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Obituary

William E. Duellman (1930–2022)

His endless study and legacy on the Ecuadorian amphibians

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William Edward Duellman (Bill) passed away on February 25, 2022, at age 91. Two years earlier, in December 2019, Bill described a hylid frog—hylids and hemiphractids were his most loved amphibians—in a publication in the Brazilian journal *Phyllomedusa* (Duellman 2019). This new yellow-eyed Colombian spiny-backed treefrog was named as *Osteocephalus omega,* and its specific epithet—the last letter in the Greek alphabet—was intended to call attention to his realization that this was going to be the last description he would write. This meticulous publication (having him as the sole author) was the epilogue of his species descriptions during a long, multifaceted life dedicated to the systematics, evolution, ecology, morphology, and natural history of amphibians, and the building of one of the largest herp collections and herpetological academic programs in the world at The University of Kansas (KU).

Bill´s biography was written in part and with many details in his book *Herpetology at Kansas: A Centennial History* (Duellman 2015). However, the efforts to write his complete biography, including his strengths and weaknesses, and to recover the essence and legacy of Bill, one of the most influential and prolific herpetologists of this era, is a pending issue. But given that Bill´s life was closely tied to the Neotropics, and specially to Ecuador, Peru, and Central America, we write this essay to briefly summarize and highlight a few aspects of his monumental contribution, especially as related to Ecuadorian amphibian research which we (as his students) partially witnessed and in which we participated.

The numbers are unreal! Bill described or co-described 252 (currently recognized as valid) species of frogs from the Neotropics (93 from Ecuador), a monumental task for a scientist! He started publishing at a young age; Bill was 17 years old when he co-authored his first paper, a range extension of Kirtland's snake (Wood and Duellman, 1947).

The first species that he described was the Peters' Shiny Peeping Frog (*Tomodactylus petersi;* now in the genus *Eleutherodactylus*) from Mexico (Duellman 1954). Sixty-five years later, in 2019, Bill completed, on his own terms, his contributions on new species, with the description of *Osteocepahlus omega*. By no means, however, did he intend to finish his writing, despite his advanced age and acute pain caused by some twisted sacral vertebrae. On the contrary, he was in a fresh dawning of a herpetologist and fully committed to the *Encyclopedia of Ecuadorian Amphibians,* an opus on which his extraordinary intellect, passion, and heart were placed. Two

weeks before passing away, Bill met online with Patricia A. Burrowes, Joseph R. Mendelson, and Ignacio de la Riva (former graduate students and postdoc) at an intensive care unit at the hospital, and he told them that he would soon be going home because he had to finish the work of the amphibians of Ecuador. Unfortunately, his wish did not materialize and he could not continue with the encyclopedia. Nonetheless, most of his contributions were already in place and the opus will be published soon.

Bill´s activity in Ecuador could be divided in two major periods, the first in which he was directly working in Ecuador from 1966–1990, when he and his KU students carried out field work, and another one from 1988–2022 when he and Linda Trueb (his wife and scientific partner) mentored Ecuadorian students, specialized in systematics, evolutionary biology, and ecology at KU, and continued publishing on Ecuadorian frogs.

Bill´s first period began in 1966, when his taxonomic research and resulting publications already included Ecuadorian frogs. For this first paper, on the Neotropical genus *Smilisca,* he examined Ecuadorian specimens of *S. phaeota* deposited at several museums in the U.S., and it was published by the Museum of Natural History of the University of Kansas (Duellman and Trueb, 1966). Next would be a paper that appeared in 1968 in the U.S. journal *Herpetologica,* in which Bill reviewed the taxonomic status of some Americas hylid frogs, among them the Ecuadorian *Trachycephalus coriaceus,* based on specimens from Limoncocha (Duellman 1968). Then, in 1969, three consecutive papers dealt with the Ecuadorian frogs: *Agalychnis buckleyi* (Duellman 1969a), *Atelopus ignescens*, *A.* sp. (*spumarius* at that time) (Duellman and Lynch, 1969), and *Dendropsophus carnifex* (Duellman 1969b). The latter was the first new species described by Bill from Ecuador. These initial studies were followed by an explosion of research and publications about Ecuadorian taxa. During his life (between 1968 and 2020), Duellman published 73 titles that included Ecuadorian frogs of a total of 386 herp publications; 68 of the 73 were journal publications, whereas the others were components in five of his major books: *The Hylid Frogs of Middle America* (1970), *The Biology of an Equatorial Herpetofauna in Amazonian Ecuador* (1978), *The South American Herpetofauna* (1979), *Patterns of Distribution of Amphibians: A Global Perspective* (1999), *Marsupial Frogs: Gastrotheca & Allied Genera* (2015). Also, in seven of the journal publications, he authored (1) or coauthored (6) with Ecuadorian researchers.

Bill´s field work in Ecuador started in November 1966, when he was 36 years old. With this trip, Bill began his lifelong journey related to Ecuador, toward which he focused a large portion of his professional life. He flew from Miami to Quito and then traveled, for the first time, to the Amazonian rainforest, specifically to Santa Cecilia, on the banks of Río Aguarico, in Sucumbíos Province. The forest was virgin or only slightly disturbed; it was located at 340 m above sea level and right on the Equator. In a prolog of a photography coffee table-book of Ecuadorian frogs, he described his experience at Santa Cecilia as follows:

"As darkness fell, I donned my boots and a headlamp and walked along a trail in the rainforest. Everywhere I looked I saw frogs of all sizes, shapes and colors—big green frogs that made a soft cluck call, large brown frogs with acute snouts that had a laugh-like call, and many kinds of small yellow frogs, some of which had red feet. These were only the tree frogs. By day on the ground there were various kinds of toads and poison-dart frogs. And then there was the frog with a long, fleshy nose and what seemed like horns on its head. Had I died and gone to heaven inhabited by the world's greatest diversity of frogs? No, I was in the Oriente (Amazonia) *of Ecuador."* (Duellman 2009).

In this first trip of 11 days, he collected 191 specimens of amphibians and reptiles at Santa Cecilia and Limoncocha adding to his 30,933 field series of amphibians and reptiles he had collected before in U.S., Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Nicaragua,

Panama, and Venezuela. Bill would return to conduct field work in the Lago Agrio region (Santa Cecilia, Limoncocha, Puerto Libre) in 1967, 1968, 1969, 1971, and 1972. At that time the oil industry in the Ecuadorian northern Amazonian had just begun its activities, and deforestation along with some of the worst oil spills in world history would shortly follow (Kimerling 1993). Nonetheless, the virgin equatorial rain forest at Lago Agrio and surroundings in Ecuador offered Bill a unique opportunity to lead and conduct inventories and ecological studies, and to document natural histories, sometimes walking behind or stopping bulldozers that were clearing the forests. At Santa Cecilia, one of his graduate students, Martha L. Crump, undertook an analysis of the ecology and reproductive modes in a tropical anuran community with the assistance of John E. Simmons (the renowned collection manager at KU). Bill commented on his student Marty *"What a significant addition (to the field team) that turned out to be!"* Marty is now one the main authorities on amphibian awareness and conservation, having written books such as *In Search of the Golden Toad* (2000) and *Extinction in Our Times: Global Amphibian Declines* (Collins and Crump 2009).

Numerous papers were written by Bill, John D. Lynch, and others, describing new species from this region, but the completion was reached with the publication, in 1978, of his opus entitled *The Biology of an Equatorial Herpetofauna in Amazonian Ecuador*. In this study, he revealed a record of the greatest diversity of herps for a single site in the world and provided novel information on the ecology and natural history of numerous species. He also challenged what was the rule (mostly from the avian works by Robert MacArthur) at the time in community ecology. Duellman emphasized: *"Herpetological communities in aseasonal tropical forests are not structured in the same way as bird communities. The models generated from bird communities do not generally apply to herpetological communities."* This landmark monograph was well received and soon began to be an obligatory lecture for anyone interested in herps, natural history, and tropical communities. This monograph and his impressive book *Biology of Amphibians* (Duellman and Trueb 1986) inspired several Ecuadorian herpetologists, among whom was Coloma, who later undertook graduate studies in Systematics and Ecology at KU, with Bill as his advisor.

Bill carried out a total of 11 fieldwork trips to Ecuador (1966, 1967, 1968, 1969, 1970, 1971, 1972, 1974, 1975, 1984). They varied in length from a short one in 30–31 January 1971 to the longest one from 6 March–18 May 1975. This field work provided Bill with the opportunity to travel throughout much of Ecuador, including the lowlands of the Pacific coast, the cloud forest of the Andes (western and eastern slopes), the highlands, and the Amazonian lowlands, and collect 6981 specimens of amphibians and reptiles. Needless to say, he collected for the first-time hundreds of species new to science. For example, in just 3 days on 20, 21, and 23 October 1971, after walking at the margins of the Azuela River in Napo Province, in the cloud forest of the Amazonian slopes of the Andes, Bill (with Simmons, Collins, and MacBryde) found 12 new species of frogs (4 centrolenids, 1 bufonid, 2 dendrobatids, 5 *Pristimantis*).

During his field work, Bill was accompanied mostly by his graduate students and some colleagues: Henry S. Fitch, William G. Saul, Linda Trueb, Martha L. Crump, Stephen Edwards, James W. Waddik, Werner C. A. Bokermann, Ildefonso Muñoz B., Thomas H. Fritts, Charles F. Walker, Sandy Echternacht, Bruce MacBryde, Joseph T. Collins, John E. Simmons, Dana T. Duellman (daughter), Alan Savitzky, Patricia A. Burrowes, and David M. Hillis. As part of his and KU's focus on Ecuador, Bill mentored additional KU students who participated in his fieldwork in Ecuador until 1990. Among them were John D. Lynch, David C. Cannatella, Richard Montanucci, John J. Wiens, and David A. Kizirian, who did collecting trips by themselves.

The KU graduate students mentioned above currently are widely recognized in the herpetological world and the contributions of most of them to the knowledge of Ecuadorian herps have been immense. Their studies were summarized by Bill (Duellman 2015), and herein we briefly highlight the taxonomic contributions of Lynch, Edwards, Cannatella, and Hillis. Lynch's field work in Ecuador added 8410 specimens to the KU collection and described or co-described the amazing number of 116 new amphibian species from Ecuador. Bill and Lynch's combined efforts resulted in seven titles, including three of the most important and classic studies, one on glassfrogs (Centrolenidae) (Lynch and Duellman 1973) and two on cutín frogs *Eleutherodactylus* (most of them currently under *Pristimantis*) (Lynch and Duellman 1980, Lynch and Duellman 1997), in which they jointly described numerous new species to science. Bill also supervised Cannatella's Master's thesis on the systematics of the *Phyllomedusa* (currently *Agalychnis*) *buckleyi* group work in Ecuador. Cannatella has published descriptions of 13 species of Ecuadorian frogs, and has continued a strong research and academic cooperation program on dendrobatids and *Engystomops* with Ecuadorian partners during the 2010s, extending Bill´s legacy to his contemporary graduate students to this day. Another one of Bill´s students who did fieldwork in Ecuador was Edwards, who undertook a phenetic taxonomic revision of the Neotropical genus *Colostethus* (currently under *Allobates, Aromobates, Colostethus, Ectopoglossus, Hyloxalus, Epipedobates, Leucostethus, Mannophryne, Paruwrobates, Rheobates, Silverstoneia*), in which he recognized 19 species as new, some of them from Ecuador. He published two papers about Ecuadorian frogs, and most of his dissertation research (Edwards 1974) remained unpublished before Bill, Lynch, Enrique La Marca, Juan A. Rivero, and Coloma began to undertake such difficult tasks. In 1988, Bill suggested that Coloma review the Ecuadorian *Colostethus* for his Master's and enthusiastically supported additional field trips. In the same year Bill described (with Lynch) an Ecuadorian species from Cordillera de Kutukú, in which they expressed their frustration in the etymology paragraph as follows:

"The specific epithet is Latin meaning irritating or rasping. We use the name in reference to the exasperation endured for nigh onto a decade and a half by students of neotropical frogs awaiting the publication of a revision of Colostethus *by Stephen R. Edwards."* (Duellman and Lynch 1988).

The completion of Bill´s travels to Ecuador and the beginnings of a new stage in Peru was marked by his 3-month field work on marsupial frogs in the Ecuadorian Andes in 1984, in which he was accompanied by David Hillis (among others). Hillis spent a memorable time with Bill, collecting and studying frogs in the Ecuadorian Andes. Hillis would remark:

"He lived and breathed herpetology. In my mind, I see him with a headlight on, catching frogs."

Bill and Hillis would publish two seminal systematic papers, one on frogs of the *Hyloscirtus larinopygion* Group (Duellman and Hillis 1990) and other paper describing three new species of marsupial frogs, and resolving taxonomic problems, and their phylogenetic relationships (Duellman and Hillis 1987). When Bill began his journey of discovery of *Gastrotheca* in the Andes in 1967, only two species of biphasic marsupial frogs (*G. riobambae* and *G. lojana*) were known from the Ecuadorian Andes, and four monophasic species (*G. guentheri, G. plumbea, G. testudinea,* and G. *weinlandii*) were known from Ecuador. Currently, 20 species are known and such a task took him about half of a century. After his paper with Hillis, in 2015, he published his major book about the marsupial frogs on which the Ecuadorian species were included (Duellman 2015). He also contributed, along with Ecuadorian researchers, studies on tree frogs (Duellman and Coloma 1993, Ron *et al.* 2018), endangered harlequin frogs (Ron *et al.* 2003, Coloma *et al.* 2007, 2010, Guayasamin *et al.* 2010), and the description of additional

Andean marsupial frogs (Carvajal-Endara *et al.* 2019).

By the end of his *Gastrotheca* and Andean Ecuadorian trip, he gave a somewhat emotional lecture in an event that filled an auditorium in Quito at Pontificia Universidad Católica del Ecuador (PUCE) on April 3, 1984. In his lecture, entitled "Los Batracios Andinos: 20 años de estudios y los prospectos para el futuro," he referred to the unparalleled wealth of frogs of Ecuador. He went further and to complain about the difficulties and bureaucratic frustrations of obtaining collection permits for research—paradoxically, a similar lament still is shared by Ecuadorian scientists. As an epilogue of his talk, he said with remarked emphasis, the following:

"Interesting and necessary research could be done here in the parks of Quito. And I have a question. Where are the Ecuadorian, Peruvian, and Bolivian herpetologists? The richest region in the world herpetologically, and there are no herpetologists here." Translated from Spanish (hear the original audio at: http://www.anfibiosecuador.ec/recursos/audio/DuellmanTalk-PUCE_3April1984.wav. Courtesy of Guillermo Paz-y-Miño).

In the Ecuadorian nationalistic mood of that time, Bill´s reclaim was not necessarily well received, especially by the local bureaucracy and some of the biologists. Anyway, that day, he would not know that in the auditorium was the seed of the first Ecuadorian herpetologists: Ana Almendáriz C. and Luis A. Coloma. The former was in charge of the Escuela Politécnica Nacional herp collections since 1983 and the latter has been making collections for Ecuadorian museums since 1982. Bill also could not imagine that 4 years later, Coloma would be his and Linda´s first Ecuadorian graduate student at the University of Kansas. In fact, Coloma arrived in KU in January 1988 and completed his MA in 1991 and PhD in 1997, after conducting systematics studies on *Colostethus* and *Atelopus*, and then he was followed by other Ecuadorians: Santiago R. Ron (1996–1998, MA), Omar Torres-Carvajal (1999–2005, MA and PhD), and Juan M. Guayasamin (2001–2007, MA and PhD).

When Coloma arrived in Lawrence, Kansas, in January 1988 he stayed a few days at Bill and Linda´s house and he was received with welcoming and open arms. He recounts this experience as follows:

"After visiting the amazing herp division facilities and museum and being presented to the herp people therein I went to his house. As darkness fell, after dinner I walked downstairs to his and Linda´s large office. Everywhere I looked I saw hundreds of reprints and books of all sizes, shapes and colors—the big opus of Biology of Amphibians, the two volumes of Hylid frogs of Middle America, the huge volume of the Amphibian Species of the World (promoted by him and edited by his student Darrel R. Frost). There were also large original paintings and illustrations hanging on the wall such as the colorful plates of the frogs and reptiles from Santa Cecilia and the skull drawings of casque-headed frogs (done by Linda Trueb). And then, there were brand new computers, and all ordered in perfection. Had I died and gone to heaven? No, I was at Bill´s and Linda´s empire of knowledge."

Two and a half decades after his last visit to Ecuador, he had these generous words when talking about Ecuadorians.

"The people of Ecuador are fortunate to have such talented scientists who can convey their knowledge so concisely. The people of Ecuador are also fortunate to live in a land of such great frog diversity, but they also are obligated to maintain that diversity for future generations of both frogs and humans." (Duellman 2009).

In 1997, Bill's planned completion of work with Ecuadorian frogs was clearly stated in the influential monograph about the *Eleutherodactylus* (now most are in the genus *Pristimantis*) in western Ecuador:

"Little did we image [sic] three decades ago that the 20th Century would be waning before our endeavors on the Eleutherodactylus *in western Ecuador would come to fruition. In the intervening years we have learned much about these frogs and have become increasingly aware that there is so much yet to be known. We leave this challenge to our successors, to whom we bid: !Que les vaya bien!"* (Lynch and Duellman 1997).

Bill retired in 1997 to become, most likely, the most prolific Curator Emeritus in the field of

Herpetology. Some of his most important publications—a revised edition of *Hylid Frogs of Middle America* (2001), *Cusco Amazónico: the Lives of Amphibians and Reptiles in an Amazonian Rainforest* (2005), *Terrestrial Breeding Frogs (Strabomantidae) in Peru* (2009), *Marsupial Frogs: Gastrotheca & Allied Genera* (2015), *Herpetology at Kansas, A Centennial History* (2015), and the yet unfinished *Encyclopedia of Ecuadorian Amphibians* (Coloma and Duellman, in prep.)—were part of his "retirement" hobbies.

Bill's influence on Ecuadorian herpetologists also extends to Omar Torres-Carvajal and Santiago R. Ron, both currently working at PUCE on reptiles and amphibians, respectively. Torres-Carvajal is the leading researcher on Ecuadorian Squamata, having made numerous contributions that follow the KU tradition (e.g., Torres-Carvajal 2000, 2003). Ron has also played a role in amphibian studies, with a focus on systematics of frogs, especially of the genus *Engystomops* (e.g., Ron *et al.* 2006) and *Osteocephalus* (e.g., Ron and Pramuk 1999).

When Guayasamin started his graduate studies at KU (2001), under the mentorship of Linda Trueb, Bill always was in his office next to the entrance of the Herpetology Division. His door always open, his mind always working. Every printed publication was perfectly organized, as were his field notes, slides, and recordings. Although the idea of "integrative taxonomy" may have a catchy new air, it was clear that for Bill that was just day-to-day taxonomy. The collections that Bill and his students obtained in the 1970s were so complete that they even included tissues for allozyme studies. These very tissues were used 40 years later to generate the first molecular phylogeny of Ecuadorian harlequin frogs, co-authored by Bill (Guayasamin et al. 2010). Also, Bill's work on direct-developing frogs (Lynch and Duellman 1997) and glassfrogs (Lynch and Duellman 1973) inspired Guayasamin to pursue these taxa for his MA and PhD theses, transitioning from the classic Truebean osteology (Guayasamin 2004, Guayasamin and Trueb 2007) to the novelty of molecular systematics in centrolenid frogs (e.g., Guayasamin et al. 2008, 2009). Many productive Ecuadorian herpetologists have been inspired and enchanted by Bill's work, as well. For example, Ana Almendáriz C., Alejandro Arteaga-Navarro, Sofía Carvajal-Endara, Diego Cisneros-Heredia, Mauricio Ortega-Andrade, Mónica Páez-Vacas, Carolina Reyes-Puig, Juan Carlos Santos, Verónica Urgiles, and Mario Yánez-Muñoz all visited him at KU or interchanged correspondence for many years.

It is difficult to measure the impact of Bill in Herpetology, but we can certainly say that the status of Ecuador as one of the most diverse countries on Earth in terms of amphibian species, is Bill's legacy. We can also say that we, the authors of this note, had in Bill and Linda true mentors, friends, and colleagues. The University of Kansas Natural History Museum was a second home where we listened to endless frog stories, worked in one of the largest collections of Neotropical amphibians, and learned how to study these beautiful animals in the heaven of amphibian academy. Everything in this very special, blue (democrat) town, called Lawrence, surrounded by prairies, and on the shoulders of the herpetology giants.

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(**A**) From left to right: Linda Trueb, Charles F. Walker, Ildefonso Muñoz B. William E. Duellman, and Thomas H. Fritts at Santa Cecilia, Provincia Sucumbíos, Ecuador, April 1969. (**B**) Bill recording a treefrog near Tandayapa, Provincia Pichincha, Ecuador. April 1975. (**C**): Bill at the Second Latin American Congress of Herpetology in Mérida, Venezuela in 1990 (photographer unknown). (**D**): Bill with three of his Ecuadorian students in Lawrence, Kansas, in September 2005. From Left to right: Omar Torres Carvajal, Luis A. Coloma, Juan M. Guayasamin. Photos by Blanca Muñoz (A), Linda Trueb. (B, D).