

## MEMORIAL RESOLUTION

### Rudolf Raff

(1941-2019)

Rudolf (Rudy) Raff, recognized internationally for his groundbreaking work on the evolution of organismal development and as one of the founders of evolutionary developmental biology (*evo devo*), retired from the Department of Biology on January 31, 2018, the same department where he began his long and accomplished career as an assistant professor in 1971. Rudy was born in 1941 in Canada in the Quebec City of Shawinigan to his mother, the daughter of a local physician, and his father, a polymer chemist with a Ph.D. from the University of Vienna, who emigrated from Austria in 1938, escaping the worsening political climate of central Europe. Rudy Raff died on January 5, 2019.

Rudy's family moved to Pittsburgh in 1949. Not knowing exactly how close to the equator he was headed, Rudy remembers watching through the train window, searching for waving palms and coiled rattlesnakes, only to be disappointed. That disappointment was quickly remedied, however, by his discovery of the Carnegie Museum and its collections, especially dinosaurs, and the growing realization that life on earth had gone through many changes, leaving traces of past worlds, recognizable to those who cared to look closely.

Rudy left Pittsburgh in 1959 to attend Penn State University, enrolling in the Navy Reserve Officer Training Corps. During this time, Rudy's fascination with all things biological blossomed—searching and collecting, rearing and observing everything that slithered, jumped, or swam. Dragonflies, in particular, became an object of affection. Upon graduating from college, Rudy started graduate school at Duke University, a move that was to bring about foundational changes in his life. Chief among these changes was meeting his wife, co-adventurer, and closest colleague Beth Raff, herself a professor emerita of biology at IU Bloomington. He also completed his Ph.D. in biochemistry on bacterial surface proteins; in the process, finding himself drifting closer towards questions focusing on evolutionary origins and transitions. Completing his Ph.D. in 1967 as a U.S. Navy officer carried with it the significant likelihood of service in Vietnam; instead, Rudy was assigned to the National Naval Medical Center in Bethesda, MD with surprising freedom to carry out any research so long as it involved exposing biological materials to radiation. It wasn't until 1978 that Rudy learned that his position, and the entire institute, served as an elaborate cover-up to mask the cold war-era neutron bomb development program. Rudy transitioned to a second postdoctoral position in 1969 at the Massachusetts Institute of Technology under Paul Gross, beginning his first deep journey into the nature of developmental biology, the role of maternally derived messenger RNA in guiding early development of embryos. It also marked Rudy's first use of sea urchins as a study organism, a relationship that continued through his career.

Rudy joined Indiana University in 1971, finding himself drawn increasingly to questions relating to how organisms develop during their lifetimes and how they evolve over eons. Rudy was among the first to realize and articulate that because the way organisms look and function emerges through development, evolutionary changes in looks and functions must require modifications to the developmental processes that allow organismal complexity to come into being. At the same time, how organisms develop should in turn bias in some ways—but perhaps also facilitate in others—how they diversify over evolutionary time scales. By then, however, developmental and evolutionary biologists had diverged in their research approaches to such a degree that neither thought much could be learned from the other. Rudy became a leading force

in reintegrating both fields, founding a new discipline in the process, and inspiring a new generation of scientists along the way.

Many holy cows ended up slaughtered due to Rudy's work. For example, the revered evolutionary biologist Ernst Mayr argued that it would be useless to search for genetic similarities between distantly related animals. Rudy confronted this highly influential intuition with data from the then novel DNA sequencing, unearthing remarkable conservation that exists on the level of genes and developmental pathways across vast evolutionary distances. Rudy's work allowed organisms as distant as sea urchins, flies and mice to be considered like Lego creations—reassemblies of the same conserved building blocks. He thereby allowed a newly forming discipline—*evo devo*—to begin to resolve a fundamental question neither parent discipline could do so on its own: how novel traits and organismal groups emerge from within the confines of ancestral variation. Similarly, Rudy's work overturned longstanding opinion that evolutionary change should be restricted to the adult stage (embryos turned out to evolve just as readily) or that developmental evolution relies primarily on changes in the timing of developmental events. Rudy published three highly influential books in the process (the first with his IU colleague and friend Thom Kaufman) and founded the flagship journal *Evolution & Development*, of which he was longtime editor-in-chief. Through these efforts, Rudy established the intellectual foundation which enabled a discipline to be built by a generation of graduate students, postdocs, and faculty, many of whom are his direct academic offspring, all of them inspired by his pioneering work. *Evo devo* is now, thanks to Rudy's work, among the most vibrant biological disciplines, complete with conferences, societies, and dedicated funding panels.

Rudy received numerous awards and honors, including the inaugural pioneer award of the Pan American Society of Evolutionary Developmental Biology, a Guggenheim fellowship, and election to the American Association for the Advancement of Science and the American Academy of Arts and Sciences. He was named the James H. Rudy Professor of Biology in 2000 and was promoted to Distinguished Professor in 2002. Rudy's interests expanded yet again later in his career, to include the microbiological processes that underlie fossilization, but also the role that science plays in society and the increasing threats science faces. His busy research work slowed down, however, only when he was out in nature, whether it be as far away as Australia where he traveled nearly every year, or nearby at his beloved Griffy Lake Nature Preserve. He seemed to follow Yogi Berra who famously said that one can see a lot by just looking. For example, at dragonflies. And especially when the adult form emerges from the last nymphal stage.

Rudy was a wonderful colleague, friend, and mentor to many of us at IU, and he was vital to the growth and success of the department over the last half-century.

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