, 8/28/2015) visited Nickerson Farm in Miller County, Missouri (in 1970), and talked to Max about herp localities. He thought the only Cnemidophorus were those shown in "Reptiles of Missouri" by Paul Anderson (employee of Standard Oil). But, Max described nearby localities of Cnemidophorus in Miller County:
> Near Eldon, at U.S. Hwy 54 x State Hwy. 52, a lot south of truck stop on the SE corner (cleared area formerly oak hickory).
>
> And E along Hwy 52 along road cuts (also Ophisaurus).
>
> Also, Eurycea cirrigera could be from Stark Caverns, near Eldon, Missouri.
>
> (There is a large series at the Milwaukee Public Museum collected by Leeland Payton)
>
> Missouri Dept. of Conservation could help out (Max has connections)"

Beelman, a high school teacher from Saginaw, MI, told Max he was going to take animals back to Michigan.

Appendix 2: Employees

Steve **Albee-Scott** [2002/2003], Emanuel Alvarez [2005/2006/2007/2008], Lou Anne Reich Cooley [1997], Courtney Asman [2016], Jennifer Ast [1997/1998/2001], Elizabeth **Bacus** [1987], Anat Belasen [2015], Cindy Bick [2017], Robert Bloye [1992], Claudia Bowman [1993], Kinsey Brock [2010/2013], Kai Bullard [2000], Russ Burke [1990], Matthew W. **Chattfield** [2008], Kevin Coburn *[2009]*, Isabel Constable [1996], Kate **Da Rin** [2000], Vincent Deem [2014], Sara Diamond [2004], Peter Ducey [1986], Stephen Dueppen [2004], John **Emerick** [2008], Glenn **Fox** [1997/1998/1999/2000 /2001/2002], Jeffrey **Gonzalez** [1995], Jason Good [2013], Michael Grundler [2017], Lance **Hamilton** [1993], Lance Hamilton [1989/1991/1992], Hayden Hedman [2014/2015/2016], Heather Heying [1995/1996], Stephanie Hibbs [1988/1989], Helen Huetteman [2015], Takehito **Ikejiri** [2009], Eve **Konopnicki** [1988], Sandy Kosek [1989], David **Lamb** [2004], Joanna Larson [2018], Rick Lehtinen [1999/2000], Thomas Leuteritz [1993], Kieth Linder [1987/1988/1989], Marco Lopez [1993/1994/1995/1996], Chris Lumpkin [1995], Ann Marie **Macara** [2013], John Marino [2010/2013], Brad Moon [1994], Annemarie **Noel** [2001], Greg **Pandelis** [2017/2018], Keith Pecor [2002/2003/2004], Theresa Peterson [1996/1997], Mike Pfrender [1989/1991], Mary A. Potts [1996/1997], Jay **Reed** [2009/2011/2012], Rick Relyea [1995], Cori Richards [1999/2000/2001/2002], Danny Rizk [2015], Rennie **Scotten** [1990], Sirirat Siripattrawan [1998/1999/2000], Jinny Suh [1997], Kyle Summers [1987/1988], Pascal **Title** [2014/2015/2016], Yoshio **Wagner** [2014/2015], Cristy Watkins [2005/2007], Abe Weiner [2013/2014/2015], Erin Westeen [2017], Courtney Whitcher [2016/2017/2018], Upekala Wijayratne [1998], Mark Wilkinson [1986], Heather Williams [2015], Tiffany Wilson [2000], Daniel Winfield [2011/2012], Jessica Winkler [1989/1990/1992], Alan Wolf [1993], Sheng-Hai Wu [1986/1987/1988/1991/1992], Brian **Yang** [1996], Lily Young [2000], Kerry Yurewicz [1994].

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Greg has worked as the Collections Manager of the UMMZ's Division of Reptiles and Amphibians for nearly 34 years. He completed his Master's degree at UC–Santa Barbara with Sam Sweet on geographic variation in Pacific rattlesnake populations. Greg is particularly adept at managing and manipulating large databases. He has been on the forefront of the transition from paper to digital records of museum collections and dissemination of these data to the scientific community. He is deeply dedicated to the curation of Michigan's reptile and amphibian collections and its associated records and maintains a long-term interest in the history of the Division of Amphibians and Reptiles at the UMMZ.

RUSSELL BURKE

Six Years at the UMMZ

1988 —

When I arrived at the University of Michigan as a Ph.D. student in Fall 1988, I was unfamiliar with the campus, having only seen it for the first time when attending the Joint Meetings of Ichthyologists and Herpetologists there that previous summer. I was quickly welcomed into the UMMZ family and found that the program was similar to my experience as a M.S. student at University of Florida (UF), where I had been closely associated with the Florida Museum of Natural History. The Museum of Zoology was my home until I defended my dissertation in 1994 under Ron Nussbaum and moved across the street to the School of Natural Resources & Ecology for a postdoc with Terry Root. I wrapped that up in summer 1996 when I left to join the faculty at Hofstra University, where I have been ever since.

Those 6 UMMZ years were amazingly valuable to me, forming much of the core of the scientist and teacher that I am today. Right from the start, many of the faculty treated me a developing professional, anticipating that I had something to offer them and that I would learn the important things I didn't know. I made good friends, many of whom are still important to me, and settled in comfortably with the other students who were also passionate about studying evolution, ecology, and especially herpetology. Having grown up nearby in Ohio, I was familiar with the local environment, which was a help to me in the field. My Florida graduate experience provided me with a decent educational background. Because my UF advisors had pushed me to publish my Master's research, I had already begun to learn the fundamentals of scientific writing and publishing, and had been encouraged to join professional societies and present at meetings—similar advice that I received from my advisors at UMMZ . Consequently, as a Michigan graduate student, I published a paper with a UMMZ faculty member (C. Badgley), two papers with fellow UMMZ graduate students (A. E. Wolf and J. Burch), and another with an undergraduate whom I advised (L. Little). I remember writing a paper for publication in *Herpetologica* on the "new" computer (big monitor, dark screen, pale green characters) in the Herpetology Division in a single weekend, jumping up over and over to use the valuable literature in the Herp Division library right behind me. That library was instrumental to my training because nothing can beat having resources close at hand to answer questions as they come up.

The UMMZ provided copious opportunities for writing grant proposals. While there I wrote (and received) a Rackham Dissertation Improvement Grant, a Rackham Pre-Doctoral Fellowship, a Hinsdale-Walker Scholarship, an E. S. George Reserve Scholarship, a Peter Olaus Okkelberg Award, and multiple Rackham Block Grants. These modest grants funded lab supplies and field time, and perhaps more importantly, forced me to formulate my ideas into written proposals suitable for review by professionals, an experience that prepared me well for proposal writing as a faculty member.

I look back on my time at the UMMZ fondly. I think that I received a balanced mix of direct instruction and freedom to do as I liked, although at the time, I occasionally didn't think so. Nussbaum traveled a lot, and I learned to get along in his absence by relying more on other faculty members than did most graduate students. This allowed me to explore a wide range of biological topics and spend considerable time in other divisions such as mammals, birds, and invertebrates, as well as in the School of Natural Resources & Ecology. The time I spent reading papers on a wide variety of topics serves me well today. Although I had a dissertation project in mind when I arrived at Michigan, I quickly began to search for another. For a year or more, I hopped from one potential dissertation topic to another. The projects changed so much that I remember walking into Nussbaum's office and his asking me what this week's proposal topic would be.

Russ Burke *ca. 1989 with turtle.*

Because of my previous experience and strong interest in the application of life-history theory to long-lived organisms, I worked with Justin Congdon at Michigan's E. S. George Reserve in Pinkney, MI, in the summers of 1989 and 1990. This experience proved especially valuable to me when I started long-term turtle demography projects in New York, where I applied many of the research questions and techniques that I had learned from Justin.

One of the valuable things that I learned at the UMMZ was a way of thinking—i.e., I became used to thinking about a wide variety of topics in evolutionary terms. My UMMZ colleagues were strong selectionists, and this led me to read about evolutionary theory and practice much more deeply than ever before. It affected my thinking on everything from animal behavior to life-history theory to systematics, and still is very important to me today. This background prepared me to teach evolution my first semester at Hofstra, and continues to influence me today in nearly every way.

Another two particularly influential UMMZ experiences involved travel opportunities. One spring, a friend told me about an opportunity to do some quick and lucrative consulting work in the Mojave Desert, where a natural gas pipeline was being installed across parts of Nevada and California. A team of "biologists" who could drop everything, fly west, and supervise huge construction vehicles while they traveled through sensitive desert tortoise habitat was needed. The pay was great, and all the UMMZ grad students who could skip classes and teaching for a week, or even two, flew out for the jobs. We wore hard hats and vests, rented rooms in cheap hotels, crammed into beds at night, and ate junk food. At least one student completely retired his credit card debt in two weeks of this "work." I had never seen the Mojave in bloom before; the diversity of reptiles I saw was astonishing and included many species I saw for the first time there. The next year one of the ichthyology students heard of an opportunity to join groups of tourists on trips to the Amazon, all expenses paid, as long as the travel agency organizing these trips could claim we were English-speaking "biologists." This accounted for my first two trips to South America and laid the foundation for taking Hofstra classes there many times since.

Probably the most commonplace UMMZ experience that I remember and miss the most was regular lunch time conversations in the Herp library. The lunches weren't formalized; it seemed that whoever was around in the middle of the day would gather around the table to eat and talk. I remember Tom Jones, Greg Schneider, Alan Wolf, Thomas Leuteritz, Chris Raxworthy, Mike Pfrender, Dan Erickson, and Sheng-Hai Wu particularly, but also anyone visiting the lab at the time, including faculty members Arnold Kluge and Ron Nussbaum, also dropped in. We grabbed references off the surrounding shelves to settle disputes. We hatched plans for field trips and professional meetings; we teased each other and trotted out crazy ideas. It was an experience not to be had again until many years later with my graduate students in my own lab.

Finally, I benefited from learning basic museum curatorial techniques while working as a Research Assistant at the Herpetology Division. During the course of my subsequent research and teaching career, I have needed to collect and preserve alcoholic and dried specimens. Nearly every time I tie strings onto a strip of collection tags, I think of doing the same thing at the benches in the division many years earlier. When my students ask me why it has to be done the particular way I do it, I say, that it's "because that's the way it is done right."

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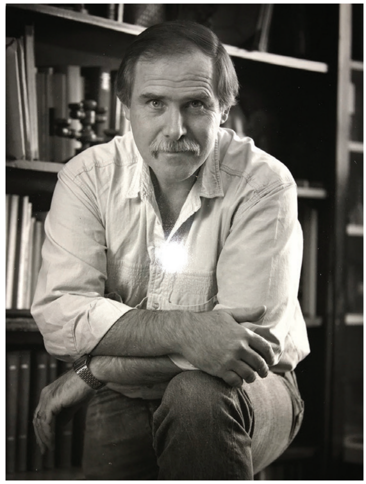
Russell Burke's primary interests are the ecology, evolution, and conservation biology of vertebrates, with an emphasis on introduced or rare species. Currently, Burke is conducting three major research projects—diamondback terrapins at nearby Jamaica Bay; wood turtles in northern New Jersey; and wall lizards on Long Island. The terrapins are challenged by decreasing salt-marsh habitat, pollutants in the bay, raccoon and plant predation on eggs, and rat predation on hatchlings. Burke is studying the evolution of temperature sex determination in the terrapins. His wood turtle research explores behavior of the species, in which sex is determined genotypically. Italian wall lizards were introduced to Long Island in 1967; the population, which now numbers in the thousands, is spreading rapidly. Burke's lab has investigated the freeze tolerance, food habits, parasite load, reproductive cycling, survivorship, seasonal behavior and diel behavior of this population. Burke has found that U.S. populations of this lizard, which are great models for studies of invasive species, mature more rapidly than their Italian counterparts.

CHRISTOPHER RAXWORTHY

Madagascar and the Endless Michigan Summer of 1990–1996

1988 — I first visited the Division of Reptiles and Amphibians in 1988, during the Joint meetings of Ichthyologists and Herpetologists (JMIH) that was being hosted that year by the University of Michigan. The Division was offering tours of the research collections, and Greg Schneider (as Collection Manager) was holding court. The collections were impressive—rows upon rows of bail-top jars containing incredible species arranged in perfect alphabetical and systematic order. Although I had seen other large research collections, I had never seen one as well-curated as Michigan's at this point in my career. But then I made my first mistake—I spotted a bottle of mis-identified *Lissotriton,* European newts (that were the subject my Ph.D.), and picked it up. The wrath from Greg was instant—nobody moved the specimens but Greg. Fast forward to my first day starting as a postdoc 2 years later, and Greg marches me back into the collection and demands to know which specimens needed to have their species names changed; the specimens were re-cataloged the same day! We always joked that Greg had the mentality of a collection manager. On that first day starting as a postdoc, I also was called into the Museum Director's office (Bill Dawson) for what I expected would be a warm welcome speech. But instead, he explained that Michigan was very proud of its faculty and graduate students, but that postdocs were the lowest status researcher in the museum. Welcome to Michigan! Nevertheless, I was well treated as a postdoc at Michigan. I had a large office (with windows), tons of resources, almost no duties or demands, and the opportunity to submit NSF grants as a co-PI. This was the ideal place for a postdoc to flourish, and this position gave me and many others at UMMZ the chance to be successful researchers.

My reason for being at Michigan centered completely on my work in Madagascar with Ron Nussbaum. Ron had been contacted by Ken Creighton (a mammalogist based at the Smithsonian) about joining a faunal environmental assessment team to work at sites on and around a proposed titanium mine (QIT, now RTZ) near Fort Dauphin in Madagascar. Ron had a huge amount of experience in the Seychelles, but had never worked in Madagascar, so he contacted me about joining him on this survey. By this point (1989), I had been to Madagascar on three student expeditions, and having just completed my Ph.D., I was free to go into the field. That first field season working with Ron was amazing. I learned so much; and we really had a blast. Ultimately it led to a second field season of environmental assessment working in southeast Madagascar, and then three NSF-funded grants during an endless summer lasting from 1989–1996. Between May and October I was in Ann Arbor; then I flew south for the Madagascar summer (rainy season) from November–April. As a result, most of my Michigan experience was during the sticky dog days of summer, when the undergraduate students had left town, and the living was easy. However, I clearly remember never having an office with AC during all my years at Michigan. These were the days of Red Hot Lovers hot dogs, Dominic's Long Island ice tea, cold beers at the Del Rio and Grizzly Peak Brewery, steaks at Knight's, and the madness of the Ann Arbor Art Fair. By the time the new class of students arrived in Ann Arbor in the fall, it was time to start preparing for the next field season in Madagascar.



Ron Nussbaum, *UMMZ Curator ca. 1989. (Photo by Chris Raxworthy.)*

For the first NSF Biotic Survey grant in Madagascar, the focus was on the humid evergreen forests, especially those at more remote sites and reserves that had been previously poorly sampled.

Zahamena Strict Reserve, *1994, at the Rangovalo Ridge summit marker (left by map surveyors) with top row (left to right): Falitiana Rabemananjara, Andry Ravoninjatovo; bottom row: local guide, Chris Raxworthy, and Jeannot Rafanomazantsoa.*

These early expeditions included such classic sites such as Zahamena, Marojejy, Manongarivo, Tsaratanana, Ambatavaky, Masoala, Mantadia, Montage d'Ambre, Ankarana, Lokobe, Andringintra, Ranomafana, Ankaratra, and Ambohitantely and were conducted in collaboration with the University of Antananarivo. The first two graduate herpetology students from the University of Antananarivo to work with the University of Michigan were Achille Raselimanana and Jean-Baptiste Ramanamanjato, both of whom worked in the collections at Michigan during the summer of 1991. The

At the summit (Maromoktro) of ***Tsaratanana,*** *2876 m, in 1993 with top row (left to right): Pierre Soga (Service de Eaux et Foret), Angelin Razafimanantsoa; middle row: Jean-Baptiste Ramanomanjato, Angeluc Razafimanantsoa, bottom row: Chris Raxworthy and 2 local guides (photo taken by Achille Raselimanana).*

early expeditions yielded many important specimens that were used to describe new species and continue to serve as critical morphological and genetic vouchers that are heavily used in ongoing research work. Some expeditions such as Zahamena, Ambatovaky, Andringitra, and Tsaratanana involved 6–10 days of hard walking to complete the surveys during 3 or 4 weeks; the logistics during the peak rainy season from November–April were complicated and involved large teams of porters, Typically, Ron was in Madagascar during part of the U.S. summer, as well as the fall semester, before returning to Michigan to teach in the spring, which often involved his Herpetology class and its famous Appalachian salamander field trip to the Great Smoky Mountains. I would return to Michigan from Madagascar in the late spring after 6 months, almost always hand-carrying the last season's collection with me, and often, DNA tissues in a cooled and drained liquid nitrogen tank (amazing what they used to let us take on planes!). Once the collection cleared U.S. Fish and Wildlife Service, we would soak the specimens for several days in water to drive off most of the formalin, and then host a specimen unpacking and sorting party in the prep. lab. These were great times, and there really is not much that feels as good as seeing your field collection finally sorted and safe in alcohol, in labelled bottles on the cart!

Ron Nussbaum was an incredible mentor with his huge breadth of herpetological knowledge that included taxonomy, biogeography, phylogenetic reconstruction, morphology, development, karyology, behavior and ecology. But probably the most valuable thing Ron taught me was the art of examining specimens in as many creative ways as possible to search for new characters that could help identify new species. This may sound easy, but you need a lot of patience and skill to do it well. We would spend hours discussing all types of research topics, primarily in reference to species in Madagascar, but he also would bring up issues that related to research experiences in Africa, the Pacific Northwest, and elsewhere. And there were always tangents that included his massive and ever-expanding music collection, crazy news from Madagascar, and politics (academic and international). Ron always worked long hours at the Museum of Zoology—getting in by 8 am (and always getting the best parking spot by the Ruthven loading dock) and usually leaving late in the evening. He was always approachable. So, it was a surprise to me that many students at the museum viewed him as a man of mystery, save for the few who dared knock on his closed office door. Unlike most of the museum staff and students, Ron frequently dropped in the prep. lab, where Greg, myself, and usually students would be working (listening to the Detroit Classic Rock station or NPR) and drinking huge quantities of cheap bitter coffee. Dave Bay (Department of Biology Photographer) and the museum artist Margaret Van Bolt were the exceptions. Dave was famous for recording a new telephone answering-machine message twice a day (with a morning or afternoon greeting and the day's date), whereas Margaret probably had the world's shortest voice-mail message.

One of the routines in the Division of Reptiles and Amphibians was lunch in the divisional library, although we also frequently went to South University Street to eat. Greg always headed to the golf course on Fridays (using his vacation time during the summer!). Although Ron never joined the library lunches (which were more like informal brown-bags), Arnold Kluge frequently was there. With the mix of students, postdocs, professors, and Greg, the conversation would swing wildly among any topic, including cladistics, evolution, classic cars, house repairs, grantsmanship, and academic gossip. A favorite theme was making fun of the lunches everybody brought to the table—Greg always had a bag of Fritos, and I became famed for my stinky Bovril sandwiches. Lunch attendees might include Jennifer Ast, Russ Burke, Isabel Constable, Doug Eernisse, Heather Heying, Tom Jones, Moises Kaplan, Fred Kraus, Tom Leuteritz, Brad Moon, Mike Pfrender, Dave Skelly, Kyle Summers, Alan Wolf, Dan York, or Sheng-hai Wu. Occasionally the discussion would erupt into a heated debate over issues like Total Evidence or Iterative Character Weighting or even bicycle access on roads, and often it was a great way to get information, and discuss and explore research ideas. I am sure many research publications benefited from these discussions. I leaned so much during these times, especially from Arnold Kluge. Occasionally, we would also join Carl Gans (viewed as the"Grandfather" of Michigan Herpetology by many students) from the Biology Department for coffee or lunch, or for one of his famous evening BBQs at which we would have the opportunity to tour his huge personal herpetological library and ask him questions on any aspect of reptile biology.

There was always a friendly feel in the Division, even if the huge and sterile interior corridors of the Ruthven Building did not communicate this. Greg kept morale up with his friendly memos about issues such as pest infestation, that always started "It has been brought to my attention…" and there was the famous dual between Russ Burke and

Greg Schneider on the Michigan running track to settle who was the fastest-runner dispute; Greg won that day. Some of our most memorable times were the long road trips we made to attend the herpetological society meetings in New Orleans and State College, which included catching hellbenders and intense discussion about science, Doritos, and who was to blame for missing the last highway exit.

The Division was a great place to learn everything about collection care (under the demanding oversight of Greg) and various preparation types. For example, taking X-rays (without killing yourself), clearing and staining, and database collection management. During my time at Michigan we had one real fire (in an electrical box) in Ruthven. It was then that I realized there was no fire alarm system fitted in the building (the alarm was banging hard on every office door on your way out) and no sprinkler system in the alcohol collections. The Division also always seemed to have live animals around- caecilians, lizards, tortoises, turtles, woodlice (as a trial to prepare delicate skeletons), geckos, as well as the ever-present roach issue in the building. Alan Wolf and I even had our pet Blanding turtle and Greek tortoise (*Persephone*) roaming in our shared office one summer.

Looking back on those years at Michigan, these were some of the best memories of my life. There were always new people and exciting ideas flowing through the Museum of Zoology, even during the supposedly slower months of summer. It was the first time in my life that I felt I was in a place where herpetology was actually taken seriously. Ron Nussbaum and Arnold Kluge had complementary deep knowledge in so many areas of research, and the collections themselves were an amazing resource to wander into and explore. Probably the best thing about my time at Michigan was learning how to ask interesting and exciting research questions and how to develop hypotheses and approaches to solving them. The breadth of expertise among the staff and students at the museum during this time was remarkable, and it heavily influenced my research at a critical point in my career.

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Chris Raxworthy has been studying reptiles and amphibians in Madagascar since 1985. He has found (and continues to describe) many new species and has added a wealth of information to the knowledge on known species. Currently, his research is focused on gecko and chameleon molecular and morphological systematics, and the use of remotely sensed data (from satellites) to help predict the distributions and model the ecological niches of species. Raxworthy's research includes field surveys of mountainous areas of northern Madagascar, as well as fieldwork in Vietnam, Ghana, and Mali. His broader research interests include the applications of Geographic Information Systems (GIS) to inform conservation priorities, and exploring patterns of speciation and endemism in Madagascar. Chris is the PI for the Sackler Institute for Comparative Genomics. He is a Professor at the Richard Gilder Graduate School (AMNH), and holds adjunct appointments at Columbia University, the University of Michigan, and the University of Antananario in Madagascar.

JENNIFER AST

Snakes 'n' Lizards 'n' Stuff

1993–

I know our focus here is the Museum of Zoology's Division of Reptiles and Amphibians, but the University of Michigan is a state school, so I'm hoping that I can be indulged in a few lines about the influence that Michigan's primary educational system had on me, because it is responsible for my becoming a herpetologist and evolutionary biologist. I graduated from Saint Joseph High School (St. Joseph, Michigan) in 1988, where I was lucky to have two excellent science teachers, Tim Pschigoda and Joseph Collins. Mr. Collins was particularly fascinated with genetics and molecular biology's central dogma of DNA to RNA, RNA to protein. One day he told us that, if you taught a flatworm to always turn left or right in a simple T-maze, and you then chopped it up and fed it to some other flatworms, they would know how to run the maze. "They think it has something to do with memory being stored in RNA," he said. And so I proposed doing an independent senior project with my two science teachers—I was going to teach flatworms to do a maze so that we could try it for ourselves. Looking back on it, this experiment was a bit of a stretch for a high school student who had one hour a day to devote to it (and the "memory RNA" hypothesis may itself be a bit of a stretch), but my teachers didn't say a single discouraging word, and simply being given the chance to attempt it was important. Of course, none of it worked, but I learned that it is just plain fun to get to poke around in a lab.

Mr. Collins and Mr. Pschigoda took students in their advanced chemistry and biology classes to evening science lectures sponsored by the colleges and universities in Kalamazoo. One Saturday, a few of us went to a day of science lectures for high school students at the University of Chicago. The University's stonework, Gothic architecture, high-ceilinged classrooms, and generally rarified atmosphere were all very attractive to a nerdy high school student like me.

When I started as an undergraduate at the University of Chicago, I was already quite sure I was going to be a biology major. I took some great classes there, including evolution from Jerry Coyne and paleontology from Jack Sepkoski, but my favorite was Steve Pruett-Jones' field ecology class, which started with a spring break trip to Florida's Archbold Biological Station on the Lake Wales Ridge, the state's highest and driest part. The habitat is distinct and quite unlike the rest of the state, with its sand live oaks and other scrubby brush, its cattle ranches, and its denizens such as indigo snakes, sand skinks, and the endemic and endearing Florida scrub jay. ("As you can see, the scrub jay is quite shy and retiring," said a resident biologist one day on a walk through the reserve, as a jay landed on his head and attempted to eat the button on the top of his ball cap.)

Our TA was Fredric Janzen, a doctoral student working with Steve Arnold, whose interest was the physiological ecology of turtles. As an ornithologist, Professor Pruett-Jones would get up and go out before dawn, but some of us preferred Fred's approach. Fred said that herps were better than birds for two reasons; first, herps didn't get up before noon, and second, because you could catch them and hold them in your hands. And he was very, very good at putting herps into our hands. The class would be walking to the cattle grazing pastures where we were doing our projects on cattle egrets and without warning, Fred would dive headfirst off the path, always coming back up with a snake, a frog, a gecko, or a skink. The class was mostly city kids, but even I and the other farm kids had never seen a person do this sort of thing before. We were all enthralled, and we tried hard to emulate him. Fred made the "mistake" early in the trip of saying "Brownie points!" to the first student who managed to catch a gecko, and after that it was a herp-catching free-for-all. (One classmate was suspected of diving into the underbrush even though he hadn't seen anything.)

All the field ecology students were somewhat childishly pleased on the one occasion we saw Fred's feeling for herps fail. In May, the class took another field trip, this time to Fred's field site on the Mississippi

River, where he put us to work finding map-turtle and snapping-turtle nests, and teaching us how to carefully dig up turtle nests, and how to prepare the eggs for safe return to the lab in Chicago. We learned that it's not easy to extract dozens of small, fragile eggs from a nest cavity without turning the egg over and disturbing the embryo—all while lying on your stomach on the ground. On the drive back, Fred had us stop at a scrubby field where he had found a box turtle once. As we piled out of the vans, he told us that box turtles were rare and hard to see, and so we shouldn't be disappointed if we didn't find any. "Isn't that one right there?" said a student, pointing at the ground about a meter to Fred's left. The student hadn't even moved away from the van yet. "Umm, yeah," said Fred. "And isn't that one?" asked another student, pointing. "Hey, here's one," called a third student less than a minute later. Within 10 minutes, we had found two more, for a total of five box turtles—four males, distinguishable by their red eyes, and one brown-eyed female. Before we drove away, we were careful to check under the vans, loudly telling Fred that he better let *us* check, because obviously *he* couldn't see turtles at all.

I talked to Fred and Professor Arnold to see if they had any projects that I could help out with to get some research experience as an undergrad. Fred did indeed need some help with his turtles, and that June, he and I and another student from the field ecology class, Chuck Hanifin, drove back to his Mississippi River site to collect more turtle eggs. Fred's main goal with this collection was to test the effect of different nest environments on the eggs and hatchlings of two different species of map turtle (*Graptemys ouachitensis* and *G. pseudogeographica*). I spent the summer tending the eggs and hatchlings, and the project was the basis for my undergraduate honors project, eventually becoming my first publication.[1] Years later, while sitting my office in the UMMZ herp division, I noticed that our research had been funded in part by an ASIH Gaige Fund award to Fred. The name hadn't meant much to me as an undergraduate at Chicago, but it pleased me mightily as a UMMZ graduate student, who was perhaps sitting not too far from where Helen and Frederick Gaige themselves had sat.

The taxonomic aspect of the turtle project bothered me. These two species of map turtles are sympatric, and their nests and eggs are indistinguishable. Thus, we didn't know which species our eggs were until the eggs hatched, and even then, I didn't like the way we distinguished them. A hatchling *Graptemys ouachitensis* has a thick bright yellow stripe behind the eye, but a hatchling *Graptemys* *pseudogeographica* has a thinner, dimmer stripe. However, there were plenty of individual hatchlings with intermediate stripes, in which case, an individual's identity was determined by that of its clutch-mates, but there was plenty of within-clutch variation too, and how did we know they were *really* two different species? I started pestering Fred with questions about what species are. Fred thought we could try to see whether the hatchlings' colorful head or plastron patterns could be quantified in some more precise way that could then be used to distinguish the species. We took close-up slides of each hatchling's head, and we set each baby turtle (more than 300 of them!) on the departmental Xerox machine to photocopy the dark concentric patterns on the plastron. (We did this photocopying after hours, feeling that a certain amount of tact was called for when setting damp baby turtles on the machine's glass. "Steve *probably* wouldn't mind," Fred said, "but why bother people with things they don't need to know about.")

Encouraged by Fred and Professor Arnold, I applied to the University of Michigan and started the Master's program in biology in 1992 (thereby ensuring me years of grief from my father, a Michigan State alum who is still strongly partisan). I hoped to learn something right away to help me with my map-turtle–patterns project, so I took George Estabrook's class on mathematics in evolutionary biology in my first term; this course involved learning his method (i.e., Character Compatibility Analysis) of inferring evolutionary relationships. In the course of reviewing each student's class-project ideas, George told me outright (but in a very kindly manner) that his methods wouldn't be appropriate for what I wanted to do. A fellow grad student in the class, George Hammond (from the Museum's insect division) suggested that I meet with Russell Burke (a nearly finished doctoral student with Ron Nussbaum) who was working on turtles. Russ and I hit it off, and with his guidance I did a class project on higher-level groups of turtles. Eventually, the project expanded to include fellow turtle-enthusiast and Master's student Tom E. Leuteritz, and the three of us each gave talks on different aspects of our project at the SSAR conference in Bloomington in 1993.[2]

George Estabrook's class was my first hands-on experience with reconstructing evolutionary relationships. I was a little worried by how sensitive the results were to seemingly minor changes in the parameters; it was easy to generate clusters that broke up taxonomic groups, and turtle biologists probably wouldn't like the groupings that I was seeing. It's no surprise that changing parameters changes results, but somehow, I had thought that an evolutionary tree, because it reflected *reality*, ought to be more robust to small perturbations. (Oh to be so young again, and naïve.) "Maybe your character data are bad," someone in the class suggested. But what does that mean, I wondered. I was using a suite of morphological characters gathered by various turtle experts. If these characters weren't "good" then what on earth was? If my "good" characters could be used to make a "bad" tree so easily, would it be better to make a "good" tree with "bad" characters? Hang on— what's a "good" tree and a "bad" tree, anyway?

I completed my Master's degree at the end of the fall term of 1993 and immediately re-applied to Michigan's doctoral program because systematics was fun and I wanted to keep doing it. In the fall of 1994, I took Arnold Kluge's "Principles of Systematics." If I said the class was transformative, it would be an understatement. Here was a class that dove head-first into discussion of those pesky details that had been bothering me since those map-turtle projects. Professor Kluge asked us to think about abstractions like characters and species concepts in a rigorous and philosophically consistent way, and to not be satisfied with empirically expedient answers. We built trees by hand using the Wagner algorithm. We re-analyzed published articles and found trees differing from those presented by the authors. We discussed the (sometimes profoundly) different evolutionary implications of our trees versus the published trees. We learned to test everything, and to be especially alert to authority figures claiming special knowledge about a group of organisms. Professor Kluge was careful to make a distinction here. The point, he said, was not to question the authority's biological knowledge *per se,* because that person probably in fact did know a lot more about those organisms than we did. Rather, the point was to take a good hard look at how the authors were using that knowledge and authority. Often enough, it seemed that when such a person said, "I don't agree with this phylogeny," they meant something like "The results from a rigorous, inclusive analysis do not agree with *what I know to be true about these organisms*." Then it was fair game to ask the person, "How do you know what is true about these organisms?" The answer usually was "Because I do."

Naturally much of the class's materials were about herps, and a particularly interesting paper that we re-analyzed was by David Wake,[3] concerning the evolution of the feeding apparatus in plethodontid salamanders. Most phylogenetic analyses of this group were based on the arrangements of bones and muscle attachments of their complicated projectile tongues. Wake had studied these systems extensively, and he saw a lot of parallel or convergent evolution. He worried that these problems were so profound that plethodontid phylogeny simply could not be tested properly, and his paper includes the provocative statement "If homoplasy is rampant, existing cladistic methods fail."[4] Professor Kluge perceived the attitude as defeatist, and it grated on him (perhaps especially as it was coming from a friend of his, a contemporary student of Jay Savage), and I remember him practically quivering with frustration during the class discussing that paper. "How can David say such a thing? He hasn't even *tried*!"

I was completely taken with the cladistic method (which I thought that I truly understood, on both computational and philosophical bases) and the spirit of rigorous inquiry and intellectual honesty that Professor Kluge engendered. I asked him to mentor me through my preliminary exams, for which I wrote a review paper about species concepts (using the western plethodontid species *Ensatina* as an empirical example of how different concepts would address the problem of a ring species), and tested Wake's pessimistic statement as a research project. I presented the results[5] of that analysis at my first Hennig meeting in College Station, Texas in 1995; word apparently got around, and I was subsequently invited to give the same talk at the SSAR meeting[6] in Lawrence, Kansas, in 1996, where I distinctly remember being closely grilled by the well-known anatomist, David M. Sever. David started his questions to me after my talk with the sentence "Are you aware that you've been using the wrong terminology this whole time?" I was taken aback to say the least. Fortunately a gentle chuckle rippled through the crowd at that point, and I knew that the questioner must be one of the people actively engaged in the contemporary debates about the developmental origins of the ceratobranchials (and that his dispute about terminology was therefore aimed more at David Wake than at me). I'm not sure whether he was completely satisfied with my answer (which was that, for my narrow purpose of retesting Wake's claim, it didn't matter whether I was "correct" as long as I was consistent), but he was willing to let it go and we had a good exchange after that about my work.

After such a positive prelim experience, I asked Arnold if I could keep working with him on phylogenetics, even if it meant abandoning turtles or salamanders. I was especially interested in using DNA data for phylogenetic reconstruction, which at the time was still rather rare in zoology, being both expensive and logistically difficult. Fortunately, the Museum had recently acquired its own DNA sequencer, and it was suddenly not unthinkable for a graduate student to do quite a bit of sequencing, as long as they were willing to do all the lab work themselves. Arnold and I talked about a few ideas, settling quickly on the molecular systematics of monitor lizards (*Varanus*). He had done previous field work in Australia where *Varanus* is the most diverse, had good contacts with local herpetologists and institutions, and had already collected some tissue samples from vouchered specimens.

We wrote an NSF grant together in hope of getting funding to go to Australia to collect more tissue samples for me and more whole specimens for the morphological work he was going to do. We sometimes talked about our plans in the herp division library during lunch, and one time he said, hardly able to hide a big grin, "If we're going after big goannas, we're going to need to get a big gun. You can't use a .22, those just bounce right off of 'em." He had very much been looking forward to collecting in Australia again, and he was upset when we didn't get the grant; I had not seen him so unhappy before, and I didn't again until years later when his pet Australian blue-tongued skink Grooter died. I was disappointed too, but at least I learned a lot about writing a grant, though the day-to-day experience of it was occasionally a little like a Dilbert cartoon, with Arnold standing behind me while I typed, pointing at the screen and saying "Click there!"

Life as a herp division student was really good and took on a satisfying, if short-lived, rhythm. Ron Nussbaum and Chris Raxworthy would return from research trips to Madagascar loaded with specimens, and it would be all-hands-on-deck in the herp division for a few weeks. I served as the division research assistant (RA) during a few of these specimen influxes, learning much about curation and specimen preparation from collection manager Greg Schneider. Under his tutelage, my lizard-skinning skills went from zero to "not bad," and he taught me important taxon-specific tips like how to skin a *Varanus* skull without damaging or detaching its palpebrum; this tiny thin slice of bone partially protects the orbit and is nearly indistinguishable from skin, and therefore easy to miss and slice off. (To this day I am still proud of a beautiful *Varanus beccari* specimen that I prepared solo.) Greg's commitment to good curation practice extended to data management, on the theory that collection data need to be planned for and tended almost as much as physical specimens do. I adopted his attitude and still consider data as a collection that needs to be curated; this attitude has saved my bacon on more than one occasion, both in my scientific life and in more mundane things like accounting and dealing with modern media libraries. Because I was the person who had most recently ransacked the herp division's burgeoning tissue collection, Greg put me in charge of starting to catalog and curate this growing divisional resource. Curation is hard work requiring an alert mind; fortunately, Greg made excellent and strong pour-over coffee—clearly a hipster well ahead of his time.

Another great thing about being a herp division grad student was the chance to go on the herpetology class's spring field trip to the Great Smoky Mountains, which is a hotbed of diversity for lungless salamanders (i.e., the same salamanders with the complicated tongue-projection mechanisms that we had analyzed in Arnold's systematics class). Enrolled students had priority, but there was usually enough room for others to tag along, and I ended up going three times. I have a lot of fantastic memories from these trips—of the beautiful nature, of the brightly colored salamanders to be caught everywhere, of the freezing cold hip deep meltwater that we were standing in, looking for hellbenders, and there are many stories that are not of general interest. However, I would like relate one small anecdote, because it taught us some fantastic local dialect. During a salamander collecting outing, a student ran into two local fellows, who asked him what we all were doing running around in these middle-of-nowhere backwoods. "We're collecting salamanders," he told them. They laughed. "Salamanders! You don' want to be messin' with *salamanders*, they'll bite your fingers off!" The student replied that there were 15 of us pulling salamanders out of the creek, and no one had lost any fingers, and anyway, how could one

Herpetology class trip, 1995. *At rest after a hard morning collecting salamanders. Foreground: Jennifer Ast. Next row, left to right: John Constable (sitting by tree), Karen Glennemeier (lying down), Heather Heying (sitting). Back row: Three unknown students from the class. Photo by Brad Moon, Teaching Assistant (whose note accompanying the picture read "What a bunch of lazy herpetologists!"*

of these bite your finger off? The student held up his plastic baggie with orange *Gyrhinophilus* and yellow *Eurycea* as evidence. "Oh, them? Them ain't salamanders, them is spring lizards," they said. The student replied, with as much dignity as he could muster, "I assure you, sir, these are salamanders." The locals laughed loudly, gave him some of the ramps they had been collecting, and went on their way. "Them ain't salamanders, them is spring lizards" became the go-to catchphrase for the rest of the trip. (In this volume, Brad Moon mentions that someone on one of these trips may have kissed a hellbender. I plead the Fifth.)

Herpetology class trip, 1995. *Four young herpetologists lunching in front of the Franklin Motel. Left to right: Jason Head, Karen Glennemeier, Heather Heying, Jennifer Ast. Photo by Brad Moon, Teaching Assistant.*

Meanwhile, in Michigan, Arnold's *Varanus* tissues were a serving as a good start for my thesis project, but we wanted more, and it wasn't always possible to get DNA samples with good vouchers. Some species of *Varanus* are popular in the pet trade, and we got two of our samples as live hatchlings from a herp swap meet (the museum equivalent of "they fell off a truck"). The baby lizards lived in Arnold's office in terraria on the larger of his two desks, and we took turns feeding them pinkies. One day it was my turn to feed the lizards—Arnold had left for the day—and I got two pinkies from the freezer to warm up, putting them on Arnold's desk so that I wouldn't forget about them, and then promptly forgot about them. There is no feeling in the world like waking up at 2:00 am because you've suddenly remembered about the two dead mice you've left thawing on your advisor's desk. I got myself to the Museum extra early the next morning, but not early enough. I knocked politely on his half-open office door, preparing my apology, but I noticed that he had been sitting at his smaller computer desk instead of his larger desk, where I could see the mice (now lying in a small pool of melt). My planned apology quickly turned into a request for something from his personal library; when he got up to fetch it, the mice (now quite squishy) disappeared into my pocket. I thought back to my late-night turtle photocopying in Steve Arnold's lab at Chicago: why bother people with things they don't need to know about? (To this day I still don't know if he had noticed.)

Even though we never made it to Australia, I still met some interesting characters in my quest for samples of *Varanus*. A thriving pet trade in monitor lizards means that there are businesses providing those animals, and one source we heard about was something called "The Goanna Ranch" somewhere outside of Tucson. Arnold said that most herp enthusiasts have plenty of mortalities, even with the best care, and that there might be some specimens to be had there. I had reason to visit Tucson anyway, as my in-laws live there, so I thought I'd give the Ranch a try. I bought a big red picnic cooler and some ice packs and one afternoon we drove my father-in-law's pickup truck out to The Goanna Ranch. The owner, Frank Retes, was a gracious host, giving me a tour of his elaborate facilities (these animals were cosseted and well cared for), and he did indeed have a freezer full of dead lizards. He asked what I wanted and gave me them, then kept throwing in a few more, and I left with a cooler packed to the brim (and he was left with considerably more freezer space).

Later in my project, I added several snake sequences to test the widely held idea that snakes are especially closely related to varanids. At this time, Arnold was running a seminar that we called "Jokers," the purpose of which was to think about Hume's problem with inductive inference. Other Jokers members besides myself were John Sparks (from the fish division) and Dan Graf (from the mollusk division). One day I told the group about an interesting thing that has happened in snake mitochondrial DNA: the more advanced snakes have a duplicated control region. "But how on earth could you tell whether having an additional replication origin is adaptive?" either John or Dan said. "You'd have to fight 'em!" answered the other one. We had a good laugh about that, but Dan went further, somehow roping Jerry Smith (contemporary Museum chair) and Diarmaid Ó Foighil (current Museum chair) and two other grad students into a photo stunt. The five of us stood in the downstairs lobby of the Museum clutching fistfuls of cash and cheering, and Dan photoshopped in a stock image of couple of entwined snakes (probably they were mating not fighting but never mind), drew black bars over our eyes, and passed around the picture as a "Wanted"-type poster about the Museum's underground snake-wrestling gambling ring.

Around this time, some fossils were adding fuel to the debates about snake origins. One particular fossil, *Pachyrhachis*, had originally been identified as a varanoid lizard, but a report in *Nature*[7] re-identified it as a snake. I added lots of morphological characters to my dataset so that I could include *Pachyrhachis* and fossil varanoids like mosasaurs, and I was trying to write up the results in a short manuscript appropriate to submit to *Nature* in response to the *Pachyrhachis* paper. I handed Arnold a draft with an accurate but boring title; among his comments back to me were "Needs a better title." I couldn't think of anything good and was annoyed (both at myself and his comment), so the next draft he saw from me had the sensationalist title *Snakes: Horrifying New Evidence!* The text I got back from him had the word *Horrifying* crossed out in red ink and replaced with the word *Horrific*. (And then we had a long discussion about which word was more grammatically appropriate. The vestigial hind limb of this incident survives in the text's final title, *Snakes*: *Not what you thought they were*, which Arnold approved of, and eventually I presented my results in a talk at Chicago's Field Museum.[8])

My understanding is that Arnold has a tough reputation in certain circles, and some other graduate students were intimidated by him. But he was also tough when defending the program against outside threats, for example from the University's own administration. The year that I was serving on the graduate affairs committee, the chair announced that the administration wanted to cut block grant funds drastically to biology students. Arnold was furious, and he accepted the task of personally going around to administrators to convince them that these cuts were going to be disastrous for many students. And he managed to do it, too. I am sure that the administration eventually won out and cut funding, but at least for that year, any biology or Museum graduate student who got a block grant funded had Arnold to thank. He was also supportive of the (fortunately short-lived) graduate student strike that happened when the administration threatened to no longer provide health insurance to graduate students, even those who were teaching. (I'd like to note in passing that the call for a strike vote was made by Museum of Zoology graduate student Nancy Shefferly, who was working with Dick Alexander.) When I started working with Arnold I was his only student (and I was his first female student, I later learned), but I was soon joined by my friend Heather Heying, who I believe had been encouraged by my positive reports. Heather and I were frequent officemates over the next couple of years and talked quite openly about many, many things, both academic and not: one thing we always agreed on was that Arnold had our backs.

And anyway, Arnold's intellectual tough-guy act had its limits. I remember a graduate student in paleontology giving a talk about dinosaurs, in which he extrapolated an amazing amount of natural history data from a tooth fragment. Some of his conclusions seemed a little far-fetched to me, and I said so. Arnold chuckled. "Oh lighten up, it's *dinosaurs*," he said in an indulgent tone I hadn't heard before. At the time, I was completely scandalized!

The incident about "should the title read 'horrifying' or 'horrific"' had made me a little hesitant about presenting Arnold texts with crappy titles, and this timidity would come back to bite me. At this point, I was getting close to defending my thesis, and I had to go to the University printing office to arrange various mundane aspects. This visit had to be made many, many months in advance of the thesis defense[9] itself, and one question they had that I (ridiculously enough) wasn't prepared for was *Title of thesis:* _______. I hadn't yet come up with anything that I liked, so I asked the office worker taking down my information if I could change the title later. "Oh sure, no problem" she said. I relaxed; this was just a bureaucratic placeholder. Feeling frivolous, I filled out that line like this: *Title of thesis: Lizards 'n' snakes 'n' stuff.* Predictably, that's the title that ended up on subsequent official emails and announcements about my thesis. As far as I know, to the University of Michigan bureaucracy, that is still its official title.

Acknowledgements. I thank Greg Schneider for inviting me to contribute to this volume, and for his comments and suggestions on early drafts. Linda Trueb and Brad Moon also offered valuable comments on previous versions. Many people helped and encouraged me throughout graduate school, more than can be comprehensively listed here. That said, I'd like to especially acknowledge the help and support from Arnold's other students, Glenn Fox (whose enthusiasm for herps buoyed me up more than he knows) and Heather Heying (for meaningful chats and moments of hilarity, and for giving me the impetus to see Crater Lake and Yosemite). I would also like to thank the Museum's administrative staff, both of 25 years ago and now—they tend not to get as much glory as professors, but their contributions and knowledge are vital for our work.

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As an evolutionary biologist, Jennifer undertook research on reptile evolution at the University of Chicago as a part of B.A. completed in 1992. She continued to study reptiles for her M.S.(1993) and Ph.D.(2002) at the University of Michigan. Subsequently, Jennifer had two postdoctoral positions at Uppsala University; in the first, she studied the luminous bacterial symbionts of marine organisms, and in the second, she used metagenomics to investigate the ecology and diversity of free-living fresh-water bacteria in Swedish lakes.

Jennifer elected to stay in Sweden, where she studied Swedish at the university and worked as a tutor in academic English at the university's Language Workshop. This experience brought home the difficulties scientists encounter in writing and speaking in English as a second language. She has started her own company, AST Clear Text, in an effort to help researchers at all levels communicate their academic, scientific, and technical ideas.

BRAD R. MOON

A Herpetologist at The University of Michigan in the 1990s

1992–

Finding My Way

When I spoke with Greg Schneider about writing this essay, he suggested writing about what it took to become a successful herpetologist. Having taught herpetology, advised students in herpetological research, published in herpetology, and served as the editor for the journal *Herpetologica*, I certainly had become a successful herpetologist. So, does that mean I know what it takes for others to become successful herpetologists? Even though I was successful, I found it hard to answer that question because the answer must vary greatly from one herpetologist to the next. Each person has to make their own way through their training and career—to develop the knowledge and skill they need for advanced study, find mentors, gain experience and complete projects, develop professional relationships, address difficulties that come up along the way, and so on. Besides requiring a deep interest in and research on amphibians or reptiles (Figure 1), for me it also took guidance from teachers, hard work in a wide range of courses, professional engagement through conferences, as well as reviewing manuscripts and grant proposals, and also nearly an entire second education in the process of writing, revising, and ultimately publishing solid work. Although I had begun building this foundation in college, some of the strongest elements were developed in graduate school at the University of Michigan and the Museum of Zoology.

My first connection with herpetology at The University of Michigan was indirect, in late 1988 or early 1989, when Carl Gans (Figure 2) visited George Zug at the Smithsonian Institution while I was working as an informal intern with George. It was shortly after I had graduated from UC Santa Cruz and moved across the country from the West Coast. I think Carl was in Washington on other business and visited George to discuss work on the *Biology of the Reptilia* series. Carl and George had known each other and worked together for years, and they seemed to enjoy the meeting. I knew of Carl from reading *Biology of the Reptilia* chapters for undergraduate projects, and the meeting served as the starting point for some deeper conversations with George about my interest in snakes and their movements.

Figure 1. *In 1994, I had the opportunity to take some measurements on a 3.5-m long Reticulated Python (*Python [Malayopython] reticulatus*) in Carl Gans' lab at Michigan. Although large snakes such as this python have beautifully large muscles that can be studied easily, my dissertation research was on locomotor and feeding movements in smaller colubrid snakes because they were available in larger numbers and were easier to house and handle. Photograph by Leandro Monteiro.*

I didn't know much about experimental research at the time. I had grown up in California chasing, catching, and learning about lizards and snakes, like so many herpetologists-to-be. I had also recently done field work for my undergraduate thesis on the biogeography of amphibians and reptiles in the Providence Mountains, far out in the eastern Mojave Desert, under the supervision of Ken Norris and Maggie Fusari. From my field experiences, I knew that snakes could move in surprisingly complex ways. I was particularly fascinated by constriction, which involved a snake coiling around prey and squeezing to incapacitate or kill it before consuming it. A similar coiling-and-squeezing behavior was often used defensively around the hands and arms of a person handling a freshly caught wild snake.

I had always wondered how snakes could squeeze so strongly during constriction. George had also observed the same behaviors and movements in snakes, as many others have. We talked about whether or not snakes might use some kind catch mechanism to sustain squeezing pressure without using too much energy or fatiguing, perhaps like the mechanism that mollusks use to keep their shells closed for long periods. We didn't think that seemed likely, but nobody knew because the mechanism of constriction had never been studied beyond simple observations that suggested it suffocated the prey animals. I went back to work with George on morphological differentiation among unisexual and bisexual geckos in the South Pacific[1], but I kept the ideas we had discussed in mind for a long time. I thoroughly enjoyed working with George Zug and living in Washington, D.C., for a year, and I later wished that I had stayed longer.

Instead of taking a second year off from school, I chose to go to graduate school at the University of Arizona (UA) in Tucson because I had become interested in desert environments and animals through my undergraduate thesis project and wanted to return to them. The Sonoran Desert and northern ranges of the Sierra Madre were wonderful places to learn about deserts, environmental transitions, and associated faunas, especially the diverse and abundant reptiles in those environments. However, at the time, most of the faculty members and graduate students in the Department of Ecology and Evolutionary Biology at UA were strongly focused on question-based research, with a bent toward theoretical work, rather than on organismal systems. They gave the impression, at least to me as a beginning graduate student, that some of the classical fields in zoology, such as herpetology and the other vertebrate "ologies," as well as the museums that supported them, were considered to be old fashioned, no longer cutting edge, and therefore not particularly valued. The department did house a museum, but I didn't have much opportunity to see it or make use of it. The curator Chuck Lowe was nearly retired and not available for meetings, and his students were close to graduation or in the field most of the time I was there. The herpetology collection, and to a degree the museum as a whole, did not seem to be a very visible or active part of the department at the time. This all came as a shock to me, because I had been impressed with the research activity in herpetology and organismal biology from earlier visits to the Museum of Vertebrate Zoology at UC–Berkeley and the California Academy of Sciences, and then in my work with George Zug at the Smithsonian. But most of those previous experiences with herpetology and museums came very early in my training, and I hadn't learned enough yet for me to develop any deep understanding of their value and place within biology. So, encountering this seeming disregard for organism-based research started a kind of professional identity crisis for me that has been reignited by circumstances several times. By "identity crisis," I mean a struggle to define my research and career goals for myself, as well as how I might describe and promote myself as a job applicant, speaker, author, grant proposal writer, etc., in the future. One of the first important steps in beginning to resolve the crisis was my move to The University of Michigan, where productive question-based research, organism-focused research, and an active museum all thrived side by side.

Initially, I visited Michigan the summer of 1991 to work in Carl Gans' lab and learn some specialized techniques. I had gotten in contact with Carl and asked about the possibility of learning techniques for studying movement, and said that I would be happy to work on any project that would also be of interest to him. He welcomed me and suggested that I could do a project on snake locomotion, one of his many well-established lines of research. Carl's willingness to let me visit his lab and start a project when I had essentially no experience, as well as no commitment or accountability because I wasn't even a student at Michigan, showed an admirable flexibility. In retrospect, knowing what I

Figure 2. *Carl Gans with a small Puerto Rican Boa (*Epicrates [Chilabothrus] inornatus*) in 1996 when Carl taught part of short course on functional morphology at the University of Puerto Rico and I went as his assistant. Richard Thomas took us in the field where we found* Amphisbaena schmidti, *which Carl had described, and the boa.*

know now about the many demands on a professor's time and how risky it can be to assign inexperienced students to work with delicate and expensive equipment, I'm still stunned and impressed by his open-minded willingness to give an unknown beginner a chance. He welcomed me to the lab, taught me his techniques, and gave me the freedom to use the lab space and equipment as if it were my own. That welcome and freedom were incredibly important to me as an aspiring scientist, and ultimately gave me a new direction for my training and career. My visit to Michigan and work with Carl turned out to be pivotal professionally and personally. By the end of the summer, I knew that I had found the kind of work I really wanted to do. When I returned to Tucson that fall to finish my Master's degree at the University of Arizona, I already had the goal of returning to Michigan for my Ph.D. if possible, and finally did make the move to the doctoral program at Michigan in 1992.

Rumors of Peril

Before I visited Carl's lab and joined the doctoral program at The University of Michigan, I had heard about some of the larger-than-life reputations and strong personalities there. The university and museum were well known and well respected, and many of the faculty were recognized as excellent scientists, but also for being extremely challenging to work with. I had also heard that certain faculty members didn't get along with one another, particularly between the biology department and the museum, and even that they wouldn't serve on dissertation committees together. Although these things were a little discouraging, I didn't let them deter me. I don't know why I felt that way, because I certainly didn't think I had any special ability to deal with these kinds of interpersonal challenges. I suppose I thought that if that's what it took to get the degree and career I was after, then that's what I'd have to go through. Also, there might be similar professional perils anywhere, but at least here I was forewarned.

Fortunately, I learned fairly quickly that I could make my own way through graduate school without those kinds of conflicts becoming serious obstacles. Carl and every other person I had heard rumors about was welcoming to me and to other students. They each recognized that their colleagues had valuable things to teach, whether they liked each other or not, and they welcomed students who were willing to learn from everyone.

When I joined the doctoral program and Carl Gans' lab at Michigan, I already knew a bit about what I was getting into from my experience on the summer project with Carl on snake locomotion. That summer had gone well, and it had given me a direction for a dissertation. I had also experienced many of Carl's strengths as a scientist and mentor, as well as a few of the challenges of working with him. I had already learned to be as straightforward as I could with Carl, and that he would be so with me. In one of our early advising meetings, Carl told me that, over time, I would likely meet people who would be very helpful to me because of their friendships with him, as well as some people who would probably not be very helpful to me because of a difficult history with him. I appreciated that he was willing to be straightforward about topics that not every advisor would discuss with students. His honesty was a great help to me then and over the coming years.

Not long after I arrived and had become friends with other grad students at Michigan, Russ Burke told me that some of the more advanced herpetology students had wondered aloud with each other how long I would last in Carl's lab. He explained that they weren't talking about me, because they hadn't even met me when they first heard a new student was joining the Gans lab, but rather about Carl's reputation for being hard on students and having few graduates from his lab. I knew about this history, and I even wondered about my own likelihood of surviving. I didn't think I could do anything that others before me couldn't do. I had just given it a try with the first summer project, found that it went well, and went for it. Sometimes you just have to hold your breath and jump in, sink or swim, even if you see risks ahead. Happily, it worked out, I swam (Figure 3).

When I had a few conflicts with Carl, I decided that I had to sit down with him and talk about them. Each time, I said that working there was important to me and I hoped to him too, explained what I was having trouble with and why, and then talked about how I wanted to work things out so that I could continue. It wasn't easy to go through at the time, and on at least one of those days I really thought it might be the end of my work there, but each time Carl surprised me. After a little resistance to my suggestion that his behaviors were partly at issue, in addition to mine, when I persisted as diplomatically and respectfully as I could, he responded well and supportively. Had others before me tried a similar strategy? Or had they lashed out with angry arguments, like I sometimes felt like doing? I don't know. Did I have some diplomatic skill that they didn't have? I doubt it, given the kinds of leadership roles that many of those people went on to achieve in their careers after leaving Carl's lab.

Had Carl changed by the time I arrived in his lab? Although I didn't know him earlier, I had spoken with his most recent students about their experiences, and I do suspect Carl had mellowed. I also somehow—miraculously—figured out early on that even when I was feeling stressed or angry, I had to approach Carl with calm respect, and not with anger. Somehow, I knew I couldn't speak harshly with him the same way fellow students and friends can often do with one another. I think each of these factors, things I had learned and ways he had changed, contributed to my success with Carl.

The lesson I learned was to take every opportunity to learn from people, even if scary reputations precede them. It may not hurt to have a backup plan if something doesn't work out. But even in that case, do the same thing with new people, approach them openly and seek those opportunities. Each professional relationship you make is unique to you and that other person; and people change over time, so even people with famously difficult personalities might turn out to be valued mentors and colleagues.

Figure 3. *Evidence of my successful Ph.D. dissertation defense with, from left to right, Carl Gans, Paul Webb, myself, Ron Nussbaum, and Dan Fisher. The University of Michigan, 1998. Photograph by David Bay.*

Working in Carl Gans' Lab

To me, as a student with little experience in functional morphology, Carl Gans' lab looked like part biology lab and part electrician's shop. The main lab room was long and rectangular, and partly divided by a long wall that made the room into a large U-shape. You entered at the top of one arm of the "U" near Carl's private office, and went to the right around the dividing wall to reach the benches by the windows. Just inside the door from the hallway, cabinets and a lab bench were lined with jars of chemicals for anatomical preparations. Around the dividing wall there were dozens of cables and tools organized on a neat array of hooks along one wall, and there was a long work bench with microscopes and space to work in the bright light of the tall windows. It was a wonderful work environment that provided the peace and quiet needed for focused detail work, even if there were people coming and going in the outer office and hallway. Along the side wall at the turn of the U-shaped room, there were three smaller adjoining rooms that housed recording equipment, space for experiment setups, and the live research animals. The two rooms closer to the windows were designed as walk-in Faraday cages, each with walls lined with heavy copper screening and copper plating on the insides of the doors to isolate them from any electrical noise. The rooms connected internally via small circular ports, through which we ran cables between the recording equipment and the experimental arrays. It was always an interesting experience walking into the small, dark, copper-lined rooms that felt like—and actually were—big cages. As I walked in, and especially whenever I closed the door, it almost felt like I was one of the experimental animals.

In Carl's lab that first summer, we started a project on the muscular control of lateral undulation in snakes. To set up the experiments, we needed to build an elaborate set of small environments in which the snakes could move, so a lot of the work involved basic carpentry and mechanical problem solving. We bought 4 × 8′ sheets of plywood, sanded them smooth, and then painted one with sand in the paint to give a consistently rough texture, whereas the paint on the other was completely smooth; then we fitted a series of pegs for the snakes to push against as they crawled. That was the first of many times that I had to build something I needed for research, and these essential mechanical skills have been useful many more times over the years.

In the recording room, I set up the rack of amplifiers for recording muscle-activation patterns and a large reel-to-reel tape recorder for recording the signals. That was before equipment like this became small enough to fit on a desk, just as personal computers were becoming powerful enough to digitize multiple channels of data in real time, and more than a decade before all of those data could easily fit on a USB drive you could carry in your pocket. For the experiments, I ran cables through the ports in the wall from this array of recording equipment to the experimental chamber where I had set up the testing surfaces. The cables passed through the wall and hung from the ceiling down to the testing area so that they could be linked to electrodes implanted in the snake's muscles without interfering with the snake's movements. A video camera on a tall tripod above the testing area was set up so that we could sync the visual recording of the movements with the electrical activity of specific muscle groups. One of the trickiest skills I had to develop was how to make tiny wire electrodes under a microscope and implant them precisely into the muscles along the snake's back and sides to record the patterns of muscular activation as the snakes crawled across the different test surfaces and pushed against arrays of pegs with different spacings.

I continued this work as part of my dissertation project and expanded it to include similar recordings of muscular control in other movements, including constriction and swallowing. While I was at Michigan, I read David Hardy's 1994 paper[2] arguing that circulatory arrest, not suffocation, was the key mechanism of incapacitating prey during constriction. His evidence for this idea was mainly that rodents succumb much faster during constriction than they would if suffocation alone was the primary mechanism. At a conference and through email, I was glad to have the opportunity to show Dave my work and discuss the possible mechanisms of circulatory arrest with him. As a physician, he understood and explained possible mechanisms for how pressure exerted during constriction could disrupt circulation and incapacitate prey faster than suffocation alone. His 1994 paper, coupled with my interest in the strength and diversity of constriction behaviors, and the techniques available in Gans' lab, inspired to me to study constriction as part of my dissertation work. I could test whether the same large spinal muscles were used in constriction movements as in locomotion, and if constriction pressures were high enough to disrupt circulation in rodents[3]. I also started thinking that a snake swallowing a large meal was somewhat like an inside-out form of their locomotion movements: They used similar undulatory movements of the spine to swallow prey once it was past the jaws, but must be exerting those forces inward instead of outward. So I decided to let my snakes swallow their prey after constriction, while I continued to measure their patterns of muscle activation and the pressures exerted. I spent many long hours across several years in the Faraday-cage rooms, recording the snake movements across plywood surfaces, and feeding them so that I could study their constriction and swallowing.

Working with Carl was rewarding, even through a few challenging times. In those years, Carl worked long hours at home on writing in the morning, and then would come to campus for the afternoons to do some lab work and editing work on the *Journal of Morphology*, and check in on my activities in the lab. I made a point of asking him to come in and look over my experiments before I began anything new. I needed the guidance, especially early on, and he valued being included. I also asked for Carl's help when I had technical problems or made mistakes with my experiments, such as mixing up the cable connections during one early experiment and getting very confusing results. Carl always helped me troubleshoot the problems and try to understand unexpected results. He was good at helping me systematically check the experimental setup, and when that looked good, he was always willing to be convinced by data about unexpected ways that animals work. These regular interactions with my advisor were incredibly important for my success in graduate school and may have been one of the key reasons why my interactions with him typically went smoothly. Asking for help with the problems I encountered early on was so productive that I never, or at least rarely, gave in to later temptations to avoid Carl when I was embarrassed about mistakes or felt guilty about delays. A few times, I certainly was tempted to avoid him or hide problems, but I knew that doing so would be self-defeating, because I needed help and I needed him to see that I was trying to keep up progress even when it felt like I wasn't making any. I've seen a lot of graduate students struggle with this balance, and run into serious conflicts with their advisors because they keep evidence of their mistakes or discouragement hidden to try to avoid being criticized or thought less of by their advisor. I've learned since then that many times when an advisor pushes for frequent progress reports, or even seems angry or disappointed about problems, it usually means at least that he or she still cares about the student's progress and wants things to work out. These kinds of problems in a lab aren't really that serious until this kind of avoidance goes on so long that an advisor stops asking for updates and stops caring about progress. The truer sign of a graduate career being in peril is when as advisor stops paying attention at all. At that point, it can be hard to rebuild the relationship or count on your advisor having good things to write in recommendation letters for the next move you need to make. I didn't know about all of these dynamics while I was in graduate school, but fortunately I chose early on to face difficulties rather than avoid them. Carl's positive responses and support made it easy to keep up that good habit later. And this lesson has been invaluable to me as an advisor myself.

Carl's afternoons often started with coffee. At first, he had a habit of asking me to go get it for him from the café across the street. I saw this kind of request as a bit out of bounds. It's the kind of personal errand one can reasonably assign to a personal assistant, but I felt that this chore shouldn't be the duty of a student. Instead, I suggested we should go together and talk about our current work. It turned out that walking together on this small errand on so many days provided valuable opportunities to get to know each other more personally. I often had a list of questions ready, because I wanted to make sure I didn't forget any of them, but there was never a shortage of things to talk about. We talked about my preparation and lab work, relevant papers both new and classic, and work he was doing on the journal. We started many afternoons that way, after which he would join me in the lab to see how things were going and give guidance as needed, and then he would head home while I worked on in the lab. It was very fortunate for me that my preference for afternoon and evening work was compatible with his similar preference and schedule, because having these regular easy interactions provided opportunities for questions and discussions that might never have come up if all our meetings had to be scheduled around other activities. Importantly, it also gave me consistent and easy access to his knowledge and feedback, and the chance to show him my progress regularly.

We resolved a major mechanism of limbless locomotion in snakes together[4] and, with Carl's guidance, I figured out a critical mechanism of constriction[3] and how snakes swallow large meals whole[5]. Some of these problems, such as the mechanism of undulatory propulsion in snakes, had been perplexing to observers for centuries, and all of them were important not just in herpetology but also in comparative morphology and physiology as well as evolutionary biology. We enjoyed feeling that we were solving some long-standing biological mysteries together and understanding better how snakes moved in such complex ways given their simple body form.

The Museum of Zoology

Carl's faculty appointment and lab were in the Department of Biology, which was housed in the Kraus Natural Science building, a few blocks across campus from the Museum of Zoology. Soon after I arrived at Michigan, Carl recommended that I get to know Ron Nussbaum, Arnold Kluge, and other faculty. He encouraged me to develop my own relationships with everyone I could in my fields of interest, independent of his own sometimes difficult relationships with the same people. I had also hoped to have the opportunity to get to know the museum anyway, so I gave it a try, even when I was a little anxious about the difficulties that I might encounter. I soon met fellow grad students who were doing their research in the museum, the collection manager Greg Schneider, and curators Ron Nussbaum and Arnold Kluge.

Figure 4. *Lunch in the herpetology library at The University of Michigan Museum of Zoology, 1997, showing me (left), undergraduate Glenn Fox, and Arnold Kluge (right).*

I remember being shown the herpetology library for the first time and marveling that there was such a fantastic library with virtually everything relevant to the field of herpetology all in one place. The herpetology group at the museum had lunch in the library every day, and before long I started joining them. At the time, the lunches usually included Greg Schneider, Arnold Kluge, Alan Wolf, Sheng-Hai Wu, and Russ Burke. Ron Nussbaum would drop in occasionally as well, but often worked through lunch in his office. Then one day, within the first few weeks after I started to attend, everyone was out except for Arnold Kluge and me. I knew Arnold's fierce reputation, but I hadn't had the chance to speak with him much yet and hadn't really gotten to know him, so I was a bit nervous about saying something stupid, or just showing my inexperience and getting eaten for lunch myself. Fortunately, it turned out that the nerves were unfounded. I was surprised—and relieved—to learn that Arnold had a relaxed attitude about chatting over lunch. I continued having lunch with everyone in the herp library for years, and never ended up becoming the lunch (Figure 4).

Figure 5. *Greg Schneider in the herpetology library at The University of Michigan Museum of Zoology, 1997.*

Over time, I also had the good fortune to work with Greg, Ron, and Arnold. Greg was friendly from the beginning, which helped make it easy for me to get to know the people and facilities in the museum quickly. We had both gone to school in California and enjoyed talking about snakes and field sites we had known there. Before too long, I came to work with Greg as a curatorial assistant for a summer (Figure 5). Greg showed me how they recorded data for the specimens, and how the collection database as a whole was organized, maintained, and protected from damage or loss. He was serious about the work, but also had a good sense of humor that made the serious work fun.

Several aspects of working with the herp collection were particularly engrossing for me. In the process of moving the collection to another room temporarily while the main room was renovated for greater fire safety, we took an inventory of the entire collection and made sure everything was in the right place and in good shape, with all jars topped-up with alcohol and labels accurate and up to date. Because I especially enjoyed seeing species I hadn't known before, even the seemingly mundane work of collection maintenance was exciting for me. Sometimes unusual things would turn up. At one point, I was moving amphibian specimens with Sheng-Hai Wu, a senior grad student with Ron, and saw that many jars of frogs from Madagascar and elsewhere contained hollow but perfectly complete skins in their correct three-dimensional shape. Sheng-Hai said that he had cleared and stained the specimens for his dissertation research. He had done such a meticulous job of keeping the skins intact that they looked like the ghosts of those frogs floating in the jars. On another day, Sheng-Hai and I came across one jar with just a large snake's head in it from his home of Taiwan. Sheng-Hai said he collected that specimen. I asked what had happened to the rest of the snake, and with a big grin he replied, "I ate it!" I suppose I'll never know if he was telling the truth or just joking, but I suspect it was the truth. I've always wondered if that history is part of the data for the specimen. I would bet it is, knowing how thorough Greg was about specimen and collection data.

Another activity that usually drew in everyone in the herp division was sorting large collections of specimens that had just arrived from a field expedition. Christopher Raxworthy was a post-doc with Ron at the time, and they would bring back fascinating animals from their field work in Madagascar. Some of the specimens, such as some tiny frogs and burrowing lizards, may have never been seen before Ron and Chris discovered them.

As we processed the new specimens, many of them served as launching points for talking about things Ron and Chris had learned from previous work in Madagascar, things they had observed on this most recent expedition, and what they planned to study next about these and other specimens. Over several years of work in Madagascar, they discovered dozens, probably even hundreds, of new species of amphibians and reptiles, some with surprisingly distinct anatomies and lifestyles. Although I wasn't a systematist, I already appreciated the desire to learn about the identity, diversity, and relationships of animals, and it was exciting to see that modern systematists also used specimens and phylogenies to study broader topics, such as how history, speciation, and diversity related to environmental variation and ecology, among other things. Yet there was clearly still a critical need to recognize and document species diversity before more species were lost to extinction as we humans expanded our use of the environment.

In the course of Sheng-Hai's dissertation work on microhylid frogs, he had separated specimens into jars with letters, labeling them "Sp. A" and so on, as temporary labels for each new species before they acquired a formal name. When he ran out the alphabet, he began using double letters, Sp. AA, Sp. BB, etc. At the time I was there, I think he had nearly finished the double letters, and was ready to start using triple letters. And those were the new species just for one group of frogs. Ron, Chris, and several students were documenting the diversity of all of the amphibians and reptiles in Madagascar's rapidly dwindling native habitats. The need to document species diversity was and is still particularly acute in places like Madagascar and other hot spots of biodiversity where environments are being altered and lost faster than the full species diversity there can even be recognized. One of the many critical roles of the museum was to document natural diversity, both to help demonstrate the need to protect natural environments before they and their biodiversity were lost forever, and so that it could be studied into the future. Working in the museum gave me a sense of contributing to this critical mission, even if only indirectly. I was also glad to see again, and to understand much more deeply than before, that herpetology and the other organismal fields were still vibrant parts of modern biology and were continuing to make major discoveries about the diversity, history, and mechanisms of life on Earth.

Key Teaching Experiences at Michigan

After Ron Nussbaum's students had graduated, I had the good fortune to be his Teaching Assistant for herpetology three times. Teaching herpetology with Ron was a fantastic and formative experience for me. Ron's extensive knowledge and experience of the field was an exceptional model for me and having such an amazing world-class collection available for use in the course was a truly incomparable privilege. I got to teach with specimens of herps that I had never seen before, might never see again, and quite likely will never get to see in the wild. I also had the opportunity to lead herpetology class field trips with Ron to the Great Smoky Mountains for long weekends in early April for those three years (Figure 6), which first showed me how many undergraduates had really lacked the opportunity to encounter a diversity of animals in the wild. Our caravan of budding herpetologists would drive overnight the 650 miles from Ann Arbor to Highlands, North Carolina. We stopped only for a short breakfast in Pigeon Forge, Tennessee, and then headed into the Great Smoky Mountains for herping before continuing on to Highlands for some rest before afternoon and evening excursions. Our first field stop of

Figure 6. *Ron Nussbaum on a herpetology class field trip to North Carolina in 1996.*

the morning usually produced a spectacular variety of salamanders, including predatory *Gyrinophilus porphyriticus*, red-cheeked *Plethodon jordani* and *Desmognathus* mimics, and tiny *Desmognathus wrightii* as well as impressively large *Desmognathus quadramaculatus*. Throughout the trip, as we located each new kind of salamander, Ron would talk about predation, mimicry, life-history variation, and other topics, illustrating each concept with the details of the species in hand. In addition to opportunistic searching, we conducted timed surveys of a headwater stream and adjacent woodland along the shoreline for plethodontid diversity, to include a realistic sample of life as an amphibian researcher in the students' field experience. In the hour we would spend each time, we would count more than 300 salamanders!

Having class sizes that required several vans meant that I didn't often have the opportunity to talk to Ron on the long drives. Back on campus, I had found Ron to be quiet and sometimes hard to draw out in conversation, but I also always found our conversations very useful and engrossing once we did get going. On one trip, at last, I jumped at a chance to ride with Ron when we had to go back to retrieve something that had been left at our last stop in the afternoon, so I finally got the chance to know him a little better. In that hour or two, we got to talk more extensively about amphibian diversity in the southern Appalachian Mountains and some of the key people who had mentored him on his early field work. I wished that I had more opportunities like that to have long conversations with him, but there is always limited time and so many salamanders to see. We kept busy through the whole weekend, and always ended the trip by all wading in to a beautiful, clear, and very cold mountain stream to lift the larger, flatter rocks and find *Cryptobranchus alleganiensis*, before climbing back into the vans for the long drive home.

I took Arnold Kluge's course on phylogenetic systematics with friends and fellow grad students Jennifer Ast and Heather Heying, and Arnold's then-student Alan Wolf was the Teaching Assistant. Some of Arnold's early work had involved developing methods for inferring phylogenetic relationships, and he maintained deep interests in the processes of evaluating evidence and doing science throughout his career. He incorporated these interests into all of his research, including his current project on the phylogeny of varanid lizards and the evolution of snakes, and into his teaching. In Arnold's course, we studied ontology and epistemology, the nature of science, what constitutes evidence and how it can be interpreted, the nature of species, the nature of history and historical sciences, and how to read and critically evaluate scientific papers with these and other concepts in mind. It was one of the most stimulating learning experiences of my life. Jennifer, Heather, and I spent a lot of time asking Alan and Arnold questions about the more complicated material. In the second half of the course, we applied these concepts to phylogenetic systematics, then did our own course projects and gave presentations on them at a mini-conference at the end of the semester. We all worked incredibly hard that semester, but enjoyed it immensely. Jennifer and Heather eventually worked with Arnold as their advisor.

A year or so later, after Alan Wolf graduated, I had the opportunity to work as Arnold's Teaching Assistant for his course. This experience reinforced for me the importance of understanding the philosophical foundations of what we do as scientists. It's hard to overstate how important this has been to me professionally, to have spent this time early in my career studying the nature of science and scientific evidence, as well as the nature of evolution, with such deep thinkers as Arnold. Having taken the course with Arnold, and then having helped him teach it, I realized that I could easily have been hooked on systematics if I had been introduced to it earlier. But I was already too deeply interested in functional morphology and physiology to want to change fields by then.

Finishing and Starting

Through my experiences working in both the biology department and museum, and teaching in both practical lab and field settings as well as in more abstract arenas, it became clear to me that so many fields in biology, including herpetology, overlap and integrate extensively with one another, and most particularly at the leading edge of the field. The range of research within herpetology and this interaction among fields also underscores for me that there's more than one way to be a herpetologist. You can and should chart your own path through a career focusing on your own particular interests, experiences, and skills. You certainly don't have to be a systematist to be a herpetologist or work with a research museum. Herpetologists are also biologists in general, of course, as well as specialists in many other vital fields in their own right, such as behavior, biomechanics and functional morphology, conservation, development, ecology, evolutionary biology and systematics, genetics, neurobiology, paleontology, physiology, and many others. Although I didn't learn this lesson well until grad school at Michigan, it's probably nearly universal for herpetologists to consider themselves biologist in several broader senses.

Some of these lessons may seem obvious in hindsight, but they may not be obvious to many undergraduates and early graduate students, and they weren't clear for me until I went to Michigan. I learned that part of my struggle to define my professional identity was because of the complexity of the ways in which all the fields of biology interact and contribute to one another in fundamental and critical ways. The central importance of these interactions has been reinforced consistently since then, throughout my own research, teaching, collaborations, publishing and editing, and communication with colleagues around the world. After studying and teaching herpetology for more than 20 years, and eventually serving as the editor for *Herpetologica* (2009–2013), the world's highest-impact herpetology journal, I realized that my professional identity crisis was finally over. I'm a herpetologist and a functional morphologist, comparative physiologist, and evolutionary biologist. These definitions coexist peacefully and in a useful coordination. This identity helps me to understand and better explain the ways my work is important to scientific progress as a whole and how it integrates with and supports work in other fields in biology. This identity also helps me recognize the value of diverse approaches and resources, including experimental labs as well as museums and herbaria, to understanding the full complexity of biology. And this understanding, in turn, is important in guiding how I advise and educate students.

Early in graduate school, it was hard to imagine myself running my own lab and research program as a future faculty member, even though that was why I went to graduate school. I had felt intimidated by how much there was to learn, especially in comparison to how little I knew. Later, as I taught comparative anatomy with Carl and herpetology with Ron for the second and third times, I began to think about how I'd like to run my own courses, which topics I'd cover and how, and what I'd like to do differently than they did. I recognized that thinking about how I'd like to change courses by well-established and successful professors was a bit presumptuous, but also felt and hoped that maybe it meant that I was actually, finally, developing some independence that would help me run my own courses as a faculty member one day. I had the sense to keep many of the more presumptuous thoughts to myself at those early stages, although now

I wish I had taken the opportunity to ask both of them more about how they came to develop their particular courses, labs, and field trips, among other things about teaching in those fields.

My experience in working with strong personalities, although not something I sought out or initially wanted, turned out to be beneficial to me as a post-doc, faculty member, administrator, author, and journal editor. I have weathered some bad behavior from famously difficult people since then, including some extraordinary tantrums by senior professors who really should know better, and I knew how to respond. I also know how *not* to behave to my colleagues and students, thanks at least in part to some of the more difficult experiences I went through in grad school.

Carl Gans used to say that a Ph.D. was just a "union card," meaning that finishing a dissertation and earning a Ph.D. was really just the beginning of a scientific career. That thought seemed daunting to me as a grad student. We go to graduate school because we are interested in careers that require the degree. Yet while we're working on it, it seems like finishing a dissertation is such a monumental task, how could so much hard work really be only the beginning? That realization felt exhausting. Although the exhausted part of me didn't want to believe that, I knew it was true when I heard it. My post-doctoral work certainly drew on my knowledge and skills from graduate school, but extended well beyond that to fields and techniques I hadn't even encountered before. As a post-doc, I used many of the skills I had obtained in graduate school, including learning new things quickly and understanding, organizing, and communicating large amounts of complex information at a much more competent and confident level than I ever could have before. Additional skills I hardly knew I'd developed, such as advanced troubleshooting and problem-solving, making adjustments while under pressure and on a schedule, and understanding and being able to use statistics at the level of advanced reasoning rather than as received wisdom, also came to be vital in my new work. Finally, post-doctoral work also helped me complete the transition to independence by giving me a broader context and vision for my own future research. Carl was right, finishing graduate school was just a beginning, but by then at least I knew how to start.

Acknowledgments. In this essay, I focused on herpetologists at Michigan while I was there. However, I also valued interactions, even some very brief ones, with and guidance from many other individuals

at Michigan and elsewhere, including Kraig Adler, Peter Aerts, Dan Beck, Jim Birch, Beth Brainerd, E.D. Brodie, III, David Carrier, David Cundall, Tom Daniel, William Dawson, Stephen Deban, Frits De Vree, Robert Dudley, Dan Erickson, George Ferguson, Mark Fishbein, Dan Fisher, Jeannine Fret, Darryl Frost, Jean-Pierre Gasc, Gary Gillis, Karen Glennemeier, George Good, Harry Greene, Jason Head, Anthony Herrel, Sue Herring, Laurel Hester, Bruce Jayne, Ken Kardong, Paul Kosnik, Nate Kley, Fred Kraus, Harvey Lillywhite, Jay Meyers, Joe Mitchell, Leandro Monteiro, Ricardo Montero, Kiisa Nishikawa, Tim O'Connor, Jim O'Reilly, Tomasz Owerckowicz, Rob Raguso, Rick Relyea, Dale Ritter, Phil Rosen, Chris Sanford, Al Savitzky, Cecil Schwalbe, Kurt Schwenk, Mark Siddall, Jake Socha, Anna Bess Sorin, Adam Summers, Tom Taylor, Stephen Tilley, Garr Updegraff, Raoul Van Damme, Bieke Vanhooydonck, Katherine Wadsworth, Paul Webb, Bret Weinstein, and Bruce Young. I'm sure I had valuable interactions with others as well, but have temporarily forgotten the details; for that, I apologize. Many of these professional relationships continue to this day, and I hope into the future.

Endnotes

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Photograph by Dave Patton

After completing his B.A. in Biology at the University of California at Santa Cruz in 1988, Brad Moon completed an internship at the National Museum of Natural History with George Zug. He then moved to the University of Arizona in Tucson for his Master's before entering the University of Michigan doctoral program in 1992.

His research program is focused on the mechanisms and evolution of animal movement—in particular, the ways in which muscles work in natural behaviors such as locomotion, constriction, and swallowing in snakes. Brad also studies the relationships among muscle anatomy, mechanics, and energetics. His model system for this work is the tail-shaker muscle in rattlesnakes, which is specialized to sustain high-frequency contractions that reflect the relationships among muscle speed, strength, motion, and energy use. Moon's research also includes studies of the ways in which muscle strength and energy use are modulated by muscle-tendon interconnections and activation patterns.

Brad maintains an active graduate student program, curates the herpetological collection at the University of Lafayette, and has contributed professional editorial services to herpetological societies, as well as the International Congress of Vertebrate Morphology.

HEATHER HEYING

Specimens Don't Behave Much, but Scientists Do

1993–

Growing up in Los Angeles, I spent time with lizards. I watched them in the nearby dry hills, which fires ravaged periodically but which sprang into bloom every spring. My cat brought tailless lizards to my room alive and then rested on my bed; this was her signal to me that there was something for me to find. And so, I began to develop the observation skills necessary to study animal behavior, and the hands necessary to grab an unwilling herp and handle it gently, doing minimal harm to it or myself.

Years later, when considering graduate school, my unofficial undergraduate advisor at the University of California at Santa Cruz, the great Bob Trivers, gave me the following advice: "Go someplace with a museum," he said. "A really good museum."

"But I want to study animal behavior," I had protested. "Specimens don't behave much."

"You have no idea what questions you will want to ask," he said. "But more to the point—a world-class museum is a crossroads; it pulls people from all over the world. Go to such a place, and every week, every day maybe, there will be someone giving a talk, taking data in the collections. While they're there, talk to them. There's your education."

As in so many things, Bob was right.

During my time in grad school (1993–2001), I took relatively poor advantage of what the UMMZ offered in this regard, but it wasn't for lack of opportunity. For a few summers, I worked as the curatorial assistant for the Herp Division, tagging and preserving Malagasy herps that Ron Nussbaum and Chris Raxworthy had collected, while Greg Schneider reliably kept the mood upbeat and the work both honest and enjoyable. Researchers often did come through, along with faculty and grad students; casual conversations that arose during these visits while specimens were being examined and measured had a value that is impossible to quantify. We are encouraged to switch institutions between our undergraduate and graduate work to be exposed to a diversity of scientific backgrounds, epistemologies, and methods. I found that in the course of talking to people whose presentations I might never attend at a conference or whose papers I wouldn't read in a journal revealed assumptions of mine that I didn't even know that I had. As natural history collections began to fall out of favor worldwide by administrators who preferred high-tech research (and therefore high-dollar funding), it was ever more obvious to those of us on the inside what we would lose.

I stumbled into working on herps, when the monkeys I was trying to study in Costa Rica never showed up, and a natural experiment was happening right in front of me with dart-poison frogs. I was in Sarapiquí at a small field station (down the road from large and famous La Selva). *Dendrobates auratus,* a species with particularly vibrant green and black coloration, had been introduced by a local "ecotourist lodge," thereby illustrating that their priorities were rather more economic than ecological. It seemed to me that in the presence of *D. auratus,* the native dendrobatid, *Oophaga pumilio* (then *Dendrobates pumilio,* a congener), was more scarce and when found, the frog seemed quieter as well. My observations and experiments to test these hypotheses were fruitful, suggesting that the introduction by the ecotourist lodge would likely cause the native *O. pumilio*—smaller, but not exactly uncharismatic—to go extinct locally.

I spent one more season in Costa Rica working on dendrobatids, this time in Talamanca, near the border with Panama. Both *Dendrobates auratus* and *Oophaga pumilio* occur there naturally, so I could compare the behavior of the species in Talamanca with that of the frogs in Sarapiquí; in Talamanca, where the species were natively sympatric, they mostly ignored each other. But what I really wanted to do was test hypotheses about sexual selection and territoriality and study the evolution of social behavior and parental care. This meant I needed permits to collect some adult frogs and bring them back to do captive experiments on them. Whole screeds could be written on the difficulty of procuring and using such permits, of course, but three moments stand out for me.

Michigan's in-house vertebrate care committees—ULAM/UCUCA—mostly deal with applications for medical and psych research. Their paperwork asks questions about infectious agents, and monkeys and rats, and animals procured from breeding stores. Their paperwork did not see me coming. I wrote a very long application, filled out reams of forms, and gave it my all, because one thing I wanted to do was to test a hypothesis about cannibalism in tadpoles—specifically, that individuals would preferentially eat unrelated conspecifics instead of their own close kin. I found the hypothesis interesting and important but understood that it might not seem so to those whose job it was to protect animals from unnecessary suffering.

My application came back with all mention of my tadpole experiments crossed out. Steeling myself, I called them, prepared to defend the need to do this work. Did the eradication of my experiments from the application mean that I could not do them? Not at all! The kind people at ULAM/UCUCA were very patient with me, whom they perhaps regarded as a little dim. They explained, slowly, repeatedly, and in unbearably clear English, that tadpoles are outside of their purview because, of course, while frogs are vertebrates, tadpoles are not. I dropped the matter and continued on my merry way.

The second thing that stands out for me in the permitting process was the end result of the months I spent navigating the Costa Rican permit process to collect animals there. Armed with an abundance of thoroughly stamped and vetted and very official paperwork, I went through Miami International Airport on my way back to Ann Arbor with several frog condos—small Tupperware® containers each containing one frog, breathing holes punched in each, duct taped into towers. I was rather pleased with myself, knowing that the months of permit gathering had left me fully on the right side of the law. The customs people who stopped me didn't see it that way, however, and vaguely suggested that I would have my frog condos taken from me. Then I said the words "poison frogs" and the tables turned. They became terrified. I offered to show them the frogs—even made a move to take the lid off the top frog condo—and the customs officials literally backed away from me (and my frogs), barked at me to keep the frogs in lock down, and waved me through.

Finally, to make my frogs and tads fully comfortable in their new homes, which comprised vivaria on the fourth floor of the museum just down the hall from the odorous dermestid room, I had a case of shot glasses delivered to the Herp Division. This, I hoped, would further cement the reputation of herpetologists as hard-drinking louts. In fact, I used the shot glasses as faux-bromeliads, the phytotelmata of choice for dendrobatids. My frogs did hang out in their shot glasses, but they never did reproduce, so there was no opportunity for cannibalism. Ultimately, after only a few incidents of losing crickets into the hallway, my frogs all died, and my brief career as a captive experimenter on animal behavior was over. I took a couple of the would-be bromeliads home, to use as shot glasses, where I drink from them still.

As part of Ron Nussbaum's Herpetology class in 1995, we went on a spring excursion to the Great Smoky Mountains, which was the tradition every year the class was taught. It was also tradition to drive straight through, overnight, from Ann Arbor. In the very early hours of the morning, I was at the wheel of one of those high-center-of-gravity vans when I passed a semi, found another vehicle approaching far faster than I would have thought possible, and pulled sharply back into our lane just in time, the van rocking theatrically side to side. Jennifer Ast, riding shotgun, was the only other eyewitness to this event, but the unexpected forces nearly woke some of the passengers in the back, one of whom wondered sleepily, "everything okay?" "Just fine!" we both called back, as our heart rates began to normalize.

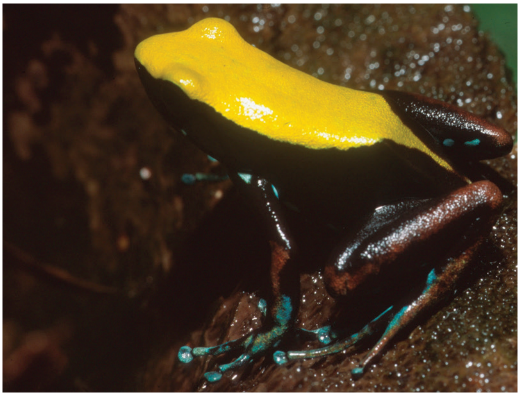
After that, the rest of the trip seemed tame in comparison. Sure, we found all the expected species of 'manders in the hills—species of *Ambystoma* and *Desmognathus* and *Plethodon* and more—and in the streams we procured hellbenders (*Cryptobranchus alleganiensis*), which Jennifer dutifully kissed, because that is what one does. Brad Moon attached a lizard whose identity I don't remember to his earlobe, and wore it as jewelry for a time, as the lizard seemed reluctant to let go. We stayed up late drinking at least one night, and on our way to field sites we passed Dollywood and wondered what wonders lay beyond those gates. We met locals out foraging for ramps—wild leeks—who

Brad Moon and Jennifer kissing hellbender.

could not grok a bunch of Yankees out looking for salamanders.

Later that same year, in the fall, I was lucky to TA for Carl Gans the last time he ever taught. It was from him, and his other TAs, and indeed our (mostly) driven and motivated undergraduates, that I learned comparative anatomy. That class had two 3-hour anatomy labs every week, and after lab practicals, all the TAs stayed, often until the middle of the night, to break down the practical and grade all of the tests. This is the only model I ever saw for comparative anatomy, so I took it with me when I later TA'd for Bill Fink in the class that he and Arnold Kluge co-developed and taught in alternate years—Chordate Anatomy and Phylogeny. When I created my own Vertebrate Evolution curriculum after I left Michigan, I changed how I taught from how I had been taught in many ways; however, I didn't mess too much with either the labs or grading sessions because comparative anatomy labs foster a kind of camaraderie and grading lab practicals with my own TAs always took me back to those early days at Michigan.

After two field seasons working on dendrobatids in Costa Rica, I had a choice to make. I could keep working on dendrobatids, a clade so well studied that I would be able to go deep on questions that are difficult to address before the natural history and basic social structure of a species have been established. Or I could head to Madagascar and find a site where there was a suitable species to study of *Mantella,* the clade of poison frogs that Boulenger had found so similar to the dendrobatids that he had, in 1882, thought them close relatives. The advantage to the latter plan was that, if I was able to collect any data, anything I found would be new to science. The disadvantage, of course, was that Madagascar was far more remote and difficult to work in than Central America.



Mantella laevigata

Madagascar it was. I spent three field seasons (about a year) observing and conducting research on *Mantella laevigata* in Madagascar. During those seasons, I also found and came to understand *Mantella's* predators (crane-fly larvae, as it turns out), and competitors (several species of paternal care-giving frogs, including *Plethodontohyla notostica* and *Anodonthyla boulengeri,* the males of which I observed moving into territories of *M. laevigata*, attracting females to mate with, and displacing the *M. laevigata* with their own clutches). I conducted most of my research on a small island, Nosy Mangabe, in the Bay of Antongil, in steamy northeastern rainforests. My now-husband Bret Weinstein, who back at the UMMZ found his home in the Insect Division, was with me for much of this research, and on each of two longer field seasons, I had one of two remarkable, and remarkably different, field assistants as well—Jessica Metcalf, and Glenn Fox (who would later become a herp division alum).

In Madagascar, I watched a boa attempt to eat of one of my tattooed frogs, but after chewing thoughtfully on her for a several minutes, the snake released her. The frog went on to become a mother. For one long field season I tried to figure out what it was that was causing *Mantella* eggs to die in their wells—their oviposition sites—and ultimately figured out that crane-fly larvae, which were very cryptic in most wells, were voracious egg predators. Females prefer males with desirable territories to males with stamina or nice voices. A good territory is one with a water-filled well, which is a limiting factor for *Mantella.* I discovered that *M. laevigata* had biparental care, but no relationship between the parents. Thus, males guard their clutches, both eggs and tads, fiercely, against all would-be intruders, and females return to their tads every few days and feed them trophic eggs. The most successful males are highly territorial, defending tiny patches of forest floor that contain wells. But that's just one of three distinct male strategies. Some males have no territory at

Madagascan boa

Mantella laevigata *at well site*

all. Males without territories may encounter females as the females head toward high-quality territories, masquerade as territory-holders, and sometimes be successful in courting a female into a mating. And, of course, there's more.

In Madagascar, in service of learning as much as possible about the social system and sexual selection of these small poison frogs, I lived in a tent and showered in a waterfall and contended with monsoons and angry lemurs and naked spice-ferrying sailors, all of which I have catalogued elsewhere in a book, and so will not revisit any more of that here.

There was conflict in the UMMZ between the macro—those who study deep history, discovering both pattern and relationship; and the micro—those who look at modern populations and infer evolutionary process from them. Most grad students picked a side, at least de facto, and faculty tended to do so as well. Two of the giants, in terms of both intellectual contributions and personality, from opposite sides of the divide, were Arnold Kluge and Dick Alexander. I was lucky to work with both of them. Kyle Summers, who had graduated shortly before I started at Michigan, had done so as well, but both of us were told repeatedly that it wasn't an advisable plan. The conflicts in world view between these two men were imagined to mean that positive critique from one guaranteed negative critique from the other.

But this wasn't the case. Both Kluge and Alexander were analytically rigorous and epistemologically driven. They were also both passionate and intense and not prone to keeping their opinions to themselves. And they disagreed on some fundamental concepts. But the very fact that they were both rigorous, and interested in understanding not just that, but how we were making knowledge claims, meant that each had a deep respect for the other. (Granted, neither tended to shout that respect from any rooftops.)

So, I spent my time going back and forth between the Herp Division, where rigorous phylogenetic systematics was done and discussed (mostly on herps), and the Insect Division, where rigorous evolutionary ecology and animal behavior was done and discussed (occasionally on insects). Because my intellectual interests were more in the micro end of things, many of the big, sprawling discussions that I was privy to at UMMZ were in the Insect division, with a host of grad students, as well as faculty from across the university, including Anthropology, Psychology, Natural Resources and the Med

School—Barb Smuts, John Mitani, Randy Nesse, Beverly Strassmann, Warren Holmes, Bobbi Low, Laura Betzig, and more. It was an intellectually rich stew of inquiry, insight, and disagreement, and it was glorious.

In the Summer of 1997, several of us went to the 3rd World Congress of Herpetology, in Prague, having received NSF funds to present there—Jennifer Ast, Brad Moon, Karen Glennemeier, and myself. I had spent the first 5 months of that year in the field in Madagascar, and at that meeting, I presented the first notes on the natural history and evolutionary ecology—the social system, territoriality, mating system, parental care, competitors and predators, and more—of *Mantella laevigata.* I knew that what I had was new, and important, but I wasn't prepared to publish until after I had collected more field data, which wouldn't happen until 1999. There was a cabal of young German scientists at the meeting who collected in Madagascar, but did no animal behavior, although they had attempted to breed *Mantella* and other species in captivity. Two of these scientists were known to other researchers as being willing to claim work that was not their own.

After my talk, four of these tall young men surrounded me and invited me to go out drinking with them, to talk more about my research. I understood the "invitation" to be an attempt to herd me out into a foreign city, where I would hopefully let down my guard and share my scientific findings such that they might be taken. We were in a broad, busy hallway at the conference, so I was mostly just amused and irritated at their antics. I said no, repeatedly, and finally they left me alone. Later, sure enough, some of them published a paper claiming that they had found my results in their captive frogs. I knew that they hadn't. So, when I did publish, I convinced the editors at *Animal Behaviour* to subvert their standard protocol and let me cite my abstract from that 1997 conference, as a way to correctly denote the history of ideas. This is, after all, what citations are for.

There were some good signs in the UMMZ. I mean this literally—we had good signs. I remember three in particular. Just inside Arnold Kluge's office, on a file cabinet so that, when his door was open, all who walked by could read it, he had posted, "It's about power and limited resources, stupid." In the basement office at the end of the hall by the Fish Division, 47A, which Jennifer Ast and I shared for some period of time that neither of us can quite remember, the exterior sign that we inherited said "NO SMOKING NO FOOD NO DRINK in this room." Neither of us had any intention of smoking in there, but we did eat and drink, so I added a sign below it which prohibited all manner of other things, including but not limited to benthic invertebrates, laughter, and farcical Shakespearean productions. Finally, inside that same office when we moved in was a music poster that had on it a large pink bird. I cannot for the life of me remember the band advertised in the poster or the species of bird, but it had a very large beak, and someone—not us—had put a speech bubble coming out of that large beak which said "Minimize ad hoc hypotheses of homoplasy." And so, because Jennifer and I were taught by Kluge to take everything on authority, especially the authority of large, pink birds, we did our damnedest to do so. For Jennifer, as a systematist, minimizing ad hoc hypotheses of homoplasy came fairly naturally. For me, as someone who spent more time over in the microevolutionary end of things, someone who was and is in fact enchanted by homoplasy—which I preferred to call convergence, reversal, evidence of adaptation, and the like—I did nevertheless work hard to not imagine homoplasy where none existed.

Fairly early in my time at Michigan, in the mid-1990s, I took Arnold's graduate course in systematics. He signaled to me, perhaps inadvertently, that I was now a scientist with whom it was worth engaging. On one of my exams, I had used the word "family" to refer to some clade—the corvids, or perhaps Aceraceae. He circled the word "family" and wrote next to it, "we eschew categorical rank." *We.* Apparently, I had forgotten myself for a moment, and had failed to eschew categorical rank. Now I would remember. Now that I was part of the *we.*

The water in which we swam at the UMMZ was epistemological. The distinct traditions, macro vs. micro, deep history vs. population level changes and behavior, inherently have distinct methods to address the questions they attempt to answer. But regardless of question, we were generating and testing hypotheses. I went on to teach undergraduates for 15 years, and when I taught animal behavior in particular, and had students do their own independent research, I made damn sure that they knew the difference between numbers they collected that are preliminary observations, and numbers they collected that actually are data. Did they, or did they not, have a hypothesis that they were testing in advance of collecting those numbers? No? Well then, they do not have data. The intellectual honesty and rigor underlying this conclusion was a staple at the UMMZ—

particularly in the Herp and Insect divisions.

My final semester at Michigan, Dr. Kluge gifted me the position of TA for his graduate course in systematics, although I wasn't then, and would not become, a practicing systematist. I could talk the talk, though, and walk the walk, mostly, certainly enough for the job that I decided needed to be done that semester. On the first day of class, I introduced myself by saying that I would act as translator for Kluge. And so, I did. And together, we eschewed categorical rank.

About the Author

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After receiving her Ph.D. with Michigan's Distinguished Dissertation Award, Heather published her first book in 2002—*Antipode: Seasons with the Extraordinary Wildlife and Culture of Madagascar.* She joined the faculty at The Evergreen State College, in Olympia, Washington, and was tenured in 2008. Heather taught evolution, animal behavior, vertebrate zoology, and tropical biology, and created and led several study abroad trips to remote sites in Panama and Ecuador.

Since leaving Evergreen in 2017, Heather's writing and speaking has expanded to venues including the New York Times and the Wall Street Journal, Oxford University, and the Department of Justice. Subjects include the evolution of sex, relationship, and consciousness; the philosophy of science; the value of risk and wild nature; contemporary threats to democracy; and the future of higher education. From 2019–2021, she has been a Visiting Fellow in the James Madison Program at Princeton University. She co-hosts "The Evolutionary Lens," a weekly livestream of the DarkHorse podcast, with husband Bret Weinstein. Their co-authored book, *A Hunter-Gatherer's Guide to the 21st Century,* will provide an evolutionary toolkit for living a good and honorable life as an ape in the 21st century, when it is published in 2021.

RICHARD M. LEHTINEN

Field Herpetology at Michigan: the Madagascar Connection

1998–

In the decades of the 1990s and 2000s, herpetological research at the University of Michigan was rich and diverse with a compelling cast of characters. The two curators at UMMZ were Arnold Kluge (1965–2003) and Ron Nussbaum (1974–2015), with several non-museum-based faculty who also studied these organisms (most notably, Earl Werner in the Department of Biology). Then and now, Greg Schneider, the long-serving collection manager, is the special glue that continues to help stick all the Michigan herpetologists together.

Of the many and diverse perspectives from which amphibians and reptiles were studied at Michigan during that period, one notable focus was on the herpetofauna of Madagascar. Nussbaum was the primary locus for this work, given his extensive experience on the island. Others involved in herpetological research in Madagascar from Michigan at that time included Chris Raxworthy, Heather Heying, Sheng-Hai Wu, and Achille Raselimanana. Some (like myself) were Nussbaum's graduate students or post docs but some were associated with other faculty either at UMMZ or the Department of Biology. Unlike today, when it is common for many or most students in a given lab to have similar research questions and be working on different aspects of the same study system, there was no single, over-riding focus of Madagascar research at Michigan. Some were engaged in systematic and taxonomic questions, others focused on biogeographical queries. Some were students of behavior, and still others studied ecology and conservation. The result was a lively mix of interests, ideas, perspectives and personalities that was intellectually stimulating. I suspect that being part of this heterogeneous lot of scholars broadened my views in many areas, or at least more so than would otherwise have been the case.

The UMMZ herpetology collections are among the finest in the world and I was privileged to help care for them as a collections assistant for several semesters. Though not necessarily appreciated by the general public, there is, of course, a great deal that can be learned from museum specimens. A very incomplete list could include: morphological variation, diet composition, parasites and diseases, conservation status, anatomy and physiology, sexual dimorphism, reproduction, geographic distribution and a source of DNA that can be used for diverse ends. While I have a great passion and respect for natural history collections, not everything of interest to a biologist can be learned from preserved specimens. Information on individual behavior, habitat use, population-level phenomena of all sorts, interactions with other organisms, and many other topics can often only be meaningfully studied in the field under natural conditions. The history of field studies in herpetology at Michigan also has a long and distinguished history. What follows here is a description of some of my experiences while in the field in Madagascar as a Michigan student.

My particular research focus in terms of Madagascar field herpetology was on the ecology and evolution of several plant-specialist frogs now placed in the genus *Guibemantis* (Mantellidae). Or at least, that became my focus, after an initial field season in 1999 that focused more on conservation-related questions led me to believe that these plant-specialist frogs were ripe for study. In any case, all the work I completed while a student at Michigan took place in the field, during the rainy season, in Madagascar. Other than that first trip in 1999, I subsequently stayed exclusively at a rustic field station near the small village of Manafiafy (still seen on many maps as "Sainte Luce") on the southeastern coast.

Most field stations have laboratory facilities, cafeterias, computer labs, libraries, dormitories, gift shops, pillows, clean linens and laundry facilities, heating and/or air conditioning, mosquito netting, not to mention floors and walls. At the Manafiafy Field Station, we had none of the above. However, we did have a thatched roof under which we ate our meals and an old, blue tarp that funneled the abundant rain into a plastic tank. This rain water collection facilitated the periodic bath from a bucket. I hauled a bucket full of rain water into the forest with a bar of soap and got as clean as I could, usually under the watchful gaze of curious children from the village. It wasn't often they got to see the butt of a *vazaha* (literally, stranger; foreigner) and my butt was apparently (to judge by the giggles) of particular interest. The last year I was there (2002), a second thatched roof structure was built; I pitched my tent under it and was able to sleep through the sultry nights without my rainfly[1] on. Ah, luxury.

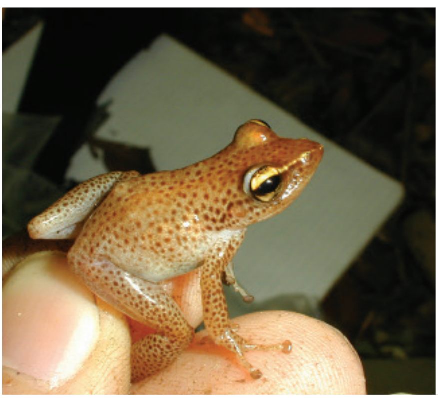
I had a mantra at the field station—never look into the belly of the beast. This referred to the inelegant toilet operations which were composed of a tattered wooden shack erected around a hole in the sand. One didn't venture there until absolutely necessary; the stench was very nearly overwhelming, and the flies were thick. Once morbid curiosity got the better of me and I did look. The vision is still with me, 17 years later.

Of course, I was at the Manafiafy field station in the shrinking coastal rainforests of southeastern Madagascar to study frogs. The foregoing paragraphs perhaps give the impression that this was not a pleasant experience. Oh, but it was. For the biologist, Madagascar is a playground, an absolute riot of biodiversity. Darwin's utmost fantasy. Isolated from all other landmasses for at least 80 million years, a unique and hyper-diverse biota has developed there, unlike anything known elsewhere on earth. Evolution has taken paths there not frequented elsewhere and not even imagined of in the midwestern United States, the only place I had so far called home. So, for someone like myself, who spent much of my childhood bringing snakes, toads, and salamanders home in my pants pockets, this was paradise.

The frogs I was studying here in paradise were odd. They did not hang around ponds or streams like most respectable kinds of frogs. Rather, they lived their entire lives (egg, tadpole, and adult) in and on *Pandanus* plants, commonly called "screw pines." These plants were shaped such that water was retained in their leaf axils, and this provided a micro-aquatic environment within which these frogs lived their lives. Not much of an aquatic habitat (maybe half a coffee cup's worth), but enough to survive on. My job was to find out as much about their lives as possible and to make this into a dissertation that would get me my degree and, hopefully, a start at earning my place in the scientific world.

There were rough spots of course—in fact, many hardships and difficulties—but I was having a real adventure. This scientific adventure was something I had been dreaming of for years, and I was determined to see it through. And besides, the frogs, indeed the whole rainforest, were everything I had hoped for and more. The more one probed nature, the more one saw the numberless layers underneath. There was so much to know and so much that was unknown; it was (and remains) a great opportunity.

There were three species of these plant-living frogs in the Manafiafy forest. I studied two of these in detail; the third remains undescribed, unnamed, and nearly totally unstudied. I learned that these specialized frogs provide parental care to their offspring by attending the developing embryos. And, with a series of experiments, I learned that the leaf-axil–dwelling tadpoles eat detritus, subsisting on fallen leaves and other mishmash from the canopy above. I learned how to distinguish males and females, how they bred, how long they lived, how long it took them to reach maturity, how their numbers waxed and waned through the seasons and years and how they interacted with one another and with their predators. An interesting twist to the story is that it ultimately turned out that these frogs that I spent all this time studying were not, in fact, the species I thought they were at the time. Years later, with the help of several colleagues, I named two of them as new species to science (*Guibemantis annulatus* and *G. wattersoni*).[2]



Guibemantis annulatus

Guibemantis wattersoni

I also quickly learned that *Pandanus* plants have tough, nasty spines along the edges of their leaves. As it was necessary to hand-capture, measure, and release thousands of these small frogs (the largest of which would sit comfortably on a 25¢ U.S. coin), my hands and forearms received many battle scars. I also learned that the local girls liked to use my plastic flagging for hair decorations. This, in retrospect, is admittedly rather charming but at the time, it totally pissed me off. It took me weeks to laboriously plot, map out, and flag all of the *Pandanus* plants in that damn forest and I wasn't going to let it fall apart because of some local hairstyle craze. After this had gone on for a while, I actually met some of the young ladies in the forest and tried to explain what I was doing and why they needed to stop taking my flagging. I even offered to give them rolls of unused flagging for their beautification needs, but I fear my message didn't get through. My French was OK by then, but only the very eldest people still spoke any in this rural area and my Malagasy was limited to a few dozen words. (Useful phrases listed in my Malagasy-English dictionary included "one is dead, send help." My wife was not inspired with confidence by this.) What kind of hand gestures could a *vazaha* use to explain to nervous children that you are a scientist studying the metapopulation dynamics of plant-specialist frogs? As I pondered this with befuddlement, they ran off screaming. I later found out from my friend Kadolfe (who was a night guard at the station and spoke a little French) that there is a local myth about white-skinned devils in the forest (the *mpakafu*) that ate unwary young girls. He was certain that the girls thought I was *mpakafu*, and he smiled his one-toothed smile. So, my reputation among the locals had taken a hit. But, I never lost another piece of flagging tape.

The nearest town of any size was Fort-Dauphin (a.k.a. Tolagnaro). This town was only 30 kilometers (~19 miles) away, but it took from 5–7 hours to get there by 4 × 4 truck, depending on the number and length of roadblocks by zebu (the revered hump-backed cattle of Madagascar) and depth of the rainy season mud. This road was pretty wretched, especially in the rainy season, and one could almost keep pace with the truck just by getting out and walking. Walking certainly would have been more comfortable; I feel like some of my vertebrae are still out of place after some of the endless, bone-jarring rides. The only thing I really cared to do in Fort-Dauphin was take a shower (no hot water, but no bucket either) and call my loved ones. The latter activity was very expensive and frustrating. (These were pre-cell phone, pre-Internet days, at least in Madagascar.) For the price of 50,000 FMG (franc malagashe, about $25 US, a substantial sum for my shoestring budget), I got about two and a half minutes talking time, most of which was spent talking over the other party as there was a three second delay between when I said something and when they heard it. I'm still alive, love you, miss you, time's up.

At the station, we were situated about a mile west of the small fishing village of Manafiafy, which was right on the Indian Ocean. Only a few hundred people lived in the town and about half of these seemed to be children under five. Like many developing nations in Africa's orbit, birthrates in Madagascar are still very high. Note that Malagasy people do not generally consider themselves African. They have a unique language, culture, and environment, all their own. The people in the corner of Madagascar where I was working were of the Anosy ethnic group. I had the good fortune to get to know a few of these folks and at night, under the stars of the southern hemisphere, I could sometimes hear their beautiful singing from the village. Because there were only headlamps and candles for illumination at night, the stars were incredibly vivid. A city dweller from the developed world looks up at night astonished; surely this is one of the uncounted costs of our many high tech comforts.

A normal day started around 5:30 am with a huge, steaming plate of white rice and a strong cup of coffee. Rice is the staple of Malagasy cuisine and takes center stage at every meal. The only way to tell whether you were sitting down to breakfast, lunch, or dinner was to see what was on top of the rice. If I was lucky, an egg on top at breakfast, manioc at lunch and perhaps a few shrimp or even zebu at dinner. One learns not to be fussy and to take the calories where you can get them. I am not a large man, yet I would come home at the end of the rainy season having left 20 pounds of myself back in the rainforest.

The coffee was wonderfully strong. Josette, the sometimes taciturn matron of the field station, would manually grind the beans in a thick wooden bowl with a large wooden stick with a rounded end that was pounded repeatedly with practice and precision. The thumping of the stick in the bowl to grind the coffee beans was my unofficial alarm clock. The coffee grounds, I noticed with interest one morning, were soaked in the boiled water inside the leg of some pantyhose. This arrangement very effectively kept coffee grounds out of the water. I found this incongruous usage humorous and tried (unsuccessfully) to explain to Josette that her coffee filters were actually worn on women's legs in westernized countries. As you might imagine, this is a pretty hard idea to get across with hand gestures and a few dozen shared words. I'm pretty sure that Josette will never leave Madagascar, but if she ever does, I imagine her going to Paris and wondering why the women wear coffee filters on their legs.

After breakfast, I would amble off toward my research plots that were scattered around the forest. I kept myself very busy monitoring the populations of frogs in hundreds of *Pandanus* plants, tracking individual movements of frogs among those plants, conducting experiments with both tadpoles and adults and much else. The lab biologist can take her bacteria out of the freezer or fruit flies out of the incubator whenever she wants to collect some more data or do another experiment. This is a very great advantage and a hell of a lot more convenient than fieldwork. If my bulb was a little brighter, maybe I could have been a laboratory biologist, too. But really, while I appreciate the advantages (and have since done much legitimate work in the lab myself), I was really born a field biologist. Yosu gotta do what you love and if you don't love slogging through fetid swamps being feasted on by malarial mosquitoes, living out of a tent for months on end and eating white rice three meals a day, then it's probably time to go home and find that white lab coat in the back of the closet.

Some of the sharp-spined *Pandanus* plants that my frogs lived in were not conveniently located on the forest floor where they could be easily accessed. Some were six or eight or ten feet off the ground and I could not see down into them, even on my tippy toes. For these situations, I paid a Malagasy friend who was handy with tools to make me a simple ladder of wood. Not wanting me to have any unfortunate accidents, he made it very sturdy and indeed I never had any problems with it. However, it was heavy. Really heavy. If you've ever been to a jungle before, you will recognize that it is often challenging to navigate just your own body through all the vines, saplings, thorns and assorted herbage to get where you need to go. Now, try it while dragging around a 25-pound, 10-foot high wooden ladder. Challenging does not even begin to describe the experience. After three rainy seasons of this Sisyphus-like task, I had a special hatred for it. On the bright side, this did provide an opportunity to invent colorful new expletives, some of which are still in regular use. Necessity is the mother of invention.

For *Pandanus* plants that were higher than about 12 feet (beyond the reach of my beloved ladder), I had to resort to a different method—the single rope-climbing technique. By climbing adjacent sturdy trees using a rope and harness, I could view and partly access the water filled leaf axils in the canopy where my frogs lived. I couldn't climb the actual *Pandanus* plants themselves as they are not woody and would quickly collapse under my weight. While I had practiced on trees in my yard back in Ann Arbor, I was no expert tree climber. While it may only have been 25 feet up to get where I needed to be, I always was drenched in sweat and shaking with the effort of hauling myself up. But once I was up there, it was nice to look around and catch a little of the sea breeze that rarely seemed to penetrate to the shady forest below.

Getting down, however, was often more difficult (for me, anyway) than getting up. After a while, I literally "learned the ropes" and got proficient at clipping in and out of the harness in the correct way and in attaching the rappelling device to slow my descent effectively. In the early going, however, there were some comical errors including one that required me to clip out of the rope system entirely and hug the trunk to shimmy back down. I ended up in a heap on the ground with some nice face burns from close encounters with tree bark. It seems funny now, as I write from the comfort of my couch, but a broken leg or other injury could easily have turned serious in such a remote area.

***Lemurs of the genus* Microcebus**

While I was usually alone while working in the forest, the clearing at the edge of the forest where the camp was located often had at least one person around, usually one of the young camp guards or the aforementioned Josette. Sometimes, other researchers were present for shorter periods, usually primatologists from Europe who were studying the lemurs in the forest. Current estimates are that Madagascar has more than 100 species of extant lemurs and more are still being discovered. And this doesn't count extinct species, some of which were gorilla-sized. There are five species of lemurs at the Sainte Luce forest (though I only ever spotted four of them) and most of the primatologists were there to study the collared brown lemurs. These are large, diurnal species important in seed dispersal. The locals had formerly hunted the lemurs for bushmeat but over a number of years my primatologist friends were able to put a stop to that by hiring local people as guides to help track the lemur movements and behaviors. Thus, no longer fleeing at the sight of humans, it was easier to study their natural behavior. While I occasionally had encounters with them in the forest, I did not see them very often. I did get hit in the face with lemur pee one time. I'm sure they got a good a laugh about that one: "Nice shot Leonard! Right in the face!" Tasted a bit smoky, hint of *Eucalyptus.*

I enjoyed and appreciated the camaraderie when other researchers were around, though this wasn't too often. Those who had the choice of researching their study organisms in the wet or the dry season almost invariably chose the dry. Who could blame them? My frogs only bred during the rainy season, so my choice was made for me. I purchased the best rain gear I could afford before leaving the States on my first trip and quickly found out that waterproof gear is worthless in the tropics if it is not breathable. My gear kept me perfectly dry from rain on the outside, but I was soon soaked in sweat on the inside. Not long after I arrived, I stopped wearing it altogether.

After months in the rainforest, chasing frogs and sweating buckets in the heat and humidity, you start to crave all sorts of niceties. What I dreamed about the most was sweets. A nice big strawberry sundae, a piece of chocolate cake or even just a vanilla cone became nearly an obsession. The only thing sweet that was available locally was bananas. Even the smallest village in Madagascar has at least a few banana trees, usually both the regular kind we get in the West as well as the "petite banane" that is substantially smaller but also a little sweeter than a more standard banana variety. One thing about bananas in Madagascar is that (at least in my experience), people generally prefer to eat them half rotten. I can remember the guards at the station one evening, wanting to be helpful and generous to the *vazaha,* absolutely insisting that I take the blackest, most putrid banana of the bunch. You put on a brave face, bat away the swarms of fruit flies, smile like you've never tasted anything better, and swallow quickly, before it comes back up. This is a part of the world where malnutrition is common and starvation is not unknown, so you won't make many friends if you turn your nose up at a local delicacy. I can remember one that was so far gone that, as I half ate, half slurped up the decaying remains, I detected a hint of alcohol from the ongoing fermentation.

In a similar vein, one of my camp guard friends named Jive once found a honey bee hive in a tree. The local people are very adept at finding hives, usually in tree holes, and bringing back the goods. Climbing up barefooted with smoldering grass clenched in his teeth (the smoke keeps the bees from stinging), Jive brought down a fist-sized hunk of comb, dripping with golden honey. Everybody was all smiles, greedily dipping in their fingers for a taste. Again, wanting to be generous and hospitable to their guest, Jive put a big chunk of the comb in a wooden bowl and insisted that I have it all to myself. After months of a nearly all-rice diet, the first few tastes were heavenly. Imagine, however, having to eat a very large bowlful of pure honey in one sitting with a half dozen smiling and expectant faces watching you. Trying to be grateful, I choked down three-quarters of the bowl, doing my best to smile. Ultimately, I had to stop to avoid vomiting and for a long time afterwards even the smell of honey made me retch a little. The moral of the story? Be careful what you wish for.

When you do fieldwork, you are not doing things on your own time; the organisms you study are the ones running the show. Luckily, the frogs I was studying were primarily diurnal, so most of my work was done between dawn and dusk. However, I did have a few side projects on other critters (other frogs, ghost geckos, snakes, etc.) that kept me busy at night, too. Some have asked me if I was scared being alone, half way round the world, out in the forest at night. I wasn't scared at all. Quite the opposite; it was exhilarating. Seemingly every crevice and crack had some new wonder to behold. Madagascar, while very well-endowed with peculiar plant and animal life, has no venomous snakes or any large predatory or dangerous animals. So, other than scaring a sleeping zebu, there is very little to fear at night in a Malagasy rainforest. On one occasion, when I was out late doing frog surveys, I was still a good hour's hike from my tent when the batteries in my headlamp died. I stopped and calmly felt around in my backpack for the spares that I always kept with me. I rummaged through the bag for several minutes with increasing annoyance but no luck; they simply were not there. What to do? As I stood thinking how I was going to follow the narrow, winding footpath all the way back to camp without losing my way, I realized that since my headlamp died, my night vision was getting better and better. So, after some minutes, by starlight and a slim crescent moon I was able to see the dirt path before me. By having to go slow to avoid tripping on unseen obstacles underfoot, I was forced to not hurry, to take one footstep at a time. Using fallen logs to cross a few streams and all the while serenaded by frogs, insects and a gentle sea breeze, I had a peaceful walk back to my tent.

***A chamaeleon,* Furcifer lineata**

I still remember the trails in that forest, I think I could walk them in my sleep. When I left the forest for the last time, to go back to Michigan, to my other life, I didn't know if I'd ever return. And if I did come back, would there be a forest to come back to? Would the great-great-great grandchildren of all those frogs that I once knew still be there to greet me? Or would the needs of a poor and rapidly growing human population eat up all the forest that remained? I haven't yet been back and, honestly, I would be a little scared to go. I'd be scared to see if all that subtle beauty and biological strangeness only now existed in my memories.

Acknowledgments. I would like to thank Ron Nussbaum, Arnold Kluge, Heather Heying, Jennifer Ast, Luis Schiesari, Greg Schneider and many others at Michigan for conversation, assistance and camaraderie. I also appreciate feedback given by Earl Werner, Beverly Rathcke and J. David Allan on my work. I also acknowledge the Horace H. Rackham School of Graduate Studies, the Museum of Zoology and the International Institute at the University of Michigan for funding and support. In Madagascar, I acknowledge Jean-Baptiste Ramanamanjato, Joe Gaby Raveloarison, all of the staff at the Manafiafy station, Manon Vincelette and Greg Feinberg for assistance great and small. Les Directions des Eaux et Forêts provided research permits. I thank Frank Glaw and Miguel Vences for teaching an ecologist some systematics. Lastly, I thank Marcy Campbell for comments on an earlier version of this essay. Any errors that remain are my own.

Endnotes

[1] A rainfly is the floorless, waterproof outer layer of a double-wall tent.

[2] Lehtinen, R.M., F. Glaw and M. Vences. 2011. Two new plant-breeding frog species (Anura: Mantellidae, Guibemantis) from southeastern Madagascar. The Herpetological Journal 21: 95–112.

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In addition to ongoing Madagascar projects, Rick is currently involved in research on the ecology, evolution, reproductive behavior and conservation of Central American glass frogs. In Ohio, he works on terrestrial salamander ecology and on a long-term study of the population dynamics of Blanchard's cricket frog. Continuing his long interest in plant-breeding frogs, he recently launched a website "Phytotelm-breeding Frogs of the World" and maintains a dart frog colony to investigate plant-animal interactions. He also has a passion for squirrels.

LAURA EIDIETIS

I Wanted to Study Whales

2000–

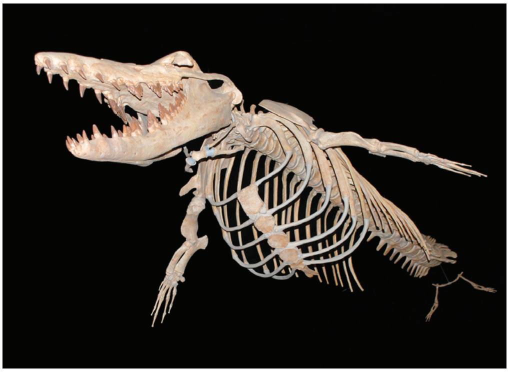
Spoiler Alert

I did not, and do not, study whales. Nevertheless, because of studying frog and toad tadpoles at the University of Michigan, I can explain to just about anyone how whales fly through the water. After navigating through an intellectual realm where colleagues knew a lot about biology and little about physics, I can explain swimming to undergraduates who, mostly, know even less about physics. They love it—the topic remains in my course because of popular demand. I think they love it because they have never before been in the position of imagining the perspective of a whale which does not have to worry about water's dislike of deformation anywhere near as much as a human does (more on that later). Looking at the world from a new perspective is exciting to many and challenging to all.

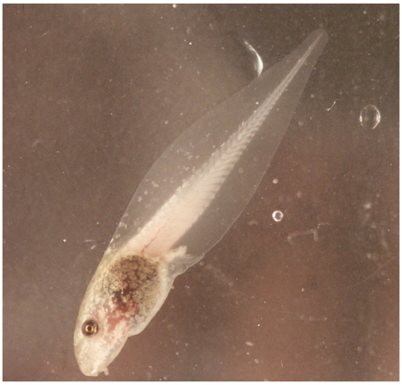
Before working in herpetology at Michigan, I had never even thought about frogs, and the only type I had ever touched was a toad (the brown, common, *Bufo americanus*). It has been more than a decade since I have studied tadpoles. Still, I listen for frogs when others listen to birds. I feel anxious excitement at the first warm day in March or April, when I know the Wood Frogs are defrosting and readying to mate. When toads call in the night, I wake from dreams about not having my kiddy pools ready to become tadpole nurseries. I love frogs, now. And, more importantly, I am very aware of frogs and their place in our natural and developed environment.

I will tell you of my journey from whale-lover to toad-lover. First, though, I need to convince you that the themes of *relativity of perspective* and *existing in an intermediate realm* are important to tadpoles moving through water. I think they are similarly critical to understanding my progression through the Ph.D. program, while studying frog tadpoles, at the University of Michigan.

Relativity of Perspective



An animal moving through water finds that fluid prefers not to deform; this is viscosity. Water dislikes being sheered or torn a lot more than air does, all things being equal. But, when biology meets physics, little is equal and most is relative. Whales fly through the sea, worrying about as much about water's viscosity as a sparrow worries about that of air. If you are very large or you are very fast (or both), then the relatively high stubbornness of water is trivial. But, for the tiny and slow, like *Daphnia* (~1 mm), the whale's ether seems like pancake batter to which you are adding flour, just before it transforms from batter into dough. Tiny animals must push, pull, and twist themselves through the same medium that supports whale flight. Relativity of perspective is necessary if you want to study animals swimming.



Similarly, awareness of the relativity of human perspective is vital to appreciating my experience of constructing a Ph.D. program at Michigan in the early 2000s. Some can soar through the medium of academia, forming a dissertation as easily as a humpback whale glides. My social perspective created an experience that is a lot more like the experience of a swimming *Daphnia*, or, maybe, a tadpole.

At < 3 g, tadpoles can weigh in on living in an intermediate realm. For a Michigan tadpole, water is sometimes more ether-like and sometimes more almost-dough-like and most of the time somewhat in-between. Wood frog, toad, and other common Michigan tadpoles are usually and mostly too big to push, pull, or twist themselves effectively like *Daphnia*, and they are usually and mostly too small to fly through water like a whale. The Michigan tadpole lives in an intermediate realm, most of the time, though not always. (I apologize for overuse of qualifiers; in an intermediate realm, absolutes are not accurate.)

When I trained and studied at Michigan, I often felt that I was navigating in a zone between realms, though never as an outsider. I accepted a role as a bridge in several realms, including between physics and biology and, sometimes, between my worldview and that of many academic peers and mentors.

I have empathy for a Wood Frog tadpole living in an ephemeral pond in the upper-Midwest of the United States, perhaps at the E. S. George Reserve in southeast Michigan. As I write, this is early July, they do not exist, that is, they have all either become frogs or died of desiccation after a week of hot, dry weather during which the trees sucked the water out of their arboreal nursery pools. Imagine that perspective—Wood Frogs hatch in April and either metamorphose or die by July. Imagine being a swimming animal that can be killed by the thirsty roots of trees. Doing science as a graduate student seemed, sometimes, like that. The faculty provided the metaphorical pool in which to grow and develop. However, I needed to develop first by two years and then, finally, metamorphose into a professional researcher by Year 5 or 6, or the very structure that supported my academic life would cut it off.

This is a reality that academics have lived with for so long. Because of its familiarity, it takes effort to look at this reality from a non-academic perspective. It takes effort to honestly consider its effects on psychology and emotion outside of the personal perspective of “If I made it through, other young scientists should be able to." For us in academia, this effort may be as difficult as asking a Wood Frog to consider its disappearing pool of water. Yet, for a person coming from outside an academic culture, the ephemeral pool of dissertation research can be as jarring as if you tried putting a minnow into a Wood Frog's disappearing nursery. The minnow does not have the adaptive background to survive; it will end up flopping around and, then, die.

To understand me as a scientist, you need to know that I came from a non-academic background. I applied to the Department of Biology, an ancestor of the current Department of Ecology and Evolutionary Biology, because my mother told me to. Though living in Mississippi, I was still a resident of my natal Michigan, and she did not know that one does not pay tuition for doctoral research in science. For context, I am the first STEM Ph.D. in my family, and my brother is the second.

Paul Webb,
Professor Emeritus

I intended to study whales and assumed that I needed an ocean to do that. But, when the University of Michigan and Professor (now emeritus) Paul Webb recruited me and offered a trip from Mississippi, I accepted. Paul Webb wrote me the absolutely nicest and most personalized recruiting letter that I have ever seen and followed up with a similar phone call. Dr. Mara Zimmerman (Washington Dept. of Fish and Wildlife), then a student of Prof. Earl Werner, met me at the airport and hosted my visit in her home. I note these details because, from my perspective, this personalized approach was more important than the reputation of the school or labs.

My perspective was that of a young teacher from a Catholic school who aspired to be a wife and mother but who thought learning how to do biology would be intriguing and useful. This was not different from all my mentors and colleagues, but it seemed to be different from most. I entered with a cohort of nine men and two women. When I began at the University of Michigan in the then Department of Biology, the diversity of social perspective was lacking. If, in 2000, you looked at the printed magazine of faculty profiles, the mode was a male of a certain age. (I invite you to contrast with today's online profiles, https://lsa.umich.edu/eeb/people/faculty.html, and see how society can evolve.) Certainly, there were gaping holes in the glass ceiling (thank you women of EEB!), but the form of the ceiling seemed, to me, to still be there.

I thought I was the only one who assumed that Saturdays were for football (North American). I thought I was the only one who thought renting an apartment above my church was normal, as well as convenient. I learned that my mode of speech and communication sounded different to my ears than to those of my mentors and many of my peers. I tended to make analogies to babies swimming and American football. Whether a person thinks that reasonable in academia or inappropriate somewhat depends on social perspective. To several of my mentors, the style of communication seemed uneducated, which I know because they told me so.

Unlike everyone I talked to, I had no intention of becoming a research scientist, post-graduation. I came to Michigan with a National Science Foundation pre-doctoral fellowship, and, every so often, I re-read my statement in the NSF application. I wrote that my doctoral research was a means to the end of becoming a more relevant biology instructor. I intended to teach.

Another very important difference: I did not know about evolutionary theory. As a child, I attended religious schools which, though not fundamentalist, did not have the stamina to bridge between biological evolution and the more conservative families attending the schools. My undergraduate department excelled in ecology and cellular biology but told me that evolution was unimportant. Even worse, I was largely ignorant of my level of ignorance, which made conversations with my museum colleagues very challenging.

Even my research was not from the same perspective as most of the researchers with whom I conversed. I studied the biomechanics of aquatic locomotion with Paul Webb. My colleagues did not use the tools of physics, as a general rule. In fact, at the time, no graduate student in Paul Webb's lab did that. Almost every time I tried to talk about my research among my research community, I needed to start with, "A force is a push or pull. Forces can be decomposed into orthogonal vectors. A vector has magnitude and direction." I honed the art of picturing my research from the perspective of my colleagues.

I often felt like a tadpole swimming in the intermediate realm where water is neither ether nor almost-dough. Sometimes one set of skills worked in one environment and, then, I would walk to another building and need to use another set of skills. For example, I walked from my home in a religious environment into a department that was most definitely not religious. Then, when I least expected it, a non-religious colleague would engage me in a conversation about spirituality, usually just when I was focusing my brain on trying to comprehend the basics of a materialist explanation for the patterns of life. Sometimes, I needed to use all my skills at once, as when I taught evolution to a fundamentalist Muslim student who had a lot of questions.

Because no mode really works well in an intermediate realm, it may seem that tadpoles are not meant to swim. But, to eat, they must swim. Their swimming often looks like what my 5-year-old does when she accidentally ends up in the deep end without her flotation device. Like my tadpoles, I cannot say I was a very graceful academic swimmer, but grace may not be possible when you are between environments. Graceful or not, I made it to metamorphosis. Even a tadpole manages to accomplish some pretty remarkable things.

How did someone who was in love with whales and about as academically graceful as a tadpole manage to successfully defend a dissertation about frogs and toads?

A Story

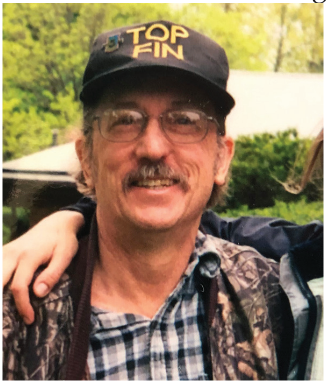
When I first set foot on the campus, Paul Webb took me to the Exhibit Museum of Natural History (now retired) and pointed to bones hanging from the ceiling, the *Basilosaurus,* an extinct whale with legs. To find that skeleton in 2018, look in the atrium of the new Biological Sciences Building.

Paul talked about "peduncles" and "degrees of freedom" and "lift" and thoroughly lost my comprehension, as I nodded and smiled and committed the conversation to memory. His was arguing that the theoretical problem was far more interesting to a biologist than the specific animal of study. I did not have the educational background to understand his lesson, but I listened.

Today, I appreciate with the enthusiasm of a convert: Excellent biologists study problems. The organism provides the setting to study the problem and, later, often the real-world application of the findings. From my current perspective, I now struggle to coach budding students of biology toward such an appreciation of concepts and problems. Picture me conversing with a student team, "Yes, you like Golden Toads, but maybe there are some data on anurans that are extant in the wild that can inform your understanding of *Bd* infection, as data on Golden Toads may be a little hard to collect, these days."

Back at the turn of the millennium, I did not know a peduncle from a bicycle pedal, and I wanted to study whales. But Paul Webb convinced me of a truth: Michigan is a place of opportunities. He managed to show me the wonder of the world of the fishes, and, 18 months later, I was ready to start a dissertation on … fish. As my narrative progresses, please remember my analogy: As a graduate student, I was not a soaring whale, I was an ungraceful tadpole in an intermediate realm. Moving from whales to fish to tadpoles was likely not the most efficient route to anywhere.

I recall talking to Prof. Earl Werner (now emeritus) about plasticity of tadpole tail shape in his lab in the Kraus Natural Science Building (also retired). He suggested that there were so many possibilities for reshaping tails and testing the results for swimming and escape responses. Paul Webb is renowned for his seminal work on fish escape responses, so I thought it made sense for me to bridge between the fishes and the tadpoles. I thought "nobody's done that before" and jumped into the world of tadpoles, figuring it would be just like studying fish. I was naïve.



Jim Gapczinski

Perhaps there were reasons why nobody had attempted to biomechanically investigate the problem of an aquatic escape response in tadpoles. Reshaping tadpole tails did not work; they tend to die when you take a scalpel to them. You cannot successfully sew things onto them using surgeon's tools, like we did on fish. Furthermore, I will reveal a secret: I am a terrible naturalist. I could not find the eggs! I asked for help from peers and was gently told I had to do my own work—honest, but not helpful. That almost led to my personal glass ceiling.

A lifeline came in the form of Jim (Gappy) Gapczinski, who ran the Saline, MI, fisheries station for the Michigan Department of Natural Resources. Jim is a naturalist, and he treated me like a daughter. He took me to the right ponds, showed me how to recognize frog eggs from a distance, taught me the frog calls, and was a necessary safety-partner as I slogged through muck to capture the eggs.

Gappy was also strong, and I am not. This is another reality of my perspective—field work is far more fun if you are strong. For me, field work meant a lot of physical pain, every day. I took up weight lifting to help (and to make me able to move around lab equipment), but, despite the weight-lifting and playing sports consistently and competitively, I was not built for hard physical labor. Some people are, but I am not.

Despite 3 years of hard work and the patient tutelage of Drs. Miriam Zelditch and Don Swiderski in quantitative shape analysis, I could not document the shape plasticity that was supposed to happen when tadpoles, especially Wood Frogs, are exposed to predator cues. As it turns out, tadpoles are complicated. To make matters worse, Michigan tadpoles do not swim away from predators. Or, to put it another way, they usually do not move until they are touched. And, the predators do not usually chase, so steady swimming is not very relevant. Steady swimming is a lot easier to study than the twisting and rolling accelerations of tadpoles. My study of tadpoles was often an uphill battle.

While I clumsily attacked tadpole swimming, the environment around me was exciting and inspirational. Scientists were doing really exciting things in the ecology and evolution of anurans at the University of Michigan. My peers studied the evolution of frogs in Africa. I remember one who worked in Madagascar, sleeping on the ground with only an inflatable mattress and maybe a tent between her and whatever the tropical forest had to offer. Just before graduation she talked to me about possibly starting research on some South American frogs that seemed to be "speciating right before our eyes." Now, that's exciting! Some colleagues discovered the ecological mechanisms of plasticity in Michigan frogs. There is not room here to describe the progression in ecological theory that the study of ponds and lakes in southeast Michigan has produced, largely in association with the Werner lab and the E. S. George Reserve.

Faculty in the newly formed Department of Ecology and Evolutionary Biology (EEB) found grant money to bring in all the best ecologists in the world to give talks and talk to us, the graduate students in a seminar. George Estabrook taught me how to test hypotheses, quantitatively. Prof. Bill Fink tried to teach me about phylogenetic hypotheses. (I was not the most adept student, but I was enthusiastic.) And, of course, Paul Webb patiently gave me back manuscripts with many useful red markings (hard copy, of course), and taught me how to study and write about biomechanics. The new Department of EEB and professional societies, as well as occasionally Paul Webb's NSF grants, made sure I networked and talked to peers and experts at conferences every year.

The early years in EEB were wonderful and exciting, if sometimes confusing. Surely a scientist would emerge out of such a rich natal pool. Admittedly, I often felt out of my league. Nonetheless, I took hours and hours of high-speed video of escape responses of several species of Michigan tadpoles. I spent weeks of 14-hour days in the basement of the DANA building (then, the School of Natural Resources), in the dark, capturing tadpoles on film. Finally, the engineer on my dissertation committee members made a definitive statement that I should "not be allowed" to collect any more data until I had analyzed and written about the data that I had already collected.

I made it work. It was not pretty or graceful, but there was a scientific story hidden in all those videos, and I found one. My most exciting discoveries were, somewhat unfortunately for my scientific career, negative results. Tadpoles do not run away from dragonfly nymphs like fish run away from moving predators. The tadpoles move upon being touched. Thus, I focused on their strength

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Laura completed her B.S. in Biology at the University of Notre Dame, her M.A.T. at the University of Portland as a part of the Alliance for Catholic Education, and her Ph.D. in Biology at the University of Michigan. She accepted a position as an assistant professor of biology education at Eastern Michigan University and then, later, another position as assistant professor of science education at Hunter College of the City University of New York before joining the faculty of the Department of Ecology and Evolutionary Biology at the University of Michigan in 2009.

In biology, Eidietis uses biomechanical tools to help understand the migrations of lamprey. Specifically, she has explored Pacific lamprey making their way up manmade ramps. She has used similar tools to investigate the behavior of frog tadpoles in predator-prey situations. She enjoys investigating the interaction between the physics of the environment and animals.

In science education, Laura is looking at factors that influence the inclusion of topics and activities in classroom, and specifically exploring teacher/instructor decision making. She teaches courses in Quantitative Reasoning in the Biological Sciences, Animal Diversity, and Envionronmental Physiology of Animals, and most recently, she has become interested in incorporating environmental sustainability themes into introductory biology courses.

KEITH W. PECOR

A Herpetologist Who Studies Arthropods

2000–

When I entered college, I had no idea what I wanted to study. I had positive experiences with English and Art History teachers in high school and those areas seemed promising. The sciences were not even on my radar. My good friend from childhood attended the same university that I did, and he was a dyed-in-the-wool herpetologist. For as long as I could remember, he was interested in snakes, turtles, and other herps. During an impressionable period, I had the opportunity to tag along on some of his adventures as a student researcher, and I found that herpetology spoke to me as well. I conducted some independent research, presented it at the National Conference on Undergraduate Research, and set my eye toward graduate studies to begin in the fall of 2000. I remember speaking with Ron Nussbaum on the phone in January 2000 and his encouragement even then. After I received my admission letter to Michigan, I was on board. Much like athletes on signing days, I followed up the mailing of my acceptance letter with the purchase of a Michigan ball cap (which I still have) from a store in the local shopping mall.

I arrived in Ann Arbor with a flurry of potential projects in my mind. I used the access provided by my UMMZ keys to wander the collections and envision my dissertation on the library shelf next to the graduate works of so many scientists whose publications I had read and respected. Perhaps I would study salamanders in the Appalachians, or maybe it would be turtles at the E. S. George Reserve. But a funny thing happened on the way to the reserve. During the Biology Weekend at the University of Michigan Biological Station (UMBS) in fall of 2000, I met Brian Hazlett. We shared an interest in behavior, specifically those behaviors elicited by chemical stimuli, but I was committed to studying herps and he studied crustaceans. I did a lot of soul searching in the weeks and months that followed. As before I matriculated, Ron was supportive of my decision to study crayfish for my dissertation and was unwavering in his support and commitment to being my dissertation co-chair.

In retrospect, I could not have asked for a better arrangement. Having a co-chair in Biology (later Ecology and Evolutionary Biology, EEB) and a co-chair in UMMZ gave me entrée into both worlds. I spent my days in Ruthven interacting with Greg Schneider, Arnold Kluge, Ron, and others, and I spent my nights (crayfish are nocturnal) in Kraus watching crayfish under the glow of red lights. I met and learned from so many good people in EEB, UMMZ, UMBS, and the Saline Fisheries Research Station. Now, as a Full Professor and Department Chair reflecting upon those days, I want to highlight the following three elements of the Herp Division that have meant so much to me—the herp trip, the space, and the people.

The Herp Trip

I had the pleasure to serve as the Graduate Student Instructor (GSI) for Herpetology on four occasions, and I participated in the herpetology class field trip five times. This class field trip was a 3-day excursion to the Smoky Mountains and surrounding areas to collect salamanders, and other herps as the weather permitted. My first trip was in 2001, and at that time, the motor pool primarily consisted of 15-passenger vans. To drive these vans, you were required to attend a special training session, and I was the only grad student to take the training. As a result, I had to drive

Keith Pecor *with his first hellbender* one van the entire trip while Ron drove the other van. It was also my first hellbender experience. After an excruciating period of fruitless searching, I saw a hellbender swimming toward me in the cold waters of the North Carolina river that we were sampling. I reached down with both hands and somehow managed to snag the slippery beast and lift it into the air, announcing my success with a profanity-laced expression of personal excellence. I returned to Ann Arbor triumphant, and immediately learned a key lesson from Ron. It is better to give the course evaluations to the students after the herp trip.

My second trip was the only one I took as a visitor rather than GSI and was most memorable for an interaction with a decidedly non-herpetological member of the Ohio fauna. By this time, the motor pool had been converted from 15-passenger vans to Dodge minivans. This meant that any licensed driver could drive and marked a major increase in the comfort for the herp trip. I was driving the first shift near Wapakoneta, Ohio, when two whitetail deer leapt from the median into the southbound lanes of I-75 immediately in front of our van, the lead vehicle in a four-van convoy. I had no time to react and plowed into one of the animals at full speed while the other bounded off the interstate as quickly as it had arrived. Given the aerodynamic shape of the hood and windshield, the deer that we hit slid up and off the van, catapulting though the air and landing back in the median. The driver's side headlight was smashed in the process, and the occupants of the trailing vehicles described the scene as something out of an action movie, with the pieces of broken headlight reflecting the lights from other vehicles in all directions as if there had been an explosion, followed by an airborne cervid in the dark Ohio night. I borrowed a student's cell phone to call the number listed on the insurance card in the glove box, and the voice at the other end said to just leave the van on the side of the road with the keys in it and carry on. We had enough space in the remaining three vans to keep going, and the remainder of the trip was smooth sailing. I expected to be blacklisted upon my next trip to the motor pool, but it was as if the incident never happened. For his part, Ron endorsed my "decision" to ram the deer and bought a Caravan soon after the trip ended, telling me that he felt safe in it given how it handled a deer at high speed.

The other trips were memorable in their own ways, and they collectively rank among my favorite experiences in grad school. As for the various hijinks and shenanigans over the years, this (thankfully) pre-dated social media.

Ruthven / The Herp Division

Despite my regular visits to Kraus, the Ruthven Museums Building where the Herp Division was located was my grad school home and played a significant role in my grad school story. The museum building was not especially old, having been built in 1928, but it was just old enough to have the kinds of detail that made it feel regal and marked it as the product of an earlier time. From the elegance of the first-floor rotunda to the large, solid-wood doors with transoms, this was a place with character. From the theses and incredible collections of journals, books, and reprints in the division library (not to mention the larger museum library) to the ranges full of magnificent specimens from around the world, this was a place that had witnessed generations of hard work and academic excellence. To be in such an environment while making the transition from undergrad to grad student to Ph.D. had a great impact on me. It inspired me to think bigger, to work harder, to be worthy of the opportunity granted to me to study here and have my name in the annals of Michigan herpetology, and I never took it for granted.

Camaraderie

The Herp Division was always a fun place to be. Everyone was friendly, and it was interesting to see who might be visiting from week to week. My close fellow students at the time—Glenn Fox and Steven Albee-Scott—were good friends and remain so today. I recently saw Glenn in Ann Arbor, and in spite of a gap of 12 years since we last were in the same space, it was as if scarcely a day had passed. Steve and I shared an office for most of my time at Michigan, and we spent untold amounts of time together in Ruthven and elsewhere. Finally, I gained so much from and enjoyed tremendously the interactions I had with Arnold Kluge, Greg Schneider, and Ron Nussbaum.

I learned a lot from Arnold Kluge, both in his systematics course and in our frequent informal chats. I have three favorite Arnold anecdotes, the first two of which are related to that systematics course. As part of the course, we were assigned to complete a systematics project. Many of the students were budding systematists, so the project was related to what would become their dissertation research. I had more or less decided by this point that my interests were more ecological than phylogenetic and that I would likely be studying crayfish rather than salamanders, so I chose to study the question of crustacean monophyly. Arthropod systematics were under much scrutiny at the time, and the possibility of Crustacea being paraphyletic had been suggested. I gathered DNA sequences from various online repositories and ended up determining that different data sets gave different answers and that there were some issues regarding taxon sampling. I felt good about my work, but I was a novice. As such, imagine my surprise when Arnold informed me that he had shared my project with the curator of invertebrates at the American Museum of American History. I was terrified, but Arnold's demeanor suggested that my conclusions had been, if not validated, at least not rejected out of hand.

Near the conclusion of the systematics course, Arnold hosted a dinner at his house. Knowing that I was from the south and perhaps feeling a bit homesick in the winter of my first year in Ann Arbor, he asked his wife to make an iconic southern dessert—pecan pie. I strongly dislike pecan pie, but I was so touched by this gesture that I fought through a nice, thick slab and had nothing but praise for the chef.

In the latter part of my time at the museum, Arnold had taken over as editor of *Cladistics*, and during one of our chats, he handed me a manuscript and asked for a review. I was taken aback. If I recall correctly, I had not at that point reviewed a manuscript within what I considered my specialty, much less a field in which I considered myself much less than an expert. However, I was also inspired by Arnold's confidence and determined to write the best possible review. I pored over the manuscript and put everything I had into the review. I still smile when I see *Cladistics* on my CV, nestled among the journals for which I have served as a reviewer.

I can go no farther without mentioning Greg Schneider. It is impossible to summarize him briefly or to praise the work he has done for the Herp Division and for the museum adequately. While I frequently poked fun at his quirks (e.g., using an ancient dot matrix printer to make specimen labels), his commitment to the maintenance of the collections and the accuracy of division records was without equal. And he is a really good guy. I always enjoyed popping in for a visit and hearing about his campus squash rivalries or some long-missing loan that he successfully tracked down. I had the opportunity to work alongside Greg as the division's Research Assistant on two occasions. From the tedious (a full inventory of the skeletal collections), to the smelly (curating the turtle range), to the mundane (cataloging specimens), it was never dull when Greg was around. I especially liked how

Greg had a nickname for everyone. Somehow, I was dubbed Keith-mon (spoken in a Jamaican accent), and I returned the favor with Greg-mon. We still address each other as such on the phone and in emails.

In addition to herps, Greg and I share an interest in golf, which was a topic of much discussion and some adventure. In particular, I recall a trip we made to South Bend, Indiana, to receive a donation of salamander specimens from David Sever. My very first "real" herp project was a survey of Junaluska salamanders, a species that David Sever co-described, so this was a trip I was looking forward to taking. We left quite early in the day, so that we could play 18 holes at the Notre Dame golf course after taking delivery of the specimens. When I finished grad school, ever the gentleman, Greg treated me to a round at Radrick Farms and a steak dinner at Knight's. One of these days, I hope to return the favor.

Last but not least, I have nothing but praise for Ron Nussbaum, my dissertation co-chair and mentor in many areas of life. It was Ron who fielded the nervous inquiry about graduate study from an undergrad at the University of Memphis, and it was Ron who spent the next 5 years helping me to become the scientist I am today. Our relationship started off in the typical mentor-mentee fashion. I met with him a handful of times during my first fall semester at Michigan and put my hat in the ring to be the GSI for Herpetology my first winter. There was a more senior student ahead of me in the queue, but she took another assignment. The job was mine, and I started in the deep end. The class I GSI-ed in the fall was fairly structured, but Ron expected the GSI to be fully in control of the lab and the herp trip. I had some notes from previous GSIs and much to learn. I spent hours determining which specimens were needed from the teaching and research collections and then carting them across campus (the lab was in Kraus that year) in the snow and ice. I secured permits from the National Park Service and the state of North Carolina. I made hotel reservations and attended van training. It was nerve-racking, time-consuming, and so much fun.

Following that first herp trip, my relationship with Ron began to deepen. We discovered our mutual interest in good music, irrespective of genre, and good beverage, irrespective of genre, and spent many evenings enjoying both while talking science and other topics. Through Ron, I learned about not only herpetology but also the history of the discipline and the history of UMMZ. We went to concerts and had dinner together and generally enjoyed each other's company. I have an entire volume's worth of anecdotes, but I will share two that emphasize both our friendship and professional relationship.

In the winter of 2004, Ron and I were enjoying an evening of science and music when he let slip that it had been his birthday recently. I will not share the exact date here, but I filed that nugget away, determined to do something special the next year. As the following winter approached, Steve Albee-Scott and I set about narrowing down the possibilities. We decided to wait until Ron left campus and then decorate his office. For those who never saw Ron's office, he had an impressive collection of carved wooden figures from his travels overseas. We adorned each figure with a party hat and hung streamers throughout the two bays of his office. We covered the door and transom with the most obnoxious wrapping paper we could find. It was quite the sight, and we giddily awaited his arrival the next day. As luck would have it, he was under the weather on his birthday, so we removed the external decorations, but left the items inside in place. After a day or two, Ron was back on campus and discovered our gift. We were rewarded with a brief email that included a few phrases not to be repeated here, followed by, "Well done."

The same winter of 2005 that saw the birthday prank was the semester that I defended. I had a date in April picked out and Museums Room 2009 reserved. I had a job in hand, and most of my dissertation was written. And yet, I was a wreck. I am not normally nervous about public speaking, but this was a different animal. The night before, I was in Room 2009 practicing for the umpteenth time when there was a knock at the door. It was Ron, and he had decided that my practicing was finished. We had a few drinks, chatted about this and that, and he sent me home. I was not sure at all that this was the best strategy, but I followed the advice. Everything went better than I could have hoped during my defense, and I still remember Ron sticking his head out of the Herp Library after the deliberations, grinning, and saying, "Dr. Pecor, I presume?"

I have benefited tremendously, both professionally and personally, from my association with Michigan Herpetology and the university more generally. From the teaching experiences to the scholarships to the seminars, it was an incredible time. When I was searching for a job in my final year in Ann Arbor, it was the sponsorship of a fellow Herp Division alum, Alan Jaslow, that led to me serving as a Faculty Fellow at Rhodes College. That position prepared me for my current position at The College of New Jersey, which I have held since 2007.

On a more personal note, I feel that my time at Michigan is largely responsible for who I am today. It was a transformative experience. I am proud to be a Michigan alumnus, and I am honored to contribute to this volume. GO BLUE!

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Keith Pecor received his M.S. in 2002 and his Ph.D. in 2005 from the University of Michigan. After an appointment as a Faculty Fellow in the Department of Biology at Rhodes College (2005–2007), Keith accepted a position in the Department of Biology at The College of New Jersey. His early research interests focussed on freshwater ecology and invertebrate biology primarily of crayfish, which is reflected in the courses he teaches—Ecology and Field Biology, Biology of Invertebrates, Freshwater Ecology, and Community Ecology. His most recent publications reflect his interest in ways to teach biological principles (e.g., genetic drift) effectively to undergraduate students.

JOHN A. MARINO, JR.

Context-dependent Development of an Amphibian Ecologist

2007–

As an ecologist, I recognize the important role that environmental context plays in influencing animal development and species interactions. Variation in abiotic and biotic factors can be the determining factor for the timing when larvae go through metamorphosis, what competitor dominates, which prey suffers greater predation risk, or how parasites are transmitted between hosts. In my own research, context dependence has been a major focus, especially with respect to amphibian interactions with parasites. However, I also recognize that environmental context applies to more than just the amphibians in the ponds where I do my research. Figuratively, my own environmental context—i.e., the conditions under which I trained and developed toward my own research program—has played a fundamental role in shaping the scientist, teacher, and mentor that I am today.

Perhaps the most critical conditions that influenced my professional (and in many ways, personal) development were those I experienced during my years at the University of Michigan for my dissertation and postdoctoral research. At Michigan I was trained to think, work, write, and speak like an ecologist. It was there that I learned many of the approaches that continue to play a critical role in my research on amphibian ecology and freshwater biology, more generally. Michigan also gave me my first opportunity to teach and mentor undergraduate students, which grew into a passion that I continue in my current role at a primarily undergraduate institution. Finally, and perhaps most importantly, the university also gave me the chance to form some of my most valued lasting collaborations and friendships.

By far the most influential person in my time at Michigan was my advisor, Dr. Earl Werner. I was Earl's final Ph.D. student before his retirement, and he taught me more than I can possibly summarize here. Crucially, Earl provided the guidance I needed, along with the freedom to pursue my own research interests throughout my Ph.D. He instilled a recognition of the importance of knowing the natural history of my study system, but also how insights from one system can inform our understanding of general ecological processes more broadly. As I was first getting started, he helped me learn how to read scientific literature effectively and to communicate about my research and ecology. Later on, he provided the guidance to overcome challenges I faced in interpreting messy data, responding to challenging reviews, or figuring out next steps. As I finished my dissertation, he was a vital source of advice and support during my transition to postdoctoral research and beyond.

A central focus of research in Earl's lab, and one of the topics that drew me to work with him, was that interactions among species depend on ecological context.[1,2] The presence of a predator, for instance, can dramatically affect prey foraging behavior that can, in turn, strongly influence competitive interactions between species. Using larval anurans as a model system, Earl and members of his lab had explored such effects extensively. Coming into the lab, I wanted to build on their work and continue to advance our understanding of context dependence, although was unsure what my contribution would be.

Inspiration came about when I had the opportunity to sit in on Barry O'Connor's parasitology course in the spring of my first year (a course I later had the good fortune to teach as Barry's teaching assistant for several years). It was during my time in that class that I started to recognize how parasites seldom received the same attention from community ecologists as predators, although parasites were increasingly being recognized as critical components of food webs.[3] Thus, the context-dependence of host-parasite interactions was ripe for exploration, and I suspected that amphibians could be a useful model system in which to address this topic. In addition, parasitism of amphibians was and continues to be a topic of great concern given recent declines in amphibian populations, in part due to infectious disease.[4] However, I had much to learn to be able to offer an intellectual contribution to our understanding effects of parasites on amphibians and ecological communities more generally.

Fortuitously, during the following summer, Manja Holland, a former Ph.D. student of Dave Skelly at Yale (himself a former Werner student) jointed Earl's lab as a postdoc. Manja had done extensive work on trematode parasites of amphibians for her dissertation research and was more than willing to share her expertise. She graciously helped me get acquainted rapidly with research on trematode parasites of anurans, and our work together soon bloomed into a productive collaboration.

In the subsequent years working with Earl and Manja during my dissertation research, we explored a range of different dimensions of the problem of context dependence in amphibian-parasite interactions. For instance, in a series of experiments, we showed that predators and parasites can synergistically affect larval frog survival and identified the likely mechanism for the synergism.[5] The presence of trematode infective stages (cercariae) induce tadpoles to increase activity levels, thereby increasing their visibility to predators and therefore, predation. Collaborating with another student in Earl's lab, Jess Middlemis Maher, we further showed that predators and parasites have non-additive effects on larval frog behavior, developmental rates, and stress hormone (corticosterone) concentrations.[6] In other work, we showed that host-parasite interactions can also critically depend on other environmental factors, including individual size and competitive interaction,[7] food resources,[8] and species identity.[9] These studies formed the core of my dissertation. Further, my interest in the context-dependence of amphibian-parasite interaction has not gone away but continues to be a focus of my ongoing research.

Besides Earl, Manja, and Jess, other members of Earl's lab were also greatly influential in my scientific and personal development as an amphibian ecologist. My first real field experience with amphibians was during the spring of my first year at Michigan helping Mike Benard, Earl's postdoc who is now an associate professor at Case Western Reserve University, with his long-term mark-recapture study of Wood Frog populations. We were collecting adult Wood Frogs and salamanders at drift fences that Mike and Earl had installed around six ponds on the Edwin S. George Reserve (i.e., the ESGR, where I performed most of my Ph.D. research), checking for individuals that Mike had marked with injectable dye as metamorphs in previous years. Wood Frogs are explosive breeders, and I remember being astounded by the sheer number of adults coming into ponds at one time. I was also greatly impressed by the scale of the study and the potential for unparalleled insights into amphibian demographics.

Another formative experience only a short time later was my first time looking for and collecting Wood Frog eggs with Amanda Zellmer, another of Earl's students, for her research on genetic population structure of these frogs. It was a first step toward my current appreciation for the usefulness of combining field and molecular approaches for informing ecological understanding, which I would later explore as a postdoctoral fellow. Shortly thereafter, I ran my first experiment with Sarah Seiter, a Master's student who was an unofficial member of the lab, assessing parasite effects on larval Wood Frog behavior. Unfortunately, the results were inconclusive, but I learned a great deal from the experience

Figure 1. *Crane Pond, which was one of the ponds included on the Edwin S. George Reserve.*

Figure 2. *A "pipe" sampler used during the Edwin S. George Reserve pond survey.*

on the challenges of experimental research with animals that I carried with me throughout my Ph.D. I also have fond memories later on in the summer collecting *Anax* dragonfly larvae (common predators of tadpoles) with Mike Fraker, who had recently completed his Ph.D. with Earl and was doing a postdoc with Bob Denver on amphibian physiology, as I was first starting to think about interactive effects of predators and parasites. The amazing combination of people and mix of interests in Earl's lab provided a fantastic environment for a student first getting started in graduate research and figuring out my focus.

Probably the most memorable experience in Earl's lab, however, was joining the long-term survey of larval amphibians, predators (large invertebrates and small fish), and snails in ponds on the ESGR (Figure 1). The survey happened every May and again in July for 3 or 4 days, to assess the communities of both spring- and summer-breeding amphibian species. While Earl was the lead investigator, it was his amazing lab manager, Chris Davis, who actually ran the show and kept everything on track. The survey included a combination of timed dipnet sampling, seining, and "pipe" sampling (Figure 2)—the last of which involved quickly thrusting down a large piece of aluminum pipe into the pond and collecting all animals in the water column inside the pipe to get an estimate of density. Making our way through the woods between ponds lugging a large pipe while wearing waders was physically exhausting but a lot of fun, fueled by the traditional donuts each morning from the Dexter Bakery, which we passed on our way from Ann Arbor to the ESGR. It was a great opportunity to learn quickly to identify

Figure 3. *The 2008 survey crew for the Edwin S. George Reserve survey. Mike Benard, John Marino, Manja Holland, Kerry Yurewicz, Dave Skelly, Chris Davis, Rick Relyea, Earl Werner. Photo credit: Mike Benard (shared with permission).*

amphibian larvae and other aquatic animals in the field and see some of the patterns in nature that I had read about. The ESGR survey not only gave me a new appreciation of amphibian natural history, but also the chance to meet and discuss research with some of Earl's former students and collaborators (Figure 3), such as Dave Skelly, Rick Relyea, Jason Hoverman, and Shannon McCauley, who were involved with the survey and whose research had been profoundly influential. Finally, the survey results became important in offering data and ideas for my own research,[10] and continue to guide my research on ecological communities.

Of course, I had many other formative experiences during my Ph.D. outside of those with Earl's lab and his former lab members, most of which I do not have the space to recount here. One memorable experience relevant for this essay, though, was my time working with Greg Schneider in the Museum of Zoology (UMMZ) Herpetology Division as a curatorial assistant, which I had the pleasure of doing for a semester during my third year and again during my final year of my Ph.D. Prior to my first semester working in the UMMZ, I of course had appreciation for the history of research on amphibians and reptiles at Michigan, especially the groundbreaking research done at the ESGR by the likes of Henry Wilbur, Jim Collins, and Justin Congdon, among others. However, in the UMMZ, looking at field notes and walking by shelves full of thousands of herpetological specimens from around the world collected during many decades by researchers from Michigan (and other institutions) gave me a much deeper appreciation of the rich history that surrounded me, going from Alexander Ruthven's work on garter snakes to the cutting-edge research in the museum today.

My time in the Herpetology Division also provided a deeper understanding of what museum work entails and its critical importance in biological research. I learned many invaluable skills in my time assisting Greg, from how to formalin-fix specimens, to taking tissue samples, to digitizing records, to the logistics of adding new accessions to the collection, arranging loans, and maintaining such a huge number of specimens. One especially great memory was Greg taking the time to show me for the first time how to clear and stain a specimen, when I had never had the chance previously. Before working in the museum, even though Earl's lab was just down the street in the Kraus Natural Sciences Building, I had not spent much time in the Ruthven Museums building outside of my classes and a weekly lunch seminar. Working at the museum gave me more opportunities to interact with and learn from UMMZ herpetologists, such as Ron Nussbaum, Dan Rabosky, Alison Davis Rabosky, Fred Kraus, and others, as well as a number of graduate students and postdoctoral fellows. Finally, working in the museum during the last semester of my Ph.D. allowed my time in graduate school to come full circle, when I had the opportunity to help Greg catalog the large collection of specimens from the ESGR survey that I had participated in since my first year.

The experiences and relationships I developed during my graduate work paved the way for my postdoctoral positions, first working with mycologist Tim James in Michigan's Department of Ecology and Evolutionary Biology (who himself had an interest in amphibians from the fungal disease perspective and had joined the ESGR survey several times) and subsequently with co-mentors Ed Ionides in Michigan Statistics and Scott Peacor (another former Werner student) at Michigan State University Fisheries and Wildlife. While these postdoctoral projects represented a significant transition from my graduate work, with new systems (freshwater plankton) and approaches (e.g., next generation sequencing, computational modeling), they built on the rich understanding of aquatic population and community ecology I developed during my Ph.D. research on amphibians. Fortunately, even though my "day job" was now focused on plankton, I did not totally have to stray from my roots in amphibian research. Working with Tim, for instance, I had the opportunity to collaborate on a couple projects related to amphibians, including a survey of amphibians on the ESGR for infection by the fungal pathogen *Batrachochytrium dendrobatadis* (*Bd*), which has had a decimating impact on amphibians in many parts of the world, although fortunately not at the ESGR. Staying in Michigan but getting to work in new labs on new questions was a valuable experience for me, as my interests and skills were broadening but my fascination with the original questions and systems never went away.

Of course, I have happily returned to amphibian research since beginning a faculty position in the Biology Department at Bradley University in Peoria, IL. I have greatly enjoyed the opportunity to work with a number of undergraduates and even high school students as I continue to investigate amphibian-parasite interactions, and other topics, in a new environmental context—the highly modified, predominantly agricultural landscape of central Illinois. Sampling tadpoles in farm ponds in the heart of the corn belt is a big contrast to the idyllic (to my mind, anyway) ponds of the ESGR, but it is useful to address some of the pressing impacts of land use change for amphibians and wildlife more generally. I am still interested in the context dependence of parasitism, but now am starting to take into account human impacts as a critical aspect of environmental context in the 21st century.

As I continue forward in my challenging but exciting role as a relatively new faculty member, I can say without a doubt that my experiences at Michigan continue to be vital and relevant, whether I am planning experiments and field studies for ongoing research projects using the skills I learned, meeting with a collaborator I first met during graduate school, or sharing my knowledge and enthusiasm with students, modeled after my own mentors. It was the rich environment for research and learning during my time at UM, facilitated by a fantastic group of people, that guided my metamorphosis from an incoming student unsure of how I could make a contribution into an ecologist passionate about advancing science. My time at Michigan led me to the point where I can now try myself to provide the right context for the next generation of developing scientists and citizens to meet their goals.

About the Author

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John completed his Ph.D. in 2013 and continued as a postdoctoral fellow at Michigan until 2017, before accepting a position at Bradley University. As an aquatic ecologist, Marino seeks to understand how environmental context mediates species interactions in food webs. His research addresses freshwater systems ranging from small, ephemeral ponds to the Laurentian Great Lakes. John uses a range of tools, including experimental and observational studies, and modeling. His goal is to confront major challenges to sustainable freshwter systems, including infectious diseases, harmful algal blooms, and invasive species.

Endnotes

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KINSEY BROCK

From the Farm to the Field

2007–

Had you told me on my first day at Michigan in the fall of 2006 that before leaving Ann Arbor, I'd travel to four continents, become a herpetologist, and have three degrees from the University of Michigan, I would have laughed and asked what a herpetologist was. I grew up on a farm in a small town in southeast Michigan. Neither of my parents went to college but they raised me with very few rules, high expectations, and the mantra "If you work hard and do the right thing, you can be anything." Being a first-generation college student had many drawbacks, but it also had some advantages. Without parental academic guides, I quickly sought out mentorship from a wide variety of professors, staff, and upperclassmen spanning the School of Art & Design, College of Literature, Science, and the Arts, and the School of Music, Theatre, and Dance. Surprisingly, it was my art school mentor, Professor Joe Trumpey, who brought my varied interests and experiences into focus, inspired and challenged me, and set my life in a direction I never would have expected—herpetology.

Joe had appointments in both the School of Art & Design (now the Stamps School of A&D) and the School of Natural Resources and Environment (now the School for Environment and Sustainability); he taught an Art & Design Perspectives course (now no longer in the curriculum) on art, environment, and technology. The class was engaging—we read books (classic and contemporary) and primary literature, watched art world films and documentaries about human overexploitation and land use, had a semester-long project that required us to establish a relationship with a wild plant in Ann Arbor, and *more!* But more important than the class, to me, was the professor. Joe was familiar—he lived on, and ran, his own farm; he was an artist, a scientist, a bit of a nerd, and brought enthusiasm, positivity, and healthy dose of realism to everything. I went to office hours, sent lots of e-mails, and asked Joe lots of questions. Joe became my mentor during that fall semester, and I enrolled as a dual-degree student in both the School of Art & Design and Program in the Environment. Having a foot firmly planted in each of the schools (across two campuses!) made me a perfect fit for the trip of a lifetime—Joe's EcoExplorers class to Madagascar for Art & Design and PitE students. Perfect!

In the spring of 2010, the EcoExplorers set out into the wild for several weeks to carry out a sustainability outreach project in partnership with Ho Avy, an NGO conservation program based in the spiny forest of Madagascar, and a few graduate students from the Michigan School of Natural Resources and Environment. Delays caused by the 2010 volcanic explosion in Iceland left us stranded in Nairobi for an overnight sleep on the floor before we arrived in Antananarivo tired, smelly, and missing some baggage. So it goes. We checked in to our accommodations for the night just as the sun was setting, and while most everyone else was rushing to the dining hall to eat what they thought was chicken but turned out to be crocodile, I was entranced by a little object in a tree bursting with flowers. A few steps closer and there it was, one conical eye whipped around to look right at me, then another (Figure 1). Even though I'd never encountered a living chameleon before, it was as though I had known this lizard forever; I swiftly reached for it without a second thought. It was a Carpet Chameleon, a little rainbow with a big mouth and freaky feet living and breathing in my hand. What a

***Figure 1. Brock** and Carpet Chameleon.*

wild thing! I spent the rest of the trip searching for herps and writing down questions. "Why do chameleons have weird eyes, weird feet, and weird tails when geckos that live in the same trees do not?" "Why are some lizards out during the day and others at night?" "Why are there so many species that only exist on Madagascar?" "How can I spend the rest of my life asking questions and chasing lizards?"

Figure 2. ***Brock*** *as Student Assistant in Herpetology.*

Upon returning from Madagascar in the fall of 2010, I got a student position in the Herpetology Division at the University Museum of Zoology (Figure 2). I would be working as a collection's assistant with the herpetology Collections Manager, Greg Schneider. I didn't realize at the time how lucky I was—there was only funding for one paid position, and I was in the right place at the right time. It turned out to be doubly so because Chris Raxworthy, the herpetologist I had recently read about in a book on Madagascar's unique flora and fauna "The Eighth Continent" by Peter Tyson, had just deposited hundreds of herp specimens from Madagascar in the collection and would be coming for a visit later that semester. I'll never forget those days in the museum. Pulling open the heavy iron door to the rotunda of the old museum, I felt that I was part of something special that was more than 100 years in the making. Scanning field notebooks from Ruthven's field expeditions and learning herpetological history from Greg was my ideal afternoon. I opened boxes chock full of jars filled with herps pickled in ethanol, double-checked taxonomy, tied tags to specimens (the right way; there is a right way and a wrong way), and put jars away in the massive collection. I gained a deep love and appreciation of museum collections and an equally strong distaste for vodka. When Chris Raxworthy arrived, I showed him around the newly catalogued specimens he collected in Madagascar and all the work I'd done. I remember his kindness—I was still learning, and he took me to lunch to talk about all those questions I had and how I could turn those questions into a graduate thesis project. The conversations with Chris Raxworthy, Greg Schneider, and Joe Trumpey led to my decision to apply graduate school to study reptile evolution on islands.


Figures 3 and 4. *Fieldwork in the Aegean islands.*

I applied to several programs but decided to stay at Michigan because the teaching and research opportunities were unbeatable. I'd be a teaching assistant in the Michigan Marching Band (in which I played in the trumpet section for 4 years) in the fall and the Program in the Environment classes in the winter. On top of getting paid to get my degree, I found an advisor in the School of Natural Resources & Environment who was going to the Greek islands every summer to study the ecology and evolution of the herpetofauna. Johannes Foufopoulos was a conservation biology professor in the undergraduate PitE program; and we designed a fun study that leveraged the hundreds of Aegean islands as a natural laboratory of evolution. After taking Dr. Bobbi Lowe's behavioral ecology class, I became interested in the evolution of behavior and my Master's thesis would look at the evolution of anti-predator behaviors in the Aegean island endemic lizard, *Podarcis erhardii*. I received research funding from the Museum of Zoology to spend two summers living in the Greek islands to collect specimens, which involved kayaking and haggling with salty fishermen to take me to extremely isolated and uninhabited islands where lizards were the only vertebrates. In addition to climbing up rocky cliff faces in search of lizards while waves crashed beneath me, I put my specimen-prep skills from the lab to use in the field—pickling specimens on the beach and balconies (Figures 3, 4) while the locals questioned my sanity. I'm proud to have contributed unique specimens from far away islands to the herpetology collections. Having graduated from my Master's program with several publications all about the behavior, life history, and evolution of *P. erhardii*, I knew I wanted to continue studying lizards but focus on using genetics to study their evolution (Figure 5). Dan Rabosky and Alison Davis Rabosky had just arrived

Figure 5. Podarcis erhardii.

at Michigan, and I volunteered to help Alison look after her colony of Western Ground Snakes (*Sonora*).

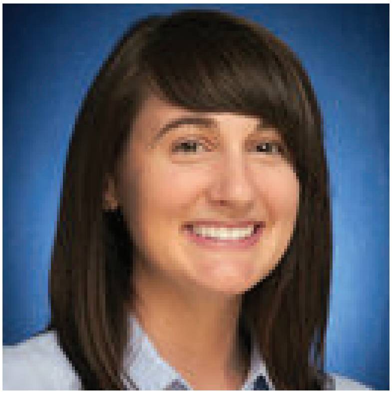
Alison was the first woman in herpetology whom I'd ever met, and she immediately became a mentor and inspiration to me. Conversations with Alison led to my feeling that I truly belonged in science, and that my ideas were my own and worth pursuing. We would meet in her office in the basement of the old natural history museum and talk about snakes, mimicry, color polymorphism, and correlated evolution of behaviors. Her enthusiasm and passion encouraged and invigorated me. As an artist and scientist, I was fascinated with the evolution of color and pattern, and the ways in which these signals could be under different forms of selection, both natural and sexual. The lizards I studied for my Master's were color polymorphic, though no one had ever described them as such or studied it. Alison and I came up with some questions and designed behavioral experiments to test for different anti-predator behaviors in different color and pattern morphs of *Sonora*. The museum, ever present in my personal and research life at Michigan, came to the rescue again and Janet Hinshaw from the Bird Division provided us with a stuffed Cooper's Hawk, one of the primary birds of prey native to range of *Sonora semiannulata,* to simulate predation! After working and talking with Alison, I decided to pursue a Ph.D. at the University of California, Merced, looking at the evolution of color polymorphism.

Currently, I am a fourth-year Ph.D. Candidate in Quantitative &

Systems Biology at the University of California, Merced (Figure 6). I chose UC–Merced because I found advisors (initially working with Dr. Danielle Edwards and now with Dr. Jessica Blois) and an interdisciplinary graduate program where I could pursue my dream project—i.e., figuring out the evolutionary causes and consequences of color polymorphism in my Greek-island system. In addition to advising me academically in graduate school, Jessica has provided me with strong mentorship on how to use my experience and intellect to advocate for myself and others and be a strong and empathetic member of the scientific community. Herpetology has long been a male-dominated field, and scientists such as Alison, Dan, and Jessica have given me hope, inspiration, and advice to carry on and battle through sexism. There have been trying moments and tough times, but I'm still here and glad I stayed in herpetology. I'm a National Geographic Explorer and now recruit, train, and mentor my own undergraduate students in the lab and field. In particular, I've focused on working with women and underrepresented students as my research mentees. I spend my summers hitching rides with fisherman and kayaking to uninhabited islands to chase and measure lizards no one has studied before. The BBC came out and shot a natural history special, *Animals Behaving Badly*, on the intense cannibalism we've observed on small dry islands. I'm living my dream. Sometimes on really good days I say to myself, "How did I get here?" The University of Michigan Herpetology Division gave me a strong foundational knowledge of herpetology and the history of our field. I was part of a community of sharp and motivated students, one of the world's greatest collections of amphibians and reptiles, and a group of great mentors who allowed me to accomplish my first independent research project and set me off on a great career. As a student, I am so grateful to all the talented and hardworking people who have contributed to Michigan herpetological community. Michigan Herpetology will always be my home, and wherever I go, I go blue.

Figure 6. *Fieldwork in Greece*

About the Author



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At the time of this writing, Brock was still a Ph.D. candidate in Quantitative and Systems Biology. From her website, we learn the following. "How species form is a central question in evolutionary biology. A major challenge in contemporary speciation research is linking microevolutionary processes, such as natural and sexual selection, within populations to broader macroevolutionary patterns of divergence among species. Much of my research is focused on the evolution of color, pattern, behavior, chemical signals, and other traits under both natural and sexual selection that vary geographically within and among species to understand how species diverge into distinct lineages. I take an integrative approach that leverages phylogenetics, morphology, behavior, and both field and lab work to study species traits in space and through time. My Ph.D. dissertation is on the evolutionary causes and consequences of color polymorphism."

ERIN WESTEEN

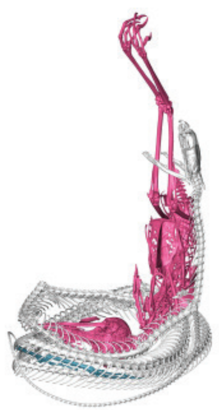
The Secret's in the Scan: Michigan Herpetology from the Inside Out

2013–

Getting Started

As a girl growing up in northern California, a favorite pastime was chasing and observing the "blue belly" lizards in my yard. Fun though it was, I never dreamed I would be able to make a career of this hobby. Because I am writing this essay, you can probably surmise that I am, in fact, a herpetologist—but for many years I did not know what a herpetologist was, or that I could be one. When I began my undergraduate studies at the University of Michigan, I admittedly knew very little of the Museum of Zoology. My first job was in food prep in a campus café; as soon as I learned that I could be paid to do research instead of making egg salad sandwiches, I promptly quit and applied to as many research jobs as I could find. I was interested in biology and accepted a position to study pollinator diversity across the metro-Detroit area. After spending several months carefully identifying bees, I began to wonder why some genera were so species-rich whereas others were species-poor. Though I found bees to be fascinating, I wanted to work with vertebrates and especially herps. At the same time, I was taking a course called "Animal Diversity," in which our final assignment was to pick any animal with a salient adaptation and discuss its natural history. Finally, an opportunity to write about the coolest thing I could imagine—venomous snakes! Upon reading my paper, my professor suggested I get in touch with the herpetology curators, Drs. Dan Rabosky and Alison Davis Rabosky. As luck would have it, an advertisement went out to the undergraduate biology majors that week: the Rabosky lab was seeking research assistants to study patterns of species richness in squamate reptiles. It was the perfect opportunity to combine my budding thematic research interests with herpetology. I responded to the email as quickly as I could and began work shortly after on a project to collect morphological data for a variety of snake species in the collections.

On my first day at work in the museum, I felt like Charlie in the Chocolate Factory as veteran collections manager Greg Schneider showed me and the other research assistants around. Thousands upon thousands of specimen jars sat neatly in their rows, waiting to be studied by students like me. Each specimen had a story, many of which were written in the original field notes held in the UMMZ. Greg showed us the largest and smallest frogs in the collections, tanks with boas and vipers, Gila Monster skins, and more. Once we were familiar with collection protocols, we were able to pull specimens from the shelves ourselves. I learned all the tricks of the trade, like how to open pesky specimen jars with Greg's "universal tool"; how to tie specimen tags and which pens to use so the writing wouldn't fade in ethanol; and how to measure the snout–vent length of a coiled snake (with a wet string, of course!). Before long, we had amassed a large dataset of snake morphological measurements, and my interest in squamate evolutionary ecology had grown exponentially.



CT-scan of snake and its prey.

Once I had proven myself a worthy collection assistant, it was time to begin an independent research project under Dan and Alison's advisement. As always, they had many wonderful suggestions, but one sounded particularly interesting. Alison had been wondering about the evolution of rear fangs in the traditionally "non-venomous" family Colubridae, and would I be interested in looking at the teeth of some of these snakes? At the time I was learning microCT methods by working with one of Dan's graduate students, and we thought this would be a suitable method to investigate the rear fangs of many colubrid snakes. I happily accepted the offer and began work on my first-ever independent research project. The UMMZ was the perfect place for this project to grow, too. As I read about cool snake dental adaptations (*Psammodynastes* and their front and rear fangs; deadly rear-fanged Boomslangs and twig snakes; *Pareas* snail-eaters with uneven sets of teeth) I thought, "wow, how cool would it be to see some of these species?" As luck would have it, UMMZ had all of them! This turned into a years-long collaborative project in which we quantified a variety of fang phenotypes from microCT scans and examined the relationship between dentition and snake diet/prey capture methods. Hopefully by the time this is published, you can read about it!

SOME REMARKS ON THE HISTORY OF CT-SCANNING AT UMMZ

Nowadays, the UMMZ has a state-of-the-art industrial CT scanner that produces a high volume of beautiful scans. But my story takes place several years ago, when we were just getting started. At the outset, we used a scanner in the Michigan Dental School; the scanner could take eight specimens at a time, but they all had to be less than about 8 cm total diameter. This limited our options, and in the beginning, we were mostly scanning skulls from skeletal preps (rather than wet specimens). Though the UMMZ has a fantastic skeletal collection, there were some challenges associated with scanning them: because snake teeth are not truly socketed to the tooth-bearing bones, when soft tissue is removed a lot of teeth tend to fall away. Additionally, the skull couldn't move at all during scanning or the result would be unusable. Ever the engineers, Greg and I took several trips to a recycling center in town to pick out suitable materials to keep the specimens safe during scanning and prevent them from moving—think small plastic containers for 10¢, recycled foam and cotton batting for 20¢, etc. We produced a set of scans that I used for my honors thesis, but the story doesn't stop there.

After using the Dental School scanner with success for several years, we took our system to the next level using larger scanners in the Medical School and Paleontology Department. At last, we could scan specimens in ethanol! But as soon as I started scanning wet specimens, I noticed a lot of…junk (the correct scientific term?) in the mouths of some specimens. This impaired my ability to measure the teeth; so I did what any logical researcher would do—ordered tiny toothbrushes to give each specimen a dental cleaning before it went into the scanner. This method worked well, and with these larger scanners, we were able to rapidly increase the number of specimens that we could digitize. We ended up creating "snake towers," or several specimens stacked atop one another for overnight batch scans. And just before I left Ann Arbor, the curators purchased their very own UMMZ scanner to really take specimen digitization and dissemination to the next level.

Now, there are standardized protocols and workflows, making the whole process of micro-CT–scanning specimens much more efficient. But the initial stages of CT scanning were fun and creative, as we were continually trying to optimize specimen prep, packaging, and processing. And, creating a blown-up version of a skull the size of your fingernail for the first time is pretty cool. (I've done it hundreds of times since then and still find it very cool, by the way.)

On Fieldwork

After working in the museum for a couple of years, I began to express an interest in working with living animals, aka fieldwork. Luckily for me, Greg was in contact with a former UMMZ postdoc, Tom Jones, who was then the program manager of the amphibians and reptiles branch of Arizona's state wildlife agency. He encouraged me to reach out to Tom and see if there were any opportunities—and there were! Arizona Game & Fish has an internship program, and every summer they hire a batch of interns to help with wildlife surveys. He put me in contact with the herp people, and soon after, I was hired as the official "garter snake intern" for the summer. For someone who had never left North America at this point (and had never done fieldwork), Arizona was basically herp heaven. My main job was to survey two species of threatened garter snakes—the Northern Mexican (*Thamnophis eques*) and the narrow-headed (*T. rufipuncatus*)— but I was also able to help on surveys for Chiricahua Leopard Frogs (and other ranids), desert tortoises, mud turtles, and even a variety of fish. As this was my first real field experience, I basically agreed to everything I could to gain experience. And of course, by spending so much time in the field, I was able to see lots of other herp species besides those we were surveying! Some highlights included seeing my first Western Hognose Snake, eight species of rattlesnakes, Arizona Tree Frogs, Canyon Tree Frogs, collared lizards, horny toads, and a Gila Monster! This experience was extremely valuable in several ways. First, it made me realize how much I love fieldwork and gave me the confidence to seek out more field opportunities, and second, I was able to make connections with some amazing biologists with whom I still keep in touch. (Part of my dissertation research is taking place at one of the sites I visited while an intern!) For any student who is seeking field experience but not able to go abroad, I highly recommend this and similar internship programs.

After this field experience, I returned to Michigan to finish my Bachelor's degree. Having been around the museum for a number of years now, I had heard tales of collecting trips but couldn't fully imagine what they entailed. In 2017, I would find out. I was thrilled when Dan asked if I would like to accompany the team (Dan, postdoc Rudi von May, grad students Pascal Title, Mike Grundler, Iris Holmes, Joanna Larson, Peter Cerda, and Imani Russell) on a herpetological collecting trip to the Peruvian Amazon. When we arrived at Los Amigos Biological Station (after 4 flights and a 5-hour boat ride), we were greeted with approximately 1000 stairs as the first test: "Gulp," are you ready for this? Once we had gotten

***"Peru team."** Back row (left to right): Peter Cerda, Imani Russell, Dan Rabosky, Michael Grundler, Mark Cowan, and Rudi von May. Front row: author, Iris Holmes, Joanna Larson, Pascal Title, and a number of Peruvian students including 2nd from right, front: Ciara Sanchez-Paredes & 2nd from right, back: Roy Santa Cruz*

all of the field gear up to the station, we hit the ground running. At long last, I got to see how animals were caught, processed, and prepared for the museum. The first few days were spent setting pitfall traps and drift fences. Each day we woke up at the crack of dawn (thanks to the howler monkeys) and checked traps. Afternoons were for processing animals, and the evenings were for night walks in the jungle in the hopes of spotting nocturnal species. In addition to all this, I was also able help Joanna Larson (Rabosky grad student) and Ciara Sanchez-Paredes (Peruvian collaborator, now MS student) with snake behavioral experiments. As part of Alison and Dr. Talia Moore's (former postdoc, now at UM Robotics) groundbreaking work on coral snake mimicry, we sought to quantify the defense behaviors of every snake we found. This meant catching snakes, putting them in an arena, and taking high-speed videos of their behaviors in response to a variety of stimuli (e.g., vibrations or overhead shapes). The experiments were fun and ran smoothly, with one exception—every time we put a *Chironius* into the arena, it escaped (almost immediately), shot across the room, and proceeded to defecate violently on whoever had the honor of catching it. Between all of these tasks, I'm not sure if I had ever been busier, or happier, in my life. Through the years, the Rabosky and Davis Rabosky labs have made several trips to Los Amigos and other field stations in Peru—their work plus the extensive work of Rudi von

"Nica team." *Left to right: Greg Pandelis, Daniel Nondorf, Maynor Fernandez Mena, Julio Loza Molina, José Martínez-Fonseca, Iris Holmes, Maggie Grundler, author. Photo by Ivan Monagan.*

May (former Rabosky postdoc) has shed tremendous light on this herpetological hotspot, and I would encourage everyone to check it out.

Once I had caught the fieldwork bug, there was no shaking it. When Alison's graduate students Iris Holmes and Peter Cerda invited me to join an expedition in Nicaragua, I was elated. The trip was eventful and productive in many ways, especially because the biodiversity of Nicaragua is significantly under-studied, and our trip resulted in a number of range extension records. Our guides, José Martínez-Fonseca, Maynor Fernández Meña, and Julio Loza Molina were like herp magnets. On the drive up to our first site (Mogoton, cloud forest climate, one of the highest points in the country) we found one of my most-wanted species—*Scaphiodontophis annulatus*, a snake that wants to be a coral snake mimic but hasn't fully committed. (The individuals that we found were patterned uniquely with red-and-black-bands on the anterior half and brown on the posterior.) We set traps going up the highest point in Nicaragua (seriously) and searched for animals in the adjacent coffee farms. Here, I met another of my most-wanted species—*Oxybelis aeneus*, a snake for which I had measured teeth many times over but never encountered alive. It was charismatic and gaped at me the whole time I spent admiring it. Other cool highlights from this site included finding a *Micrurus nigrocinctus* and then shortly after, a *Lampropeltis abnorma* that looked a lot like the former; watching our guides skillfully climb a really large tree and use a machete to catch a huge, grumpy *Spilotes pullatus;* meeting my first *Drymarchon;* and seeing the species (*Sceloporus malachiticus*) that would eventually inspire my dissertation work.

I didn't think the trip could get much better than that, but our next site, near Momotombo Volcano, was the snake-iest place I have ever been. The site is supposedly considered lowland dry forest, and we were all looking forward to a chance to properly dry out before heading to our final site in the lowland rainforest. As luck would have it, a tropical storm rolled through and we were rained upon for almost the entirety of our stay. We had no proper shelter, no electricity, and we processed animals in the back of our rented truck—it was fabulous! But back to the snakes. We caught several *Leptodrymus pulcherrimus* (an appropriately named species, this is one of the most beautiful snakes I have ever seen); *Oxybelis aeneus* and *O. fulgidus*; *Trimorphodon* and *Leptodeira*; *Conophis*; and many, many others. Though we had only several days here, we had a blast and I think it's safe to say that we would all like to return one day!

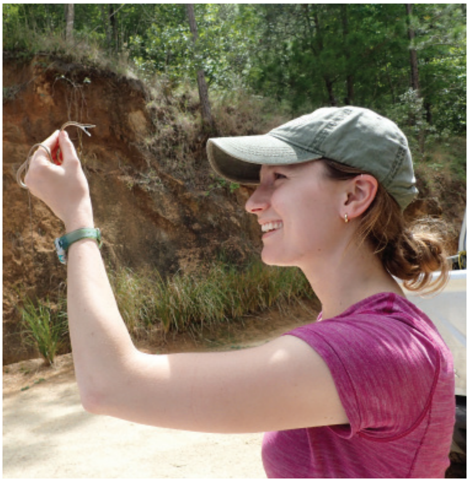
The last site in Nicaragua, Refugio Bartola, produced another herpetological dream—caecilians (yes, plural). Situated at the confluence of the Río San Juan and Río Bartola and just across from the border with Costa Rica, with lush vegetation and hammocks swaying in the breeze, the field station was a welcome site. Here we found our first salamander of the trip, and some of my personal favorite arboreal snakes (*Imantodes, Dipsas, Sibon*, and more *Oxybelis*). One night, in the pouring rain, we decided to walk up a small tributary. After a few hours of the water levels getting increasingly higher and our hopes dropping ever lower, two amazing things happened—we found a *Bothriechis schlegelii* charismatically wrapped on a branch overhanging the river, and nearby, four species of glass frogs calling! This whole trip was magical, and permanently cemented my interest in herping in Central America.

I am fortunate that even after leaving Ann Arbor and beginning my doctoral studies at UC–Berkeley, my connections with UMMZ remain strong. In 2019, I was reunited with my former advisor and lab-mates (Alison Davis Rabosky, Iris Holmes, Peter Cerda, Michael Grundler, Courtney Whitcher, John David Curlis, Briana Sealey, and my current cohort-mate and travel buddy, Maggie Grundler!) in Belize for another exciting trip. We stayed at BFREE, an eco-lodge in the tropical broadleaf forest that borders four nature reserves. Of all the wonderful animals we found, my favorite will remain the *Sibon sartorii* that convinced many of us that it was truly a coral snake. We also had the opportunity to watch Hickatee turtles hatch as part of BRFEE's effort to conserve this species. Another wonderful surprise was the high abundance of geckos (*Coleonyx elegans*) —Briana Sealey was the master of catching these! We traveled to another site in the

Mountain Pine Ridge Area where I happily caught some *Sceloporus* lizards (*S. lundelli* and *S. variabilis*). Here, we also had an opportunity to see giant limestone caves, several massive tapirs, and a ~5-foot long *Bothrops.* I can't wait to work with my UMMZ colleagues again soon!

I believe that landing a research assistantship in the UMMZ was the catalyst for my career as a herpetologist. I am fortunate to have had incredible mentors who were willing to take a chance on me, in both research and field settings. The history of herpetology at Michigan is extensive, and recent efforts to grow the collections by visiting new places and making the collections available to the public through micro-CT scanning show how committed UMMZ Herpetology is to maintaining this rich legacy. Though I miss my time in the UMMZ dearly, I know my journey with the museum and the people I met there has just begun.

About the Author



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Born in the San Francisco Bay Area, Erin Westeen became fascinated with herps at a young age: her first encounter was surely a western fence lizard, which she would observe and catch in her yard. Her formal herpetology education began at the University of Michigan, where she studied biology as an undergraduate and worked as a research assistant at UMMZ. Currently she is a Ph.D. candidate at UC–Berkeley, where she studies trait evolution and speciation in Sceloporus lizards. When not in the field, you can find her in one of the many natural history museums where she has been lucky to work.

HAYDEN HEDMAN

CHARYBDIS OR SCYLLA?

2014– Like Odysseus struggling to navigate his daunting voyage, I encountered many unexpected obstacles that greatly altered my trajectory as an entering herpetologist at the University of Michigan. Fortunately, these encounters offered opportunities for growth and expanded my overall tenacity as a research scientist.

My first field season for dissertation research began not far from Homer's homeland on Naxos, Cyclades, under Dr. Johannes Foufopoulos. Here, I was intrigued by the idea of sharing data collected on the native herpetofauna with local shepherds. I attempted to design an observational study to monitor the spread of ticks from goats to surrounding herpetofauna. On paper, this was my dream project that combined my zealous passion for herps and supporting local communities at the same time; however, I encountered many unforeseen pitfalls.

Given that I was working in a foreign environment, largely on my own, I had to rely heavily on my nascent (i.e., at the level of a 3-year-old child) command of Greek vocabulary. This resulted in frequent charades as I attempted to communicate technical information (e.g., did you apply acaricide to your goat?). Consequently, I made minimal progress at developing positive community relationships. At one point, a shepherd even accused me of poisoning his goat. My project suffered greatly because I couldn't clearly communicate with local community members. Fortunately, I collaborated with researchers of the Panayiotis Pafilis Lab at Athens University. Through two side projects, I made a unique finding of *Podarcis peloponnesiacus* outside of the Peloponnese and also recorded an observation of potential *P. erhardii* cannibalistic behavior. Despite my efforts to salvage my field season, I was forced to reflect seriously on my future potential as a herpetologist studying in the Mediterranean.

The question was difficult—how do I indulge my passion for herpetological research and make it relevant to local communities? After many late-night ponderings, I decided that there were two potential paths for my future research career. In the first path, like Charybdis, I could continue spiraling down a whirlpool of my early childhood dreams and continue to study Aegean reptiles despite the low societal impact of my research. In the second path, I could diverge from Charybdis and steer toward Scylla by transitioning to an entirely new field of research. The latter, of course, could prove initially more difficult because I would have to learn entirely new laboratory and analytical methodologies. I chose Scylla and pursued a doctorate in field epidemiology.

Before I am labeled as a pariah by the herpetologist community, I must explain that I was not eager to completely abandon my previous training. Prior to my work in Greece, I had worked for five years in six different countries studying animal behavior, community ecology, and thermal biology of reptiles and amphibians. My previous experience as a herpetologist taught me invaluable lessons about writing field notes, meta data annotation, and even speaking Spanish because I had worked on previous projects in Latin America. Such training prepared me for enduring rough field conditions, because epidemiologists typically have a different definition of "the field" compared to that of herpetologists. Thus, my typical day in the field of chasing chickens through marshes or recording field notes during a tropical storm were a bit of a novelty among public health professionals, yet common practice for me.

For my dissertation I used a mixed methods approach focused on studying the spillover of antibiotic-resistant bacteria from chickens to humans in rural Ecuador under the guidance of Dr. Joseph Eisenberg and Dr. Lixin Zhang. This topic encompasses both rigorous molecular techniques and spatial statistics, while also complementing my strong desire to relay findings with local communities. One of the key findings of my research was the presence of clinically relevant drug-resistant bacteria collected from chickens in one community.

Regardless of my change in dissertation topics, I remained steadfast about supporting the herpetological community at University of Michigan. During my first year at Michigan, Dr. Earl Werner helped me complete a manuscript on combat behavior of the Emerald Glass Frog (*Espadarana prosoblepon*). I founded the Herpetology Group to help build community among students, faculty, and outside professionals interested in herps, and also an excuse for me to wear my old herp meeting shirts. For a few years, I worked in the Reptiles and Amphibians Division within the Museum of Zoology under the mentorship of Gregory Schneider. It was a humbling experience to be part of the archiving process of so many historic herpetologists that were not only foundational to the university's collection but also the entire field of herpetology. On my last semester, I was awarded the position of Graduate Curatorial Assistant (GCA) under the mentorship of Dr. Alison Rabosky, Dr. Dan Rabosky, and Gregory Schneider. While serving as the GCA, I photographed Peruvian specimens because of my experience conducting Amazonian surveys under the mentorship of Dr. Robert Jadin and Dr. Sarah Orlofske. Working for the museum collections offered me an opportunity to still contribute to the field of herpetology.

My odyssey towards scientific research followed a nonconventional path as an aspiring herpetologist working in the Mediterranean to a field epidemiologist studying in South America. Despite this drastic transition, I still retain much of my core training as a herpetologist; however, now I am applying those skills towards different problems. I am extremely grateful for the community and mentorship gained while working under the Division of Reptiles and Amphibians. I radically transitioned my field of study and career trajectory to better accommodate my passion of working alongside local communities; none of this change would have been initiated if it were not for my first exposure to herpetology at the University of Michigan.

About the Author

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Hayden Hedman received his Ph.D. in Resource Ecology Management from the University of Michigan. His overall interests include GIS analysis, surveillance, spatial and infectious disease epidemiology, antimicrobial resistance, and community-based intervention design. Hayden participated in postdoctoral research programs at the Duke One Health Team and the Wildlife Veterinary Epidemiology Laboratory at the University of Illinois Urbana–Champaign. Currently, he is the Lead COVID-19 Epidemiologist for Summit County, Colorado, and AAAS Science and Technology Policy Fellow for the U.S. President's Emergency Plan for AIDS Relief with the Department of State. Outside of the laboratory environment, he has extensive experience in leading field epidemiological projects. Hayden still enjoys herping while conducting fieldwork.

COURTNEY WHITCHER

From the Shelves of the Collection

2015–

My journey into the field of herpetology, at the University of Michigan, did not truly start until a simple e-mail landed me a job as a curatorial assistant in the Herpetology Division of the University of Michigan Museum of Zoology. An e-mail of inquiry to Dr. Chris Raxworthy, Curator of Herpetology at the American Museum of Natural History, from an eager third-semester undergraduate student asking for advice on how to procure a career in the field ended with a same day meeting with the UMMZ Herpetology Division Collection Manager, Greg Schneider, and a position working for the division. From my experiences during a high school Spanish class trip to Costa Rica, I came to the University of Michigan with a desire to find the path that would take me back to the rainforest. However, finding this tropical connection in the freezing winters of temperate Michigan often felt hopeless. As a self-defined "inquisitor," I loved the unknown aspects of research. While my path to the field was (spoiler alert) fulfilled, it started in the dark, windowless room of a lab.

After being accepted to the Undergraduate Research Opportunity Program, I began my first semester in college working for the Dr. Julie S. Biteen lab on a project that examined the use of metal nanostructures in enhancing intrinsic biomolecular fluorescence. Entranced by the biological production of light, I found this project to be the closest to bioluminescence I could get. During the year and a half I spent in the Biteen lab, I gained confidence and learned techniques, but also felt a strong desire to work with the wildlife that I found so interesting. At the start of my sophomore year, I started as a Wildlife Curator Intern at the local Leslie Science and Nature Center. Despite a close call with the snapping turtle, this experience gave me the hands-on practice I was craving. I loved the public interaction element—my own opportunity to excite children about animals. While I enjoyed my time as an intern, I was missing the research aspect. This is where the e-mail comes in. December of my sophomore year I started working with the Herpetology collections. Despite the fact that I was surrounded by one of the largest museum research collections of reptiles and amphibians, it was the collection manager, Greg Schneider, who took me from being just an ordinary student to a scientist on the pathway of research in the 2 years I had the pleasure of working with him.

Greg Schneider is a man of many stories, and one who altered how I thought about myself and the world around me. I was constantly encouraged to go beyond just doing the work. As a diligent and nervous undergraduate, I would tend to quiet my own urge to engage fully with the specimens I was cataloging, remembering a name in my head to look up at home later to make sure my interest did not come at the expense of efficiently completing my designated task. Greg was able to fight this, making sure that I immersed myself in the historical and scientific significance of the specimens we received from the most recent expedition to Peru or Papua New Guinea. The constant exposure to massive numbers of specimens provided me with an appreciation of the biological diversity of amphibians and reptiles that otherwise, I would not have had. I kept a list in my phone of the unique characteristics that would catch my eye while cataloging. The intraspecific pattern variation of *Dendropsophus triangulum* and *Dendropsophus leucophyllatus* or the unique lure of a specimen

Intraspecific variation in Dendropsophus triangulum.

of *Pipa pipa;* these notes eventually turning into a research project to pursue in graduate school.

Greg went above and beyond to listen to my goals and took the time to connect me to a post-doc at the university, Rudolf von May. Here began my first true experience as a herpetologist. From the winter of my sophomore year through the summer of my junior year, I utilized the incredible research collection to take 14 morphological measurements on each of nearly 650 specimens to examine the effect of abundance and habitat on the morphological divergence of a diverse tropical anuran community. Completing a multi-year study as an undergraduate allowed me to understand the true nature of scientific research. Throughout this time, I was surrounded by incredible mentors. I learned a great deal from Dr. Dan Rabosky about how to conduct research, analyze my data, and most importantly think critically. He was a great advisor who showed me incredible support during my project. Similarly, I worked very closely with Rudi, who tirelessly supported me through and beyond my thesis, most notably through all of the imperfect drafts. His care for his students and willingness to help a crucial part of my success.

Throughout this process, my love for the study grew even more. However, my favorite part of the process has yet to be discussed. Again, my sophomore year at the University of Michigan was the most transformative. I spent the summer of 2017 solidifying my passion for field work. First, I spent a month at the University of Michigan Biological Station gaining appreciation for the ecology of the state I had called home for so many years. I then traveled almost immediately 40 hours across the Pacific Ocean to the Atherton Tablelands of Australia. Another month spent in the field, now in the Australian rainforest surrounded by new and exotic flora and fauna, increased my love for not only ecology and evolution but for herpetology as well. Finding a majestic leaf-tailed gecko while spotlighting on a night walk was the start to my herpetology field experience. However, something else continued to rack my brain and my eyes. After a long rainy day in the field, I caught a glimpse out of the corner of my eye of something while walking back to the cabin; a group of glowing mushrooms clustered at the side of the path, and I almost missed them in the intense beam of my headlight. I stopped to admire them and over the next few days as the individual mushrooms passed off the luminescence between themselves—a new one in the group shinning the brightest each night. My fascination of bioluminescence had yet to subside and seeing it for myself in nature (besides the lightning bugs I had watched in my backyard) was incredible.

For the next couple years, my research experience, specifically in herpetology, increased. While I continued my thesis work and working in the collections, I also became more integrated into the Rabosky lab. I began helping a Ph.D. student, Joanna Larson, with her frog-diet research. I learned the process of photographing frog stomach samples and later flushing frogs to get those samples. I was also welcomed to join in on Dr. Alison Davis-Rabosky's lab meetings my senior year. Again, an e-mail I sent explaining my interest in her work with polymorphism provided me with an incredible opportunity. I was warmly welcomed into another group of supportive scientists, who also happened to study the color and pattern variation in herps that so intrigued me. Her willingness to include me in her lab, and my acceptance by the members of the lab, enhanced my experience at the University of Michigan. I was now surrounded by two groups of herpetologists who encompassed my interests from speciation to color polymorphism and allowed me to flourish.

As I began narrowing down my interests, I was stuck between my continual curiosity in "glowing" organisms and a new-found love for herps that I gained at the University of Michigan. Now timing was really on my side when, the semester I began looking into graduate schools, I came across a newly discovered quality in frogs—biofluorescence. In the year prior, two species of frogs were found to be biofluorescent, and a third was discovered as I was preparing my applications to graduate schools. My two worlds came together with this discovery, and the questions I had began to bloom. It was the first time biofluorescence had been discovered in an amphibian, and I was captivated with what it might mean. Furthermore, the specimens with fluorescence were found in distinct localities of Costa Rica, Brazil, and Argentina. How many more species had this quality? Was it a byproduct? Did it have functional significance—

Boana rufitelus. *One of the three species of biofluorescent anurans (permission by Pablo Deschepper).*

perhaps in mate choice or predation? These are some of the questions that I hope to have begun to pursue by the time you read this essay.

I graduated in December 2018, a semester early, and then continued on the herpetology path. I spent my semester off volunteering as a teaching assistant for the first Biology of Amphibians and Reptiles course offered in 4 years. With an all-female herpetologist teaching team, I not only gained skills in how to transfer knowledge to students, but I learned what a female herpetologist could do. Again, Alison and Joanna were incredible mentors for me in this aspect.

As I prepared my thesis data for publication,[1] I continued working with the Peruvian specimens collected by the Rabosky lab for various projects and began helping to mentor Rudi's new UROP student. I was now passing along the knowledge I had gained to a new student in the same place I had started my herpetology career just 2 years before. I applied to graduate schools and the NSF Graduate Research Fellowship Program—processes for which I was grateful to have had the support of my lab groups. I was accepted as a doctoral student into the Dr. Emily Moriarty-Lemmon lab at Florida State University. I received an Honorable Mention for my proposal to the NSF GRFP about the functional significance of biofluorescence in anurans.

For my last experience at the University of Michigan, I traveled to Belize with the Davis-Rabosky lab group. The group's composition of current, as well as former lab members, allowed me to realize that support from Michigan herpetology did not necessarily terminate with graduation. Again, I found myself surrounded by vast amounts of knowledge and experience- an environment in which I work best. I went to Belize to gain field experience, hoping that I might also encounter a glass frog to test for biofluorescence.

Davis Rabosky lab group *in Belize.*

Although we did not find a glass frog, I was pleasantly surprised to see green "glowing" armbands on a *Gastrophryne elegans*—a small brown microhylid that until that moment, I had written off as just a small brown frog. I also found fluorescent flanks on *Smilisca, Rana,* and *Bromeliohyla,* as well as intraspecific variation in these species.[2] The florescence ranged from small inguinal patches to extensive fluorescence across the entire flank. A new world was opened to me. My tenure at the University of Michigan was marked by, and ended with, discovery.

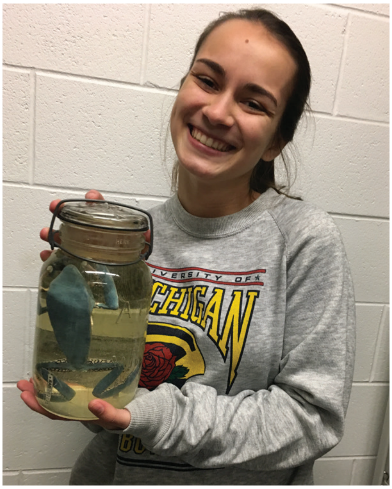
Now my herpetological and undergraduate journey has been laid out. The reason for the title of my essay is likely clear; I started in the collections and that experience matches the words of the headline. But it also connects to a larger story I am trying to tell, a story of discovery that characterizes my experience at the University of Michigan. In many ways, I think that humans are not unlike the jars of specimens that line the shelves of the collection. Each specimen and each person is surrounded by similar ones, but each individual unique. Each are separated geographically and by group. However, every individual has something special to provide—perhaps a pattern that is unique, an extra limb, or, for the extraordinary, a holotype status that places it in a protected cabinet. My point is that each specimen, like each human, has special qualities awaiting discovery. While working with and admiring the amphibian and reptile specimens in the seemingly boundless collection, I realized my own individuality, not just in the scientific community, but in the collections of the world. While I have much more to learn and many more experiences to have, I am fortunate to have begun my career with the collection and people associated with herpetology at the University of Michigan. From the shelves of the collections, I am making my debut.

Endnotes

[1] Whitcher, C., von May, R., Rabosky, D. (MS) The morphological structure of a diverse anuran community. Manuscript in preparation.

[2] ——. (MS) Intraspecific variation and new account of biofluorescence in several anuran genera. Manuscript in preparation.

About the Author



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Courtney Whitcher grew up in southeastern Michigan. She attended the University of Michigan–Ann Arbor from September 2015 to December 2018, where she received her Bachelor of Science. She had a double major in Ecology, Evolution, and Biodiversity with a specialization in Wildlife Biology. As an undergraduate, Courtney resided in the Dr. Dan Rabosky Lab and completed an Honor's Thesis under Dan's mentorship. She also worked as a Curatorial Assistant for the University of Michigan Museum of Zoology Herpetology Division for two years during her time at the University of Michigan. She is currently a Doctoral Student in the Dr. Emily Moriarty-Lemmon Lab in the Florida State Department of Biological Science. For her dissertation, she is examining the functional significance of biofluorescence in mate choice and predation of anurans.

Greg Pandelis

The Tale of a Cliff Side and Herpetology at the University of Michigan

2016–

As I teetered on the edge of a 75-meter drop into the waves and rocks of the Mediterranean Sea with a backpack full of collecting gear and live snakes and a steep cliff face 50 meters above me, I contemplated the decisions that had led me to this predicament.

I had decided, foolhardily as it turns out, to travel alone to an uninhabited island off the coast of the island of Kythera, Greece, to conduct the first herpetofaunal survey of the area. Known only as "The Egg" by locals, this little island certainly resembles one from a distance, rising an impressive 200 meters above sea level and coming to a point on top. It is valued by the inhabitants of the nearby island of Kythera, owing to the proliferation of a certain yellow flower on its precipices; the flowers are preserved and sold to tourists. The island is accessible at only one point along its coastline, where an inconspicuous path, visible only when recently trampled by the yearly flower gatherers, gradually winds back and forth up the cliffside to the top. Upon learning that I was an undergraduate herpetologist conducting a collecting expedition in the region on behalf of the University of Michigan, the flower-gathering team immediately reported that there were droves of snakes on The Egg. Despite warnings from the group as to the treacherous nature of the island, my excitement at the prospect of being the first herpetologist to explore and record species from this island was overwhelming. I had to identify the species of snakes and collect specimens for the University of Michigan Museum of Zoology, where they would serve as permanent records of my novel survey.

A view of my transport from the top of "The Egg" (left) and the first record of Hierophis gemonensis *from the island (right)*.

Finally managing to convince a reluctant local fisherman to take me to the island a few hours before dark, I climbed up its sheer path, with the fisherman shouting after me "Don't lose the path and come back down before dusk!" Once on top, I was ecstatic. The flower team had not exaggerated; there was in fact a large population of the snake, *Hierophis gemonensis,* as well as one species of gecko, *Mediodactylus kotschyi,* on which these usually generalized colubrids must have subsisted. I collected several specimens of each species and began my descent, thinking it best to leave early rather than risking a descent in the dark. At the top, however, the head of the path by which I ascended was no longer clear. A few misjudged turns later, I found myself in the predicament above, not quite knowing how I ended up there or how I would manage to get off the cliffside. I began contemplating the protocol for calling a helicopter lift and wondering whether the crew would mind having snakes in the cabin.

Sitting on this cliffside with no help forthcoming because the fisherman, half a kilometer away, could not hear me yelling at the top of my lungs, I pondered my life choices. Why, I asked myself, did I have to become a herpetologist? What drove me to visit a veritable rock in the middle of the ocean for a couple of snakes? And maybe my grandmother was right and I should have gone to medical school. (That last one was a fleeting thought, thankfully.) The driving factor, I realized, and the one that guided me and shaped my passion for fieldwork, reptiles, and research, was the herpetology program at the University of Michigan. Here were the people with whom I interacted with and learned, as well as the remarkable field experiences in which I was lucky enough to participate. These things, I realized, were what for better or for worse had ultimately led to my current plight. My later experiences at the University of Michigan, however, were in no small part determined by my earlier background.

My interest in zoology began so early that I cannot remember what sparked it—by the time I was eight years old, whenever a good-natured aunt or teacher would ask me what I wanted to be when I grew up, fully expecting me to say "astronaut" or "firefighter," I would adamantly proclaim that I was going to be a zoologist. They would then often tell me that it was fantastic that I wanted to work in a zoo, and later regretted it as they found themselves in a long conversation with an eight-year-old about why zoologists don't necessarily work in zoos.

***Seventh-grader Greg** in Alaska with a snow-white mix of game—a brace of snowshoe hares and three willow ptarmigan. He later photographed, measured, and preserved skeletal preparations of these specimens.*

After I finished the sixth grade, my family moved to Marshall, Alaska, a village of approximately 500 people on the Yukon River. Every day after school, I hunted and fished with the local kids in the pristine tundra environment where we saw moose, bears, and all manner of natural splendor. This was paradise for me. Alaska was the intellectual breeding ground for my love of wildlife and my beginnings as a scientific collector. I quickly began amassing a vast collection of animal parts that I would carefully preserve, label, and later compare to other species, noting differences in morphology. Though my parents thought I was crazy, my hobby was well organized; I kept a careful ledger, recording all animals that I collected or that others gave to me. I took systematic measurements of foot, wing, and body size, recording them in my ledger along with photographs of the specimens. I found out much later, while working in the Museum of Zoology at the University of Michigan, that many of the measurements I had decided on then were actually standard measurements taken in most museums around the world.

My growing specimen collection led me to establish a dermestid beetle operation when I learned that this was the method of skeletal preparation employed by museums around the world. These beetles consumed the flesh from my specimen, leaving behind cleaned skeletal material that I could study. I began this operation in Alaska, cleaning skulls for my personal collection, which quickly grew to several hundred specimens. When my family moved back to the Midwest, I continued this operation, turning it into a business – offering skull cleaning services to hunters and scientists in the Wisconsin area, and nationally, through a website I created.

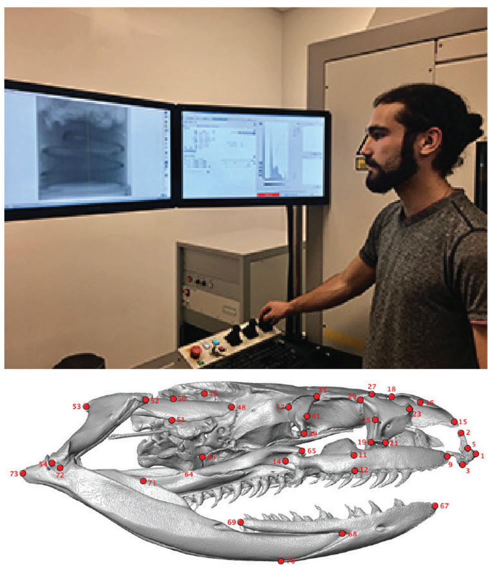
While always fascinated by all animals, it was about this time that I caught the "snake bug." I began learning everything I could about snakes from the literature and through observation, amassing a collection of about a dozen live boas and pythons. During high school, I began a small-scale business keeping and breeding these animals and producing educational videos through Youtube, increasing awareness for these misrepresented reptiles while learning more about them.

After abandoning my businesses and entering the University of Michigan where neither dermestid beetles OR snakes were welcomed in the dormitories, the series of events began that ultimately led to my precarious situation on a cliff in Greece. When looking for a job as a first-semester freshman, I came across an ad for a dermestid colony technician at the University of Michigan Museum of Zoology. Scarcely believing how fortuitous this was, I went to the museum and was interviewed by Dr. Cody Thompson, the mammal collections manager at the UMMZ, who promptly told me that I had the job. I became caretaker of the University of Michigan Museum of Zoology's dermestid colony and also began preparing specimens and assisting in the curation of the mammal collection. One of the most memorable moments of this first exciting year at the Museum of Zoology, however, was when Greg Schneider, collections manager of the reptile and amphibian division, brought in two large *Varanus* (monitor lizard) skeletons to be cleaned by the beetles. While I marveled at the interesting skeletal anatomy and large claws, Greg introduced himself and explained to me some aspects of reptile and amphibian specimen preparation, which were new to me, given that reptiles in Alaska were few and far between.

While working as a mammal curatorial assistant and dermestid colony technician was an incredible experience, I never lost sight of my interest in herpetology. I had expressed my interest in herpetological research to my mentor, Dr. Cody Thompson, who despite a few protests, referred me to Dr. Dan Rabosky in my second year; this was my first introduction to herpetological research at the University of Michigan. (To this day, Cody insists that I have "turned to the dark side.")

I remember my first meeting with Dan and the excitement I felt to be conversing with a real herpetologist. As we talked at length about snakes and research projects, I felt incredibly lucky that I had come to a university where it was possible for a second-year undergraduate to discuss research with a professor, and not only assist with, but have the freedom to design their own projects.

I began work as an assistant for a project of Dan's, the "Scan all Snakes" project, the goal of which, as you might imagine, is to CT scan every species of snake. As someone who had spent a considerable amount of time physically cleaning, preserving, and curating skeletal collections, this virtual skeletal preparation was astonishing. With a few clicks on some very expensive software, a virtual model of a skull could emerge from a set of files gathered by an even more expensive machine. This knowledge was pivotal for me.



***Greg** operating a CT scanner and the resulting 3D model of the skull of* Clelia clelia*, landmarked to quantify its shape.*

It was also during this time that I began working more closely with Greg Schneider, herpetological collections manager. (We quickly worked out that he would be Greg 1 on account of seniority, while I would be Greg 2.) Greg and

I collaborated to ensure that the specimens being scanned as part of the Scan all Snakes project were handled appropriately and returned to their correct locations in the collections after scanning. Although I always had a predisposition for specimen work, Greg is undoubtedly the person who hammered home the importance and value of a specimen from the perspective of a collections manager. Greg's willingness to go beyond what we were working on at the moment to teach and mentor me was undoubtedly a large factor in my later success, and this is where I learned a number of essential skills in collections management.

After working for a semester as an assistant, I talked to Dan about beginning my own research project utilizing CT-scan data, to which he enthusiastically agreed. After bouncing about a number of ideas, I decided to investigate the link between ecology and morphology in the snake skull. In other words, I was interested in uncovering the evolutionary impact of factors such as habitat use, activity, and diet on the shape of the wonderfully unique snake skull. I began work by CT-scanning more than 150 species from the Dipsadinae and proceeded to quantify each virtual skull's shape with geometric morphometric techniques. I then spent countless hours poring over the literature, trying to decipher how each species lived, when it was active, and what it ate. Reading the accounts of other herpetologists was thrilling, although I admit I made it only halfway through Duellman's monograph on *Leptodeira;* nevertheless, I yearned to see the animals I was studying in their natural environments.

I did not have to wait long for this opportunity. At the end of my 3rd year at the University of Michigan, I was invited by one of Dan's Ph.D. students, Iris Holmes, to take part in an international collecting expedition to Nicaragua. When I stepped foot in a coffee plantation with a brand-new headlamp during that first night, I couldn't help but feel like a real herpetologist, taking part in the very same types of collecting efforts whose reports had assisted me so much with my own research just a few short weeks earlier. Here I could merge my love for specimen work and research with the fascination and thrill of working with live animals. I do not hesitate to say that this experience, brought about by my involvement in the Rabosky lab, was life changing. I employed the techniques taught to me by Greg in the lab to prepare wet specimens in the field and had the opportunity to learn further techniques such as tissue sampling, using funnel and bucket traps, and proper techniques for the handling of venomous snakes. By the end of this 6-week trip, which encompassed surveys in the cloud forests of northern Nicaragua, dry forest volcano habitat in the center, and lowland rainforest at the border with Costa Rica, I was hooked. I could not imagine pursuing a career that did not feature this type of work as an important component. The thrill of discovering something new, whether it be a range extension, novel variation, behavior, or otherwise, was intoxicating. Furthermore, I realized that collecting expeditions provided the most basic and therefore essential data on which all other studies in the zoological sciences are based; and I wanted to continue taking part in that type of science.

***Greg** preparing reptile and amphibian wet specimens in Nicaragua (left) and Greg with a hard-earned specimen of* Spilotes pullatus *collected through a group effort that involved machetes, climbing, and a lot of shouting (right).*

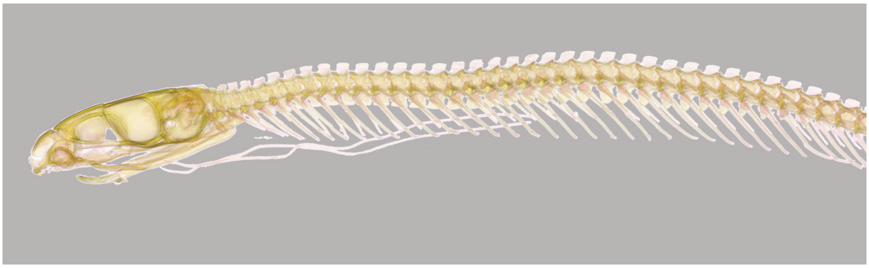
It was in the airport in Managua, Nicaragua, that the idea struck me—what was preventing me from organizing my own collecting expedition? In two weeks, I would be visiting family in Kythera, Greece, and I decided I would multitask and do some collecting while I was there. I began asking the graduate students in Dan's lab numerous questions about organizing a trip, and they readily gave me advice and recommendations. When I mentioned to Greg that I was planning my own collecting trip, he not only offered advice but also provided me with the equipment I would need to successfully carry it out. I was overjoyed that so many people in the herpetology division would look positively on an undergraduate hoping to conduct their own independent expedition, and indeed offer advice and supplies so readily.

Once in Greece, it felt incredible to be solely responsible for a novel effort to understand a region's biodiversity; historically, the island of Kythera had been ignored by herpetologists because of its low species richness relative to other Greek islands. After a resolving a few complications with the permits, I was on my way. With a brand-new pair of snake tongs in my hand and armed with my experience from Nicaragua, I was able to document most of the species known to occur on the island successfully, including one (*Zamenis situla,* the Leopard Snake) that had not been recorded from the island since the early 1900s. Prior to my visit, the last targeted collecting expedition had taken place on Kythera in the 1930s by Frantz Werner. Thus, I was obtaining the first tissue samples from the island for most of the species I was collecting. If I was not hooked before, I certainly was now. After this invigorating several consecutive months of fieldwork in Nicaragua and then Greece, the return to the U.S. was bittersweet.

***Greg** with a Greek Grass Snake,* Natrix natrix, *plucked from the water amidst a group of tourists.*

When I returned to the U.S., however, telling the stories of my recent experiences brought back that feeling of excitement and discovery for which I had developed a craving. Greg and Cody were both eager to hear about my travels, which assuaged the pain of their coming to an end. Moreover, the Museum of Zoology had just purchased a new CT scanner to be located just outside the collections space, and the research and new responsibilities that came with this machine allowed me to keep my mind off of fieldwork for the time being.

I became the lead technician at the University of Michigan responsible for producing CT scans for the oVert project, an inter-institutional effort with the aim of producing CT scans for every extant genus of vertebrate. Needless to say, running the new CT scanner full time while also managing, curating, and uploading the CT data to a digital repository was an onerous responsibility, but one for which I am grateful. I learned a great deal on my own, as well as from my mentors about digital data management, archiving, and curation, as well as essential programming skills. These digital skills complemented my recently acquired fieldwork experience, equipped me with a well-rounded skill set that would later become vital. I continued to work on my own research project as well, working in a CT scan of a snake whenever I could, and incidentally picked up a few side projects along the way (e.g., *Elachistodon,* below).



The first complete figure of the vertebral column of the Indian Egg-Eating Snake, Elachistodon. *I borrowed the only U.S. specimen to obtain a CT scan, which documents the first evidence of ontogenetic variation in the specialized vertebral anatomy of this species. [Editors note: figure placed on neutral gray background to visualize the scan better.]*

Free from classes for a semester and attempting to become more involved in research and my own project, I was available when the invitation arrived to accompany the Rabosky lab to the Peruvian Amazon for a 3-week long collecting expedition. Nicaragua was incredible, as was Peru, but in a different way. This was the real Amazon rainforest, and I was able to encounter many of the species that I had included in my own analyses in their natural habitat. This was a fascinating experience for a number of reasons, and was especially significant for me because I could link the organisms I had been studying digitally with their natural environment and habits. This led to many insights that later were important in interpreting the findings of my research. In addition, I was able to learn firsthand from Dan, Dr. Alison Davis Rabosky, and their graduate students on this trip. I also took part in more independent survey efforts, prepared unique specimens (e.g., Green Anaconda, *Eunectes murinus*), learned to handle venomous snakes independently, and practiced my growing interest in herpetological photography.

***Greg** inspecting a funnel trap in the Peruvian Amazon (left), photographing an Annellated Coral Snake (*Micrurus annellatus, *top right), and a photograph of* Chironius fuscus *at bottom right*.

Upon returning to Michigan, I completed my last semester of studies and graduated in May of 2019. My independent research project, with the help of my advisor Dr. Rabosky, was brought to successful completion as an honors thesis, which I am currently preparing for publication (Pandelis et al. 2020. Habitat Use and Diet as Drivers of Morphological Evolution in Dipsadine Snakes), along with several other side projects.

With three international collecting expeditions under my belt, I once again planned to return to Kythera, Greece, to conduct a more thorough survey of its surrounding islets. With funding from the UM herpetology division, I traveled by boat to most of the surrounding islets, none of which had previously been sampled by herpetologists.

I discovered species of reptiles on each one, each constituting a range extension into a previously unexplored region. The excitement and satisfaction of conducting these surveys, knowing that I was positively contributing knowledge to the herpetological community, was indescribable. At the same time, I knew that if it were not for the University of Michigan herpetology program, I would have acquired neither the skill set nor the motivation to carry out such a study. My field experiences with the Rabosky lab had instilled in me an unquenchable yearning for discovery; my time with Greg Schneider, graduate students, and others in the herpetology division had taught me the skills I would need to be successful. Together, these things drew me to Kythera, Greece, where I engaged in my own independent study, striving to come to a better understanding of the region's herpetological biodiversity.

A view from the site of the cliff predicament on The Egg at left. A specimen of an endemic subspecies of Cat Snake, Telescopus fallax intermedius, *from the nearby island of Antikythera (above right), and a European Green Toad,* Bufotes viridis, *from the island of Kythera. All photos by author.*

In many ways, therefore, it was University of Michigan Herpetology that landed me on the side of that cliff. If it were not for the people and the opportunities that I encountered there, I would not have pursued the path that ultimately found me in a precarious situation. Despite the momentary panic, I would not trade my experiences at the University of Michigan for anything, knowing that it would make me the person and the scientist that I am today.

Perhaps you wonder how this story ends. After regaining my composure, I decided it would be irreparably embarrassing for myself and my family on Kythera (Greeks being extremely conscious of reputation) if they were to hear I was rescued by a helicopter from The Egg while catching snakes. So, after gathering up the courage, I free-climbed the approximately 50 meters to reach the top once again, snakes still in my pack. Once there, I managed to find my way back to the correct trail and made my way back to the meeting spot in the dark, two hours after the prescribed time, utterly exhausted (thankfully the fisherman was still there, because he had been about to return to Kythera to request a team to come rescue me. When I finally returned home, I related a milder version of this story to my father, ending it with "But I got the specimens, so it was all worth it. I can't wait to see the look on Greg's face when I get them to the museum!" He looked at me and replied: "You're crazy."

That "craze" for science and for herpetology in particular, I owe to my mentors, and now friends, from the University of Michigan Herpetology, as well as the opportunities and experiences that they opened for me. As a direct result of this undergraduate experience, I was offered the position of Collection Manager of the Herpetological Collections at the University of Texas at Arlington, where I began work in September of 2019. As I embark on this next chapter of my career, engaging in precisely the type of work that I feel I have been working toward my entire life, I cannot help but feel I was incredibly lucky to have been a part of the University of Michigan herpetological community, despite its having landed me on the side of a cliff!

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Gregory Pandelis is Collections Manager of the Amphibian and Reptile Diversity Research Center at University of Texas at Arlington, where he pursues his lifelong interest in natural history specimen preservation, curation, and use. Greg graduated with a B.S. in Ecology, Evolution, & Biodiversity from University of Michigan in Ann Arbor—the many experiences with his mentors at the UMMZ having refined and guided his fascination for the natural world.

Greg's research interests include ecomorphology of the vertebrate skull, snake biology, and techniques in natural history specimen curation and data management. With a strong interest in organismal biology, Greg can often be found surveying for herps locally in Texas as well as at his study sites in Greece. He spends considerable amounts of time on fieldwork in the summer months, documenting the herpetofaunas of the uninhabited islands surrounding his family home in Kythera, Greece.

DANIEL L. RABOSKY

The Secret Lives of Snakes in the Era of Big Data

2012 —

Doing herpetology in the steamy lowland tropics is a profound and life-changing experience. Nothing compares to a night spent knee-deep in the muck of a *Mauritia* palm swamp, where the slightly sulfurous smells of anaerobic fermentation mix (pleasantly, to me) with the odors of rotting palm fruits amidst a raucous chorus of treefrogs and katydids. In these Amazonian *aguajales,* the thick canopy of rainforest trees and lianas gives way to a virtual monoculture of palms, and the thin shade afforded by the spindly palmate leaves provides the bare minimum of protection against the torrid midday sun. But after sunset, this more open cover provides a coolness that is missing from the nearby terra firme and floodplain forests. With no landmarks, one can easily get lost stumbling around such a place at night; a light shown in any direction reveals vistas of seemingly identical palm trunks and the densely spiked trunks of understory ferns. Boot prints are quickly swallowed by the peaty brine, and we rely on strategically placed orange flagging to find our way our back out of the swamp after a night of searching.

We find few snakes in the swamps by day during these Museum of Zoology (UMMZ) expeditions, but the macaws are abundant when the palms are fruiting. We frequently see large flocks of blue-and-yellows overhead, and any such swamp is usually good for a nesting pair or two of scarlets. There are other denizens of these low places: caimans and anacondas in the deeper waters, and tapirs where the muddy substrate can support their weight. We stumble through the *aguajal* to set and check lines of funnel traps and drift fences. The fences, traps, and even researchers sink into the peaty tannin-rich suspension, but trapping brings a wealth of insight into ecological communities that can't be obtained any other way.

By night, the *aguajal* is a magical place, simultaneously weird and disorienting and unlike any other habitat that I've explored in the Amazon. Our headlamps reveal brown-banded water snakes (*Helicops angulatus*) hunting in the thin skim of clear water that lies atop the suspension of peat and rotting plant debris. If disturbed, the snakes instantly vanish into the neither-liquid-nor-solid suspension of muck below—a poorly known region haunted by snake-eels (synbranchid fishes) and the enigmatic and rarely seen *Hydrops* water snakes. Above the water, a regular pattern of vertical lichens on a vine catches the eye and materializes into an ornate snail-eater (*Dipsas catesbyi*). The reflections of tree-boa eyes (*Corallus hortulanus*), as bright as any nocturnal gleam in the rainforest, reveals the taut body of a meter-long snake in ambush position, with its neck cocked and head strategically positioned just a few inches above a well-used rodent trail.

One night, I found two aquatic coral snakes (*Micrurus surinamensis*) foraging amidst soggy palm debris in the *aguajal* shallows. A few hours later, I haphazardly flipped some palm debris and found a third. That day—and those three aquatic coral snakes—will forever define a moment that captures for me both the mystery and the challenge of tropical biodiversity. Here was a snake that had eluded me for years, a robust coral snake with gleaming reds and a fine black mesh tracing the boundaries of its scales, a fascinating and indescribably beautiful snake that had evolved a substantially different way of life from so many other *corales.* Collectively, our expeditions to the Peruvian Amazon have involved many thousands of person-hours searching for snakes at night and by day, with an appreciable fraction of time in *aguajal* habitats like the one in which I found those three *surinamensis.* We've trapped and flipped and raked palm thatch until our backs were sore, yet never (as of this writing) have we encountered another individual at this location. For the briefest moment in time, the surinamensis worldline intersected mine, as though a portal had opened through which I could glimpse an ecological dimension beyond our own. This experience, and many others like it, have led me to question my assumptions about snakes and the worlds they inhabit.[1]

*One of three aquatic coral snakes (***Micrurus surinamensis***) featured in this essay, captured in an aguajal in the southern Peruvian Amazon. This specimen is catalogued in the UMMZ Reptiles & Amphibians collection as 246861.*

Experiences like these are valuable because they humble us, teaching us about the limits to our understanding of biological diversity more generally. Working in the Peruvian Amazon, our daily lives are imbued with the mystery of tropical diversity, which surely represents one of the greatest unsolved puzzles in the natural sciences. Why are there so many species in the humid tropics? The *aguajales* described above are part of a mosaic rainforest landscape that accounts for a greater number of animal and plant species than any other comparable biogeographic region on Earth. A square kilometer of lowland rainforest in southern Peru, indexed solely by the number of distinct taxonomic species it contains, would harbor about 100 species of frogs, 85 snakes and lizards, 300 (resident) birds, 800 trees, and countless insects. Depending on the taxonomic group, species diversity in Amazonia is approximately five to fifty times greater than you would find in regions of a similar size in temperate North America.[2]

Such a numerical deconstruction of the rainforest provides a convenient, but wholly inadequate description of the experience of tropical diversity—the haunting trills of tinamous at dusk, the mottled diamonds of a bushmaster (*Lachesis muta*) in dappled understory light, a nighttime glimpse of a large cat that lingers in the mind long after the animal has melted into the shadows. Nonetheless, the numbers give us a yardstick with which to measure and compare biological diversity. One doesn't need any special taxonomic expertise to appreciate order-of-magnitude differences in species numbers between tropical and temperate regions. These massive discrepancies in species diversity define one of the most exciting problems in all of science—a problem I refer to as the tropical diversity puzzle. To study tropical diversity, we must consider evolutionary and ecological phenomena that play out across vastly larger scales of space and time. These scales are measured not in human lifetimes, but in the million-year lifespans of species and clades. Given this scale of pattern and process—geological, epochal, continental—what can singular natural-history encounters tell us about the tropical diversity puzzle?

My own singular natural-history encounter involved those three *surinamensis* coral snakes in the *aguajal*. Had I spent my day somewhere else, I'd have concluded that this snake was either not present in the region or too rare to detect; we would have recorded zero such snakes during the many days we had spent working in the region. But finding three individuals in such a short period of time made me realize that this is perhaps a common snake the activity of which is regulated by factors that we cannot perceive. The weather on that fateful night in the *aguajal* was no different than dozens of similar (snakeless) nights before and since. In fact, the most solid conclusion that I can draw from my observations is that we probably know far less than we think about the ecology of most Amazonian snakes.

All of this leads us to a question that lies at the heart of our attempts to answer the "big questions" about biodiversity—i.e., is our present knowledge adequate to solve the tropical diversity puzzle? We know little about the abundance and geographic distribution of many (perhaps most) Amazonian snakes, much less the way in which species abundances change across space and through time. Even for seemingly common Amazonian snakes, such as blunt-headed tree snakes (*Imantodes cenchoa*), we don't really know how our opportunistic encounters align with true species abundances, and we have no information about how those abundances vary across the range of the species. In fact, beyond some coarse generalizations, field studies have yielded relatively little about the natural history of most Amazonian snakes. What do they eat? How do their diets shift with age, season, and geographic location? What is their social system, and how do they select mates? How do they interact with predators and parasites? These questions are fundamental to the comprehensive baseline of understanding needed to solve the tropical diversity puzzle, yet our ignorance is staggering. And of course, there are still undiscovered and undescribed snake species from the Amazon, plus many more "known" species in need of wholesale taxonomic revision. It is true that some taxa are easier to study than snakes (birds, trees), but some are far more difficult (nearly all fossorial animals, including amphisbaenians and caecilians). In terms of knowledge accessibility, I would wager that most species in the Amazon are more like snakes than trees.

Thus, my seemingly chance encounter with coral snakes seems to me to represent the profound challenges we face in trying to solve the tropical diversity puzzle. Those three *surinamensis* give a resounding "no" to the question of do we know enough to answer the big questions in biodiversity science. Today, the study of biodiversity dynamics—e.g., what regulates the number of species in space and time—is increasingly driven by a trend towards digitization and automation, such that modern science exists in a torrential stream of "Big Data" that was unimaginable several decades ago.[3] In astronomy, for example, digital sky surveys yield terabyte-to-petabyte data dumps that have increased the numbers of known black holes and exoplanets by orders of magnitude. In the life sciences, the amount of publicly available DNA sequence data has increased exponentially since the release of the first draft human genome, with the total amount of available genomic data doubling every 8 months or so.

In many ways, trends within the biodiversity sciences are no different. It sometimes seems as though we are surging ahead with the view that we can get what we need by analyzing a mere shadow of the natural world, provided we can maximize both the coverage of our data (i.e., how many species in our databases) and the accessibility of that data (i.e., is it digitized?). As we project ecological complexity into something amenable to SQL queries, we increasingly find ourselves reducing emerald tree boas (*Corallus batesii*) and other animals to a convex-hull estimate of their geographic range plus a few coarse descriptors ("eats mammals and birds," "uncommon to rare," "arboreal"). While taking nothing away from the achievements of Big Data, I wonder if the pendulum has shifted too far.

Perhaps a side effect of the Big Data philosophy is that we overvalue research that consumes data while undervaluing research that produces data. I expect that this side effect is particularly severe whenever the cost of that data is measured not in CPU time but in the blood and sweat and mud that comes with fieldwork in the tropics and elsewhere. One lesson for me from those three coral snakes on a humid night in a Peruvian *aguajal* is that our field needs a renewed appreciation for and revaluation of the primary natural history data that are required for us to have any chance of understanding the creation and maintenance of tropical biodiversity.

Another lesson from these snakes is that we need to recognize, support, and invest in the institutional structures that facilitate our understanding of tropical (and other) biodiversity. The single most important reservoir of natural history data—the raw materials that we draw on as we study the tropical diversity puzzle—is undoubtedly the resources that exist through our natural history collections, of which the UMMZ is just one. For most organisms on Earth, natural history collections represent the central locus of information on taxonomy, geography, and morphology. But we sometimes fail to appreciate that natural history collections also represent our primary window into the ecology of many organisms. For organisms that are infrequently encountered, hard-to-sample, or simply rare, our understanding of many ecological dimensions—their predators and prey, parasites and pathogens—is most likely to emerge from the collective wisdom of the specimens that are carefully maintained in the world's natural history collections. Most of what we know about snake diets, for example, comes from the systematic examination of stomach contents held in museum collections. Natural history collections provide access to these and other raw materials on a scale that vastly exceeds what any single researcher could hope to collect in his or her lifetime.

Our UMMZ field expeditions to the Peruvian Amazon have created a legacy of natural history information that will remain in place beyond the lives of the researchers who collected the specimens. For three particular specimens of *Micrurus surinamensis*—now carefully archived in research collections in Michigan and Peru (UMMZ 246861, MUSM 37352, MUSM 37353)—their "hard" scientific legacy includes numerous tissue preservations, such that future researchers will be able to access and study DNA, RNA, venoms, parasites, and pathogens. The "soft" legacy of these specimens includes the associated digital information: field notes, full-spectrum color photographs, metadata associated with the captures (weather, habitat, etc), as well as in

UMMZ Herpetology field team *from the November-December 2017 expedition to southern Peru. Participants included researchers and students from at least seven institutions in Peru, Australia, and the United States.*

situ and experimental video documentation of antipredator behaviors. These specimens likely represent the only information the world will ever have about the lives of aquatic coral snakes from this particular point in space and time.

The specimens that we've collected in Peru provide an admittedly imperfect snapshot of what may be the world's most complex ecological community. We've archived a fragmentary record of life and death in the rainforest, one that is filtered through a prism of sampling biases and constraint—money and time—that limits the scale and scope of any scientific endeavor. But for biodiversity science, the opposite of imperfect data is not perfection—it is the absence of information. The incomplete snapshot afforded by our specimens is both unique and priceless, providing a reference point to which any future ecological "photographs" of Amazonian communities can be compared. As I walk the halls of the UMMZ's herpetological collections, I view the seemingly endless jars of preserved specimens with feelings of pride and awe, knowing that I've had the opportunity to contribute something tangible to the future of biodiversity science. The animals we've collected will have a scientific lifetime that far exceeds the lives of the individual researchers involved in procuring them. In a very real sense, the dead animals in our jars have been resurrected into "living data"—data that will continue to yield insights into the tropical diversity puzzle and, with a bit of luck, some deeply hidden wisdom from the secret lives of snakes.

Endnotes

[1] Many have noticed this enigmatic, almost otherworldly property of snakes. See H. W. Greene (2000): Snakes: *The Evolution of Mystery in Nature* (University of California Press), and W. E. Magnusson (2019): *Snakes and Other Lizards* (Open Science Publishers). Magnusson (2019) writes of snakes that seemingly "occupy a parallel universe and only come into our world for brief moments before returning to somewhere beyond our understanding."

[2] A patch of Amazonian rainforest just one hectare in size (~2 U.S. football fields) harbors about the same number of tree species as you would find in the entirety of Europe.

[3] Selected references on this topic:

Farley, S. S. et al. (2018). Situating ecology as a Big-Data science: current advances, challenges, and solutions. BioScience 68:563–576.

Qi, Z., and X. Liu (2019). Big data: new methods and ideas in geological scientific research. Big Earth Data 3:1–7.

Zhang, Y., and Y. Zhao (2015). Astronomy in the Big Data Era. Data Science Journal 14:1–9.

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Dan Rabosky, pictured here with 2.8 meters of neotropical indigo snake (Drymarchon corais) in southern Peru, studies large-scale patterns of biological diversity in space and time. Much of his empirical research is focused on speciation processes, community ecology, and biogeography of squamate reptiles. He has been studying the evolution and ecology of Australian desert lizards since 2004 and has conducted fieldwork throughout the Australian arid zone. More recently, Rabosky's group has worked in the field with reptile and amphibian communities from the Peruvian Amazon to understand how and why these ecological assemblages are so much more diverse than those from the temperate zone. Dan received his Ph.D. from Cornell University in 2009 and has been Professor and Curator in the University of Michigan's Division of Reptiles and Amphibians since 2012.

ALISON DAVIS RABOSKY

Building a Tangled Bank: Today's Michigan Herpetology Community

2012 —

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us."

—Charles Darwin, *On the Origin of Species* (1872)

The first time I walked into the Ruthven Museums Building, I felt profoundly humbled. I don't think that this experience is unique to me, although I do predict that this response is not uniformly distributed across members of our community. To some, membership in a community like the UMMZ is "expected," but there is very little in my own past that predicted my opportunity for leadership in such an influential and historic program. To me, every specimen jar radiates its own exciting history: the many UMMZ and local collectors who worked together to fill it, the many global scientists who have relied on these specimens to make science happen, and the century of curatorial teams who worked every day in the service of something bigger than themselves to ensure that these specimens live forever. It is impossible for me to step into such a collection and not see the power and value of what our community has produced, as well as a deep responsibility to both continue and grow that legacy as a curator. But what makes a community great, and how does one cultivate those links in a meaningful and positive way?

Although Darwin is a complex figure whose work has been used in many ways, his famous "tangled bank" metaphor about the complexity and interdependence of life on Earth has always been a powerful metaphor for people in science. I've always been astounded by the way our knowledge advances through such complex networks of collaboration and community, in ways so different from other industries. These links can be both easily visible and unseen, and collaborative data can span such vast amounts of time and space that most herpetologists today (myself included) cite people they have never met as primary forces who make their own science possible. The Michigan Herpetology of today stands upon the shoulders of all the people whose words you read in this book, as well as an even larger group of people whose voices are missing. In my opinion, one of the most notable missing voices is Helen Gaige.

Helen Thompson Gaige, along with Alexander Ruthven, founded the first formal incarnation of the Division of Reptiles and Amphibians within the UMMZ in 1917. She served as an official curator from 1923–1945, during which time she also was an unofficial advisor to many of Ruthven's students, especially after he began taking demanding administrative roles within the University. The first woman to publish in the journal *Copeia (*now known as *Ichthyology and Herpetology)* in 1914, she eventually served as an influential editor-in-chief there for more than a decade. She was a talented and thoughtful scientist, who invested heavily in the UMMZ community, 90 years before the next woman would be chosen for a curatorial role in herpetology at Michigan. Everything that has been written about her focuses on how inclusive and welcoming the Division of Reptiles and Amphibians was under her leadership, especially toward students and visitors, and how that, in turn, promoted great science. She shared her resources and expertise so broadly across her community, her legacy is now celebrated through the Gaige Fund Award for students by the American Society of Ichthyologists and Herpetologists. I wish she had written more about her personal experiences and especially her views of her own responsibilities and goals, both fulfilled and unfulfilled. I think of her often, and there have been many times that I wish I could have asked her for advice. She has left huge shoes to fill, but there's no way

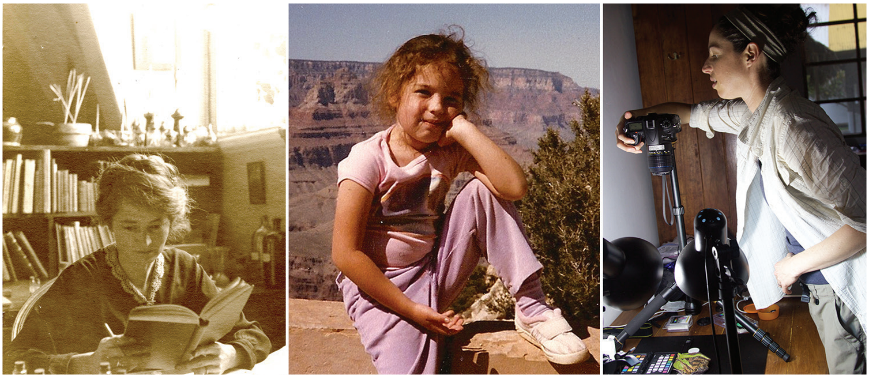

Figure 1. *The women herpetology curators of the UMMZ. Left:* ***Helen T. Gaige,*** *courtesy of Bentley Historical Library. Center:* ***Alison Davis,*** *age 5, at Grand Canyon National Park in her home state of Arizona, USA. Photo credit to Judith Richards. Right:* ***Alison Davis Rabosky,*** *using full spectrum imaging to photograph a Surinam horned frog (*Ceratophrys cornuta*) at Los Amigos Biological Station, Madre de Dios, Peru. Photo by Dan Rabosky.*

around the fact that she and I are forever united as the only women to have ever been curators of herpetology at the UMMZ (Figure 1).

Co-Curator Dan Rabosky and I arrived at the University of Michigan in 2012, full of hope and vision for museum science in the 21st century. We came from the Museum of Vertebrate Zoology at UC–Berkeley, where we had met (and later married) as postdocs 3 years earlier. Neither of us likely fit the "traditional" expectations of a future curator. We were the first in our families to pursue a career in science; both of us had backgrounds with little economic privilege, and neither one of us was focused on systematics as our primary research objective. However, we both cared deeply about biodiversity science, and we championed the critical importance of museum collections to answering the most fundamental and important questions in ecology and evolutionary biology, past and present. Most of all, we were motivated by our shared desire to combine our different, but complementary, strengths to frame a trajectory for the herpetology program at Michigan that neither one of us could have accomplished alone.

When I arrived, I had three priorities that have continued to guide my curatorial decisions. First, the enormous catalog of nearly 450,000 specimens, which had been fully digitized for internal use since the 1960s, needed to be incorporated into data aggregators such as VertNET and GBIF, where our collection was notably absent. By remaining a "dark" collection for so long, our data had been literally invisible to the greater research community that relied on these online databases to identify records of interest. By 2013, we were live! Second, I sought to leverage the incredible resources and opportunity available at Michigan into scientific excellence across the largest community I could, especially targeting students. How many papers could we get out of each collection trip, with first authorship spread among the greatest number of people? How could we maintain and enhance Michigan Herpetology as a welcoming community, where people felt empowered to succeed in the science they envisioned? Third, we needed to innovate the ways in which we think about expanding collections. I wanted to prioritize high-level training for students in museum science that was grounded in the principle that as museum scientists we must be (1) careful stewards of the historical specimens in our collections and (2) active contributors to collections for the benefit of future generations. Rather than collections being consumables for us to use to enhance our personal research, they are an entity in which we invest and transform for the benefit of others. I wanted to leverage emerging technologies for specimen digitization and public archiving, and make these data accessible on a massive scale.

How did these goals manifest in practice during the last 8 years, and what can I say about the community that we have built here? Like all ambitious plans, some things have worked better than others, and we are not a perfect division. However, I'd say that we've changed in some major ways, and I'm proud of our achievements. From 2014–2018, the research collections and the public museum (UM Museum of Natural History) were moved out of the Ruthven Museums Building; this offered the opportunity for complete redesign of all spaces to meet best practices for the 21st century. Our specimens, labs, and interactions with the public are all now in bright, modern spaces specifically designed to invite collaborative access and community engagement. In addition, we leveraged some of the moving funds into the purchase of our own CT scanner for the UMMZ, which led to an ongoing collaboration with the University of Florida and 14 other museums to make publicly available digital models of representatives from every living vertebrate genus on Earth (the "oVert" project). Today, we are using this machine in high-throughput fashion to generate an enormous quantity of three-dimensional morphological data ready to pair with existing/emerging molecular phylogenies in a comparative

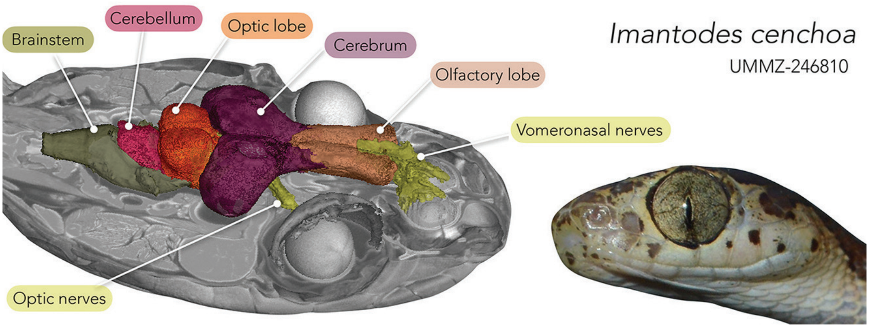

Figure 2. *3D digital dissection of the brain of a Blunthead Tree Snake (***Imantodes cenchoa***) made possible by diffusible iodine contrast enhanced ("dice") CT scanning. After seeing just a few of these digital segmentations, you never look at the outside of a snake the same way again. This specimen was collected by Joanna Larson, Consuelo Alarcón Rodriguez, and Talia Moore, CT scanned by Ramon Nagesan, and segmented by Jenna Crowe-Riddell. Photo by Consuelo Alarcón Rodriguez.*

framework. This combination is revolutionizing the ways in which we study and teach morphological evolution. In a marked departure from traditional approaches, digital specimens and virtual dissections dramatically increase pedagogical impact because the data are more accessible (Figure 2). A visit to our wet collections today reveals our dynamic and exciting workplace—many busy students, the CT scanner humming along, and lots of interaction among the Mammal, Fish, and Herpetology divisions lining up specimens to scan and marveling over the incoming accessions and loans. These are some of my favorite memories of our community in action.

Another defining feature of our community during the past decade has been the major neotropical field expeditions that we undertook from 2016–2019, which united undergraduate and graduate students from both Michigan and Latin America in collaborative collection teams. Expeditions on this scale are a huge amount of work and paired with the low encounter rates typical of many neotropical taxa, you simply can't do this kind of work alone. UMMZ curators have participated in collaborative collection expeditions for a century; so, this is one way in which our community resembles those of the past and of other museums. The way in which specimens are processed in the field is complex. Before preserving whole-body specimens, samples of every data type imaginable that could be associated with a reptile or amphibian voucher were taken, including high-speed videos of behavior to skin swabs and ecological data. Each specimen collected has a standardized

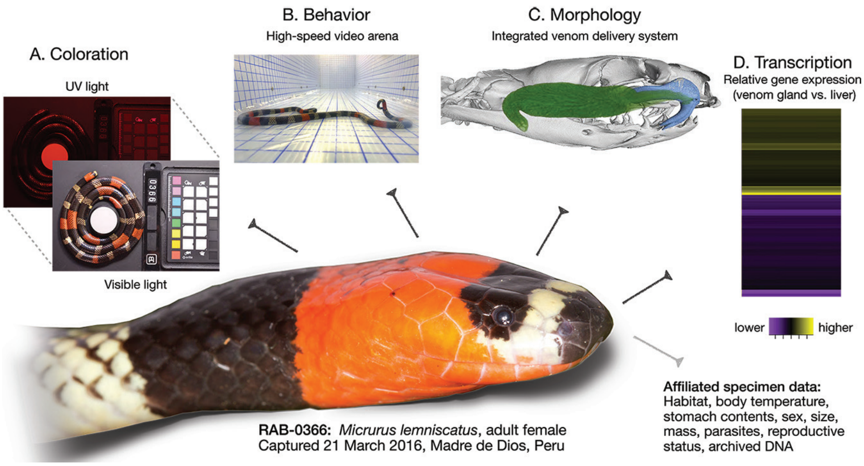

Figure 3. *Data types collected for every "super specimen" vouchered into the UMMZ or partner museums in country of collection. This specimen was collected by Mike Grundler, imaged by Alison Davis Rabosky, CT scanned by Greg Pandelis, and sequenced by Peter Cerda. It was vouchered by Michigan Herpetology for the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, Peru (MUSM-35905). Photo credit to Pascal Title.*

set of samples collected from all the phenotypes that aren't fully analyzable from a fixed specimen in a jar; these include habitat use, full spectrum coloration, behavioral and physiological responses to experimental stimuli, all stomach contents, skin and digestive microbiomes, and parasites and pathogens. Because formalin degrades genetic material, samples of a wide range of cephalic and corporal organs are taken for subsequent RNA sequencing; when possible, we try to leave one of a paired organ undamaged for later CT scanning (Figure 3). Using a strategically coordinated approach whereby everyone learns how to collect every type of data, we are creating one of the few archived records of biodiversity change that specifically examines how these extra-specimen traits interact across time and space. Although collection manager Greg Schneider has never gotten entirely accustomed to our specimens missing so many (small!) pieces, we have great hopes that these "super specimens" will have a long future and be used in novel ways that we didn't envision when we collected them. Moreover, these trips were important for figuring out how to nurture our own connections as a community. Whether it was joking about the "team-building properties" of Rudi von May's torturous frog plots (meticulous nighttime leaf litter surveys on hands and knees, a testament to both steely nerves and permethrin-treated clothing), sweetly optimistic bilingual discussions of using grassroots collaboration to solve global conservation issues while doing early morning trapline checks, or late-night frog barfing sessions to get stomach contents from beefy cane toads, we built personal connections and datasets that we hope will last lifetimes.

These are some of the things we have done, but does that tell you who we are? Is a community best defined by its actions, its goals, or even its failures? My answer is that we are best defined by the people themselves (Figure 4). All of us have worked hard to provide opportunities to each other across a broad set of research questions and projects, continually bringing in as many new people as possible to our community in some way or another. We recognize that together, we can do things that none of us can do alone, and that our capacity grows exponentially as new members bring diverse ideas, experiences, and expertise to the table. If we hadn't had that kind of universal buy-in from the people we invited into our community, we wouldn't have been able to sustain such collaboration across challenges. The people in this figure and those who have contributed to this book have been instrumental creating the herpetology program today at Michigan herpetology, and they are a huge part of my own tangled bank.

This, in a nutshell, is the reason that we have designed *Letters from Michigan Herpetology* in the way that we have—no single person can speak for all of us, past and present. We have been a vibrant and complex community since our inception in 1917, and we continue to grow along axes of diversity and representation. We foster the ideals set by Helen Gaige and Alexander Ruthven of giving collective support to others and of pursuing new science with a valued museum collection. With these priorities, we hope to link the powerful, positive threads that you have read in each author's story about what Michigan herpetology meant to them and ensure that the community is a place we can continue to be proud of in the future.

While our initial vision was to distribute this book to everyone visiting Ann Arbor in person at the Society for the Study of Amphibians and Reptiles (SSAR) standalone meeting in 2021, the COVID-19 pandemic of 2020 delayed the meeting for 3 years to accommodate safe attendance in large groups after successful vaccines had been deployed.

This book, however, was delivered on the original schedule thanks to the impressive efforts of Greg Schneider, Linda Trueb, and the chapter authors. We now hope that the purpose of the book similarly expands, and that this window into the many facets of Michigan herpetology will encourage the reader to visit us in person in 2024 and beyond. We welcome you to our community!

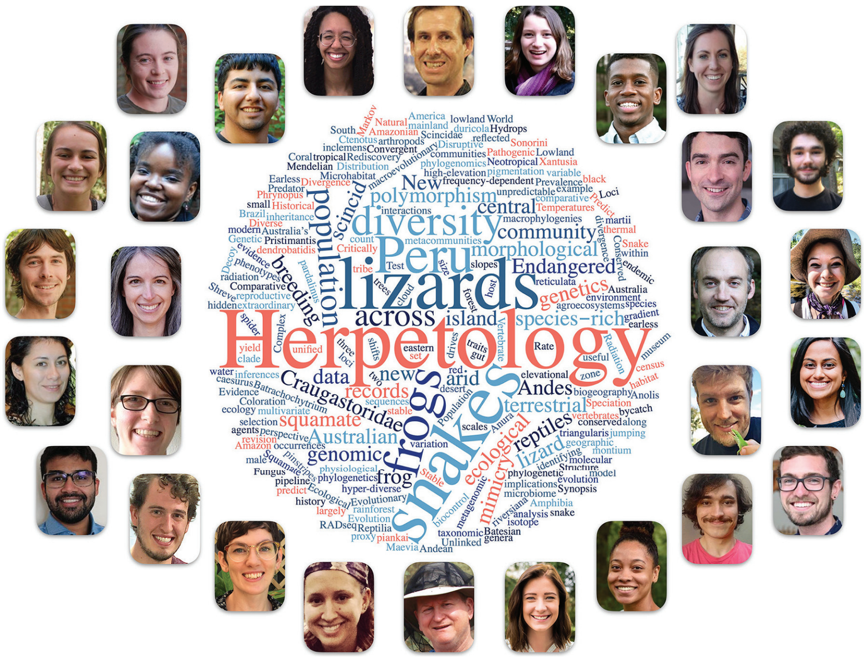

Figure 4. ***Michigan Herpetology faculty, graduate students, postdoctoral researchers, and technicians from 2016–2020.*** *Photos, from top center, clockwise: Rudi von May (postdoc), Erin Westeen (undergraduate and technician), Ivan Monagan (graduate student), Joanna Larson (graduate student), Greg Pandelis (undergraduate and technician), Pascal Title (graduate student), Maggie Grundler (undergraduate and technician), Dan Rabosky (faculty), Sonal Singhal (postdoc), Ivan Prates (postdoc), John David Curlis (graduate student), Matheus Januário (graduate student), Brianna Mims (graduate student), Taylor West (graduate student), Greg Schneider (collection manager), Hayley Crowell (graduate student), Jenna Crowe-Riddell (postdoc), Sean Callahan (undergraduate and technician), Ramon Nagesan (technician), Natasha Stepanova (graduate student), Talia Moore (postdoc), Alison Davis Rabosky (faculty), Michael Grundler (graduate student), Briana Sealey (graduate student), Courtney Whitcher (undergraduate and technician), Iris Holmes (graduate student), Peter Cerda (graduate student), Imani Russell (graduate student). Center: Word cloud of our paper titles showing the breadth of topics we study within herpetology.*

About the Author

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Museum of Zoology
University of Michigan
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After completing her undergraduate degree at Pomona College, Alison received her Ph.D. in Ecology and Evolutionary Biology from the University of California, Santa Cruz, in 2009 and was appointed a postdoctoral fellow in the Museum of Vertebrate Zoology at the University of California, Berkeley, from 2009–2012.

As an evolutionary biologist and behavioral ecologist, Alison combines molecular, field, and laboratory studies to answer research questions in three main areas: (1) character evolution and phylogenetics; (2) animal behavior and evolution; and (3) the conservation and management of island endemics. Although much of her recent work has involved reptiles and amphibians, her research interests span a broad range of taxa.

Broadly interested in the origin and evolutionary stability of phenotypes in nature, a major focus of her research involves color polymorphism and the evolution of mimicry. Currently, Alison is using comparative genomics to test hypotheses about the role of color polymorphism in phenotypic evolution within Batesian and Müllerian mimicry systems. Her primary study systems include snakes across the Western Hemisphere, including the colubrid snake genus *Sonora* with varying levels of color polymorphism and mimicry of venomous coral snakes.

Appendix

This chronological list of Michigan herpetologists and/or herpetological dissertations documents research conducted at the University of Michigan since 1876. Square brackets indicate information garnered from sources other than the actual thesis.

Student	Year	Thesis Title	Committee Chair
William Henry Smith	1876	The Tailed Amphibians Including Caecilians [in Proquest as "The Zoology of Anoura and Caecilia"]	[Mark W. Harrington]
Alexander Grant Ruthven	1906	Variations and genetic relationships of the garter-snakes	Charles C. Adams
Frank N. Blanchard	1919	A Revision of the King Snakes: Genus *Lampropeltis*	Alexander G. Ruthven
Frieda Cobb (Blanchard)	1920	A Case of Mendelian Inheritance Complicated by Heterogametism and Mutation in *Oenothera pratincola*	Alexander G. Ruthven
Arthur Irving Ortenburger	1925	The Whip Snakes and Racers: Genera *Masticophis* and *Coluber*	Alexander G. Ruthven
Olive Griffith Stull	1929	Variations and Relationships in the Snakes of the Genus *Pituophis*	Alexander G. Ruthven
Charles Earl Burt	1930	A Study of ohe Teiid Lizards of the Genus *Cnemidophorus* with Special Reference to Their Phylogenetic Relationships	Frank N. Blanchard
Walter Mosauer	1930	Ueber Die Ortsbewegung Der Schlangen; Eine Kritik Und Ergaenzung Der Arbeit Wiedemann's. [About the local movement of the snakes: a criticism and supplement to the work of Wiedemann]	[G. Carl Huber]
Gordon Lynn Walls	1931	The Early Evolution of the Visual Cells of Vertebrates	[John F. Shepard]
Laurence C. Stuart	1933	Studies on Certain Neotropical Colubrinae	Alexander G. Ruthven
Norman E. Hartweg	1934	A Study of Genetic Variation in the Genus *Chrysemys*	Alexander G. Ruthven

Student	Year	Thesis Title	Committee Chair
Theodore E. White	1935	Adaptive Evolution of the Pelvic Musculature of the Turtles of the Genera *Clemmys, Emys* and *Terrapene*	Ermine Cowels Case
Charles F. Walker	1935	The Generic Relations of the North American Terrestrial Hylidae, *Pseudacris*	Alexander G. Ruthven
Howard K. Gloyd	1936	The Rattlesnake Genera *Sistrurus* and *Crotalus:* A Study in Zoogeography and Evolution	Frank N. Blanchard
William M. Clay	1937	The Taxonomy and Phylogenetic Relationships of the Water Snakes *Natrix erythrogaster* and *Natrix sipedon*	Frank N. Blanchard
W. Frank Blair	1938	Ecological Distribution of the Mammals of the Bird Creek Region, Northeastern Oklahoma	Lee R. Dice
Joseph Randle Bailey	1940	Relationships and Distributions of the Snakes Allied to the Genus *Pseudoboa*	Alexander G. Ruthven
Karl Frank Lagler	1940	Ecological Studies of Turtles in Michigan with Special Reference to Fish Management	[Carl L. Hubbs]
Ira Dearing George	1940	A Study of the Life History of the Bullfrog, *Rana catesbeiana* (Shaw) at Baton Rouge, Louisiana	Frank N. Blanchard
Laurence Wilfred Roth	1940	The Effect of Hypophysectomy upon the Respiratory Quotient of Snakes	[Alvalyn E. Woodward]
James Arthur Oliver	1941	Distribution and Relationships of the snakes of the Genus *Leptophis*	Alexander G. Ruthven
Hugh Daniel Clark	1941	The Anatomy and Embryology of the Hemipenis of *Lampropeltis, Diadophis* and *Thamnophis* and Their Value As Criteria of Relationship in the Family Colubridae	Frank N. Blanchard
Fred Ray Cagle	1943	The Growth of the Slider Turtle, *Pseudemys scripta elegans*	Norman E. Hartweg

STUDENT	YEAR	THESIS TITLE	COMMITTEE CHAIR
Grace Louise Orton	1944	Studies on the Systematic and Phylogenetic Significance of Certain Larval Characters in the Amphibia Salientia	Norman E. Hartweg
Mahlon Clifton Rhaney	1948	Some Aspects of the Carbohydrate Metabolism of the Kingsnake (*Lampropeltis getulus floridana*)	Alvalyn E. Woodward
Lucille Farrier Stickel	1949	Populations and Home Range Relationships of the Box Turtle, *Terrapene carolina* (Linnaeus)	Peter Okkelberg (Frank N. Blanchard / Hartweg / Test)
Charles Congden Carpenter	1951	Comparative Ecology of the Common Garter Snake (*Thamnophis s. sirtalis*), the Ribbon Snake (*Thamnophis s. sauritus*), and Butler's Garter Snake (*Thamnophis butleri*), in Mixed Populations	Frederick H. Test
Herndon Glenn Dowling	1951	A Taxonomic Study of the American Representatives of the Genus *Elaphe* Fitzinger, with Particular Attention to the Forms Occurring in Mexico and Central America	Norman E. Hartweg
Emanuel Cassel Hertzler	1951	The Red and Black Pigments of the Salamander, *Plethodon cinereus* (Green)	Frederick H. Test
Bernard Stephen Martof	1951	An Ecological Study of the Green Frog, *Rana clamitans,* in Southeastern Michigan	Frederick H. Test
George T. Baxter	1952	The Relation of Temperature to the Altitudinal Distribution of Frogs and Toads in Southeastern Wyoming	Lee R. Dice
James Arthur Peters	1952	The Snake Subfamily Dipsadinae in South and Central America	Norman E. Hartweg
Albert Schwartz	1952	The Land Mammals of Southern Florida and the Upper Florida Keys	William H. Burt
Gordon Wieland Ballmer	1953	The Microdistribution of Some Proteolytic Enzymes in the Gastric Mucosa of Several American Turtles	Alvalyn E. Woodward

Student	Year	Thesis Title	Committee Chair
Thomas Mann Oelrich	1953	The Anatomy of the Head of *Ctenosaura pectinata* (Iguanidae)	Alfred H. Stockard
Bryce C. Brown	1955	The Herpetology of the Coastal Prairie Region of Texas	Norman E. Hartweg
Paul Schultz Martin	1956	Herpetology of the Gomez Farias Region, Tamaulipas, Mexico. A Biogeographic Study of a Neotropical Area	Charles F. Walker
James Emile Mosimann	1956	A Morphometric Analysis of Allometry in Shells of the Turtles *Graptemys geographica, Chrysemys picta,* and *Sterontherus odoratus*	Norman E. Hartweg
William E. Duellman	1956	The Phylogenetic Relationships and Zoogeography of the Snakes of the Genus *Leptodeira*	Norman E. Hartweg
Kenneth Leonard Fitch	1957	The Development of *Necturus maculosus*	Alfred H. Stockard
George Bernard Rabb	1957	A Study of Variation in Iguanid Lizards of the *Leiocephalus carinatus* Complex	Charles F. Walker
Owen James Sexton	1957	The Spatial and Seasonal Distribution of a Population of the Painted Turtle, *Chrysemys picta marginata,* Agassiz	Frederick H. Test
David Edgar Delzell	1958	Spatial Movement and Growth of *Hyla crucifer*	Frederick H. Test
Harold A. Dundee	1958	Habitat Selection by Aquatic Plethodontid Salamanders of the Ozarks, With Studies on Their Life Histories	Nelson G. Hairston
Richard Emmett Etheridge	1959	The Relationships of the Anoles (Reptilia: Sauria: Iguanidae): An Interpretation Based on Skeletal Morphology	Norman E. Hartweg
Harold Franklin Heatwole	1960	The Forest Floor and Its Utilization by Selected Species of Terrestrial Amphibians	Frederick H. Test
James Albert Organ	1960	Studies on the Local Distribution, Life History, and Population Dynamics of the Salamander Genus *Desmognathus* in Virginia	Nelson G. Hairston

Student	Year	Thesis Title	Committee Chair
Arthur Erle Dammann	1961	Some Factors Affecting the Distribution of Sympatric Species of Rattlesnakes (Genus *Crotalus*) in Arizona	Norman E. Hartweg
Thomas Marshall Uzzell, Jr.	1962	Morphology and Biology of the Salamanders of the *Ambystoma jeffersonianum* Complex	Charles F. Walker
Calvin Boyd Dewitt	1963	Behavioral Thermoregulation in the Iguanid Lizard, *Dipsosaurus dorsalis*	William R. Dawson
Jim Walter Dole	1963	Movements and Spatial Relations of *Rana pipiens* in Spring and Summer in Northern Michigan	Frederick H. Test
Marilyn Dorothy Davidson Bachmann	1964	Maternal Behavior of the Red-backed Salamander, *Plethodon cinereus*	Frederick H. Test
Paul Licht	1964	The Relation Between Thermoregulation and Physiological Adjustments to Temperature in Lizards	William R. Dawson
Vaughan Hurst Shoemaker	1964	Physiological Effects of Water Deprivation in a Toad, *Bufo marinus*	William R. Dawson
Floyd Leslie Downs	1965	Intrageneric Relationships Among Colubrid Snakes of the Genus *Geophis* Wagler.	Norman E. Hartweg / Charles F. Walker
William Albert Dunson	1965	Sodium Regulation in Freshwater Turtles	William R. Dawson
Peter Allen Lee	1965	Histological and Biochemical Analysis of the Annual Cycle of Growth and Secretion in the Oviduct of *Rana pipiens*	Norman E. Kemp
William Ryder. Healy	1966	The Effect of Alternative Life Histories on Population Structure in the Common Newt *Notophthalmus v. viridescens*	Charles F. Walker
Walter Ray Moberly, II	1966	The Physiological Correlates of Activity in the Common Iguana, *Iguana iguana*	William R. Dawson
Priscilla Hollister Starrett	1968	The Phylogenetic Significance of the Jaw Musculature in Anuran Amphibians	Charles F. Walker

Student	Year	Thesis Title	Committee Chair
Kraig Kerr Adler	1968	Environmental Control of Locomotor Activity in a Salamander (*Plethodon glutinosus*)	Charles F. Walker
Patricia Ruth Stocking Brown	1968	Growth Responses of Larval and Post-metamorphic *Rana pipiens* to Prolactin and Growth Hormone	Billy E. Frye
Warren Yalding Brockelman	1968	Natural Regulation of Density in Tadpoles of *Bufo americanus*	Nelson G. Hairston
John Edwin Minnich	1968	Maintenance of Water and Electrolyte Balance by the Desert Iguana, *Dipsosaurus dorsalis*	William R. Dawson
Marvin Henry Bartell	1969	The Role of the Pituitary in Blood Glucose Regulation in Larval and Adult Salamanders, *Ambystoma tigrinum*	Billy E. Frye
George R. Zug	1969	Locomotion and the Morphology of the Pelvic Girdle and Hind Limbs of Cryptodiran turtles	Charles F. Walker
Gary Wright Ferguson	1969	Geographic Variation and Evolution of Stereotyped Behavioral Patterns of the Side-blotched Lizards of the Genus *Uta* (Iguanidae)	Donald W. Tinkle
Charles Oran McKinney	1969	Analysis of Zones of Intergradation in *Uta stansburiana*	Donald W. Tinkle
Louis Peter Visentin	1969	A Biochemical and Morphological Analysis of the Renal and Hepatic Peroxisomes of the Frog, *Rana pipiens*	J. M. Allen
James Harvey Asher, Jr.	1970	Parthenogenesis and Genetic Variability	Morris Foster / Charles F. Sing
Paul Alfred Debenedictis	1970	Interspecific Competition Between Tadpoles of *Rana pipiens* and *Rana sylvatica:* An Experimental Field Study	Francis C. Evans
Stephen George Tilley	1970	Aspects of the Reproductive and Population Ecology of *Desmognathus ochrophaeus* in the Southern Appalachian Mountains	Donald W. Tinkle

Student	Year	Thesis Title	Committee Chair
Ronald John Flaspohler	1970	Evolutionary Basis for Species Discrimination in Iguanid Lizards	Donald W. Tinkle
Albert Curtis Allen, Jr.	1970	Ossification of the Skull and Deposition of Aragonitic Crystals in the Endolymphatic Sacs of the Urodele, *Ambystoma maculatum*	Charles F. Walker / Norman E. Kemp
Benjamin Willard Snyder	1970	Physiological Responses of Larval and Postmetamorphic *Rana pipiens* to Growth Hormone and Prolactin	Billy E. Frye
John Charles Hegenauer	1970	Studies on Ferritin, Phosvitin, and Non-heme Iron Metabolism in the Frog Embryo	George W. Nace
Priyambada Mohanty Hejmadi	1970	Transfer of Maternal Serum Proteins into the Egg of *Rana pipiens* and Their Role in Development	George W. Nace
David Saul Ostrovsky	1970	Lysozyme Ontogeny in *Rana pipiens*	George W. Nace
Albert Farrell Bennett	1971	Oxygen Transport and Energy Metabolism in Two Species of Lizards, *Sauromalus hispidus* and *Varanus gouldii*	William R. Dawson
Henry Miles Wilbur	1971	Competition, Predation and the Structure of the *Ambystoma–Rana sylvatica* Community	Charles F. Walker
Stevan James Arnold	1972	The Evolution of Courtship Behavior in Salamanders	Arnold G. Kluge
Ronald Edwin Beiswenger	1972	Aggregative Behavior of Tadpoles of the American Toad, *Bufo americanus,* in Michigan	Frederick H. Test
Eugenia Sue Smith Farrar	1972	Some Aspects of Carbohydrate Metabolism and Its Regulation by Adrenalin and Glucagon in *Rana pipiens*	Billy E. Frye
Ann Elizabeth Pace	1972	Systematic and Biological Studies of the Leopard Frogs (*Rana pipiens* Complex) of the United States	Richard D. Alexander

Student	Year	Thesis Title	Committee Chair
Alan Robert Templeton	1972	Statistical Models of Parthenogenesis	William R. Dawson
Sandra Joyce Smith Gill	1972	A Genetic and Developmental Analysis of the Cytophysiology of the Disruptive Pigmentary Patterning in *Rana pipiens*	George W. Nace
Robert Edward Gatten, Jr.	1973	Aerobic and Anaerobic Metabolism During Activity in the Turtles *Pseudemys scripta* and *Terrapene ornata*	William R. Dawson
Marian Ellen Blank Vinegar	1973	Evolution of Life History Phenomena in Three Forms of the Lizard Genus *Sceloporus*	Donald W. Tinkle
James Paul Col-lins	1975	A Comparative Study of the Life History Strategies in a Community of Frogs	Donald W. Tinkle
Daniel Rittschof	1975	Some Aspects of the Natural History and Ecology of the Leopard Frog, *Rana pipiens*	George W. Nace
Robert Wayne Van Devender	1975	The Comparative Demography of Two Local Populations of the Tropical Lizard, *Basiliscus basiliscus*	Donald W. Tinkle / Nelson G. Hairston
Cynthia Carey	1976	Thermal Physiology and Energetics of Boreal Toads, *Bufo boreas boreas*	William R. Dawson
Douglas Early Ruby	1976	The Behavioral Ecology of the Viviparous Lizard, *Sceloporus jarrovi*	Donald W. Tinkle
Michael Charles Devine	1977	Chemistry and Source of Sex-attractant Pheromones and Their Role in Mate Discrimination by Garter Snakes	Donald W. Tinkle
Paul Edward Feaver	1977	The Demography of a Michigan Popula-tion of *Natrix sipedon* with Discussions of Ophidian Growth and Reproduction	Ronald A. Nuss-baum
Richard Duncan Howard	1977	The Evolution of Mating Strategies and Resource Utilization in Bullfrogs, *Rana catesbeiana*	Richard D. Alex-ander

Student	Year	Thesis Title	Committee Chair
Robert Anthony Noonan	1977	Seasonal Control of Carbohydrate Metabolism in the frog *Rana pipiens*	Billy E. Frye
David Conwell Smith	1977	Interspecific Competition and the Demography of Two Lizards.	Donald W. Tinkle
Arthur Earl Dunham	1978	An Experimental Study of Interpspecific Competition Between the Iguanid Lizards *Sceloporous merriami* and *Urosaurus ornatus*	Donald W. Tinkle
Terry Steven Dugan	1978	Collagenolytic Activity During Regeneration of Hind Limbs of the Frog, *Rana pipiens*	Norman E. Kemp
Walter Wilczynski	1978	Connections of the Midbrain Auditory Center in the Bullfrog, *Rana catesbeiana*	R. Glenn Northcutt
John William Levinson	1979	Characterization of Fertilization Antigens of *Rana pipiens* Ova	George W. Nace
Scott Michael Moody	1980	Phylogenetic and Historical Biogeographical Relationships of the Genera in the Family Agamidae (Reptilia: Lacertilia)	Arnold G. Kluge
Cynthia Kagarise Sherman	1980	A Comparison of the Natural History and Mating System of Two Anurans: Yosemite Toads (*Bufo canorus*) and Black Toads (*Bufo Exsul*)	Richard D. Alexander
Alan P. Jaslow	1982	Factors Affecting the Distribution and Abundance of Tadpoles in a Lowland Tropical Stream	Arnold G. Kluge
Edward Lee Hover	1982	Behavioral Correlates of a Throat color Polymorphism in a Lizard, *Urosaurus ornatus*	Ronald A. Nussbaum

Student	Year	Thesis Title	Committee Chair
Thomas Clayton Scanlon	1982	Anatomy of the Neck of the Western Painted Turtle (*Chrysemys picta belli* Gray; Reptilia, Testudinata) from the Perspective of Possible Movements in the Region	Carl Gans
Peter J. Tolson	1982	Phylogenetics of the Boid Snake Genus *Epicrates* and Caribbean Vicariance Theory	Arnold G. Kluge
Frederick Joseph Carey	1985	The Development and Organization of Spinal Motoneurons in Urodele Amphibians (horseradish peroxidase, motor pool)	Bruce M. Carlson
Joseph Robert Fetcho	1985	The Motoneurons Innervating the Axial Musculature of the Goldfish (*Carassius auratus*), the Mudpuppy (*Necturus maculosus*), and the Florida Water Snake (*Nerodia fasciata pictiventris*)	Stephen S. Easter
William Stephen Bartels	1987	Fossil Reptile Assemblages and Depositional Environments of Selected Early Tertiary Vertebrate Bone Concentrations, Bighorn Basin, Wyoming	Gerald R. Smith
Edward Frederick Kraus	1987	An Evaluation of the Ontogeny Polarization Criterion in Phylogenetic Inference: A Case Study Using the Salamander Genus *Ambystoma*	Arnold G. Kluge
David Rodgers Carrier	1988	Locomotor-Ventilatory Coupling in Lizards and Early Tetrapods	Carl Gans
Kenneth Mark Crawford	1988	Osmoregulatory Function in Summer and Winter Acclimatized Painted Turtles, *Chrysemys picta*	William R. Dawson
Peter Karl Ducey	1988	Variation in the Antipredator Behavior of *Ambystoma* Salamanders	Ronald A. Nussbaum
Kyle Summers	1990	Parental investment and Sexual Selection in Dart-poison Frogs (*Genus Dendrobates*)	Arnold G. Kluge

STUDENT	YEAR	THESIS TITLE	COMMITTEE CHAIR
Joel Thomas Heinen	1992	Behavioral Anti-predator Strategies in Newly-metamorphosed American toads (*Bufo americanus*) in Response to Predation Risk by Eastern Garter Snakes (*Thamnophis sirtalis*)	Bobbi S. Low
David Kiernan Skelly	1992	Larval Distributions of Spring Peepers and Chorus Frogs: Regulating Factors and the Role of Larval Behavior	Earl E. Werner
Russell Lewis Burke	1994	Reproduction and Survival Strategies in Various Animals: Assumptions and Predictions of Adaptational Hypotheses	Ronald A. Nussbaum
Sheng-hai Wu	1994	Phylogenetic Relationships, Higher Classification, and Historical Biogeography of the Microhylid Frogs (Lissamphibia: Anura: Brevicipitidae and Microhylidae).	Ronald A. Nussbaum
Daniel Scott York	1995	Taxonomic and Functional Implications of Dorsal Scale Characters in the Viperidae (Reptilia: Serpentes)	Ronald A. Nussbaum
Alan Jeffrey Wolf	1996	Systematics of the *Rana catesbeiana* Species Group and the Phylogenetic Informativeness of Anuran Vocalizations	Arnold G. Kluge
Jana Yonat Beth Swimmer	1997	Physiological Consequences of Basking, Disease and Captivity in the Green Turtle, *Chelonia mydas*	Terry L. Root
Brad R. Moon	1998	Structural and Functional Integration of the Snake Axial System	Carl Gans
Rick Alan Relyea	1998	Phenotypic Plasticity in Larval Anurans	Earl E. Werner
Karen Ann Glennemeier	2000	Roles of Corticosterone in the Development and Physiological Ecology of *Rana pipiens* Tadpoles and the Disruption of This Endocrine System by Organochlorine Contamination	Robert J. Denver

STUDENT	YEAR	THESIS TITLE	COMMITTEE CHAIR
Scott D. Peacor	2001	The Role of Phenotypic Plasticity and Indirect Interactions on the Structure of Ecological Communities	Earl E. Werner
Heather Elizabeth Heying	2001	The Evolutionary Ecology and Sexual Selection of a Madagascan Poison Frog (*Mantella laevigata*)	Arnold G. Kluge
Jennifer Catherine Ast	2002	Evolution in Squamata (Reptilia)	Arnold G. Kluge
Kerry Lynne Yurewicz	2002	Size Structure and Intraguild Interactions in Larval Salamanders	Earl E. Werner
Richard Matthew Lehtinen	2003	Ecology and Metapopulation Dynamics of Two Pandanus-dwelling Frogs from Madagascar	Ronald A. Nussbaum
Graham C. Boorse	2004	The Roles of the Corticotropin-Releasing Factor System in Amphibians	Robert J. Denver
Luis C. Schiesari	2004	Performance Tradeoffs Across Resource Gradients in Anuran Larvae	Earl E. Werner
Laura Eidietis	2005	A Biomechanical Description of the Anuran Tadpole Startle Response and Some Implications of Anatomical Diversity	Paul W. Webb
Keith Pecor	2005	Some Aspects of the Chemical Ecology of the Crayfish *Orconectes virilis* and *Orconectes rusticus*	Ronald A. Nussbaum
Glenn Michael Fox	2006	Total Evidence and the Evolution of Ophidia (Reptilia: Squamata)	Arnold G. Kluge
Michael Edward Fraker	2007	Predation Risk Assessment and the Anti-predator Behavioral Dynamics of Larval Anurans	Earl E. Werner
Corinne L. Richards	2008	Ecological and Evolutionary Implications for the Conservation of Panamanian Golden Frogs	Ronald A. Nussbaum / Laura Lacey Knowles

Student	Year	Thesis Title	Committee Chair
Matthew W. Chatfield	2009	Evolutionary Dynamics Among Salamanders in the *Plethodon glutinosus* Group, with an Emphasis on Three Species: *Plethodon jordani, Plethodon metcalfi,* and *Plethodon teyahalee* (Caudata: Plethodontidae)	Ronald A. Nussbaum / Priscilla Tucker
Takehito Ikejiri	2010	Morphology of the Neurocentral Junction During Postnatal Growth of Alligator (Reptilia, Crocodylia)	J. Wilson
Amanda June Zellmer	2010	Ecological and Evolutionary Consequences of Population Connectivity in an Amphibian With Local Adaptation	Earl E. Werner / Laura Lacey Knowles
Clayton E. Cressler	2011	Multi-trait Selection and the Evolution of the Integrated Phenotype	Aaron A. King
Jessica E. Middlemis Maher	2011	Ecological and Evolutionary Context of the Stress Response in Larval Anurans	Earl E. Werner
Jay Reed	2014	Analysis of the Function and Evolution of Mite Pockets in Lizards	Ronald A. Nussbaum / Barry O'Connor
John A. Marino, Jr.	2014	Interactions Between Echinostome Parasites and Larval Anurans Across Ecological Contexts and Scales	Earl E. Werner
Pascal O. Title	2018	Species Richness in Time and Space: a Phylogenetic and Geographic Perspective	Daniel Rabosky
Anat Belasen	2019	The Impacts of Habitat Fragmentation on Amphibian Health in the Brazilian Atlantic Forest Biodiversity Hotspot	Tim James

Student	Year	Thesis Title	Committee Chair
Hayden Hedman	2019	Don't Count Your Eggs Before They Hatch: A "One Health" Investigation of Antimicrobial Resistance at the Intersection of Small-scale Agricultural Development and Global Health in Northwestern Ecuador	Joseph Eisenberg / Johannes Foufopoulos
Mike Grundler	2020	Exploring the Roles of Models and Natural History in Macroevolution	Daniel Rabosky
Iris Holmes	2020	When Does Gene Flow Stop? A Mechanistic Approach to the Formation of Phylogeographic Breaks in Nature	Alison Davis Rabosky
Joanna Larson	2020	Frog trophic and morphological diversity: phylogenetic and spatial patterns	Daniel Rabosky

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