

Dan Salah Tawfik (1955–2021)

Pioneer of molecular evolution.

We are deeply saddened by the premature and unexpected passing of our dear friend and mentor Dan Salah Tawfik (דן סלח תופיק) in a climbing accident on 4 May 2021. Danny was born in Jerusalem in 1955 to an Iraqi-Jewish family, and he cherished both sides of his heritage: he was a Jew and an Arab. Throughout his life, Danny took great pleasure in subverting any simple classification: he was a scientist, a former construction worker, and a retired major in the Israel Defence Forces.

Danny's contributions to science were immense, and his insights into enzyme catalysis have shaped an array of fields, including marine biology, metabolic engineering, astrobiology and the origin of life. He is, perhaps, best known for developing *in vitro* compartmentalization — which links genotype to phenotype in artificial cells — and revealing the critical role of promiscuity in enzyme evolution. For these technical and theoretical advancements, Danny was awarded the prestigious EMET Prize for Biological Science by the Israeli government in 2020.

The major through-line of Danny's work, enzyme evolution, requires an understanding of forces that operate across vastly different scales of length and time: from the effect of a mutation on protein function (for example, binding and catalysis) to the overall fitness of an organism or a population in the environment. Although Danny was trained as a chemist, he was never constrained by divisions between disciplines. Instead, he deftly navigated his research across and between the different levels of life's organization, from small molecules and proteins to cells and microbial communities. Restless by nature, Danny was never content to stay put; he was always transforming himself and his lab. In recent years, Danny focused his efforts on understanding early protein evolution, ever eager to uncover biological secrets that are billions of years old. His work helped explain how complex protein structure and function could have emerged from 'so simple a beginning' by demonstrating the surprising functional repertoire of short, oligomerizing peptides.

Danny's success as a scientist can be understood, in part, through his love of rock climbing: namely, his embrace of risk and his persistent desire to challenge himself



Danny climbing the cliffs at Ein Farah in 2020. Credit: David Salem, Zoog Productions

both physically and mentally. Although the inherent danger of rock climbing can be mitigated with training and practice, it can never be abolished. It was with this attitude that Danny pursued his curiosity and conceived of scientific projects. First, with extensive reading and discussions with peers; then, by setting ambitious goals where risk — in this case, of project failure — was an intentional part of the design. Danny understood that to push the boundaries of human knowledge, as with climbing, you must continually challenge yourself to overcome your limitations. The elevated perspective at the summit — be it views of the desert or a deepened understanding of biological phenomena — was the reward. By embracing risk, Danny was able to consistently ask provocative questions and do important, relevant research, spanning some 30 years and 160 original research articles.

Danny's legacy also lives on through his unique style of mentorship. In the lab, Danny embraced disagreements and discussions. He suppressed and minimized social or professional hierarchies, instead encouraging everyone to engage in science together as equals. Despite significant responsibility, Danny foremost enjoyed

analysing and discussing data and ideas with students in his lab. Irrespective of your lab seniority, Danny had time to meet with you. When results were bad, he brought optimism; when results were good, he brought a critical eye. Indeed, Danny's optimism was a powerful motivator, especially when the path forward was not clear. He understood the value of rest, of long lunches and of play.

During his years as a principal investigator at the Medical Research Council Centre for Protein Engineering, Cambridge, UK, and the Weizmann Institute of Science, Israel, Danny mentored over 50 aspiring scientists — many of whom have gone on to establish independent research groups. Just as he valued diversity in his research topics, so did he value human diversity, both scientifically and culturally. Danny championed the inclusion of women and under-represented minorities in science. On weekends, he would lecture at underserved schools throughout Israel, hoping to inspire disadvantaged students.

Dan Tawfik was not just a scientific visionary; he was generous and humane. A confident, unpretentious man with a strong passion for science and mentorship. A man who openly embraced risk and playfulness,

and ultimately transformed the field of enzymology. He is dearly missed.

Liam M. Longo ^{1,2} ,
Dragana Despotović ³  and
Lianet Noda-García ⁴ 

¹Earth-Life Science Institute, Tokyo Institute of Technology, Tokyo, Japan. ²Blue Marble Space Institute of Science, Seattle, WA, USA.

□ ³Department of Biomolecular Sciences,
Weizmann Institute of Science, Rehovot, Israel.

⁴Institute of Environmental Sciences, Robert H. Smith Faculty of Agriculture, Food and Environment, Hebrew University of Jerusalem, Rehovot, Israel.

e-mail: llongo@elsi.jp;
dragana.despotovic@weizmann.ac.il;
lianet.noda@mail.huji.ac.il

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Additional information

L.M.L. was a postdoctoral fellow in the Tawfik Lab from 2015–2020. D.D. was a postdoctoral fellow in the Tawfik Lab from 2012–2017 and a senior research associate in the Tawfik Lab from 2018–2021. L.N.-G. was a postdoctoral fellow in the Tawfik Lab from 2013–2018.