

Antonio and Sturt: an interaction

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Antonio García-Bellido arrived at Caltech in the late 1960's to work with Ed Lewis. He had been a postdoc with Hadorn for several years before then. As a result he had clear ideas about what research to do. One of his ideas was to apply genetics, in the form of homeotic gene mutations, to the developmental studies he had started previously in Zurich. That included using homeotically transformed discs in his mix and match aggregation experiments.

Drosophila was a well known organism for developmental studies, principally because of the separation of growth from differentiation. "Determination" was the key term and the goal was to uncover examples of determination at the single cell level. Antonio was using X-ray induced mitotic recombination to describe basic parameters in cell multiplication (rates and orientations) in imaginal discs (García-Bellido, 1968; García-Bellido and Merriam, 1971a). He used Nöthiger's technique for larval isolation (Nöthiger, 1970) and kept track of larval time by measuring the time to pupariation after X-irradiation. I arrived to be a postdoc with Ed late in 1967 with the goal of studying developmental genetics. Antonio and I began collaborating by using mitotic recombination to compare changes in cell genotypes at developmental times in a study that led to the concept of "perdurance" (García-Bellido and Merriam, 1971b).

Ed's lab was an informal place but it didn't take long for me to meet Antonio. As I recall, he came over from his cubicle in the office to join a conversation I was having with James F Crow, there on sabbatical from Wisconsin. I recognized instantly two characteristics about Antonio: his love of conversation -Antonio was interested in and could talk on any subject- and his openness to new ideas and viewpoints. When I arrived, Antonio already had the habit of talking

in the afternoon with A. H. Sturtevant, then an emeritus professor with a room next door, and he led us into his frequent conversations. "Sturt" loved to talk or listen to visitors talk; he kept his office door open, attracted in traffic from the hall and nabbed you as you went by to talk with him a bit ("Rather like a spider at its web," Antonio once commented). This expanded to become an important series of regular lab meetings where Erik Bahn (another post-doc), Antonio and I took turns with Ed in presenting our recent results and thoughts. Sturt responded by describing data on thoracic bristle numbers and patterns he had collected for several years. As a result of these meetings Sturt was persuaded to publish his results (Sturtevant, 1970). For much of 1968 our routine was to adjourn on Wednesday afternoons to Sturt's nearby house where Phoebe Sturtevant fed us beer with cheese and crackers.

Sturt kept his pipe going and just grinned from ear to ear as we chattered on about whatever. One of these sessions anticipated future regional meetings when it was held at Ed and Pam Lewis' house and included as well Michael Ashburner, with Herschel Mitchell, and Ron Konopka and Yoshiki Hotta with Seymour Benzer and David Hogness also who was down from Stanford to start a sabbatical with Ed.

Small events may have large consequences. And so it was that the work Antonio and I did on gynandromorphs owes much to our drop-in talks with Sturt. This work began in an interesting way: Antonio's work habit was to concentrate on a problem to the exclusion of anything else such as food, time of day (night). One day I found him digging at an abstract of Bill Lee's on mosaics introduced by irradiating sperm, with descriptions of several

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gynandromorphs that were mosaic for yellow. Lee *et al.* (1967) described the results as a "chocolate swirl" during development. Antonio was initially puzzled by the absence of any regular pattern, but he worked on that with Poulson's and Sonnenblick's descriptions of fly embryogenesis until he understood what was happening.

My contribution when he told me his conclusions was to bring out Sturt's 1929 paper on the claret mutation in *D. simulans*, that I had read in a book with Sturtevant's collected works, to compare with Lee's descriptions.

There Sturt used marked gynandromorphs to develop an analysis for individual discs. When Antonio and I went to Sturt to tell him about extending his model to compare relations between discs, he literally reached into a drawer and handed us 379 drawings of the 1929 gynandromorphs. Without those drawings we would probably not have done the analysis that we published in 1969 (García-Bellido and Merriam, 1969a). After that we made and analyzed *D. melanogaster* gynandromorphs using the unstable ring X chromosome, now called R(1)2 In(1)w[vC], that we knew about from Hinton's paper (1955) (García-Bellido and Merriam, 1969b). At the time, Antonio and I were deep into using mitotic recombination to change the genotype of cells during development. This was all Antonio's inspiration, and it fit my interest in chromosome manipulations (my graduate subject). In that sense the gynandromorph paper was slightly the stepchild.

One side note on the mitotic recombination work: Bill Dwyer came into the lab one day to discuss a notion of his that antibodies were put together covalently from different genes located on different chromosomes, and did we know of any gene translocations that occurred developmentally in *Drosophila*? We thought it unlikely based on how cleanly mitotic recombination worked in development. Control ex-

periments with known translocations gave the anticipated reductions in mitotic recombination frequencies so we assumed they didn't normally occur and didn't consider them further. Dwyer's different genes (known now as the V and C regions) turned out to be syntenic; we perhaps missed a great opportunity.

Social activities had other consequences as well. The Bahns, Merriams and García-Bellido's started pick up dinners with each other. Maria-Paz García-Bellido's chicken stuffed with prunes and roasted with olive oil was legendary. We made trips to the unique lower desert region of the Anza-Borrego for camping where we were sometimes joined by Antonio's close friends Rolf and Ursula Nöthiger. Rolf was then a post doc in San Diego in a mammalian development lab. The lure of *Drosophila*, or of Antonio, however, was strong and he used to join us for conversations about mitotic recombination.

Sometimes this group joined a regular monthly camping meeting consisting of Dean Parker and John Williamson from Riverside and Dan Lindsley from San Diego, with their families, for even more fly talk.

At one of these joint events a decision was made to convert it into a regional fly meeting held at a campus and accessible to all. Accordingly, the Southern California regional *Drosophila* meetings started in 1968 and rotated between Cal Tech, Riverside, City of Hope (Bill Kaplan, Bill Trout, Rodney Williamson), Northridge (George Lefevre) and San Diego. When Howard Schneiderman arrived at Irvine with this students and postdocs (Peter Bryant, Cliff Poodry, John Postlethwait, Gerald and Margrit Schubiger) the meetings moved to Irvine as the central location where they still continue.

The year 1968 spent at Cal Tech was a study in contrasts. The campus itself was quiet, even monastic. It seemed far from the major currents ripping the country: Vietnam, the deaths of Martin Luther King, Jr. and Robert F. Kennedy, the election of Nixon to the presidency. My wife Virginia contributes this recollection of Antonio and the period. After the 1968 election (when Nixon won) Antonio asked her how was it possible that Nixon could win when "none of the people he (Antonio) knew were for Nixon?" We were almost totally immersed in our science; in retrospect it was a thrilling period. *Drosophila*, after a long pause, seemed again to be gaining influence. Part of this was work on development, part was the nascent field of neurogenetics.

Genetics was an indirect science before molecular cloning, in contrast to biochemistry. Our activities were obtaining mutants and analyzing phenotypes. Mosaics analysis and cell lineage were also indirect approaches to developmental biology. But they provided an analytic basis for much of the work done today. Especially important in this regard was the steady push towards always earlier stages as holding the keys to determination, from analysis of adult phenotypes to their larval progenitors (Lewis, 1978) to discussions of the relationship between maternally inherited factors and embryonically active factors. The questions leading to the compartment theory were set in those days. Antonio and his family returned to Spain at the end of 1968. Shortly before he left he gave a Biology division seminar (a great honor). There he described his vision of groups of cells behaving as social communities. The theme of how cells affect each other has appeared repeatedly in his work. Max Delbruck, normally a severe critic of speakers, was enthralled: instead of his usual comment, that this had been the worst seminar he had ever heard, he said was one of the best ever and predicted that this new type of thinking would have a lasting effect. It has.

Those were different days; I have often thought of them to contrast with today. Not better, perhaps, even with my rose colored glasses, but special.

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