

## In memoriam—Crodowaldo Pavan

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Crodowaldo Pavan (Fig. 1) was born in Campinas, in the state of São Paulo, Brazil, on December 1, 1919. In 1941, he obtained his Bachelor's degree in Natural History at the Faculty of Philosophy, Sciences and Letters (FFCL), University of São Paulo (USP). He concluded his Ph.D. in 1944, working in the Department of General Biology of the FFCL under the supervision of Prof. André Dreyfus, director of the FFCL (1943–1947). In 1943, Pavan started collaboration with Theodosius Dobzhansky and a school of Animal Evolutionary Genetics was born in Brazil. In that year, they published two papers, the first on *Drosophila* species reared in the laboratory (Dobzhansky and Pavan 1943a) and a second on chromosomal evolution of *Drosophila* species (Dobzhansky and Pavan 1943b). Other results obtained by Pavan, Dobzhansky and colleagues were published in later years.

In 1951, Pavan collected the lower dipteran *Rhynchosciara angelae* (Diptera: Sciaridae; renamed *Rhynchosciara americana*) in coastal regions of the state of São Paulo. This fly was particularly suitable for cytogenetic studies, given its oversized polytene chromosomes. After identifying local decondensation patterns in polytene chromosomes from different tissues of *Rhynchosciara*, he and Marta MMEE Breuer concluded that all the cells of a multicellular organism have the same “disc patterns” (namely the same gene set). However, there were differences in the degree of condensation of “discs” (polytene bands) in certain chromosome sections from distinct cell types (Pavan and Breuer

1952). Although this paper is considerably simpler than Beermann's (1952) outstanding treatise made with the lower dipteran *Chironomus*, both were in agreement and the view of differential gene expression as the central process in cell differentiation and development has since then been firmly established. Perhaps the most remarkable achievement of Pavan's scientific career would come one year later when, together with Marta Breuer, he observed an increase in the DNA content within certain polytene bands, uncoupled from polyteny, during larval development of *R. angelae* (Fig. 2). According to the authors, “Another point suggested by our data in *Rhynchosciara* is related to the theory of the constancy of the amount of DNA in all cells of a species.... The observations on bulb formation suggest to us that this theory may not hold in all cases. We observed an increase of the DNA content in certain bands (Feulgen reaction), which reaches an amount several times greater than that which the band had before going through the process. This increase of DNA is however not uniform along the length of the chromosome. There are some bands where the increase of DNA is very great while in some other bands there is no evidence of increase or decrease at all. The increases of DNA in the regions which we have studied in detail.... are independent of the process of polytenization”.

The paper containing this observation (Breuer and Pavan 1955) presents the first description of developmentally controlled gene amplification in specific genomic regions undergoing puffing, later called “DNA puffs”. Pavan said on several occasions that, in discussions at scientific meetings, Prof. Beermann as well as other researchers expressed their doubts about that finding. This was not surprising, since the observations challenged the invariability of the amount of genetic material in the cells of an organism, a dogma of that time. Also contributing to the

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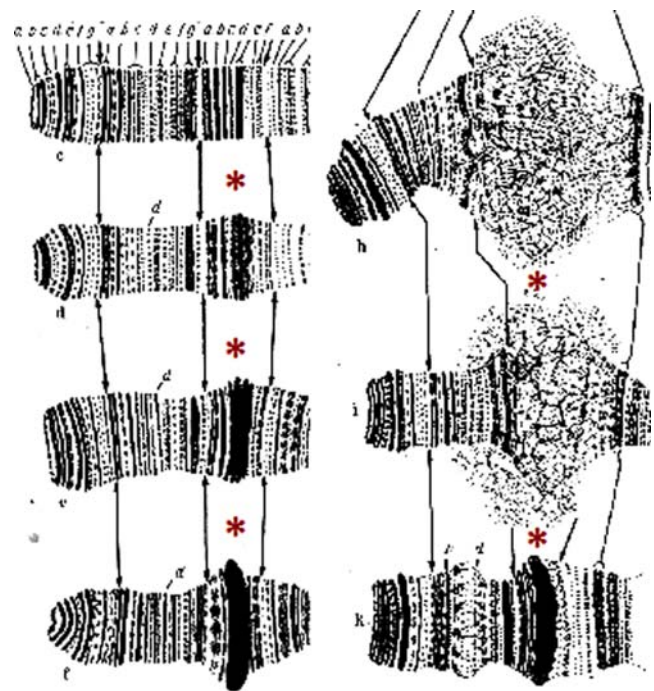


**Fig. 1** Crodowaldo Pavan at the age of 83

doubts about Pavan's findings was the factor that no similar process had ever been seen in salivary gland chromosomes of other dipterans such as *Drosophila* and *Chironomus*. Some years later in collaboration with Adrienne Ficq, autoradiographic data using tritiated thymidine (Ficq and Pavan 1957) confirmed that differential DNA synthesis in specific puffs was indeed occurring, as he had described previously. Many years later, the occurrence of gene amplification was widened when this process was characterised in other cell types subjected to either normal or abnormal growth.

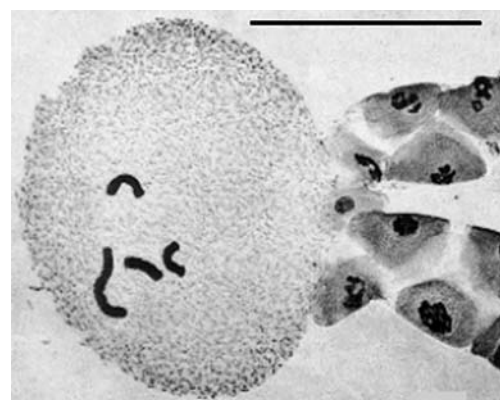
From 1964 to 1965, Prof. Pavan was a researcher at the Biology Division in the Oak Ridge National Laboratory (Oak Ridge, TN, USA), where he led a laboratory dedicated to the study of the effects of radiation and infectious agents on chromosome behaviour and gene activity. Other impressive results documented by Pavan and collaborators were related to infections caused by microsporidia and viruses in *Rhynchosciara* and in other sciarid species. Drastic changes in the morphology of cells and chromosomes were observed, as well as changes in nucleic acid synthesis (Diaz and Pavan 1965; Pavan et al. 1969). Of particular interest was the amazing increase in size of cells and chromosomes during infection (Fig. 3).

Research in the Department of General Biology was initially focused on animal genetics. Prof. Pavan was advised by Harry M Miller Jr. of the importance of human



**Fig. 2** Camera lucida drawings of the distal end of salivary gland chromosome C of *R. angela* throughout different stages of larval development (modified from Breuer and Pavan 1955). The asterisks indicate chromosome section 3 in which “DNA puff” C3 develops. *c–k* Increasing larval age toward *k*. Developmental points *a*, *b* and *g* from the original drawings were omitted

genetics, a discipline that was flourishing in the USA as well as in other countries. Through fellowships from the Rockefeller Foundation, he managed to send Brazilian researchers to reference centres for training with the aim of introducing human genetics in the department. Also importantly, the introduction of molecular biology in Brazil was conducted by Prof. Francisco JS Lara in the early 1960s, still in the Department of Botany of the FFCL-USP. On the basis of the work initiated by Pavan, *Rhynchosciara*



**Fig. 3** Part of the distal region of the salivary gland from early fourth instar larva of *Sciara ocellaris* showing some uninfected cells and one abnormally large cell infected by microsporidia (modified from Pavan et al. 1969). Bar represents 200  $\mu$ m

research with a molecular focus was then carried out by Prof. Lara.

Prof. Pavan was invited to teach in the Department of Zoology of the University of Texas (UTA, Austin) where he stayed from 1968 to 1975. There, together with scientists from the Department of General Biology of the FFCL, he established a laboratory where another species of *Rhynchosciara* was successfully raised. At UTA, he supervised several postgraduate students and a postdoctoral fellow. His time at UTA resulted in publications on the control of DNA amplification and puffing by the insect moulting hormone, ecdysterone (example in Stocker and Pavan 1974). After returning to Brazil, he became Vice-Director of the Biosciences Institute at the University of São Paulo (IB-USP; 1977–1978). He then decided to move to the Department of Biology of the University of Campinas (UNICAMP) where he worked with fruit fly biology applied to the control of agricultural pests. Years later, back in the city of São Paulo, he was appointed as researcher in the Biomedical Sciences Institute (ICB-USP). Prof. Pavan appears in the authorship of more than 100 scientific articles.

Prof. Pavan took part in the first Council of the Foundation for Research Support of the State of São Paulo (FAPESP; 1961–1963), presided over FAPESP (1981–1984) and also the National Council of Research (CNPq, 1986–1990). He played a key role not only in the expansion of resources for FAPESP from its beginning but also in the substantial increase of fellowships for students offered by the two agencies. While still in the CNPq, Pavan was responsible for creating the Science Station (“Estação Ciência”), open to the public for diffusing science to society. Prof. Pavan was president of the Brazilian Association for Science Diffusion and also coordinated the “Cátedra UNESCO José Reis” for science outreach. He became Professor Emeritus of USP (1989) and of UNICAMP (1991).

He was a member of international scientific committees and of scientific societies, including president and member of the Brazilian Society for Genetics and the Brazilian Society for the Advancement of Science (1981–1986). He was also member of the Brazilian Academy of Sciences, honorary member of the Academy of Medicine of São Paulo, member of the Physiography Society of Lund, of the Academies of Sciences of Lisbon and Chile and of the Pontifical Academy of Sciences of Vatican. Prof. Pavan was awarded a number of prizes in Brazil and in other

countries. Several times, he has referred to himself as “a lucky man”. Such a statement gives a good measure of his modesty.

Prof. Pavan often came to the Department of Genetics and Evolutionary Biology at the IB-USP, which had formerly been the Department of General Biology of the FFCL. I had the pleasure of receiving his visit many times here in my laboratory. In 2007, to my surprise and satisfaction, he told me that he wanted to join us for a trip to collect *Rhynchosciara* on the coast of São Paulo. Last year, I expressed to some colleagues my concern about Prof. Pavan, since for the first time in many years, I heard him complaining about his health. After a life devoted to science, Professor Crodowaldo Pavan, a person of unique strength of character, enthusiasm and polemic ability, died on April 3rd of this year in the city of São Paulo.

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