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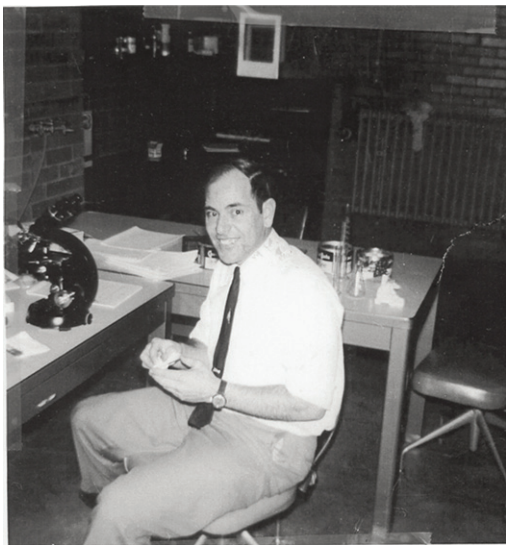
# OBITUARY



## Uzi Nur
## (12.6.1928-20.6.2007)

The early and mid 20th Century was a golden age of comparative cytogenetics. All manner of bizarre chromosome behaviours were discovered during that period, but they were poorly understood. It wasn't until the late 20th Century that evolutionary theory developed the key conceptual tools that would allow us to understand how the crazy diversity of chromosome systems could have evolved. These two eras were separated by a gap. Around 1953, when Watson and Crick proposed a structure for DNA, the prestige of comparative cytogenetics began to decline, giving way to newer fields like molecular biology. But it wasn't until the 1960's that the needed theoretical insights - especially the concepts of selfish genes and intragenomic conflict - were developed, and years later until they became widely understood. In the late 20th Century there were very few individuals who were able to bridge this gap, and none who did so more effectively than Uzi Nur. Uzi had a broad and deep understanding of the enormous body of factual information that was classical cytogenetics, and yet he also understood the most innovative facets of evolutionary theory, and had a better understanding than any of his contemporaries of how classical cytogenetics and modern evolutionary theory fit together.

Uzi Nur was born on Kibbutz Ein Harod in 1928 in what was then Palestine. His parents, Simcha and Tzipora, had emigrated from Poland and were some of the original founders of the settlement. Life on the kibbutz was very difficult in the years before the establishment of the State of Israel, due to malaria and other challenges; Uzi contracted both malaria and typhus. Growing up with his two younger brothers, Ido and Zvi, Uzi was in love with natural history. As a teenager he tried to reach an eyrie of an eagle, climbing on nearby Mount Gilboa, and fell, sustaining serious injury to his leg and head. Luckily, he fully recovered. After graduating from high school, he was involved in the many facets of agriculture on the kibbutz, including operating a combine to harvest wheat and barley.

In 1948, the State of Israel was declared and Uzi joined the Israeli Defense Forces in the War of Independence, serving in the Negev. According to legend, he once snuck into Jordan - risking death - to view the ancient stone city of Petra.

In 1950, he came to the United States to serve as an instructor and leader for the Youth Zionist Organization at a settlement in Canada that prepared Americans and Canadians who desired to immigrate to the kibbutzim of Israel. It was there, in Smithville, Ontario, that he met Irene Glick. They were married in 1952, and the couple moved to Ein Harod several months later. In 1953, their elder son, Nadav, was born; five years later their younger was born, William. Uzi

was sent by the kibbutz to Hebrew University in Jerusalem to learn agriculture, but he soon decided to switch to Botany. He studied gene flow between diploid and tetraploid grass species with Danny Zohary and this work resulted in his first publication. During this period he learned many of the cytological techniques that he would continue to use throughout his career. In December 1959, Uzi left Israel for the United States and the family moved to Berkeley where he studied cytogenetics with Spencer Brown, obtaining his Ph.D. in June 1962. During this time he studied the cytology of both grasshoppers and scale insects.

***Selfish B chromosomes***

One of Uzi's most important contributions to the field was his work on B chromosomes. These supernumerary chromosomes are not essential for an individual's survival and often are only present in certain individuals. Their presence in many taxa had been previously described. However, their existence remained a puzzle and it was often assumed that they must be somehow beneficial for their carrier. Uzi was strongly influenced by an early suggestion that B chromosomes might exist because of their selfishness. From his work on B chromosomes in pseudococcids, he learned that they can spread even when they reduce the fitness of their carrier, because the chromosome encodes a "trick" with which it increases it own transmission. He described how in pseudococcids, B chromosomes take advantage of paternal genome elimination and hitch a ride on those chromosomes that remain active whether offspring become male or female. He also described the behaviour of B chromosomes in a grasshopper species and showed that, although their B chromosomes use a different trick than those found in pseudococcids, they also manage to spread by enhancing their own transmission. However, the discovery that received most attention is his work on a B chromosome found in the parasitoid wasp *Nasonia vitripennis*. Uzi's colleague Jack Werren had discovered that some males only produced male offspring and that they transmitted this phenotype to their sons. However the factor causing this unusual phenoltype was not known. Uzi discovered that it was caused by a B chromosome that enhances its transmission by turning diploid daughters into haploid males by eliminating all the paternal chromosomes except itself. Uzi described this chromosome as the most selfish genetic element yet discovered.

***Intracellular bacteria associated with parthenogenesis***

The presence of micro-organisms living within the cells of their host has been described for many scale insects. However Uzi was the first to describe the presence of bacteria living within the host cells of some individuals of the coccid *Parthenolecanium cerasifex* and he noted that the presence of these bacteria was associated with parthenogenesis. Now, nearly 40 years later, most biologist are familiar with the fact that bacteria such as *Wolbachia* can induce parthenogenesis in their hosts, but back in 1972 the significance of Uzi's observation was not understood.

***Function and suppression of the deactivated paternal genome in male pseudococcids.***

Like most male scale insects, male pseudococcids undergo paternal genome elimination (chromosomes of paternal origin are deactivated and subsequently lost during spermatogenesis). Uzi studied the function, deactivation and loss of the paternal genome in several mealybug species. First of all, he showed that, although the paternal genome is deactivated in most tissues, it is active in a few tissues, most importantly the male

reproductive tract, the very place where the paternal chromosomes are lost from the germline. This finding explained earlier observations that, when the paternal chromosomes of males were damaged by radiation treatment, this did not affect survival but did cause a decline in fertility. He also showed that the paternal chromosomes are actively suppressed by the maternal chromosomes: in cells of embryos where the maternal chromosomes are destroyed, the paternal chromosomes reverted to an active state. Finally, Uzi was the first to show a direct relationship between the deactivation and loss of the paternal chromosomes. In cases where the deactivation of the paternal genome in the germline failed, he showed that the paternal chromosomes are incorporated in the sperm.

***Active polar bodies in pseudococcids***

With few exceptions, an animal is a single clone of cells, which developed from a single zygote. But a remarkable exception occurs in mealybugs, in which polar bodies are inherited from the mother and incorporated into the bacteriocytes. This had been observed cytologically in the 1920's, but Uzi was the first to show that the genes in these polar bodies are expressed. The expression of these genes remains an unsolved evolutionary paradox, as the inclusive-fitness interests of the genes in the polar bodies are at odds with those of the embryo.

***"Uzi knew everything"***

Uzi's published record does not begin to convey the extent of his reputation among his colleagues. It was in conversation, teaching, and correspondence, that he had some of his most profound impacts. When colleagues who knew Uzi speak about him, they often express astonishment at the breadth and depth of his knowledge. "Uzi knew everything" is how several of his colleagues put it. "I was in awe," says Nancy Moran, summarizing her impression of her first conversation with Uzi. "He read all the journals cover to cover," says Howard Ochman. "He knew your field as well as you did, but he also knew fifteen or twenty other fields that well".

Not only did Uzi know the relevant fact, but he knew the number of the table in the decades-old reference where you could find the fact. When it was suggested to John Jaenike that Uzi's colleagues must have turned to him in much the same spirit in which we today turn to Google, Jaenike objected - Uzi was much better than Google, because he could put the facts together for you.

In 2007, the primary endosymbiont of Diaspididae was given the generic name *Uzinura*, in honour of Uzi. Uzi passed away on June 20, 2007, just 8 days short of his 79$^{th}$ birthday.

***"I owe a world to Uzi Nur" A remembrance by Robert L. Trivers***

I owe a world to Uzi Nur. I first met him in 1976 on a visit to Rochester as a guest of Robert Selander, who told me there was one person in the department I had to meet and that was Uzi. Uzi kindly showed me around his lab and introduced me to B chromosomes as well as paternal genome loss. I scarcely knew what he was talking about.

Then, in 1985 I published my book on “Social Evolution” and in a state of wild excitement unwisely sent nearly 200 copies to colleagues. They scarcely responded, with the singular exception of Uzi, who thanked me for the gift with a return gift, Jones and Rees’ (1982) book on “B Chromosomes”. I knew of selfish genetic elements and had incorporated a short discussion in my book but I did not know that there existed such a huge literature on one case. I thought the subject consisted entirely of a set of dis-

jointed examples of various kinds of elements.

The book entered my life like religion. I carried it everywhere, reading it even in the check-out lanes of super-markets. From that grew a lifelong interest in B chromosomes, selfish genetic elements and genetics itself. I owe it all to Uzi Nur.

The authors express their gratitude to Nadav Nur, who provided the biographical overview, photos, and other assistance, and to Robert Trivers, for contributing his remembrance of Uzi. We also thank everyone else who shared with us memories of Uzi and helped us to correct errors in this manuscript, including Jack Werren, John Jaenike, Norman Johnson, Molly Hunter, Howard Ochman, and Nancy Moran.

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