

Rudolf A. Raff (1941–2019)

Pioneer of evolutionary developmental biology and supportive mentor.

Rudolf Raff was a creative experimental biologist, passionate naturalist and author of books that laid the intellectual foundations for modern evolutionary developmental biology ('evo-devo'). With Indiana University colleague Thomas Kaufman, he published *Embryos, Genes, and Evolution* in 1983, anticipating the rise of evo-devo by a decade. Its central theses of labile early development and the importance of key 'switch genes' were later supported by experimental work in various organisms. Rudy's own laboratory pioneered the comparison of closely related species at a time when evo-devo was largely focused on ancient changes in animal body plans. Together with his students and wife (and frequent collaborator) Beth, Rudy visited Sydney, Australia, for 29 consecutive years. There, he used the sea urchin genus *Heliocidaris* as a model of rapid divergence of early development. Rudy's 1996 book *The Shape of Life* stressed the concept of modularity. By this time, evo-devo had become one of the most exciting topics in evolutionary biology and was attracting bright minds from fields as diverse as palaeontology and genetics.

Although best known as an intellectual leader of evolutionary developmental biology, Rudy's research spanned a remarkable range of subjects. While a post doc, Rudy demonstrated for the first time that maternal messenger RNAs (mRNAs) encoding tubulin are deposited into eggs, and remain untranslated until after fertilization (R. A. Raff et al. *Nature* **235**, 211–214; 1972). This provided key support for the masked messenger hypothesis, which was further confirmed by experiments in his new lab at Indiana. Another important contribution of his was the first large-scale molecular phylogeny of the animal kingdom (K. G. Field et al. *Science* **239**, 748–753; 1988). Along with subsequent studies, this work reconfigured our understanding of bilaterian phylogeny: traditional Protostomia was replaced by the now-familiar Lophotrochozoa and Ecdysozoa. A final example of the astonishing breadth of Rudy's intellect came towards the end of his career. The discovery of what appeared to be fossilized metazoan embryos from the late Precambrian of China begged the question of how such delicate objects could be preserved. With typical fearless curiosity, Rudy spent his last years exploring embryo



taphonomy experimentally, studying what happens to real embryos under reconstructed postmortem conditions (E. C. Raff et al. *Proc. Natl Acad. Sci. USA* **103**, 5846–5851; 2006).

Rudy was born in Québec in 1941, the son of a local doctor's daughter and an Austrian scientist who had just fled the impending Holocaust. His family moved to Pittsburgh in 1949. The young Rudy spent much of his time exploring the nature that surrounded him. As a high school student, he volunteered at the Carnegie Museum of Natural History, which deepened both his understanding of the history of life and his love of fossils. Indeed, when invited to speak at other institutions, Rudy often asked his hosts to arrange a field trip to a noteworthy local fossil site.

Rudy graduated from Penn State University and its Navy Reserve Officers' Training Corps (ROTC) program in 1963. With the Vietnam War intensifying, he deferred active duty to pursue a PhD on bacterial biochemistry at Duke University, which he completed in 1967. He spent his brief career as a Naval officer at the National Naval Medical Center in Maryland, researching the biological effects of radiation. Though deemed important by his superiors, this was not where Rudy's heart lay. After fulfilling his Navy obligation, he joined the lab of Paul Gross at the Massachusetts Institute of

Technology, where he turned his attention to what would become his life's work: the molecular workings of echinoderm embryos. By 1971 he was an assistant professor at Indiana, where he stayed for the remainder of his life.

Though an early leader in probing the molecular mechanisms of development, Rudy's commitment to field work was surprisingly constant. The annual trips to Sydney included snorkelling in Botany Bay to collect sea urchins and excursions to the Blue Mountains to gather onychophorans (velvet worms) for phylogenetic analysis, with fossil hunting worked in whenever possible. A more urban sort of fieldwork was visiting bookstores to augment his world-class collection of travelogues by naturalists (both famous and not-so-famous). It would be a mistake, however, to see Rudy's interest in fossils and old books as a hobby. These habits reflected his ravenous curiosity about the natural world, which formed the basis for his remarkable intellectual creativity. He had a rare talent for recognizing deep connections between seemingly unrelated topics. In an era when science was becoming increasingly specialized, he cheerfully swam the other way, basing his scientific success on his ability to synthesize ideas and methods from disparate fields.

In hindsight, it is easy to understand how Rudy came to be an early leader of the evo-devo revival. Studying the molecular details of development, his simultaneous immersion in fossil forms and classic comparative embryology treatises begged for a synthesis of these truths. In the 1980s, evolutionary biology was largely unconcerned with the roles of specific genes and gene networks in shaping the evolution of morphology. While the strong hierarchies and modularity that mark development were emerging, the long-standing mysteries of comparative embryology remained unsolved—something new was clearly needed. Rudy argued that real progress required the comparative study of species at the molecular level, performed in the context of a robust phylogeny. Today we take this for granted, but few did as much to articulate this strategy.

Beyond Rudy's personal scholarship, he contributed greatly to the development of evo-devo as a field. A 1994 conference that he organized at Indiana University is widely regarded as a watershed gathering. In 1999, feeling that developmental biology journals

were excluding important interdisciplinary work and studies of non-model organisms, he launched the journal *Evolution & Development*, for which he served as the founding editor. His last book, *Once We All Had Gills: Growing Up Evolutionist in an Evolving World* (2012), is a memoir that also demystifies evolution for the non-specialist reader. His efforts to increase public understanding of the centrality and wonder of evolution constitute another of his important legacies.

Though Rudy will be remembered by most for his championing of evo-devo, what stands out for us, his trainees, was his unfailingly supportive mentorship. He gave his students and post-docs a remarkable

degree of freedom and agency in their research projects, yet somehow kept the lab funded. He was an unflagging cheerleader eager to follow the latest development of each project, and his door was always open for conversations both on- and rather off-topic. When these discussions occurred over lunch in the lab, one couldn't help notice that for nourishment, Rudy favoured a pound of very dark chocolate (never, ever milk chocolate), washed down with a non-alcoholic beer. Though we strove to emulate him in many ways, this was a habit that remained uniquely his. □

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