



Fotis C. Kafatos

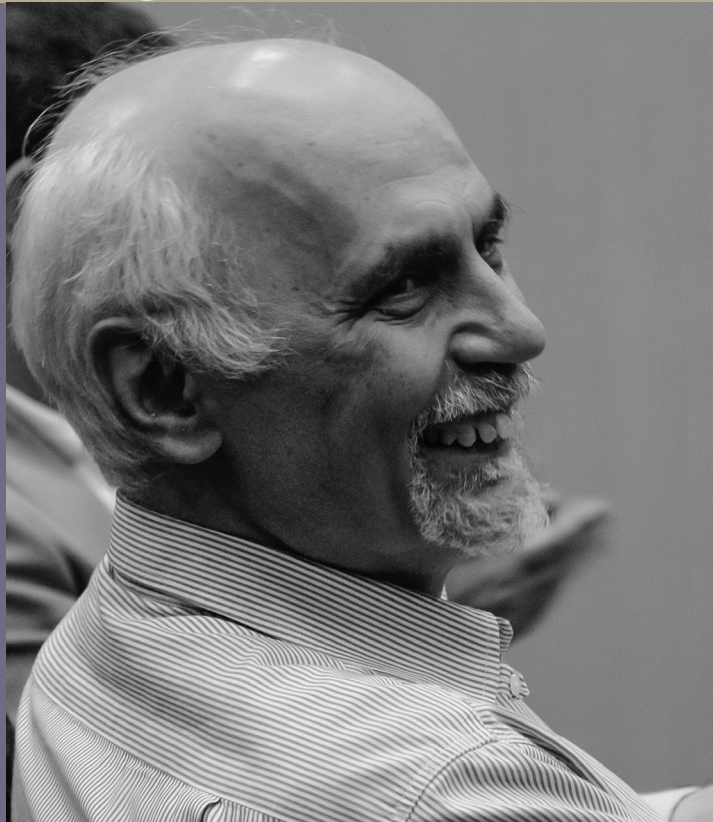
1940–2017

BIOGRAPHICAL

Memoirs

*A Biographical Memoir by
Christos (Kitsos) Loui
and Marian R. Goldsmith*

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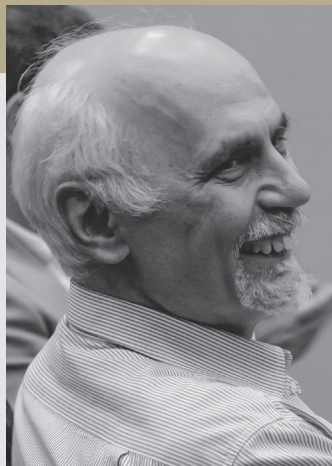
FOTIS C. KAFATOS

April 16, 1940–November 18, 2017

Elected to the NAS, 1982

Beginnings

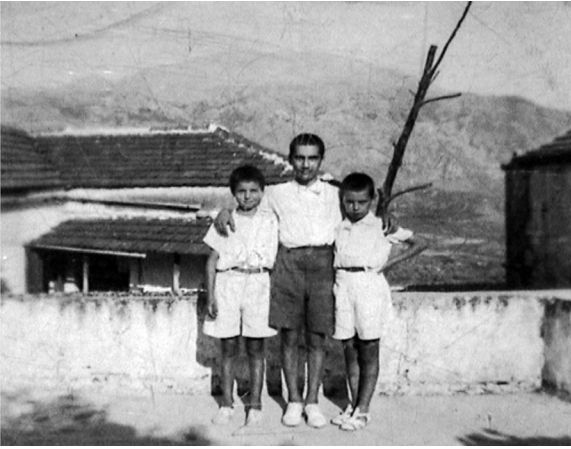
Fotis Kafatos was born in Heraklion, Crete, Greece, on April 16, 1940. His father Constantine had been born to a family of subsistence farmers in the village of Monastiraki, in the beautiful valley of Amari in central Crete. Constantine, or “Costas”, emigrated to the United States at the age of fourteen, and there managed not only to support himself but to earn a BA from Lafayette College and a graduate degree in agronomy from Cornell. At age thirty he returned to Crete, where he met and married an elementary school teacher, Eleni Ksiroudaki. He and she were distant cousins, both being related to the intellectually distinguished Prevelakis family. Costas first led an agricultural school in the Amari district, then accepted a post with the Government Agricultural Service with an office in Heraklion. In 1950 the book *Crete*, detailing the results of a socio-economic survey sponsored by the Rockefeller Foundation, was published; the book’s subtitle was “A case study of an underdeveloped area.” Costas Kafatos provided assistance to the survey and was acknowledged in the book.



A handwritten signature of Fotis Kafatos in black ink, written in a cursive style. The signature is located below the portrait and above the caption.

By Christos (Kitsos) Louis
and Marian R. Goldsmith

Fotis was the second of Costas’ and Eleni’s three sons. Both he and his younger brother Menas, now a Professor and Institute Director at Chapman University, grew up to be scientists; their older brother, Antonis, became an insurance executive in Greece. Fotis had a happy childhood, even though his family lived in modest circumstances and with considerable material hardship, including the acute stresses of life in an occupied country during World War II. He and his brothers were educated at the historic Korais Lyceum in Heraklion, a coeducational private school then rightly regarded as one of the best in Greece. He was an excellent student, encouraged by his teachers, and liked and admired by his fellow students. His most cherished experiences of those years were the family’s visits to his father’s home village of Monastiraki.



Fotis (right), his brother Antonis (centre) and his cousin Antonis at Monastiraki in the '50s.

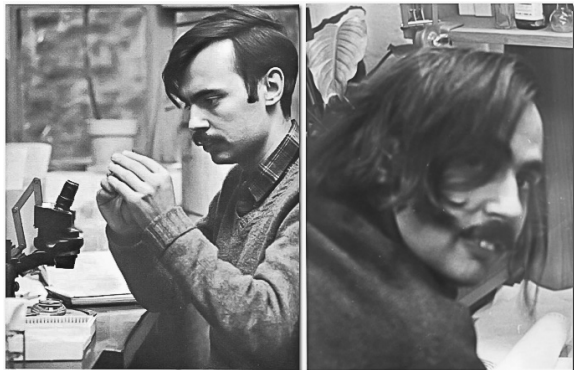
Fotis entered Cornell in 1958. He was supported in part by a Fulbright grant, but the most meaningful support for his studies came in the form of a scholarship endowed and personally curated by the distinguished French philanthropist Anne Schlumberger, whom he came to regard as his “spiritual mother.” A daughter of Conrad Schlumberger, who had founded, together with his brother, the giant firm Schlumberger, she was dedicated to the fostering of the arts and sciences. In addition to her work in France, where she created the Fondation des Treilles, she was active in Greece, where she built a network of children’s libraries in poor neighborhoods and where she sponsored the studies of promising young people

from the provinces. Not only did she support Fotis’ studies, but she continued to counsel him throughout life, the two of them sustaining an intimate friendship based on mutual admiration and trust that lasted until her death in 1993.

At Cornell Fotis majored in Biological Sciences, graduating after only three years, in 1961, at the top of his class. While there he was fortunate to work with the great entomologist Thomas Eisner, who warmly invited the eager freshman to join his very lively research group. Fotis co-authored his first scientific publication with Eisner in 1962 (Eisner and Kafatos 1962). When asked about the title of the paper referring to “an aposematic distasteful insect,” Fotis replied that he tasted the insect himself and still remembered the highly unpalatable experience! On Tom’s advice, Fotis went on to graduate school at Harvard, where his doctoral advisor was another great entomologist, Carroll Williams. In 1962, while working toward his PhD, he met, and in 1967 he married Sarah Niles, his companion of 55 years. Sarah, an accomplished poet, novelist, translator, painter, and musician, quickly learned to share his deep love of Greece. Fotis and Sarah have two beautiful daughters, Helen Beccard (born in 1969) and Zoe Myrto (1972), and four grandchildren.

Harvard

Fotis joined the Harvard Department of Cellular and Developmental Biology as an assistant professor immediately after receiving his PhD in 1965. In 1969, while making use of a sabbatical term to do six months' compulsory service in the Greek army, he was promoted to full professor, at that time, the youngest person to achieve that status in the modern history of the university. From 1978 to 1981, as Chair of the Department of Cellular and Developmental Biology, he was instrumental in elevating the CDB from a departmental subcommittee to a department (see W. Gelbart's statement in the *Harvard Crimson*; Note #1): an early indication of his career-long administrative strengths.



Fotis at Harvard: as a graduate student (left) and Assistant Professor (right).

The Kafatos lab at Harvard was active 24/7, with members' interests ranging from biochemistry and insect science to marine invertebrate biology. Fotis provided strong encouragement and support for people wishing to pursue their own projects, usually but not necessarily in cell biology, development, differentiation, or the newly emerging field of molecular biology/gene regulation, which eventually became the lab's primary focus. Projects on mathematical modeling of developmental phenomena (Kafatos and Reich 1968, MacWilliams et al. 1970, Nardi and Kafatos 1976, Mazur et al. 1982) and bioinformatics (Pustell and Kafatos 1982) reflected Fotis' eclectic, experimental, open-minded approach to doing science.

Carrying on a tradition initiated by Carroll Williams, lab members gathered daily to discuss ongoing research, hash over new ideas, and meet colloquium speakers, guests, and regular visitors to the lab. This, along with weekly soup lunches made in-house, periodic visits to local restaurants, and annual potlucks hosted by Fotis and Sarah, provided opportunities for socializing that generated lab spirit and enriched many future careers. A memorable lab activity was the annual summer rearing of wild silk moths, which involved weekly expeditions to sites in Concord, MA, where larvae were tended, as well as to Carroll's home where oak "perfume" from nearby woods induced lab females to "call" and attract wild males, so as to avoid inbreeding and consequent depression of the

lab's stocks. These practices continued until a hurricane wiped out a summer's crop just before the harvest, persuading Fotis to purchase cocoons from commercial dealers thereafter, much to some people's disappointment.

Fotis was always eager to explore new avenues for research. Projects on wild silk moth chorion (eggshell) synthesis and structure (Paul et al. 1972) were well underway when someone in the lab said that it might be worthwhile to study chorion mutants. This notion involved an emerging approach for uncovering unsuspected developmental mechanisms which, at that time, had been applied almost exclusively to the fruit fly, *Drosophila melanogaster*. Fotis used an NSF grant renewal to send a lab member to Japan in 1972 to learn silkworm genetics. Carroll helped them to contact Yataro Tazima, the foremost Japanese silkworm geneticist, and he agreed to host the postdoc who was to bring *Bombyx* back to Harvard. Thus began a new direction which resulted in many projects, encompassing basic chorion genetics, gene structure, function, and regulation, which could not have been accomplished using wild silkmoths alone. Plus *Bombyx* was much easier to rear and maintain than the wild silk moths had been. As was *Drosophila*, which was brought into the lab later for the sake of its complementary technical advantages, such as much more powerful genetics and its capacity to support transgenesis, an emerging technology which could only be applied in that insect at the time. Fotis' work on fruit fly and silk moth eggshell genes earned him his well-deserved place among leading developmental geneticists (Kafatos et al. 1977).

What was perhaps one of Fotis' most significant contributions to modern biology did not involve insects directly at all. That was the cloning of the rabbit β -globin mRNA, the first ever cloning of a "mammalian gene" (Efstratiadis et al. 1976a). Fotis' involvement in that effort was based on the thought that one should obtain a proof of principle for the technology, so as to then use it to study silkworm and fruit fly chorion genes. The project's success, involving Argiris Efstratiadis, Tom Maniatis, and John Vournakis as key players, made worldwide news.

Athens and Crete

In 1972, while continuing his research and teaching at Harvard, Fotis was invited to assume the position of Professor of Biology at the University of Athens and began to divide his time between the US and Greece. He did so at a difficult time in Greek history, since a military dictatorship had taken power in 1967, dissolving parliament and setting aside many political freedoms. Fotis shocked his colleagues at the oldest, largest, and most conservative Greek university through his young age and also his

appearance: bearded, his hair at shoulder length, and almost never wearing a suit and tie. His preference for close interaction with students was unique in the Greek university environment of the time. He organized parties with Cretan dances, evenings with lots of singing, and excursions with hikes in the countryside. He also, though this was known to few, gave discrete support to the democratic student movement. Although Fotis rapidly became a favorite of the majority of students, there were those whose feelings toward him ranged from reservation to extreme mistrust. He was lucky to find an ally in Professor Costas Sekeris, who had moved to Athens from Germany. Interestingly, his opponents were to be found among both very conservative faculty members and extreme leftist students, who disliked the fact that he had studied and worked in the US, and who imagined that his presence in the university was due to backing by the CIA!

Fotis remained in Athens for about 10 years, and can be credited as the person who introduced modern molecular biology to Greece. He modernized the department structure and curriculum, writing a three-volume textbook in Greek in order to do so, and brought back to life previously dormant research efforts. He also enabled many Greek and Greek-American students, postdoctoral fellows, and more mature researchers to expand their capabilities by doing advanced work in his US lab. Among them were George Rodakis, George Thireos, Christos Delidakis, Kostas Iatrou, Rena Lecanidou, Sonia Tsitilou, Elengo Manousaki, and Mary Konsolaki. To name them all is impossible here. Fotis' felt great gratitude and loyalty to all of them, and to all of his students and collaborators.

After the fall of the Junta in 1974 the Government decided to found a new University in Crete which was to have campuses in two of the three major cities of the island. Fotis, together with Basil Nafpaktitis (a marine biologist at the University of Southern California), were called upon to organize its Department of Biology, becoming its first two Professors. Fotis gladly left his more prestigious position in Athens and moved to Heraklion to devote himself to the new enterprise there. He and Nafpaktitis agreed to make the new department



The campus of the Foundation of Research and Technology-Hellas at Heraklion where the IMBB building is located.

organizationally different, and much more collegial and democratic, than those preexisting in the country. To staff the Department, they urged young, research-oriented Greek scientists from abroad to apply. They also, crucially, obtained a promise from the Greek government to support a cluster of relevant research institutes adjacent to the new university and medical complex.



At the 1986 *Drosophila* meeting. From left: Spyros Artavanis, Fotis, Dave Hogness, Ed Lewis, Alekos Papaderos (Director of the Orthodox Academy of Crete), Bishop of the Kissamos Province Eirinaios, Pam Lewis and Walter Gehring

For some, Fotis' greatest contribution to Greek science was the creation of the Institute of Molecular Biology and Biotechnology (IMBB). With the support of Giannis Lianis, the first Minister of Research and Technology in Greece, and other members of the government, this brainchild of Fotis soon became part of a cluster of five very lively institutes making up the new Research Centre of Crete (whose name was later changed to Foundation of Research and Technology Hellas, with its attractive acronym FORTH). It is an astonishing fact that the island of Crete, a scientific desert until that time, was to develop into the most important technology and research centre of the Eastern Mediterranean

region, being the home not only of FORTH, but also of the expanded university in Heraklion, which is currently the leading research university in Greece, the university's second campus for social science and the humanities in the city of Rethymnon, a Centre for Marine Research, and a technical college, both in Heraklion, a technical University and International Agronomic Institute in the city of Chania, and several smaller research units of the Ministry of Agriculture. Although Fotis was only involved in a few of these, it is a common belief that if it hadn't been for the rocket-style take off of the IMBB, the current remarkable state of development would have never been achieved.

Heidelberg

In 1993 Fotis was chosen by the Council of the European Laboratory for Molecular Biology (EMBL) to succeed Lennart Philipson as its third Director General (DG), and life changed dramatically for him. He moved to Heidelberg, Germany, where the central



Fotis (EMBL's DG), Iain Mattaj (Fotis' successor) and Lennart Philipsson (Fotis' predecessor).

organization of EMBL is located, and resigned his positions at Harvard, at the University of Crete and at the IMBB. To his own research effort, which continued in full, he added the responsibility of running Europe's main research organization in the life sciences, with more than 800 scientific and administrative personnel. His tenure there was a great success. During his twelve years as DG the European Bioinformatics Institute (EBI) opened a new EMBL outpost—a logical development of the pioneering EMBL Data Library—in Hinxton, UK, conveniently at the Sanger Center/

Wellcome Trust Sanger Institute (now Wellcome Genome Campus). Then, in 1999, yet another outpost, focusing on Mouse Biology, was opened in Monterotondo near Rome. Fotis' wish to expand research in developmental genetics (then still an obscure sub-field of biology) at EMBL found increased support after Christiane Nüsslein-Volhard and Eric Wieschaus (along with Ed Lewis) were awarded the 1995 Nobel Prize for Medicine for their pioneering genetic analysis of embryonic development in *Drosophila*. Their research had been carried out at EMBL before Fotis' arrival as DG.

Fotis' move to Heidelberg coincided with a re-focusing of his research on a new model organism, one that had been understudied and that held enormous implications for human health: mosquitoes! From its formation in 1989, he was a member of the John D. and Catherine T. MacArthur Foundation-sponsored Network on the Biology of Disease Vectors (Beaty et al. 2009). Other leading members who remained part of the network for its duration included Barry Beaty, Fort Collins; Lou Miller, NIAID; Jose Ribeiro, Tucson then NIAID; Marcelo Jacobs-Lorena, Case Western Reserve then Johns Hopkins; Tony James, UC Irvine; Frank Collins, CDC Atlanta, then Notre Dame; and Dennis Prager, acting as coordinator on behalf of the MacArthur Foundation. By the time of his arrival at EMBL Fotis had almost completely abandoned research on Lepidoptera and *Drosophila* and switched his research interests to this insect. This brought him back to exploring the molecular-cellular interactions between vectors and the pathogens they transmitted and, inevitably, to unsolved questions regarding the various defense

mechanisms protecting insects from larger and, now importantly, smaller parasites and predators. His many scientific travels would lead him to visit many disease-endemic countries in Africa, Latin America and Asia.

Another major aspect of Fotis' presence at the EMBL was the strengthening of all science related to the field of Genomics. This was a phenomenon common to most research institutions throughout the world, but Fotis' efforts started earlier than most: already in 1987, only months after the initiation of the *C. elegans* physical mapping project, he established the European *Drosophila* Genome Project (EDGP), a collaborative network consisting of the groups of Michael Ashburner (Cambridge, UK), David Glover (London, then Dundee, then Cambridge UK), Kitsos Louis (Heraklion), Juan Modolell (Madrid) and Babis Savakis (Heraklion). Funded by the Commission of the European Union, the EDGP later expanded to include groups in France (Jacques Demaille, Montpellier and Francis Galibert, Rennes) and the UK (David Harris, Sanger Centre) (Benos et al. 2000). Fotis' genomics interests not being restricted to *Drosophila*, he soon put together the *Anopheles* Genome Consortium with funds from the NIH, the WHO/TDR (Note #2) and some European national agencies, and was also involved in several genomic projects in the field of biology of disease vectors.

In 2005 Fotis reached the European mandatory retirement age of 65, and upon leaving EMBL he made the penultimate move of his life, settling in London as a Professor at the Imperial College of Science, Technology, and Medicine.

London - The European Research Council

The lab leadership responsibilities at Imperial were shared with his longtime collaborator George Christophides, while Fotis took on the mission that he came to regard as his "most significant" achievement. While still at EMBL he had begun lobbying for the establishment of the institution which ultimately became the European Research Council. The ERC is an organization, run by scientists and scholars, whose mission is to "to encourage the highest quality research in Europe through competitive funding and to support investigator-driven frontier research across all fields, on the basis of scientific excellence" (ERC/Mission, see Note #3). In 2006 Fotis became chairman of the ERC's governing body, the Scientific Council, and when the ERC began operations a year later, Fotis became its first President, continuing in that role until 2010 when he decided to step down. At that time he was awarded the permanent title of Honorary President of the ERC.

Why was Fotis so proud of his involvement in the ERC? This often-asked question is very easy to answer. Grants awarded by the ERC from its start date till 2017 amount to 17.1 billion €, or about 17% of the funds allocated to research centrally by the European Union! During this period, six grantees won the Nobel Prize and four the Fields Medal, and more than 40,000 papers acknowledged support by the ERC. But perhaps what made Fotis even more proud was that his efforts remedied the lack of a Europe-wide agency that would fund research based on its scientific merit only. Although most countries had such institutions, EU-wide research was funded on the basis of framework programs that often left vast scientific areas outside of funding schemes. Fotis' ideas, loosely modeled on the NSF, centered on the creation of a scheme that would support bottom-up approaches, rather than concentrate on the wishes of politicians and political compromises.

It is a fact that after only a little more than 10 years European scientists have fully accepted the role of this extremely successful agency.

Endings

In 2014, 56 years after leaving Crete for the first time, Fotis returned there for good. He had long said that he wanted to see more of his daughters and their families, to spend more time with friends, to act as an advisor in matters related to science and higher education, and to walk once again in the Cretan mountains that he loved. Unfortunately his enjoyment of these things was to be curtailed as he became ever more affected by Alzheimer's disease. He died of consequences of the disease in November of 2017, and was buried in the churchyard in Heraklion where his parents also lie.

The Kafatos papers

PubMed lists 331 papers authored or coauthored by Fotis, the first of which was published in *Science* in 1963. Actually, Fotis' real first paper, the one on a distasteful beetle published in 1962, is not even listed by PubMed, nor are many others such as those written in Greek. The 1963 publication was followed by one on millipedes, then his first lepidopteran research output (also in *Science*) and then hundreds of papers mostly (more than 85%) dealing with insect biology.

Lepidoptera: Fotis' pre-doctoral and early post-doctoral work was largely devoted to cocoonase, a proteolytic enzyme he had discovered (Kafatos 1965) which is used by silk moths to escape their tightly woven cocoons. In 1971 or so he switched to silkmoth eggshell or chorion proteins, which are produced by the pupal ovaries. This was largely

based on the ovaries' many technical advantages, including their long, well-defined developmental sequence, and the fact that they are much more abundant and productive than the tiny cocoonase-producing glands (Paul et al. 1972). Fotis' studies of silk moth proteins (Regier et al. 1978) and genes (Jones and Kafatos 1980) were among the first to define and reveal properties of complex multigene families, including their clustered chromosomal organization, expression, regulation, evolutionary relatedness and diversification (Kafatos et al. 1987). Transformation of *Drosophila* with moth chorion genes, perhaps an interspecific first, showed that certain short intergenic promoters could act bidirectionally to drive normal tissue- and temporal expression and depended on an intact DNA element common to both species (Mitsialis and Kafatos 1985). Ultrastructural studies of wild silk moth chorion revealed the presence of "Bouligand figures," mathematical constructs providing evidence that chorion proteins are "biological analogue(s)" of cholesteric liquid crystals (Mazur et al. 1982), a property they have in common with insect cuticle proteins. Laser Raman (Hamodrakas et al. 1982) and other physical studies illuminated conformational features underlying these distinctive properties. Although these studies used both wild and domesticated silk moths, the low DNA-polymorphism of the highly inbred *Bombyx* genome made possible the Herculean labor of assembling a 270 kb chromosome "walk" using only short technologically feasible contiguous stretches of sequenced genomic DNA which first revealed that the chorion locus was organized into extended, temporally expressed gene clusters (Eickbush and Kafatos 1982).

Fruit flies: It took about 10 years from the first insect papers until the first publication dealing with *Drosophila* (Petri et al. 1976). This concerned chorion proteins and their biosynthesis. Although most of the early papers deal with the eggshell structure and the genes that encode its components, one can already detect the bona fide "genomic component" even before the term was coined. One early paper deals with the DNA sequence of the moth *Antheraea pernyi* and its comparison to the genome of *Drosophila melanogaster* (Eftratiadis et al. 1976b). We would like to stress the comparative component that emerges throughout Fotis' research, a sign of how interested he always was in evolution. Most of the early fruit fly research was conducted in Cambridge and in Fotis' labs in Athens and Crete. In the '90s, most fruit fly papers reported progress in the genome project that the EDGP was working on, most of them being generated first at Harvard, then at Heidelberg. It is these genomic papers as well as the mosquito genome ones that best exemplify the point about comparative studies (e.g., Bolshakov et al. 2002, Zdobnov et al. 2002).

Mosquitos and parasites: Fotis was not a follower of trends but, rather, a trend setter. This was proven several times in his career, the best examples being, first, the use of modern recombinant DNA techniques to answer questions in bio-disciplines that often looked at molecular techniques with some kind of disdain and, second, the immersion into the sea of genomics even when famous biologists criticized this technology as an expensive pastime that would simply take money away from other, more “important” research. Fotis’ adventure into the world of tropical medicine took place during the last third of his research career, in a medical field that had been long neglected. With his constant optimism, he was certain that even within his lifetime genomics and genetics would provide sustainable solutions to medical entomology and vector-borne diseases. This was not to be the case, although it is true that medical entomology made tremendous progress during the years when Fotis and his friends of the MacArthur Network pursued their research efforts. Scientists came to understand better the interactions between pathogens (parasites, bacteria and viruses) and vectors (Hoffmann et al. 1999, Christophides et al. 2004), one of Fotis’ main research foci (in a long-term collaboration with Jules Hoffmann, Strasbourg), as well as general mosquito genomics (e.g., Holt et al. 2002). As mentioned above, this research included work on insect defense, mainly the mechanisms that protect vectors from being harmed by the pathogens they carry.

Non-insect research and mathematical modeling: It is amazing to think that one of the most important and successful molecular entomologists ever may be remembered by many for his research dealing with rabbits and with the development of new technologies! It was in the early ‘70s that Fotis and his collaborators at Harvard embarked on the then pioneering work of cDNA cloning. This was the first time that a mammalian “gene” had been cloned and it opened avenues for the analysis of gene expression. With that needed technology at hand, Fotis continued to work with his beloved insects. Non-insect-focused publications include more key areas: four papers, co-authored by Jim Pustell (now Ostell) describing a novel DNA computer analysis package (e.g., Pustell and Kafatos 1982) that immediately became very popular in the early ‘80’s, as well as Fotis’ own paper introducing dot blots (Kafatos et al. 1979). These were developed by Fotis himself at the bench (!) during an in-house sabbatical; they provide the conceptual basis for the microarray techniques that were developed decades later. Finally, while at Harvard Fotis and his collaborators also published a few papers on mathematical modelling of developmental phenomena. These included the stability of the cocoonase mRNA (Kafatos and Reich 1968), the study of the spatial organization of cell popula-

tions exemplified by butterfly wing patterns (Nardi and Kafatos 1976), the ultrastructure of chorion already mentioned, and, last but not least, the regeneration of the Hydra basal disk (MacWilliams et al. 1970).

The Crete meetings: It is important to mention the series of scientific meetings held at the Orthodox Academy of Crete in Kolymbari, which bring together research communities dealing with *Drosophila* (since 1978), Lepidoptera (since 1988) and arthropod vectors (since 2004). The format, originally shaped by Fotis and Mike Ashburner for the fruit fly, is that of short talks and informal exchange of ideas and newest results, accompanied by swimming, hikes, dancing, and Cretan food and wine. Clearly the most successful and significant international meetings in their respective fields.

ACKNOWLEDGMENTS

We are indebted to Sarah Kafatou for providing important details and help editing the manuscript. We are also thankful to all who provided photographs to choose from.



Fotis and Sarah at the BioMalPar Award ceremony (European Network "Biology of the Malaria Parasite")

AWARDS AND PRIZES

- 1980 Member of the American Academy of Arts and Sciences
- 1982 Member of the National Academy of Sciences, USA
- 1991 Member of Academia Europaea
- 1995 G. J. Mendel Honorary Gold Medal for Merit in the Biological Sciences, Academy of Sciences of the Czech Republic
- 2000 Honorary Medal for Distinction in Biology, Academy of Athens
- 2000 Honorary Professor, University of Heidelberg, Germany
- 2002 Foreign Member of the French Academy of Sciences
- 2003 Medal “Taxiarchis of The Phoenix,” awarded by the President of the Hellenic Republic, for contributions to Science, Culture and Society
- 2003 Foreign Member of the Royal Society of London
- 2003 Member of Pontifical Academy of Sciences
- 2004 Medal of Honour, City of Heraklion, Crete
- 2004 “Bundesverdienstkreuz 1. Klasse”, awarded by the President of the Federal Republic of Germany
- 2005 Grosse Medaille der Universität Heidelberg
- 2007 Member of European Academy of Sciences and Arts
- 2008 Fondation Louis Jeantet – 25th Anniversary Special Prize
- 2011 BioMalPar/EviMalaR Lifetime Achievement Award

NOTES

1. <https://www.thecrimson.com/article/1993/5/12/kafatos-to-leave-cdb-pprofessor-of/> retrieved, January 16, 2019.
2. TDR: WHO’s Special Programme for Research and Training in Tropical Diseases. (<https://www.who.int/tdr/en/>)
3. <https://erc.europa.eu/about-erc/mission>, retrieved January 16, 2019.

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